CENTRAL NERVOUS SYSTEM AND WEB BUILDING IN SPIDERS

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December 1983

This thesis is submitted as partial fulfilment for the requirements of the degree of Master of Agricultural Science at the University of Adelaide.

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SUMMARY

Using Palmgren silver staining, and other histological methods, the supraoesophageal association areas in one Uloborid and six Araneid spider genera are investigated and compared.

The Araneid genera studied share a common, general plan which differs from that found by other authors in non-Araneid genera. This general plan shows sequential modifications from simple to derived Araneidae. The simple Araneid supraoesophageal ganglion is characterised by a large and fibrous central body, well developed posterior fibre tracts and poorly developed lateral optic masses. The derived Araneid supraoesophageal ganglion is characterised by a smaller, more homogenous central body and a prominent, well developed, anterior nexus of association areas. In particular the lateral optic masses and corpora pedunculata, which are interconnected to the suboesophageal ganglion, show strong development.

The degree of individual association area development may be correlated with the relative importance of visual or tactile sensory modalities, based upon the spiders web building behaviour.

Using the supraoesophageal structure as a tool, the taxonomic positions of Celaenia and Tetragnatha within the Araneidae, and the relationship of the cribellate spider family, Uloboridae, to the Araneidae, are discussed.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University, and to the best of my knowledge, contains no material previously published or written by another person, except where due reference is made in the text of the thesis. Material in this thesis may be copied for private study without written permission.

Signed.

Acknowledgements

I wish to thank the following for their generous help during this work.

Dr R. Laughlin (Waite Agricultural Research Institute) and Mr D. Lee (South Australian Museum) for their supervision.

J. Wannan (BarrSmith Library) for her translation of papers.

State Water Laboratories for use of the photomicroscope.

Solomon Islands Department of Agriculture for permission to collect specimens.

My wife, Jane, for her help with many tedious nights of photography.

This study is an attempt to determine the taxonomic stability of the supraoesophageal ganglion structure in a single family of spiders. Other studies have been limited to comparisons between different arachnid orders, different families of spiders or isolated species(2,39,40,41,54). The results of these studies showed the differences in supraoesophageal structure mentioned previously, but not the amount of structural variation within a single family.

Since the family shows wide behavioural adaptation, and, in the case of web building, the behaviour is well documented, the Araneidae is a convenient group to study the taxonomic stability of supraoesophageal structure. A large body of evidence supports the hypothesis that web building behaviour is controlled within the supraoesophageal ganglion. Due to its prominent association areas and complex interconnections the supraoesophageal ganglion is regarded primarily as an integrating centre. Laser lesion studies(127,129,130) have indicated the dorsal region is involved in web construction and its function is "an overall coordinating one, somehow integrating the perceptual information with motor execution"(134). The disruption of orb web construction after injection of centrally acting drugs has also been recorded(80,133). Other evidence for a role for the central body and bridge during web construction has been suggested by histological studies(2,3,4,5,,39,40,41,42,114,115,116,117).

The Araneidae is also a convenient group to study the amount of supraoesophageal ganglion variability since, unlike many other spider families, its monophyletic origin is not questioned. None of the studies made to date have attempted to show the stability of structure or otherwise within a single family of spiders. By a study of closely related species which show a variability of behaviour, both the stability within the structure, as well as the correlation between structural features and behaviour, can be examined. Within the Araneidae, the placement of Tetragnathinae as an derived or simple form has been controversial. The family Uloboridae has been considered both as a close relative of the Araneidae and as a far removed group by different authors. The other spiders chosen in this study conform to both the behavioural and more general taxonomic classification as simple(Nephila and Phonognatha) and derived(Argiope and Celenia) web building Araneidae. Celaenia is however a special case as it is usually considered most closely related to Argiope, but has secondarily lost its web building behaviour. Recent studies have considered the Cyrtophora as a derived Araneid form due to its web form (26,70)and the lack of ampullate glands (52). The same web characters have been used to suggest Cyrtophora is a simple Araneid (49,50,79). It may be argued that the absence of ampullate glands indicates an early divergence from the main evolutionary path of the Araneids, rather than a recent modification.

Seven species of spider were used during the study. They were,

Uloboridae

Philoponella congregabilis (Rainbow)

collected Adelaide (South Aust)

Araneidae

Cyrtophora moluccensis (Doleschal)

collected Greenvale (Queensland)

Nephila edulis (Labillardiere)

collected Morgan (South Aust)

Phonognatha melania (Koch)

collected Mt Compass (South Aust)

Argiope protensa (Koch)

collected Morgan (South Aust)

Celaenia kinbergi (Thorell)

collected Adelaide hills (South Aust)

Tetragnatha demissa (Koch)

collected Berri (South Aust)

A limited number of species, related to the above, were also examined in order to assure the presence and development of major behavioural and nervous system features within a single genus. These species were,

Uloboridae

Zosis geniculatus (Koch)

collected Adelaide (South Aust)

Araneidae

Cyrtophora hirta (Koch)

collected Sarina (Queensland)

Nephila maculata (Fabricius)

collected Munda (Solomon Is)

Argiope trifasciata(Doleschall)
collected Honiara (Solomon Is)
Tetragnatha bituberculata (Koch)
collected Renmark (South Aust)

Between twenty and forty adult female spiders of each species were collected. During collection, observations and photographs of web structure and habits were recorded. Live Celaenia adults and spiderlings were also maintained in the laboratory for study.

FIXATION

After collection the legs, palps, chelicerae and abdomen were removed with dissecting scissors. The dorsal and ventral cephalothoracic exoskeleton was partially removed with a scalpel. Immediately after preparation was complete the specimen was placed in fixative. The standard fixative used was Formal Acetic Alcohol(78). The specimen required at least one week of fixation, and some specimens were stored up to twelve months in fixative with only minor problems of dehydration. Carnoy's and Blest's fixatives(8,93) were used in some instances but results were not superior to Formal Acetic Alcohol.

DECHITINISATION

Dechitinisation was performed in early experiments. Initially Moore's chlorine dioxide method(87) was used. This was discontinued as the method proved hazardous to the specimen(15) and the experimenter(personal observation). Attempts to use mushroom enzymes(128) met with limited success.

Dehydration in graded alcohols and clearing in xylene required 2 weeks to be completely effective for supraoesophageal preparation(see appendix). The extended period seems to reflect the extreme density of the tissue studied. Suboesophageal studies required only a fraction of this time. The specimen was then embedded in histowax(M.Pt.62 C),blocked and cut into serial sections of either 8 or 10 microns thickness on a Cambridge Rocker Microtome. At least four sets of serial sections in each of the three cardinal planes were made for each species.

STAINING

At least two sets of serial sections in each cardinal plane of each species were stained for cell identification and another two sets for tract identification. The routine stain used for cell identification was Weigert and Van Gieson(78,93). Haematoxylin and Eosin, Methylene Blue and P.T.A.H.(78,93) were used on some occassions. The routine stain for tract identification was the Palmgren Silver Stain(89). The Butler stain (13) was not as effective in staining the supraoesophageal fibres. The Blest method(7) in conjunction with the Blest fixative was used on some occasions.

Photomicrographs of all sections stained to show tracts were made using a Zeiss Photomicroscope III at magnifications from 150x to 300x. Specific details were also photographed at higher magnifications.

Cell localization was determined by direct microscopic observation and a limited number of photomicrographs. Cell size was determined by taking measurements from a fixed number of cells in each section they appeared. Cells were chosen at random in each section. Measurements were made using a calibrated eyepiece micrometer.

The construction of the orb web by members of the Araneidae is well described (9, 10, 19, 29, 68, 74, 79, 86, 94, 95, 97, 99, 102, 111, 119, 131, 132, 133, 135).

Initially, radii and an outer frame of non-viscid silk, from the ampullate glands, are constructed. To this is added a central, interwoven hub from which a loose, small and centrally placed spiral of nonviscid silk is spun outwards. The central core of the hub is then often removed. The spiral is neatened and completed by working from the centre to the outside of the web. After a brief pause, the spider reverses its direction along the spiral and lays down viscid silk from the aggregate glands by regularly attaching the spiral to each radius,or twice if the direction of travel is reversed. Reversal of direction occurs wherever the distance between successive radii is large. As the viscid spiral is laid down the non-viscid spiral is generallyremoved and eaten. The viscid spiral stops short of the central hub leaving a free zone. If not removed previously, the central hub is biten out and eaten. The spider may complete the web by removing some radii or adding strands to the outer edge of the hub.

Variations of the geometric orb web pattern can be seen in numerous Araneid, and non-Araneid genera. These variations can be considered derived modifications or simple precursors of the basic design.

The tangled webs of the Theridiids, sheet webs of the Linyphiids, domed non-viscid webs of Cyrtophora and heavily framed permanent webs of Nephila, some Gasteracantha and Phonognatha can be considered forerunners of the geometric orb web. An opposing view (71) has received little support (26).

The reduced webs of Zygiella(missing sector), Pasilobus(triangular web), Theridiosoma(ray web) and Mastophora and Dicrostichus(single sticky thread) have been considered examples of evolution beyond the orb web.

These web-based phylogenetic classifications are subject to the normal limitations of any classification which is based on limited features, and there is debate concerning the phylogenetic position of groups such as the Uloboridae and Tetragnathinae(49, 50, 54, 67, 71, 98, 99, 119). Knowlege of the web building habits in the particular species used for this study is very limited or non-existant. Therefore the webs of the species used were examined and compared with the webs of related species studied by other authors.

WEB STRUCTURE : PHILOPONELLA (table1)

Philoponella is a cribellate spider, unlike other spiders in this study. Its web, however, is similar to that of Araneid spiders in some ways.

It is a semi-permanent web built in protected areas and repaired when damaged. A maze of lateral supporting threads interconnect with adjacent webs, but a female spider will not leave its own web. The male spider is often observed wandering from web to web throughout the colony.

The orb of the web has a frame of non-viscid branching radii produced by the ampullate glands (51,130). On this is laid a spiral scaffold of non-viscid thread. The catching spiral of cribellate silk (33) is then laid and the scaffold spiral removed.

Detritus of wrapped prey and insects remains together with strengthening bands of non-viscid silk are found in the orb of the web. The irregular paper-like eggsacs are found amongst the lateral supporting threads. The orientation of the web may be at any angle from horizontal to vertical.

Other authors (23,24,25,76,81,83,125) have made studies of various Uloborid webs. These findings are in agreement with studies of other authors.

WEB STRUCTURE : CYRTOPHORA (table1)

The Cyrtophora web is horizontal in orientation with a domed appearance.

The whole structure is supported by an extensive maze of lateral support lines. The radii are close together, plentiful and branched. The spiral is closely woven with only non-viscid threads from the ampullate glands present (94). The web is semi-permanent, being repaired after damage rather than replaced. Webs are constructed in close association with each other and are classed as semisocial (6,11,120,121). The maze of lateral support lines between webs are interconnected. Kleptoparasites, in particular Argyrodes, are common throughout the web maze.

Lubin (77) reports mature males do not spin webs although juvenile and sub-adult males do spin small versions of the female web. In this study mature males were observed alone in small webs, but it is not known if these webs were spun by them or vacated by other spiders.

Other authors (43,60,74,75,77,82,116) have studied the webs of various Cyrtophora species. These findings are in general agreement with these other studies.

WEB STRUCTURE : NEPHILA (table1)

Nephila spins a vertical orb web. Like Cyrtophora there is an extensive maze of lateral support lines forming a barrier web. The radii are close together, plentiful and branched.

The web is semi-permanent, often showing signs of repair after damage. Detritus hanging from the hub adds to the untidy appearance. Webs are often in close association, but a female will not encroach on the web of another. Argyrodes are common kleptoparasites on the web. Unlike Cyrtophora the web contains a viscid spiral between the strands of non-viscid scaffold thread. The orb is not complete, lacking spirals at the top of the web. Mature males do not build webs but move about in the lateral support lines and outer part of the orb. Up to seven males were observed in one female web.

Other authors (1,17,18,106,108) have studied the webs of various Nephila species. Robinson (108) has observed a moulting web with a stabilimentum but lacking a viscid spiral. This form of web was not found during this study, but other results of this study are in agreement with these other authors.

WEB STRUCTURE : PHONOGNATHA (table1)

Phonognatha spins a web similar to that of Nephila. The web is semi-permanent and vertical. It contains branched radii and an extensive maze of lateral support lines. Webs are in close association, but a female will not encroach on the web of another. There is a missing sector of spirals at the top of the web. Unlike Nephila, the web is not usually infested by kleptoparasites, and, while the viscid thread is present in the completed web, the non-viscid spiral is removed.

At the centre of the web is a leaf, curled into an open ended spiral, which serves as a retreat for the spider during the day.

The male shows no size dimorphism, unlike Cyrtophora and Nephila. In a sample of over 1000 adult webs during February and March, only seven males were found. The male in each case shared a leaf retreat with the female. Separate male and female retreats within the one web has been reported (96),but this was not observed in the population studied. At no time were mature males observed to make a web of their own.

The eggsac is laid in another curled leaf within two metres of the female's web. The leaf which contains the eggsac is folded with the stem and leaf apex joined, and is supported by a few lateral support lines only.

Other authors (12,20,44,79,84) have made mention of the Phonognatha web. These findings are in agreement with other studies.

WEB STRUCTURE : ARGIOPE (table1)

Argiope spins what is normally considered the typical orb web. It is vertical in orientation, contains viscid thread and has no missing sectors. The non-viscid scaffold is removed as the viscid thread is laid. In this species there are either few lateral support lines to the web or none at all. Radii are widely spaced and unbranched.

There is usually, but not always, a stabilimentum present in the form of a cross. The spider sits in the centre of the web with its legs aligned in pairs along the lines of the stabilimentum. The web is temporary, being removed each day, when the spider goes into retreat. Webs are not often constructed during rain. Argiope is a solitary species in the sense that webs do not interlock and only one spider will normally be found in a web.

Several authors (12,69,70,36,102,104,105,107) have studied the webs of various Argiope species. These findings are in agreement with other authors.

TETRAGNATHA : WEB STRUCTURE (table1)

Tetragnatha spins a web similar to that of Argiope. It contains viscid threads, the scaffold is removed during construction, it lacks lateral support lines and it has widely spaced unbranched radii. Like Argiope the web is temporary, very rarely if ever being left erect during the day. Tetragnatha is solitary. Only once were two spiders observed in the same web. This occurred four hours after horizonal sunset when a male spider entered a female's web to mate. The web differs from that of Argiope in having no stabilimentum, and the radii of the inner hub are removed after construction of the orb.

While the species of Tetragnatha studied built a vertical web, normally close to or over water, other species construct them horizontally.

Other authors (68,79)have studied the webs of various Tetragnatha species. These findings are in general agreement with other authors.

CELAENIA : WEB STRUCTURE (table1)

The Celaenia female spins no web but is an ambushing hunter which may rely on pheromones to lure prey (86,123). The spider has been reported to attach itself to a leaf by a thin sheet of silk. (12,100) This behaviour was not observed during this study. Attempts to feed adult Celaenia females in the way described by Lowry (in 86) proved unsuccessful.

The habits of the minute Celaenia male are not known, but it is unlikely to be able to capture the large moths which the female hunts (21). During the study, in November,an adult male spider was observed ballooning.

The Celaenia spiderling spins no web but produces only a drag line and a ballooning thread. Repeated attempts using the methods of Witt, Reed and Peakall(133) to get the spider to spin an orb web met with failure. Authors (49,79) who state the spiderling spins an orbweb inaccurately cite Roberts (103).

Roberts only stated that spiderlings "wove a hammock of finest silk between the eggsac and leaf, where they remained for an hour or two, an examination of the leaves a few days later confirming young spiders construct snares and doubtless feed on small insects, abandoning this method later to prey on moths." The hammock, observed repeatedly during this study, is not an orb web but a mass of non-viscid thread. Some spiderlings were fed with a variety of small insects caught with a sweep net in tall grass. Large insects and moths were removed from the catch. Spiderlings from this group survived until the experiment was terminated, over twice as long as the control group which was not fed.

INTRODUCTION

The first studies of spider nervous systems(14,31,38,46,113) determined the basic anatomical subdivisions of the spider central nervous system (Plate1). This structure follows the standard arthropod form, with a neuropile cortex and a rind of cell bodies(16,31,85). In the spider there is complete cephalization enclosing the oesophagus. Dorsal to the oesophagus is the supraoesophageal ganglion. Lateral to the oesophagus lie the paired cheliceral ganglia. Ventral to the oesophagus is the large suboesophageal ganglion. Segmentation can be seen in the suboesophageal and cheliceral ganglia with glial septa dividing them into smaller ganglia. The anterior ganglia, which make up the bulk of the suboesophageal ganglion, are associated with the pedipalps and legs(2,3). The caudal suboesophageal region is associated with structures of the abdomen(2). Fibre tracts of the cheliceral and suboesophageal ganglia stain well and so, with the sensory and motor neurones which run to and from them, have been well described(3). The presence and paths of these suboesophageal tracts have been confirmed for species in this study. The supraoesophageal tracts do not stain well and so have been comparatively poorly studied.

Lateral to the main mass of the nervous system lie the paired neurohaemal organs. The neurohaemal organs are fed by small tracts of up to ten axons which pass through the neuropile of the central nervous system(27,28,34,53,58,59,60,61,62,63,64,65, 124). A similar study has been made of the spider neurosecretory system(36,37).

Neural cells of the spider central nervous system are of four types(4,5,62,65) Plates 2-7). Type A(globuli) cells are small, chromatin-rich cells which have been observed in the anterior supraoesophageal ganglion by some authors(116,117), but not others(5,115,117). Type B(medium) cells are the most common and are found throughout the nervous system. Type C(neurosecretory) cells are found in the arboreal ganglion on the outer dorsal surface of the supraoesophageal ganglion(4). Type D(large motor)cells are found in the ganglia of the legs, pedipalps and chelicerae, but not the supraoesophageal ganglion. A number of different glial cells are also found within the central nervous system.

The supraoesophageal ganglion(SOG) receives information through optic nerves, from the four pairs of eyes, and a number of longitudinal tracts from the suboesophageal and cheliceral ganglia(2,39,40,41,42) (CG). Within the neuropile a number of association areas have been identified.

These are primary (PLOM PMOM) and secondary optic centres(2LOM), the corpora pedunculata(CP), the glomeruli(Gl), the bridge(Br) and the central body(CB) (39,40,41,42,48,13,114, 115,116,117,122). The number, structure and development of these association areas has been found to vary between different spiders. Different arrangements of the primary optic masses have been observed(88,126). Secondary optic masses vary both in number and innervation. In the anterior dorsal position, the bridge is found in some species but not others. An inverse relationship between the development of corpora pedunculata and bridge (or anterior dorsal commissure of Babu) has been suggested. Diffuse glomeruli have been found in the same region in some species, but not in others. The central body is located in a posterior dorsal position in all spiders, but its degree of development and lobation vary. Surrounding each of the association centres the type of neurocytes found differs from species to species.

OPTIC MASSES : PHILOPONELLA (fig1a, Plate 8,9)

A common median optic nerve(MON), from the posterior median eyes, follows the midline of the cephalothorax into the supraoesophageal cellular cortex where it bifurcates, with a branch passing into the primary median optic mass(PMOM) of each hemisphere. The primary median optic mass is a discrete neuropile mass, found dorsal and anterior to the main supraoesophageal neuropile, composed of moderately dense association neuropile. Fibres which pass through it, and others which synapse within it, give the swollen bulb of the mass an onion-like appearance. On the median and dorsal margins of the neuropile is a 3-6 deep layer of B neurocytes which form a well demarcated cap over the neuropile. Fibres from the posterior of the mass form a tract which merges into the larger tract(T3) between the primary lateral optic mass(PLOM) and the lateral lobe of the central body (LL).

The lateral optic nerve(LON) from the four lateral eyes and the two anterior median eyes, follows a similar but more ventral path to the median optic nerve. The lateral optic nerve innervates the primary lateral optic mass in each hemisphere. The primary lateral optic mass(PLOM) is a discrete neuropile mass about the same size as the primary median optic mass, but more ventrally situated. The neuropile is less ordered with clumps of dense homogeneous association neuropile scattered between a diffuse mesh of fibres. Around the margins of the neuropile is a cortex of B neurocytes varying from 3 to 8 cells in depth.

Fibres leaving the posterior of the mass form a single, well-defined tract which passes around the lateral edge of the supraoesophageal neuropile. This tract has no associated neurocyte cortex. The most dorsal fibres pass into the lateral lobe of the central body. Median fibres follow the edge of the dorsal supraoesophageal neuropile to form a commissure with the corresponding fibres of the contralateral hemisphere. Ventral fibres(T1) pass into the secondary lateral optic mass(2LOM).

The secondary lateral optic mass lies on the dorsal edge of the supraoesophageal neuropile in a median position in each hemisphere. It is elongated in the anterior-posterior plane and composed of moderately dense association neuropile, interspersed with fibres running in an anterior-posterior direction. A small cortex of B neurocytes, 2 to 4 cells deep is found laterally. Fibres arising from the posterior portion of the mass are associated with the central body(CB). Fibres arising from the anterior portion of the mass pass into the primary lateral optic mass, the bridge, and into a well developed suboesophageal longitudinal tract.

OPTIC MASSES : CYRTOPHORA (fig1b Plates 14-16)

A common median optic nerve, from the posterior median eyes, follows the midline of the cephalothorax to the outer anterior edge of the supraoesophageal cellular cortex where it bifurcates, with a branch passing into the primary median optic mass of each hemisphere.

The primary median optic mass is a discrete spherical neuropile mass with a homogeneous dense staining appearance, found dorsal and anterior to the main supraoesophageal neuropile, on the edge of the cellular cortex. On the dorsal margin is a small group, 3 to 4 cells deep, of B neurocytes which send their axons into the neuropile. Fibres from the posterior of the mass form a large, prominent tract which merges with the tract between the primary lateral optic mass and the lateral lobe of the central body.

The lateral optic nerve from the four lateral eyes and the two anterior median eyes follows a more ventral path than the median optic nerve, before bifurcating to send a branch into the primary lateral optic mass of each hemisphere. The primary lateral optic mass is a discrete neuropile mass slightly larger than the primary median optic mass. It lies close to the midline of the body, in the cellular cortex of the supraoesophageal ganglion, just ventral to the primary median optic mass. Two distinct regions can be observed within the neuropile. Around the anterior surface of the mass, fibres from the lateral optic nerve fan out and feed into small very dense balls of neuropile. These balls of neuropile appear to be homologous to the rods found in the primary optic masses of Salticidae and other hunting spiders, but much smaller.

Behind the layer of rods, fibres which synapse in the rods form a diffuse fibrous area of neuropile. Around the neuropile are three groups of B neurocytes. One group covers the dorsal surface of the neuropile toward the midline of the body to a depth of 3 to 4 cells. A second group of cells, similar in size and number, covers the ventral surface of the neuropile. Between these two groups of cells another similar group is found on the outer lateral surface of the neuropile. The three groups of cells probably correspond to the three pairs of eyes which innervate the neuropile.

Fibres from the diffuse posterior neuropile of the primary lateral optic mass converge into a fibrous tract which runs posteriorly into the main supraoesophageal neuropile. The most dorsal fibres follow the lateral edge of the neuropile into the anterior lobe of the central body. More ventral fibres either pass around the lateral edge of the neuropile forming commissures with contralateral fibres or feed into the ipsilateral secondary lateral optic mass.

The secondary lateral optic mass forms a dorso-lateral lump on the surface of the supraoesophageal ganglion. It is sausage-shaped, being elongated in the anterior-posterior plane, and composed of densely staining, homogeneous neuropile. There are no fibrous areas within the neuropile. The associated cortex of the mass is formed by a ribbon of B neurocytes slightly anterior to the mass itself.

This ribbon of cortex is 3 to 4 cells deep and runs along the lateral edge of the tract joining the primary and secondary lateral optic masses. Axons from the cells are clearly seen entering the tract and travelling posteriorly into the mass. Fibres from the posterior portion of the mass pass into the central body or form a commissure with contralateral fibres in the posterior supraoesophageal neuropile. Fibres from the anterior portion of the mass form separate tracts to the primary lateral optic mass dorsally and the bridge and corpora pedunculata ventrally. A longitudinal suboesophageal tract originates from the median portion of the mass.

OPTIC MASSES : NEPHILA (figlc Plates 24-26)

A common median optic nerve from the posterior median eyes follows the midline of the cephalothorax into the cellular cortex of the supraoesophageal ganglion, where it bifurcates. A branch passes into the primary median optic mass of each hemisphere. The primary median optic mass is a discrete cup-shaped neuropile. The fibres of the median optic nerve feed into the anterior end of the cup. The open end of tne cup faces posteriorly toward the main supraoesophageal neuropile. The cup is composed of dense homogeneous neuropile. Within the cup is loose fibrous neuropile fanning out into dense neuropile. The loose fibres join into the tract between the primary lateral optic mass and the central body. The cellular cortex of B neurocytes forms a 4 to 6 cell deep cap over the posterior half of the mass.

The lateral optic nerve from the four lateral eyes and the two anterior median eyes follows a more ventral path than the median optic nerve, and bifurcates closer to the main supraoesophageal neuropile. The primary lateral optic mass which the lateral optic nerve branches feed into is 50% larger than the primary median optic mass. It contains six areas of very dense homogeneous neuropile rods arranged in three pairs. The anterior rod of each pair is twice the size of the posterior rod. The cellular cortex of B neurocytes is thickest on the posterior edge of the mass where it reaches a depth of 12 to 18 cells. Laterally the cells form a thin ribbon along the tract between the primary and secondary lateral optic masses.

Fibres from the primary lateral optic mass run posteriorly into the supraoesophageal neuropile as a large, dense, fibrous tract. A small tract passes into the central body but the majority of these fibres pass into the secondary lateral optic mass.

The secondary lateral optic mass is a peanut shaped mass of dense homogeneous neuropile situated in the dorso-lateral neuropile of each hemisphere. There are no fibrous areas within the mass, which takes up stain better than the surrounding supraoesophageal neuropile. The associated cellular cortex lies lateral and dorsal to the neuropile of the mass. The B neurocytes of the cortex lie 6 to 8 cells deep around the mass.

Axons from a longitudinal suboesophageal tract both fan out into the posterior cellular cortex of the mass and into the neuropile of the mass. Axons from the cortex enter into the neuropile of the mass. Tracts from the anterior of the mass also interconnect the mass with the primary lateral optic mass and the bridge. A small number of fibres from the anterior portion of the mass travel to the corpora pedunculata. Fibres from the posterior portion of the mass follow the posterior surface of the supraoesophageal neuropile to form a commissure with contralateral fibres.

OPTIC MASSES : PHONOGNATHA (fig1d plate 28)

A common median optic nerve from the posterior median eyes, follows the midline of the cephalothorax, then bifurcates on the anterior edge of the supraoesophageal cellular cortex. A branch passes into the primary median optic mass of each hemisphere. The primary median optic mass is a discrete mass of dense neuropile lying just anterior to the main dorsal supraoesophageal neuropile. A cellular cortex surrounds the posterior half of the mass. It is composed of B neurocytes which lie 4 to 6 cells deep. Ventrally the cortex is continuous with the cortex surrounding the primary lateral optic mass. Fibres from the posterior portion of the primary median optic mass form a small tract which enters the main supraoesophageal neuropile just behind the secondary lateral optic mass.

The lateral optic nerve from the four lateral eyes and the two anterior median eyes, follows a more ventral path than the median optic nerve, bifurcating anterior to the supraoesophageal cellular cortex. A branch of the bifurcation leads into the primary lateral optic mass of each hemisphere. The primary lateral optic mass lies just anterior to the main supraoesophageal neuropile and immediately ventral to the primary median optic mass. It is about half again as large as the primary median optic mass and composed of three dense homogeneous neuropile rods lying side by side. Each dense rod probably corresponds to one of the eyes served by the mass. Between the rods a small amount of loose fibrous neuropile is present. The cellular cortex covers the posterior and lateral edges of the mass. It is composed of B neurocytes which may be up to 20 cells deep in places. Dorsally it is continuous with the cortex surrounding the primary median optic mass.

From the posterior of the mass, a broad fibrous tract passes into the main supraoesophageal neuropile. Dorsal fibres pass around the lateral edge of the supraoesophageal neuropile. More ventral fibres travel to the secondary lateral optic mass.

The secondary lateral optic mass forms a ridge of dense homogeneous neuropile on the anterior lateral edge of the main supraoesophageal neuropile. The cortex of B neurocytes which is associated with the mass, covers the dorsal and posterior-lateral edges of the mass to a depth of 3 to 6 cells.

Fibres from a well developed longitudinal suboesophageal tract send fibres both into the cellular cortex, and the posterior neuropile of the mass. Tracts from the posterior of the mass also interconnect the mass with the contralateral mass, via a posterior commissure, and the central body. Anterior fibres pass into the bridge and the corpora pedunculata.

OPTIC MASSES : CELAENIA (figle plates 42,43)

A common median optic nerve, from the posterior median eyes, follows the midline of the cephalothorax before bifurcating just anterior to the supraoesophageal cellular cortex. A branch passes into the primary median optic mass of each hemisphere. The primary median optic mass is a discrete neuropile mass found on the dorsal anterior edge of the supraoesophageal cellular cortex. It is a cup-shaped mass of dense staining neuropile. The open end of the cup on the posterior surface of the mass is covered by a two cell deep cortex of B neurocytes which send their axons into the mass. Fibres from the posterior of the mass form a tract which passes outside the main supraoesophageal neuropile before merging with a tract joining the primary lateral optic mass with the central body.

The lateral optic nerve from the four lateral eyes and the two anterior median eyes passes immediately ventral to the median optic nerve.

The lateral optic nerve innervates the lateral optic masses in each hemisphere. The primary lateral optic mass is a discrete neuropile mass lying immediately ventral to the primary median optic mass. It is about fifty percent larger than the primary median optic mass. No lobation can be seen in the anterior part of the mass, but about ten small, ovoid, densely staining neuropile rods are found over the anterior surface of the mass. I have called these the primary rods. Fibres from the primary rods pass into the cellular cortex surrounding the mass, and posteriorly into a group of three secondary rods. The secondary rods are ovoid masses of moderately dense neuropile. Fibres running in an anterior-posterior direction can be observed within the homogeneous neuropile of the rods. Fibres from the surrounding cortex also enter the neuropile of the secondary rods. The cellular cortex of the primary lateral optic mass is composed of B neurocytes which cover the posterior surface of the mass. On the medial posterior surface this cortex reaches a depth of 8 to 10 cells and more laterally 1 to 2 cells deep.

From the posterior of the mass a large fibrous tract passes around the lateral surface of the supraoesophageal neuropile to the central body. Fibres from the posterior ventral surface of the mass form a tract to the secondary lateral optic mass.

The secondary lateral optic mass forms a bulge of medium dense neuropile on the lateral surface of the supraoesophageal neuropile. The dorsal surface of the mass contains fibres running in an anterior-posterior direction. More ventrally, the mass is composed of homogeneous diffuse neuropile. On the lateral edge of the mass is a cortex, 3 to 4 cells deep, of B neurocytes which send axons into the neuropile of the mass. The dorsal posterior fibres leaving the mass continue to the central body. Medial ventral fibres pass into the bridge and to the corpora pedunculata. Fibres from the ventral region of the mass pass into a longitudinal tract to the suboesophageal ganglion.

OPTIC MASSES : ARGIOPE (fig1f plates 30-33)

A common median optic nerve, from the posterior median eyes, follows the cephalothoracic midline until, just anterior to the cellular cortex of the supraoesophageal ganglion, it bifurcates with a branch entering each hemisphere. The fibres of a branch fan out, pass through a thin layer of neurocytes and enter the primary median optic mass. The mass is found on the anterior dorsal limit of the supraoesophageal cellular cortex. It forms a discrete, spherical neuropile which stains densely. The mass is homogeneous except in the extreme anterior and posterior regions where some individual fibres can be detected. The cellular cortex of the mass is limited to a single layer of B neurocytes over the anterior portion of the mass.

From the posterior portion of the mass a large and well defined tract travels posteriorly into the main supraoesophageal neuropile where it joins a tract from the lateral optic masses passing into the central body.

The lateral optic nerve, from the four lateral eyes and the anterior median eyes, follows a similar, but more ventral path, to the median optic nerve. It bifurcates some distance anterior to the supraoesophageal cellular cortex. A branch of the nerve feeds into the primary lateral optic mass of each hemisphere. The primary lateral optic mass is positioned more medially and has a volume thirty times greater than that of the primary median optic mass. Three lobes can be distinguished within the primary lateral optic mass, probably corresponding to the three pairs of eyes which innervate it. Junctions between the lobes are poorly defined. Each lobe receives fibres from the lateral optic nerve on its anterior surface. These fibres pass into the small spherical bundles of very dense association neuropile of the primary rods. Each lobe contains between twenty and forty primary rods spread over its anterior surface. Fibres from the posterior portion of the primary rods form into diffuse tracts. A few optic nerve fibres pass directly into these diffuse tracts without synapsing in the primary rods. Fibres of the diffuse tracts pass into a cellular cortex of B neurocytes, which may reach a depth of 30 cells, covering the posterior surface of the mass.

Other fibres of the diffuse tracts synapse within a group of three secondary rods. The secondary rods, which lie on the posterior surface of tne mass, are also composed of very dense staining homogeneous neuropile. They are ovoid in shape and lie side by side. Fibres from one lobe of primary rods feed only into one of the secondary rods. The secondary rods have their own surrounding cellular cortex which forms a ring, four to seven cells deep, around the secondary rods. Most of the cells within the cortex are B neurocytes, but ten to fifteen larger C neurocytes form a group of their own on the outer lateral edge of the cortical ring. Axons from both B and C neurocytes pass into the neuropile of the secondary rods. The combination of structures making up the primary lateral optic mass give the mass the appearance of a flaming tree, with the secondary rods as the trunk and the lateral optic nerve fibres as flames.

From the secondary rods, a dorsal fibrous tract passes posteriorly into the secondary lateral optic mass.

The secondary lateral optic mass lies directly posterior to the primary lateral optic mass, forming a large bulge on the anterior surface of the main supraoesophageal neuropile. It is composed of dense staining homogeneous neuropile. The associated cellular cortex of B neurocytes covers the anterior and medial surfaces to a depth of 8 to 12 cells.

These cells send axons both into the secondary lateral optic mass and into a longitudinal suboesophageal tract. Fibres from the neuropile of the secondary lateral optic mass form tracts which lead from the posterior of the mass to the central body, and from the medial part of the mass to the corpora pedunculata and bridge.

OPTIC MASSES : TETRAGNATHA (fig1g Plates 37-39)

A common median optic nerve from the posterior median eyes bifurcates dorsally and anterior to the supraoesophageal ganglion with a branch entering the primary median optic mass of each hemisphere. The primary median optic mass lies well anterior and dorsal to the supraoesophageal cellular cortex. It is a discrete, ovoid neuropile which stains densely. Some fine fibres running in an anterior-posterior direction can be observed amongst the generally homogeneous neuropile. The cellular cortex of the mass is made up of B neurocytes, six cells deep, lying on the posterior edge of the neuropile, dorsal to the cortical cells of the supraoesophageal ganglion. From the posterior, ventral region of the mass a thin tract of fibres travels into the main supraoesophageal neuropile where it joins a tract from the lateral optic masses before passing into the central body.

The lateral optic nerve, from the two anterior median eyes and the four lateral eyes, follows a similar, but more ventral, path to the median optic nerve. It bifurcates immediately anterior to the primary lateral optic mass with a branch entering the mass in each hemisphere. The primary lateral optic mass is forty times the volume and situated ventral to the median optic mass. Three lobes, one dorsal and two ventral, can be distinguished within the primary lateral optic mass, and probably correspond to the three pairs of eyes which innervate it. Each lobe receives fibres from the lateral optic nerve on its anterior surface. These fibres pass into elongated or V-shaped bundles of very dense neuropile primary rods. Each lobe contains forty to fifty primary rods spread over its anterior surface. Within a lobe, the primary rods may join up with each other to form a complex maze. Fibres from the posterior portion of the primary rods form into distinct homogeneous tracts which, in turn, join up to form a single tract for each lobe within the mass. Some fibres do cross from one lobe to another and axons from the surrounding cortex of cells also join the tracts. The cortical B neurocytes are densest over the dorsal and posterior surfaces of the neuropile mass where they reach a depth of 6 to 8 cells. Each lobe of the mass has its own group of cortical neurocytes forming a cresent around the lobe. The single tract from each lobe passes posteriorly into another ovoid secondary rod of neuropile.

Each lobe has one secondary rod at its base. The secondary rod is homogeneous but does not stain as deeply as the primary rods. Lateral to the secondary rods, groups of B neurocytes, up to six cells in depth, send their axons into the neuropile of the secondary rods. The combination of structures making up the primary lateral optic mass give the mass a flaming tree appearance, similar to that of Argiope, with the secondary rods at the trunk and the lateral optic nerve fibres as the flames.

From the secondary rods a fibrous tract passes posteriorly around the dorso-lateral limit of the supraoesophageal neuropile to the central body. A second, larger tract connects the secondary rods with the secondary lateral optic mass.

The secondary lateral optic mass forms a large bulge of dense staining neuropile over the anterior dorsal portion of the supraoesophageal neuropile. The associated cellular cortex of B neurocytes which covers the anterior surface of the mass, merges with the cortex of the secondary rods. Fibres from the anterior of the mass pass into the cortical cell layer. Other fibres from the mass pass into the suboesophageal ganglion through a longitudinal tract originating in the ventral portion of the mass. Fibres from the medial edge of the mass pass into the bridge and corpora pedunculata in a large and heavily staining tract. Posterior fibres form a tract to the central body.

PHILOPONELLA (fig2a Plate 8,9,11,12)

CORPORA PEDUNCULATA: The corpora pedunculata is a poorly staining, but large paired structure linking the hemispheres in the anterior dorsal supraoesophageal ganglion. They lie in a plane medial and slightly ventral to the secondary lateral optic masses(2LOM), and are composed entirely of fibrous neuropile. The corpora pedunculata are composed of two groups of fibres. The smaller, anterior group originates in the secondary lateral optic mass of each hemisphere and proceeds anteriorly and ventrally in a semicircle around the anterior surface of the supraoesophageal ganglion. It then follows a medial path to form a commissure with the corresponding contralateral fibres. The larger posterior tract of the corpora pedunculata originates in the posterior supraoesophageal neuropile. In each hemisphere fibres entering this tract can be traced to the longitudinal suboesophageal tract(T2) which innervates the secondary lateral optic mass and into the glomerular neuropile(Gl) described below. Other fibres disappear into the supraoesophageal neuropile. The fibres converge into a single tract and pass anteriorly and slightly dorsally toward the midline where they merge with fibres of the anterior tract before forming a commissure with the contralateral fibres. There is no midline bulge in the corpora pedunculata or any evidence that fibres synapse within this region.

BRIDGE: The bridge(Br) is a small, two lobed structure lying anterior to the corpora pedunculata. It is composed of diffuse, pale staining, fibrous neuropile. Each lobe reaches a maximum diameter of 15 microns. Innervation of the bridge is through a broad band of fibres from the secondary lateral optic mass which passes around the anterior surface of the supraoesophageal neuropile to the bridge lobes. There is no fibrous connection between the lobes of the bridge. A group of B neurocytes is found aterior to the bridge.

GLOMERULAR NEUROPILE: A number of large glomerular neuropile(Gl) areas(29) are situated between the anterior and posterior tracts of the corpora pedunculata. Individual fibres from the glomeruli can be traced into the posterior tract of the corpora pedunculata and into the longitudinal, suboesophageal tract (T2) to the secondary lateral optic mass.

HORSESHOE COMMISSURE: The horseshoe, or median dorsal, commissure (HC) is a well developed structure lying in the posterior dorsal supraoesophageal neuropile. It is composed of moderately densely staining homogeneous neuropile. On the midline it is 90 microns in depth. The commissure arises from the conjunction of a longitudinal suboesophageal tract (T2) in each hemisphere. Near the midline a few fibres branch from the commissure and pass through the central body (CB), dividing the central body into lobes. On the posterior surface of the central body the fibres fan out amongst the cortical cells.

CYRTOPHORA (fig2b Plates 10,13,16-22)

CORPORA PEDUNCULATA: The corpora pedunculata are well developed structures linking the hemispheres in the anterior dorsal part of the main supraoesophageal ganglion. They stretch medially between the secondary lateral optic masses, and are composed of fibrous structured neuropile. Two groups of fibres pass through the corpora pedunculata. The anterior, smaller group, which originates in the secondary lateral optic mass, follows the anterior surface of the supraoesophageal neuropile in a semicircle before proceeding medially to join the corresponding fibres from the contralateral hemisphere. The larger, posterior tract of the corpora pedunculata, does not take up stain as well as the anterior tract. Fibres of the posterior tract originate in the longitudinal suboesophageal tract, which also leads to the secondary lateral optic mass, and the glomerular neuropile found near the corpora pedunculata stalk. The fibres pass in an anterior direction before passing medially directly behind the fibres from the secondary lateral optic mass. Both the anterior and the posterior tracts form true commissures between the hemispheres. In addition to the fibrous region, the anterior tract also bulges out into a small densely staining synaptic area ventrally near the midline.

BRIDGE: The bridge is a small, elongated, U-shaped structure lying immediately anterior to the corpora pedunculata. The lateral extensions of the "U" have a few scattered fibres which connect the bridge with the secondary lateral optic mass. The thickest, and most densely staining, portion of the bridge lies lateral to the midline bulge of the corpora pedunculata where it reaches a diameter of 20 microns. The neuropile of the bridge is diffuse and unstructured. It does not stain as deeply as the corpora pedunculata. A group of B neurocytes is found anterior to the bridge.

GLOMERULAR NEUROPILE: Small patches of glomerular neuropile are observed lateral, or just ventral to, the stalks of the corpora pedunculata. Four to six glomeruli can be seen in each hemisphere. Some fibres could be traced back into the corpora pedunculata. The origin of other fibres which synapse within the glomeruli is unknown.

HORSESHOE COMMISSURE: The horseshoe, or median dorsal commissure is well developed in Cyrtophora. It is composed of moderately densely staining, fibrous, neuropile in which few individual fibres can be detected. On the midline it is 90 microns in depth. The commissure arises from the conjunction of a longitudinal, suboesophageal tract in each hemisphere. In each hemisphere a few fibres branch from the commissure, and pass between the central body lobes to the cortical cells of the central body.

NEPHILA (fig2c Plates 24-26)

CORPORA PEDUNCULATA: The corpora pedunculata are well developed paired structures linking the hemispheres in the anterior dorsal part of the supraoesophageal ganglion. Two distinct areas can be seen within the corpora pedunculata. An anterior group of densely staining fibres from the secondary lateral optic mass in each hemisphere follows the anterior surface of the supraoesophageal ganglion in a semicircle to the midline. The tract in this region is 10 microns in diameter. After tracing this semicircle the fibres then continue medially to join the corresponding fibres in the contralateral hemisphere. Just before this conjunction a small bulge of very dense homogeneous neuropile, 15 microns in diameter, can be seen in each hemisphere. The posterior region of the corpora pedunculata is broader(30 microns in diameter), but more poorly demarcated from the surrounding neuropile, and paler staining than the anterior region. Fibres of the posterior region originate in the area of the longitudinal suboesophageal tract which leads to the secondary lateral optic mass in each hemisphere, but fibres from this area could not be traced directly into the corpora pedunculata, and passes medially to join corresopnding fibres from the contralateral hemisphere.

BRIDGE: The bridge is a small, vertically standing, V-shaped structure lying immediately anterior to the corpora pedunculata. It is composed of homogeneous neuropile, which stains less densely than the anterior region of the corpora pedunculata. The dorso-lateral regions of the "V" send fibres to the ipsilateral secondary lateral optic mass. Anterior to the midline bulge of the corpora pedunculata the bridge reaches its maximum diameter of 20 microns. Only a few fibres join the bridge lobes in each hemisphere. A group of B neurocytes is found aterior to the bridge.

GLOMERULAR NEUROPILE: One or two patches of glomeruli were observed just ventral to the stalks of the corpora pedunculata in each hemisphere. The origin of the axons which synapse within the glomeruli could not be determined.

HORSESHOE COMMISSURE: The horseshoe, or median dorsal commissure is a prominent, dorsal structure lying anterior to the central body within the main supraoesophageal ganglion. It is composed of moderately densely staining, fibrous neuropile. In the midline region, where the commissure is 30 microns in diameter, individual axons can readily be identified. The commissure arises from the conjunction of a longitudinal, suboesophageal tract in each hemisphere. In each hemisphere a few fibres branch from the commissure, pass between the central body lobes to the cortical cells of the central body.

PHONOGNATHA (fig2d Plates 28,29)

CORPORA PEDUNCULATA: The corpora pedunculata are fibrous, poorly staining structures lying in the anterior dorsal supraoesophageal ganglion, spanning the midline. Loosely packed individual fibres within the structures can be clearly seen. The corpora pedunculata are divided into two groups of fibres. A smaller anterior tract originates in the secondary lateral optic mass of each hemisphere. The tract passes slightly ventrally around the anterior surface of the supraoesophageal ganglion toward the midline. On the midline, these anterior fibres form a commissure with the corresponding contralateral fibres. A larger posterior tract of fibres originates in the posterior, dorso-lateral supraoesophageal neuropile. Fibres cannot be traced to any individual area within the the neuropile mass. The tract passes anteriorly and medially until it merges with the anterior tract. Fibres then form a commissure with corresponding contralateral fibres. There is no midline bulge or any evidence that fibres synapse in the midline region. On the midline the corpora pedunculata are 40 microns in diameter.

BRIDGE: The bridge is a poorly developed, two lobed structure lying immediately anterior, and slightly dorsal, to the corpora pedunculata. It is composed of poorly staining, homogeneous neuropile. The single lobe in each hemisphere is 20 microns in diameter and innervated by a small fibre tract from the secondary lateral optic mass. This tract follows a path immediately anterior and dorsal to the anterior tract of the corpora pedunculata. The two lobes of the bridge are not interconnected. A group of B neurocytes is found anterior to the bridge.

GLOMERULAR NEUROPILE: Between the anterior and posterior tracts of the corpora pedunculata one or two small areas of glomerular neuropile are sometimes, but not always, found.

HORSESHOE COMMISSURE: The horseshoe, or median dorsal, commissure is found posterior and slightly dorsal to the corpora pedunculata. It is composed of poorly staining, homogeneous neuropile, 70 microns in depth across the midline. The commissure arises from the conjunction of a longitudinal, suboesophageal tract in each hemisphere. In each hemisphere a group of fibres branches from the commissure, passes between the central body lobes and fans out amongst the central body cortical cells.

CENTRAL SUPRAOESOPHAGEAL STRUCTURE

CELAENIA (fig2e Plates 42-44)

CORPORA PEDUNCULATA: The corpora pedunculata are deeply staining, paired, fibrous structures in the anterior region of the supraoesophageal ganglion. They are found more ventrally than it is in other species, half way between the oesophagus and dorsal surface of the ganglion. The corpora pedunculata are made up of two equally sized groups of fibres. The deeply staining anterior fibres arise from the secondary lateral optic mass. From this mass they pass by a semicircular route around the anterior surface of the supraoesophageal neuropile. They then pass behind the ventral portion of the bridge to the midline where they form a commissure with corresponding fibres in the contralateral hemisphere. On the anterior surface is a small bulge of densely staining homogeneous synaptic neuropile. Ventral fibres of the anterior tract synapse within this bulge, while dorsal fibres form a direct commissure. In the vertical plane the anterior tract takes the shape of pedal-bike handlebars. A posterior tract originates in the the posterior region of the supraoesophageal neuropile. Many of tnese fibres can be traced into a longitudinal suboesophageal tract in each hemisphere, but others disappear into the neuropile mass.

BRIDGE: The bridge is a large, moderately dense, homogeneous structure covering the anterior surface of the supraoesophageal ganglion and spanning the hemispheres. In transverse sections the bridge has a distinctive "H" shape. The dorsal wing in each hemisphere lies anterior to the ventral wing. The anterior wing reaches a diameter of 30 microns. Innervation of this portion is from the secondary lateral optic masses through a dense homogeneous fibre tract passing over the dorsal anterior surface of the supraoesophageal ganglion. The ventral wing of the bridge in each hemisphere measures 60 microns in diameter before it spreads out into the ventral supraoesophageal neuropile. A large number of individual fibres emerging from the posterior lobe can be traced into the ipsilateral tract of an anterior suprastomatodeal commissure of the suboesophageal ganglion.A group of B neurocytes is found anterior to the bridge.

GLOMERULAR NEUROPILE: No glomerular neuropile was observed in the dorsal supraoesophageal ganglion.

HORSESHOE COMMISSURE: The horseshoe, or median dorsal commissure is only poorly developed in Celaenia. It is composed of fibrous poorly staining neuropile and is 20 microns in depth across the midline. The commissure arises from the conjunction of a longitudinal, suboesophageal tract in each hemisphere. In each hemisphere a group of fibres which branches from the commissure, passes between the central body lobes to the surrounding cortical cells.

ARGIOPE (fig2f Plates 30,32-36)

CORPORA PEDUNCULATA: The corpora pedunculata are prominent, anterior facing, structures linking the two hemispheres in a U shape. They lie ventral and posterior to the primary lateral optic masses. The corpora pedunculata are innervated by two groups of fibres. A group of prominently staining fibres from the posterior ventral portion of the secondary lateral optic mass enter the corpora pedunculata laterally to form the stalks. Fibres from the longitudinal tract between the secondary lateral optic mass and the suboesophageal ganglion, which stain less densely, enter the stalk in a more ventral position. Both sets of fibres either cross to the contralateral secondary lateral optic mass, or synapse within a swollen region of the corpora pedunculata, 80 microns in diameter, situated on the midline of the brain between the hemispheres. The midline bulge is composed of diffuse neuropile, which stains more heavily than the surrounding supraoesophageal neuropile.

BRIDGE: The bridge is a small, two lobed structure. A lobe lies immediately lateral to the swollen region of the corpora pedunculata in each hemisphere. The two lobes are discrete and do not unite across the midline. Each lobe envelops the anterior and dorsal surface of the corpora pedunculata stalks. The neuropile of the bridge varies from diffuse to homogeneous. It does not stain as deeply as the neuropile of the corpora pedunculata. Innervation of the bridge is from fibres which originate in the ipsilateral corpora pedunculata stalk, and axons of B neurocytes which form a distinct group 8 to 10 cells deep anterior to the bridge lobes.

GLOMERULAR NEUROPILE : No glomerular neuropile was observed in the dorsal supraoesophageal neuropile of Argiope.

HORSESHOE COMMISSURE : The horseshoe, or median dorsal, commissure is weakly developed in Argiope, only 10 microns in depth across the midline. It is composed of fibrous neuropile which takes up stain poorly. The commissure arises from the conjunction of a longitudinal, suboesophageal tract in each hemisphere. In each hemisphere a group of fibres branches from the commissure. Some of these fibres pass dorsal to the central body and others between the lobes of the central body. Both groups of fibres terminate in the cellular cortex of the central body.

CENTRAL SUPRAOESOPHAGEAL STRUCTURES

TETRAGNATHA (fig2g Plates 37,39,40,41)

CORPORA PEDUNCULATA: The corpora pedunculata are very prominent, heavily staining structures with a characteristic "handlebar" shape. The end of the handlebar in each hemisphere feeds into the secondary lateral optic mass. It is this mass which provides the major innervation of the corpora pedunculata. Other fibres from the suboesophageal longitudinal tracts provide only a small proportion of the fibres. From the secondary lateral optic masses the corpora pedunculata continue medially and dip ventrally. The corpora pedunculata are 50 microns in diameter at these points. On the midline the neuropile expands into a large bulge, 150 microns in diameter. The entire corpora pedunculata are composed of dense homogeneous association neuropile. Individual fibres cannot be detected, even in the lateral extremities.

BRIDGE: The bridge is a small, two lobed structure. A lobe lies immediately lateral to the swollen region of the bridge in each hemisphere. The two lobes are discrete and do not unite across the midline. Each lobe envelops the anterior and ventral surface of the corpora pedunculata stalks. The neuropile of the bridge is diffuse and unstructured. The paths of individual tangled fibres can be traced within the lobes. Fibres from the secondary lateral optic mass enter the ventral surface of the bridge. On the anterior medial surface of the neuropile, axons from a group of 30 to 40 B neurocytes join together into a tract which passes into the ipsilateral lobe.

GLOMERULAR NEUROPILE : No glomerular neuropile was observed in the dorsal supraoesophageal neuropile of Tetragnatha.

HORSESHOE COMMISSURE : The horseshoe, or median dorsal, commissure is weakly developed in Tetragnatha, only 20 microns in depth across the midline. It is composed of fibrous neuropile which takes up stain poorly. The commissure arises from the conjunction of a longitudinal, suboesophageal tract in each hemisphere. In each hemisphere a group of fibres branches from the commissure. These fibres pass in tight bundles between the lobes of the central body then fan out amongst the cellular cortex of the central body.

CENTRAL BODY : PHILOPONELLA (fig3a Plates 8,11,12)54

The central body(CB) in Philoponella forms a large, discrete neuropile with a surrounding cellular cortex. It is situated over the posterior and dorsal supraoesophageal ganglion, and makes up 20% of the total supraoesophageal neuropile. The central body is divided into the anterior(AL), posterior(PL) and two lateral(LL) neuropile lobes.

The anterior lobe is situated over the dorsal supraoesophageal neuropile and makes up 20% of the total central body neuropile. It is composed of homogeneous, dense staining, association neuropile. Innervation is from cells of the surrounding cortex. Fibre tracts (FN) separate it partially from the lateral lobes, and completely from the posterior lobe.

The lateral lobes spread across the dorsal lateral surface of the supraoesophageal ganglion as far forward as the secondary lateral optic mass. Each of the lateral lobes makes up 20% of the central body neuropile. Like the anterior lobe, they are composed of dense, homogeneous, association neuropile. Innervation is from the surrounding B neurocytes of the cortex and fibres which can be traced to the primary lateral optic mass (PLOM).

The posterior lobe lies adjacent to the posterior surface of the supraoesophageal ganglion. In frontal sections it appears W-shaped and thickened at either end. It is the largest lobe of the central body, making up 40% of the total volume.

Parallel tracts which traverse the posterior lobe without branching, give the lobe a fibrous appearance. Ventral tracts are branches of the commissure(C1) which follows the outer posterior limits of the supraoesophageal neuropile and interconnects the primary lateral optic mass in each hemisphere. Fibres from the secondary lateral optic masses are also found. Dorsal fibres pass through the posterior lobe in an anterior posterior direction. These fibres split from the paired longitudinal suboesophageal tracts, which unite to form the horseshoe commissure, then pass as a band to the B neurocytes of the cortex. A branch of this fibrous band partly separates the anterior lobe from the lateral lobes.

The cellular cortex of the central body is 10 to 15 cells deep on the posterior surface, 3 to 6 cells deep on the dorsal surface and 15 to 20 cells deep laterally. The region between the neuropiles of the supraoesophageal ganglion and the central body contains no neurocytes.

CENTRAL BODY : CYRTOPHORA (fig3b plates 14,16,17,20-23)

The central body in Cyrtophora forms a large discrete neuropile with a surrounding cellular cortex. It lies posterior to the main supraoesophageal neuropile and makes up 15% of the total supraoesophageal neuropile. The central body neuropile is divided into equally sized anterior and posterior lobes.

The anterior lobe lies dorsal to the posterior lobe and is composed of dense staining, homogeneous association neuropile. The cortical cells surrounding the anterior lobe send axons into the lobe. At the lateral edges, fibres from the primary lateral optic masses feed into, and synapse within, the neuropile. Midlaterally a branch of the fibre band, which passes between and so separates the anterior and posterior lobes, also partially segments the anterior lobe. This partial division corresponds to the division between the anterior and lateral lobes in Philoponella.

The posterior lobe is made up of a fibrous central region and dense, homogeneous neuropile on its lateral edges. Axons from the surrounding cellular cortex feed into this homogeneous association area. The more dorsal fibres of the central region, which form a posterior commissure,can be traced to the primary lateral optic masses of each hemisphere. The more ventral fibres form another posterior commissure between the secondary lateral optic masses of each hemisphere.

Between the anterior and posterior lobes, runs a band of fibres aligned in an anterior-posterior direction. The fibres of this band, which divides the lobes, originate in a longitudinal suboesophageal tract as branches of the horseshoe commissure. After passing through the lobes of the central body, they disperse in the cellular cortex.

The cellular cortex, composed entirely of B neurocytes is thickest in the dorsal midlateral position where it is 20 to 30 cells deep. On the mid dorsal and posterior surfaces it is reduced to 3 to 6 cells depth. No neurocytes are found on the anterior surface adjacent to the main supraoesophageal neuropile.

CENTRAL BODY : NEPHILA (fig3c Plate 27)

The central body in Nephila forms a discrete sausage-shaped neuropile with a surrounding cellular cortex. It lies over the posterior surface of the dorsal supraoesophageal ganglion, and makes up 10% of the total supraoesophageal neuropile. The central body is composed of equally sized anterior and posterior lobes with a band of fibres separating them.

The anterior lobe is composed of dense homogeneous association neuropile. Innervation is by axons from the thick layer of cortical cells, particularly in the lateral regions. A fibre tract which originates in the primary lateral optic mass and passes around the lateral surface of the supraoesophageal neuropile also terminates in the lateral region of the anterior central body lobe.

The posterior lobe is also composed primarily of dense, homogeneous, association neuropile with innervation from surrounding cortical cells. Commissural fibres connecting the secondary lateral optic masses of each hemisphere are less developed than those found in Philoponella and Cyrtophora.

The commissure does not pass through the central body, but follows the posterior surface of the supraoesophageal neuropile adjacent to the posterior lobe.

Between the lobes run tight bundles of fibres which pass to cells of the cortex. These bundles give the line separating the lobes a notched appearance. They originate from the longitudinal fibre tracts which form the horseshoe commissure when they unite.

The cellular cortex surrounding the central body is 10 to 15 cells deep over most of the surface, but thickens to 15 to 20 cells on the dorsal lateral surface. No neurocytes are found between the neuropiles of the central body and supraoesophageal ganglion. Both B and A(globuli) neurocytes are present in the cortex. The B neurocytes are larger, unipolar cells with clearly visible cytoplasm. The nucleus is also larger (6.5microns diameter), with granular chromatin. These cells are found throughout the central nervous system as well as in the central body cortex. The A(globuli) cells are smaller with no visible cytoplasm. The nucleus is also smaller (5micron diameter) and dense staining. The globuli cells are found in dense clumps behind and above the lateral regions of the central body. Since the specimens examined were sexually mature females, these cells would not be undeveloped B cells (5). (see table 2 & figure 3)

CENTRAL BODY : PHONOGNATHA(fig3d Plates 28,29)

The central body in Phonognatha forms a large, discrete neuropile with a surrounding cellular cortex. It is situated over the posterior surface of the dorsal supraoesophageal ganglion, and makes up 10% of the total supraoesophageal neuropile. The central body is composed of an anterior and a posterior lobe. The two lobes are only partially separated laterally.

The anterior lobe is cresent shaped and made up of dense, homogeneous neuropile. The surrounding, close packed, cortical cells send axons into the neuropile. A tract from the primary lateral optic mass in each hemisphere terminates in the lateral anterior lobe.

The posterior lobe is also composed of dense homogeneous association neuropile. The association neuropile is most obvious in the midlateral posterior regions, where bulges of it give the posterior lobe a W-shape. Axons from the surrounding cortical cells run into this association neuropile. Centrally, the posterior lobe has a loose fibrous appearance. Fibres can be traced to both the primary and secondary lateral optic masses. In the midline area fibres from each hemisphere fan out and synapse with fibres from the contralateral hemisphere. Over the dorsal surface of the posterior lobe, fibres which branch from the horseshoe commissure pass to cells of the central body cortex.

Over most of the central body neuropile the cellular cortex is 4 to 6 cells deep, but this thickens to 15 to 20 cells deep laterally. No neurocytes are found between the neuropiles of the suboesophageal ganglion and the central body. Both B and A(globuli) neurocytes are present in the cortex. The B neurocytes are larger, unipolar cells with clearly visible cytoplasm. The nucleus is larger than that of the globuli cells(6.7 microns diameter) with granular chromatin. These cells are found throughout the central nervous system as well as in the central body cortex. The A globuli cells are smaller with no visible cytoplasm. The nucleus is also smaller(4.9 micron diameter) and dense staining. The globuli cells are found in dense clumps on the lateral edges of the central body anterior lobe. Staining reactions of both cell types are similar to that found in Nephila (see table 2 & figure 4). Since the specimens examined were sexually mature females, the globuli cells would not be underdeveloped B cells(5).

CENTRAL BODY : CELAENIA (fig3e Plate 42)

The central body in Celaenia forms a discrete, W-shaped neuropile with a surrounding cellular cortex. It lies over the dorsal posterior edge of the supraoesophageal ganglion and makes up 10% of the total supraoesophageal neuropile. The central body is incompletely divided into equally sized anterior and posterior lobes.

The anterior lobe is composed of dense homogeneous association neuropile. Cortical cells send axons into the anterior lobe and a small tract from the primary lateral optic mass of each hemisphere terminates in the lateral portion of the anterior lobe of the ipsilateral hemisphere.

The posterior lobe is also composed mainly of association neuropile. Axons from the surrounding cellular cortex feed into the neuropile. Fibres from the secondary lateral optic mass of each hemisphere pass through the neuropile, adjacent to the anterior lobe, to the contralateral side of the lobe, where they synapse. These fibres form the division between the lobes of the central body. Most fibres branching from the horseshoe commissure do not pass through the central body neuropile, but over its dorsal surface, to terminate amongst the cortical cells. A branch of this suboesophageal tract passes into the ipsilateral posterior lobe neuropile where it fans out.

The cellular cortex, composed entirely of B neurocytes, varies in depth from 15 to 20 cells laterally, to 10 to 15 cells deep along the midline. Neurocytes are not found between the neuropiles of the central body and the suboesophageal ganglion.

CENTRAL BODY : ARGIOPE (fig3f Plates 35,36)

The central body in Argiope forms a large, discrete, W-shaped neuropile mass lying over the posterior surface of the dorsal supraoesophageal ganglion. It makes up 10% of the total supraoesophageal neuropile and is partially divided into equally sized anterior and posterior lobes. A cellular cortex covers most of the neuropile.

The anterior lobe is composed of dense, homogeneous, association neuropile. Axons from the surrounding cellular cortex pass into the anterior lobe neuropile. Laterally in each hemisphere, a small fibre tract, which can be traced directly to the primary lateral optic mass, enters the terminal bulge of the anterior lobe.

The posterior lobe is also composed of homogeneous association neuropile with axons from the surrounding cellular cortex feeding into it, particularly on the lateral edges. Fibres from the secondary lateral optic mass split into two tracts anterior to the central body. One of these tracts forms a weakly developed posterior commissure within the supraoesophageal neuropile. The other branch passes through the junction between the central body lobes to the contralateral portion of the posterior lobe, where it fans out into the association neuropile.

Fibres branching from the horseshoe commissure pass over the dorsal surface of the central body neuropile, as well as between the neuropile lobes, before fanning out into the cortical cells. A small number of these fibres pass into the lateral regions of the posterior lobe neuropile where they synapse.

The cellular cortex, composed entirely of B neurocytes, is 6 to 8 cells deep laterally, but thins to a depth of 2 to 3 cells along the midline. No neurocytes are found between the neuropiles of the supraoesophageal ganglion and the central body.

CENTRAL BODY : TETRAGNATHA (fig3g Plate 37)

The central body in Tetragnatha forms a discrete, sausage shaped neuropile with a surrounding cellualar cortex. It lies over the posterior surface of the dorsal supraoesophageal ganglion and makes up 10% of the total supraoesophageal neuropile. The central body is divided into poorly defined anterior and posterior lobes. In the lateral regions the two lobes merge.

The anterior lobe is composed of dense, homogeneous, association neuropile. Axons from the surrounding cortex, particularly in the lateral regions, pass into the anterior lobe neuropile. At the lateral extremities a tract of fibres which can be traced to the association area between the primary and secondary lateral optic masses, enters the anterior lobe neuropile.

The posterior lobe, also composed of association neuropile, is slightly larger than the anterior lobe. Laterally, axons from the surrounding cellular cortex enter the neuropile. Fibres branch from the posterior commissure which connects the secondary lateral optic masses in each hemisphere and pass across the anterior surface of the posterior lobe. When they reach the lateral edge of the posterior lobe in the contralateral hemisphere, they branch into the neuropile.

Fibres branching from the horseshoe commissure roughly divide the central body lobes as they pass through the neuropile in tight bundles to the surrounding cortical cells. These tight fibre bundles give the central region between the lobes a vaccuolated appearance.

The cellular cortex covers the surface of the central body neuropile except in the area adjacent to the supraoesophageal ganglion where no neurocytes are found. The cortex varies from 20 to 25 cells deep over the lateral portion of the central body and thins to one to two cells deep over the median portion. Both B(medium) and A(globuli) neurocytes are present in the cortex. The B neurocytes are larger, unipolar cells with clearly visible cytoplasm. The nucleus is also larger (4.2 microns diameter), with granular chromatin. These cells are found in all other parts of the central nervous system as well as the central body. The globuli cells are smaller with no visible cytoplasm. The nucleus is also smaller (2.4 microns diameter) and dense staining. The globuli cells are found scattered amongst the B cells over the anterior lobe of the central body. Both cell types have similar staining reactions to the corresponding cells in Nephila (see table 2 and figure 4). Since the specimens examined were sexually mature females, the globuli cells would not be undeveloped B neurocytes(5).

SUMMARY : OPTIC MASSES

The two pairs of primary optic masses of Philoponella are poorly developed and equal in size. The primary lateral optic mass in each hemisphere has a poorly developed cortex of B neurocytes but shows little internal structure The secondary lateral optic mass is also poorly developed and fibrous.

The primary lateral optic mass of Cyrtophora is much smaller than the primary median optic mass. Small dense neuropile rods are found on the anterior surface of the mass. Three groups of B neurocytes form the cellular cortex of each mass. The secondary lateral optic mass of each hemisphere is homogeneous with a small cellular cortex.

Nephila has a large primary lateral optic mass in each hemisphere which is surrounded by a well developed cellular cortex. Within the mass six well developed rods are arranged in pairs. A well developed tract links the primary and secondary lateral optic masses of each hemisphere. The secondary lateral optic mass in a densely staining homogeneous mass with a well developed neurocyte cortex.

The primary lateral optic mass of Pnonognatha is also much larger than the primary median optic mass. Within the mass three large neuropile rods lie side by side. Around the mass is a well developed cortex of B neurocytes. The secondary lateral optic mass is well developed, anteriorly placed and has a cortex of B neurocytes.

The primary lateral optic mass of Celaenia is much larger than the primary median optic mass and is surrounded by a dense cortex of neurocytes. A rim of dense neuropile rods around the anterior surface of the mass are interconnected with three larger rods on the posterior surface of the mass. A broad tract runs from the primary to the secondary lateral optic mass. The secondary lateral optic mass is large, dense and homogeneous, with a well developed cellular cortex.

The primary lateral optic mass of Argiope is thirty times the size of the primary median optic mass. It contains three lobes, each with its own thick cellular cortex. Within the neuropile of each lobe many small dense rods on the anterior surface send fibres posteriorly to a larger rod on the posterior surface. From the posterior of the mass a broad, dense staining, fibrous tract passes into the secondary lateral optic mass. This mass is large, homogeneous and densely staining with a well developed neurocyte cortex.

The primary lateral optic mass of Tetragnatha, which is forty times the volume of the primary median optic mass, is the dominating feature of the supraoesophageal ganglion in each hemisphere. It is surrounded by a large and dense layer of cortical neurocytes.

Within the neuropile, dense convoluted rods on the anterior surface feed posteriorly to three large, dense, ovoid rods on the posterior surface of the mass. The tract between the primary and secondary lateral optic masses is broad, homogeneous and densely staining. It has its own surrounding cortex of B neurocytes. The large secondary lateral optic mass is found in the anterior portion of each hemisphere. It is composed of dense, homogeneous neuropile with a well developed cortex of neurocytes.

Prominent central supraoesophageal structures in the species studied are the corpora pedunculata, bridge, glomerular neuropile bundles and horseshoe commissure.

In Philoponella the corpora pedunculata and bridge are fibrous and poorly staining . Within the corpora pedunculata an anterior group of fibres is innervated from the secondary lateral optic mass and a larger posterior group from the supraoesophageal neuropile. The bridge does not form a commissure between the hemispheres. A large number of small glomerular neuropile areas are found lateral to the corpora pedunculata. Posterior to the corpora pedunculata, the horseshoe commissure is thick and dense with poorly developed connections to the central body.

In Cyrtophora the smaller group of anterior fibres within the corpora pedunculata stains more densely than the posterior group, but otherwise resembles the corpora pedunculata of Philoponella. The two lobes of the bridge are fused across the midline and have fibrous connections with the secondary lateral optic masses. Areas of glomerular neuropile are found lateral to the corpora pedunculata. The horseshoe commissure is not as large or as densely staining as found in Philoponella, but more fibres run from it to the central body.

In Nephila the anterior portions of the corpora pedunculata contain small swellings of dense homogeneous neuropile. The posterior portions are poorly staining. The homogeneous neuropile of the bridge forms a V-shaped structure across the midline. Patches of glomerular neuropile are rare. The horseshoe commissure is fibrous but prominent.

The corpora pedunculata of Phonognatha are large but fibrous. The two homogeneous lobes of the bridge are distinct, each lobe receiving a small bundle of fibres from the ipsilateral secondary lateral optic mass. Very few areas of glomerular neuropile can be observed. The horseshoe commissure is homogeneous and poorly staining with firbre tracts to the central body branching from it.

In Celaenia the deeply staining, homogeneous and swollen anterior region of the corpora pedunculata is the same size as the posterior fibrous region. There are well developed tracts from the corpora pedunculata to the secondary lateral optic masses and into longitudinal suboesophageal tracts. The bridge is a very prominent, homogeneous, H-shaped structure with well developed connections to both the secondary lateral optic masses and the suboesophageal ganglion. No glomerular neuropile was observed. The horseshoe commissure is thin, fibrous and poorly staining, but sends prominent tracts into the central body.

In Argiope the posterior regions of the corpora pedunculata are poorly developed and fibrous. The anterior portions are thick, homogeneous and dense with well developed connections with the secondary lateral optic masses and a large bulge on the midline. The bridge is small and fibrous. The two lobes do not fuse. Each lobe sends a small bundle of fibres to the secondary lateral optic mass in the ipsilateral hemisphere. No glomerular neuropile was observed. The horseshoe commissure is thin, fibrous and stains poorly. In each hemisphere a tract of fibres from the horseshoe commissure passes to the central body.

The anterior regions of the Tetragnatha corpora pedunculata are very densely staining and homogeneous with a large central bulge. The posterior tract is poorly developed, fibrous and originates in longitudinal suboesophageal tracts. The bridge is composed of two diffuse, discrete lobes with no obvious innervation. No glomeruli are found. The horseshoe commissure is thin and fibrous with tracts branching from it to the central body.

SUMMARY : CENTRAL BODY

The central body is the dominant feature of the supraoesophageal ganglion in Philoponella. It is made up of four neuropile lobes with a surrounding cortex of B neurocytes. The paired lateral lobes and the anterior lobe are composed of homogeneous association neuropile. Many axons from the optic masses pass through the larger, posterior lobe without synapsing and give the lobe a regular fibrous appearance. Axons from the cellular cortex pass into the horseshoe commissure.

The central body of Cyrtophora makes up 15% of the total supraoesophageal volume and consists of two equally sized lobes with a surrounding cortex of neurocytes. The anterior lobe is composed of homogeneous neuropile with fibrous connections to the optic masses. The posterior lobe is homogeneous laterally and fibrous medially. The fibrous portion contains commissural fibres interconnecting the optic masses of each hemisphere. Axons from the cellular cortex pass into the horseshoe commissure.

The two lobed central body of Nephila makes up 10% of the total supraoesophageal volume and is surrounded by a dense cortex of A and B neurocytes. The anterior lobe is homogeneous and densely staining with fibrous connections to the optic masses. The posterior lobe is predominantly homogeneous with a central region of regular fibrous neuropile. The axons of this region form a direct commissure between the optic masses of each hemisphere. Cortical cells send axons into the horseshoe commissure.

The two lobed central body of Phonognatha is similar to that of Nephila except in the make up of the posterior lobe's fibrous region. Fibres from the optic masses branch before entering the central body. The branch which does not enter the central body forms a direct commissure with contralateral fibres, while fibres which enter the posterior lobe form a diffuse synaptic region along the midline between the hemispheres.

The two, equally sized, incompletely divided, central body lobes of Celaenia together make up 10% of the total supraoesophageal volume. They are both composed of dense association neuropile and surrounded by a cellular cortex which sends axons into the horseshoe commissure. Both lobes are interconnected by tracts similar to those found in Phonognatha, but the incoming commissural fibres within the posterior lobe synapse in the contralateral hemisphere rather than along the midline, and the tract connecting the anterior lobe and the primary optic amsses is smaller.

In Argiope the two equally sized, homogeneous lobes which merge laterally make up 10% of the total supraoesophageal volume. Innervation is similar to that found in Celaenia except that; the fibres between the horseshoe commissure and the surrounding cortex are more prominent; the spread of synapsing commissural fibres within the posterior lobe is greater and; the direct fibrous connection between the primary lateral optic mass and the anterior lobe is less well developed.

The two, equally sized, homogeneous lobes of Tetragnatha are only weakly divided. Together they make up 10% of the total supraoesophageal neuropile and are surrounded by a dense layer of A and B neurocytes which send prominent groups of axons into the horseshoe commissure. The tract between the anterior lobe and the primary optic masses is very poorly developed. The tract between the secondary lateral optic masses which passes into the contralateral hemisphere of the posterior lobe and spreads out widely.

DISCUSSION

WEBS

Many authors have attempted to explain the origins and evolution of the orb web (10,19,49,50,79, 80,81,98,99,118,119).

While there are difficulties in cladistic analysis involving limited features(67), and in particular the orb web(70), there is agreement concerning some evolutionary features. These conclusions are supported by morphological evidence such as palpal and epigynal structure(70).

The main function of the orb web in Araneidae is the capture of prey. Selection would favour the evolution of an orb web which,

(1)makes the web more efficient in catching prey.

(2)reduces the energy expenditure by the spider making the web(57).

This analysis does not consider the influence of prey specificity, as seen in Celaenia,which is not usually important for spiders(110). Evolution of the orb web through these selection pressures may be divided into developmental stages where different living species retain varying numbers of the primitive characteristics.

The accepted view is that the Araneidae orb web evolved from a space or sheet web like the Theridiidae or Linyphiidae webs(71). Cyrtophora has a web similar to these(26,49,50,52,70,79). The chief difference is that it contains a regular spiral and radii arrangements which reduce the silk spun over a given area, compared with the sheet web.

This reduces the energy expenditure of the spider. "Web building is an economical process energetically, unless the edible mass of prey is small compared with the mass of web used in its capture. It was thus advantageous for spiders to develop superior web materials and web designs rather than lay out even larger webs"(57).

The efficiency of this web for prey capture has been increased in two ways by Nephila.

(1)As insects fly mainly in a horizontal direction, a vertical web is more efficient than a horizontal web. In an elastic structure, such as a web, this places considerable strain upon the upper portions of the web. "A weight localized at a point in a web loads the supporting filament above it and not the portion below"(57). The "missing sector"(79) of Nephila and Phonognatha webs reflect this. The radii each side of the missing sector at the top of the web form an integral part of the web frame and are able to take a large proportion of the web load which would otherwise be taken through the numerous lateral support threads. This is distinct from the neater missing sector in Zygiella which varies in position and performs a different function(66,97). Extra strengthening may be supplied by stabilimenta reported in immature Nephila edulis(Austin pers. comm.) and the moulting web of Nephila maculata and Nephila clavipes(106,108).

(2)A viscid spiral from the aggregate glands is more efficient in restraining prey than a non adhesive web, particularly in a vertical web where prey would otherwise fall from the web.

Webs of Phonognatha present 3 modifications of the Nephila web.

(1)Detritus which builds up in the web is removed, reducing the vertical strain on the web allowing a reduction in the quantity of silk used.

(2)Unbranched radii use less silk and are therefore more energy efficient.

(3)The nonviscid scaffold spiral is removed and reingested. The more efficient viscid spiral is the primary catching mechanism and by reingesting the scaffold spiral less energy is wasted for the animal.

The Argiope web contains considerably less silk for its catching area than the previous genera considered and is therefore more energy efficient. The reduction of silk content is achieved by increasing the structural stability of the frame. Stability is further enhanced by the stabilimentum which also serves to camouflage the spider in its web(79). The stabilimentum is not universal within or between species and is therefore of dubious taxonomic use(70). With the increased structural stability the large quantity of silk used to construct lateral support lines is reduced. Similarly the missing sector in the upper portion of the web is lost. Wider spread radii and spirals reduce the silk requirement without loss of efficiency(57). The temporary nature of the web may be the result some loss structural stability but this is counterbalanced by other gains in efficiency:-

The spider will reduce the energy loss of constant rebuilding by reingesting the web(9,95,127,135): Permanent webs require considerable repair as a result of rain, wind and dust(57). This energy expenditure for repair is avoided by temporary webs where web construction does not occur in adverse conditions(29,11).

The simple symmetrical web allows more precise location of prey by vibration(57) increasing the efficiency of the web in prey capture. The removal of the non-viscid non-catching, central hub of the web in Tetragnatha, and the Zygiella missing sector are argued to be adaptations for rapid localization of prey in the web(49,66).

Celaenia is considered to be an derived Araneid which has adapted its method of prey capture to its specialized diet and secondarily lost its web building behaviour.

The evolution of the orb web in Uloboridae is argued by most, although not all(67), to be convergent evolution(50,53). Morphological evidence supports convergent evolution as well as some aspects of Philoponella web structure which suggest analogous rather than homologous development.

(1)The hub is always attached to a support suggesting relationships with Filistatidae rather than Araneidae(49).

(2)The spiral is not attached at a single point to a radius but is joined to the radius over some length(49).

(3)The spiral is not attached to every radius it intersects(23,24,25).

(4)While the stabilimentum is not a good taxonomic feature to use, it was observed during the study that the Philoponella stabilimentum runs parallel to the radii, but the Araneid stabilimentum is composed of a series of threads at right angles to the radii,joining two adjacent radii.

The nature of these behavioural differences suggests different cues are required by Uloboridae and Araneidae in the web building process. Differing cues would require different methods of integration within the central nervous system which in turn might be reflected in the structure of the central nervous system.

Several studies have been undertaken to determine the stimuli needed to construct different parts of the orb web. The construction of a radius is controlled by tension stimuli measured from the hub(101,132). The catching spiral construction is controlled by measurement of angles(22). The content of the silk glands controls the spacing of threads measured by the first pair of legs(133).

To spin an orb web the spider would need at least one cue for each of the following. Most features below would need a complete set of cues.

a: lateral support thread construction

b: regular scaffold spiral and radii

c: stabilimentum construction

d: production of viscid thread spiral

e: vertical orientation

f: removal of scaffold spiral

g: complete detritus removal

h: vertical frame production

i: reingestion of web at daybreak

j: construction of web at nightfall

k: override of cue j in adverse conditions

l: removal of hub

(a) is superceded by (h) in derived Araneidae. Stabilimentum construction which appears inconsistently in webs(70) may have evolved several times (22,109).

Cues needed by each of the spiders under study are as follows:

Cyrtophora : a , b

Nephila : a , b , (c) , d , e

(stabilimenta are not universal)

Phonognatha : a, b, d, e, f, g

Argiope : b, (c), d, e, f, g, h, i, j, k

(stabilimenta are not universal)

Tetragnatha : b, d, e, f, g, h, i, j, k, l

The cues would not be needed by Celaenia which does not construct an orb web.

Philoponella : a, b*, c*, d*

(* b,c and d are likely to be examples of convergent evolution since the nature of the product is different to that of the Araneidae although its function is the same). The construction of a maze (a) is found in many spider families.

As more cues are required for web construction, more integration would be carried out at the level of the central nervous system. A corresponding increase in importance of the appropriate association areas of the brain would be expected in spiders, such as Argiope and Tetragnatha, with many cues to integrate compared with Cyrtophora with few cues.

There is a shift in the nature of the sensory stimuli, the orb web building spider being less visually orientated and more tactile. "Such capability goes a long way to make up the web-spider system viable on the basis of tactile sense alone. There may be little need for more specialized senses of sight, smell and hearing"(22). A corresponding reduction in the importance of the optic centres should be seen or they may change in function.

BRAIN STABILITY (fig 5)

Satija(112) has observed, that "apart from the confusion that exists in the relationship of the structures of the brain in spiders, there is a good deal of controversy regarding the form and number of optic masses." This uncertainty extends to other association areas of the Araneid supraoesophageal ganglion. Only two studies of Araneid spiders have been made, and the results of these studies conflict. Hanstrom(39), studying Araneus diadema, found two median optic masses and one lateral optic mass in each hemisphere. Satija(111), studying Cyrtophora, found one median optic mass and two lateral optic masses in each hemisphere. Other comparisons between the two studies are difficult to interpret. This study has clarified the controversy that the differing results have caused. Despite the wide behavioural and anatomical diversity of the Araneid species studied, the brain structure shows a consistency not previously appreciated.

All the Araneids studied possess two pairs of primary optic masses. In each hemisphere a single optic nerve runs from the posterior median eye to a small primary median optic mass situated outside the main supraoesophageal neuropile mass. The optic nerves of the anterior median eyes and the two pairs of lateral eyes fuse into a single, lateral optic nerve which passes into the lateral primary optic mass. This mass is anterior to the main supraoesophageal neuropile mass.

The lateral primary optic mass is interconnected with the lateral lobe of the central body and also a secondary lateral optic mass. This is the formation described by Satija. It can only be assumed that Hanstrom's differing findings are the result of inaccurate tracing of the optic nerves to their associated eyes.

The secondary lateral optic mass in all species is interconnected to all the other association areas of the supraoesophageal ganglion, and, through a longitudinal tract, to the suboesophageal ganglion. Similar interconnections of the secondary lateral optic mass and these areas are found in all species.

In the anterior supraoesophageal area the corpora pedunculata, bridges the two hemispheres. Laterally the corpora pedunculata fans out with connections to both the suboesophageal ganglion and the secondary lateral optic mass. In the same region the development of the bridge, or anterior dorsal commissure of Babu (2) and glomerular neuropile does vary between different species.

Abutting the posterior dorsal surface of the supraoesophageal neuropile lies the central body. It forms a well developed association area, discrete from the main supraoesophageal neuropile, in all Araneid species studied. The central body is divided into an anterior and a posterior lobe. In simple Araneids the remnants of two lateral lobes can be seen. Tracts and fibre bundles separate the lobes.

The posterior dorsal supraoesophageal neuropile contains a number of commissural fibre tracts which follow the boundary between the neuropile and the cellular cortex. These tracts are interconnected with the association lobes and cells of the central body. In the central region of the supraoesophageal neuropile, a large horseshoe commissure, corresponding to the dorsal median commissure of Babu(2), is found. Branches from this commissure interconnect longitudinal tracts from the suboesophageal ganglion with the central body.

These features were consistently found in all Araneid spiders studied and while the relative development and internal structure of each did vary, together they form a distinct, unaltering pattern within the family.

SIMPLE SUPRAOESOPHAGEAL STRUCTURE

Although dorsal supraoesophageal association areas remain constant in their presence and interconnection, a number of structural variations have been found in this study. These variations follow a consistent and gradual pattern which corresponds to the phylogenetic and behavioural relationships of the species studied. Two brain structures can be put forward, one representing the simple orb-weaver, and the other representing the derived orb-weaver. Between these two extremes this study has found a continuum of intermediate forms.

Simple web building Araneids, such as Cyrtophora, show poor development of the anterior association areas. The primary lateral optic mass is small, no bigger than the primary median optic mass. It shows little or no internal specialisation, being primarily composed of fibrous neuropile. There are only few primary rods and these are porly developed. No secondary rods are present. From the primary lateral optic mass fibres travel to the posterior dorsal neuropile. Only a small proportion of these fibres interconnect the primary and secondary lateral optic masses, most continuing to the central body directly. The secondary lateral optic mass is a small lateral bulge toward the posterior of the neuropile. Staining of the mass is poor. The fibrous appearance of the mass is indicative that it is simply an intermediate minor synaptic region between the primary lateral optic mass and the central body. The cellular cortex surrounding the secondary lateral optic mass is similarly poorly developed, as are the connections between the mass and other regions of the central nervous system. The longitudinal tract between the mass and the suboesophageal ganglion is small, suggesting it is of only minor importance in these species. The corpora pedunculata, between the secondary median optic masses of each hemisphere are small and highly fibrous. Synaptic regions within the corpora pedunculata are virtually non-existant. Anterior to the corpora pedunculata, the bridge is insignificantly developed. Lateral to the bridge lies a scattered area of glomerular neuropile.

The posterior dorsal supraoesophageal neuropile in simple web building Araneids shows strong development. In particular, fibrous tracts and commissures are prominent. The horseshoe commissure is large and takes up stain well. Branches from the horseshoe commissure into the central body interconnect the central body with the suboesophageal ganglion. The central body itself is characterized by a fibrous posterior lobe. Comparatively few of these fibres pass into the association areas of the neuropile, or into the surrounding cortex, but form commissures through the central body. A very well developed tract from the primary lateral optic mass enters the lateral edge of the anterior lobe. In the most simple species a partial subdivision of the anterior lobe into anterior and lateral portions can be seen.

DERIVED ARGIOPID STRUCTURE

Advanced web building Araneids, such as *Argiope*, show strong development of the anterior association areas and the interconnections between them. The primary lateral optic masses are prominent, and are much larger than the primary median optic masses. They are not fibrous but contain many clumps of dense staining, homogenous neuropile (rods). These rods are interconnected by more dense staining homogenous neuropile, giving the mass a "flaming tree" appearance.

At the base of this flaming tree is a further secondary swelling of dense association neuropile. Between the secondary swelling and the secondary lateral optic mass the tract is both large and densely staining, similar to other association neuropiles. The secondary lateral optic mass is situated in the lateral anterior region of the main supraoesophageal neuropile. It is large and contains very heavily staining homogenous association neuropile. Between the secondary lateral optic masses, the corpora pedunculata show strong development of their associative function compared with the simple Araneids. The anterior tract, from the optic masses, is non-fibrous and densely staining. Across the midline a bulge of tnis association neuropile suggests an integrating function fior this area. Glomeruli are few or absent. The bridge is poorly developed.

The posterior dorsal supraoesophageal neuropile in derived web building Araneids shows only weak development. The horseshoe commissure is thin and fibrous with few synapses. Similarly, the commissural fibres which travel on the outer limit of the neuropile, adjacent to the central body, are sparse. The posterior lobe of the central body has few of these fibres passing through it. The lobe itself is non-fibrous, large and composed of association neuropile.

Many of the fibres which lie between the central body and the main supraoesophageal neuropile do not form a direct commissure, but branch off and pass in tight bundles between the central body lobes to the surrounding cellular cortex. The lateral extremities of the central body are weakly developed with only a small tract of fibres from the primary lateral optic mass entering the neuropile.

TAXONOMIC SIGNIFICANCE

The Araneid species studied conform to a predictable pattern, both in the stability of the underlying structure and in the gradual modification of that pattern from a simple form to an derived form, makes the supraoesophageal structure a useful tool for the investigation of relationships within the Araneidae, and relationships between Araneidae and other spider families.

Celaenia further supports the taxonomic significance of supraoesophageal structure. The structure is consistent with the traditional placement of Celaenia within the Araneidae(21,43,96) on the basis of morphological characteristics, although the spider does not share any of the derived web-building behaviours. The presence of similarly developed association areas and their interconnections in Argiope and Celaenia not only supports a close relationship between the spiders, but also suggests that regression and atrophy of redundant supraoesophageal structures is slow, or that the structures have taken on different functions.

The relative development of lateral optic masses, corpora pedunculata and posterior lobe of the central body, and the slow regression of the posterior commissures and glomeruli are typical of a spider intermediate in development between Argiope and Phonognatha.

Tetragnatha has traditionally been placed in a family of its own(70)or as a subfamily within the Araneidae(31,42,69). The genera Meta and Leucage have been considered intermediate forms between Tetragnatha and the simple Araneids on the basis of their superficial similarity. More recently some authors have questioned the relationship between Meta and Tetragnatha and suggested that Tetragnatha is more closely related to the derived Araneidae(69). The structure of the ventral caecum in Tetragnatha is quite different to that found in Meta(86,87,88). The loss of the eye tapetum(45) and the large separation of tne lateral eyes from the median eyes(67) are evidence of a closer relationship to the derived Araneids.

The supraoesophageal structure of Tetragnatha is that of a highly derived Araneid. The anterior association nexus of optic masses and corpora pedunculata are highly developed. The primary lateral optic mass is larger and shows a more complicated pattern of rods than in any other genus studied. Similarly the secondary lateral optic mass and corpora pedunculata are large with well developed homogeneous association neuropile.

Between the primary and secondary lateral optic masses an additional area of association neuropile is found. The posterior commissures are only poorly represented as are the connections between the primary optic masses and the central body. Within the central body the posterior lobe has a non-fibrous appearance. These features are all typical of an derived web building Araneid. The results are consistent with Tetragnatha being a derived Araneid form.

The family Uloboridae has been grouped as a close relative of the Araneidae by some authors. The features used for this classification have been the similarity of genital organs, trichobothrial patterns (64,94,114) and secretory products(49), as well as the presence of an orb web (94). Other authors have grouped all cribellate spiders, including Uloboridae, as a single evolutionary branch widely divergent from the Araneidae. This classification has been supported by the presence of a cribellum in Uloboridae but not Araneidae and the differences in orb web construction between the two families (10,47,51,67). This classification regards the development of the orb web in the two families as convergent evolution.

Two other groups of workers have studied the supraoesophageal structure of cribellate spiders. Hanstrom, although supplying little data to support his findings, and contradicting his own findings in a later paper,(41,111) grouped the cribellate families Filistatidae and Amaurobiidae with the Agelenidae and placed the family Eresidae in a group of its own according to their brain structure.

Satija and his coworkers(112,113) have examined the structure of Filistatid, Erisid and Oecobid cribellate spiders. The three families show considerable differences in (1)the number and structure of primary optic centres, (2)the development and innervation of the corpora pedunculata, (3)the development and innervation of the bridge, (4)the presence or otherwise of globuli, (5)the development of the central body. From this evidence it would appear that the cribellate families of spiders are not closely related. When compared with the work of Satija, this study suggests the family Uloboridae is not closely related to either the Filistatidae or the Eresidae. The Filistatids have no corpora pedunculata and the two pairs of primary optic masses each serve two pairs of eyes. The dorsal pair serve the median eyes and the ventral pair serves the posterior eyes. Philoponella possesses corpora pedunculata and the dorsal optic mass serves only the anterior median pair of eyes. The posterior optic mass serves the three other pairs of eyes. The Eresids have a similar grouping of primary optic masses to the Filistatids and although they possess corpora pedunculata much of their innervation differs from that of Philoponella. While some differences between the supraoesophageal structure of Uloboridae and Oecobidae are suggested it is difficult to make a close comparison between the studies.

The Philoponella supraoesophageal structure, while showing few similarities with these cribellate spiders, does show a strong resemblance to the simple Araneid structure. The primary and secondary lateral optic masses are both observed with little development in either. Their innervation is similar in both Philoponella and simple Araneids. A single pair of small primary median optic masses is present. The corpora pedunculata are fibrous in form with few interconnections to the optic masses. The horseshoe commissure is a strongly developed region of homogenous neuropile. The central body is large with a fibrous posterior lobe. Remnants of the central body lateral lobe, as found in Philoponella, can be observed in Cyrtophora.

BEHAVIOURAL SIGNIFICANCE

The change from a simple to an derived Araneid web requires an increasing number of cues to be integrated within the supraoesophageal ganglion. Integration occurs in the association areas, so the development of particular association areas in these species is a useful guide to which areas are of importance to web-building behaviour.

The Celaenia supraoesophageal ganglion demonstrates not only the retention of structural characteristics despite a change in behaviour, but also the development of new structures associated with new behaviours. Celaenia differs from other Araneids in the strong development of the bridge, and in particular the ventral tracts from the bridge to the suboesophageal ganglion through the stomatodeal commissure. The stomatodeal commissure interconnects the cheliceral ganglia. Other pathways from the bridge interconnect it with the first pair of legs. Celaenia catches its moth prey by grasping them when they fly close enough. It is not suprising therefore that the most strongly developed area of the supraoesophageal ganglion is concerned with the integration of this behaviour.

In derived orb weaving spiders the more extensive integration needed for more derived webs is accomplished through six major structural changes. (1)The total volume of association neuropile is increased. (2)The density of the association areas increases. Coarse fibrous association centres are replaced by dense staining homogenous neuropiles in which fine fibres are closely packed. (3)Individual association areas become more structured with distinct subdivisions and distinct interconnections. (4)Around the association areas the cellular cortex contains more cells. (5)Between existing association areas fibre tracts become homogeneous and densely staining with numerous synapses forming new association areas.

(6)Direct commissural fibres linking the hemispheres become less evident and are replaced by synaptic areas along the midline.

Through these six structural changes there is an overall shift in the importance of association areas from a posterior nexus in simple orb weaving spiders, to an anterior nexus in derived orb weaving spiders. The posterior nexus includes the central body, posterior commissures and horseshoe commissure. The anterior nexus includes the lateral optic masses and the corpora pedunculata. As the dependence on visual information becomes less in more derived orb-weavers it seems likely that the anterior nexus of optic centres has developed a secondary function related to the suboesophageal input to the masses rather than the input from the optic nerves. The longitudinal suboesophageal tracts to the optic masses convey the tactile information to the supraoesophageal ganglion. It is this tactile information which is of primary importance in the derived web building Araneids.

The supraoesophageal structure of Philoponella is similar to that of the Araneids but the specialization of association areas occurs in the posterior nexus. The horseshoe commissure, glomeruli and the lateral and anterior lobes of the central body are better developed in Philoponella than in any Araneid studied. The components of the anterior nexus of association areas show similar development to the simple Araneids. It seems probable therefore that, while Uloboridae show evidence of a close relationship with the Araneidae, the development of the orb web is due to convergent evolution in the two families(22,26,49,50,70,71).

Due to the extreme density of the supraoesophageal neuropile many procedures required extended times for complete penetration of the tissues. For the same reason the Palmgren silver stain required some modifications. The same difficulties were not found during sectioning of the suboesophageal ganglion.

FIXATION

a) Formal acetic acid (1 hr)

b) Formal acetic acid (from 1 wk to 12 mths)

c) Formal acetic acid (1 hr)

DEHYDRATION

d) 70% alcohol (1 day)

e) 70% alcohol (1 day)

f) 90% alcohol (2 to 3 days)

g) Absolute alcohol (2 days)

h) Absolute alcohol (2 days)

i) Absolute alcohol (1 hr)

CLEARING

j) Xylene (2 days)

k) Xylene (2 days)

l) Xylene (1 hr)

EMBEDDING

m) 50% Xylene:50% Histowax (2 days)

n) Histowax (2 days)

o) Histowax (2 days)

a) Xylene (needs to be about 50 C for complete dewaxing) (5 min)

b) Xylene (room temperature) (5 min)

c) Absolute alcohol (2 min)

d) Absolute alcohol (2 min)

e) 90% Alcohol (1 min)

f) 70% Alcohol (1 min)

g) 50% Alcohol (1 min)

h) 30% Alcohol (1 min)

i) Distilled water (2 min)

j) Distilled water (2 min)

k) Solution D(acidifier) (5 min)

l) Distilled Water (2 min)

m) Distilled water (2 min)

n) Distilled water (1 min)

o) Solution E(mordant) Best results were obtained using the bath at 33 C for 7 minutes. Temperature is a critical factor.

p) Solution F(reducer) Best results were obtained when the solution was "aged" for 2 weeks in a brown bottle in a cool place before use. 300ml of solution can be used for 8 slides dipped simultaneously. A plastic holder for the slides made controlled agitation of the slides much easier, and the resulting stain more regular. (1 min at exactly 42 C)

Q) 50% Alcohol (5 to 10 sec)

r) Distilled water (2 min)

s) Distilled water (2 min)

t) Distilled water (1 min)

Wipe back of slide to remove excess stain

u) Solution G(toner) (5 min)

v) 2% Oxalic acid (15 sec)

w) Distilled water (30 sec)

x) Solution I(fixer) (10 sec)

y) Distilled water (2 min)

Rehydrate in graded alcohols

Clear in Xylene

Mount with Canada Balsam

FIGURES

99 Figure 1 Optic masses

101 Figure 2 Central Supraoesophageal Structures

104 Figure 3 Central Body

106 Figure 4 Neurocyte Cell Types

107 Figure 5 General Supraoesophageal Structure

TABLES

108 Table 1 Web Characteristics

109 Table 2 Nephila Neurocyte Types

PLATES

110 Legend

111 Plates 1 - 44

FIGURE 1

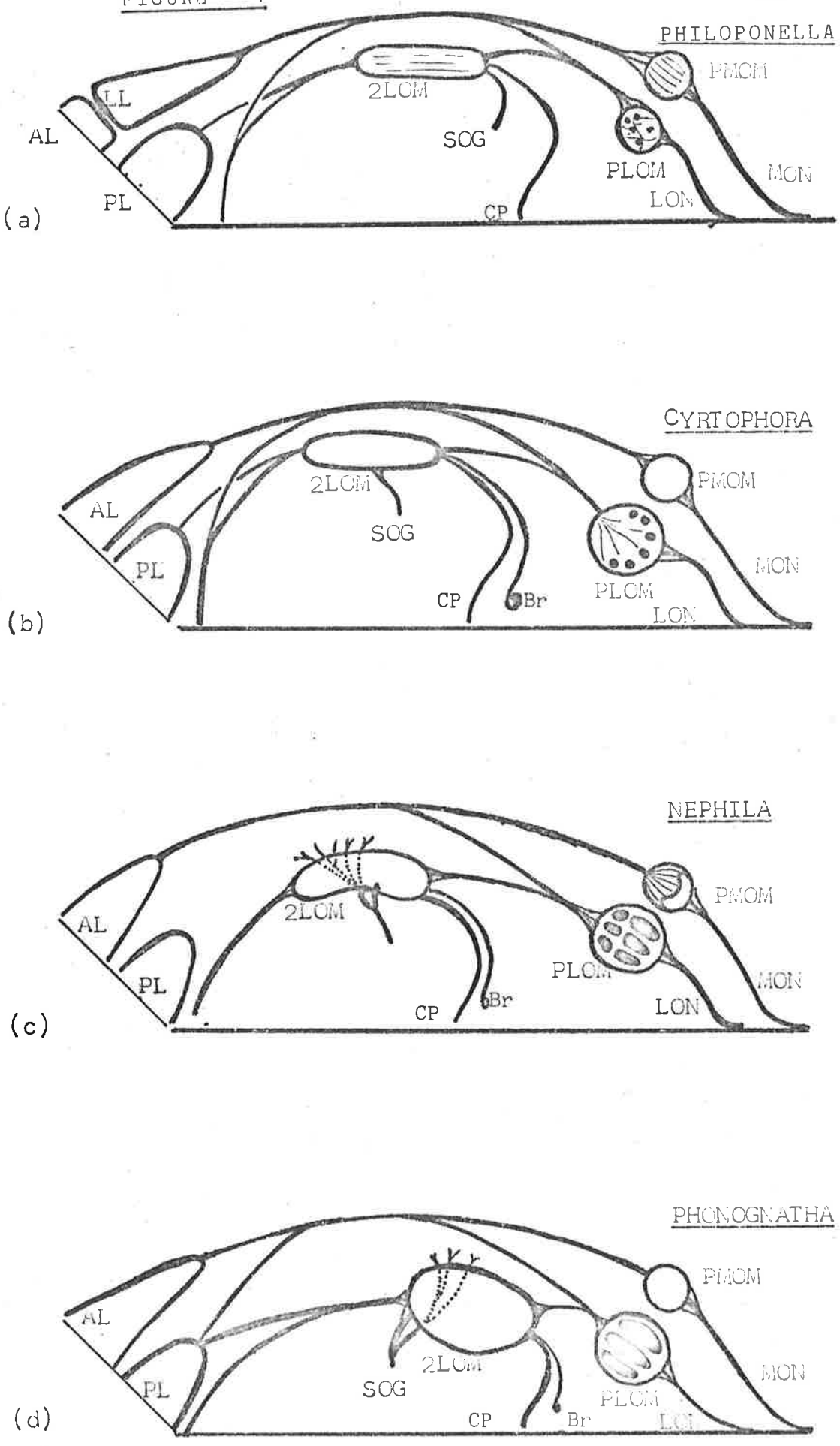
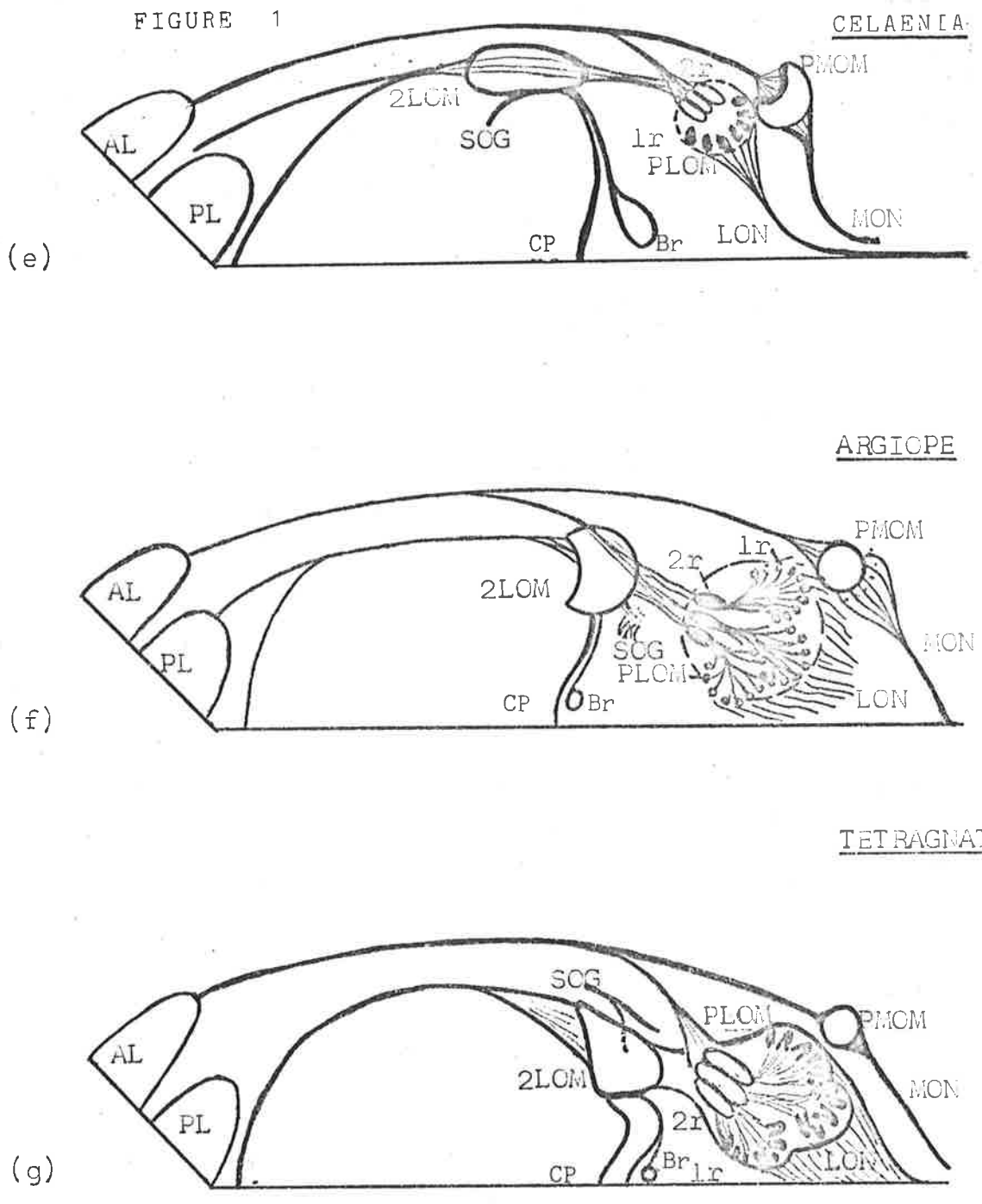

PHILOPONELLA
PMOM
2LOM
LL
AL
SOG
PLOM
MON
PL
LON
CP
(a)
CYRTOPHORA
PMOM
2LOM
AL
SOG
PL
MON
CP
Br
PLOM
LON
(b)
NEPHILA
PMOM
2LOM
AL
PL
PLOM
MON
CP
Br
LON
(c)
PHONOGNATHA
PMOM
AL
2LOM
PL
SOG
MON
PLOM
CP
Br
LON
(d)

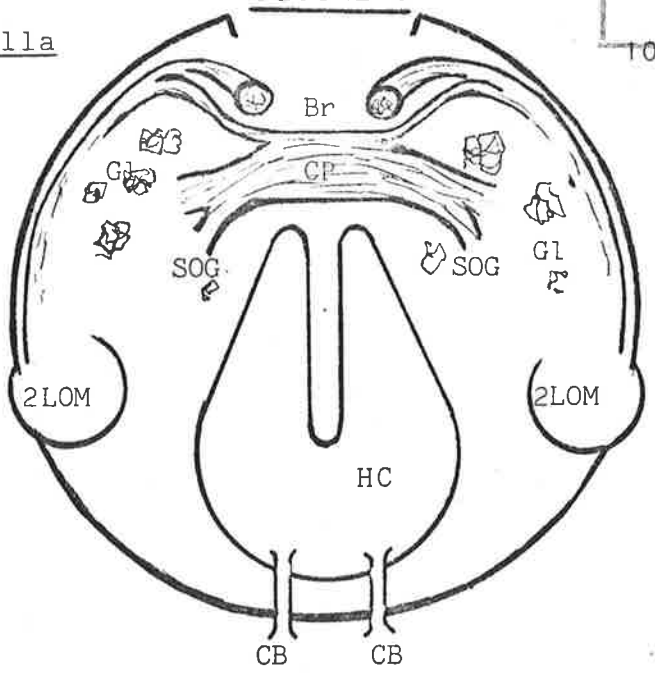
FIGURE 1



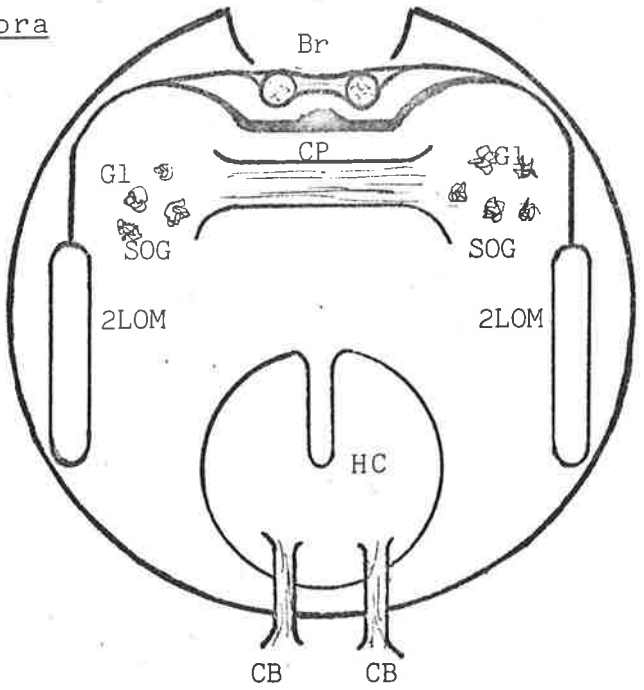
OPTIC MASSES viewed from above.
AL-Anterior lobe (central body) , PL-Posterior lobe (central body) , LL-Lateral lobe (central body) , MON-Median optic nerve , PMOM-Primary median optic mass , LON-Lateral optic nerve , PLOM-Primary lateral optic mass , 2LOM-Secondary lateral optic mass , Br-Bridge , CP-Corpora pedunculata , SOG-Sub-oesophageal ganglion , 1r-Primary rods , 2r-Secondary rods .

FIGURE 2

(a) Philoponella



(b) Cyrtophora



(c) Nephila

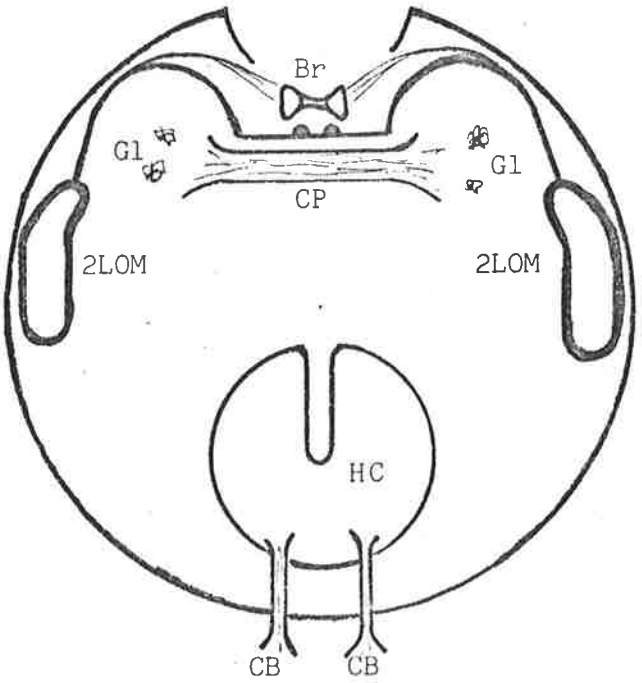
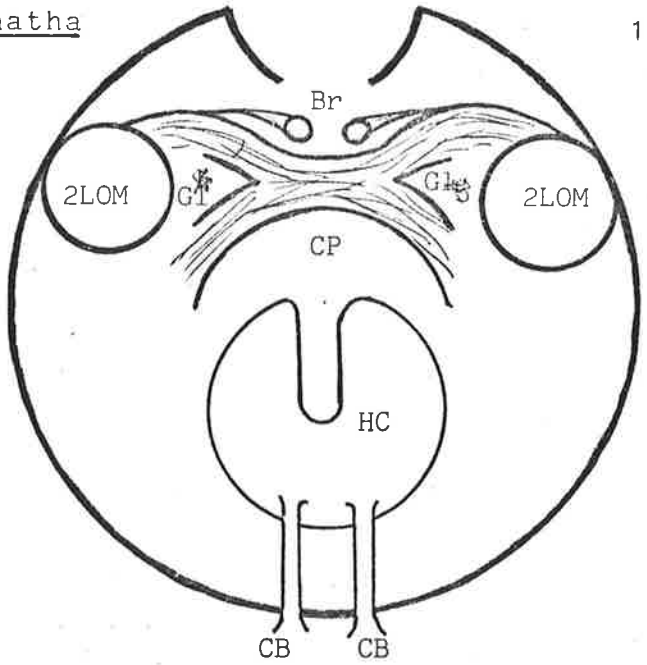
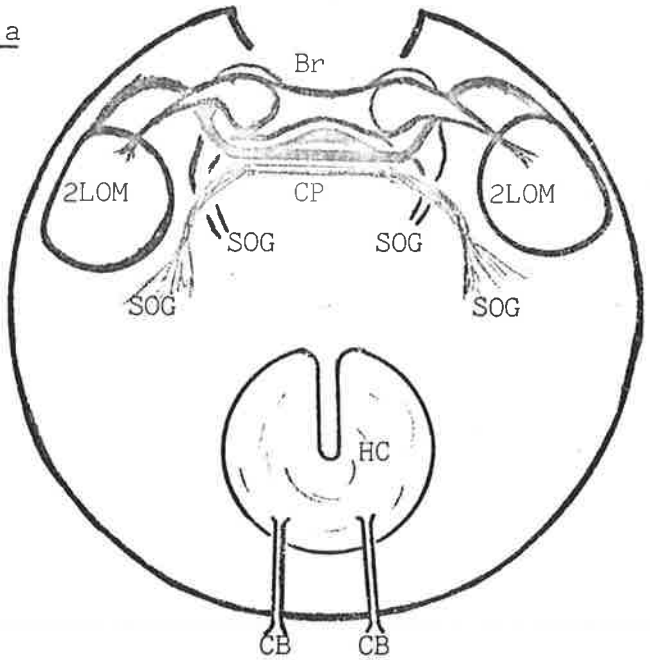


FIGURE 2

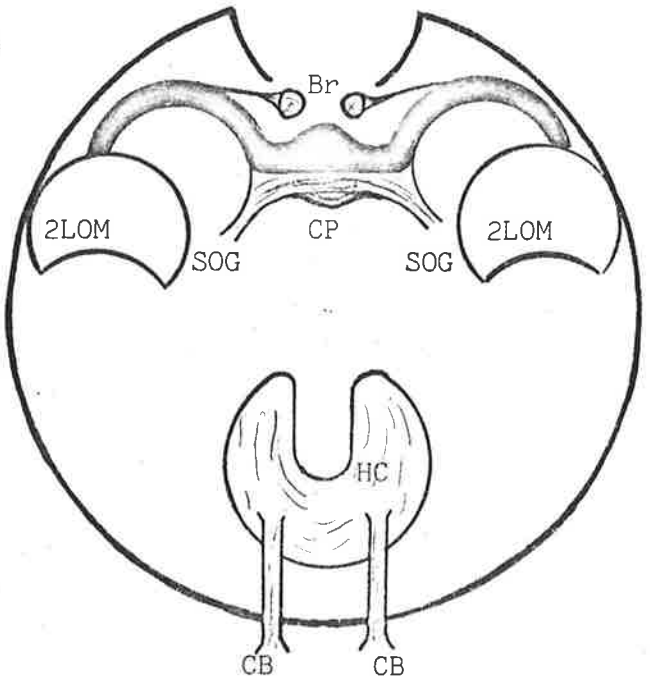
(d) Phonognatha



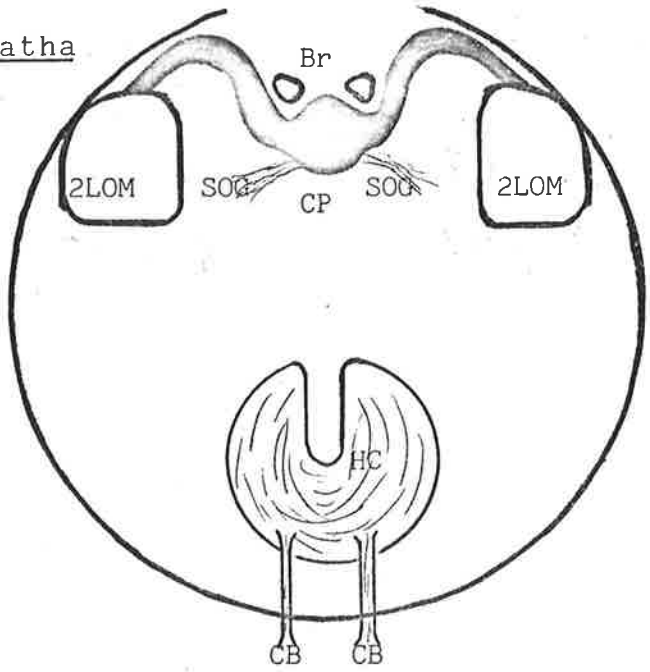
(e) Celaenia



(f) Argiope



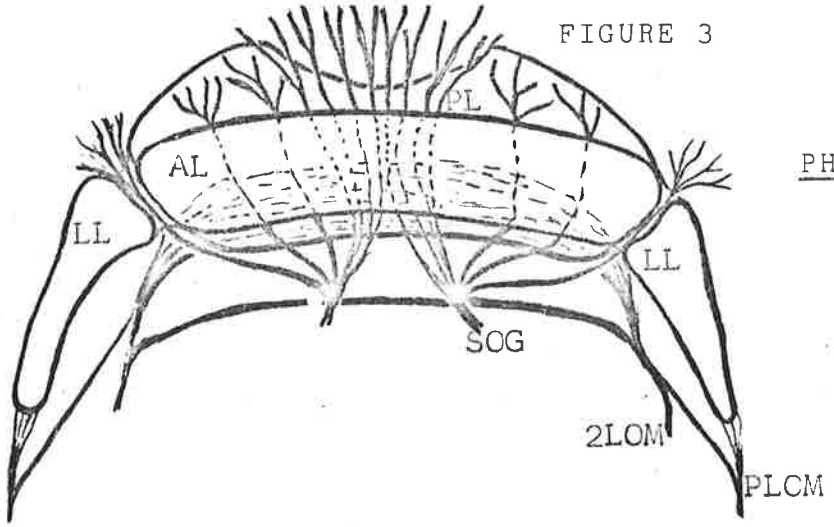
(g) Tetragnatha



CENTRAL SUPRAOESOPHAGEAL NEUROPILE viewed from above (diagramatic) showing association areas and their innervation. Br-Bridge , CP-Corpora pedunculata , HC-Horseshoe commissure , 2LOM-Secondary lateral optic mass , SOG-Fibre tracts to the suboesophageal ganglion , CB-Fibre tracts to the central body , Gl-Glomeruli.

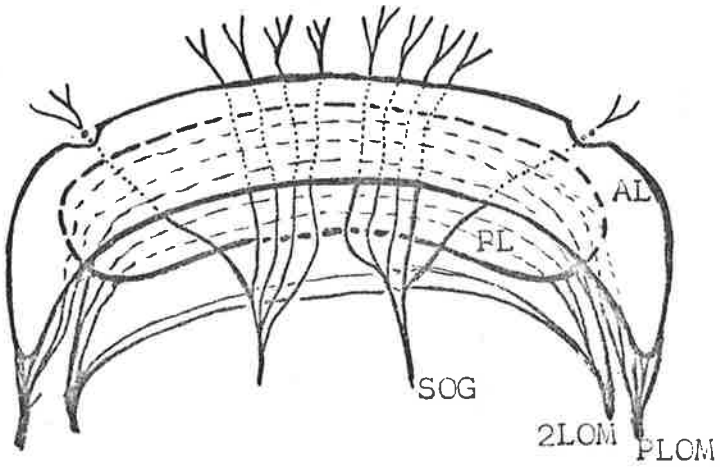
FIGURE 3

(a)



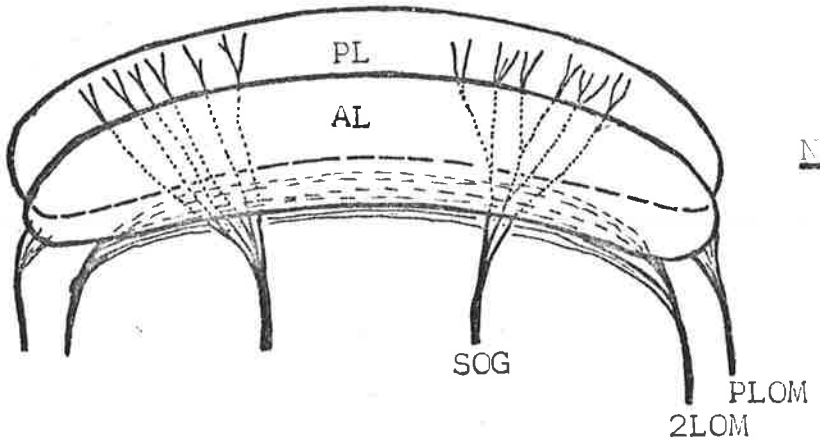
PHILOPONELLA

(b)



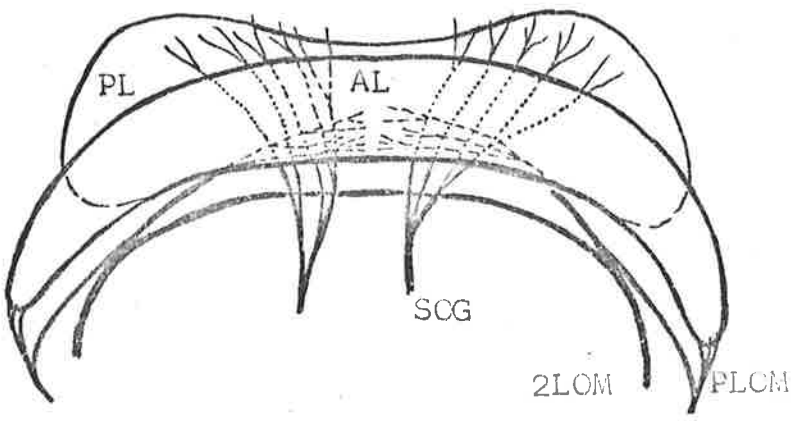
CYRTOPHORA

(c)



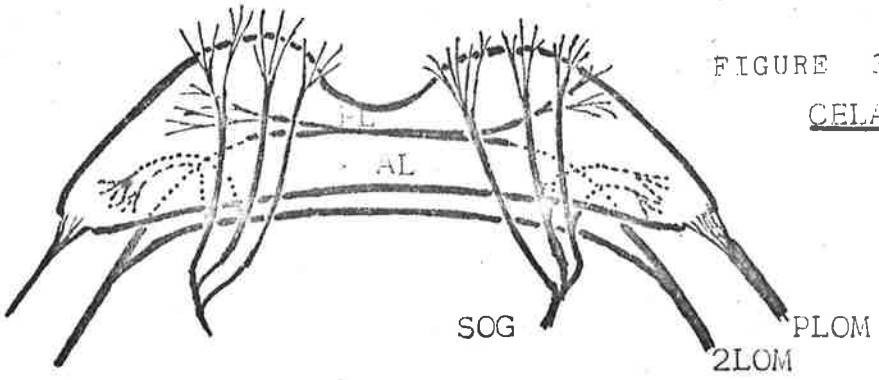
NEPHILA

(d)



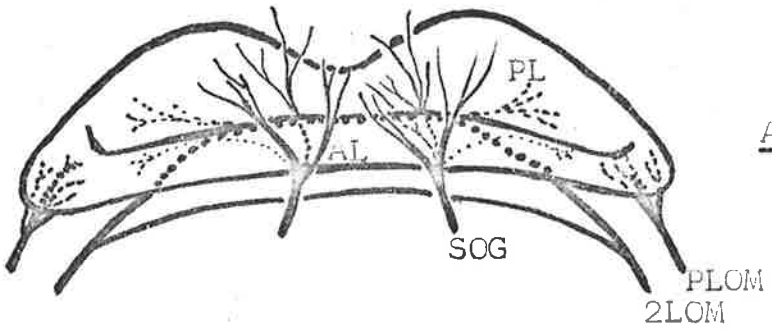
PHONOGNATHA

(e)



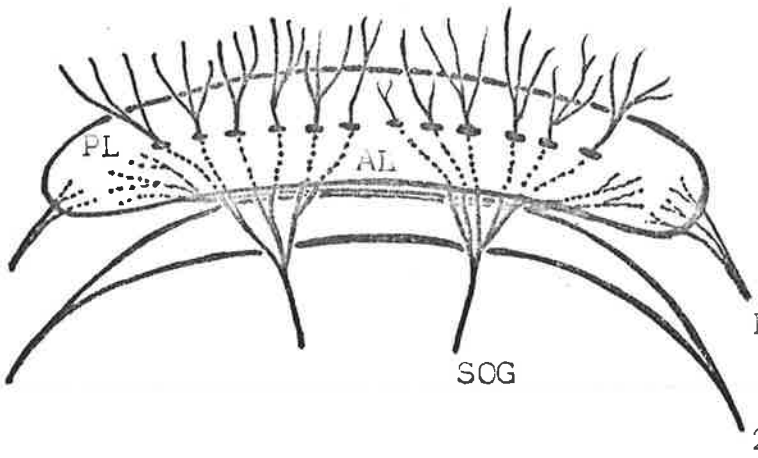
CELAENIA

(f)



ARGIOPE

(g)



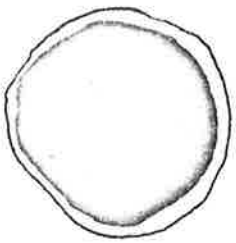
TETRAGNATHA

CENTRAL BODY viewed from above to show lobation and innervation. LL-Lateral lobe , AL-Anterior lobe , PL-Posterior lobe , SOG-fibres from the sub-oesophageal ganglion , 2LOM-fibres from the secondary lateral optic mass , PLOM-fibres from the primary lateral optic mass. Fibre tracts hidden by neuropile are represented with dotted lines.

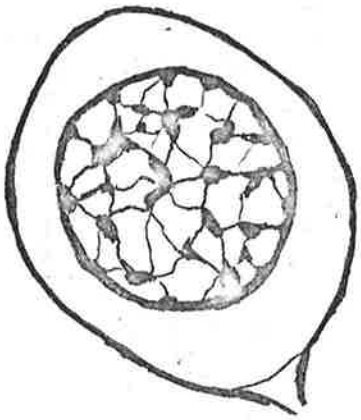
FIGURE 4

NEUROCYTE CELL TYPES

(sensu Babu (5))

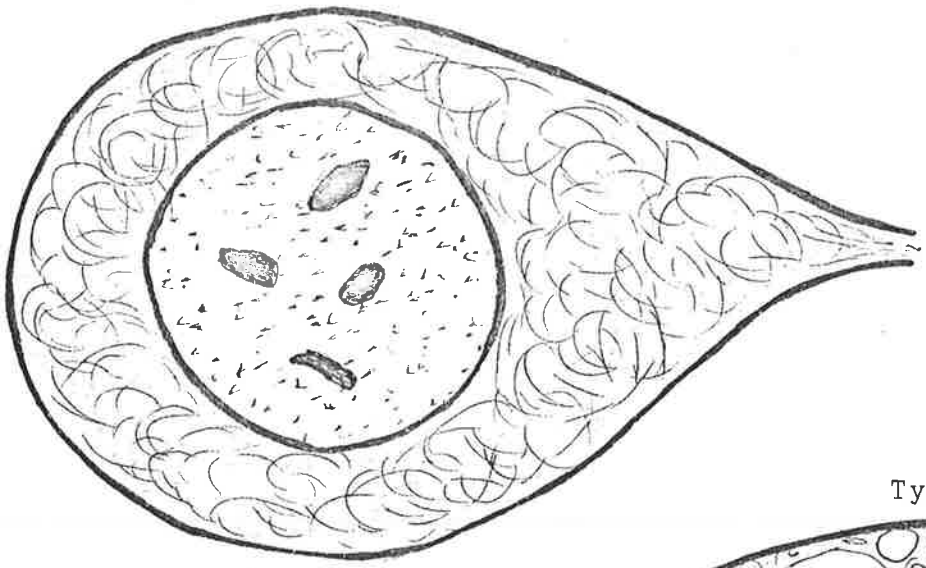


Type A (Globuli)

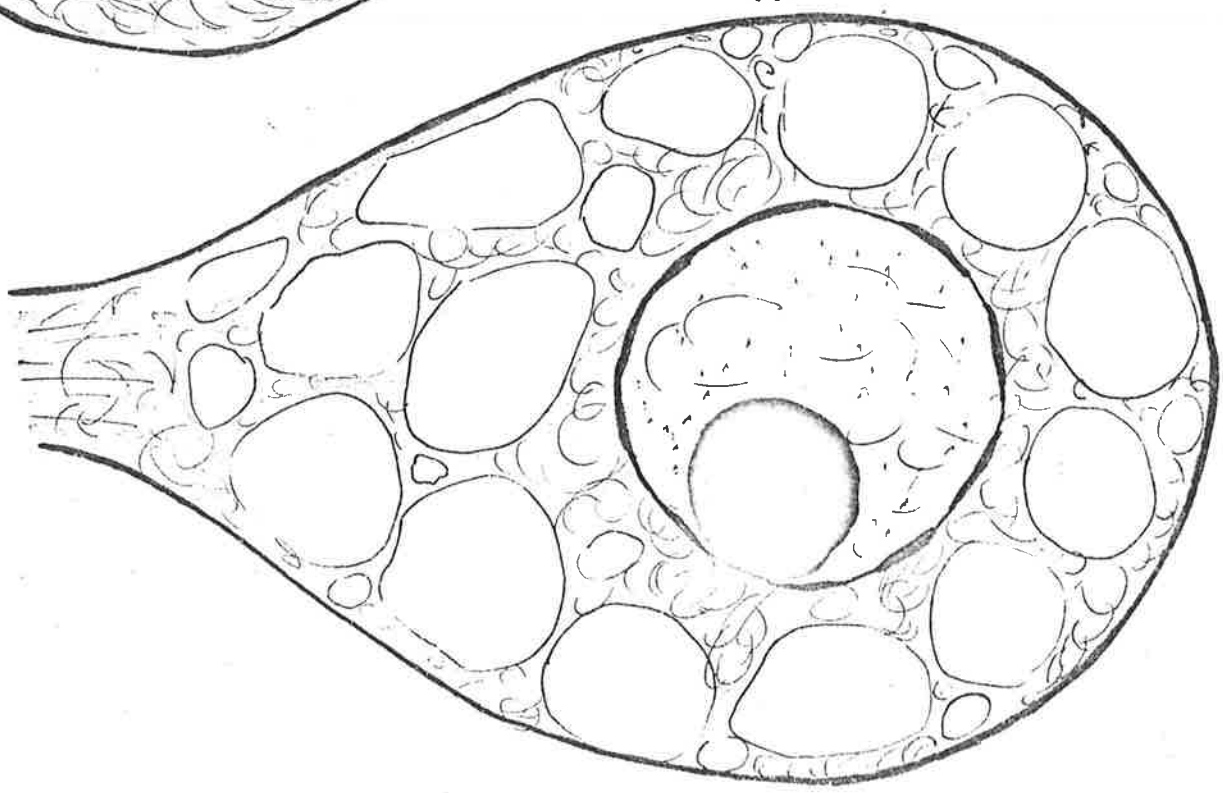


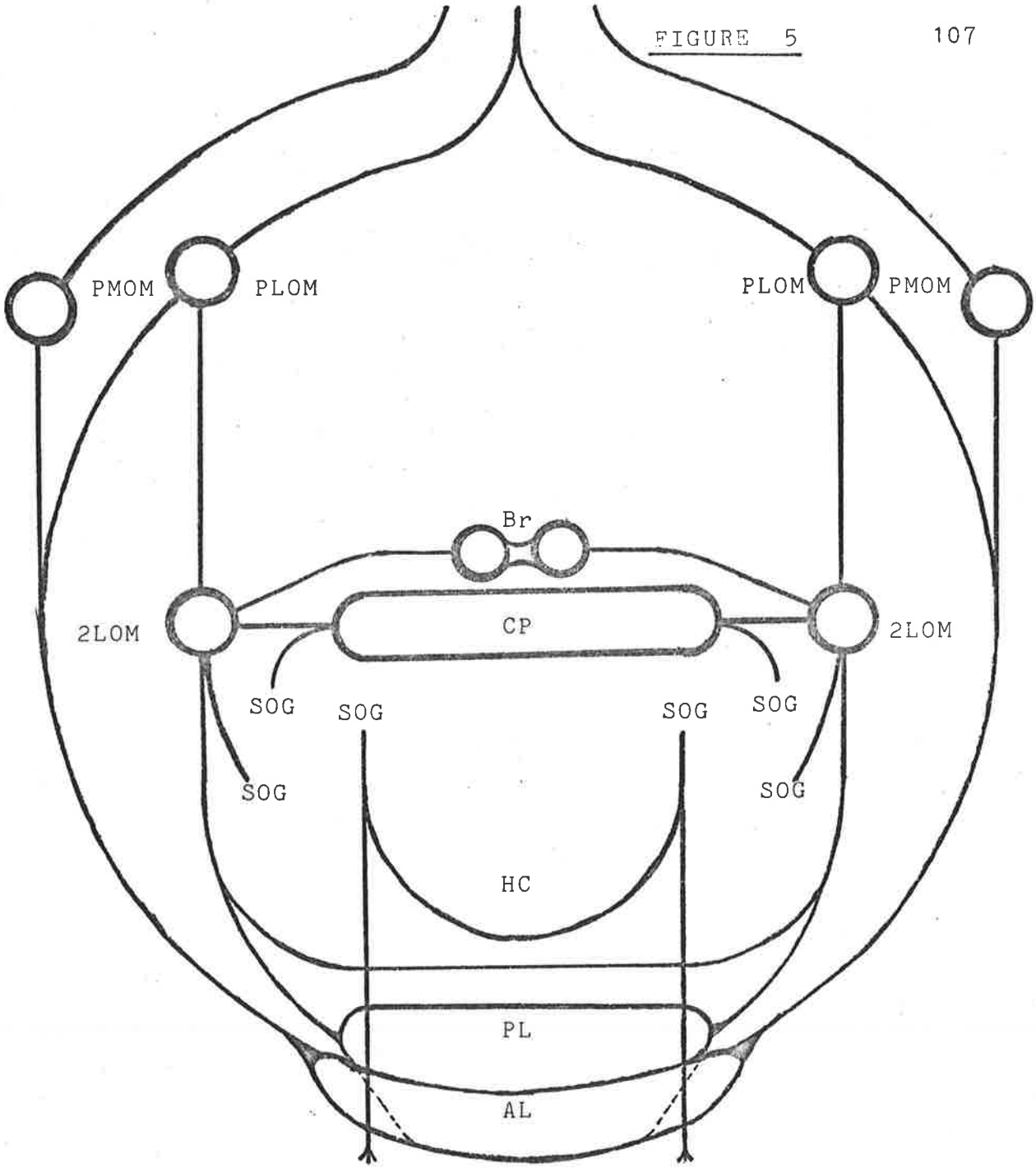
Type B (Medium)

Type C (Neurosecretory)



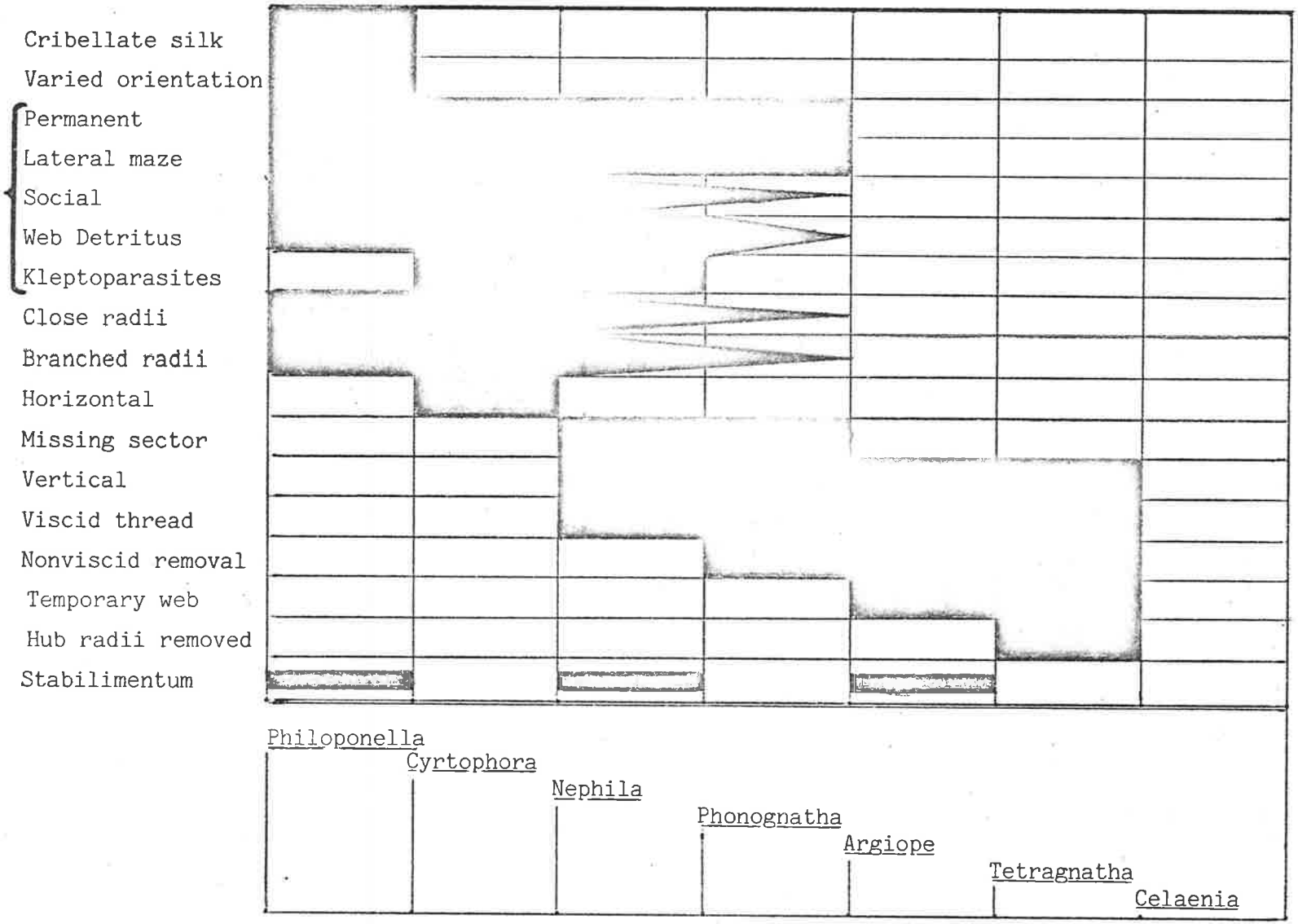
Type D (Motor)





GENERAL ARGIOPID SUPRAOESOPHAGEAL STRUCTURE

AL-Anterior lobe of the central body , PL-Posterior lobe of the central body , SOG-Fibres from the sub-oesophageal ganglion , 2LOM-Secondary lateral optic mass , PLOM-Primary lateral optic mass , PMOM-primary median optic mass , Br-Bridge , CP-Corpora pedunculata , HC-Horseshoe commissure .


Cribellate silk
Varied orientation
Permanent
Lateral maze
Social
Web Detritus
Kleptoparasites
Close radii
Branched radii
Horizontal
Missing sector
Vertical
Viscid thread
Nonviscid removal
Temporary web
Hub radii removed
Stabilimentum
Philoponella
Cyrtophora
Nephila
Phonognatha
Argiope
Tetragnatha
Celaenia

CELL TYPE	GENERAL FEATURES & SIZE	STAINING REACTIONS		
		WEIGERT VAN GEISON	PALMGREN SILVER STAIN	P. T. A. H.
A(Globuli)	Nm5.0 sd0.5 dense clumps behind & above central body merging into B cells	C ground grey N dense black	C not visible N dense black	C not visible N ground deep red with a network of chromatin
B(Medium Neurocyte)	Nm6.5 sd1.3 Throughout brain in all ganglia multipolar	C even grey N ground grey patchy chromatin	C very pale brown to pink Axon hillock often visible N ground clear with granular chromatin often in large lumps No nucleoli	C purple N ground clear network of chromatin
CA1 (Neuro-secretory)	Nm8.6 sd3.5 Cm15.2 sd3.2 Found in arboreal nucleus of supraoesophageal ganglion & many nucleii of the suboesophageal ganglion Multipolar	C even grey but darker than nucleus N ground pale grey chromatin in small dots & usually 2 large patches	C pale pink & foamy texture secretory granules not visible Distinct nerve axons pass into the neuro-pile Axon hillock expanded with a network of fibrils N dense spots of chromatin with 2-3 larger clumps	C pale pink with a foamy appearance with small clear secretory granules N nuclear membrane hard to distinguish ground clear with sparse small dots & 2-3 larger patches of chromatin
CA2 (Neuro-secretory)	Nm9.0 sd0.4 Cm13.3 sd2.7 Found only in the cheliceral ganglion Multipolar	C as for CA1 cell outline indistinct N paler than cytoplasm some large patches of light chromatin	C pale pink & foamy texture visible secretory granules N many fine spots of chrom-atin with 2-4 large patches	C as for CA1 N ground clear with patchy chromatin nuclear membrane hard to distinguish
D(Motor)	Nm10.2 sd1.7 Cm21.6 sd6.0 Xm27.7 sd6.7 nucleolus m4.1 sd0.8 eccentric position Found in cheliceral & suboesophageal ganglia	C dark grey, darkest near nucleus large clear vaccuoles N ground clear with dark patches on rim nucleolus prominent	C deep foamy red to maroon Secretory vaccuoles clear Sometimes with parallel fibrils at the axon hillock N ground foamy, dense & granular nucleolus prominent	C even pink N ground clear with some blue chromatin on rim nucleolus deep red

N, nucleus ; C, cytoplasm ; m, mean ; sd, standard deviation
All measurements are in microns

LEGEND FOR PLATES

A	A (Globuli) cells
AG1	1st Ambulatory ganglia
AG2	2nd Ambulatory ganglia
AL	Central body anterior lobe
B	B (Medium) neurocytes
Br	Bridge
C	C (Neurosecretory) neurocytes
CB	Central body
CG	Cheliceral ganglion
CP	Corpora pedunculata
C1	Posterior commisural fibres & associated tracts
D	D (Motor) neurocytes
FN	Fibrous nexus of the central body
Gl	Glomeruli
LL	Central body lateral lobe
LON	Lateral optic nerve
LS	Longitudinal section
MON	Medial optic nerve
Oe	Oesophagus
P	Perilemma glial cell
PG	Pedipalpal ganglion
PL	Central body posterior lobe
PLOM	Primary lateral optic mass
PMOM	Primary medial optic mass
SOG	Supraoesophageal ganglion
SS	Sagittal section
Sub	Suboesophageal ganglion
TS	Transverse section
T1	Tracts between the primary & secondary lateral optic masses
T2	Tracts between the supra- & suboesophageal ganglia
T3	Tracts between the optic masses & central body
2LOM	Secondary Lateral optic mass

PLATE 1

Nephila LS

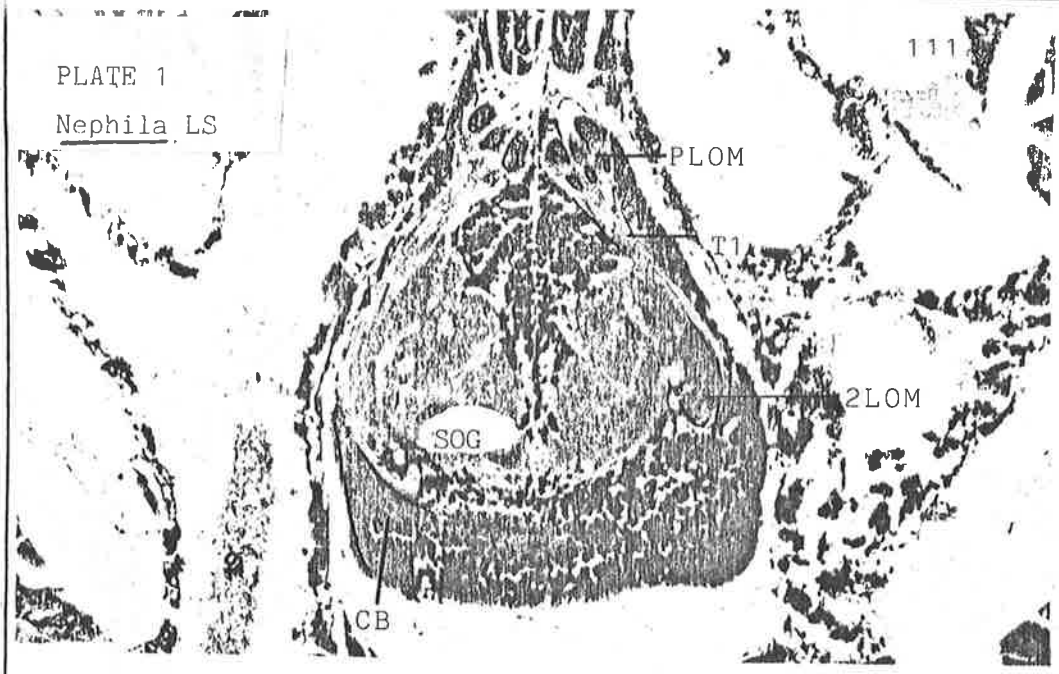


PLATE 2

Nephila cells

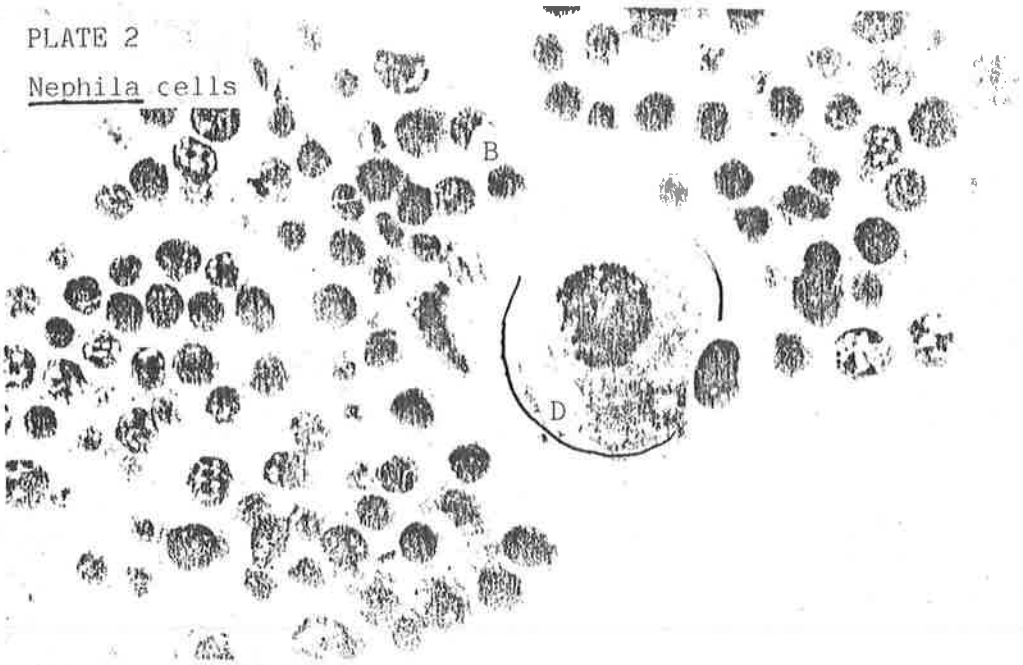
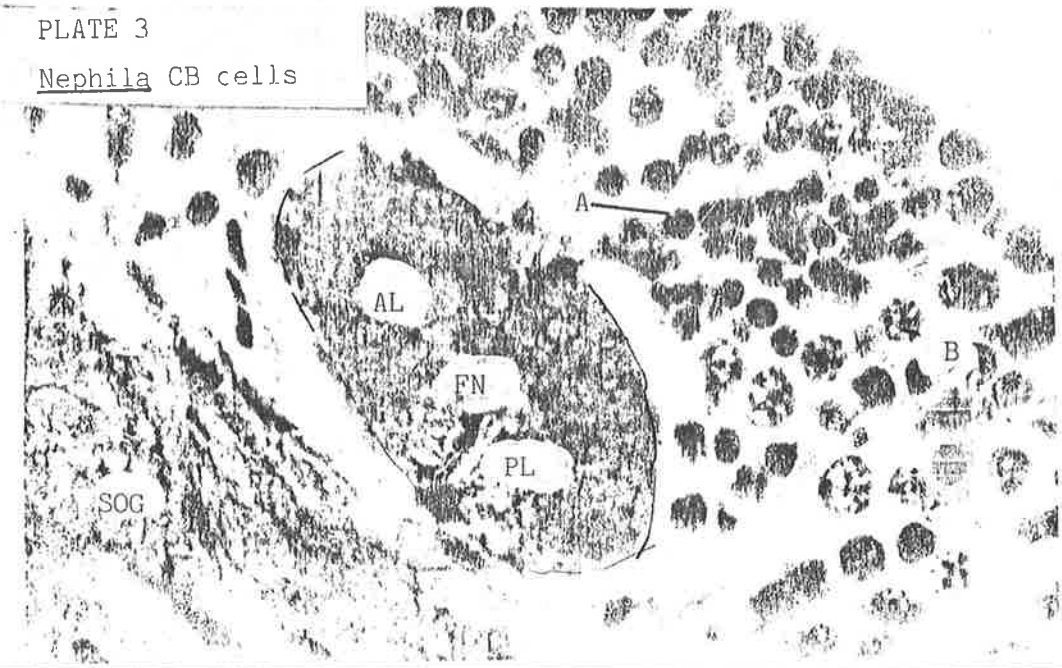
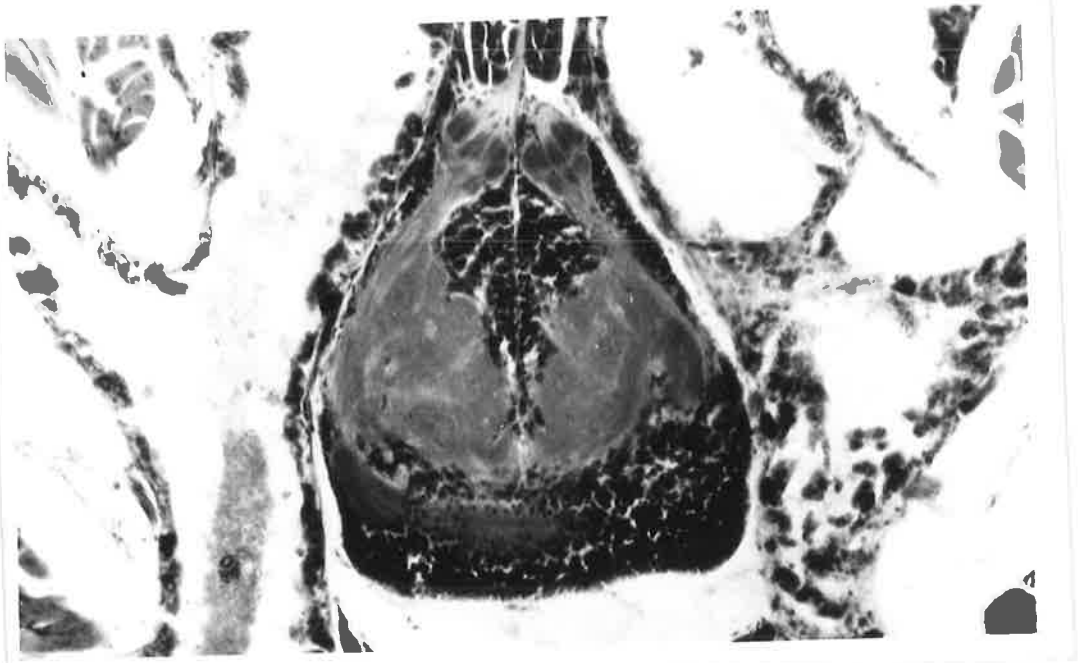
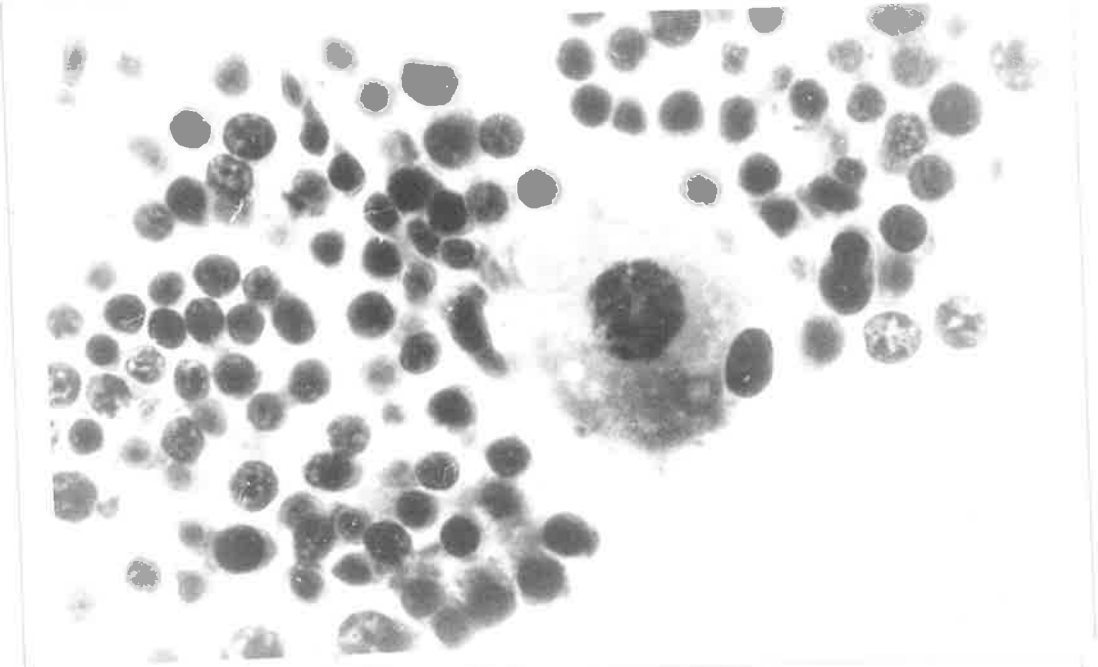


PLATE 3

Nephila CB cells







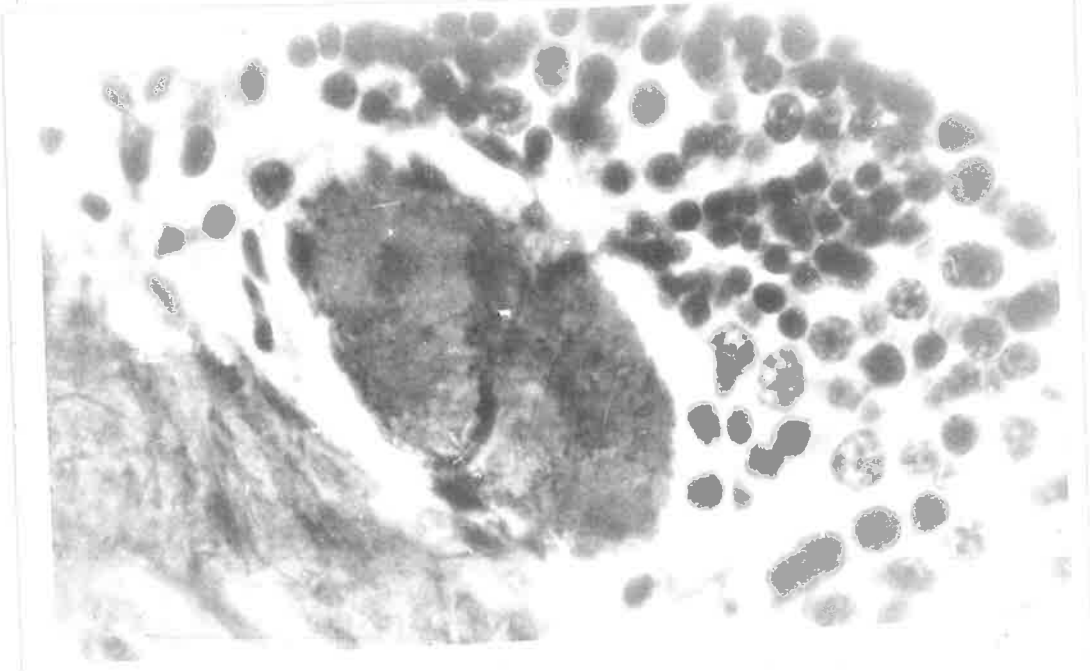


PLATE 4

Nephila CG cells

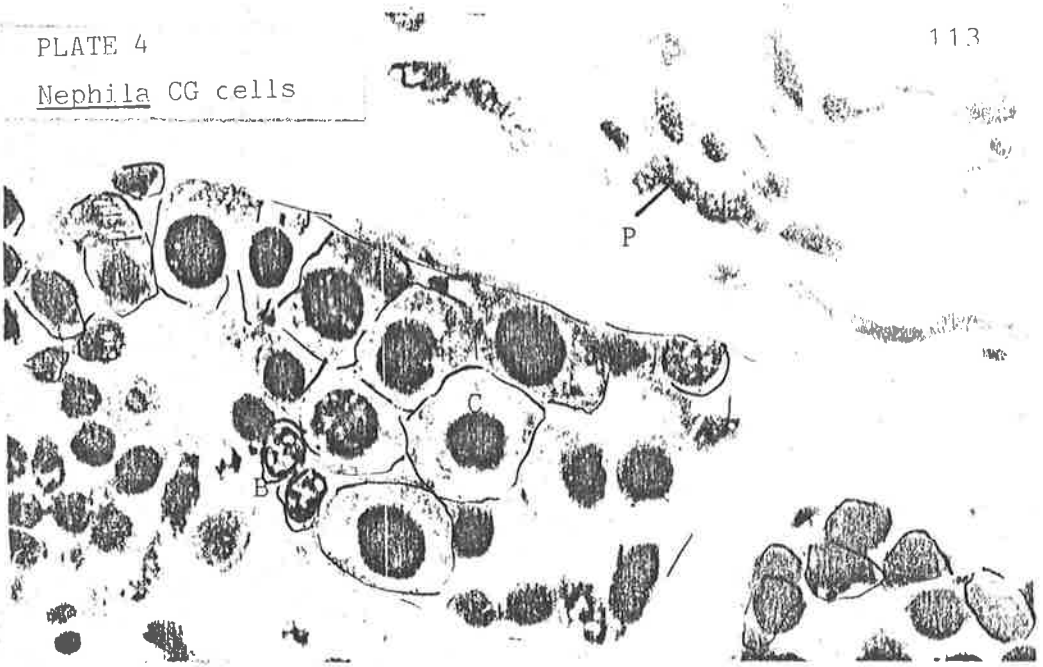


PLATE 5

Cyrtophora

Perilemma

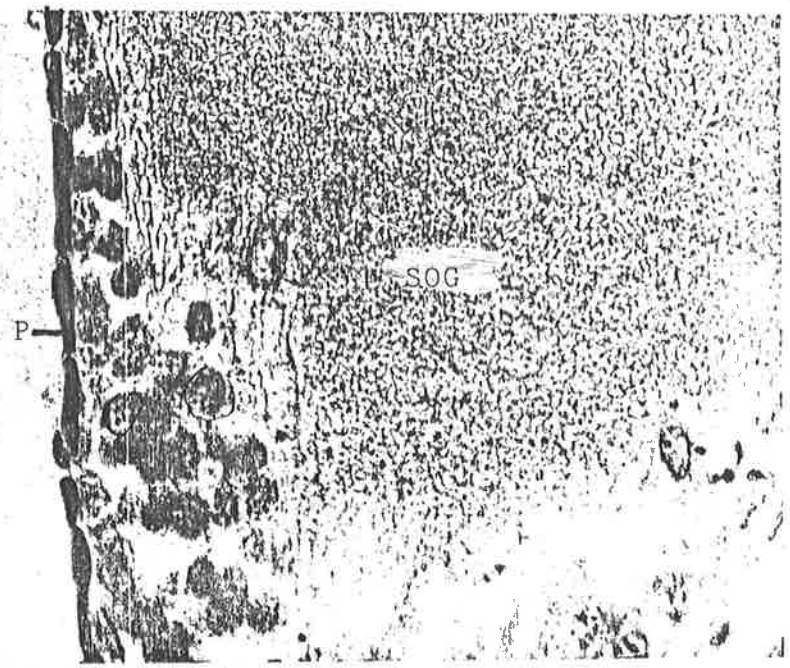
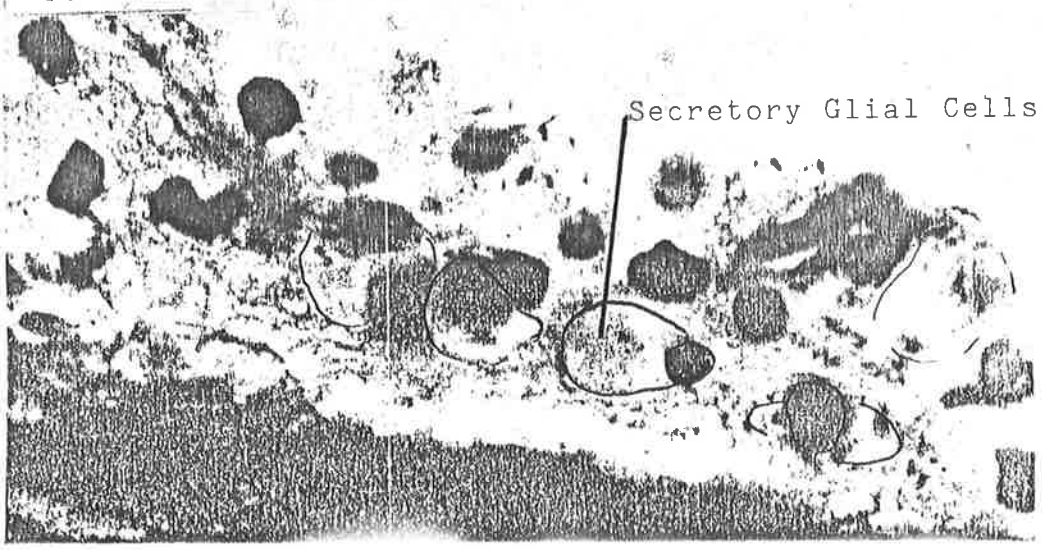
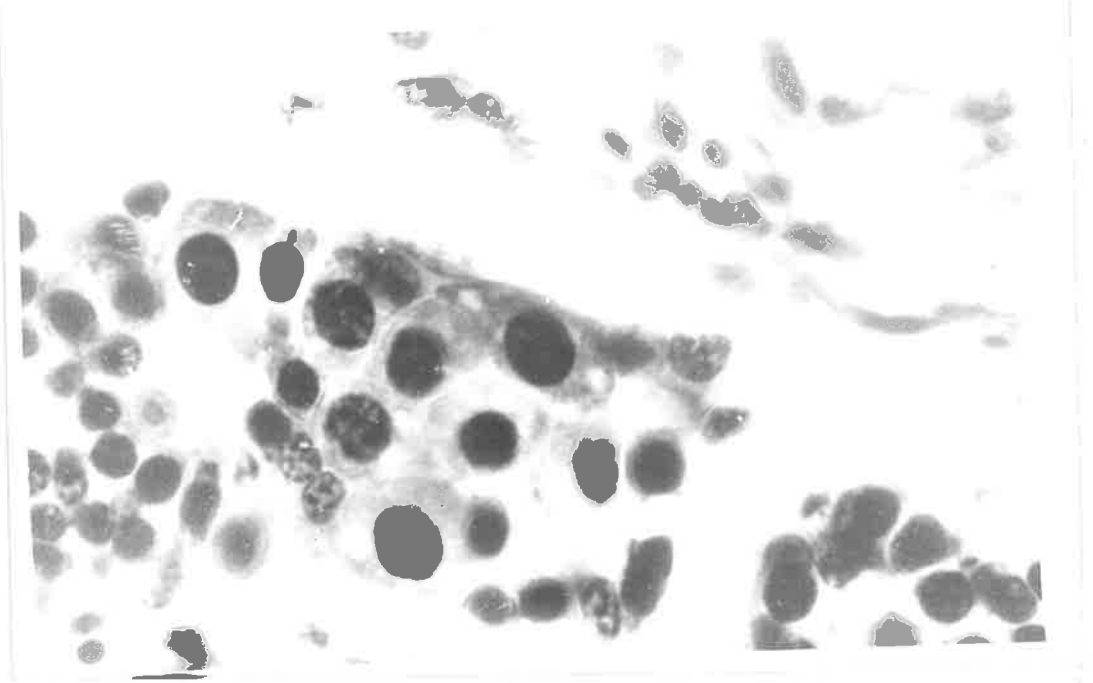


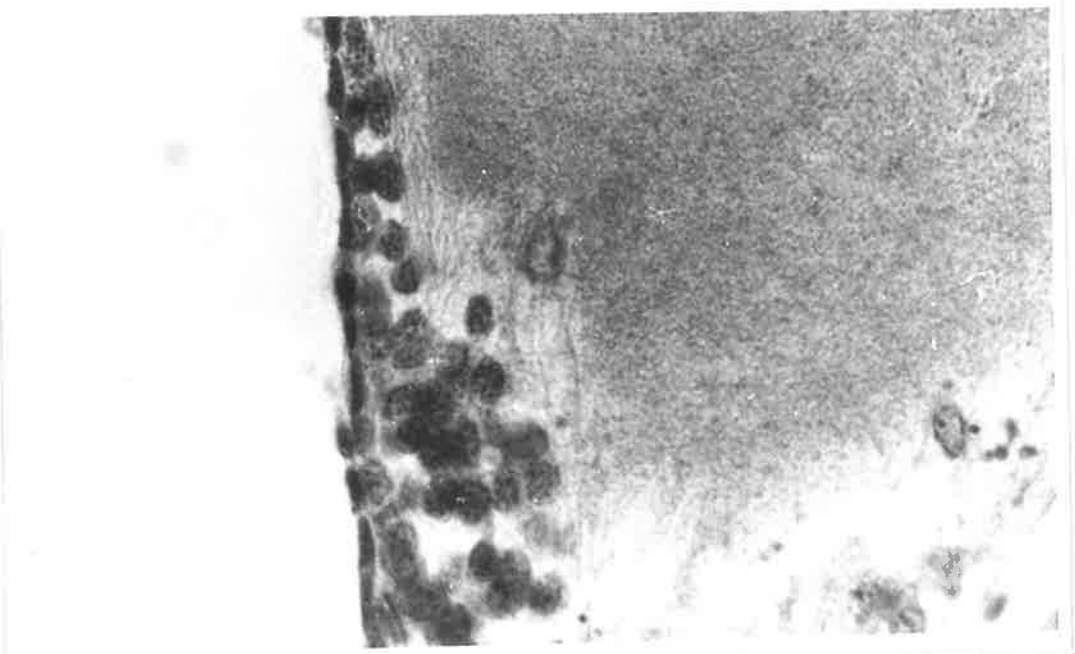
PLATE 6

Cyrtophora

Perilemma







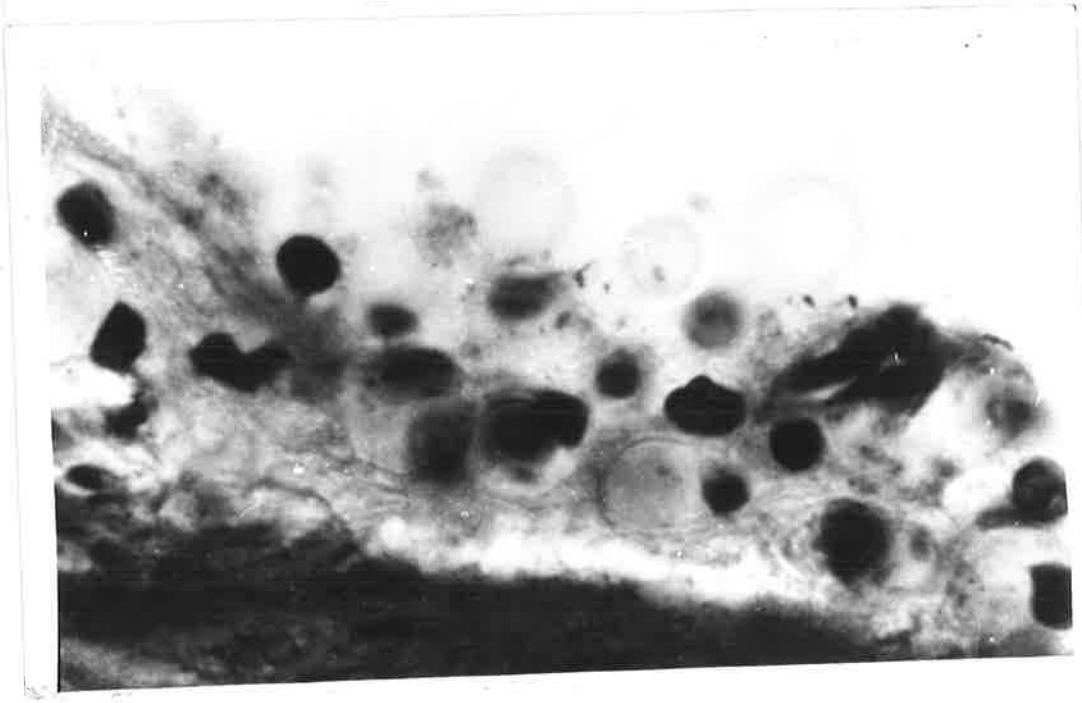
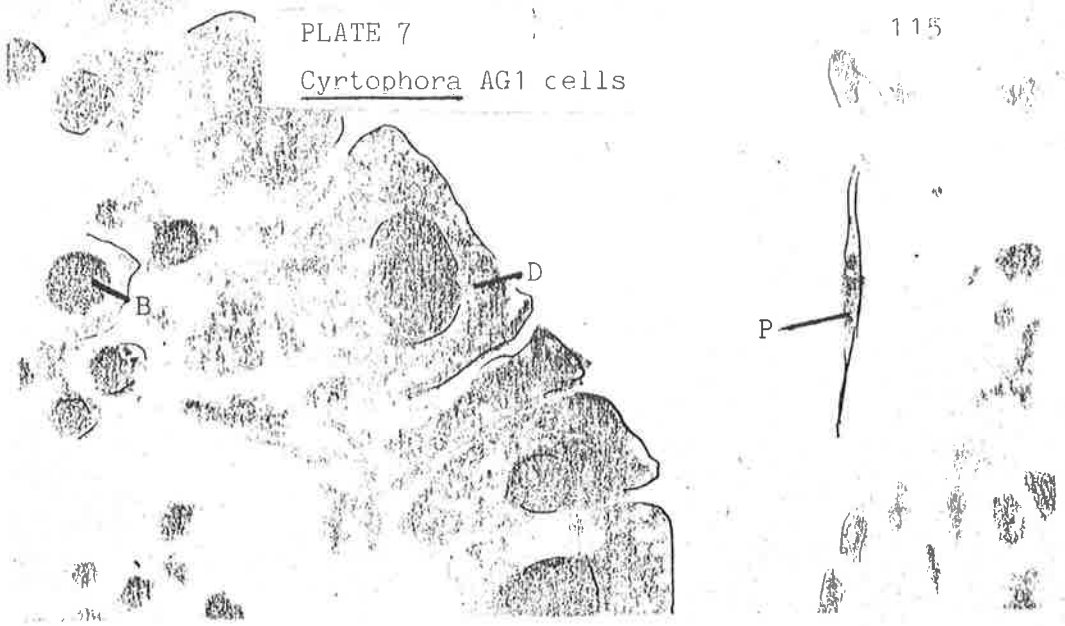


PLATE 7

Cyrtophora AG1 cells



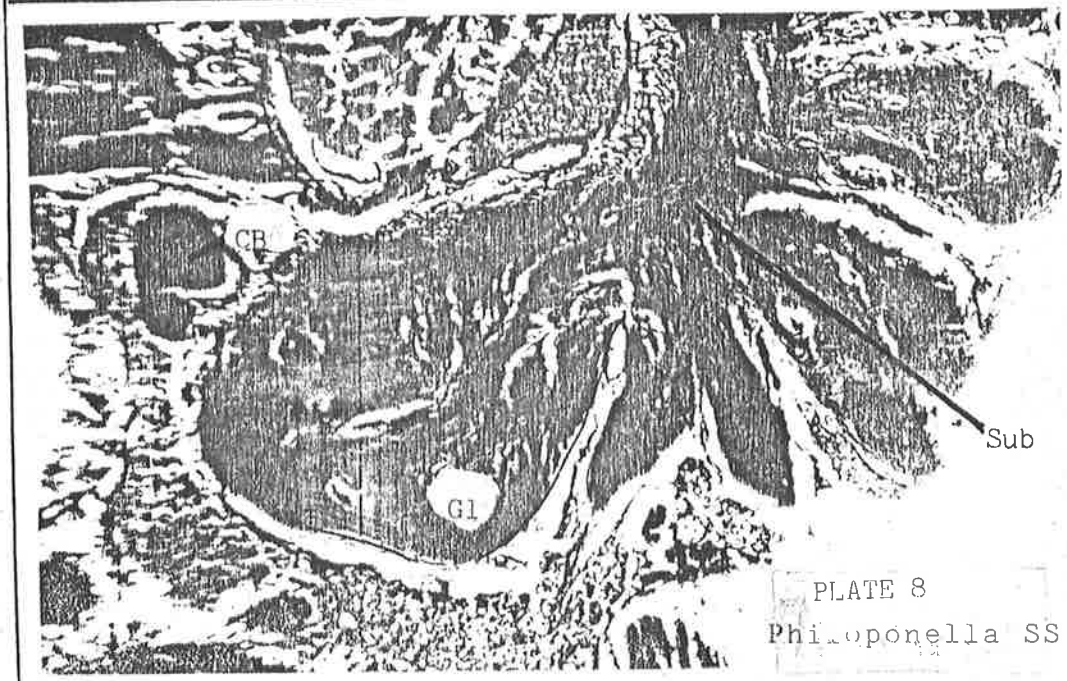
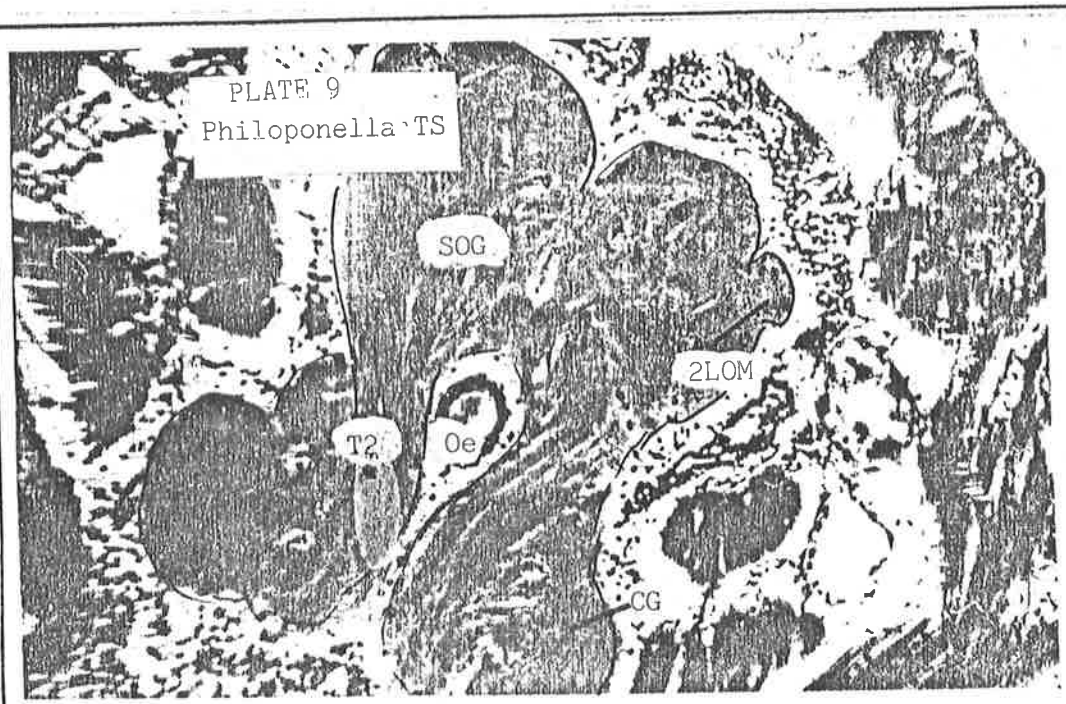


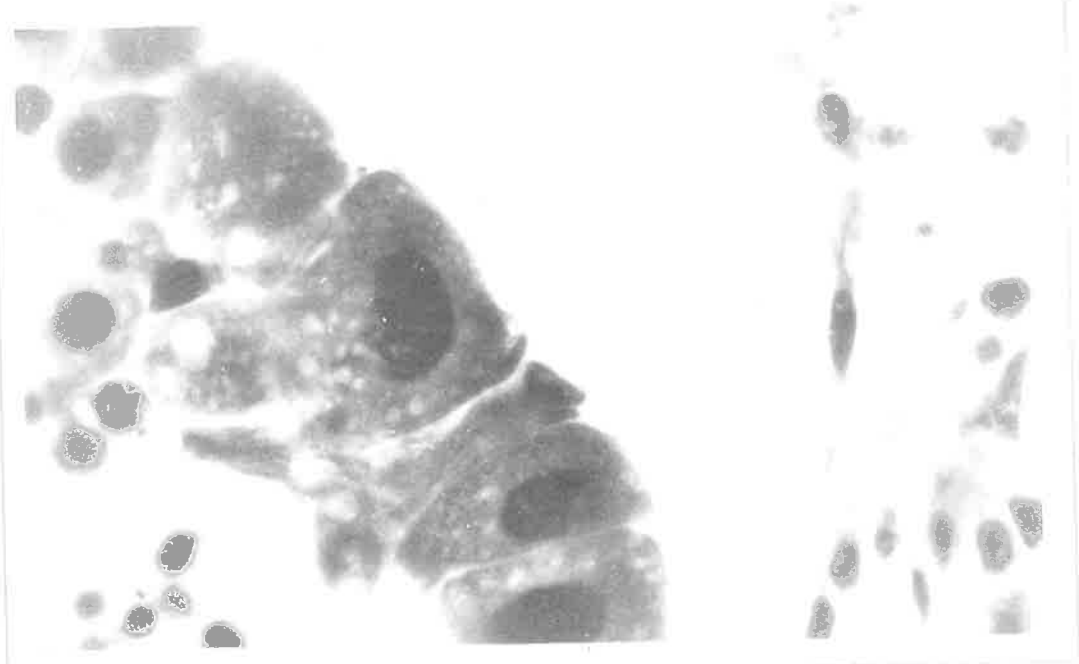
PLATE 8

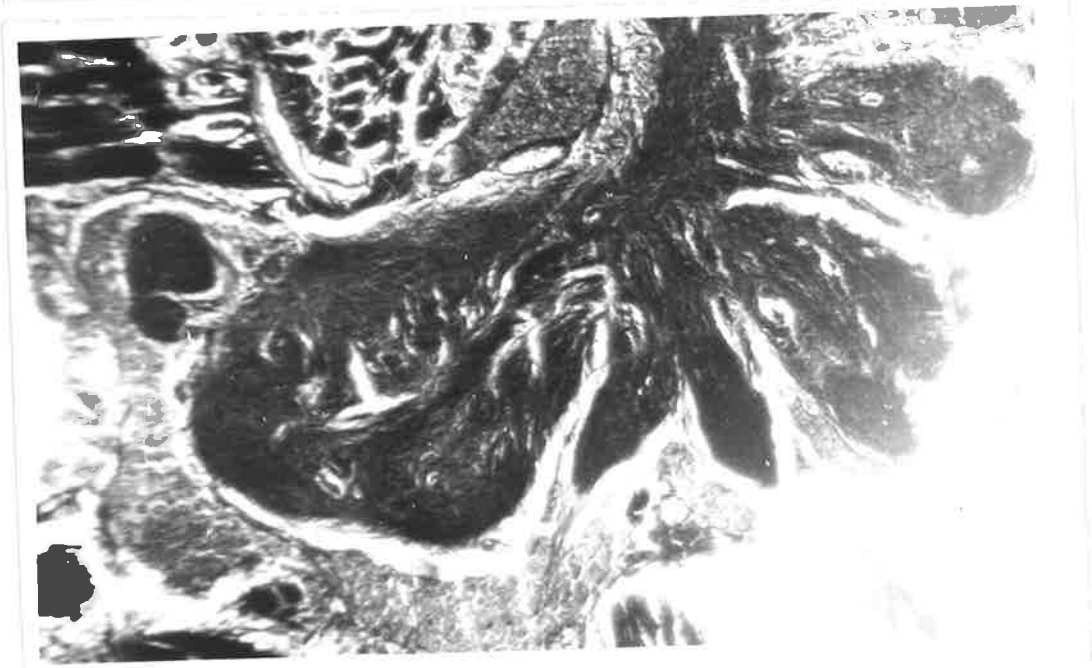
Philoponella SS

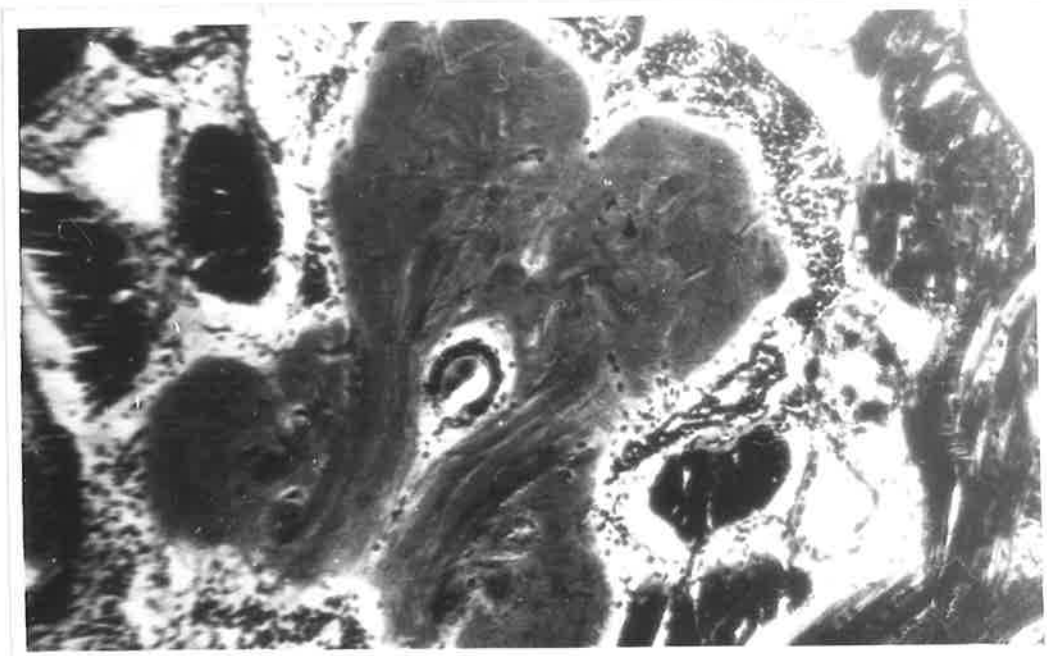
PLATE 9

Philoponella TS









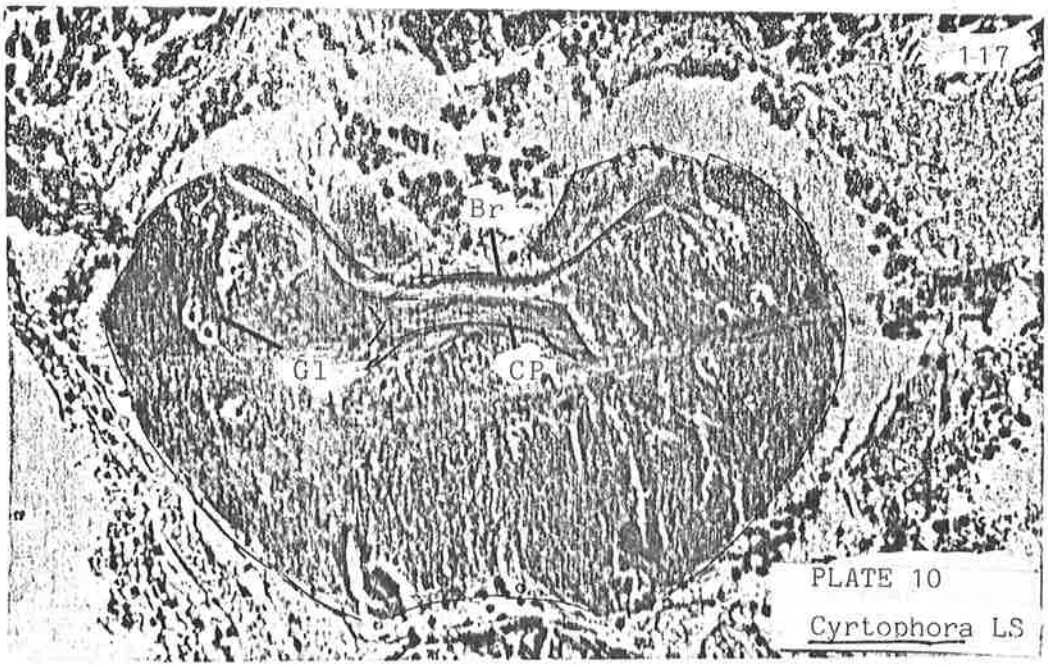


PLATE 10
Cyrtophora LS

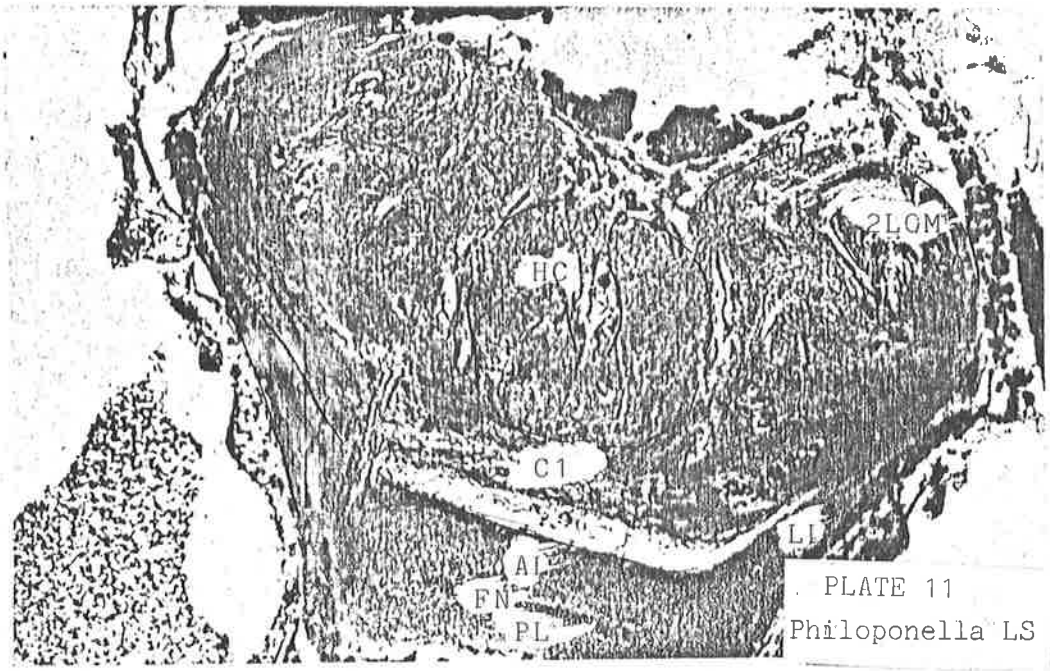


PLATE 11
Philoponella LS

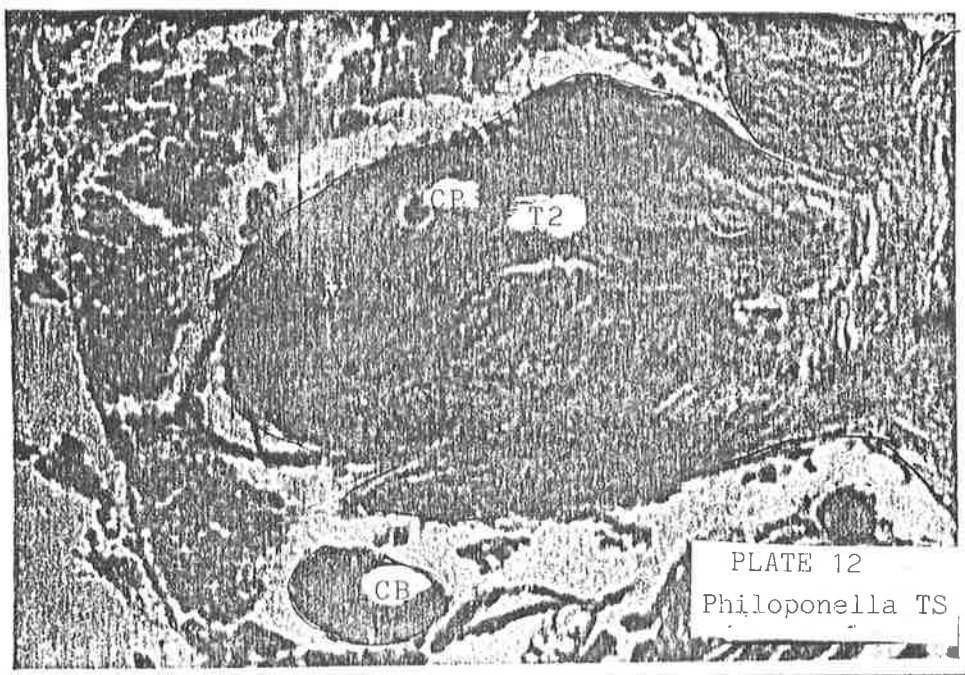
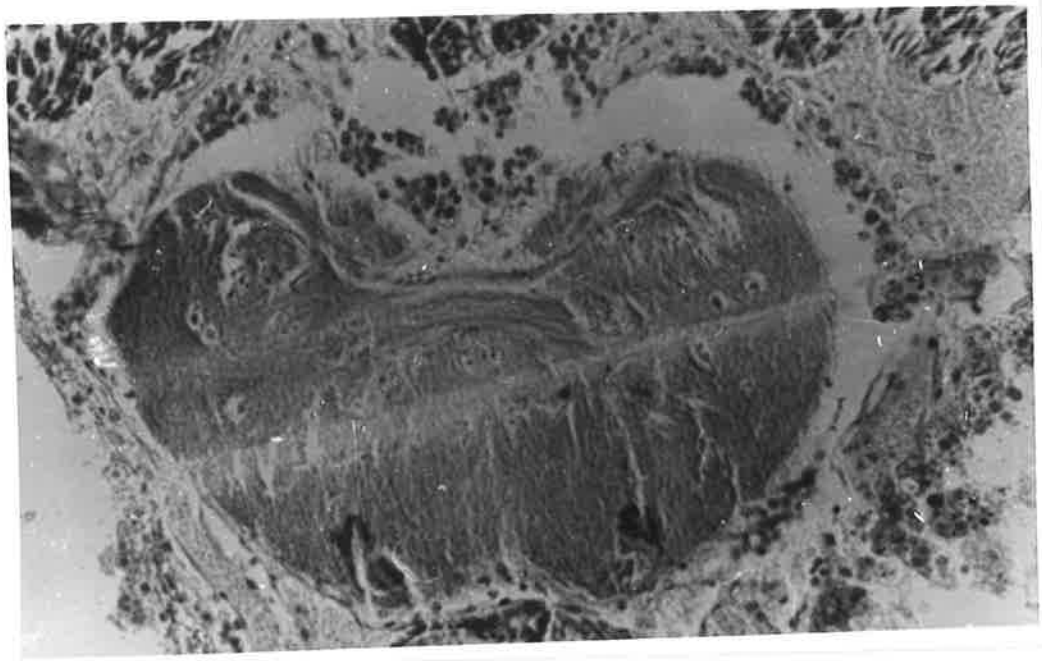
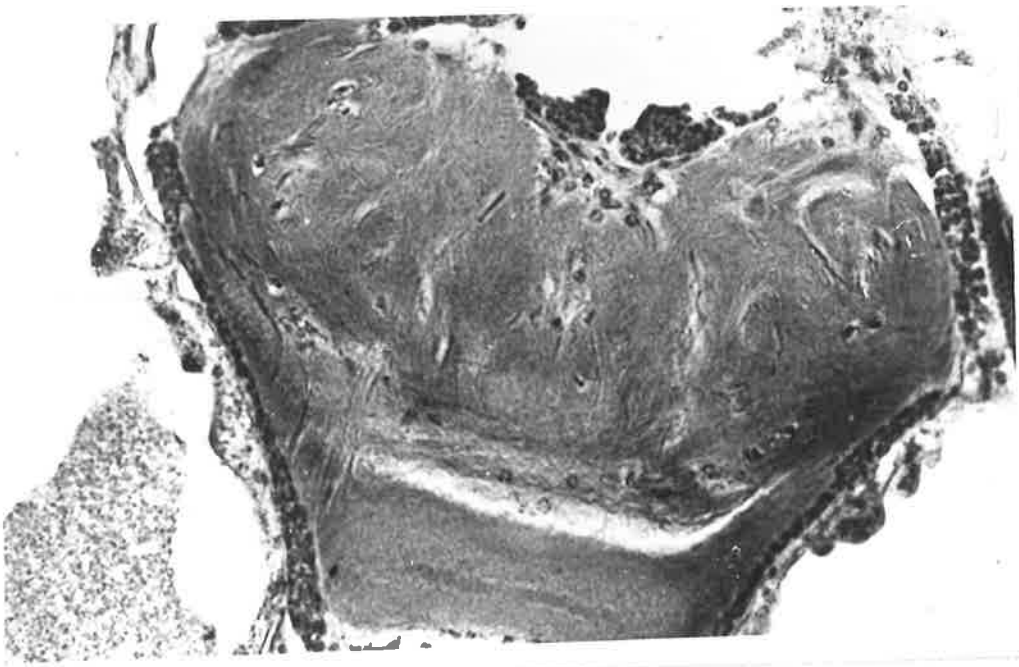


PLATE 12
Philoponella TS





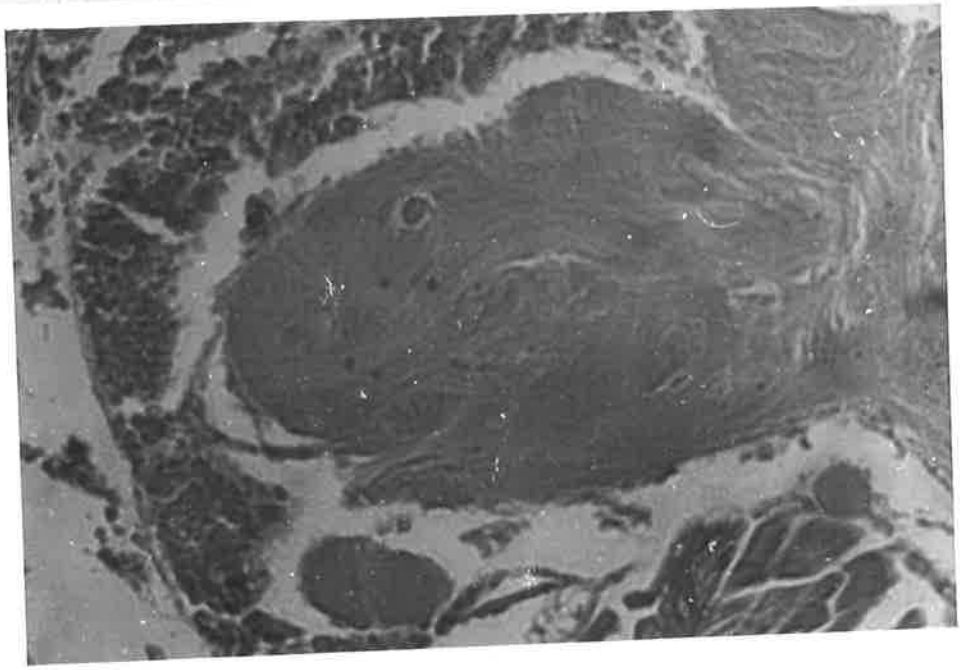


PLATE 13

Cyrtophora TS

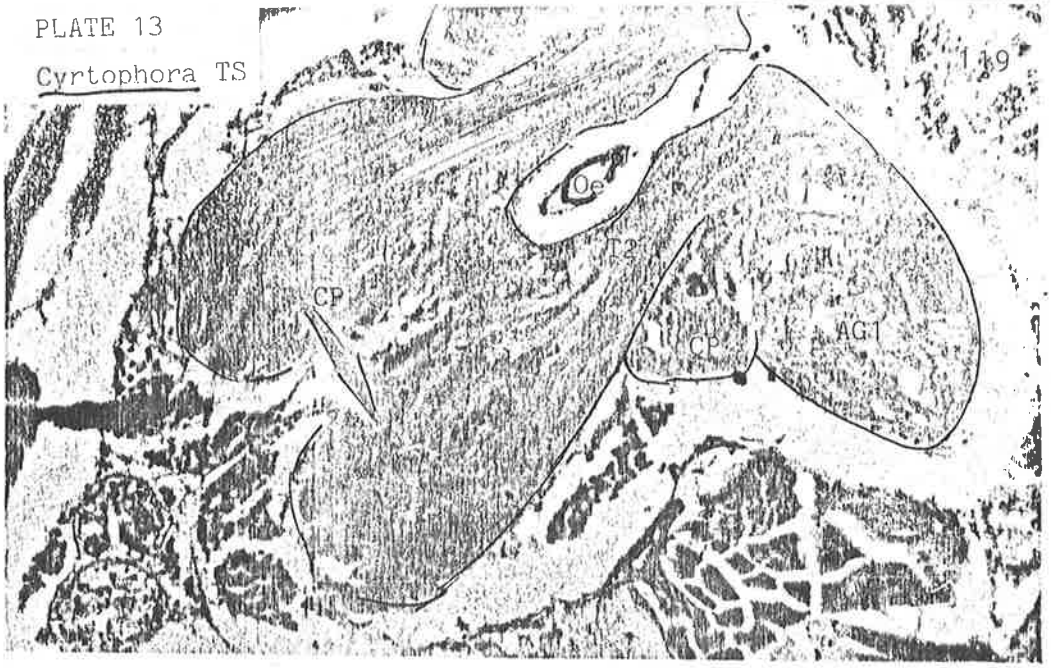


PLATE 14

Cyrtophora SS

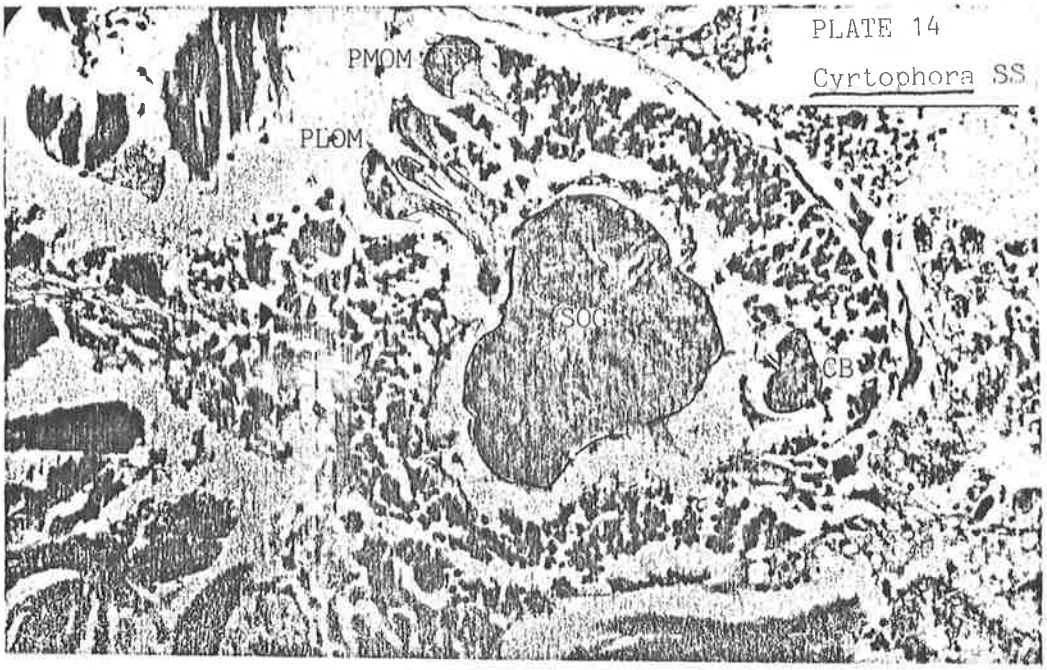
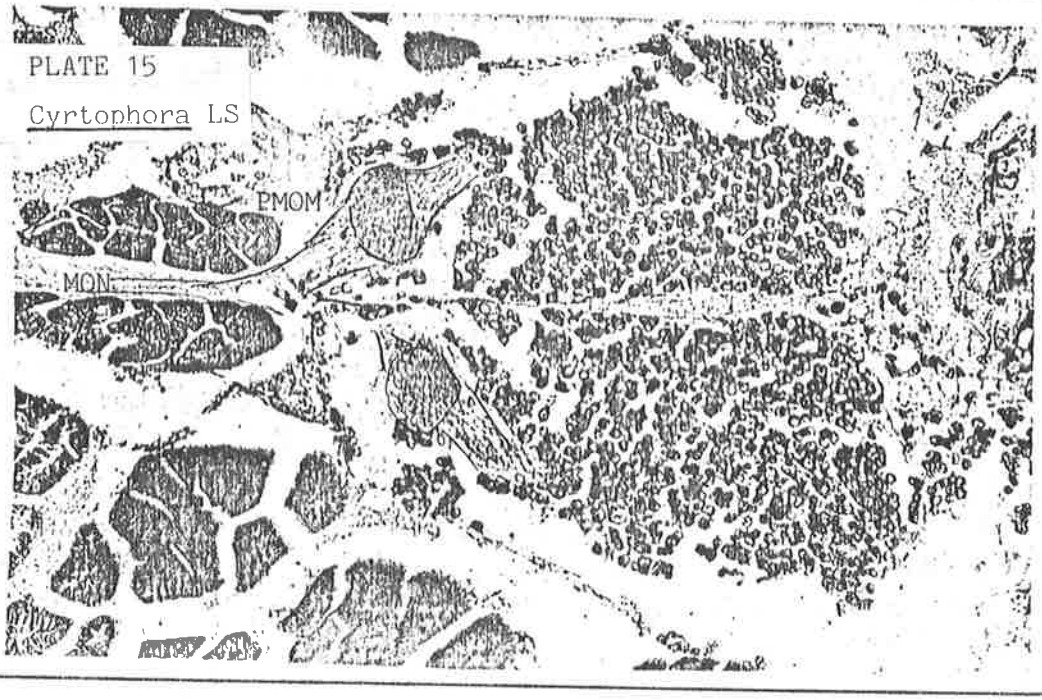
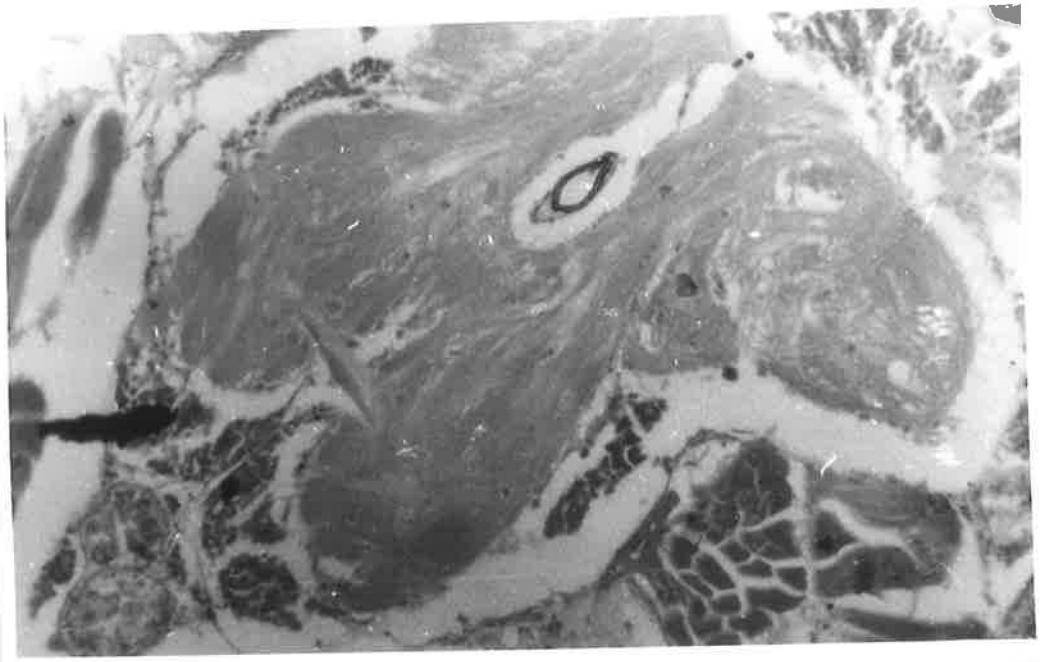
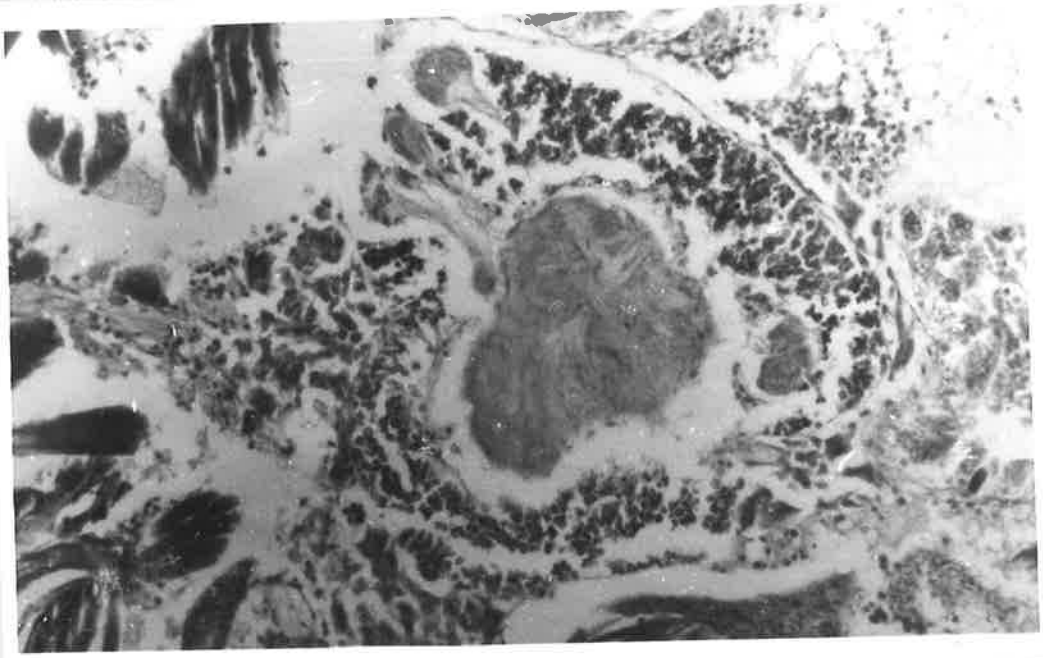


PLATE 15

Cyrtophora LS







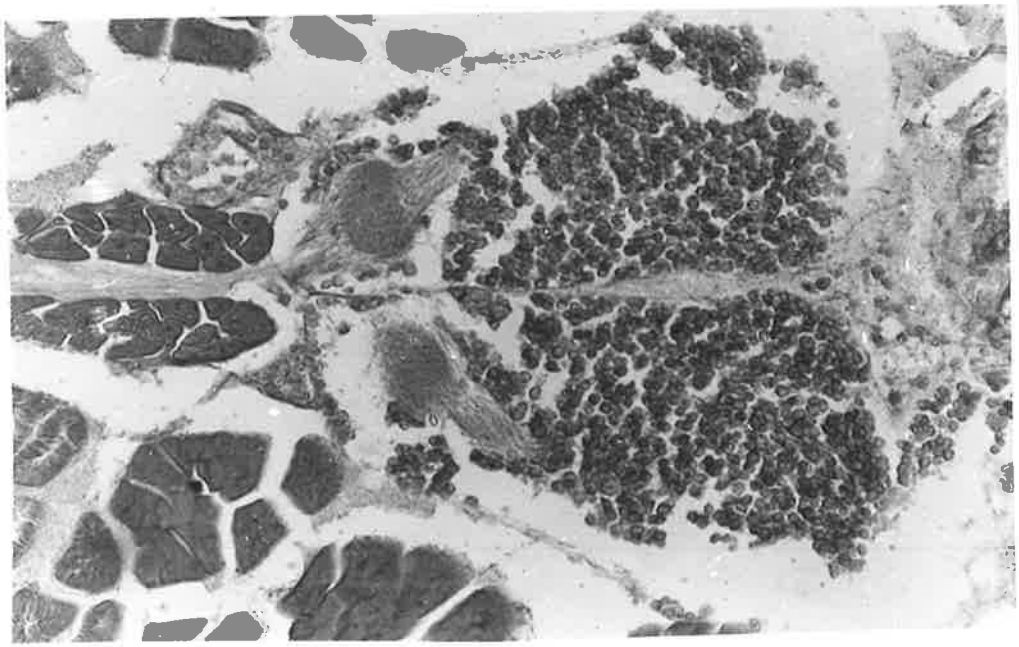


PLATE 16

Cyrtophora LS

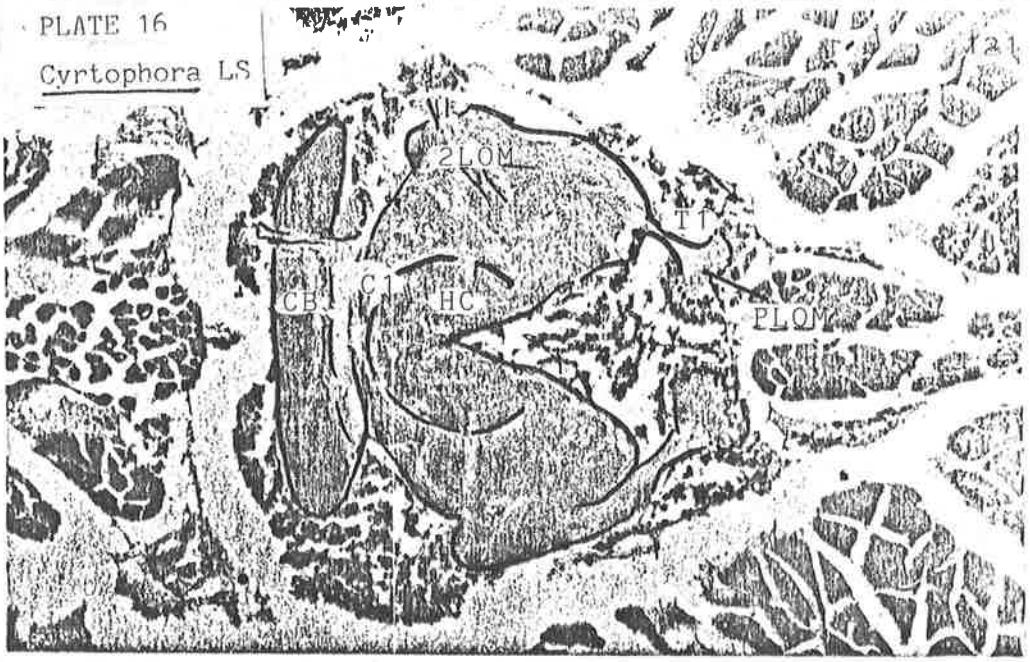


PLATE 17

Cyrtophora LS

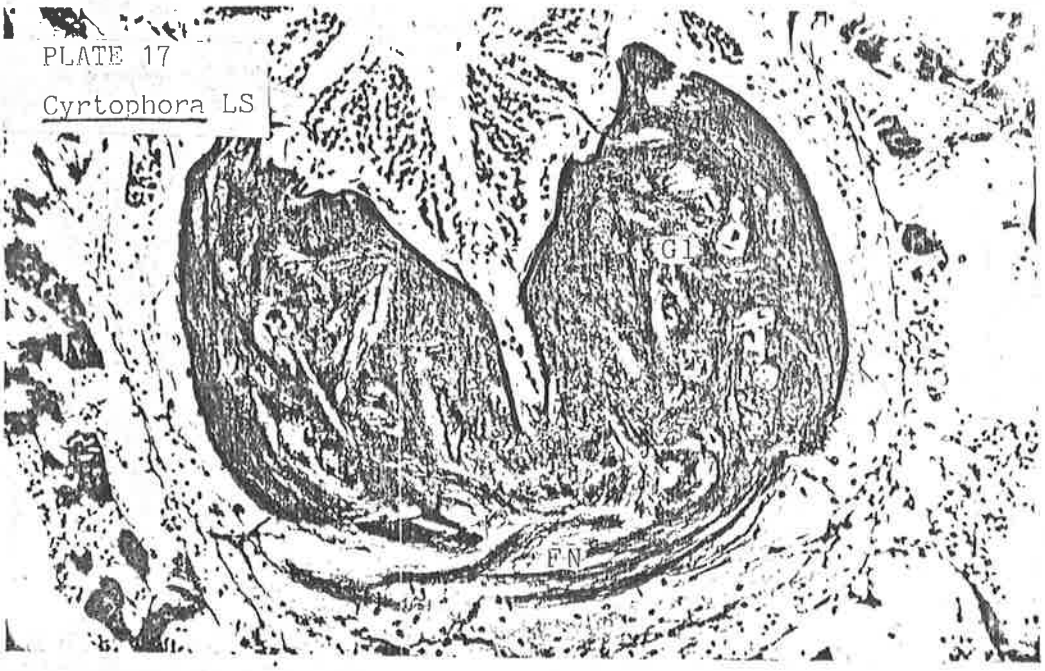
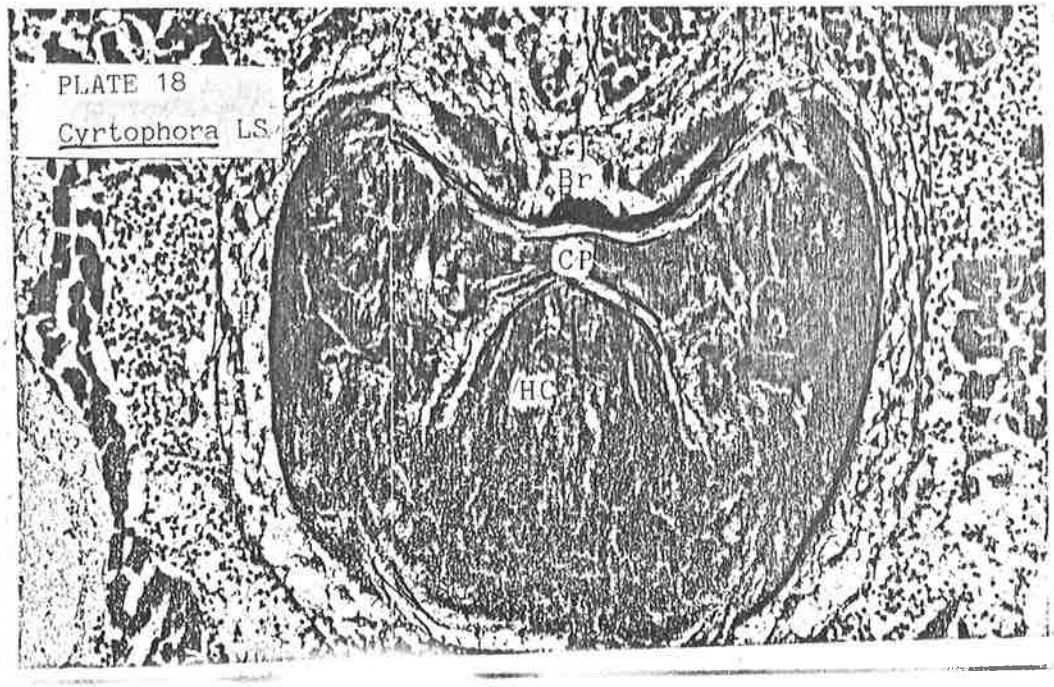
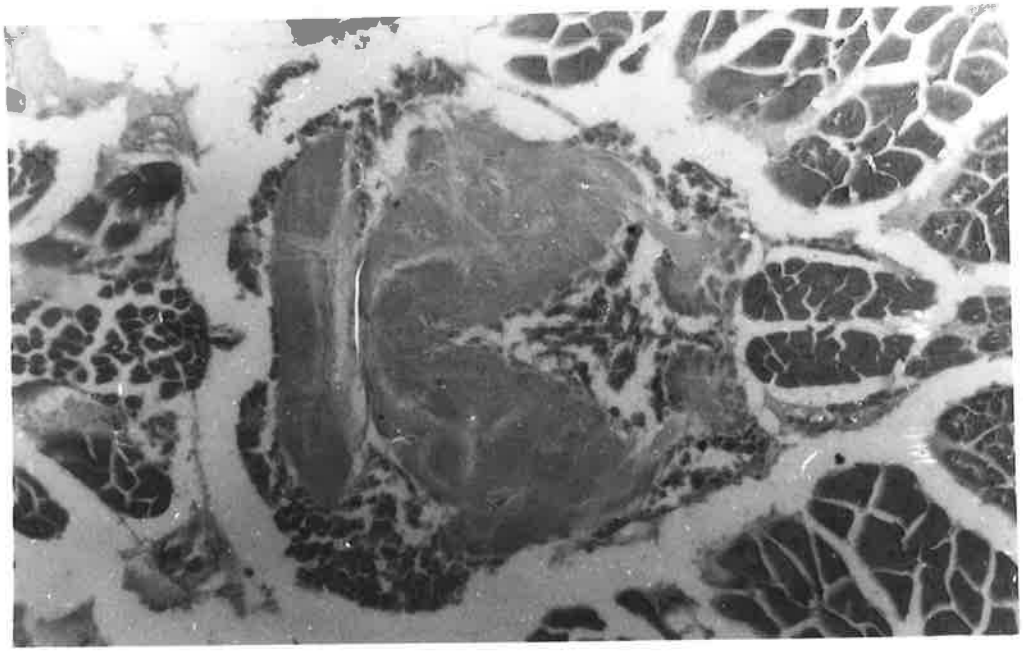
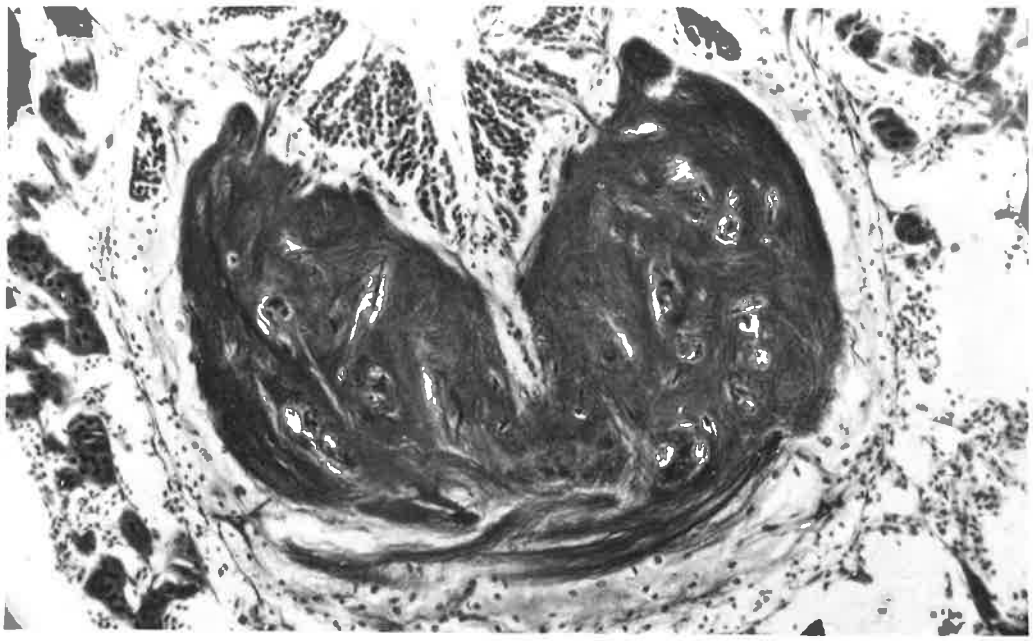


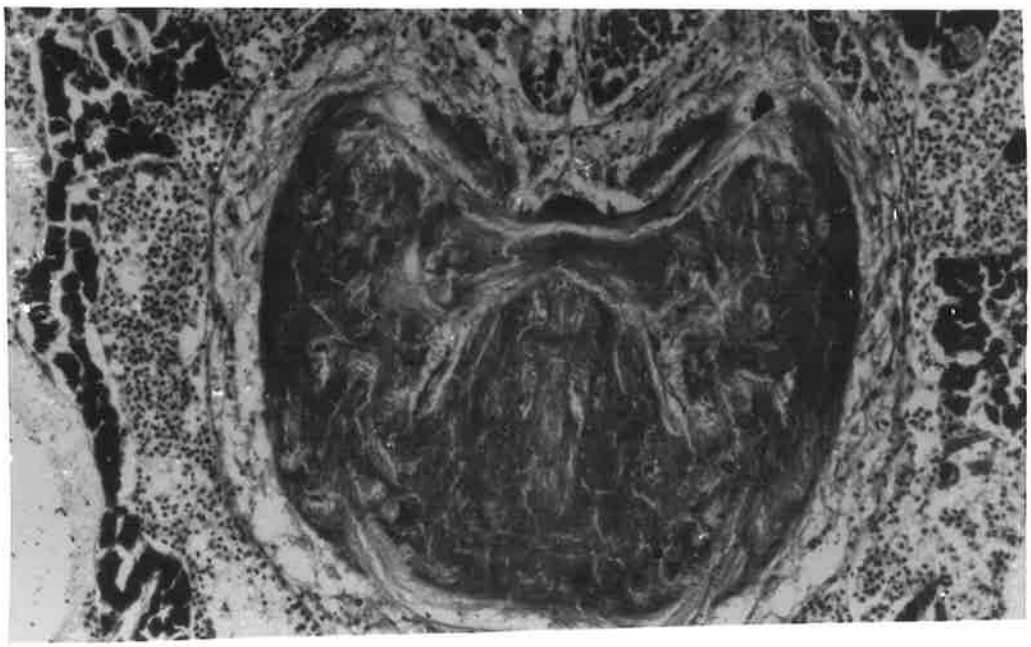
PLATE 18

Cyrtophora LS









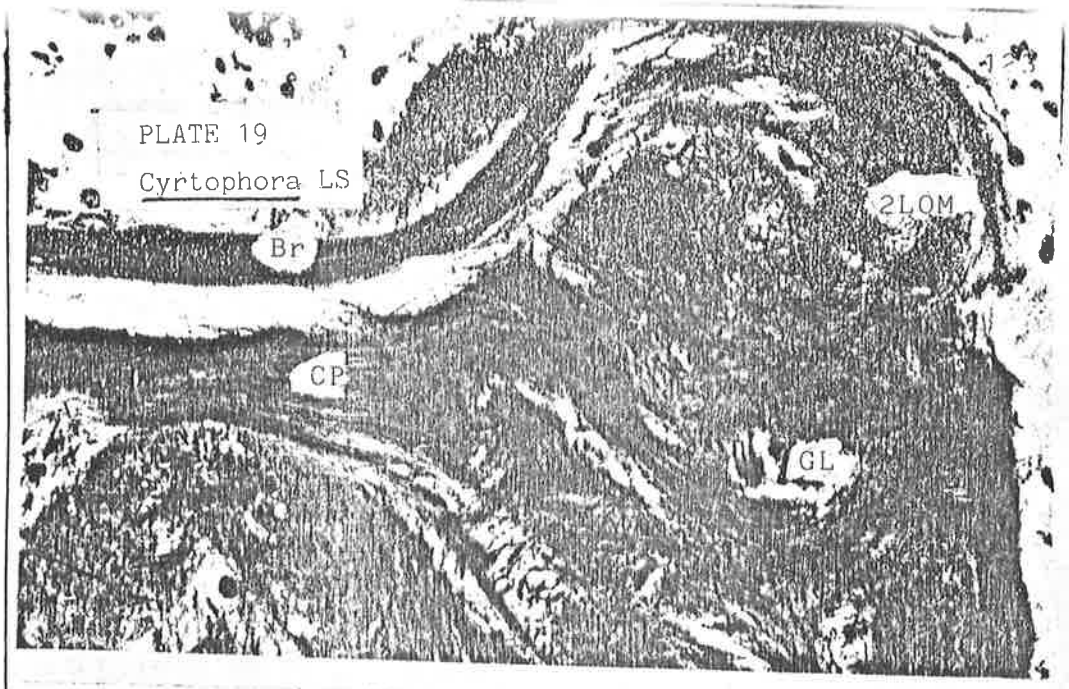


PLATE 19

Cyrtophora LS

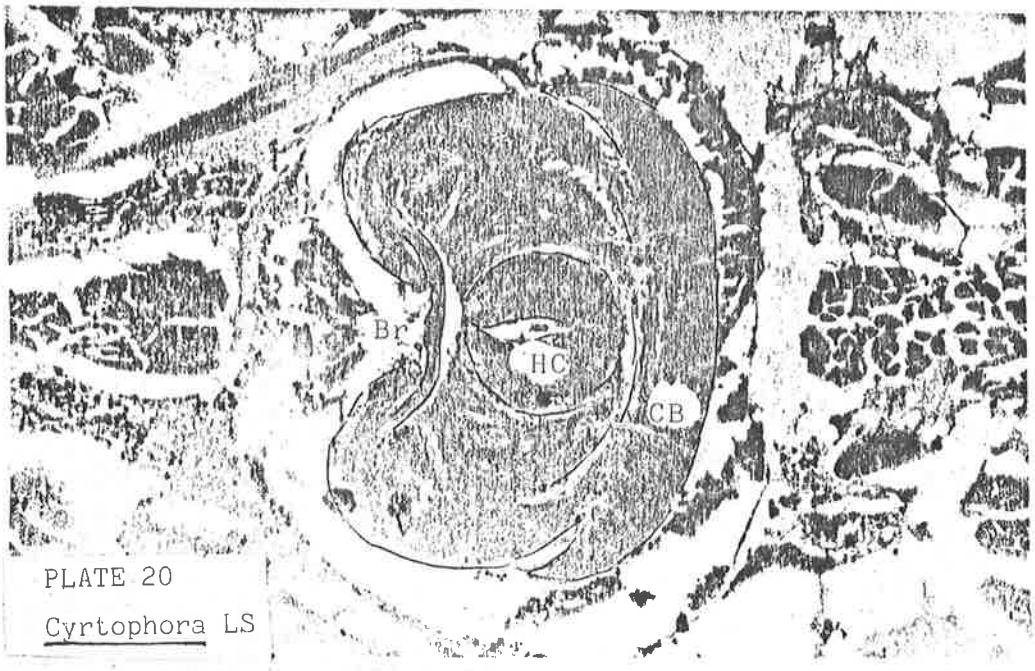


PLATE 20

Cyrtophora LS

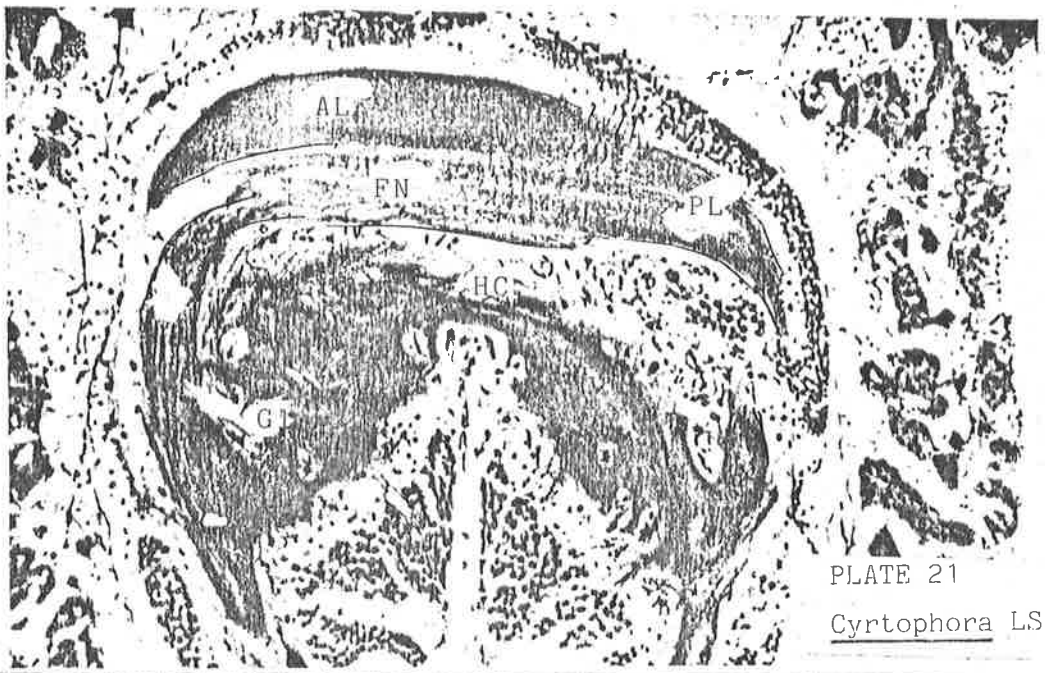
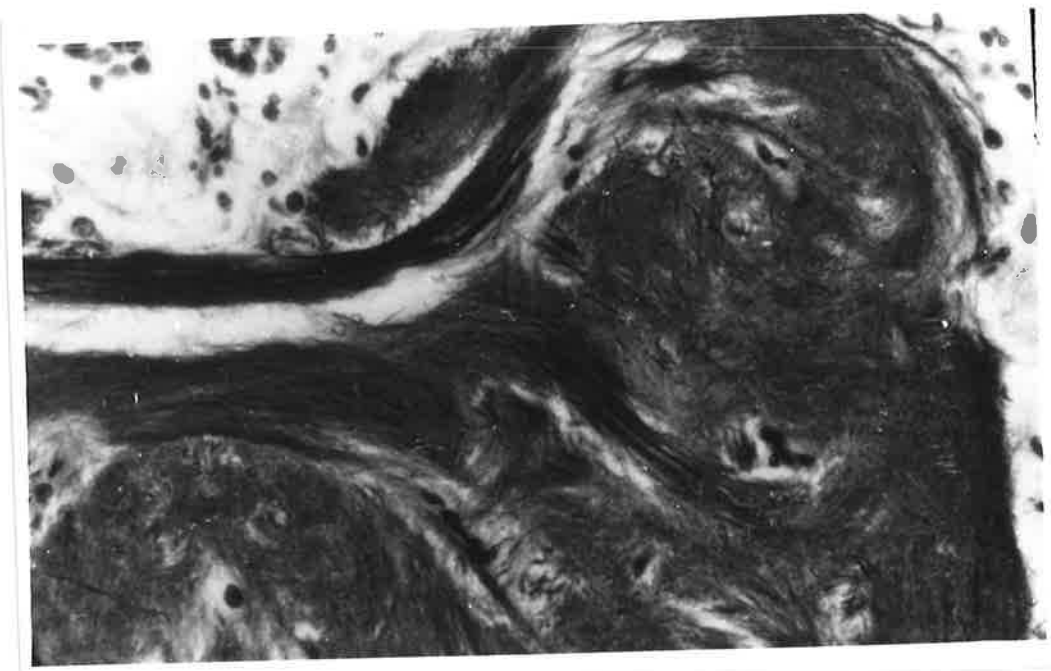
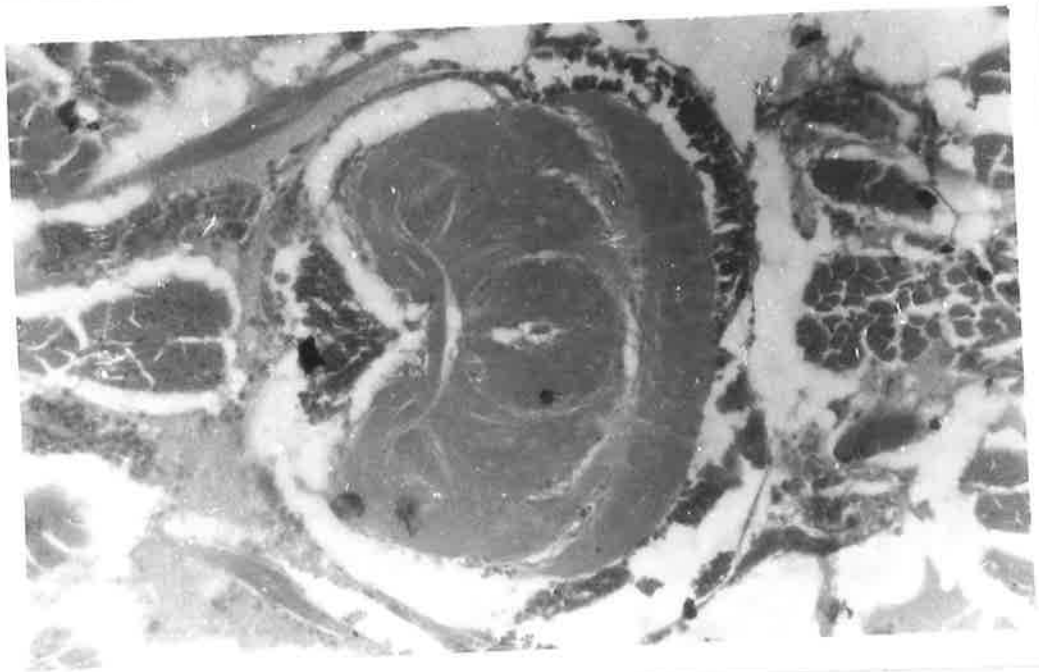
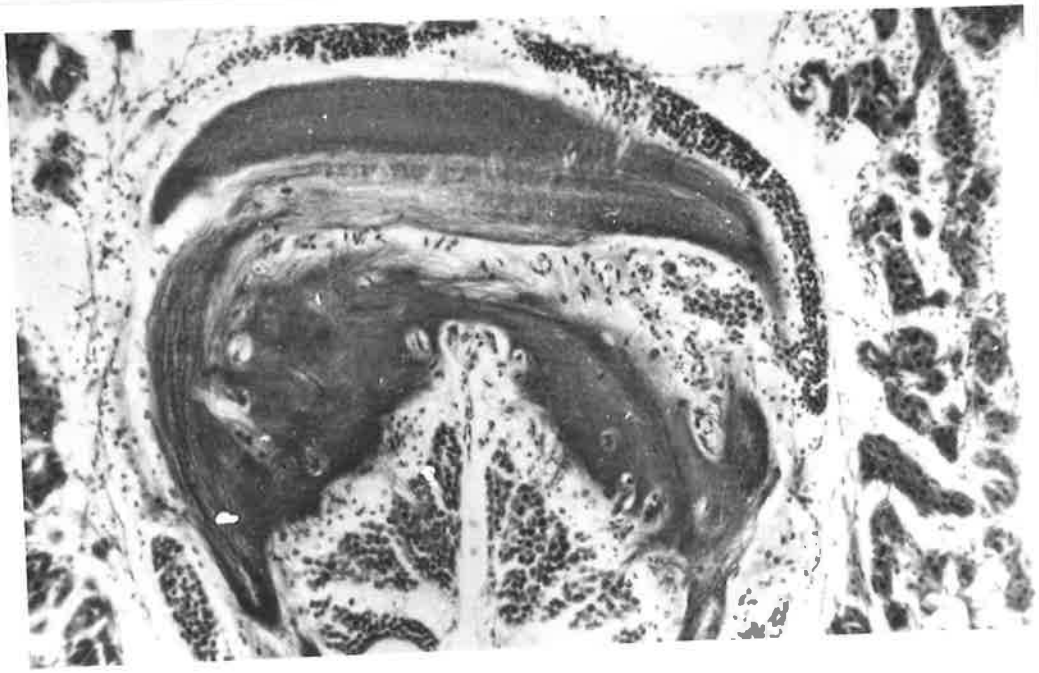


PLATE 21

Cyrtophora LS







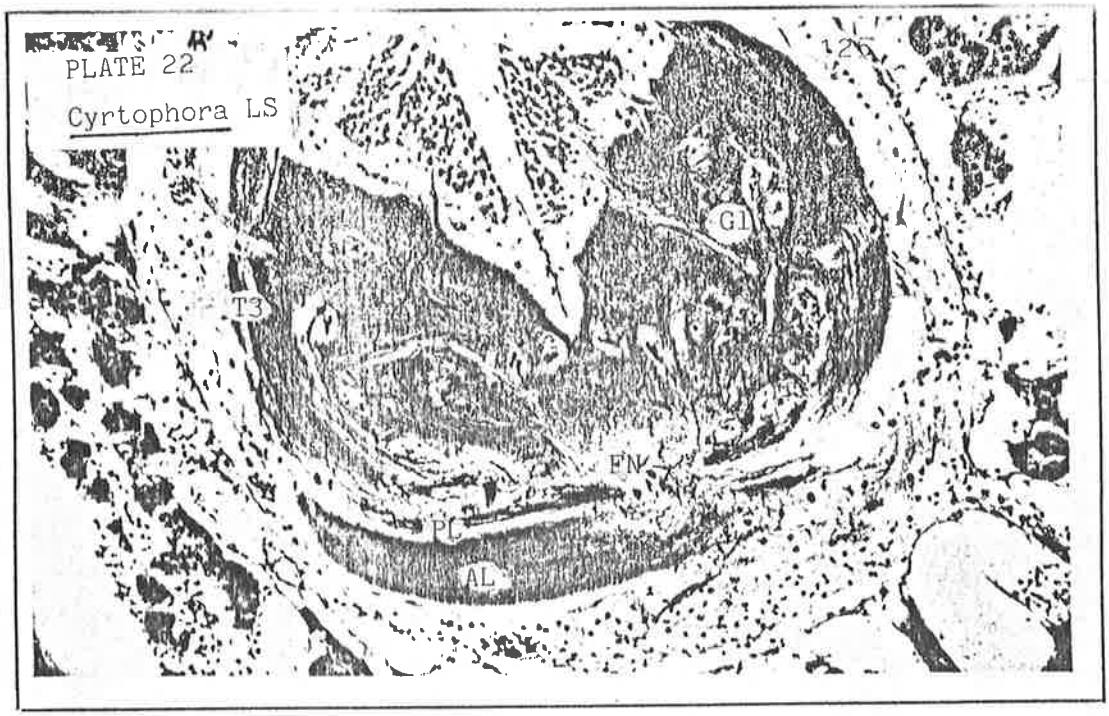


PLATE 22
Cyrtophora LS
GL
T3
FN
PL
AL

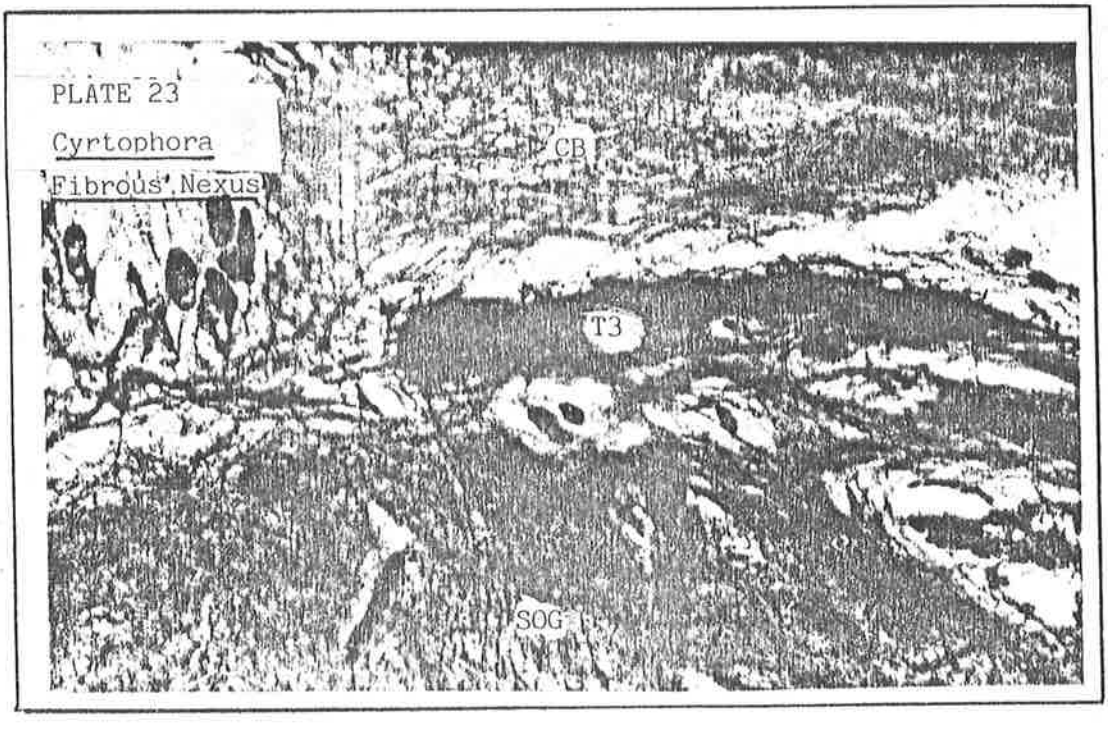
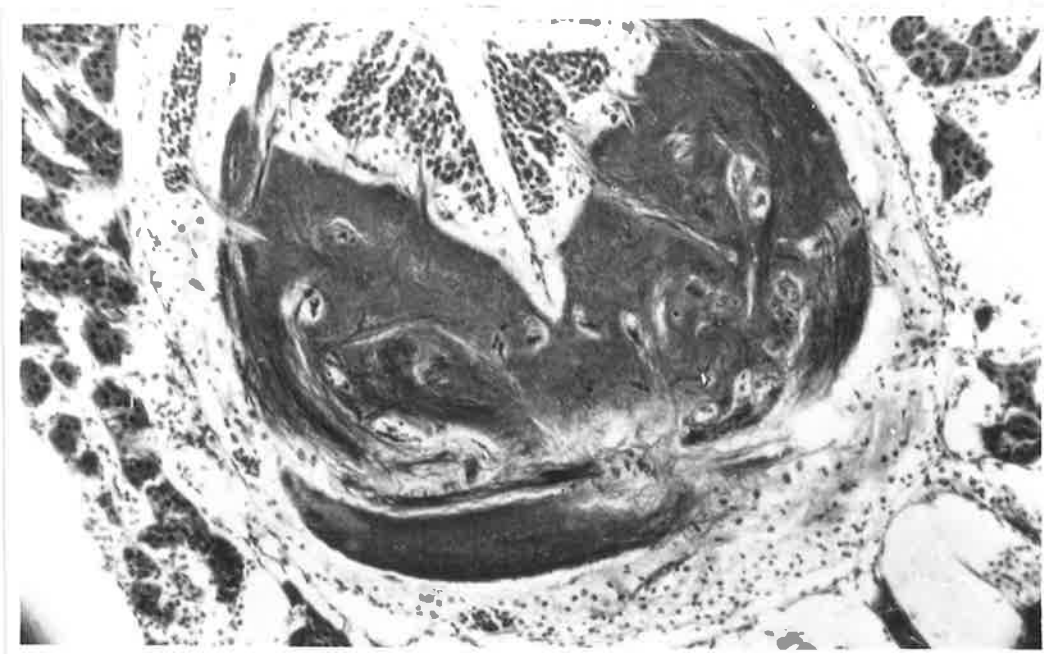
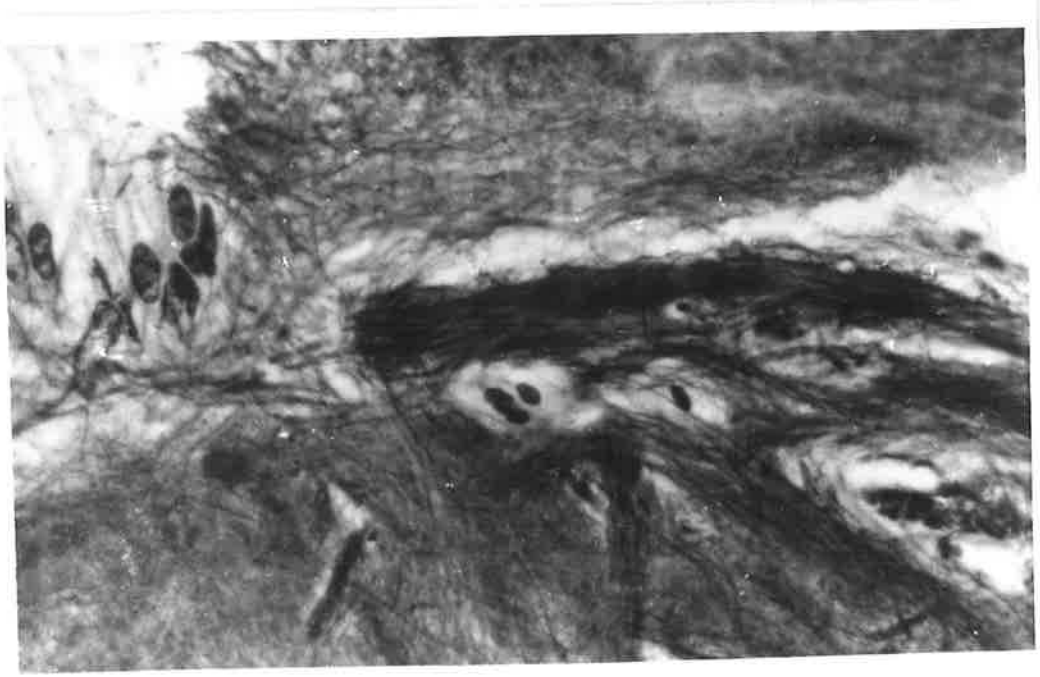


PLATE 23
Cyrtophora
Fibrous Nexus
CB
T3
SOG





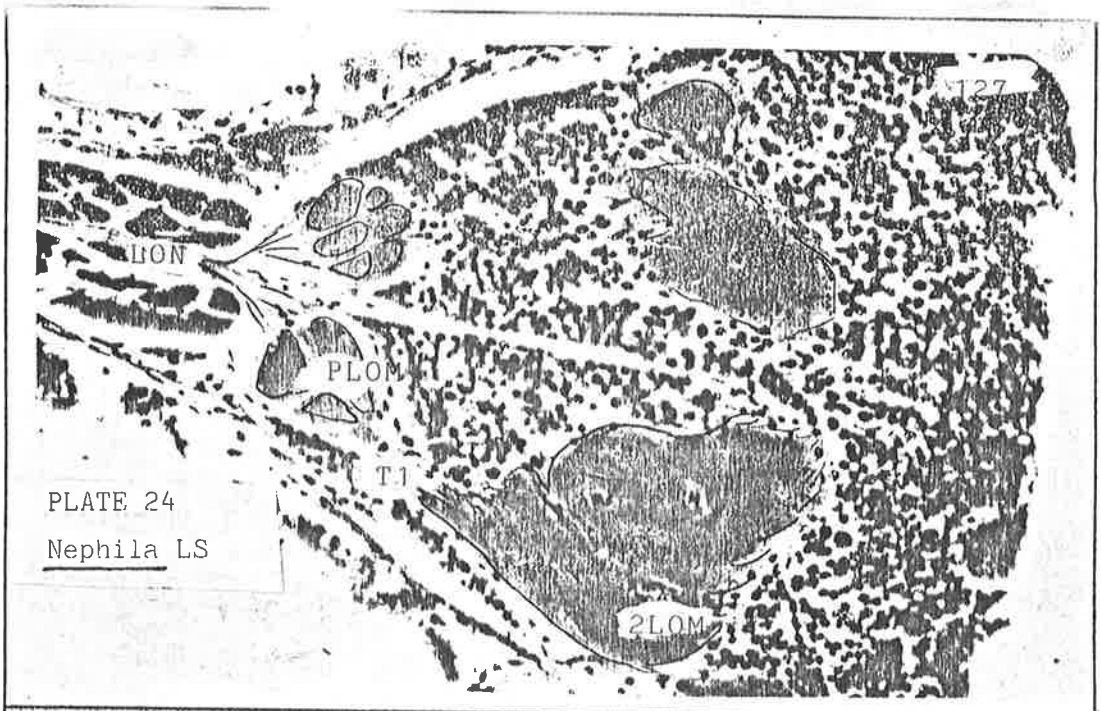


PLATE 24

Nephila LS

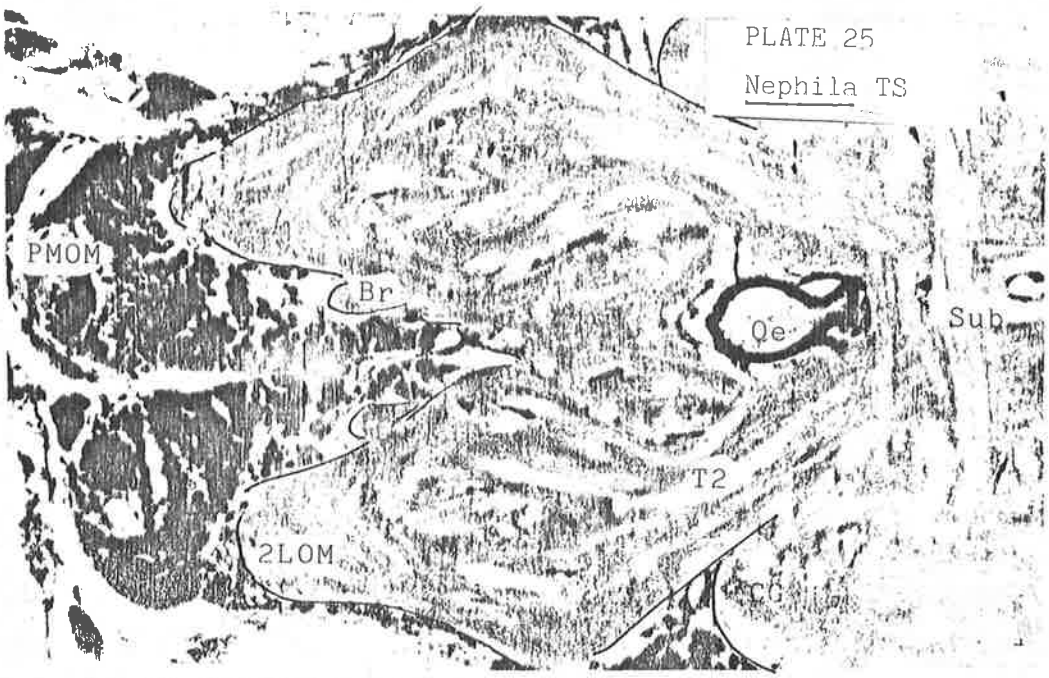


PLATE 25

Nephila TS

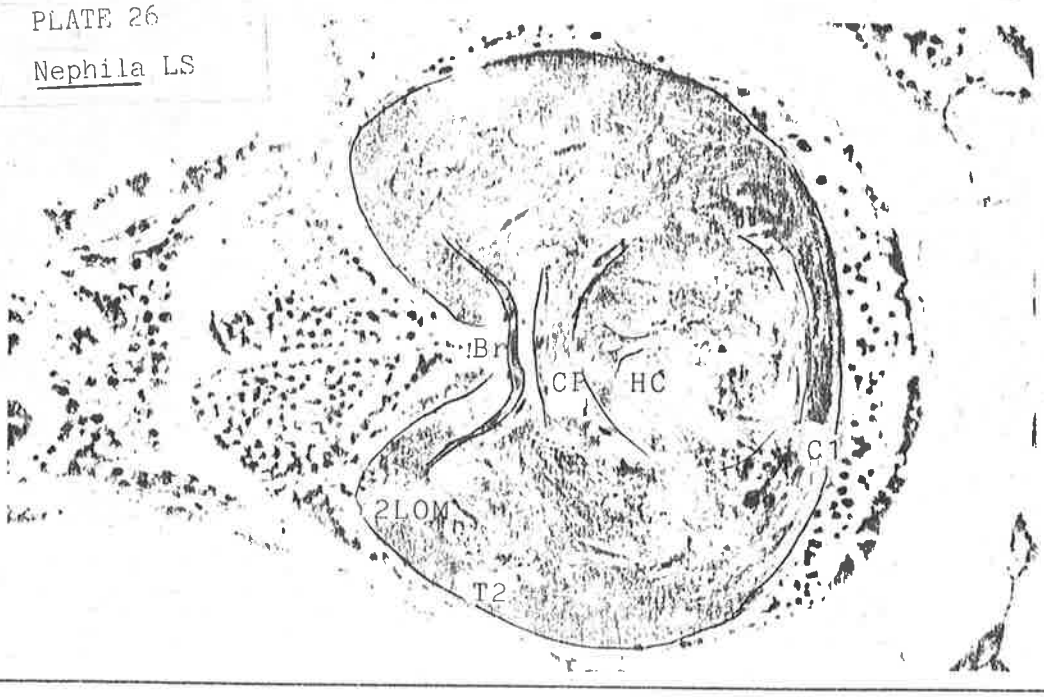
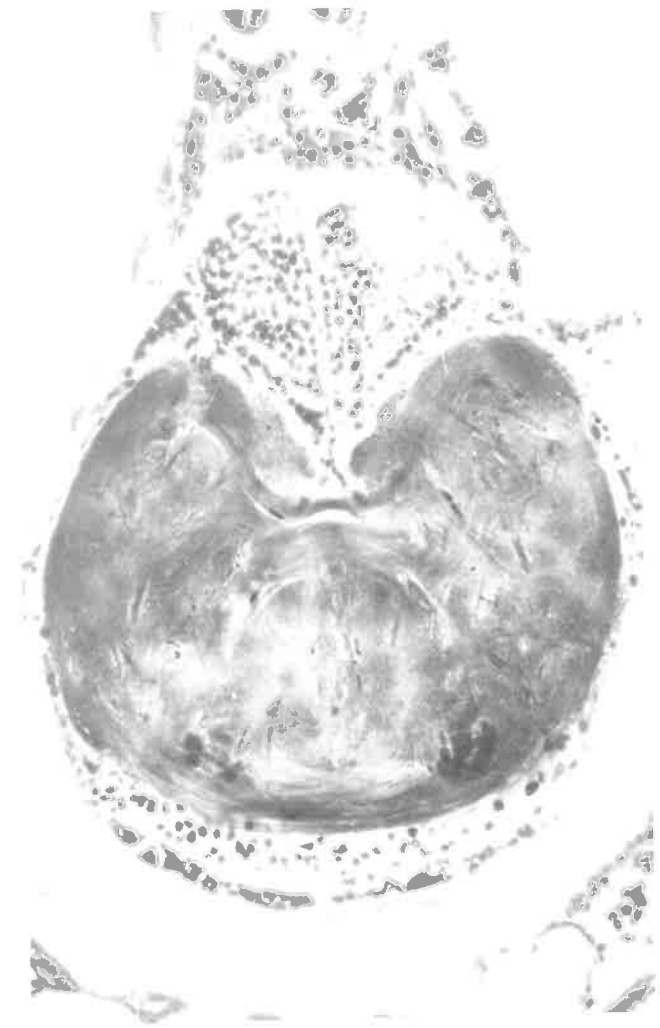
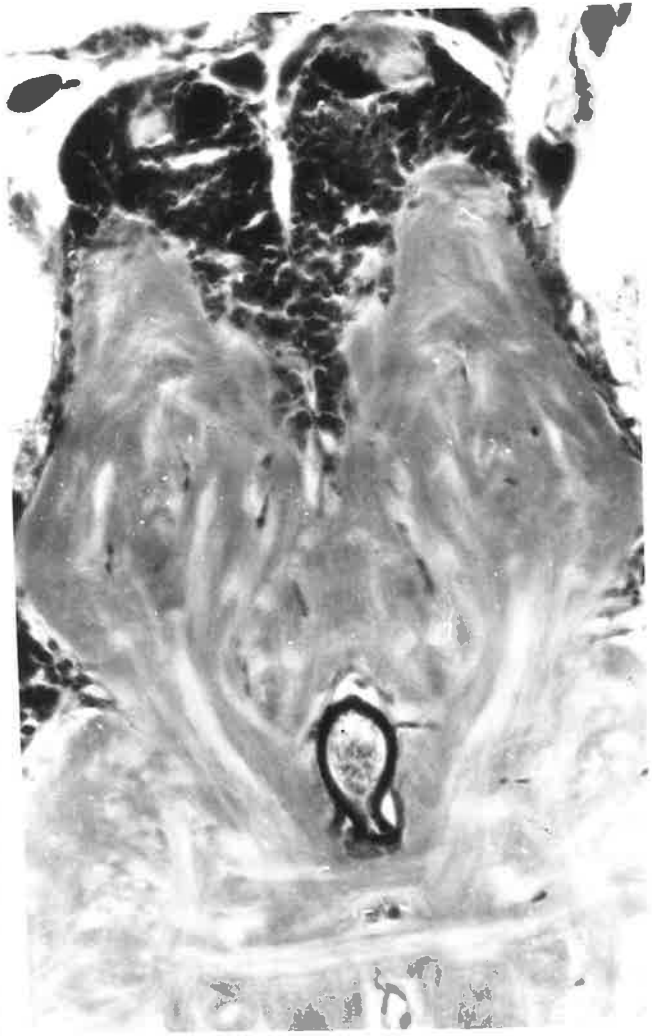


PLATE 26

Nephila LS





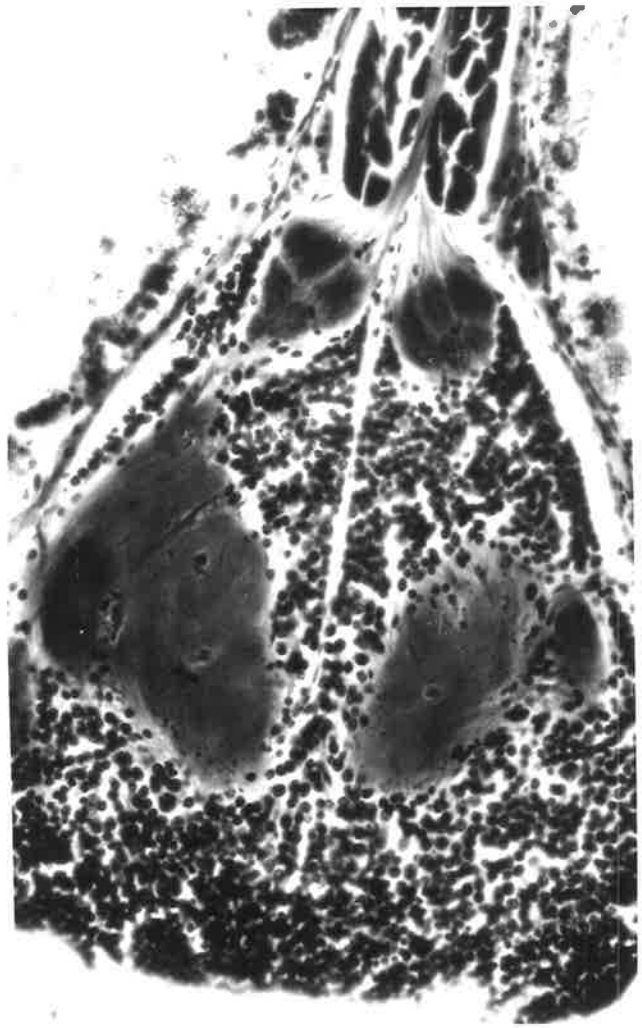


PLATE 27

Nephila TS

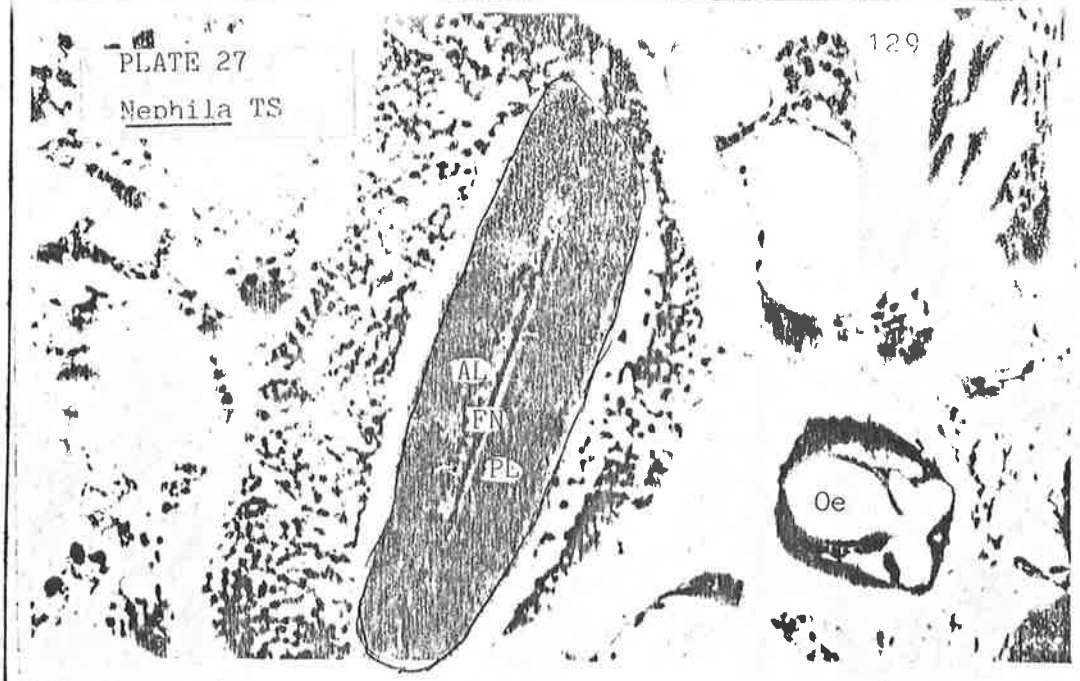


PLATE 28

Phonognatha LS

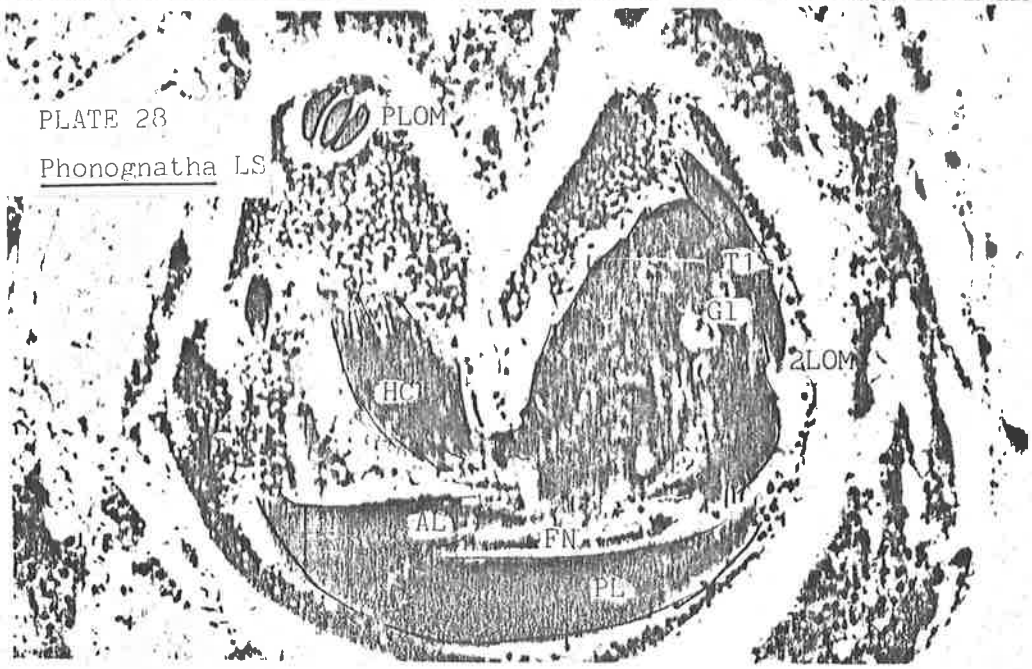
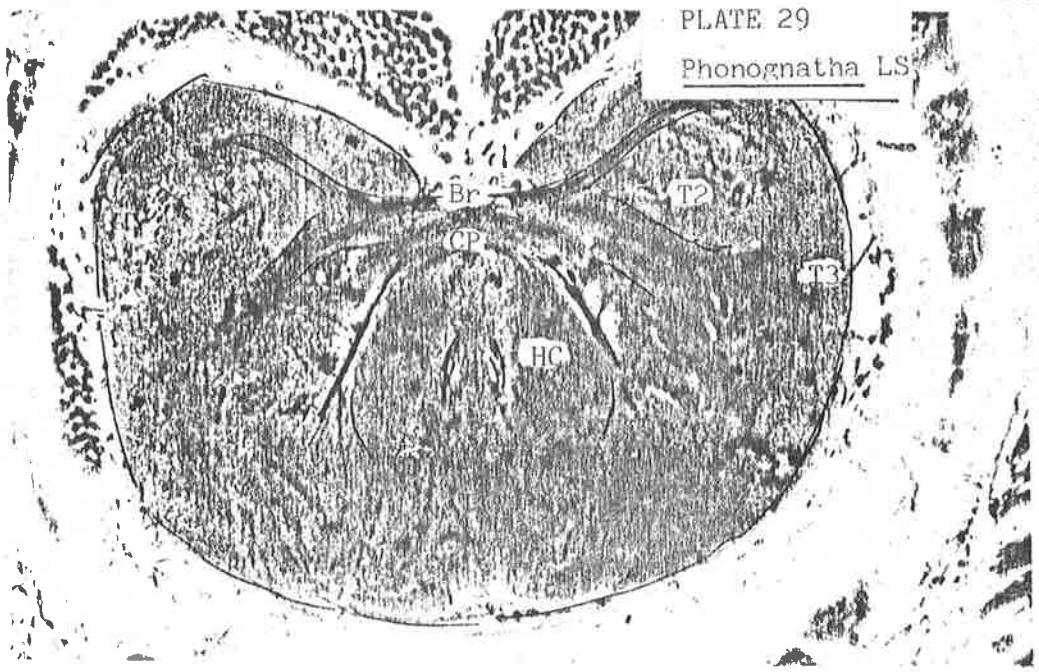


PLATE 29

Phonognatha LS



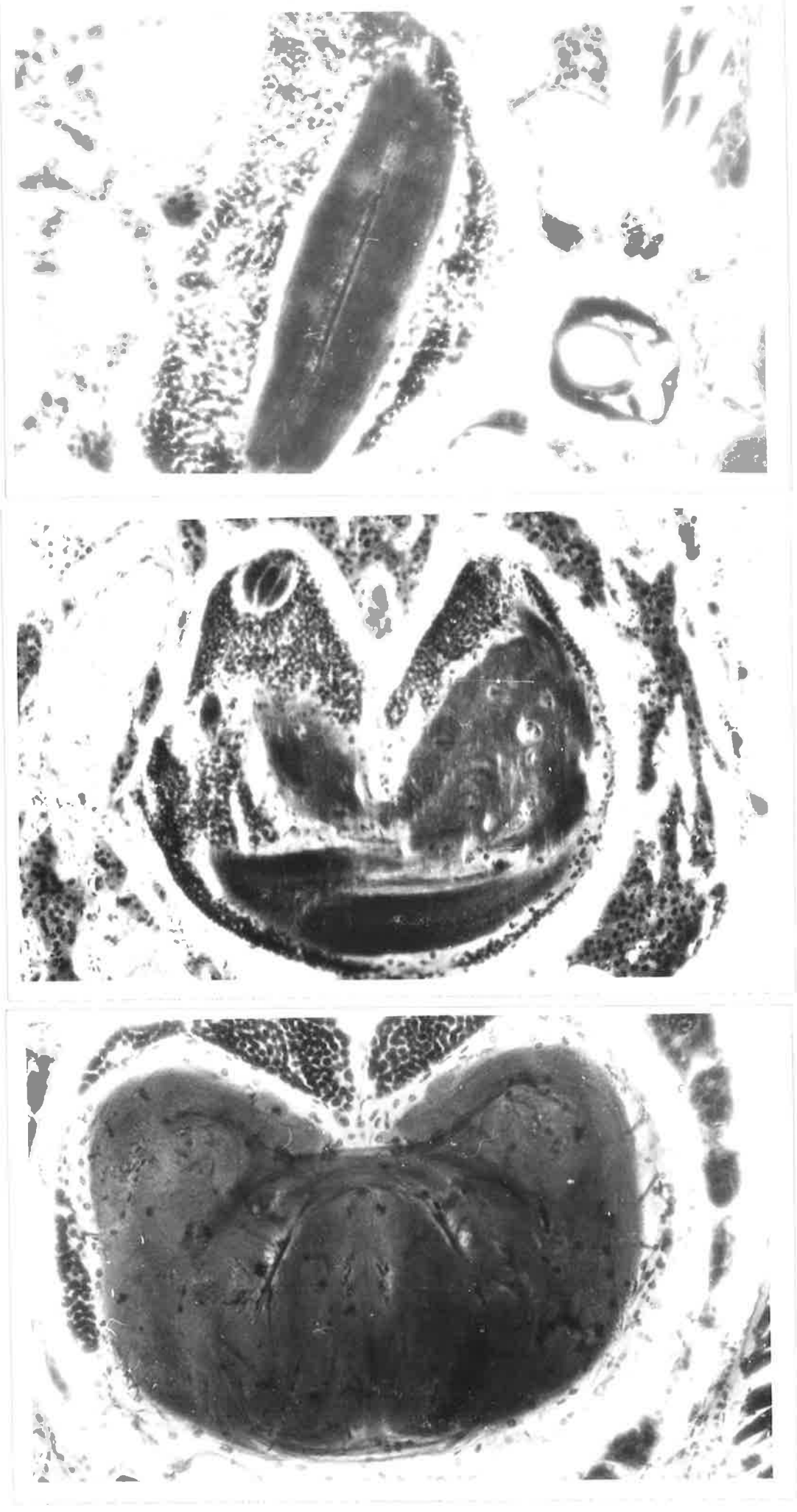


PLATE 30

Argiope LS

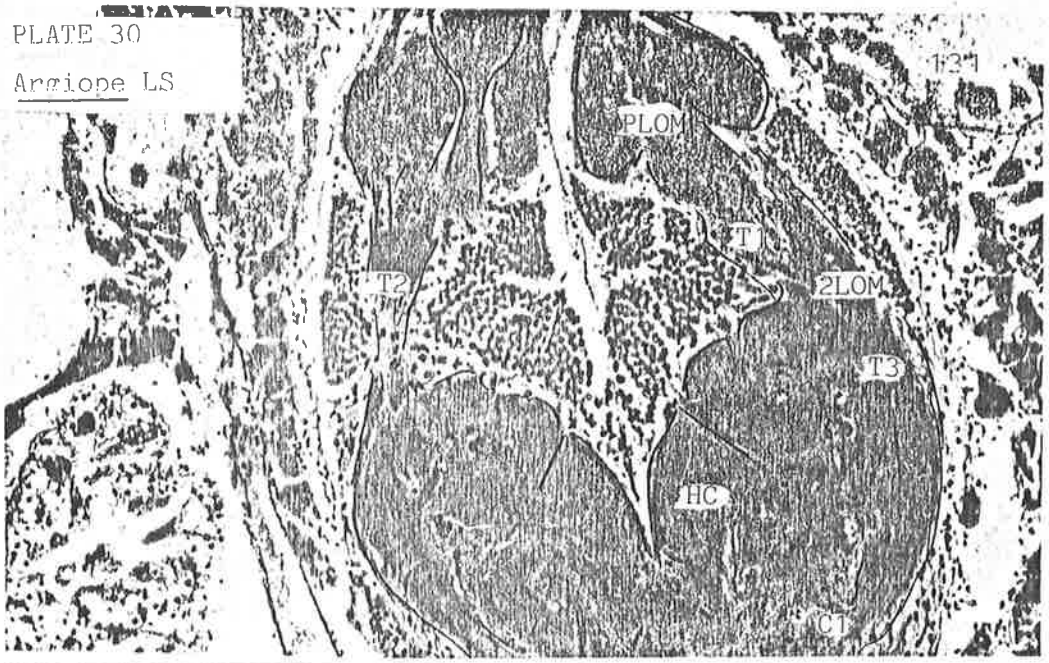


PLATE 31

Argiope SS

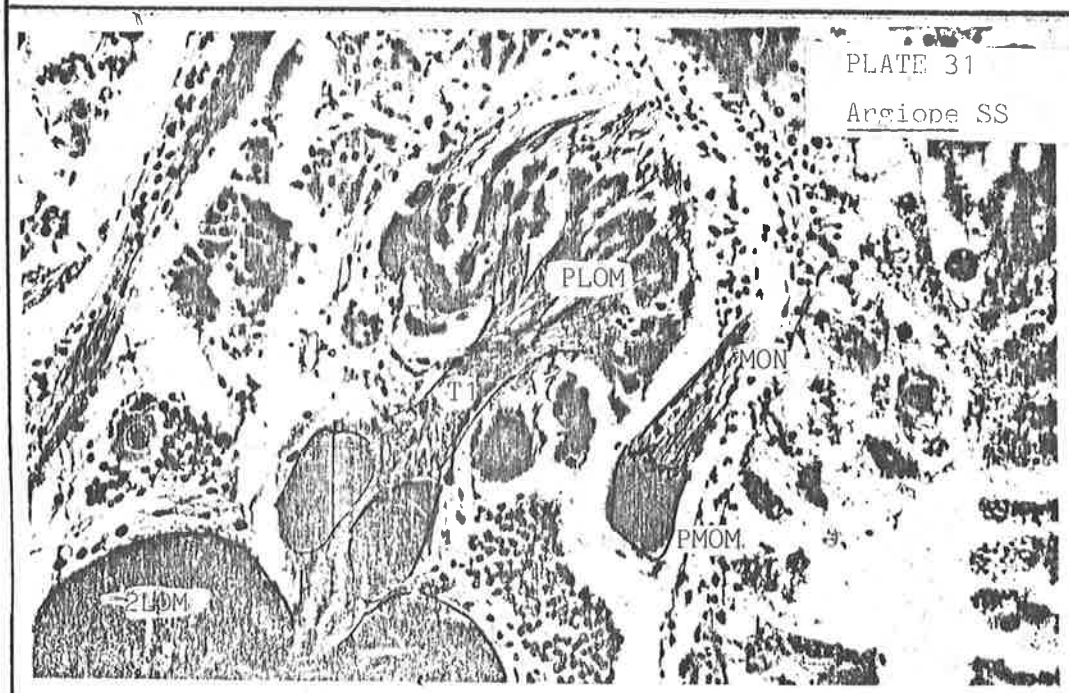
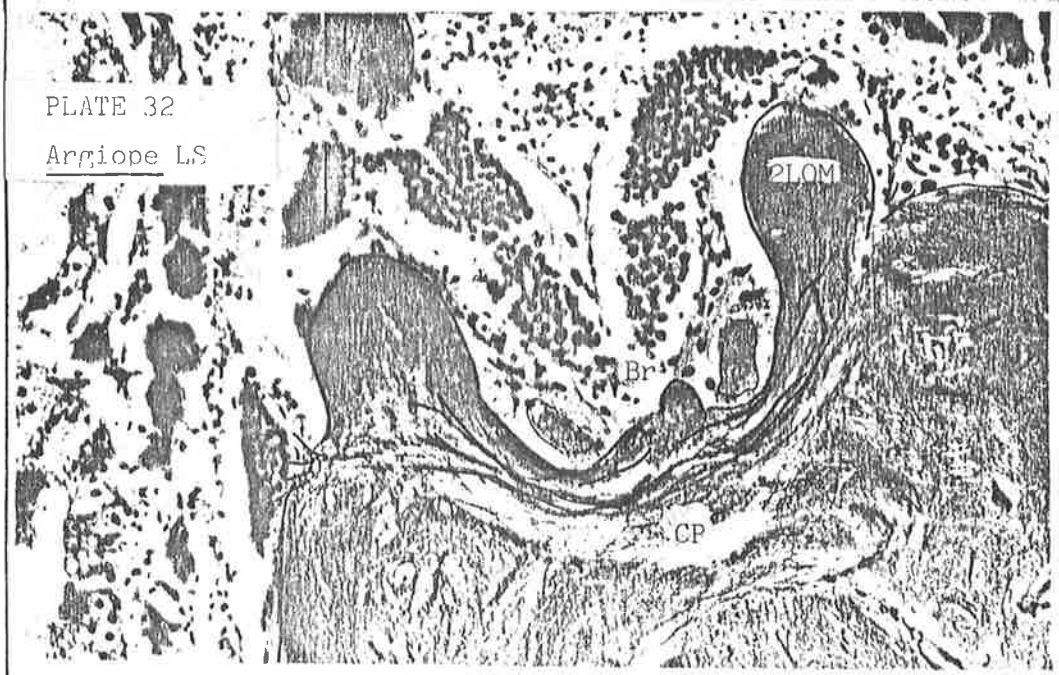
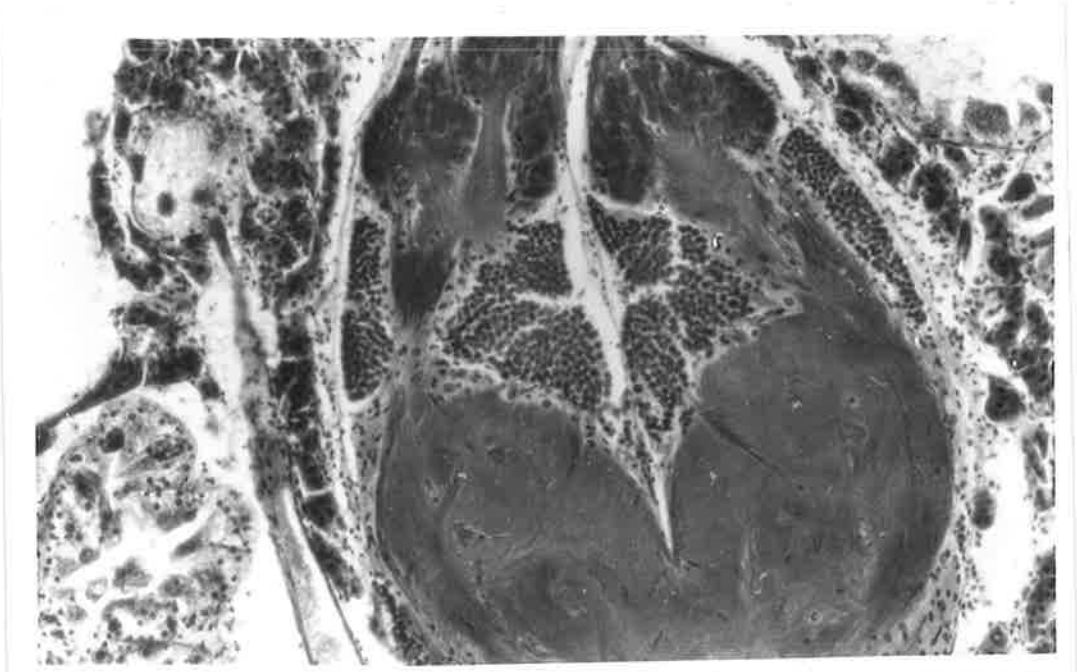
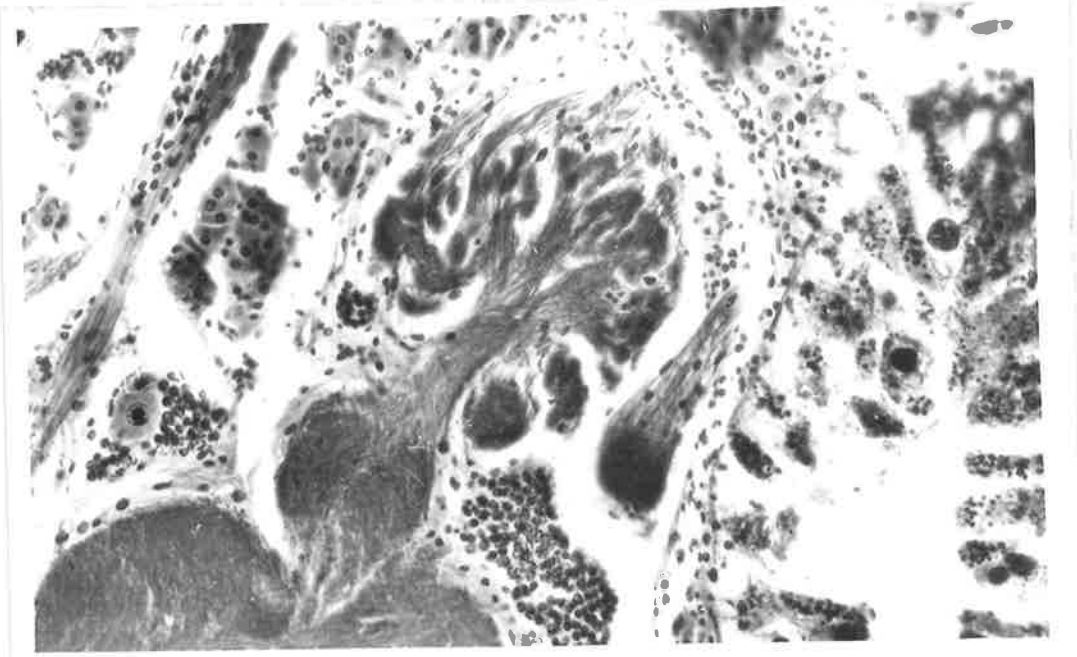


PLATE 32

Argiope LS







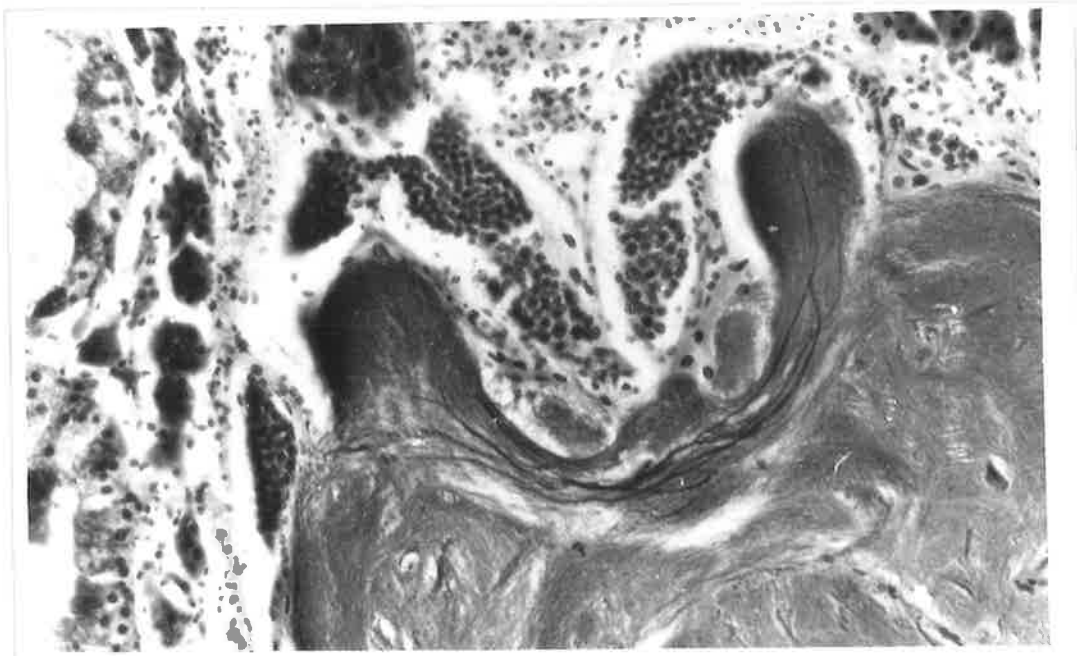


PLATE 33

Argiope LS

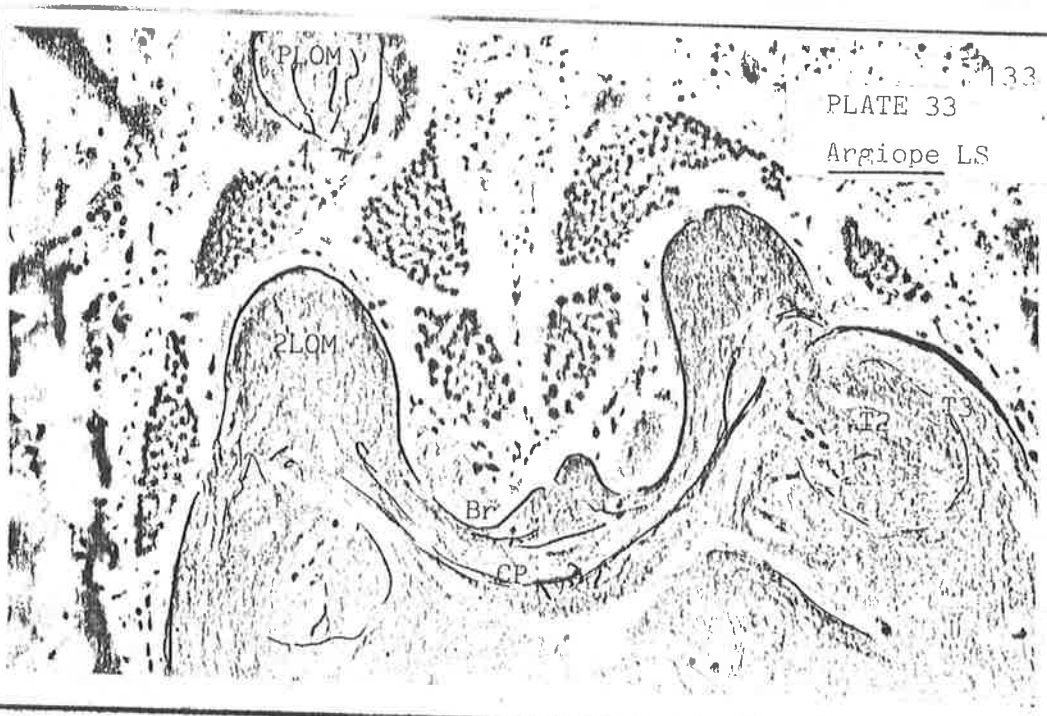


PLATE 34

Argiope LS

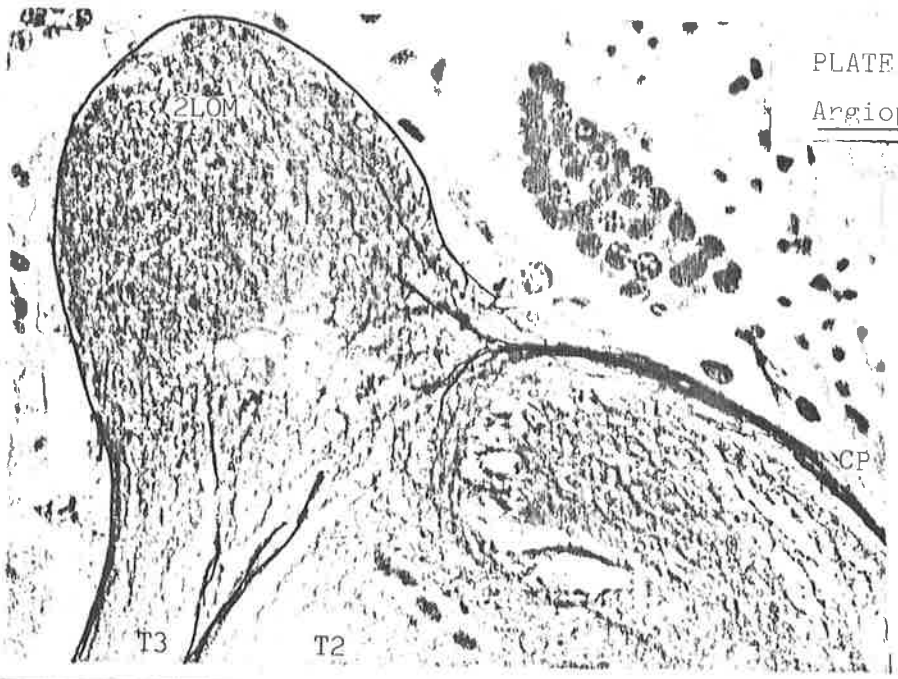
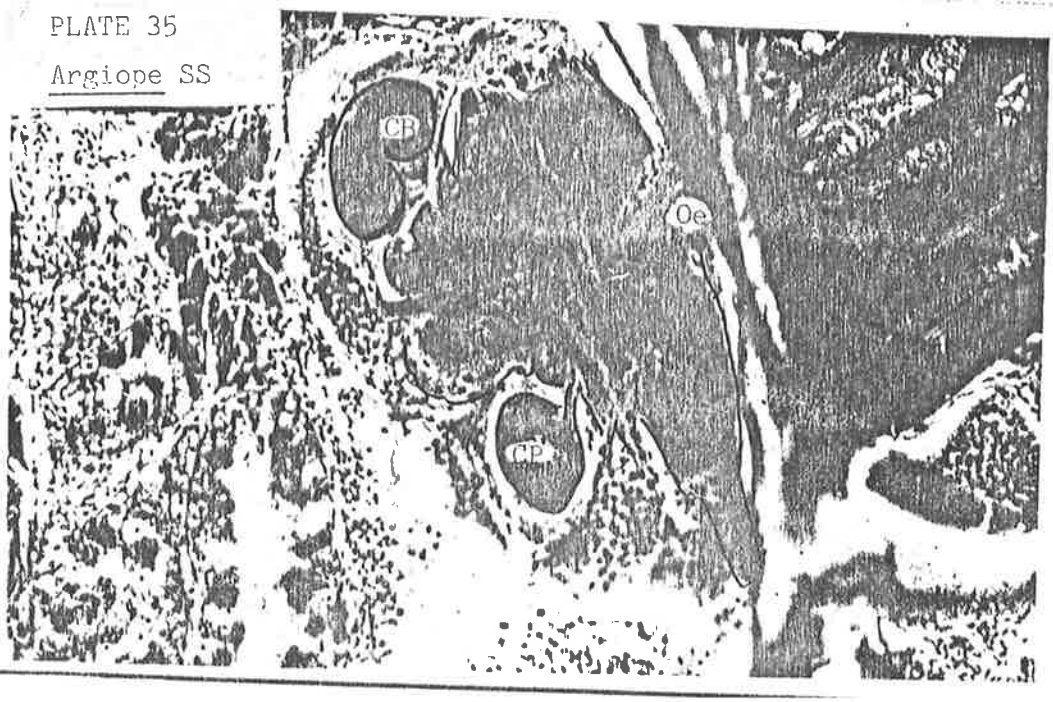
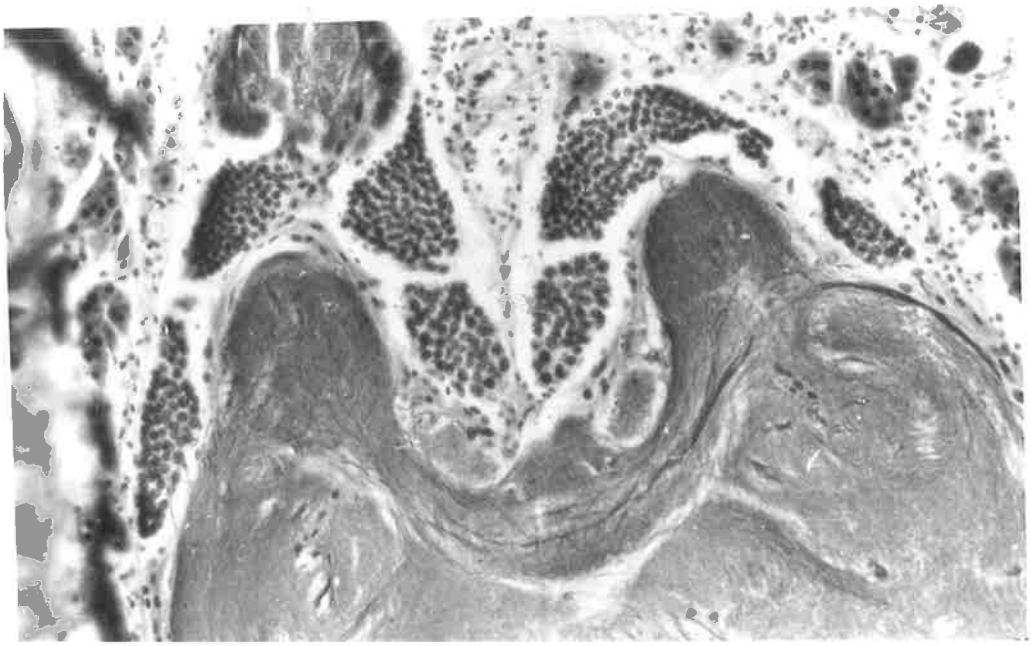
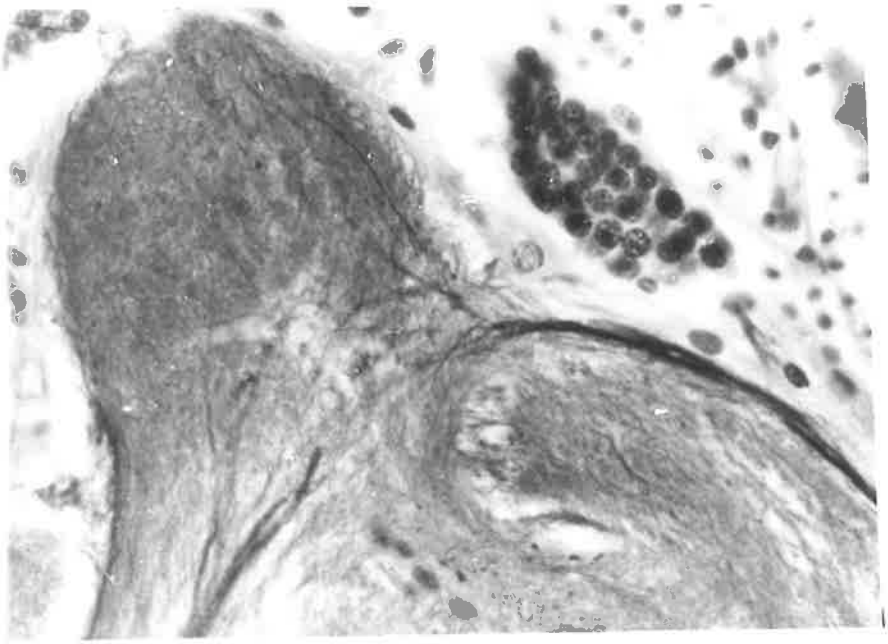


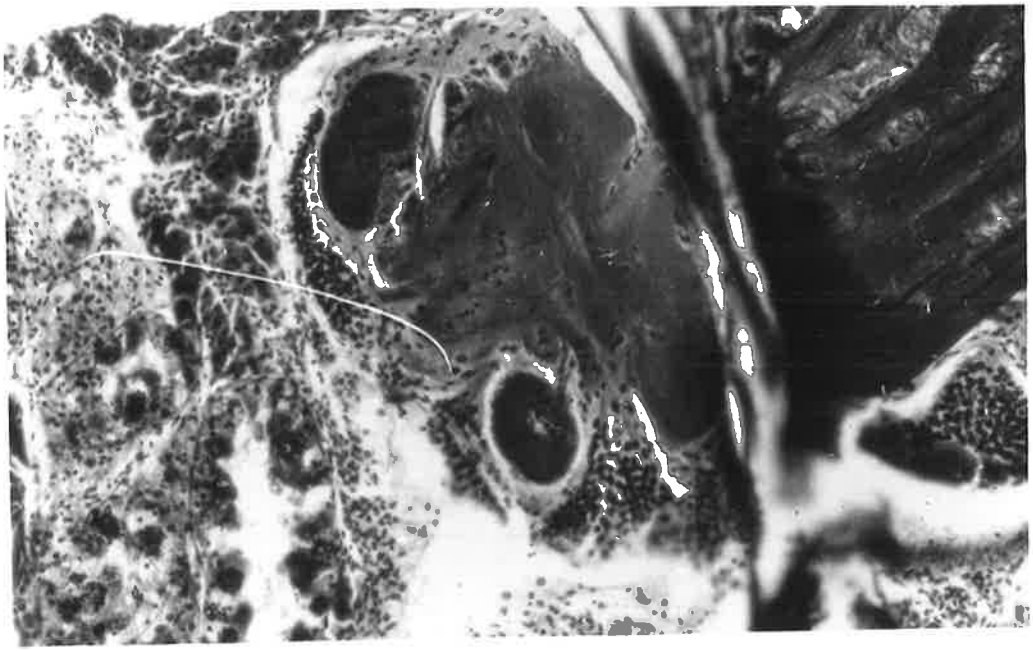
PLATE 35

Argiope SS









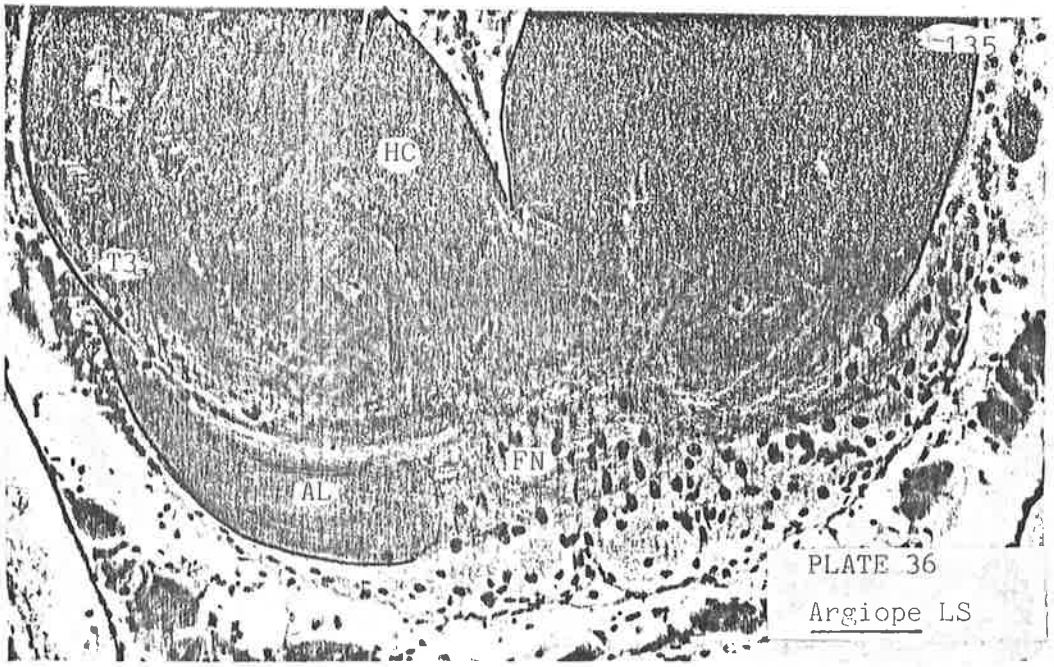


PLATE 36

Argiope LS

PLATE 37

Tetragnatha SS

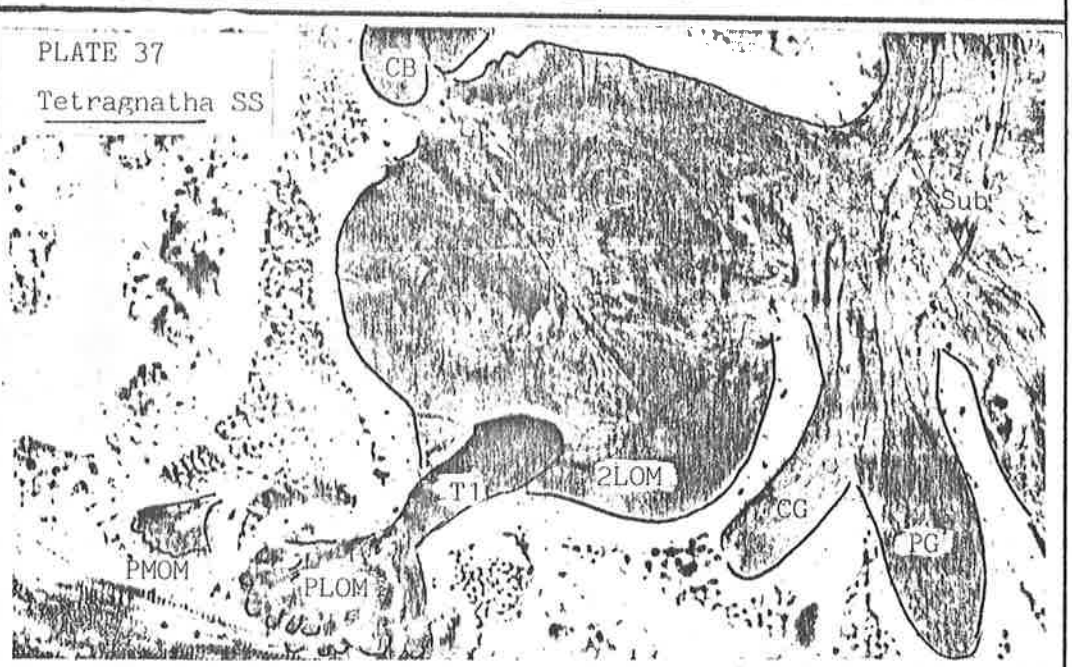
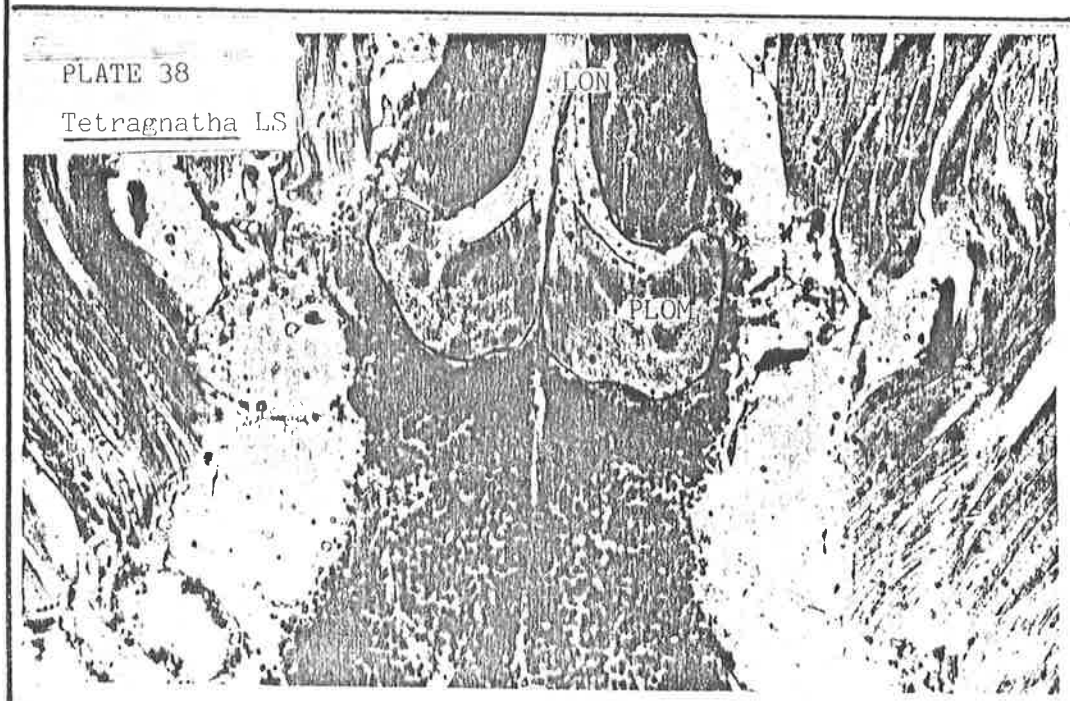
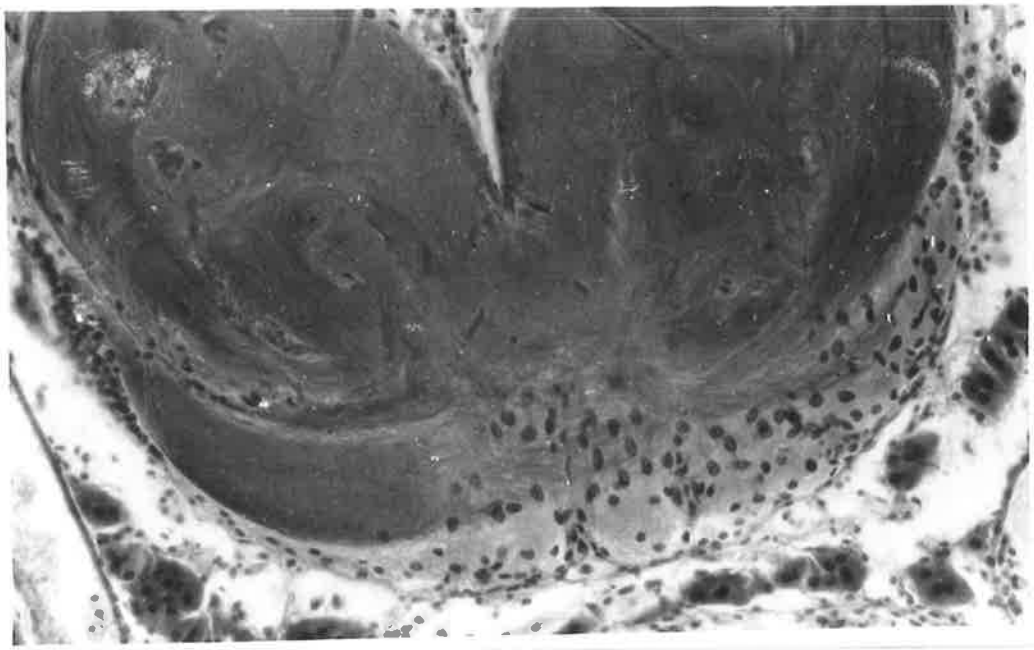
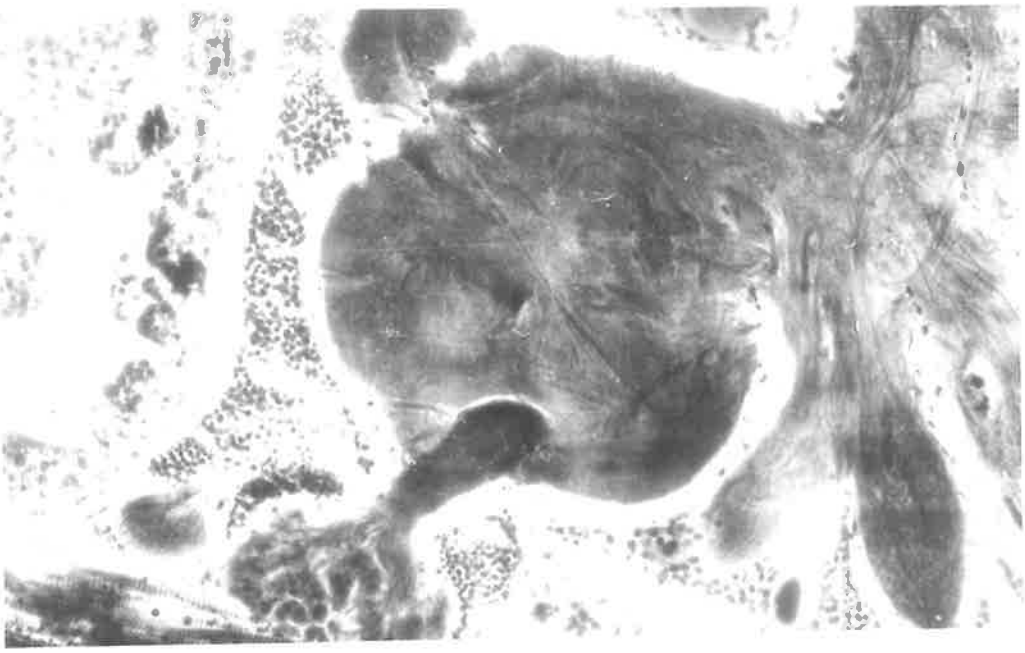


PLATE 38

Tetragnatha LS







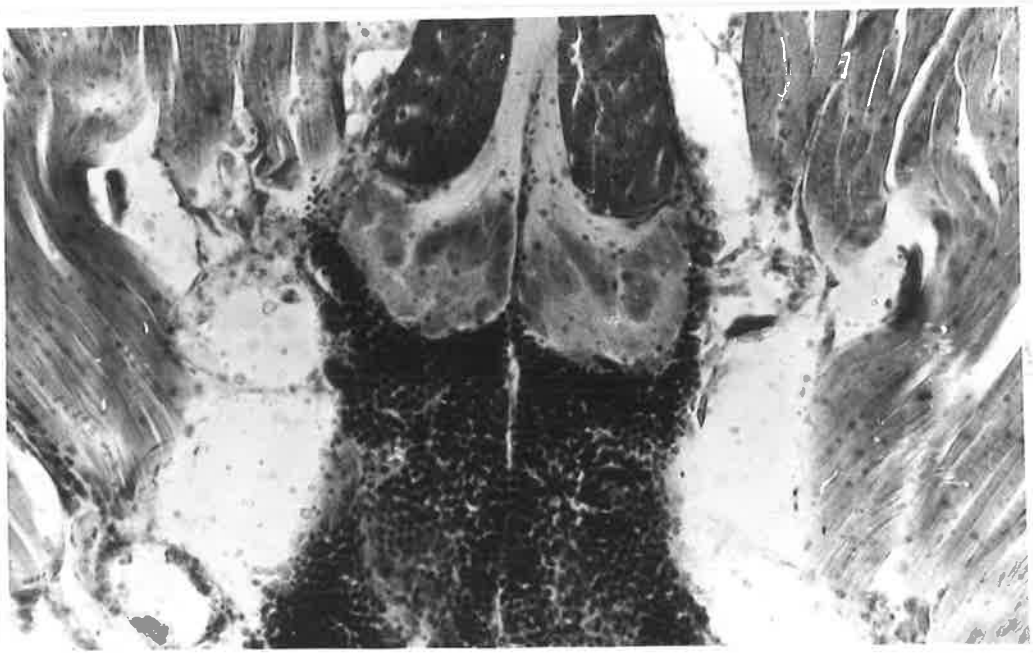


PLATE 39

Tetragnatha LS

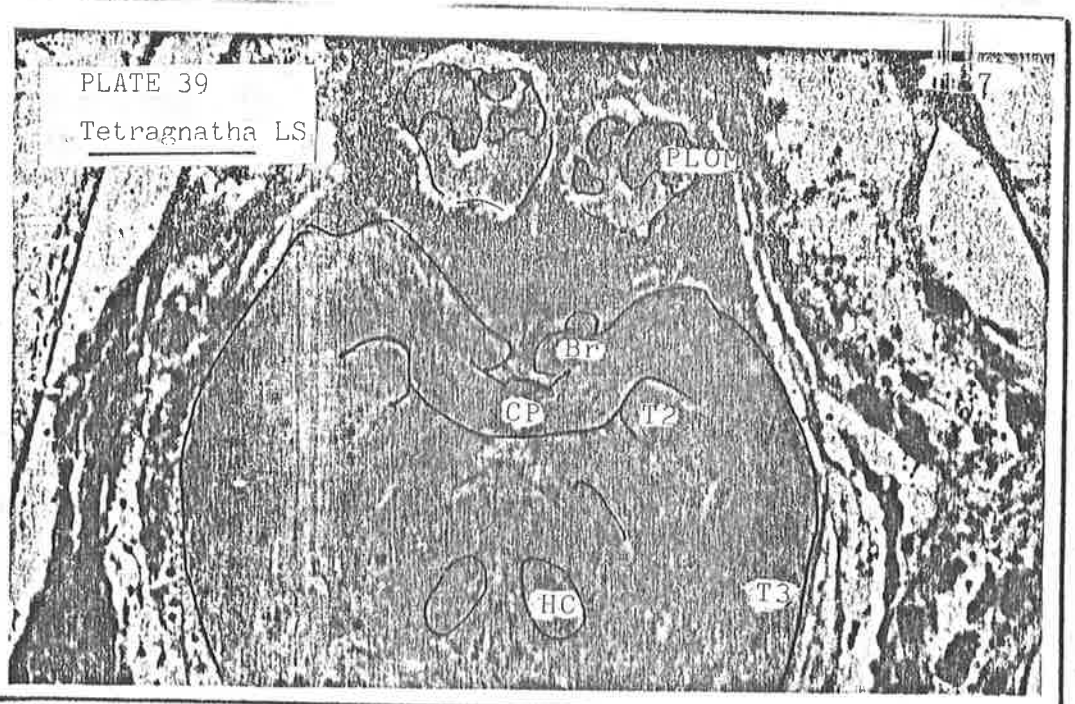


PLATE 40

Tetragnatha SS

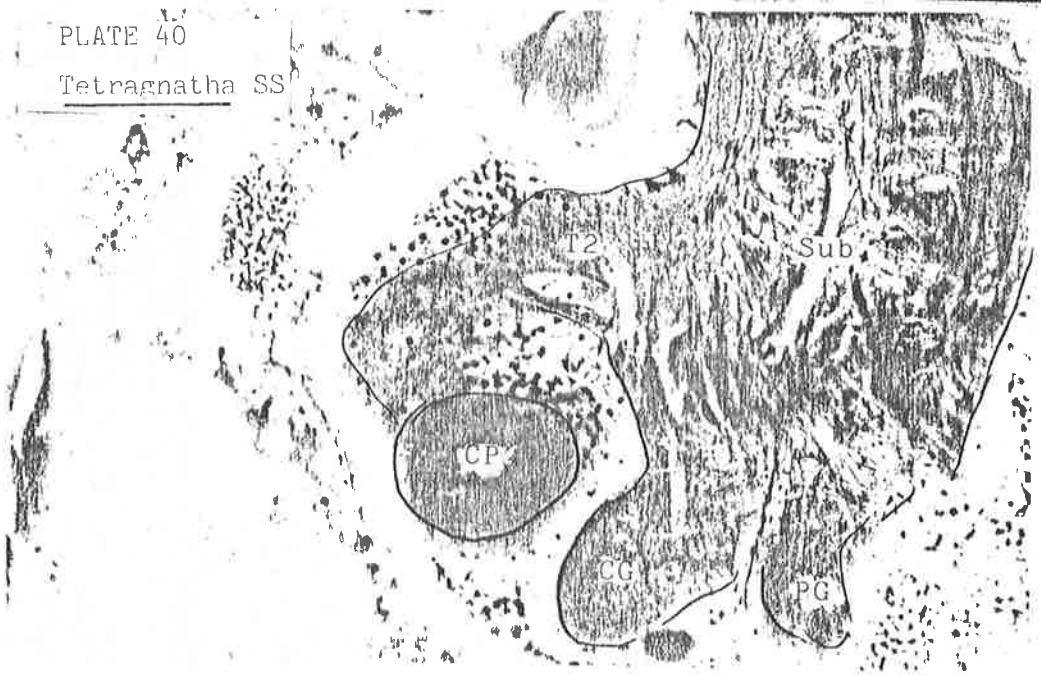
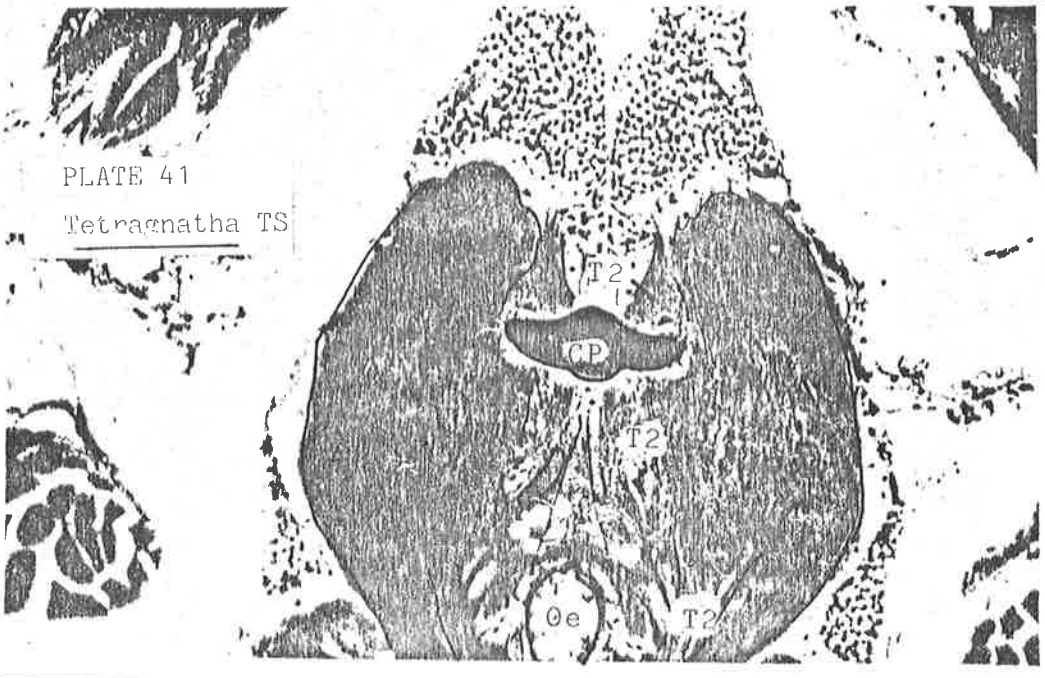
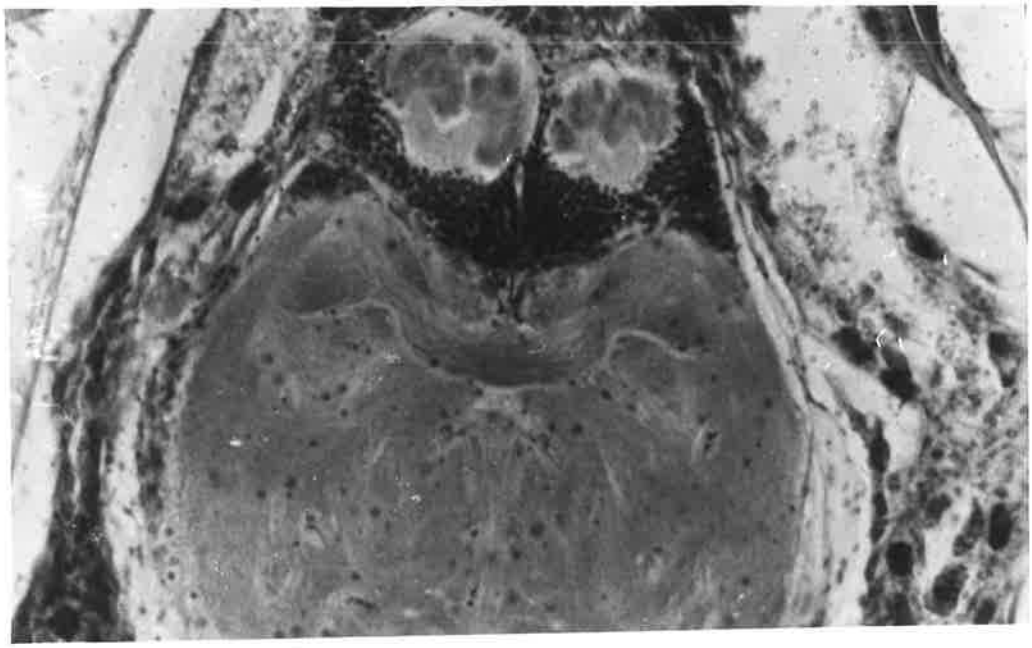
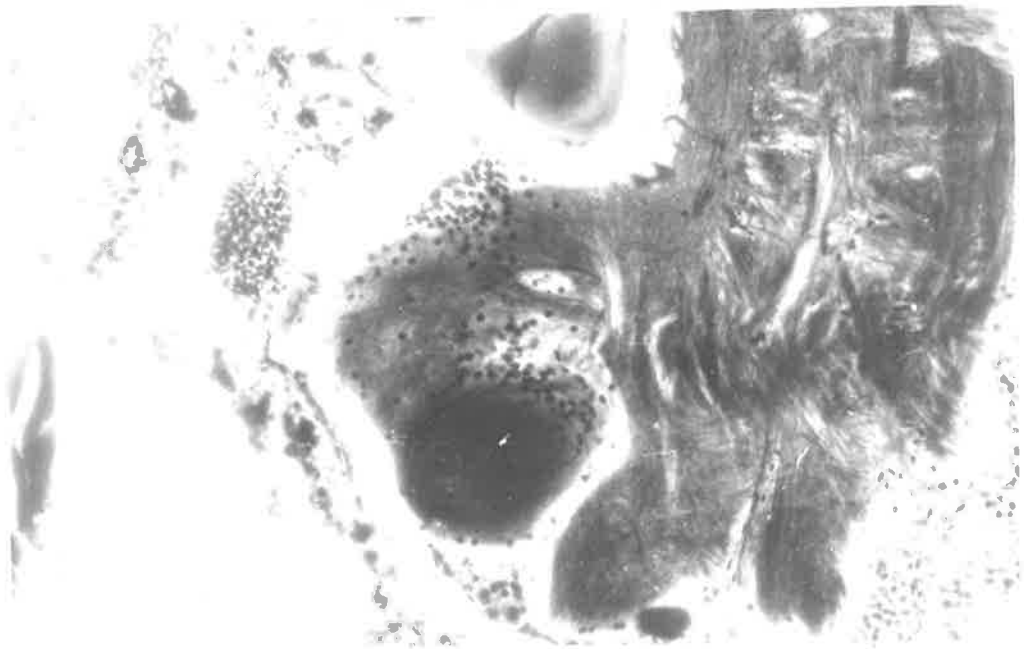


PLATE 41

Tetragnatha TS







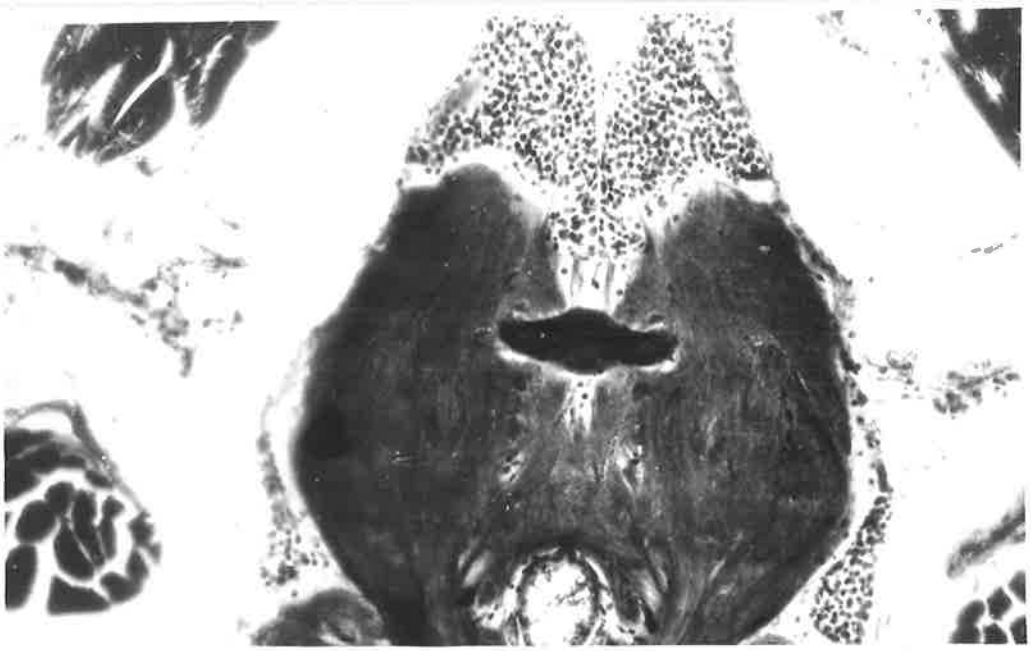
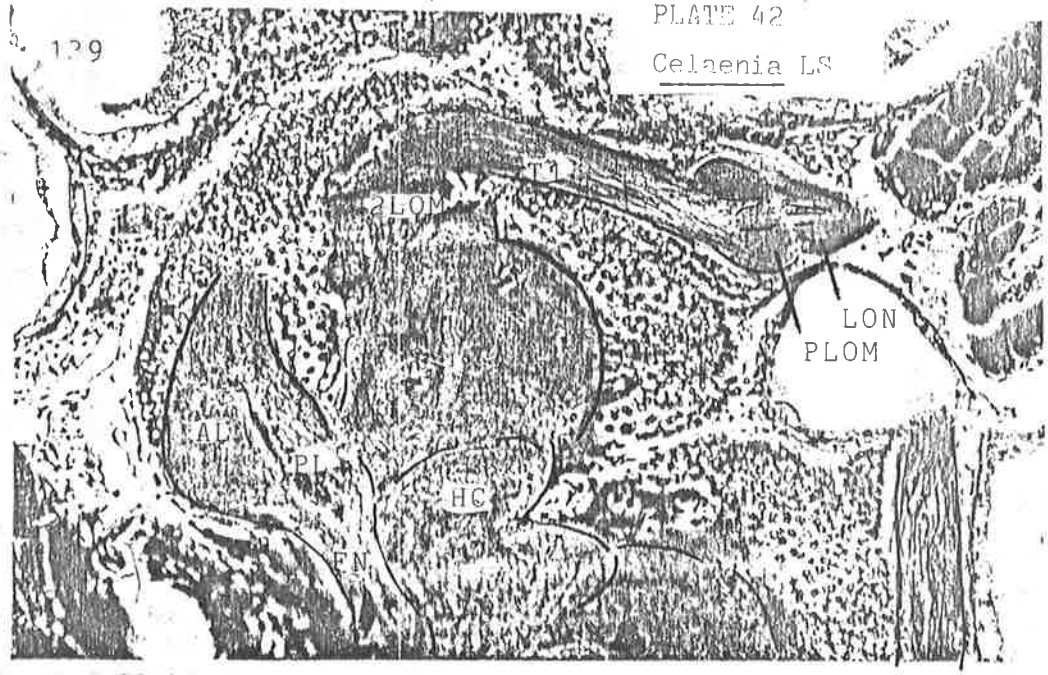


PLATE 42

Celaenia LS



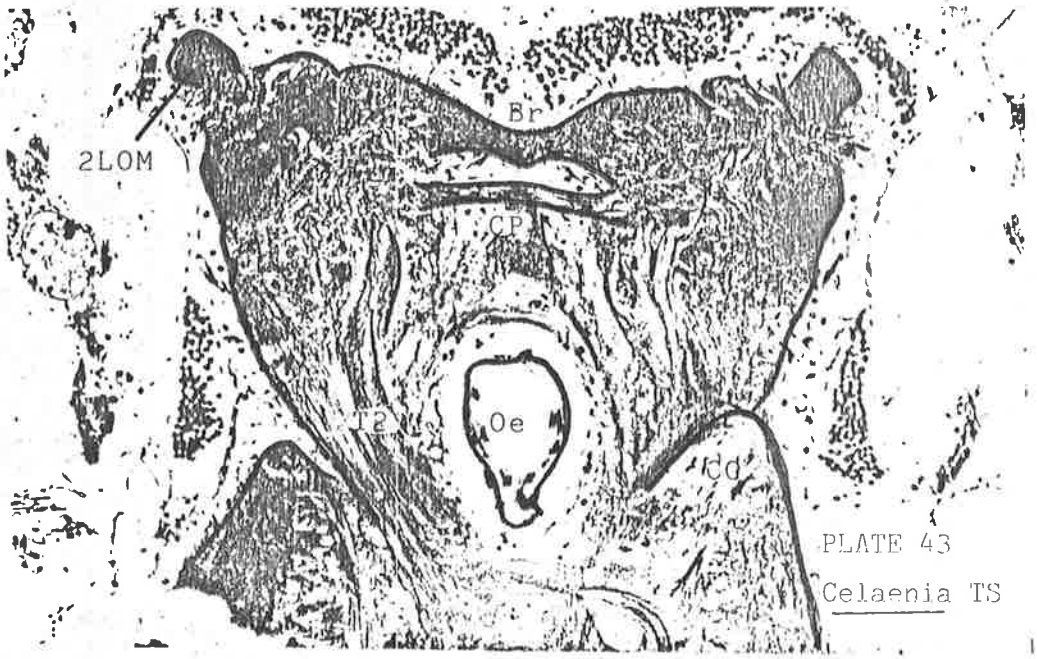
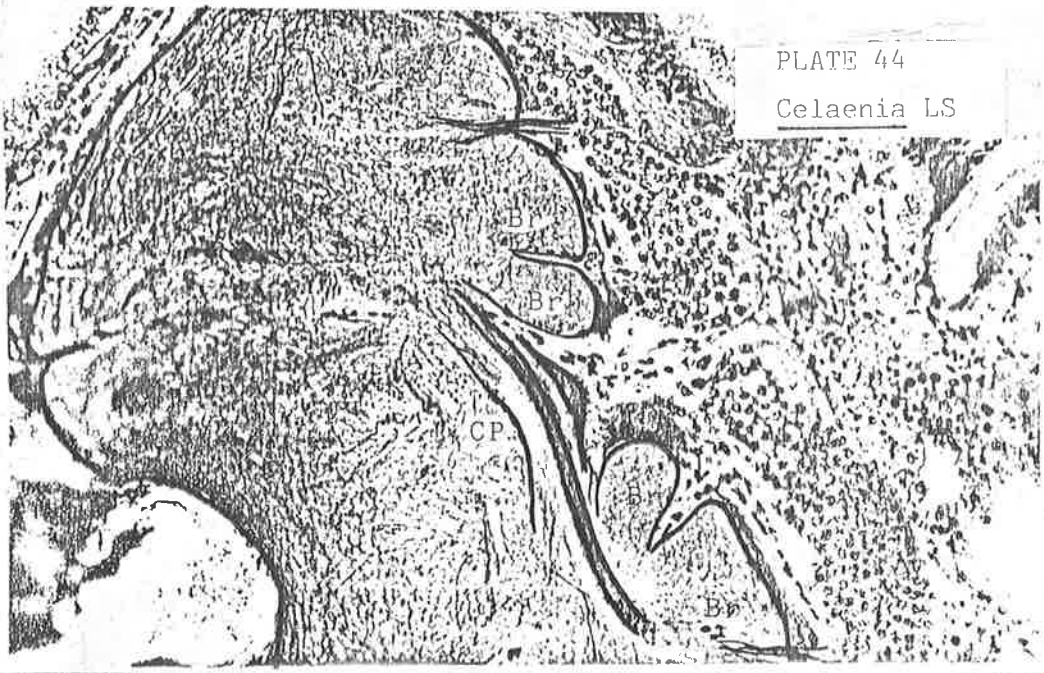


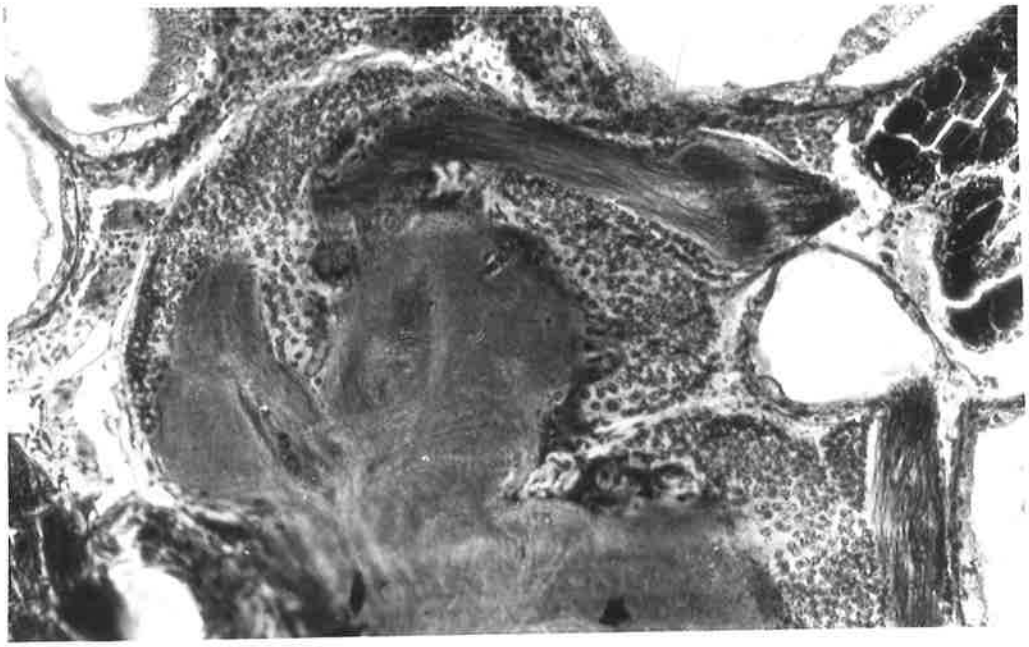
PLATE 43

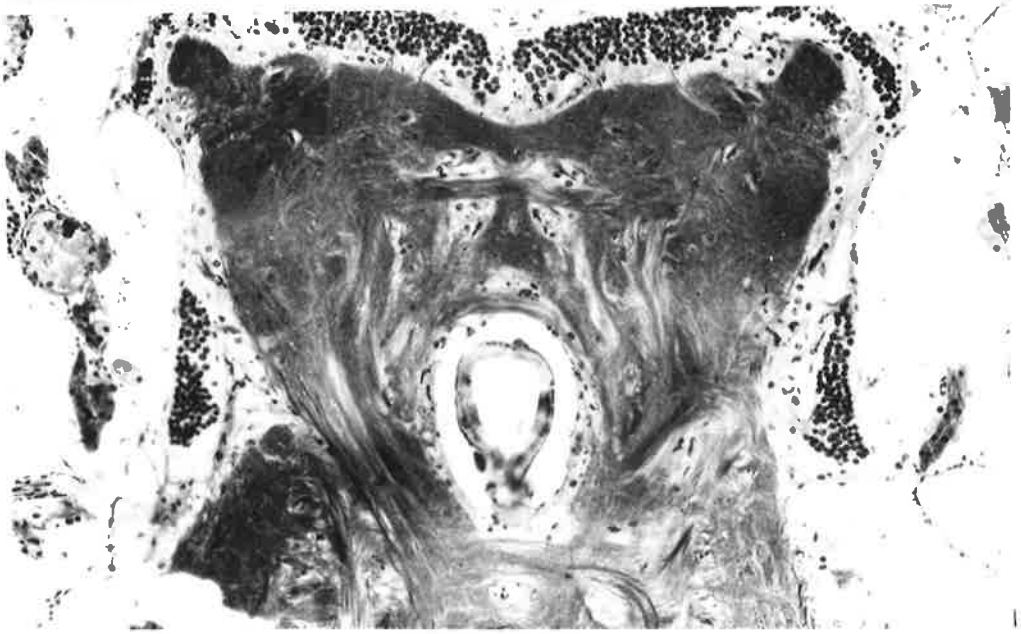
Celaenia TS

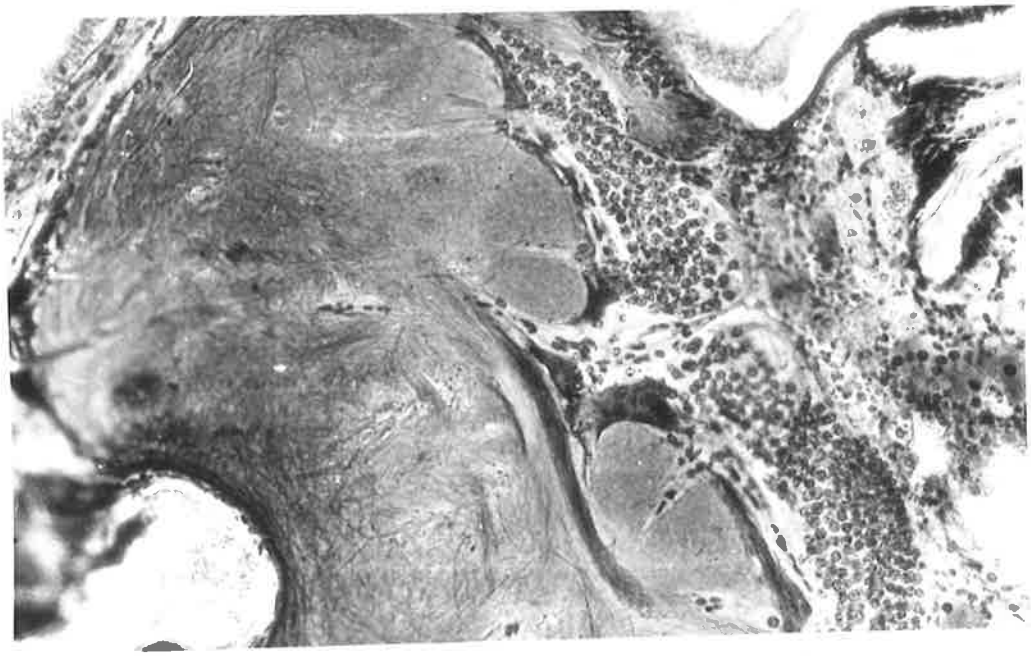
PLATE 44

Celaenia LS









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