The structure of the central nervous system of jumping spiders of the genus *Phidippus* (Araneae: Salticidae)

Republication Version 1 (October 31, 2006)

David E. Hill
213 Wild Horse Creek Drive, Simpsonville, South Carolina, 29680
platycryptus@yahoo.com

This work was originally published as: Hill, D. E. 1975 The structure of the central nervous system of jumping spiders of the genus *Phidippus* (Araneae: Salticidae). M.S. thesis, Oregon State University: 1-94. All original text and content is presented, but illustrations have been reprocessed for clarity and the text has been repaginated. In several places, pertinent material or corrections have been added [marked by red text in brackets]. A figure (6B) has also been added to Figure 6.

1. Abstract

The central nervous system of *Phidippus*, while comparable to that of other spiders in most respects, is distinguished by the extraordinary development of visual processing centers, associated with the complex visually-directed behavior of these animals.

The primary neuropile of the anterior medial eyes consists of two distinct columnar synapsing regions. There is some evidence that the geometry of this structure may correspond to the arrangement of receptors in the anterior medial eyes. First-order interneurons link this primary neuropile with a less-structured, massive secondary neuropile at the top of the syncerebrum.

The optic nerve fibers of each lateral eye synapse in a convoluted primary neuropile. Two distinct first order interneuron types join this neuropile to a lateral eye neuropile and the protocerebrum on one hand, and to the glomerular layer of the *corpora pedunculata* on the other. Each of these interneurons branches to form two separate synapsing regions in the primary neuropile.

The small optic nerve of the posterior medial eyes synapses in a glomerular neuropile. Large interneuron fibers associated with this neuropile lead to the protocerebrum. This structure suggests a special role for information provided by the posterior medial eyes, perhaps in the regulation of diurnal activity patterns.

In the *corpora pedunculata*, intrinsic fibers synapse anteriorly with first-order interneurons of the lateral eyes, and form linear fibers bearing numerous synaptic glomeruli in the pedunculus. The latter is the site of extensive synapsing with extrinsic fibers.

The *corpora pedunculata* are considered to be secondary visual centers, quite possibly concerned with directed orientation to visual stimuli. In structure they are the analogs, rather than the homologs, of similar structures observed in annelids and other arthropods. This distinction supports the separation of the Chelicerata from the latter groups.

The structure of the central body agrees with its accepted role as either a major association center, or as the source of complex programmed behavior.

2. Introduction

Within the continental United States, the genus *Phidippus* includes approximately 40 species [At least 60 species of *Phidippus* are presently known (Edwards 2004)], which B. J. Kaston (1972) termed *our heaviest and hairiest jumping spiders*. The identical chromosome number of *P. audax*, *P. johnsoni*, and *P. regius* (Pinter and Walters 1971) supports the undisputed morphological basis for the integrity of this genus.

The present work involves the study of *P. johnsoni* (Peckham 1883) and *P. rimator* (Walckenaer 1837) [now called *P. clarus* (Edwards 2004)]. Identification of the spiders was based upon Peckham and Peckham (1909, the most recent revision of the genus) and Kaston (1972). This identification was confirmed by Lawrence J. Pinter. A complete synonymy for the spiders is available in Bonnet (1945-1962) under the headings of *P. formosus* and *P. johnsoni* for the former, and likewise under the dual headings of *P. clarus* and *P. rimator* for the latter species.

In light of the continuing interest in the visually directed behavior of jumping spiders, it is surprising that little information is available in regard to the structure of the salticid central nervous system (CNS); the present work is intended to deal with this gap in our knowledge.

Figure 1. Adult female *Phidippus rimator* (Walckenaer) [*Phidippus clarus* Keyserling], collected in the vicinity of Corvallis, Oregon. The prosoma of this spider is oriented toward the camera, to facilitate scanning with the large anterior medial eyes. Moments later the spider jumped onto the lens of the camera. The apparent psyche of these spiders is communicated to visually oriented humans by the great amount of time devoted to the collection and processing (evaluation) of visual information.

Figures 2-5. [on next two pages] Four views of adult female *Phidippus rimator* (Walckenaer) [*Phidippus clarus* Keyserling] drawn to scale with *camera lucida*.

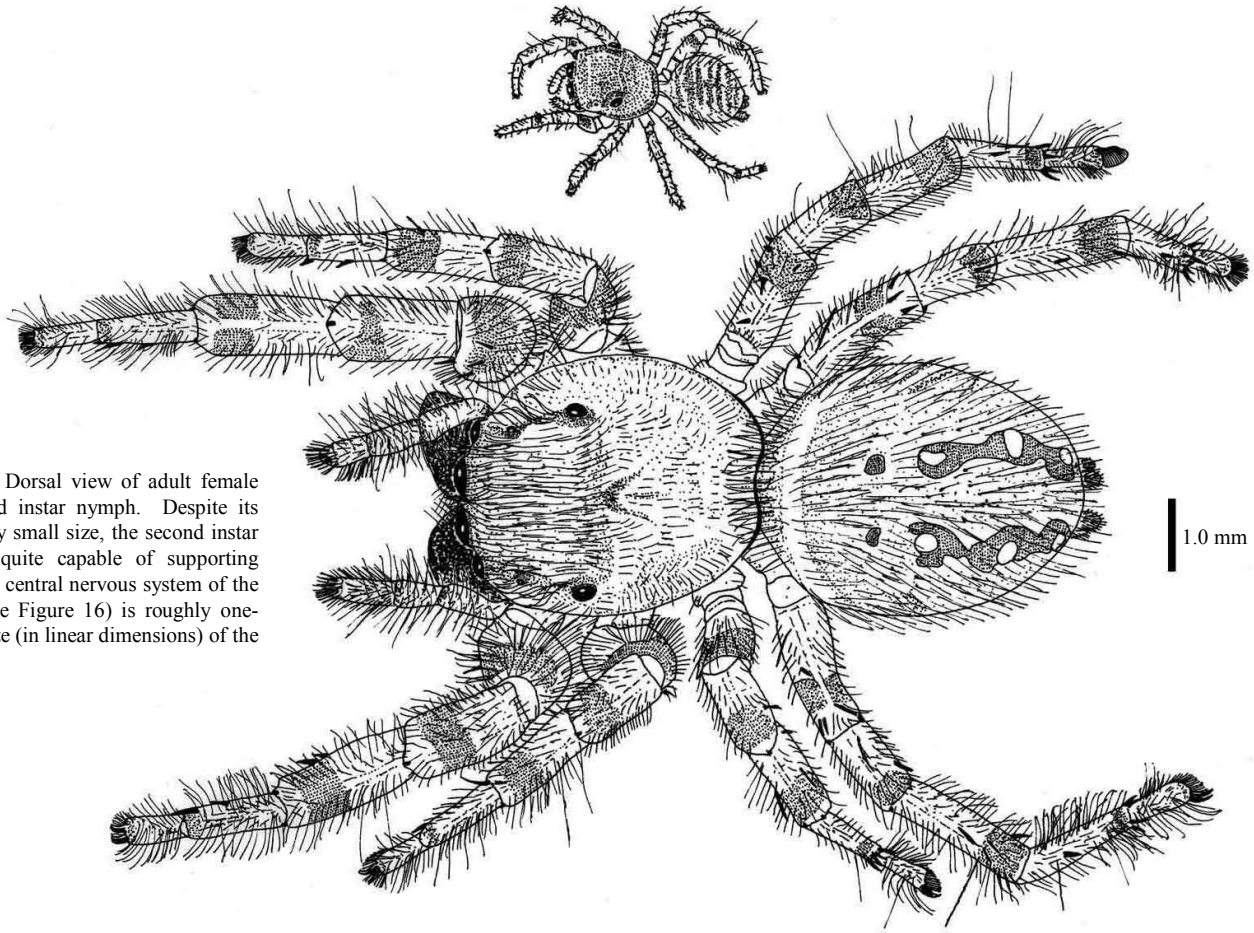


Figure 2. Dorsal view of adult female and second instar nymph. Despite its comparably small size, the second instar spider is quite capable of supporting itself. The central nervous system of the nymph (see Figure 16) is roughly one-half the size (in linear dimensions) of the adult CNS.

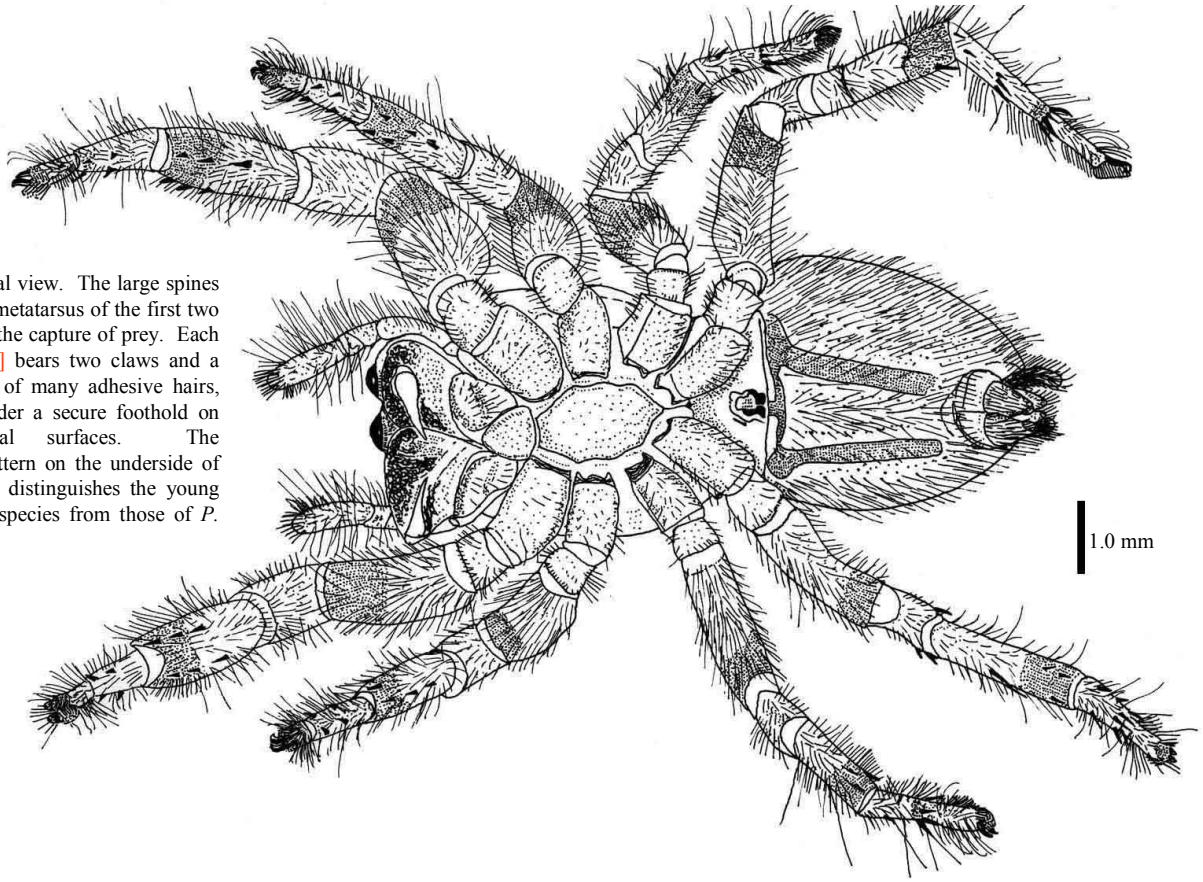


Figure 3. Ventral view. The large spines of the tibia and metatarsus of the first two legs are used in the capture of prey. Each tarsus [pretarsus] bears two claws and a tuft or foot-pad of many adhesive hairs, granting the spider a secure foothold on smooth vertical surfaces. The characteristic pattern on the underside of the opisthosoma distinguishes the young nymphs of this species from those of *P. johnsoni*.

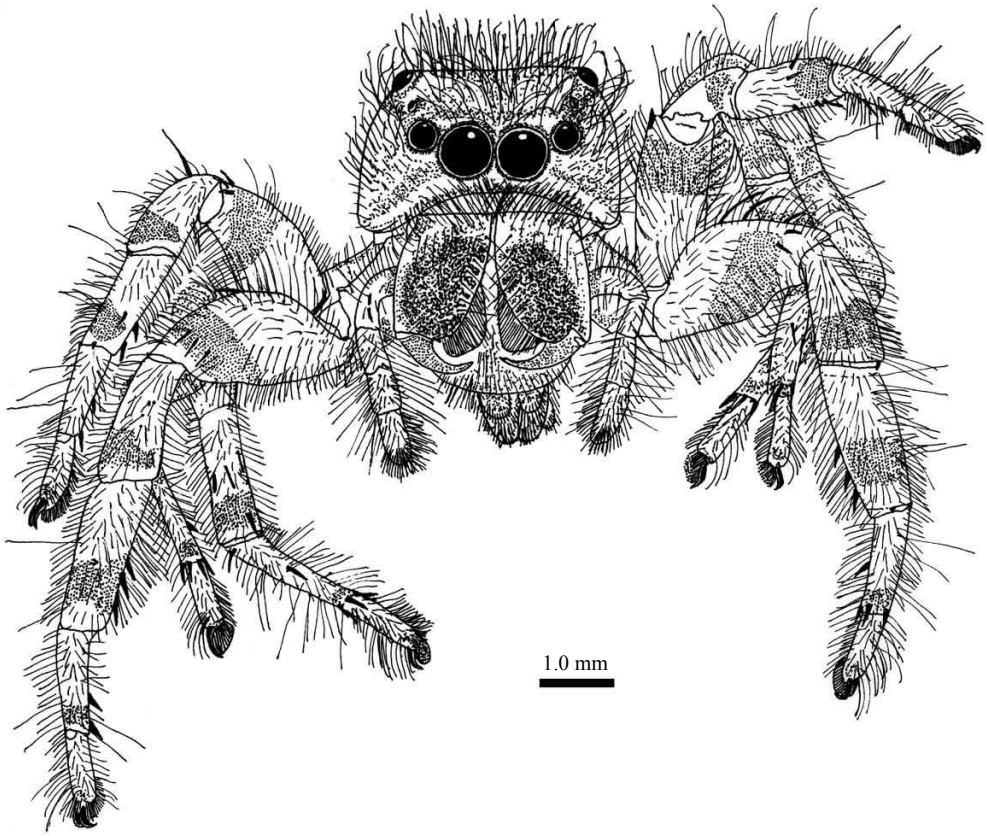


Figure 4. Anterior view. The chelicerae are iridescent green. The large pair of anterior medial eyes and the three pairs of lateral eyes (including the diminutive posterior medial eyes) are evident.

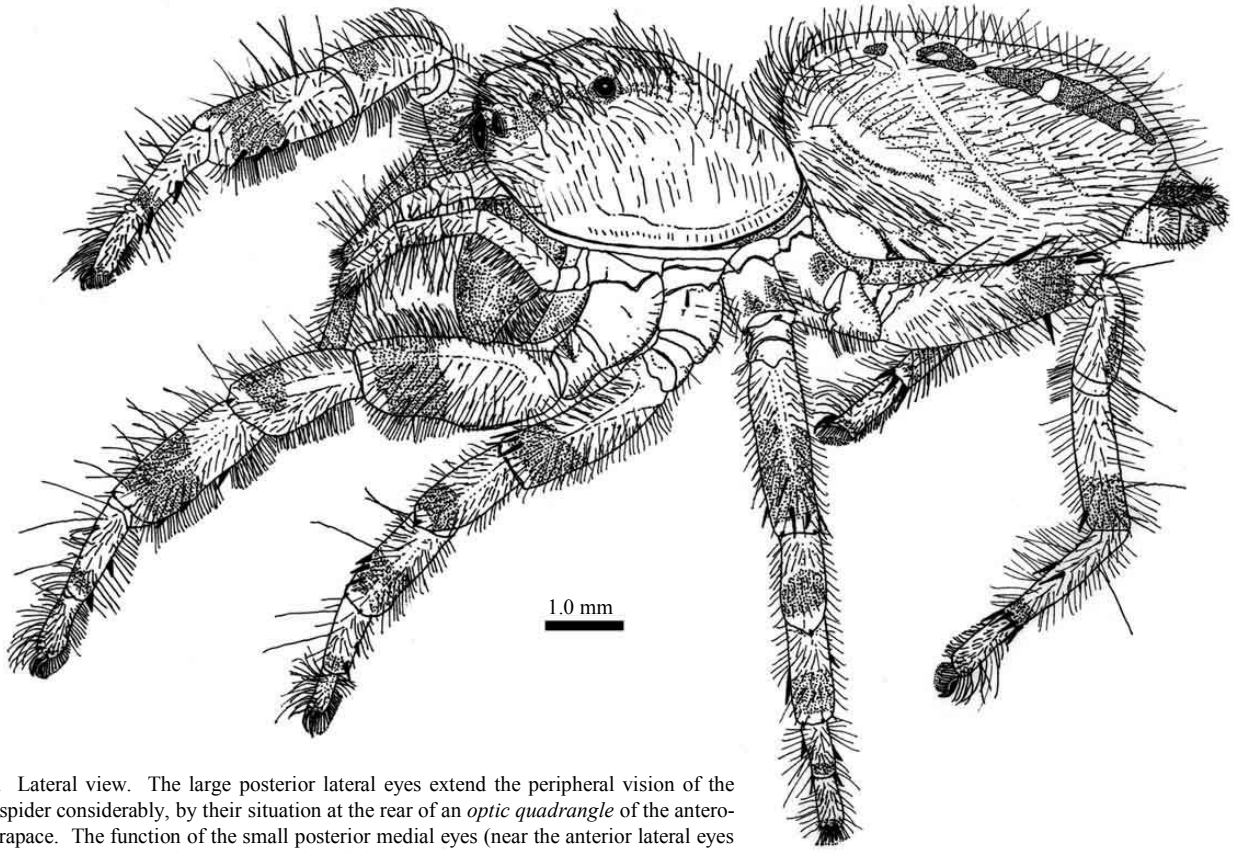


Figure 5. Lateral view. The large posterior lateral eyes extend the peripheral vision of the jumping spider considerably, by their situation at the rear of an *optic quadrangle* of the antero-dorsal carapace. The function of the small posterior medial eyes (near the anterior lateral eyes in *Phidippus*) is doubtful in this regard, as their field of vision is obscured by numerous hairs [not true in living *Phidippus*]. Nonetheless, the fact that these small eyes are retained by all salticids is significant. A number of trichobothria are shown in this view [long setae, presumed mechanoreceptors; presence of trichobothria has not been established].

3. Salticid behavior

Behavior and structure are two facets of the same phenomenon. Certainly an understanding of behavior must precede any intelligent interpretation of nervous function based upon structural evidence.

Salticid psychology has attracted a number of investigators in recent years (Drees 1952, Dzimirsski 1959, Precht 1952). Precht and Freytag (1958) were concerned with the effect of internal states upon behavior. This line of inquiry was pursued by Gardner (1964, 1965, 1966) in her studies of *Phidippus*. Gardner delimited intrinsic and extrinsic factors affecting behavior, and advanced the drive-level hypothesis in explaining the sequence of activities involved in predatory behavior. According to this hypothesis, a new or continued stimulus is required to initiate each succeeding activity of the behavioral sequence. Gardner (1966) dealt with *hunger* or deprivation as an intrinsic factor.

Although Witt, Reed, and Peakall (1968) termed the orb-weaver *an animal of simple capacities*, the behavioral repertoire of spiders is in reality quite complex. Hollis and Branson (1964) tried to list the discrete activities of *P. audax*. In Table 1 this list is expanded, although it is by no means completed, to illustrate the behavioral capacity of these jumping spiders. Discrete *behaviors* are classified as programs, or larger sequences involving many individual activities, and as activities. Thus the program of brood-sac construction involves the activities of attachment disk formation, silk release, prosomal and opisthosomal movement, and evaluation, among others. The specific sequence of activities is subject to constant sensory feedback, or evaluation. Periods of activity appear to be interrupted by *sensory interludes*.

The best summary of variations in the visual sexual display of male salticids is provided by Crane (1949). Bristowe (1971) gives a lively account of this sexual display. Kaston (1936) stresses the importance of visual information provided by this display in *P. clarus* (*rimator*), *P. audax*, and *P. purpuratus*. In *Phidippus* the visual effect of the elevated carapace and forelegs is enhanced by the iridescence of the chelicerae.

In jumping spiders, vision is of primary importance. Heil (1936) investigated the tactile and chemical senses of salticids, as well as vision. *Phidippus* is equipped with vibration-sensory trichobothria [presence of trichobothria has not been established] (Walcott 1969), sensory hairs of uncertain capacity, and lyriform (slit-sense) organs which serve as mechanoreceptors of cuticular stress (Kaston 1935, Pringle 1955), in addition to its extraordinary eyes. Vision figures most prominently in the distinctive behavior of these spiders, nonetheless.

Table 1. The behavior of *Phidippus*

Although no enduring distinction can be made between a program and an activity, in the sense that each activity could be considered as a program or coordinated sequence of behaviors in itself, there is nevertheless some justification for attempting such a distinction. Each of the programs listed here represents a definitive portion of the behavioral repertoire, involving many specific activities in an overriding objective essential for the survival of the species. The list of specific activities is presented as an illustration of the remarkable abilities of jumping spiders. Both lists are based upon the author's personal observations.

Programs

First and second instars: gregarious behavior in brood-sac
Second instar to adult (general activities): resting-sac construction and repair; daily rest; prolonged (seasonal) inactivity; travel or search for prey, water, or shelter; predation sequence
Nymphs [immatures]: molting-sac construction and molting activity or inactivity
Adult males (short-lived): sperm-web construction and pedipalp charging; courtship display and mating sequence; cohabitation with female (observed in *P. rimator* [*clarus*] in the field)
Adult females: reception of male and mating; cohabitation with male; brood-sac construction and egg deposition; brooding eggs and young

Activities

Sensory: visual evaluation of prey or environs; orientation of prosoma for view with anterior medial eyes; testing tension of dragline or balloon silk with legs [ballooning has not been observed in adult *Phidippus*]; search for water with first legs (new observation)
Locomotory: running or walking forward, backward, sideways; turning; jumping; ballooning; descending by release of silk dragline; climbing dragline with first two pairs of legs (very rapid)
Handling silk: (the spinnerets are quite agile) formation of attachment disk; release and positioning of silk in construction; dragline release; opening and closing sac entrances
Grooming: wiping appendages against substrate [surface]; grooming legs and pedipalps with chelicerae; cleaning eyes with pedipalps
Predatory: following and stalking prey; jumping and grasping prey; injecting venom and feeding
Other activities: threat behavior (raising prosoma and first legs in jerking thrusts) directed toward other spiders and insects; evasive activity and hiding; drinking water from tarsal hairs and substrate [surface]; pedipalp vibration; holding opisthosoma high in air either to dry or to avoid a wet surface; vibration of resting-sac of mate with first legs

In a recent series of papers M. F. Land (1969a, 1969b, 1971, 1972a, 1972b) dealt with the nature of salticid vision. The large tubular anterior medial eyes (AME) are moved by six pairs of singly innervated oculomotor muscles. Land described four patterns of activity involving the translation (lateral displacement) and rotation of these eyes: spontaneous activity, saccades (centering), tracking (following an object), and scanning. The scanning, Land suggests, is linked to evaluation of the line contours of a stationary stimulus; his interpretation of the nature of the perception involved, as the differentiation between a potential mate and potential prey, is without doubt simplistic.

Land (1971) also studied the peripheral vision afforded by the lateral eyes. When a moving object enters the field of vision of the lateral eyes, the salticid turns and orients the prosoma to allow evaluation by the AME. The opisthosoma does not move until the AME have begun this evaluation (Lahue 1973) [not always true, the opisthosoma (*telsoma*) can be moved freely during a facing turn]. Land demonstrated that the spiders do not need to follow an object with their eyes in order to orient, and in addition (Land 1972b) suggested that the lateral eye receiving the stimulus has control over the number of turning steps involved.

In general, learning phenomena in spiders have been ignored. Lahue (1973) reviews the literature in this area, and more specifically mentions habituation to visual stimuli observed in *Salticus*. Leguelte (1969) dealt with the short-term memory of orb-weavers in regard to web orientation, without any outstanding results.

Still, there is a great deal of evidence for learning in spiders. *Phidippus* in petri dishes come to associate the opening of the dishes with the introduction of food, and will jump on dead flies in response to this stimulus [This interpretation may be incorrect and this behavior may represent a response of these spiders to movement of the dead flies]. *Phidippus* dwelling in an open field venture out from their resting sacs in pursuit of prey on sunny days, an somehow manage to return in the evening. Some recognition of local plants and terrain seems necessary.

In summary, each activity of the jumping spider involves a complex interplay between internal states (or programs) and the external environment as mediated by the senses. In considering the integration of information and response required for a single activity, such as jumping, one may appreciate the functional significance of the extreme fusion of neuromeres in the spider CNS. In order to jump, the spider must first evaluate the nature and distance of the target accurately (not necessarily prey), secure an attachment disk with the spinnerets, form and hold a running line [dragline], and raise the internal prosomal fluid pressure by means of a series of segmental muscles (Parry and Brown 1959, Wilson 1971).

At this time the pedipalps are moved up and down rhythmically. At the time of the jump, flexors of the hind legs must suddenly relax (simultaneously on both sides of the body), the valves holding the running line [dragline] must release to allow the flow of silk (Wilson 1969), and all of the appendages, including chelicerae, must prepare either to receive the new substrate [substratum], or to seize the prey in a suitable location. All of these events must occur simultaneously, within the span of a few seconds.

4. The araneid central nervous system: historical review

Saint Remy (1890) began the study of the spider CNS with his description of the *brain* of representatives of a series of labidognath families. He noted the great variability in development of visual centers, and provided excellent drawings, but was greatly limited by a lack of specific nerve stains.

Hanstrom (1921, 1935) continued the study of the spider *brain*, applying the Golgi technique to this task. In spite of the limited scale of his studies in this area, his works are the basis of most of our current knowledge of the spider syncerebrum. Hanstrom accepted the homology of structures of the spider brain with similar structures found in crustaceans and insects (allowing for the loss of the deutocerebrum in chelicerates) [We now know that the deutocerebrum has been neither reduced nor lost in chelicerates (see Telford and Thomas 1998)]. This may have been ill-advised, particularly if the arthropods form a polyphyletic group as suggested by Anderson (1973). This apparent homology of spiders and insects persists in current literature (Babu 1965, Bullock and Horridge 1965, Firstman 1954, Legendre 1959).

Hanstrom (1935) also presented a simplified outline of four basic categories of araneid brain, classified according to differential [differences in the] development of the visual centers: attid (salticid), sparassid, argiopid, and agelenid types. Meier later (1967) pointed out the flaws of this over-simplified scheme, as well as its lack of phylogenetic significance.

More recently, a number of separate workers have provided substantial accounts of the araneid CNS. The work of Legendre (1959) is a most valuable synthesis of available information, including a study of the development of *Tegenaria* and *Dolomedes*. Legendre reviews many earlier concepts, particularly in regard to the segmentation of the anterior region. Babu (1965) deals with a series of arachnids, and more specifically the theraphosid *Poecilotheria*, in an attempt to trace the major fiber tracts in reduced silver preparations. Meier (1967) provides and accurate though limited study of the araneid CNS, including a valuable, and critical, discussion.

Several inferior [less useful] studies of the spider brain (Satija and Grewal 1970, Satija, Sharma, and Dhir 1969, Satija and Sohal 1962) are also available.

Gabe (1964), Kuhne (1959), and Babu (1973) describe neurosecretory cells as well as a retrocerebral neuroendocrine complex linked to the CNS. This work is based solely on histochemical evidence, essentially as afforded by paraldehyde-fuchsin staining.

A number of excellent reviews are available. Millot (1949) provides the best existing account of araneid biology, although information on the CNS is limited. Bullock and Horridge (1965) recount earlier information, and provide a useful bibliography. Legendre (1965) gives a comprehensive account of recent literature dealing with the morphology and development of spiders. A complete list of work published prior to 1939 is available in Bonnet (1945-1962).

5. Materials and methods

The capture and rearing of Phidippus

Crane (1948) outlined the most useful techniques for locating salticid spiders- visual search, and shaking vegetation over a ground cloth. The grass-sweep net serves as a useful modification of the latter technique for the capture of *Phidippus rimator* [*clarus*].

P. rimator [*clarus*] is an inhabitant of many open, undisturbed, and well-drained fields in the vicinity of Corvallis, Oregon. The distinctive males mature in early July, while the females mature two weeks later in the subsequent instar [may not be true, instar was not determined for animals in the field]. During the mating period in July the spiders are easily located in resting-sacs at the top of field plants. Snetsinger (1955) gives a good account of the life history of *P. rimator* [*clarus*], as well as *P. audax* which, at least in a temporal sense (both mature in early spring) replaces *P. johnsoni* in the eastern United States.

P. johnsoni is more difficult to locate in this area, as these spiders generally live on or near the ground. Most individuals were secured by visual search in areas where rock or concrete provided suitable refuge; this species is much less able to cope with water [exposure to rain?] than is *P. rimator* [*clarus*]. *P. johnsoni*, unlike *P. rimator* [*clarus*], makes use of the crevices afforded by human habitation. Mature males appear by early May, and brooding begins in June. After a single mating, the females may rear a succession of broods during the summer.

Both species mated readily in captivity; emerging broods were separated into individual 100mm plastic petri dishes at the second instar and were fed vestigial winged fruit flies (*Drosophila melanogaster*) at least twice a week. A small piece of household sponge was placed in each of the dishes to provide drinking water; as noted by Crane (1948), such water is essential to salticids in captivity. Much of the mortality associated with the molting of jumping spiders (Horner and Starks 1972) could probably be avoided by careful maintenance of the water supply. In addition, one must never disturb spiders either in the process of molting, or in preparation for a molt. Dishes should be cleaned or replaced by a clean dish several times a month (more often for larger spiders). With careful attention to this procedure, it should be possible to rear fully four-fifths of the second instars to maturity.

With regular feeding, molting occurs at three to four week intervals for spiders reared at room temperature. *P. johnsoni* mature in the eighth-ninth instars, while *P. rimator* [*clarus*] will mature as early as the fifth-sixth instars in captivity. There is some indication, but no conclusive proof, that early maturation is the result of a long photoperiod, although diet and temperature may be contributing factors. An excellent discussion of variation in the number of molts required to attain maturity in spiders is available in Levy (1970).

Gardner (1967) and Bailey (1968) give additional information on the life cycle of *Phidippus*. In as much as Russell (1970) reports the painful lesions and swelling which accompany the bite of *P. johnsoni*, one might exercise some caution in the handling of these spiders. In most situations, however, they have no cause or tendency to bite humans.

Techniques

Prior to all operations, the spiders were anesthetized with CO_2 gas released from sublimating dry ice. Opisthosoma, legs, pedipalps, and chelicerae were detached from the prosoma immediately before its immersion in the fixative.

For topographical studies, spiders of various ages were fixed in Bouin-Dubosq (alcoholic Bouin's) fixative (Humason 1972) for at least 24 hours, followed by a wash and storage in 70% ethanol. Dioxane dehydration was followed by *Paraplast*® (Sherwood Medical Industries, Inc.) embedding. The staining of 10µm sections followed Gurr's (1956) modifications of the Masson Trichrome stain as given in Humason (1972), with the use of Harris' hematoxylin and the substitution of Orange G for *Ponceau de Xylidine*.

For reduced silver impregnation, the Holmes' reduced silver method as modified by Blest (1961) and outlined by Weiss (1972) was utilized. The procedure, outlined in some detail in Appendix 2, involves fixation with Bodian's Fixative No. 2 and a terpineol dehydration.

A modification of the Golgi-Kopsch method given by Colonnier (1964) was employed. Each prosoma was embedded in soft *Epon*® according to procedures given by Luft (1961), and sectioned at 80µm, with a sharp steel knife set in an ordinary desk microtome. The details of this procedure are given in Appendix 3.

Several groups of second instar spiders were fixed in 2% glutaraldehyde and 1% osmium tetroxide after Eakin and Brandenburger (1971). The prosomata were embedded in either *Araldite*$_{TM}$ or *Epon*$_{TM}$ following procedures given by Dawes (1971) and Luft (1961). The details of fixation and embedding are in Appendix 4. The prosomata were subsequently sectioned at 0.5-5.0mm with the *Porter-Blum Ultramicrotome*$_{TM}$ and stained with toluidine blue according to Humason (1972).

All serial sections were essentially either frontal (perpendicular to the sternum and parallel to the face), horizontal (roughly parallel to both the sternum and the optic quadrangle at the top of the prosoma), or parasagittal. A few oblique sections were used.

Paraplast® sections were arranged on subbed slides (Boyd 1955) treated with Mayer's Albumen Fixative according to Humason (1972). The details are given in Appendix 2.

All sections were mounted under cover glass with *Permount* ® (Fisher Scientific Co.).

Drawings were prepared with the assistance of a *Wild* ® *camera lucida*.

Discussion of techniques employed

The excessive hardening of cuticle was avoided by use of dioxane and terpineol as substitutes for ethanol dehydration. Nonetheless a certain degree of separation of cuticle is inevitable. The appendages are removed to facilitate penetration by fixatives and embedding media.

As noted by Humason (1972), this Masson Trichrome stain allows excellent control at all stages. It gives excellent and aesthetic definition of most tissue, and connective tissue in particular, with intense nuclear staining, although it cannot stain nerve fibers.

The reduced silver technique outlined by Weiss (1972) yields excellent results with Phidippus, although there is some variation in the quality of individual preparation. Pearson (1971) rightfully noted the virtual impossibility of tracing the ramifications of an individual nerve by means of such non-selective silver methods for serial sections. One should remain skeptical of conclusions based solely upon serial tracing of the fiber tracts revealed with this technique. Still, the reduced silver techniques are indispensable for their ability to reveal nervous structures in their entirety.

The enigmatically selective Golgi techniques are [among] the best means in a study of individual neurons within the central nervous system, as they are capable of revealing the entirety of a neuron in three-dimensional space. The combination of Golgi and non-selective silver stains is very useful in a structural study of this sort. The selective nature of Golgi impregnation is a great advantage, but it is also the greatest disadvantage of the method. One must rely greatly upon chance for the most definitive results, and neurons are often incompletely stained.

The shrinkage associated with conventional fixation and embedding can be avoided by glutaraldehyde-osmium tetroxide fixation and epoxy embedding, but the small size of tissue blocks required by this technique is a distinct disadvantage. In addition, the staining methods available for paraffin sections cannot be applied to plastic sections.

5. General aspects of CNS structure

Gross anatomy

This study has not revealed any significant differences in the structure of the central nervous system of the two species of *Phidippus*.

As shown in Figures 6-8 the central nervous system of *Phidippus*, like that of other spiders, consists of a highly fused mass of nervous tissue, derived from a series of segmental ganglia, and situated in the prosoma around a rigid esophageal tube leading to the sucking stomach (Figure 10). The somata of unipolar neurons forming this mass are situated in the peripheral cortex, distinct from the central fiber mass (Figures 9 and 12). These somata are found in greatest numbers at the bottom of the subesophageal ganglia, in front of the nervous mass, and above the supraesophageal portion of the CNS.

The inner fiber portion and outer cortex of the nervous mass are separated and collectively enclosed by a single layer of flattened cells comprising the neurilemma. This thin neurilemma is typical of labidognaths (Saint Remy 1890, Legendre 1959), whereas a much thicker multi-layered neurilemma capsule is found in orthognath spiders (Babu 1965, Legendre 1961). The neurilemma surrounds nerves leading from the CNS, and forms the lining of a series of dorso-ventral *blood vessels* penetrating the subesophageal CNS in a sagittal plane. Tracheoles leading from the spiracle anterior to the spinnerets also pass through the CNS in these blood vessels (Figure 10).

In front of the CNS is situated a curious group of loosely attached binucleate nephrocytes and small endocrine cells (Figure 10), which Legendre (1959) termed the *anterior organ*. These cells allegedly combine endocrine and excretory functions (Legendre 1971).

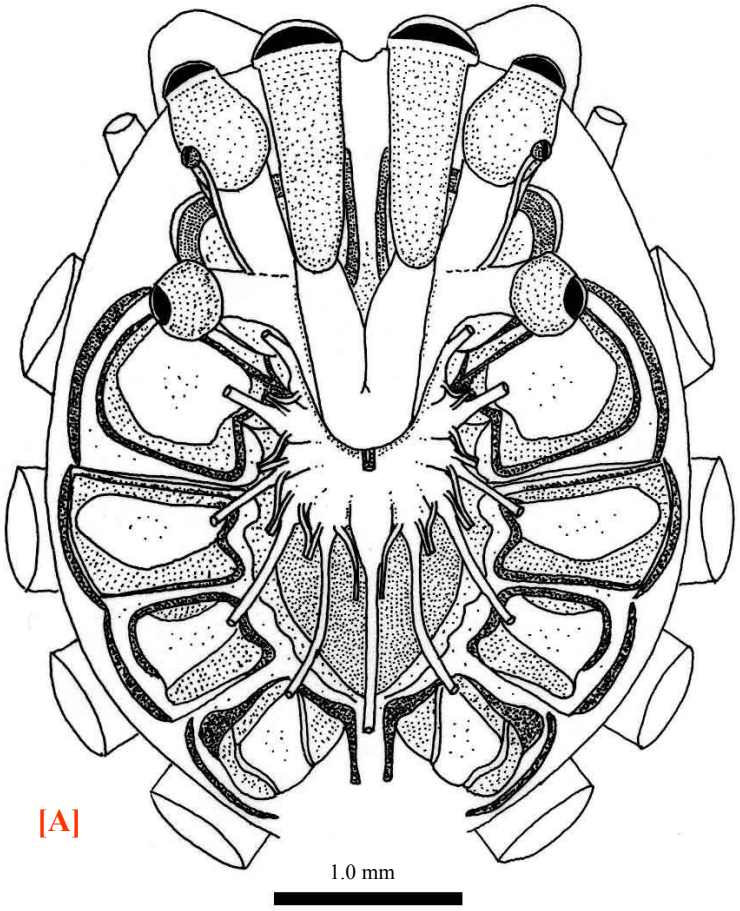
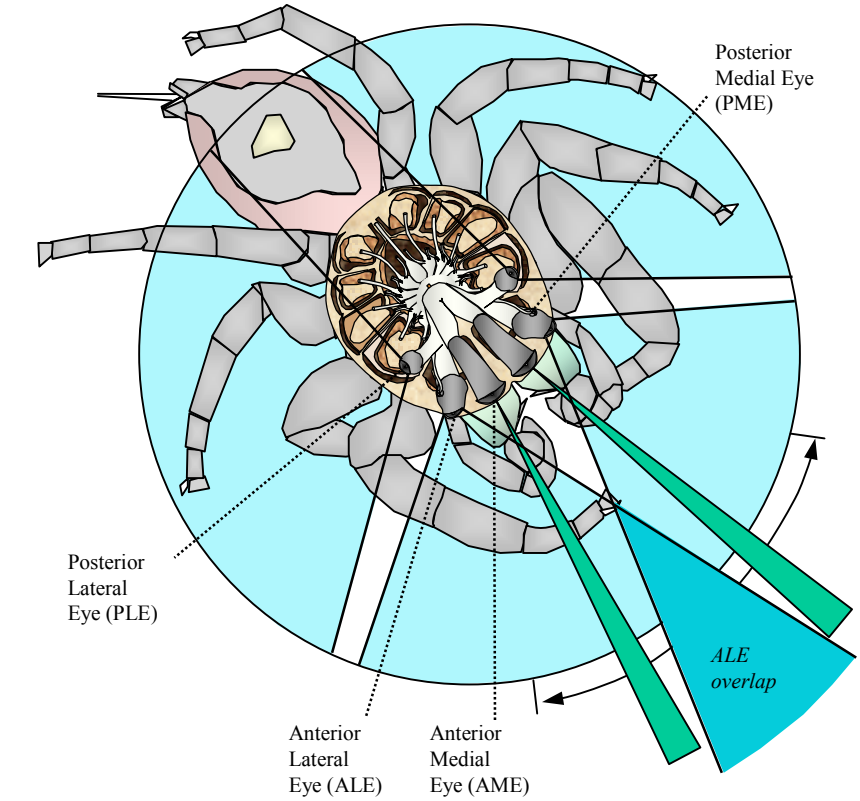


Figure 6. [A] Dorsal view of the central nervous system in the prosoma of adult female *Phidippus rimator* [*clarus*], based upon photographs of dissection [and evaluation of serial sections]. In the adult, the subesophageal ganglia lie above midgut diverticula of the anterior sternum. The supraesophageal portion is characterized by the large and separate optic nerves. For interpretation of structures, refer to figures 7 and 8.



[Figure 6. [B] (from Hill 2006) Diagram of the approximate visual fields of *Phidippus* as viewed from above, showing the eyes and their respective optic nerves connected to the prosomal CNS. The posterior lateral (PLE) and anterior lateral eyes (ALE) provide the spider with a 360-degree survey of its surroundings. Field of vision of the ALE overlap in front of the spider. Each anterior medial eye (AME) consists of a long tube that can be moved independently to scan the area in front of the spider with high resolution. The function of the small posterior medial eyes (PME) is not known.]

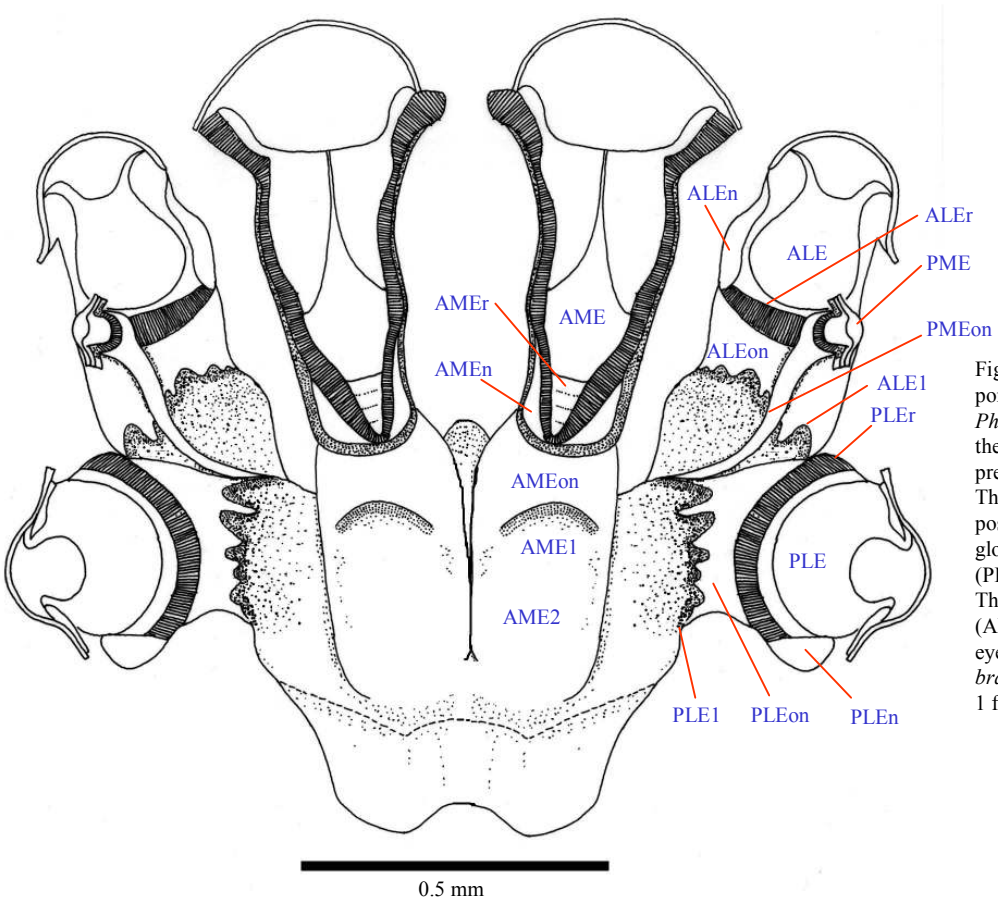


Figure 7. Dorsal view of supraesophageal portion of the CNS of a fifth instar *Phidippus rimator* [*clarus*]. Sections of the eight eyes are shown. The predominance of visual input is obvious. The optic nerves (PMEon) of the small posterior medial eyes (PME) run to glomeruli near the primary neuropile (PLE1) of the posterior lateral eyes (PLE). The primary (AME1) and secondary (AME2) neuropiles of the anterior medial eyes (AME) are situated at the top of the *brain* or syncerebrum. Refer to Appendix 1 for interpretation of other symbols.

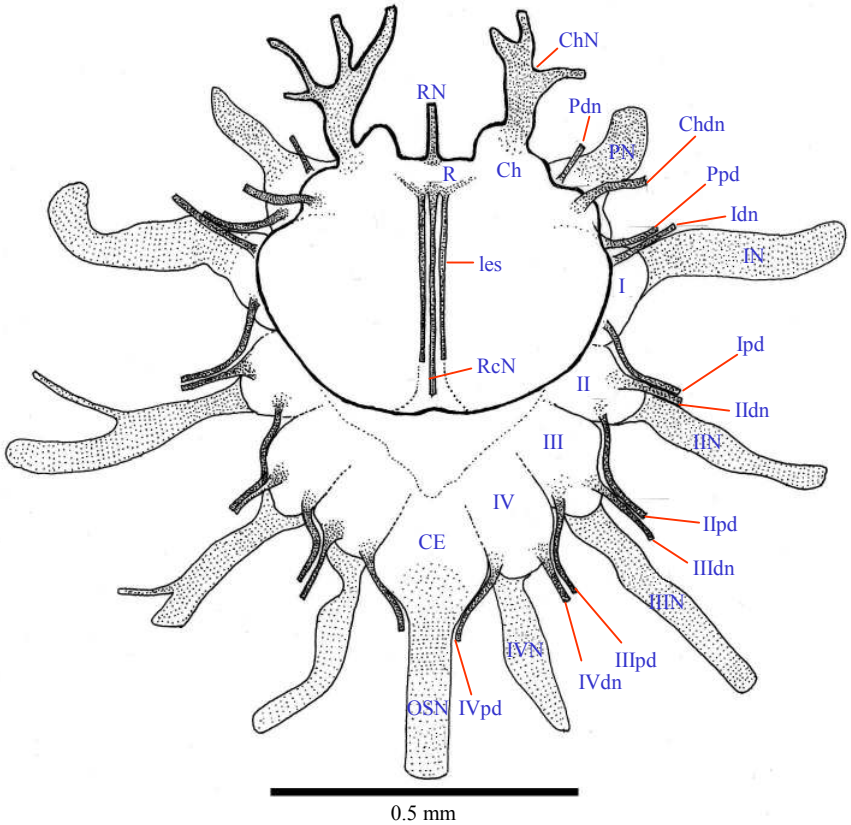


Figure 8. Dorsal view of the subesophageal portion of the CNS of a fifth instar *Phidippus rimator* [*clarus*], including the supraesophageal cheliceral and rostral ganglia. The major nerves are shown. Each of the leg ganglia sends forth a small dorsal (dn) and a small postero-dorsal (pd) nerve; the latter joins the dorsal nerve of the ganglion immediately to the rear. The opisthosomal ganglia are fused to form the *cauda equina* (CE). The segmental opisthosomal nerves depart the CNS as a composite opisthosomal nerve (OSN). For interpretation of other features, refer to Appendix 1.

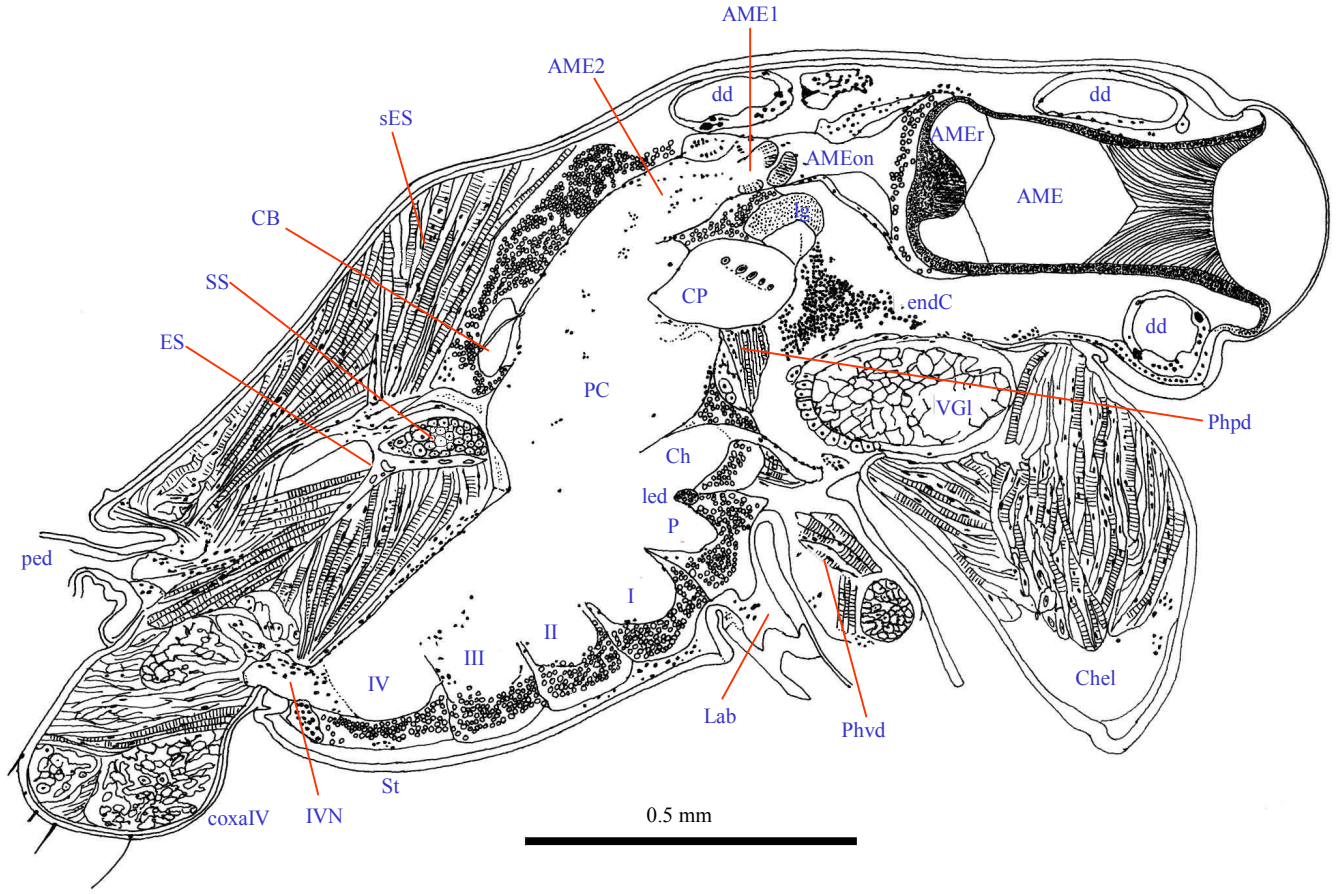


Figure 9. Parasagittal section of prosoma, fifth instar *Phidippus rimator* [*clarus*]. *Camera lucida* drawing of preparation stained with Masson's Trichrome. The neuropile and tracts of the CNS are isolated from the cortex of cell bodies by neurilemma. The lateral esophageal dilator (led) separates the chelicerae (Ch) and pedipalpal (P) ganglia. For interpretation of other features, refer to Appendix 1.

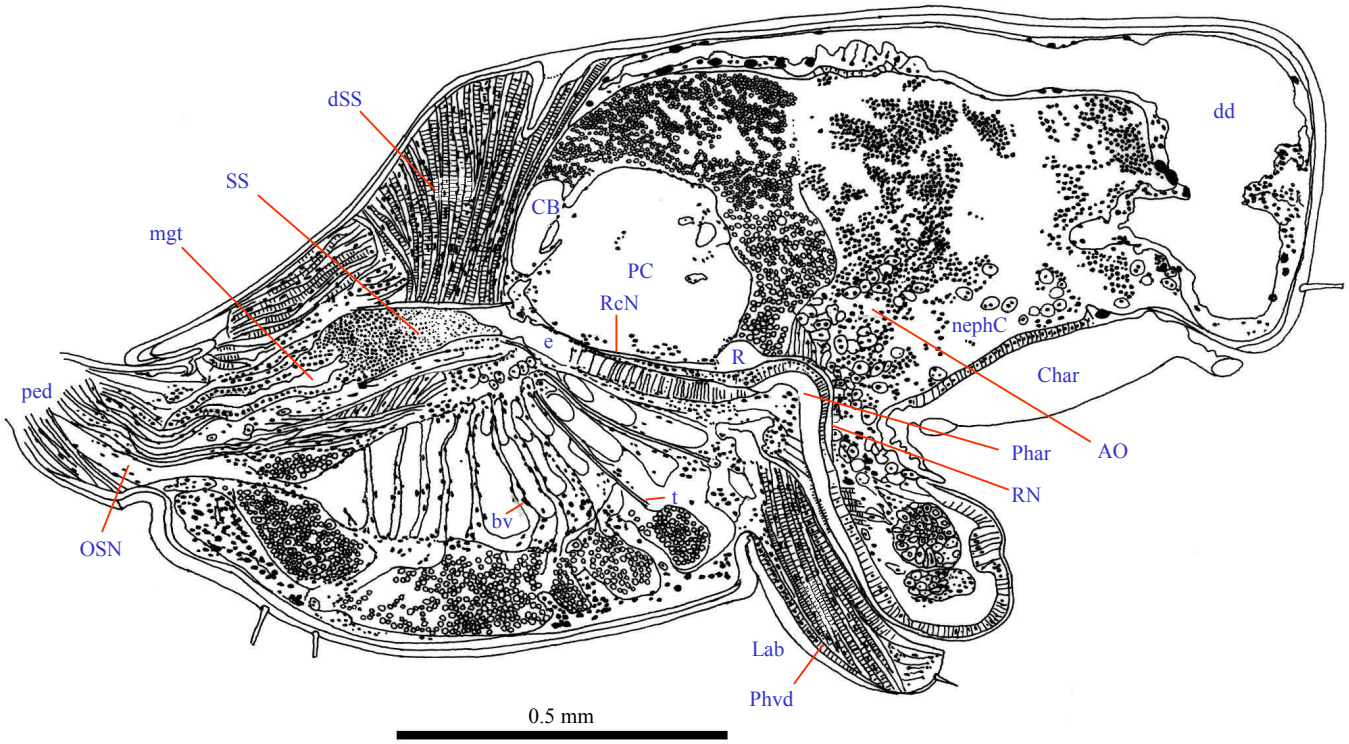


Figure 10. Sagittal section of prosoma, fifth instar *Phidippus rimator* [*clarus*]. The subesophageal ganglion complex is penetrated by tracheae (t) and a series of blood vessels (bv) lined with neurilemma. The small rostral ganglion (R) lies directly above the anterior esophagus, sending the recurrent nerve (RcN) to the rear above the rigid esophageal tube, and the rostral nerve (RN) anteriorly. Anterior to the CNS lies an unusual mass of binucleate nephrocytes (nephC) and small endocrine cells that has been termed the anterior organ (AO) by Legendre (1959). For interpretation of other structures, refer to Appendix 1.

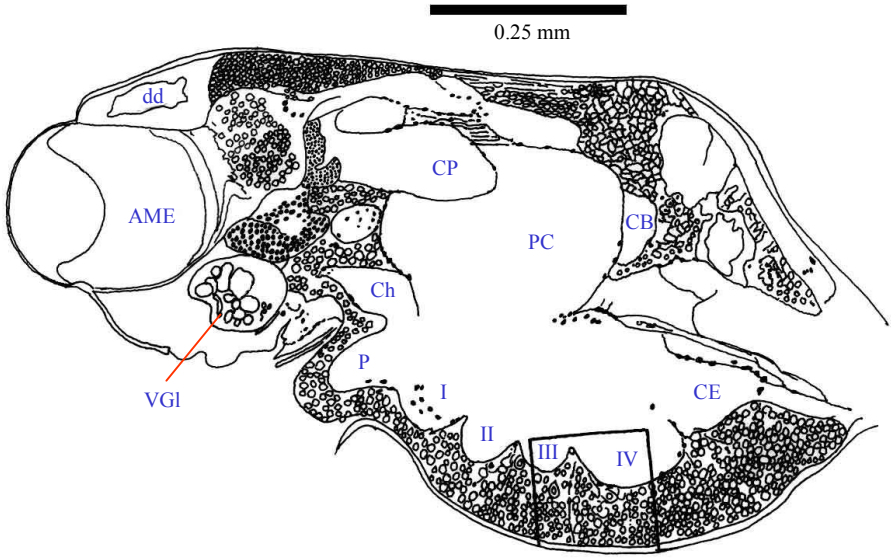


Figure 11. Parasagittal section through the prosoma of a second instar *Phidippus rimator* [*clarus*]. The central nervous system occupies virtually the whole of the central [medial] prosoma at this stage, flanked laterally by musculature. For interpretation of symbols, see Appendix 1.

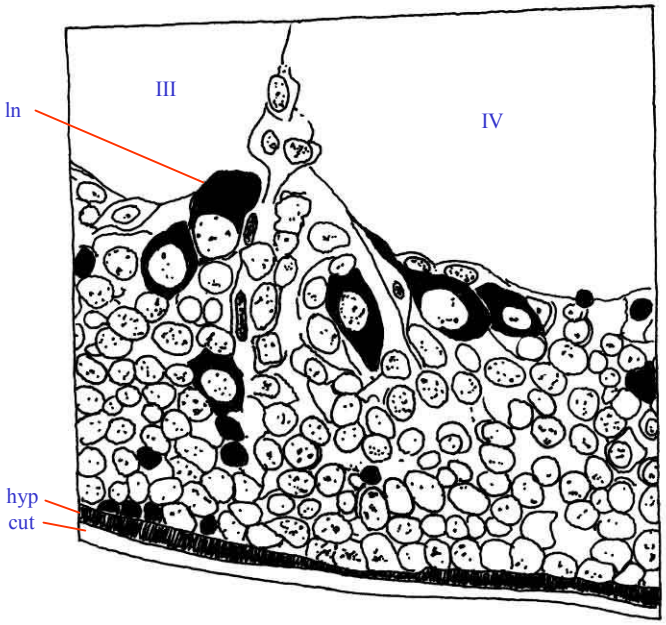


Figure 12. Enlargement of portion of neuronal cortex indicated above [inset in Figure 11]. A group of large neurons (ln) at the junction of two leg ganglia is shown. The nuclei of smaller neurons and neuroglia are [also] shown.

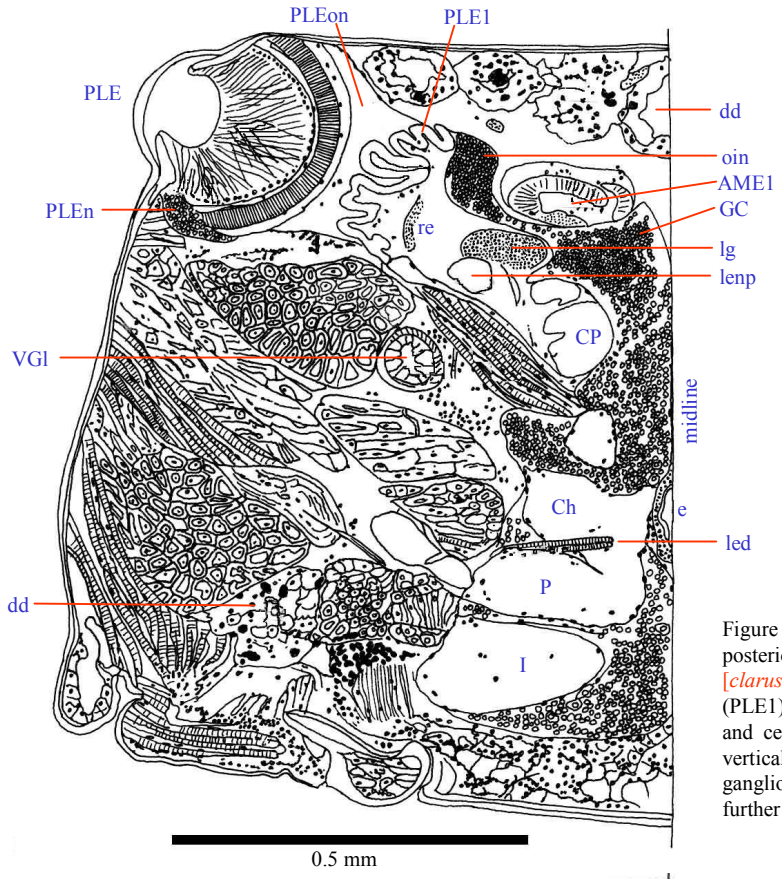


Figure 13. Half-frontal section of prosoma through the posterior lateral eye (PLE) of a fifth instar *Phidippus rimator* [*clarus*]. The relationship of the primary neuropile of this eye (PLE1) to the lateral eye neuropile (lenp), *lame glomerulee* (lg), and cell bodies of optic interneurons (oin) is evident. The vertical relationship of the first leg ganglion (I), pedipalpal ganglion (P), and cheliceral ganglion (Ch) is also shown. For further interpretation, see Appendix 1.

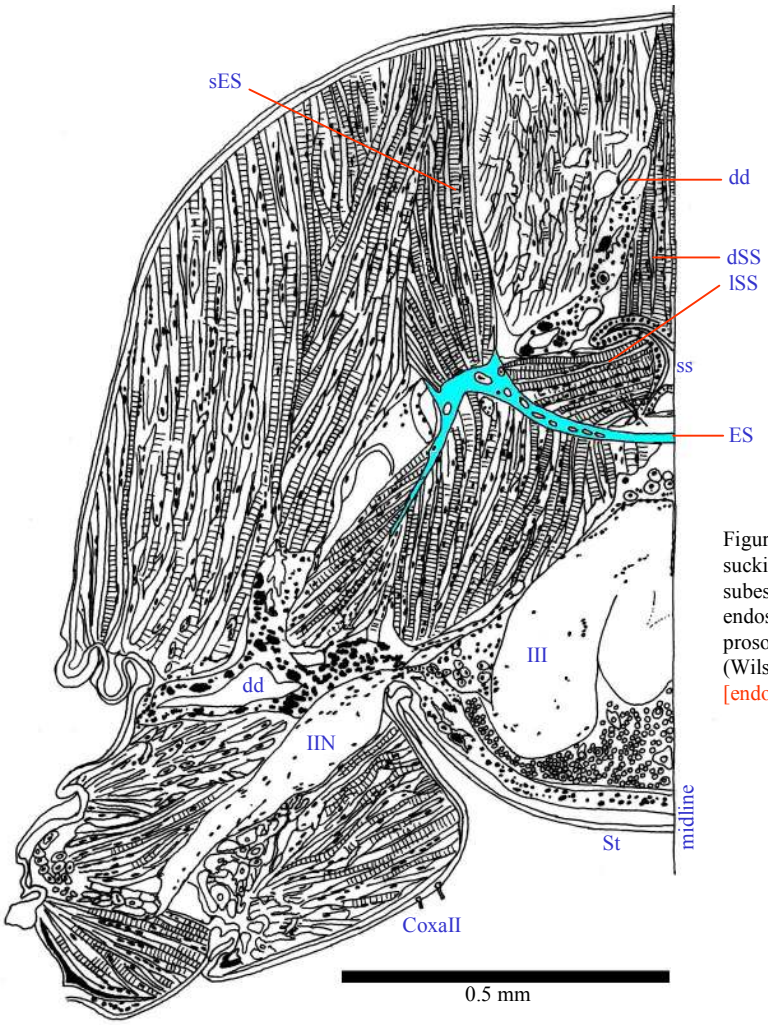


Figure 14. Half-frontal section of prosoma through the sucking stomach (SS) of a sixth instar *Phidippus johnsoni*. The subesophageal ganglia lie between the sternum [St] and the endosternite (ES). The extensive striated musculature of the prosoma is characteristic of salticids [and other spiders] (Wilson 1970). For further interpretation, refer to Appendix 1. [endosternite is highlighted in blue]

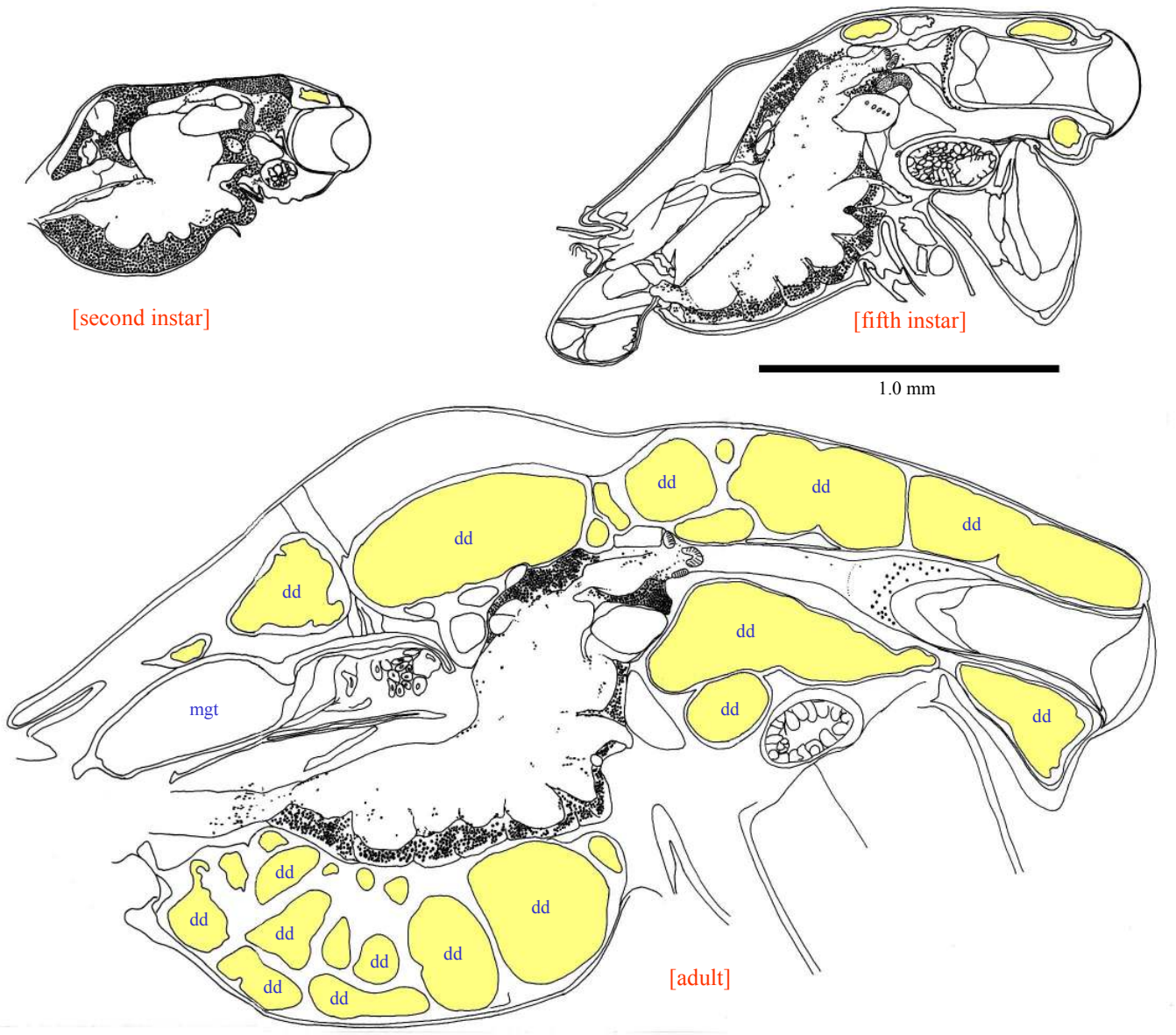


Figure 15. Comparative extent of the CNS in the prosoma of second instar, fifth instar, and adult *Phidippus rimator* [*clarus*]. Parasagittal sections. The CNS of the adult is small is comparison to body size. The adult prosoma is filled with digestive diverticula (dd) of the midgut which form a spongy layer separating the CNS from the sternum. For interpretation of other structures, see Figure 9. [Digestive diverticula are highlighted in yellow]

Figures 16-26. Half-horizontal sections through the prosoma of a sixth instar *Phidippus johnsoni*. This series of drawings illustrates the basic features of the gross anatomy and situation of the CNS at various levels. Beside the figure caption, a number in parentheses indicates the section number in a series of 10 µm sections, from top to bottom. Musculature in the plane of the section is shown with dotted lines, while predominantly dorso-ventral muscle bundles are indicated by cross-hatching. Digestive diverticula (dd) are shown at various levels. Nuclei of the neuronal cortex are encircled. For interpretation of symbols, refer to Appendix 1. All scales are 0.5 mm.

0.5 mm

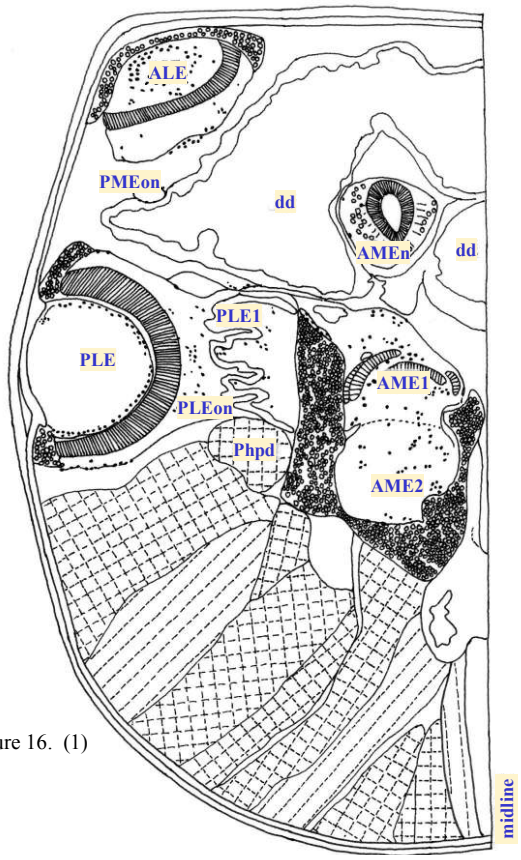


Figure 16. (1)

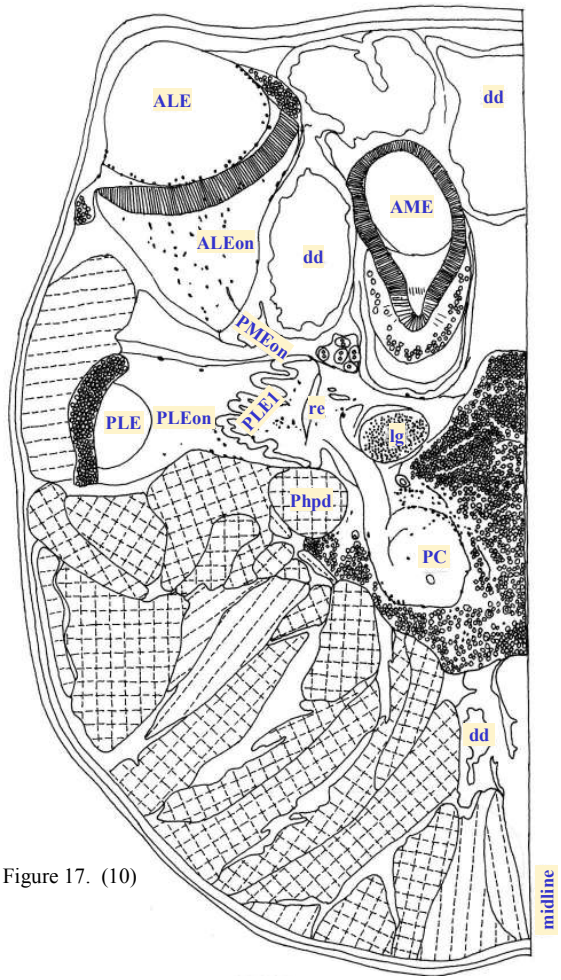


Figure 17. (10)

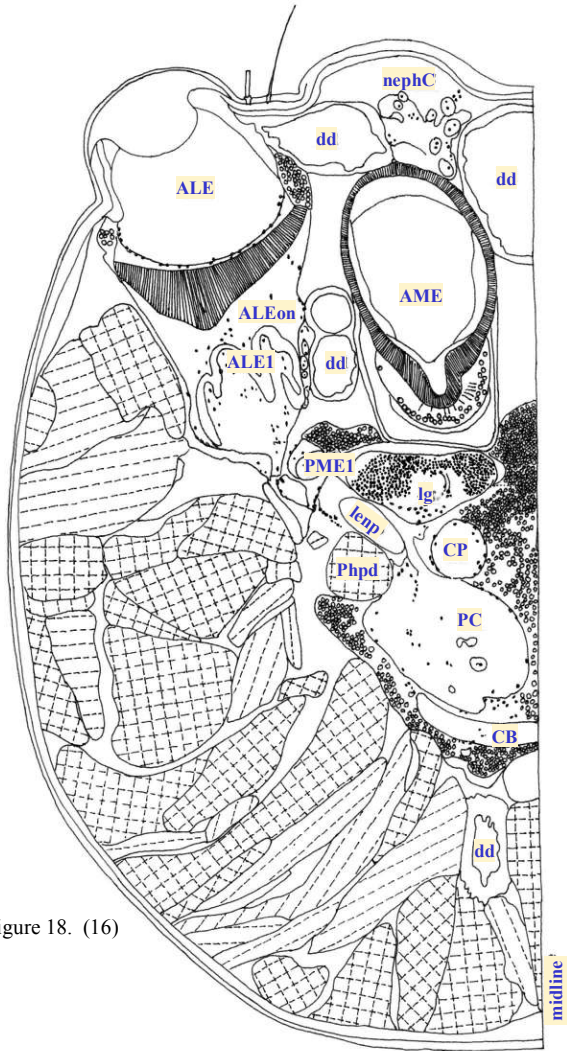


Figure 18. (16)

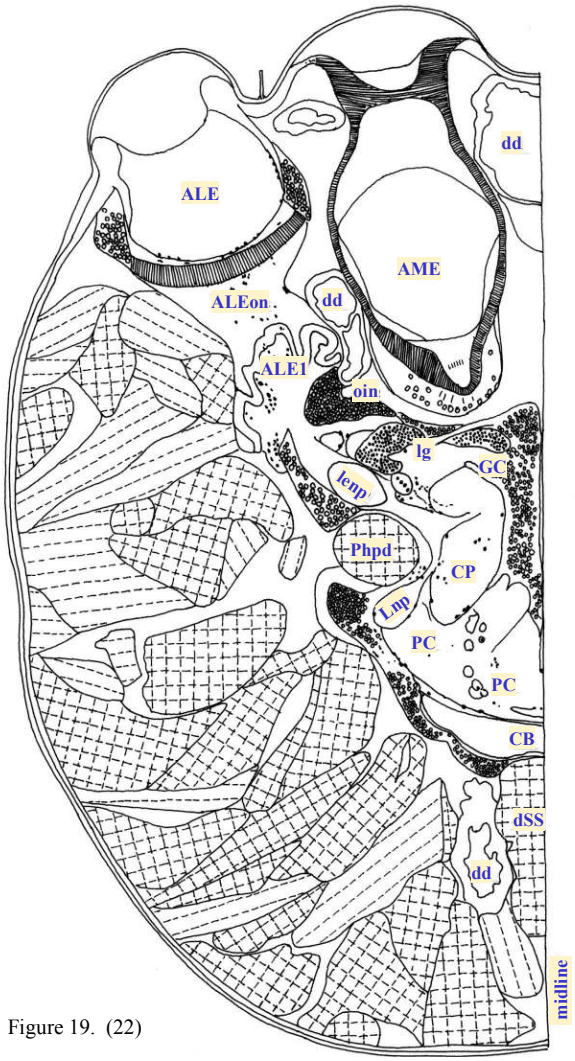


Figure 19. (22)

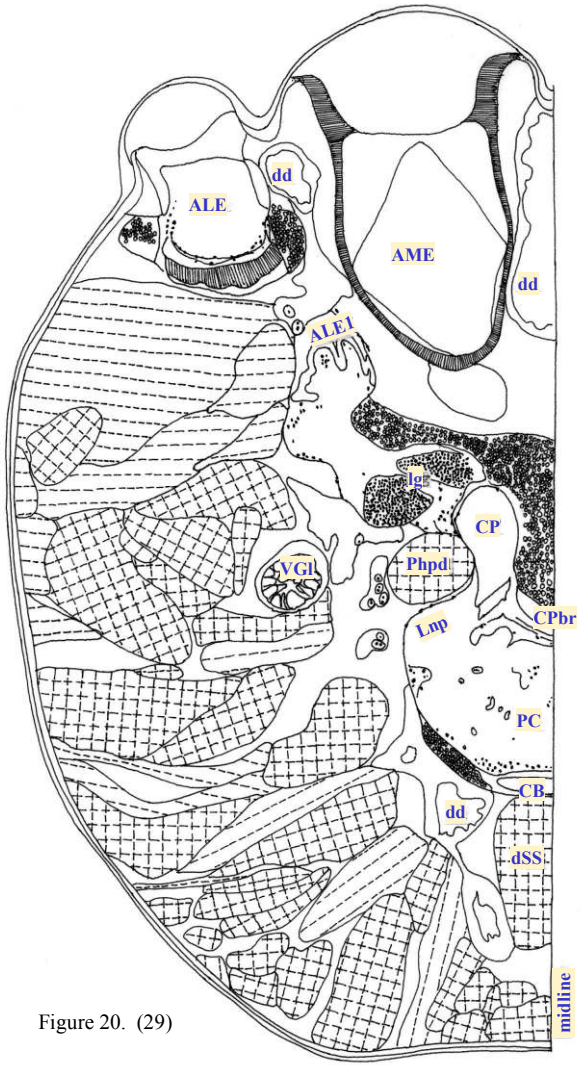


Figure 20. (29)

0.5 mm

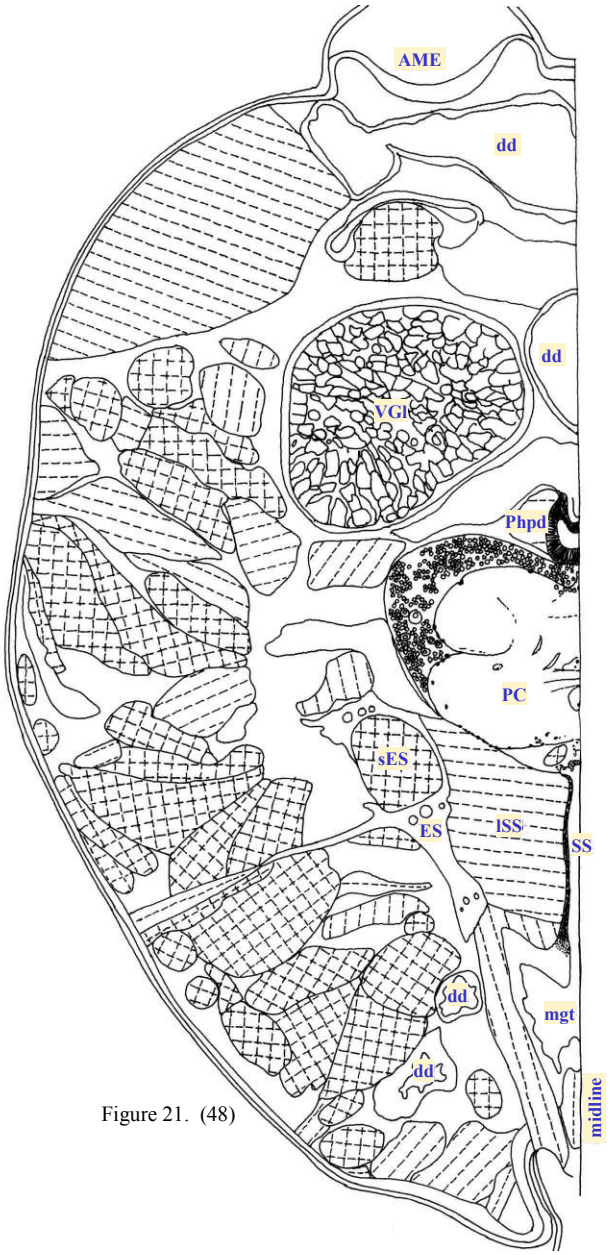


Figure 21. (48)

Figure 22. (61)

0.5 mm

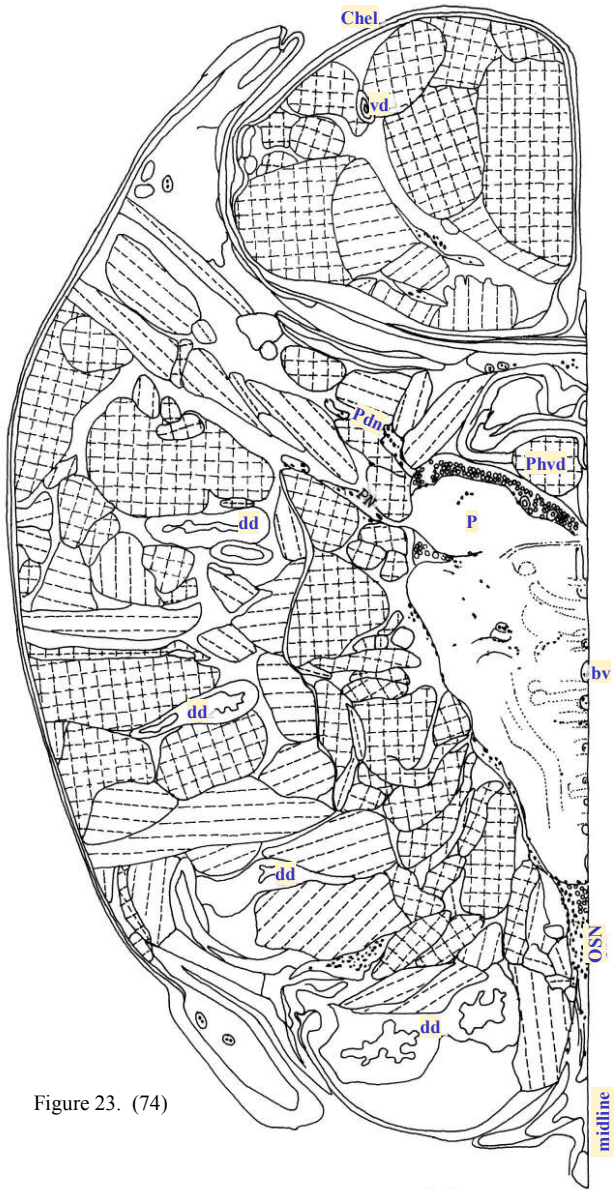


Figure 23. (74)

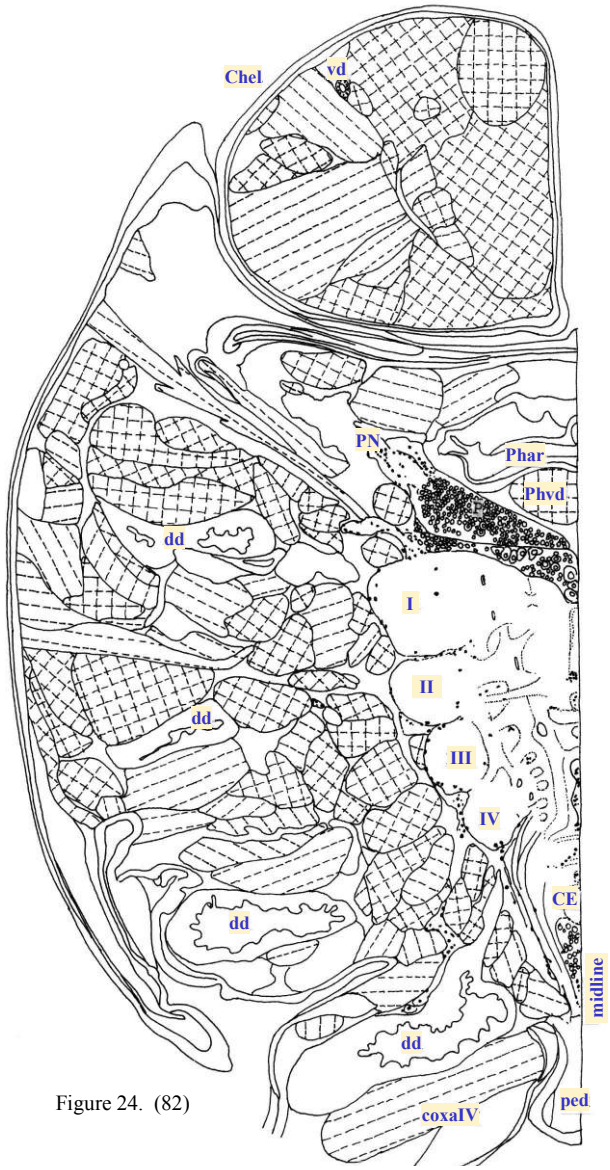


Figure 24. (82)

0.5 mm

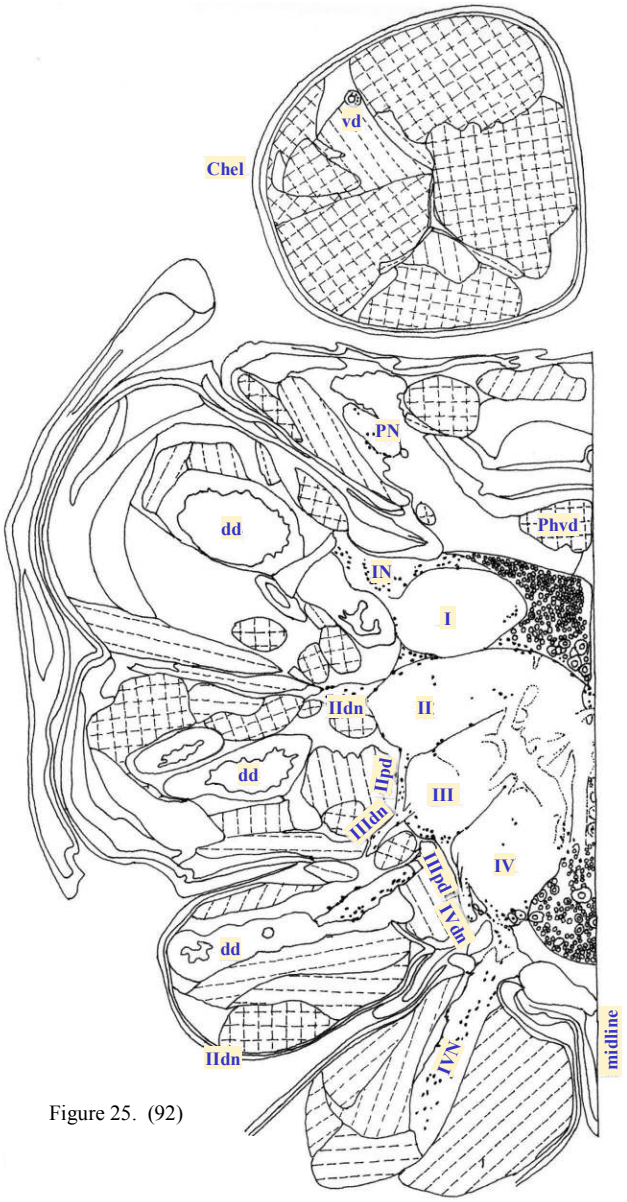


Figure 25. (92)

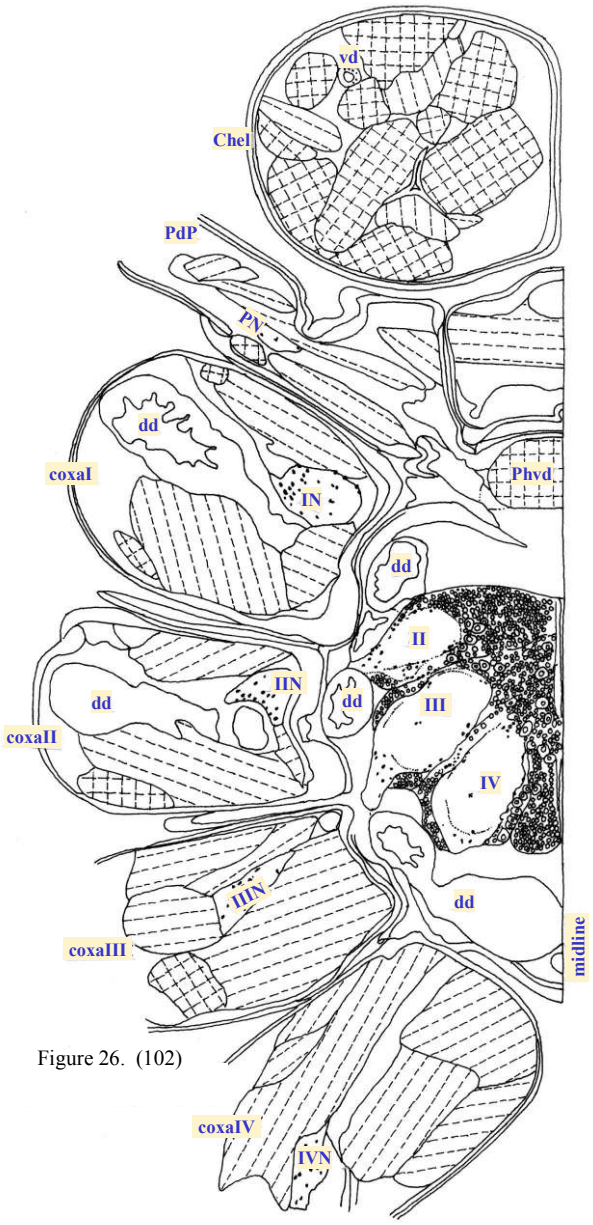


Figure 26. (102)

0.5 mm

Following Legendre (1959), the supraesophageal portion of the nervous mass is termed the syncerebrum, a complex structure formed by the fusion of a series of neuromeres (Table 2).

Table 2. Neuromeres contributing to the syncerebrum (supraesophageal portion of the CNS)

1	acronal element (archcerebrum or central body)
2	centers of principal eyes
3	centers of lateral eyes
4	neuromere of cerebral ganglion (protocerebrum)
5	rostral neuromeres (rostral ganglion)
6	cheliceral neuromeres

Meier (1967) noted the difficulty of defining individual ganglia within the central fiber mass, just as Legendre earlier (1959) described this as a region of neuropile common to all ganglia.

The protocerebrum is a major integrating center (Meier 1967) of interneurons, sending no fibers out of the CNS (according to Legendre 1959). Fibers originating in all of the ganglia communicate in this complex region of tracts and *neuropile*, the latter a term which Meier (1967) considers useful only for lack of better definition.

The chelicerae and their ganglia move to a preoral position in late embryonic development, while retaining their original subesophageal commissures (according to Rempel 1957, see also Figure 47).

The subesophageal mass is tightly fused to the supraesophageal mass around the esophagus. It consists of a single pair of pedipalpal ganglia, four pairs of ganglia associated with the walking legs, and series of at least seven pairs (Legendre 1959) of fused ganglia forming the *cauda equina*, giving rise to the opisthosomal nerves. The commissures of these ganglia are metamerically arranged between the blood vessels (Millot 1949, see also Figure 47). As in the supraesophageal mass, the central tract region is common to all ganglia and lacks simple definition. The migration of opisthosomal ganglia into the prosoma, characteristic of araneids, is completed in the late embryo (Rempel 1957), by the end of inversion (Legendre 1959).

The major nerves associated with the CNS are shown in Figures 6-8. Legendre (1959) termed the dorsal pedipalpal nerve a sensory nerve. Parry (1960) traced the dorsal nerve of the leg ganglia (small leg nerve, apparently *dn*, figure 8) to mechanoreceptors. The most striking and distinctive external aspect of the salticid CNS is the large size and separation of the optic nerves.

Legendre (1959) described a series of *axillary ganglia* associated with the branching of the principal leg nerves. A mass of neuroglia-like elements was observed in this location, but no nervous fibers were impregnated.

The gross anatomy of the CNS of *Phidippus* is summarized in a series of drawings (Figures 6-26). The terminology applied to musculature follows Whitehead and Rempel (1959).

Cells of the CNS

Neuroglial elements are associated with the neuron somata, but are generally lacking in the neuropile and tract region.

The neuron types (Table 3) are categorized according to nuclear size and nucleo-cytoplasmic ratio. This classification agrees with similar schemes proposed by Legendre (1959) and Babu (1965), although Babu described much larger neurons in the large theraphosid Poecilotheria. The classification serves to emphasize the great disparity in size of neurons associated with different structures in the CNS. According to Legendre (1959), the largest neurons are the last to be elaborated from neuroblasts.

Table 3. Neuron types

(from adult female *Phidippus rimator*) (*clarus*)

type	location in CNS	nuclear diameter	nucleo-cytoplasmic ratio
small	optic neurons of primary lateral eye neuropile	4-5µm	much greater than 1
small	globuli cells of pedunculate body	4-5µm	much greater than 1
small	underlying central body	5-6µm	greater than 1
medium	periphery of protocerebrum	7-8µm	near 1
medium	underlying leg ganglia	7-8µm	near 1
large	underlying leg ganglia	10µm	less than 1
giant	in groups under leg ganglia	15µm	much less than 1

There is some controversy in regard to the nature of the large *neurosecretory* cells revealed by histochemistry (Gabe 1954, Kuhne 1959, Legendre 1959, 1971). As noted by Meier (1967), there is no demonstration of function or correlation of activity with life functions for these cells. Meier suggests that these cells are either motor neurons, or that they possess a dual function. In addition, he notes that their major processes appear to terminate in the vicinity of adjacent blood vessels, and that there is no evidence for a direct connection between these cells and the *retrocerebral neuroendocrine complex* or the *organs of Schneider*.

Agreeing with the lack of such a connection, Serna de Esteban (1973) ascribes a purely endocrine function to the first Schneider's organ, and an autonomous nervous function to the second.

Nonetheless Babu (1973), using paraldehyde fuchsin, described an unusual set of *neurosecretory* tracts and commissures associated with neurohemal organs in *Argiope aurantia*, a system linked to metameric groups of *neurosecretory* cells in the subesophageal ganglia. Since this unusual finding is not substantiated by other workers, and relies upon uncertain histochemistry, its validity is questionable.

Post-embryonic growth

In the second instar (Figure 11), the central nervous system is essentially complete. The neuromeres are fused in the prosoma, and, according to Legendre (1959), there is no further elaboration of neurons from neuroblasts. In its proportions the CNS at this stage is large as compared to that of the adult. In further maturation, the CNS will only double its linear dimensions. The space afforded by the much greater increase in prosomal volume is occupied by midgut diverticula, which in time separate the sternum and the CNS considerably (Figure 15).

Peters (1969) demonstrated that the coordinated ability to produce webs in *Zygiella x-notata* (Cl.) develops during the brooding of second instars. Similarly in *Phidippus*, the second instars may remain in the brood-sac for several weeks, retaining the gregarious behavior characteristic of the first instars. When they finally emerge, the second instar jumping spiders are fully capable of spinning shelters and capturing prey, just as orb weavers of this age produce miniature webs of perfect construction.

With age, the nymphs [immature spiders] acquire an increasing number of trichobothria [presence of trichobothria has not been determined] and hair sensilla. This most likely corresponds to a continued elaboration and ramification of sensory neurites during the post-embryonic period. In addition, individual fibers of the anterior medial eyes double their diameter (from 0.8 to 1.5 μm) between the fifth instar and adult [stages].

Other structures of the CNS also increase in size with age. The individual glomeruli of the *lame glomerulee* (see section 6) are only about 3 μm in diameter in the second instar. By the fifth instar they are 4 μm in diameter, while in the adult they are 5 μm in diameter.

6. The visual centers

The extraordinary development of vision, particularly in regard to the anterior medial eyes, is the great distinction of jumping spiders. Indeed, Land (1972a) suggests that the Salticidae possess the best optical resolution of all invertebrates, excepting the cephalopod mollusks. Thus the jumping spider is the master of the visual world among terrestrial invertebrates- a considerable distinction for such a small animal.

The optic nerves are almost as large in diameter as the eyes themselves (Figure 7). Notably among spiders, each optic nerve is distinct in its entire pathway from eye to syncerebrum.

In salticids, the optic centers dealing with this visual information (including the *corpora pedunculata*) attain their greatest elaboration. Visual information is indispensable to these spiders in the recognition and capture of prey, in courtship, and in daily movement (see Land 1969a).

Centers of the anterior medial eyes

The anterior medial eyes (AME) are direct eyes [bearing bipolar sensory neurons] in spiders, whereas the lateral eyes (including posterior medial eyes) are indirect [unipolar sensory neurons] (Figure 41). The movement and use of these eyes is [was] described in section 3. Eakin and Brandenburger (1971) provide an excellent study of the ultrastructure of these eyes, as well as the lateral eyes. Homann (1971) gives a very comprehensive review of eye structure in spiders, with some emphasis on the uniqueness of the salticid AME. Land (1969a, 1969b) provides an excellent study of AME structure and function.

The rhabdoms of the AME are arranged in four layers within a narrow crescent-shaped retina. The innermost layer contains the smallest receptors. While bipolar sensory neurons send these light-sensitive rhabdoms anteriorly, they send the optic nerves to the rear.

The fibers of the optic nerve are of two sizes, the larger almost twice the diameter of the smaller. All optic nerve fibers synapse in the primary neuropile of the AME, a curiously shaped composite structure (Figures 27, 29) consisting of a large outer lobe and a small, essentially parallel [concentric], inner lobe. Land (1969a) furnished a highly schematic view of this structure, which he described as two horseshoe-shaped glomerular strips.

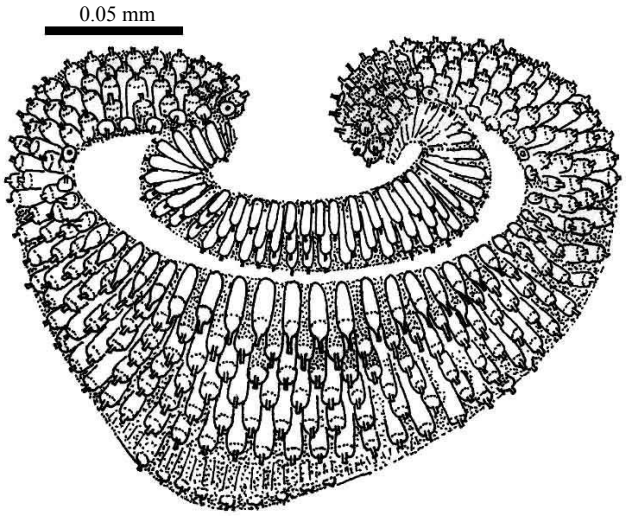


Figure 27. Diagrammatic antero-dorsal view of the primary neuropile of the left anterior medial eye of *Phidippus*. The columns of the large lobe receive large optic nerve fibers, while small optic nerve fibers run to both the inner lobe and the lower portion of the outer lobe. The columns of the inner lobe are of smaller diameter than are those of the outer structure.

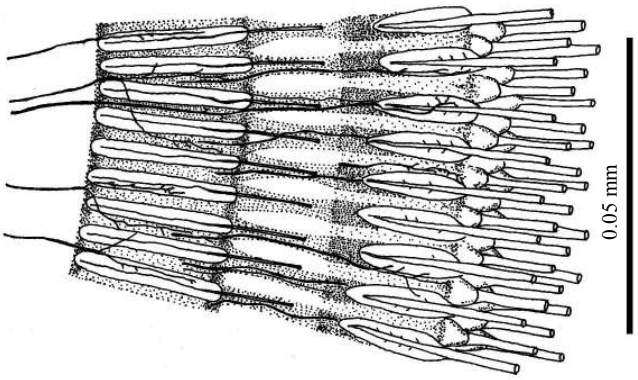


Figure 28. Enlarged portion of primary neuropile of the anterior median eye in dorsal view. The correspondence of inner (left) and outer (right) columns is apparent. A number of interneurons running to the secondary neuropile appear to synapse in both inner and outer lobes of the primary neuropile (diagrammatic).

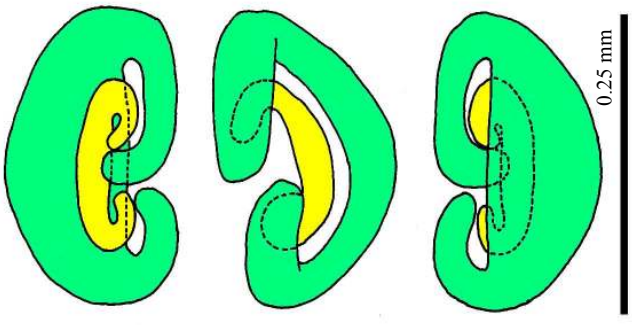


Figure 29. Posterior, dorsal, and anterior views from left to right of the primary neuropile of the left anterior medial eye. The inner and outer lobes are roughly parallel [concentric] structures.

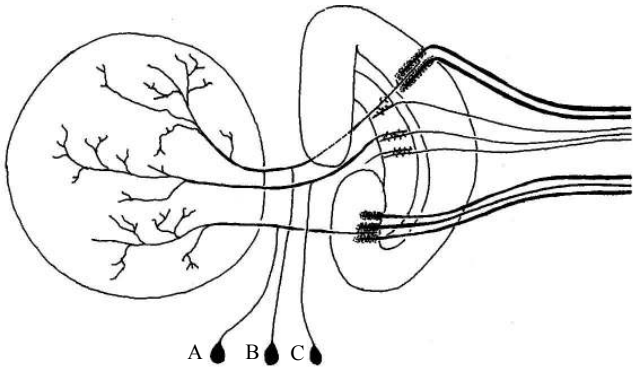


Figure 30. Three interneuron types connecting the primary and secondary neuropiles of the anterior medial eyes. The cell bodies are located in the adjoining ganglionic cortex. (A) connects the large columns with the secondary neuropile at the left. (B) forms synapses in both lobes of the primary neuropile, and (C) synapses only in the inner lobe. [schematic diagram of hypothetical arrangement]

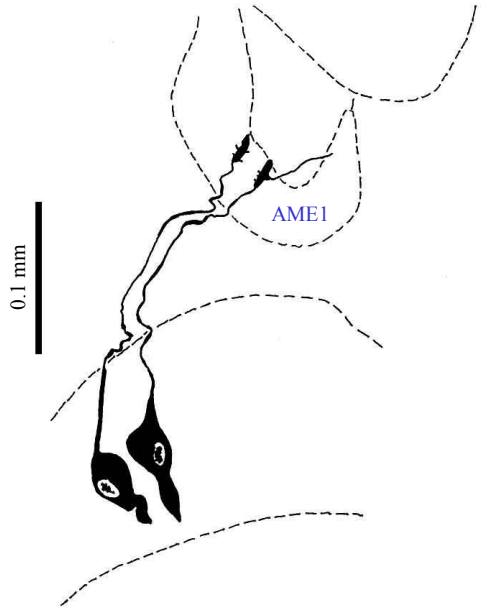


Figure 31. Golgi-Kopsch impregnation of two neurons of the left anterior medial eye, showing the correspondence of columnar synaptic regions in the primary neuropile (AME1). Sixth instar *P. johnsoni*. [camera lucida drawing]

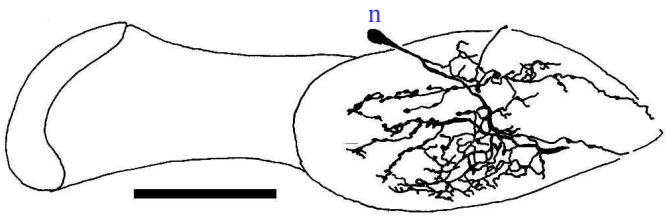


Figure 32. Golgi-Kopsch impregnation of an individual intrinsic interneuron of the secondary neuropile of the anterior medial eye. The peripheral cell body (n) is connected to an elaborate network of synaptic ramifications. [camera lucida drawing]

The larger optic nerve fibers synapse in the upper portions of the outer lobe, forming large columns where a dense network of interneuron ramifications surrounds each of the primary fibers [Figure 28]. The columns are packed in a hexagonal array. The position of the large fibers in the optic nerve corresponds to this portion of the primary neuropile, and there can be little doubt that the geometry of this structured neuropile is of great significance. Perhaps, as suggested by Land (1969a), it corresponds to the origin of the fibers in the four rhabdom layers of the AME (see Figure 31).

Small optic nerve fibers synapse in the inner lobe and the lower portions of the outer lobe, forming smaller columns. There is some correspondence between columns of the two lobes (Figure 28), and some interneurons appear to ramify and synapse in both structures (Figure 30).

Curiously, each synaptic locus of first-order interneurons with optic nerve fibers involves two post-synaptic fibers with the *large irregular bouton* of the pre-synaptic fiber ([according to] Eakin and Brandenburger 1971, also observed in the Lycosa lateral eye neuropile by Trujillo-Cenoz and Malamed 1964, 1967). Figure 30 is largely conjecture based upon sections stained by the reduced silver technique. Further definition of interneurons will require a successful Golgi study. These interneuron somata are peripheral to the tract connecting primary and secondary AME neuropiles.

The secondary neuropile of the AME receives first-order interneurons in communication with higher order interneurons. Certain intrinsic neurons (Figure 32) ramify greatly within this complex or unstructured neuropile. This neuropile forms a large mass, at the top of the syncerebrum, in close communication with the protocerebrum.

The functional significance of this arrangement is difficult to evaluate without further information about the individual interneurons involved.

The correlation of specific receptors in the eye with particular columns of the primary neuropile would probably reveal a significant pattern.

Centers of the lateral eyes

Land (1969a) noted the importance of peripheral vision afforded by the anterior and posterior lateral eyes (ALE and PLE) to the jumping spider, essentially in the accurate detection and location of movement. Land also suggested (1971, 1972b) that these eyes are the mediators of prosomal orientation to such stimuli, although flight, negative orientation [turning away], or AME activity may also result from visual stimuli received by the lateral eyes.

The primary neuropile receiving optic nerve fibers of the ALE (ALE1) is separate from that of the PLE (PLE1). Each of these structured neuropiles forms a highly convoluted surface (Figure 33), which is comparable in structure in different individuals of the same species (Figure 34). The PLE1 of *Phidippus rimator* [*clarus*] is also like that shown for *Phidippus johnsoni*, a further indication of the relatedness of these spiders.

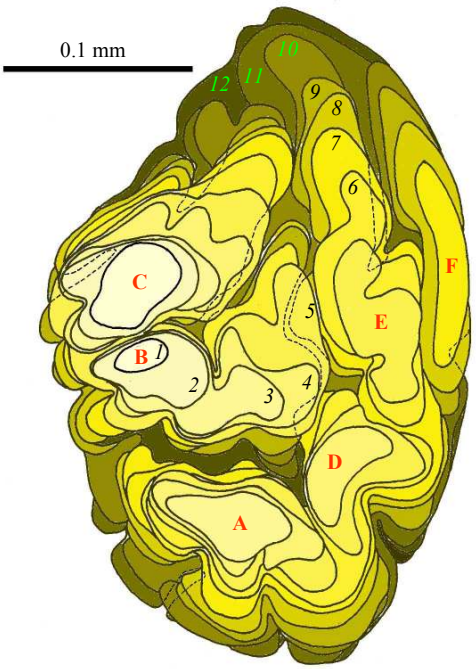


Figure 33. Contour diagram of the primary neuropile of the right posterior lateral eye, sixth instar *P. johnsoni*. The dorsum is to the right. The anterior end is at the bottom. Contours are numbered in a medial direction. The contour interval is 10 µm. Distinctive lobes of the convoluted surface are labeled (A-F).

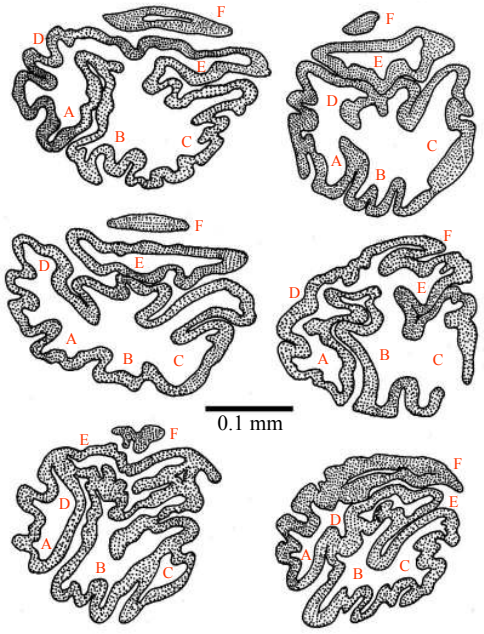


Figure 34. Comparable parasagittal sections through the primary neuropile of the posterior lateral eye of six *P. johnsoni*. Lobes are labeled as in Figure 33. Left is anterior. The top is dorsal. The stippled region is the primary neuropile. The enclosed spaces (A-F) contain interneuron fibers

The two types of first-order interneurons synapsing in this primary neuropile are shown in Figure 35. The interneurons forming synaptic trees send fibers along the lateral optic tract to the previously unreported *lateral eye neuropile* (lenp, Figure 41) and the protocerebrum. A second type of interneuron forms compact synaptic nodes in the primary neuropile, which it connects with the glomeruli of the lame glomerulee. Both first-order interneurons branch and synapse at two different sites in the primary neuropile (Figure 35), a good indication that they respond to a change in illumination, or movement. This contradicts Hanstrom's (1921) concept of a one-to-one correspondence between pre- and post-synaptic fibers of this primary neuropile. As illustrated in Figure 41, the first-order interneuron fibers divide almost equally into the lateral eye tract and a second tract of fibers destined for the *lame glomerulee*.

[Duelli (1980) studied the primary neuropile or *first optic ganglion* (FOG) in *Evarcha arcuata*. He also called the *lame glomerulee* the *second optic ganglion* (SOG).

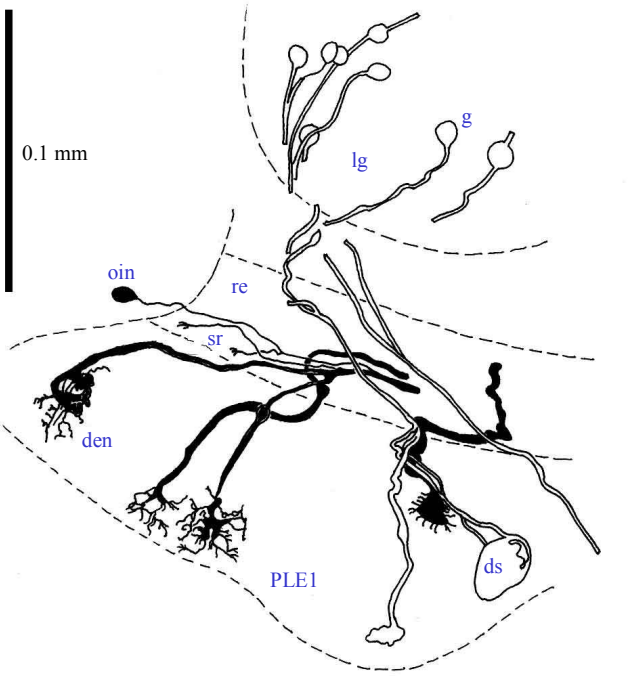


Figure 35. Golgi-Kopsch impregnation of interneurons involved in the primary neuropile (PLE1) of the left posterior lateral eye of a sixth instar Phidippus johnsoni. A zone of ramification of primary interneurons is outlined (re). Glomeruli (g) [compact synapses] of the *lame glomerulee* (lg) are joined to dense synaptic regions (ds) of the primary neuropile. Fibers of the lateral eye tract form dendritic structures (den) in the primary neuropile. A peripheral cell body (oin) is linked to dendritic synapses (den) as well as to small ramifications (sr) in the ramification zone. The two-fold branching characteristic of both types of interneurons is evident. [camera lucida drawing]

Each of the interneurons that he observed between the primary neuropile and the *lame glomerulee* connected a single glomerulus (synaptic region) in the former to a single glomerulus in the latter. He did not observe any of the branching that is described here, with respect to interneurons that terminate in the *lame glomerulee*. However, he did observe *large field* neurons with horizontal branching across the synapses of the primary neuropile, and noted that these neurons bypassed the *lame glomerulee* (SOG) and passed near a *bottlebrush ganglion*, perhaps the same as the lateral eye ganglion described here. Duelli did not observe any of the *small ramifications* shown here (*sr*, Figure 34).

A division of interneurons originating with the *primary neuropile* (FOG) of the lateral eyes into two groups, those destined for the *lame glomerulee*, and those that move toward the *lateral eye neuropile*, was described here for *Phidippus*. Very few, fragmentary examples of individual neurons are shown (Figure 35), and much larger samples are needed in future studies. It appears that the ramification zone (*re*, Figure 35) is the area where first order interneurons connect to their somata (*oin*). It is important to realize that, given the ancient lineage of these animals, we *should* find substantial differences between different genera of salticid spiders with respect to the detailed development of neurons, synapses, and neural centers.

There is still a possibility, as suggested by Duelli in an earlier paper (Duelli 1978) that either the disinhibitory off-pass filter or the inhibitory surround associated with light-to-dark stimulation of lateral eye receptors has a structural counterpart at the level of the primary neuropile. This remains to be determined.]

Hanstrom (1935) observed that the rods of this primary neuropile were most distinct in the Lycosidae, Thomisidae, and Salticidae, all groups with prominent *corpora pedunculata*. The coarser structure observed in the Araneidae agrees with the lack of corpora pedunculata in this family, as the distinct rods are compact terminals of fibers destined for the glomeruli (*lame glomerulee* [layer of compact glomerular synapses] of Saint Remy 1890) of this structure.

Many workers (Saint Remy 1890, Hanstrom 1921, Babu 1965, Meier 1967) have described a posterior commissure of fibers leading from the centers of the lateral eyes, directly in front of the central body. Hanstrom's (1921) Golgi work does not fully establish the real nature of this commissure. It is unusual that no workers have previously described the lateral eye neuropile (*lenp*, Figure 41) receiving fibers of the lateral eye tract (*let*). [It is likely that development of the *lenp* and *let* varies between salticid genera or subfamilies]

Centers of the posterior medial eyes

The posterior medial eyes (PME) of salticids are generally very small and hidden beneath the hairs [long setae] of the optic quadrangle [In live animals they have an unobstructed view in one direction, however]. In *Phidippus*, they are close to the ALE [closer than to the PLE]. Land (1972a) suggests that these eyes are vestigial. This is doubtful, if only for the reason that the PME are retained by all salticids in the course of evolution. Hanstrom (1921) could not locate the neuropile of the PME in the salticid *Marptusa* (now *Marpissa*).

Nonetheless a glomerular primary neuropile of the PME does exist in *Phidippus* between the primary neuropiles of the lateral eyes (Figure 41, *PME1*). This neuropile receives fibers from the primary neuropile of the PLE, in addition to those of the PME optic nerve.

A distinctive tract of large fibers, which appear to originate with a dorso-lateral group of protocerebral somata, synapses in the primary neuropile of the posterior medial eye. Fibers of this tract also synapse in a small neuropile (*x*, Figure 41) with interneuron fibers leading from the ALE1. Thus this tract, receiving most of its input from the posterior medial eyes, also handles a limited amount of information from the lateral eyes.

All of this suggests a special role for the diminuitive posterior medial eyes, which may be comparable to insect ocelli. These may be the mediators of photoperiod effects, or, more likely, they are diurnal activity regulators. For discussion of circadian rhythms in salticids, see Phanuel (1968).

The corpora pedunculata

The *corpora pedunculata*, or pedunculate bodies, are prominent features of the anterior salticid syncerebrum. They are essentially secondary [or higher-order] processing centers for information received from the primary lateral eye neuropiles (Figure 41). The only known sensory input to these structures involves the many first order interneurons connecting the primary lateral eye neuropiles to the *lame glomerulee* (so named by Saint Remy 1890), or glomerular layer of the *corpora pedunculata* (Figure 35 [36]). Fibers from the anterior and posterior lateral eyes synapse in separate portions of this glomerular layer.

Intrinsic fibers arise from a peripheral layer of neuron somata (the *globuli cells* of Hanstrom 1935) which is actually continuous with the layer of first order optic interneuron somata.

These give rise to fibers which synapse in the glomeruli of the lame glomerulee of the [at their] afferent terminal, and form longitudinal fibers with numerous small synaptic glomeruli in the neuropile of the *corpora pedunculata* (*mass medullaire inferieure* of Saint Remy 1890, see Figures 37, 38)

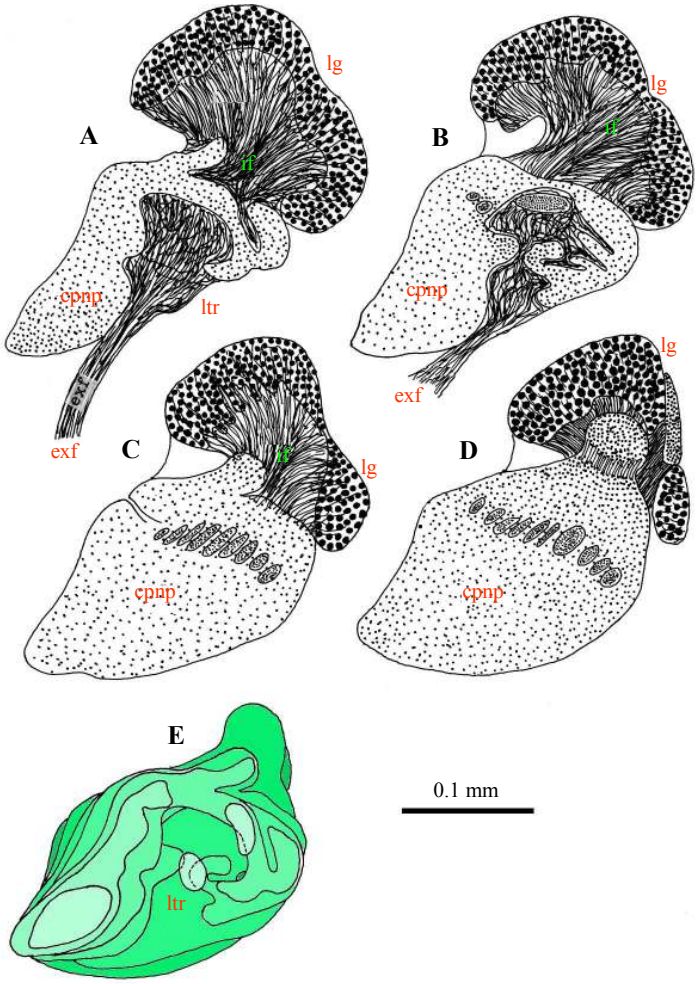


Figure 36. The pedunculate body of a sixth instar *Phidippus johnsoni*. A-D: Serial (10 µm) parasagittal sections toward the midline. E: Contour diagram (10 µm interval) of the same. Dorsum is at top, anterior is right. Extrinsic fibers (exf) enter the neuropile of the pedunculate body (cpnp) through the lateral tract region (ltr) of the latter. Intrinsic fibers (if) join the glomeruli of the *lame glomerulee* (lg) to this neuropile.

Thus the intrinsic fibers synapse with the extrinsic fibers (fibers of external origin) in the dense neuropile of the *corpora pedunculata*. The pedunculate bodies are closely connected to the lateral protocerebral neuropile (*Lnp*, Figures 39, 40), and both send fibers to the commissural bridge of the *corpora pedunculata*. The lateral tract region of the *corpora pedunculata* (Figure 36) contains fibers originating with the lateral eye neuropile (lenp), although the extent of communication between these structures is uncertain. A distinctive tract of large fibers originating with the *corpora pedunculata* and lateral protocerebral neuropile descends to form a longitudinal tract of the subesophageal mass (Figure 46).

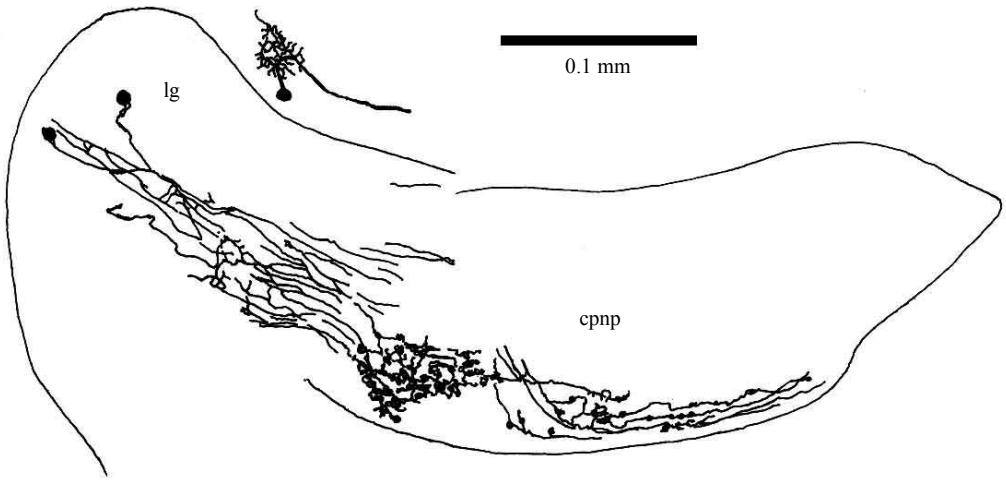


Figure 37. Golgi-Kopsch impregnation of intrinsic fibers of the right pedunculate body of *Phidippus johnsoni* (sixth instar). The intrinsic fibers form the glomeruli of the *lame glomerulee* (lg) anteriorly [left], and synapse with extrinsic fibers by means of small glomeruli of the neuropile of the pedunculate body (cpnp). Thus the intrinsic fibers are essentially second order [or higher order] interneurons of the lateral visual system.

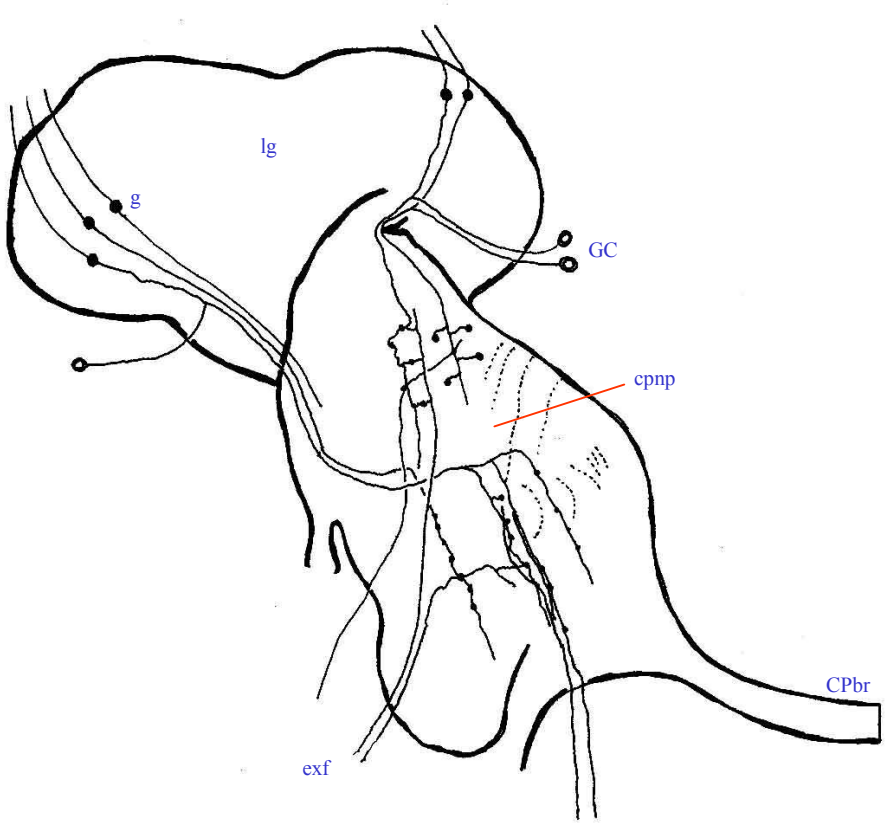


Figure 38. Diagram of a single stalk (pedunculate body) of the *corpora pedunculata* as viewed from below. Several intrinsic neurons are shown. Neurites originating with the peripheral *globuli cells* (GC) connect the glomeruli (g) of the *lame glomerulee* (glomerular layer, lg) with extrinsic fibers (exf) in the neuropile of the pedunculate body (cpnp). [Schematic based on examination of multiple Golgi preparations. See Appendix 1 for interpretation of symbols]

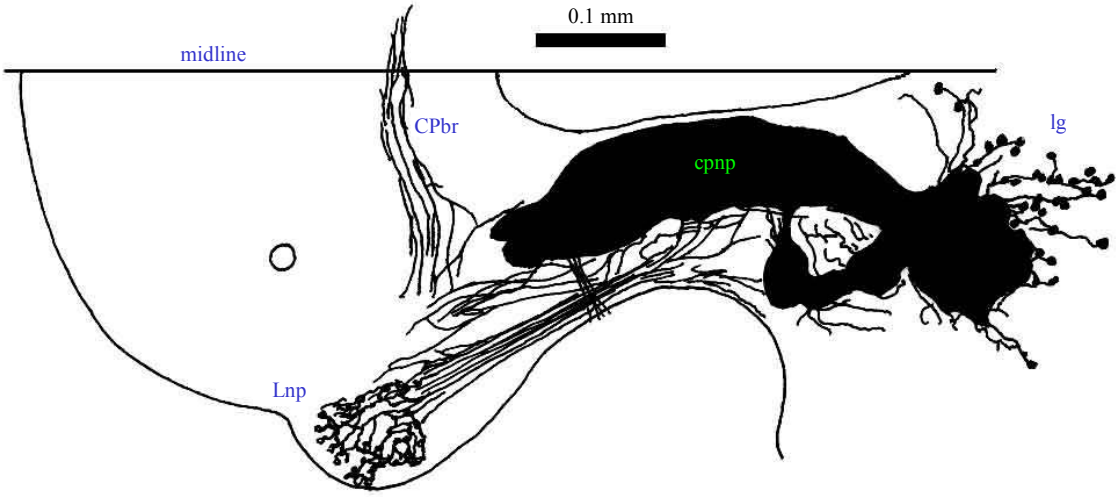


Figure 39. Golgi-Kopsch impregnation of the right pedunculate body of a sixth instar *Phidippus johnsoni*. The neuropile of the pedunculate body (cpnp) is heavily stained. The importance of the lateral protocerebral lobe (Lnp) in the processing of visual information is obvious [at least it is tied into the lateral eye processing area of the *corpora pedunculata*]. Several fibers of the bridge of the corpora pedunculata (CPbr) are shown.

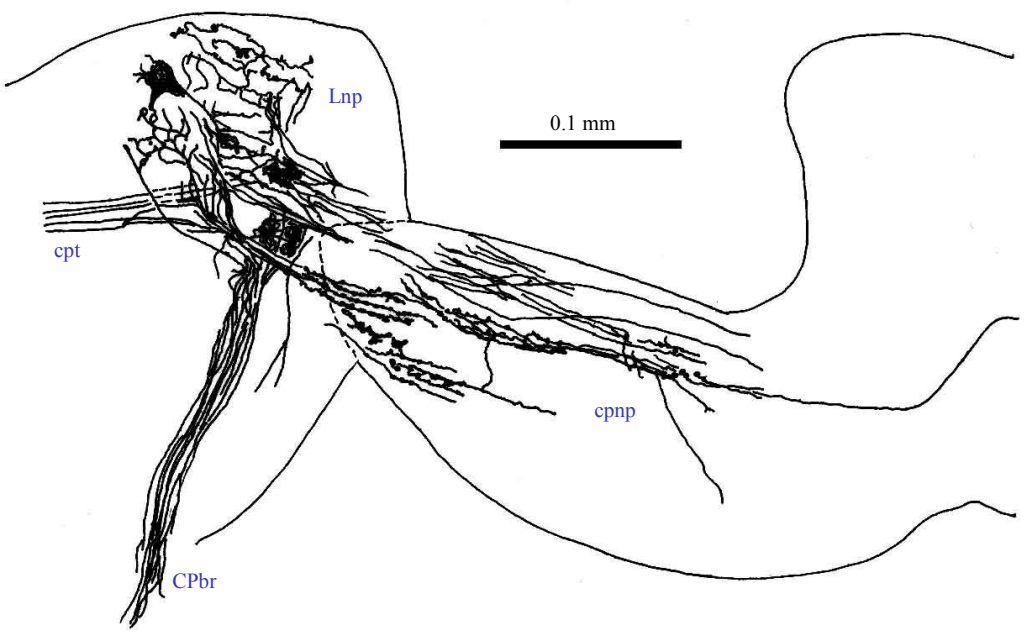


Figure 40. Golgi-Kopsch impregnation of the left pedunculate body of a sixth instar *Phidippus johnsoni*. The lateral protocerebral lobe (Lnp) is closely linked to both the pedunculate body (cpnp) and the bridge (CPbr). A tract of distinctive fibers (cpt) leads to the subesophageal ganglia.

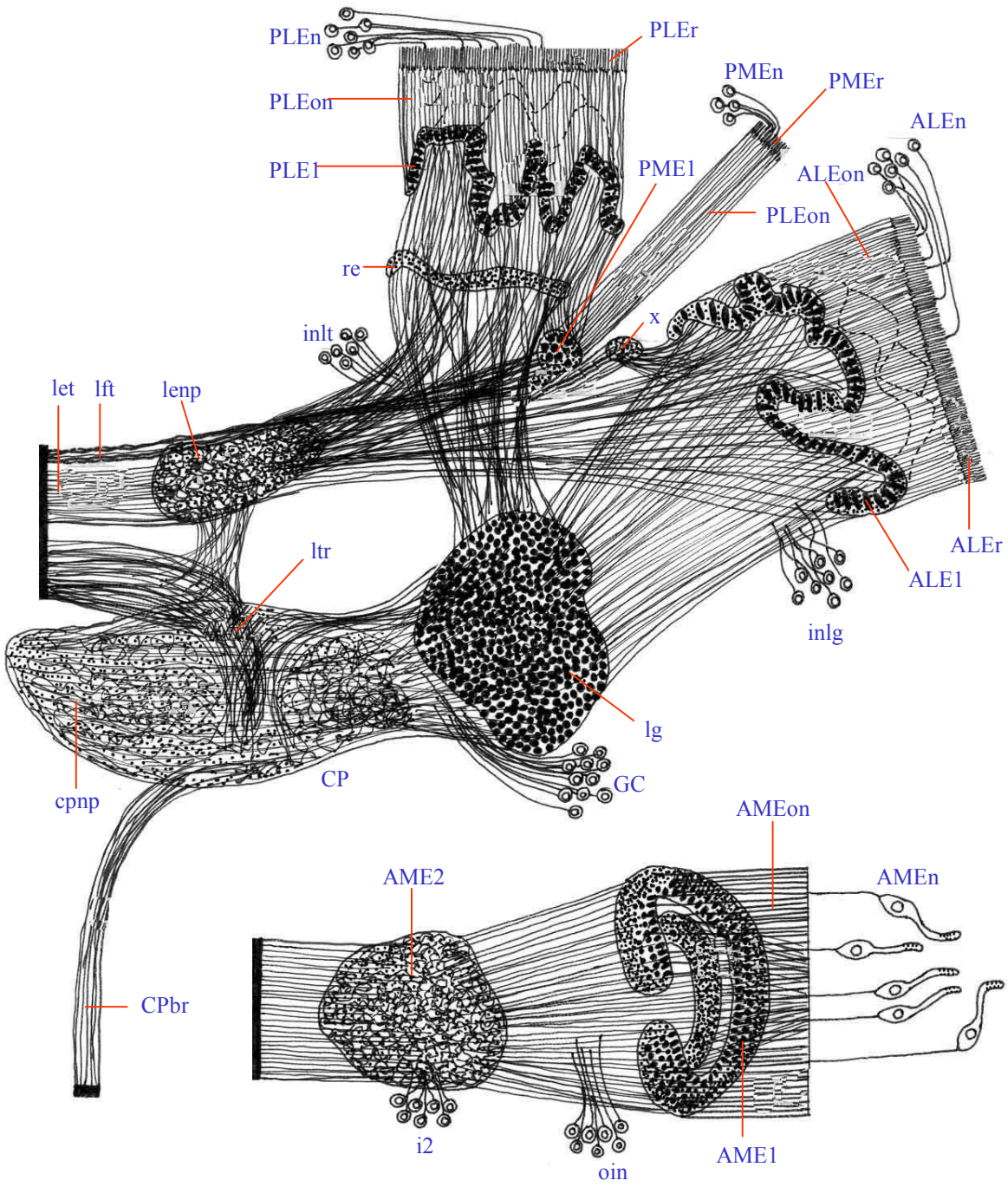


Figure 41. Summary of the visual processing system of *Phidippus* [schematic based on examination of silver and Masson Trichrome sections]. Dorsal view of left half. The first link between information received by the lateral eyes and the anterior medial eyes is in the protocerebrum. The solid black bars indicate groups of fibers entering the protocerebrum. Fibers leading from the primary neuropiles of the lateral eyes (ALE1 and PLE1) lead to either the glomerular layer (*lame glomerulee*, lg) of the pedunculate body (CP), or to the lateral eye neuropile (lenp) and lateral eye tract (let). Large, distinctive fibers of the primary neuropile of the posterior medial eyes (PME1) join similar fibers originating with a small neuropile (x) receiving fibers from the primary neuropile of the anterior lateral eye. These large fibers enter the proto cerebrum as a distinctive tract (lft). Several important groups of neuron somata are shown. For further interpretation , see Appendix 1.

Hanstrom (1921) first recognized the glomerular layer as a *secondary optic mass*. Later (1935) he noted its relationship to the *corpora pedunculata*, and accepted the homology of these structures with those of insects and other arthropods. Noting the great variation of development of the pedunculate bodies in various spider families, Hanstrom correctly associated their presence with the presence of highly developed visual centers, a correlation later supported by Meier (1967).

Although they are highly developed in certain Agelenidae, Pisauridae, Lycosidae, Thomisidae, and Salticidae, the *corpora pedunculata* of Linyphiidae and Araneidae are rudimentary. They are altogether absent in many families, including the Ctenizidae, Amaurobiidae, Theridiidae, Drassidae, and Clubionidae ([according to] Hanstrom 1935). They are also lacking in the Theraphosidae (Babu 1965).

As mentioned earlier, Hanstrom (1935) first advanced the homology of these structures with those of insects and annelids. The homology of the chelicerate syncerebrum with those [that] of other arthropods is based on a hypothetical disappearance of antennules and the associated deutocerebrum in these animals [We now know that the deutocerebrum has been neither reduced nor lost in chelicerates].

Anderson (1973) seriously questions the phyletic relationship of chelicerates with mandibulate arthropods and annelids, establishing the complete lack of developmental evidence for the integrity of the phylum Arthropoda. Thus the structure of the *corpora pedunculata* in spiders has some bearing on the argument over a polyphyletic origin of the arthropods.

[With molecular tools to study phylogeny of these animals a consensus has emerged with respect to the relationship of chelicerates to other arthropods and to annelids. The annelids are much more diverse than previously thought, and are not at all closely related to the arthropods (Halanych and Janosik 2006). Insects and crustaceans form a clade (*Pancrustacea*) that, with myriapods, is part of a larger *Mandibulata* clade. The arthropod clade can be divided neatly into chelicerate and mandibulate clades, only distantly related to each other (Giribet, Edgecombe, and Wheeler 2001).]

Meier (1967) notes that the pedunculate bodies of spiders are completely different from those of insects. If one compares the dendritic structure globuli cell ramifications in the calyces of insect *corpora pedunculata* (Bernstein and Bernstein 1969, Frontali and Mancini 1970, Pearson 1971, Schurmann 1973, Weiss 1974) with the large and compact glomeruli of the araneid [pertaining to Araneae] *corpora pedunculata*, the great difference between the two structures is immediately evident. The so-called globuli cells of spiders are ordinary optic interneurons [cell bodies of interneurons of the visual system] by all appearances, whereas those of insects are situated in a calcyl cup [calyx]. In all of these respects, the pedunculate bodies of crustaceans and annelids agree with those of insects.

Even the sensory input of insect *corpora pedunculata* is at variance with the homology. Although there is some optic input in Hymenoptera, the predominant input is from deutocerebral antennal sensory centers (Vowles 1955, Weiss 1971, 1974). The optic input is scarcely a source of homology, as the multilayered optic lobes of Crustacea (Hafner 1973) and Insecta (Strausfeld 1970) have nothing in common with the visual centers of chelicerates.

The resemblance of the synaptic *lame glomerulee* of spiders to the globuli cell layer [containing cell bodies] of insects adds to the misleading similarity in the appearance of the corpora pedunculata of these animals. Nonetheless there are some real similarities in the structure of these organs. Both receive fibers secondarily from sensory centers, and these sensory fibers synapse with intrinsic neurons at the anterior end of each pedunculate body.

The greatest similarity lies in the the structure of the pedunculus. If one compares Golgi preparations of insect *corpora pedunculata* (Frontali and Mancini 1970, Pearson 1971, Schurmann 1973) with those of spiders (Figures 37, 40), the presence of longitudinal intrinsic fibers bearing numerous small synaptic boutons or glomeruli in both cases is striking. And in both cases, this is the site of extensive synapsing with extrinsic interneurons.

Thus the *corpora pedunculata* of spiders are quite possibly analogous, rather than homologous, with those of annelids and other [non-chelicerate] arthropods. The possibility of this analogy immediately raises the question of function, a question which remains decidedly unresolved in a recent review of the subject (in [with] reference to insects) by Howse (1975).

The *corpora pedunculata* have been alternately termed organs of integration, association, coordination, and intelligence in insects. Given a particular function in the handling of sensory information, there is no reason why they could not fulfill all of these ill-defined functions. Bernstein and Bernstein (1969) made a virtually meaningless [perhaps, but look two paragraphs down in this paper!] correlation between their size and the foraging efficiency of ants.

Given the major role of lateral eyes in directing orientation to visual stimuli (Land 1971, 1972b), as well as the fact that the *corpora pedunculata* handle only sensory information arising with the lateral eyes, there is a good possibility that the pedunculate bodies of spiders are organs of orientation, whose sole function is the direction of a calculated orientation to visual stimuli. [Duelli (1980) likewise noted that these structures had relatively few external connections, and that they might play a role in extracting information relative to the direction of a stimulus or the resulting turn by a spider.]

Similarly, the *corpora pedunculata* of insects, by analogy, may serve as organs of directional orientation to sensory stimuli, in this case arising primarily from the antennae. Thus the large size of these organs in the ant worker (Vowles 1955, Bernstein and Bernstein 1969) would be indispensable to the path-finding capacity of these insects.

7. The central body

Unlike the central situation of the central body of insects (Bernstein and Bernstein 1969), the central body of spiders is isolated at the rear of the protocerebrum. In addition, the intrinsic cells of this structure are well-defined in spiders.

This distinctive structure in *Phidippus* (Figure 42) consists of two intimately connected lobes. The upper lobe is connected to lateral protocerebral lobes by several essentially horizontal tracts, while the lower lobe sends several medial tracts down toward the subesophageal ganglia. Both lobes are surrounded by the somata of small intrinsic neurons (see Table 3). The neuropile of the upper lobe is highly structured, whereas that of the lower lobe is more compact and essentially unstructured (Figure 43).

Hanstrom (1921) demonstrated the connection of the upper lobe with the primary neuropiles of the lateral eyes, using the Golgi method.

Witt, Reed, and Peakall (1968) noted the large extent of the central body in orb weavers and termed it a coordinating center. Along with the protocerebrum, it is recognized as an important association center between the visual centers and the subesophageal ganglia (Legendre 1959, Satija and Sohal 1962, Meier 1967).

The conspicuous isolation and serial ramification of intrinsic neurons within this unpaired organ agrees with the accepted theory that this is a control center of programmed behavior in spiders (Millot 1949, also see section 3). The upper lobe appears to handle sensory information, while the lower lobe may be largely a coordinating center for motor functions. [This hypothesis is based only on the relative orientation of associated nerve tracts. Barth (2002) described the central body as a visual center, based on its interconnection with other visual centers in the ctenid *Cupiennius*, but also noted that it may have other functions (e.g., "integration") based on its interconnection with other regions of the CNS.]

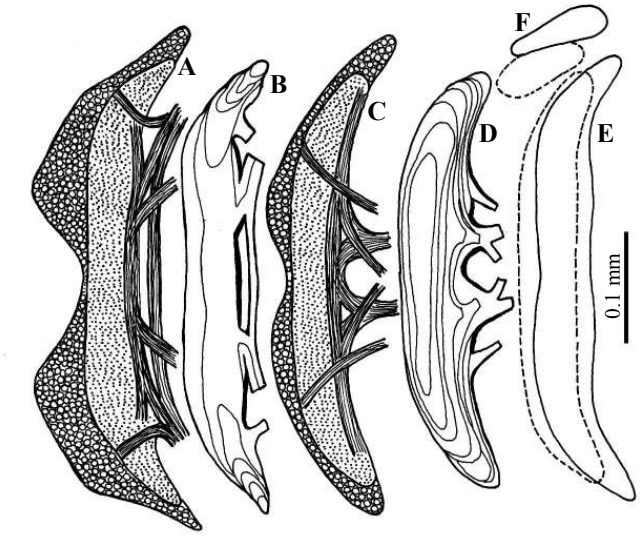


Figure 42. The central body. A: Dorsal view of dorsal lobe, showing posterior layer of cell bodies (left), stippled neuropile, and tracts leading to the lateral regions of the protocerebrum. B: Contour diagram (10 µm interval) of the upper lobe neuropile and tracts, as seen from above. Note the upturned ends. C: Dorsal view of ventral lobe, showing tracts running to the medial protocerebrum. D: Contour diagram (10 µm interval) of the lower lobe, as seen from below. E: Relative position of dorsal and ventral lobes of the central body, as seen from above. F: Relative position of dorsal and ventral lobes, from sagittal section. Based primarily on horizontal sections of sixth instar *P. johnsoni*.

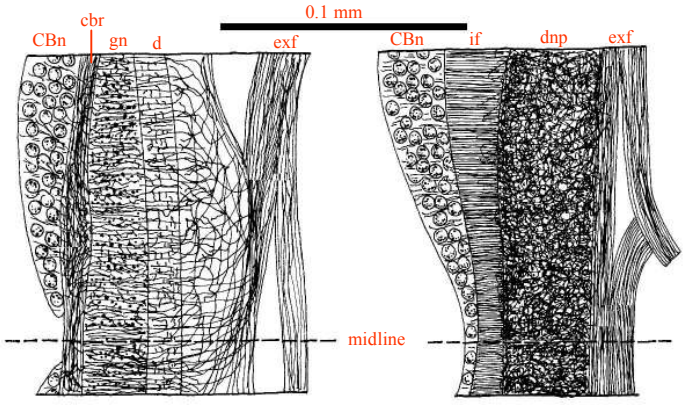


Figure 43. Semi-diagrammatic horizontal views of the central body. Left, section of the upper lobe. Right, section of lower lobe. Fibers of peripheral cell bodies (CBn) ramify in a posterior zone (cbr) and synapse with extrinsic fibers (exf) in a glomerular neuropile zone (gn) and a well-ordered anterior dendritic neuropile (d) of the upper lobe. The lower lobe is simpler in structure, with intrinsic fibers (if) joining the cell bodies (CBn) with extrinsic fibers (exf) in a dense neuropile (dnp).

8. The rostral ganglion

The rostral ganglion consists of two fused lateral lobes surrounding the anterior esophagus, with many lateral connections to the adjoining cheliceral ganglia (Figure 44). Associated neuron somata are at the anterior lateral periphery of this structure, which consists of a loose dendritic neuropile.

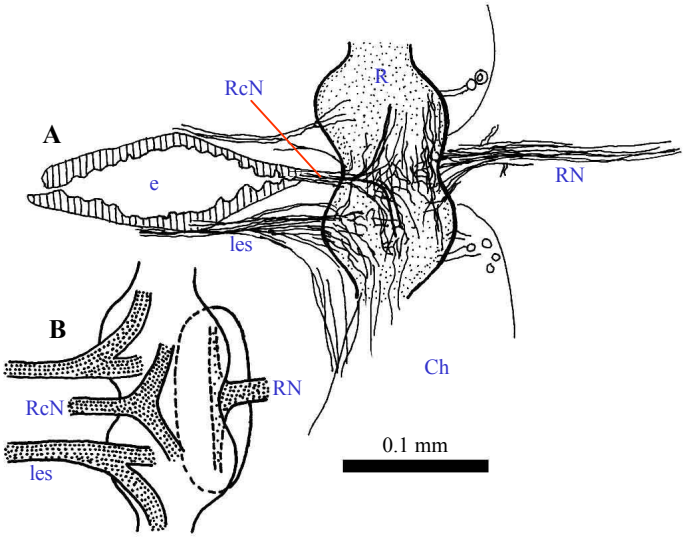


Figure 44. Structure of the rostral ganglion. A: Dorsal view based upon several sections of Bodian preparation. B: Diagrammatic view of (A). Symbols: *e*, esophagus, *les*, lateral esophageal nerve, *RcN*, recurrent nerve, *RN*, rostral nerve, *R*, rostral ganglion, *Ch*, cheliceral ganglion. Legendre (1959) considers this to be a composite structure formed by the fusion of the frontal ganglion and a pair of rostral ganglia.

Saint Remy (1890) discovered the rostral nerve, and assigned it to a rostro-mandibular ganglion. Hanstrom later (1935) depicted the separation of the rostral ganglion from the cheliceral ganglia and [he noted] its homology with the frontal ganglion of insects, as the stomodeal bridge of a so-called sympathetic nervous system (by analogy with vertebrates). Millot (1949) accepted this interpretation. Rempel (1957), in a study of [the theridiid spider] *Latrodectus mactans*, similarly noted the homology of this stomodeal bridge as a reduced insect tritocerebrum.

Legendre (1959) proposed a double origin, in which the rostral ganglion is formed by the fusion of a pair of rostral neuromeres with a *frontal ganglion*. The original paired nature of this composite structure is suggested by the lateral lobes depicted in Figure 44.

The rostral ganglion appears, by virtue of its associated nerves, to integrate pharyngeal activity with that of the sucking stomach.

9. Structure of the subesophageal ganglia

The subesophageal ganglionic mass consists of a single pair of pedipalpal ganglia, four pairs of leg ganglia, and a fused mass of at least seven pairs of opisthosomal neuromeres which is termed the *cauda equina*. While the neuron somata of each of the ganglia are isolated from each other by neurilemma, the central tract region of the subesophageal mass is common to all ganglia. The dense neuropiles associated with each of the ganglia are the sites of synapsing between incoming sensory neurites and interneurons leading to the supraesophageal ganglia. In addition, they contain the dendritic ramifications of associated motor neurons ([according to] Meier 1967).

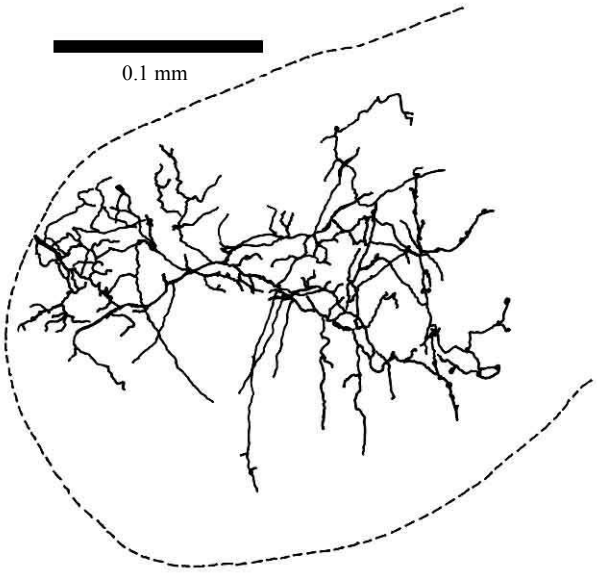


Figure 45. Golgi-Kopsch preparation showing ramification of an individual (or portions of several) neurons in the ganglion of the first leg.

Metamerically arranged commissures of these ganglia are shown in Figures 46 and 47.

Motor neurons form both ipsilateral and contralateral ramifications in the neuropiles of adjoining ganglia (Meier 1967, Babu 1969). Unfortunately, the vertical dimension is neglected in these descriptions.

Babu (1965) traced seven major paired longitudinal tracts of the subesophageal ganglia. The validity of these tracts as sensory and motor units, as determined by Babu in *Poecilotheria* (Theraphosidae) is questionable in the case of *Phidippus*. The course of constituent fibers may be quite different from that of the tract itself. There is no simple correspondence for the most part between major tracts of the supra- and subesophageal portions of the CNS. Several longitudinal fiber groups are shown in Figure 36.

The structure of the subesophageal mass is illustrated in a series of Figures (48-54).

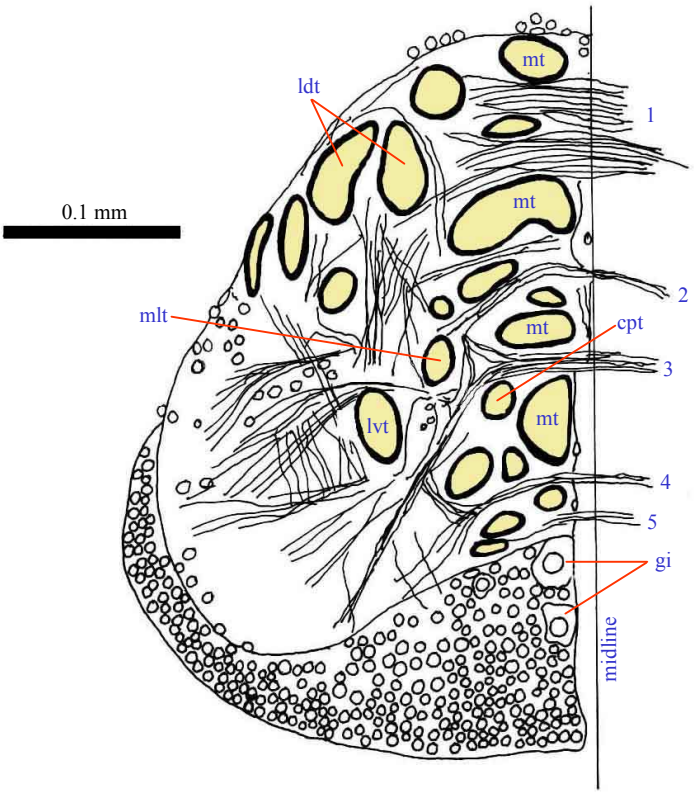


Figure 46. Half-frontal section between ganglia of first and second legs of a sixth instar P. johnsoni. The five commissure levels correspond to those in Figure 47 [1-5]. Groups of longitudinal fibers of the subesophageal ganglia are outlined with heavy lines [yellow areas]. Symbols: *mt*, major medial tract, *lvt*, latero-ventral tract, *mlt*, meso-lateral tract, *cpt*, tract originating with pedunculate body and lateral protocerebral lobe, *ldt*, latero-dorsal tracts.

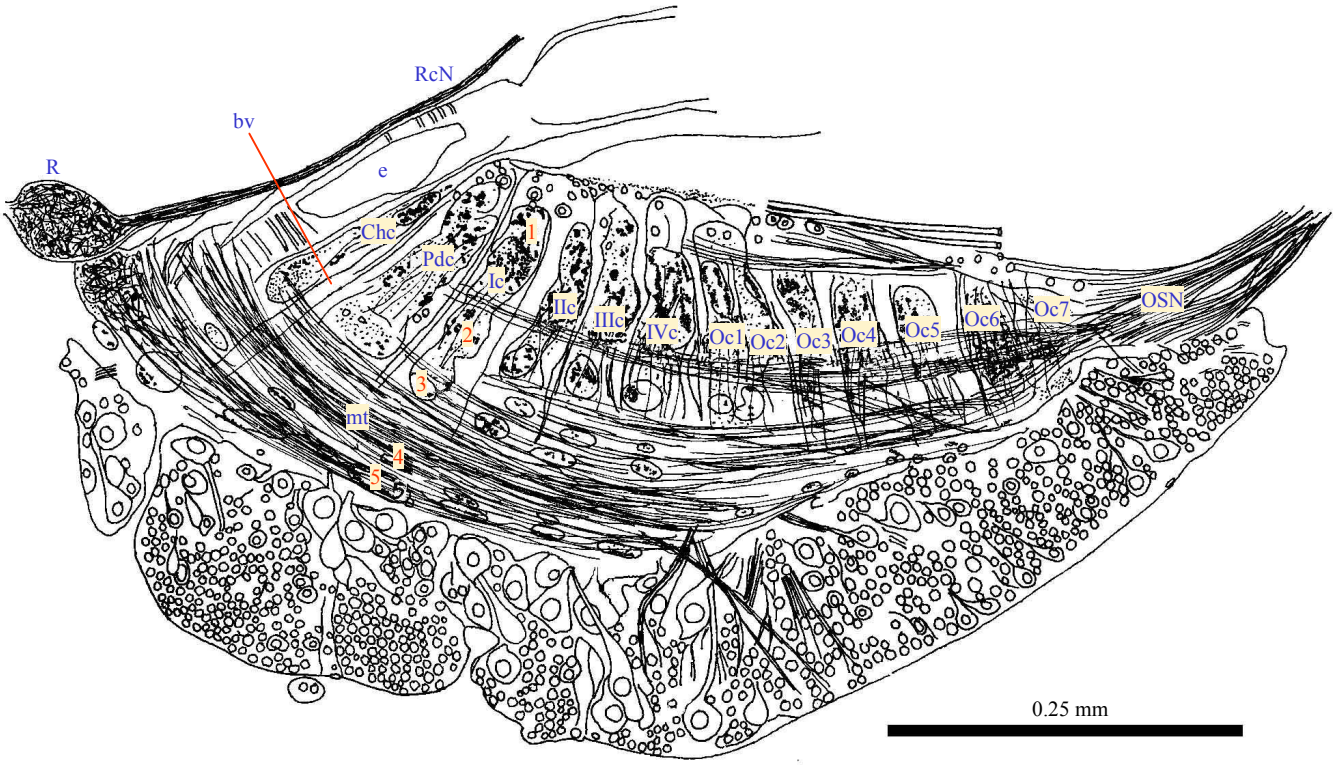


Figure 47. Sagittal section of subesophageal ganglia of a fifth instar *Phidippus rimator* [*clarus*, reduced silver preparation drawn with *camera lucida*]. The segmentally arranged commissures are separated by the medial [at mid-line or median] dorso-ventral blood vessels (*bv*). Five (*1-5*) levels of commissure fibers are labeled in the commissure of the first leg ganglia. Medial longitudinal fiber tracts (*mt*) are separated by the commissure fiber tracts. Many giant neurons may be seen in the cortex of cell bodies. Other symbols: *Chc*, commissure of cheliceral ganglia (post-esophageal), *Pdc*, commissure of pedipalpal ganglia, *Ic*, *IIc*, *IIIc*, *IVc*, commissures of the leg ganglia, *Oc1-Oc7*, commissures of the opisthosomal ganglia, *e*, esophagus, *R*, rostral ganglion, *RcN*, recurrent nerve, *OSN*, opisthosomal nerve.

Figures 48-54. Serial horizontal (10 mm) sections of the subesophageal ganglion mass prepared with reduced silver impregnation. Adult female Phidippus rimator [clarus]. The number of each section in the series is indicated beside the figure caption, beginning with the section through the top of the subesophageal mass (Figure 48). The extent of each photograph is indicated by a rectangle in the corresponding figure.

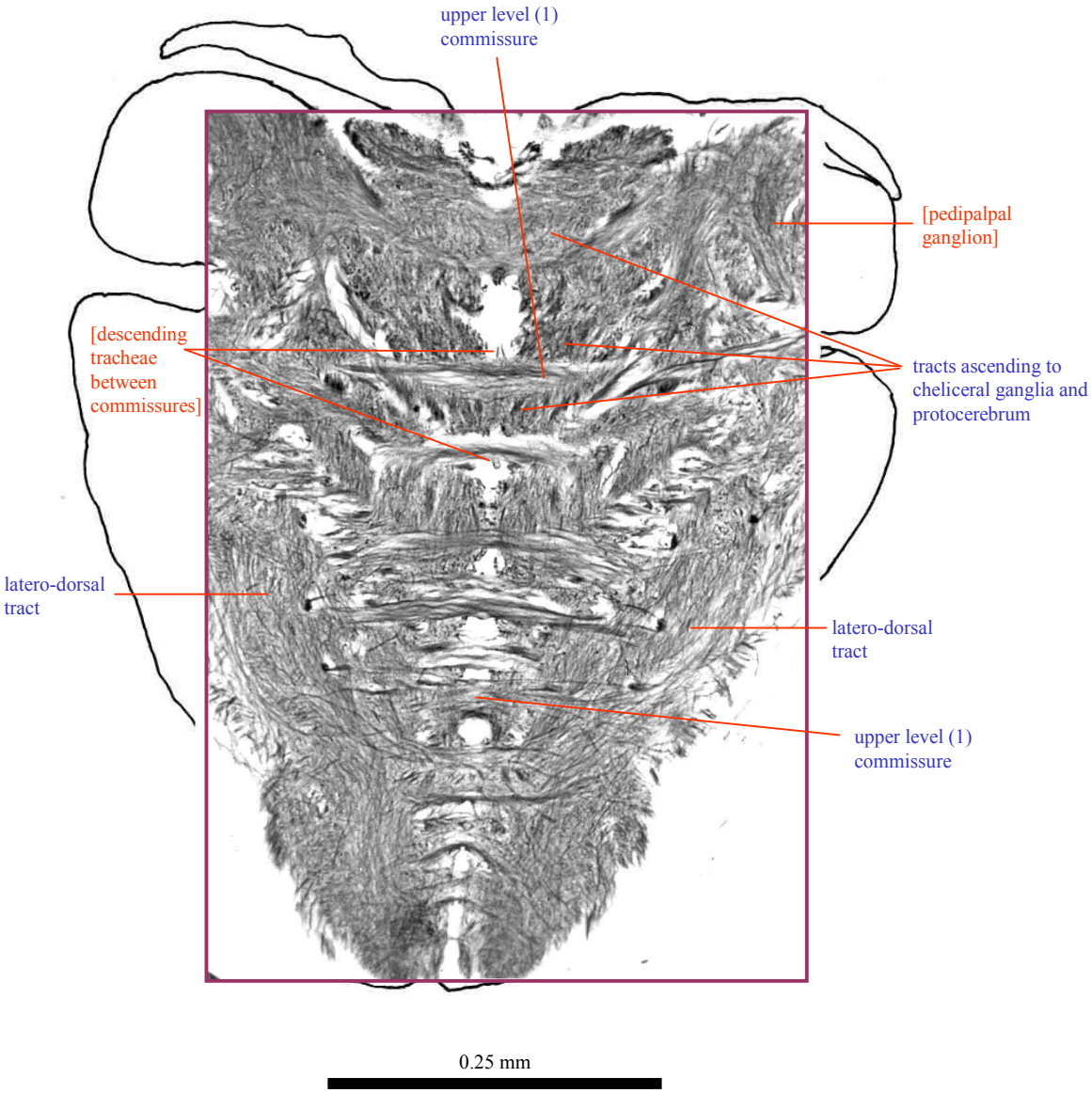


Figure 48. (1)

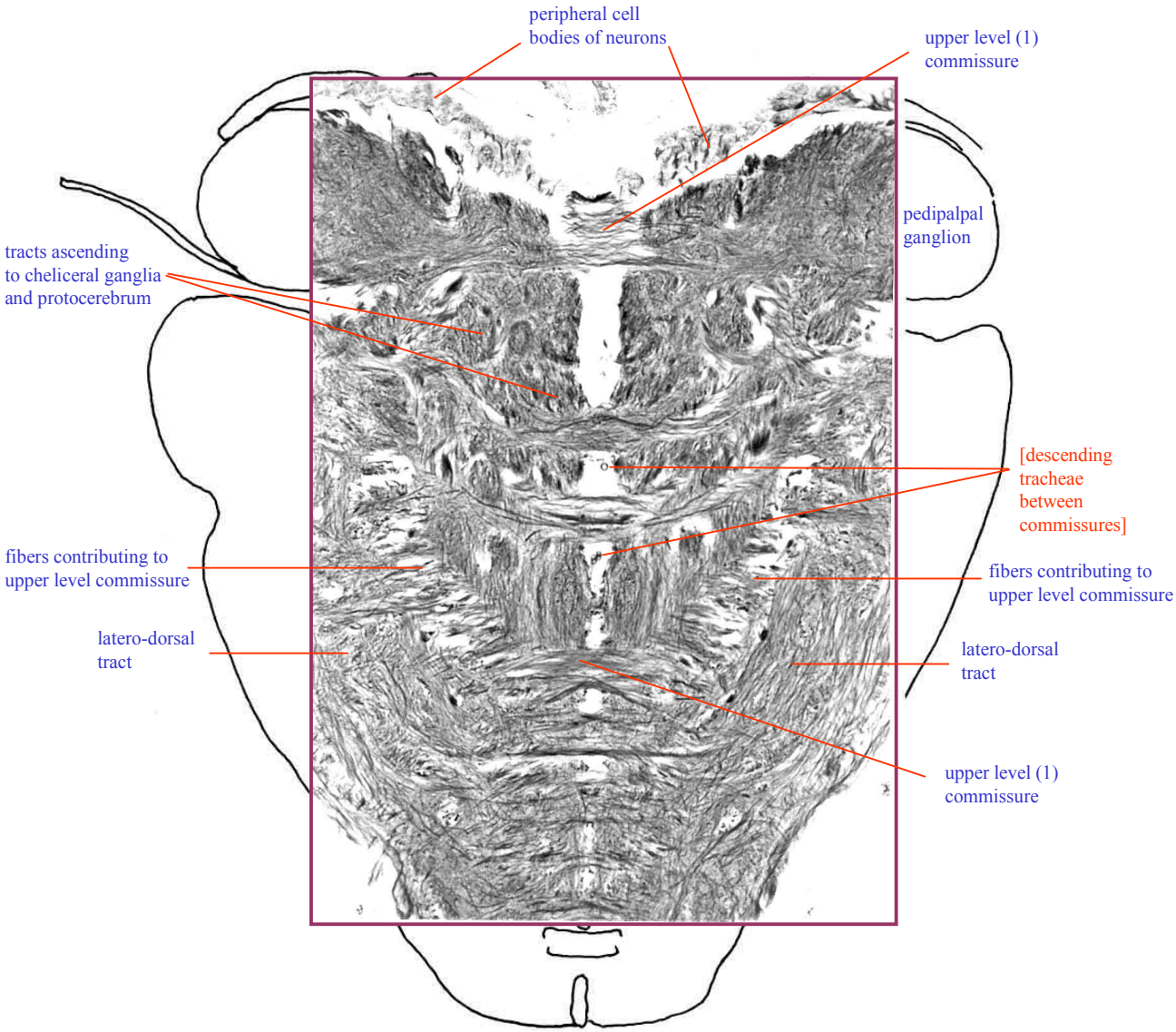

peripheral cell bodies of neurons
upper level (1) commissure
pedipalpal ganglion
tracts ascending to cheliceral ganglia and protocerebrum
[descending tracheae between commissures]
fibers contributing to upper level commissure
fibers contributing to upper level commissure
latero-dorsal tract
latero-dorsal tract
upper level (1) commissure
0.25 mm

Figure 49. (4)

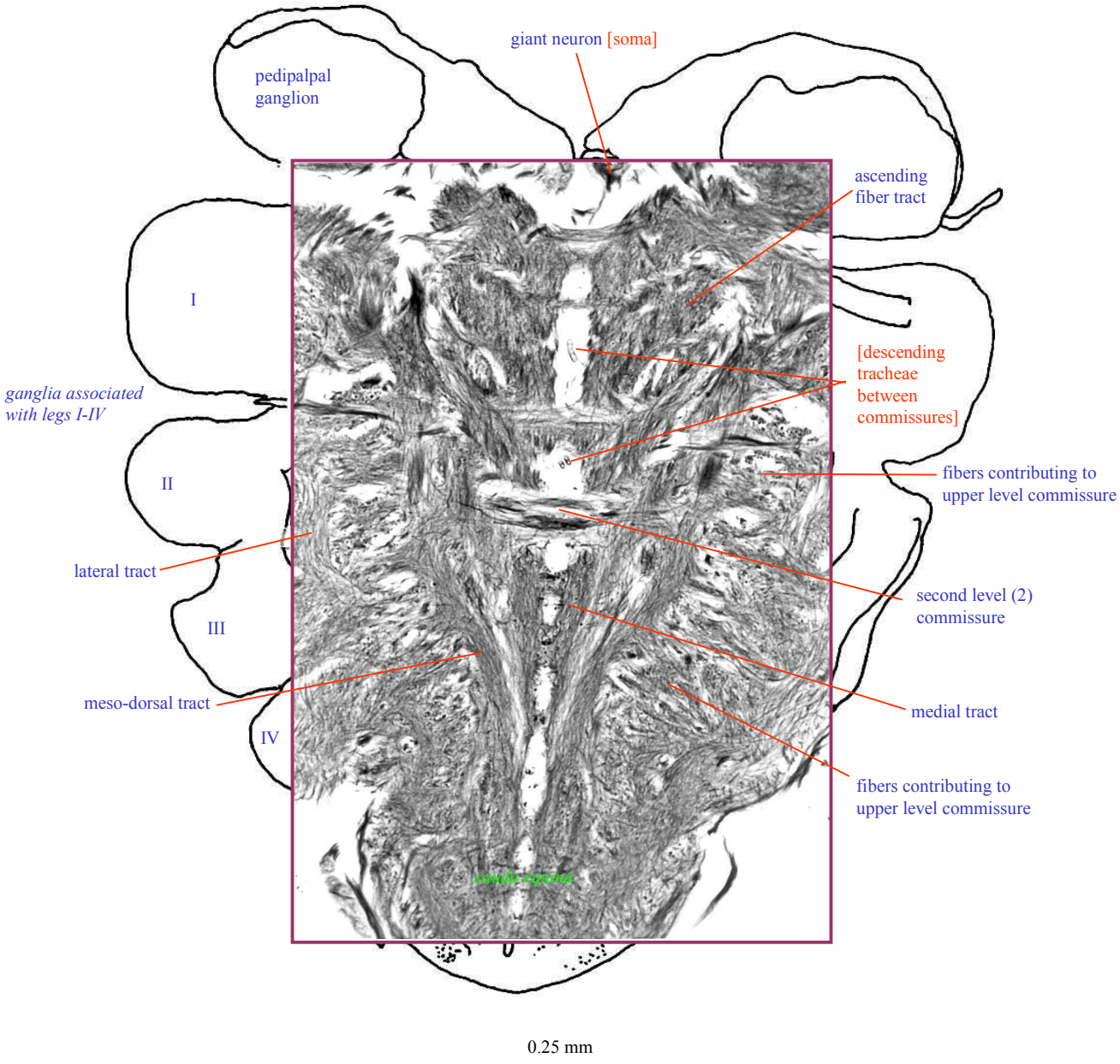

giant neuron [soma]
pedipalpal ganglion
ascending fiber tract
I
[descending tracheae between commissures]
ganglia associated with legs I-IV
II
fibers contributing to upper level commissure
lateral tract
second level (2) commissure
III
meso-dorsal tract
medial tract
IV
fibers contributing to upper level commissure
cauda equina
0.25 mm

Figure 50. (8)

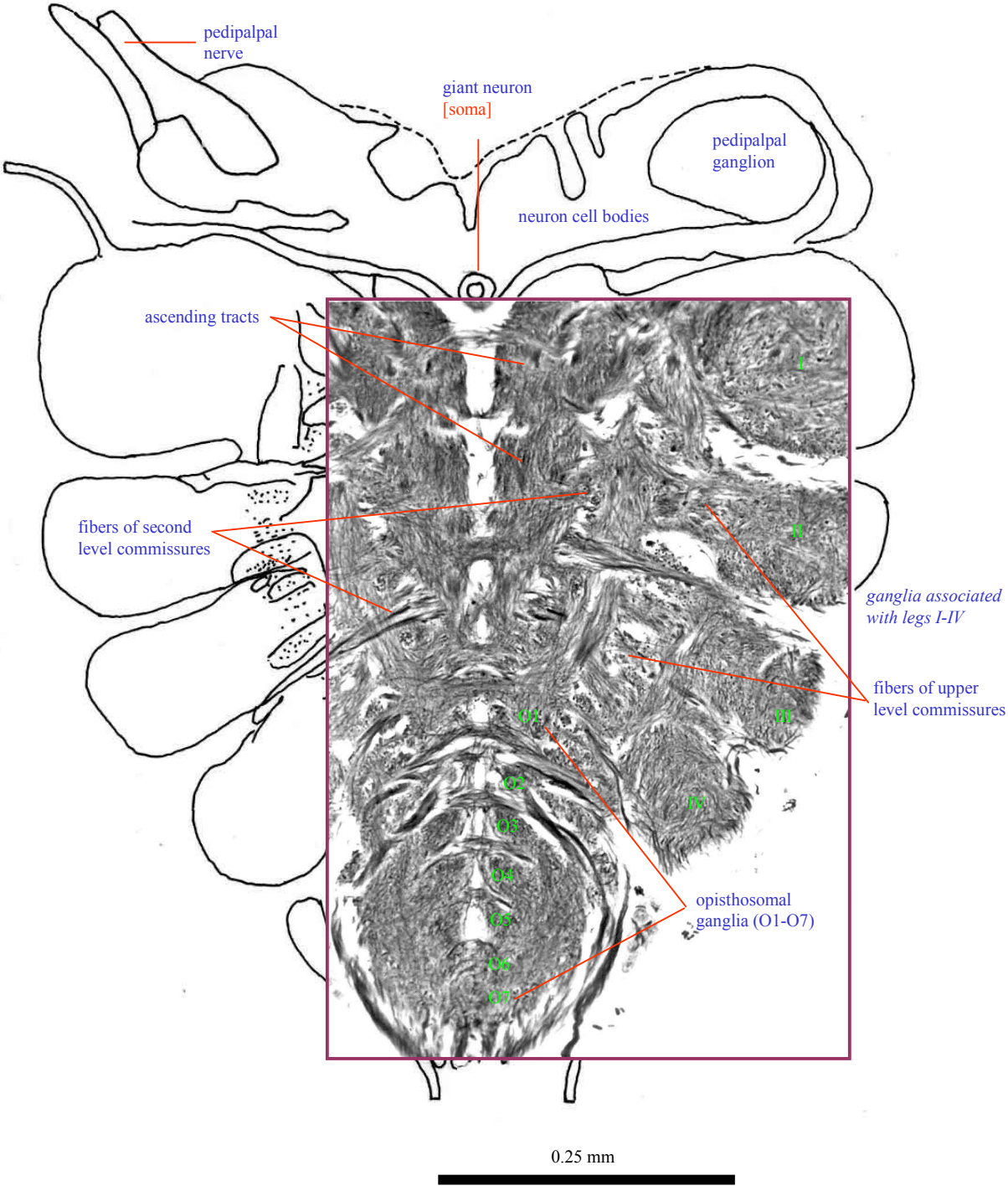

pedipalpal
nerve
giant neuron
[soma]
pedipalpal
ganglion
neuron cell bodies
ascending tracts
fibers of second
level commissures
ganglia associated
with legs I-IV
fibers of upper
level commissures
opisthosomal
ganglia (O1-O7)
I
II
III
IV
O1
O2
O3
O4
O5
O6
O7
0.25 mm

Figure 51. (12)

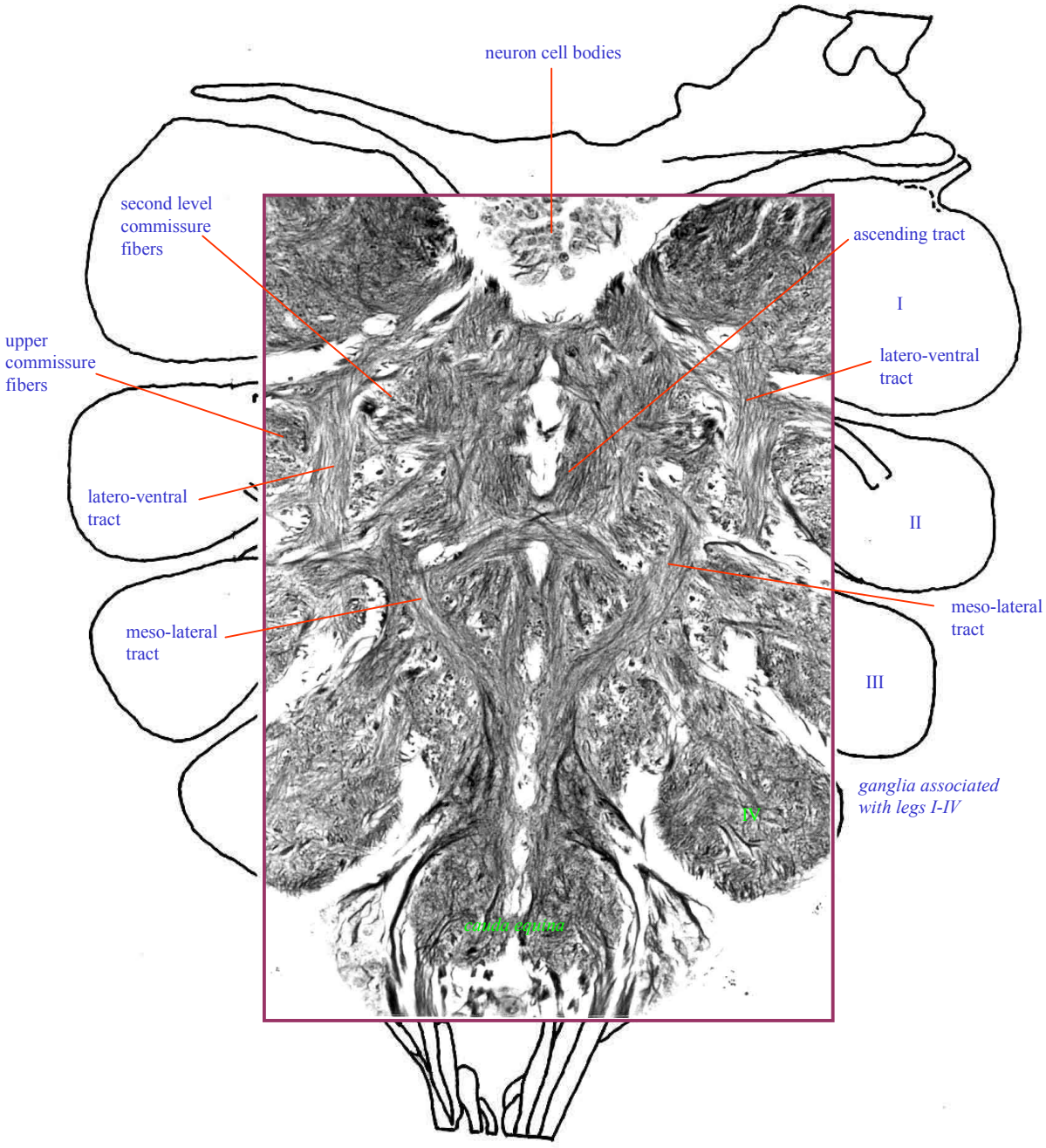

neuron cell bodies
second level commissure fibers
upper commissure fibers
latero-ventral tract
meso-lateral tract
ascending tract
latero-ventral tract
meso-lateral tract
I
II
III
IV
ganglia associated with legs I-IV
cauda equina
0.25 mm

Figure 52. (17)

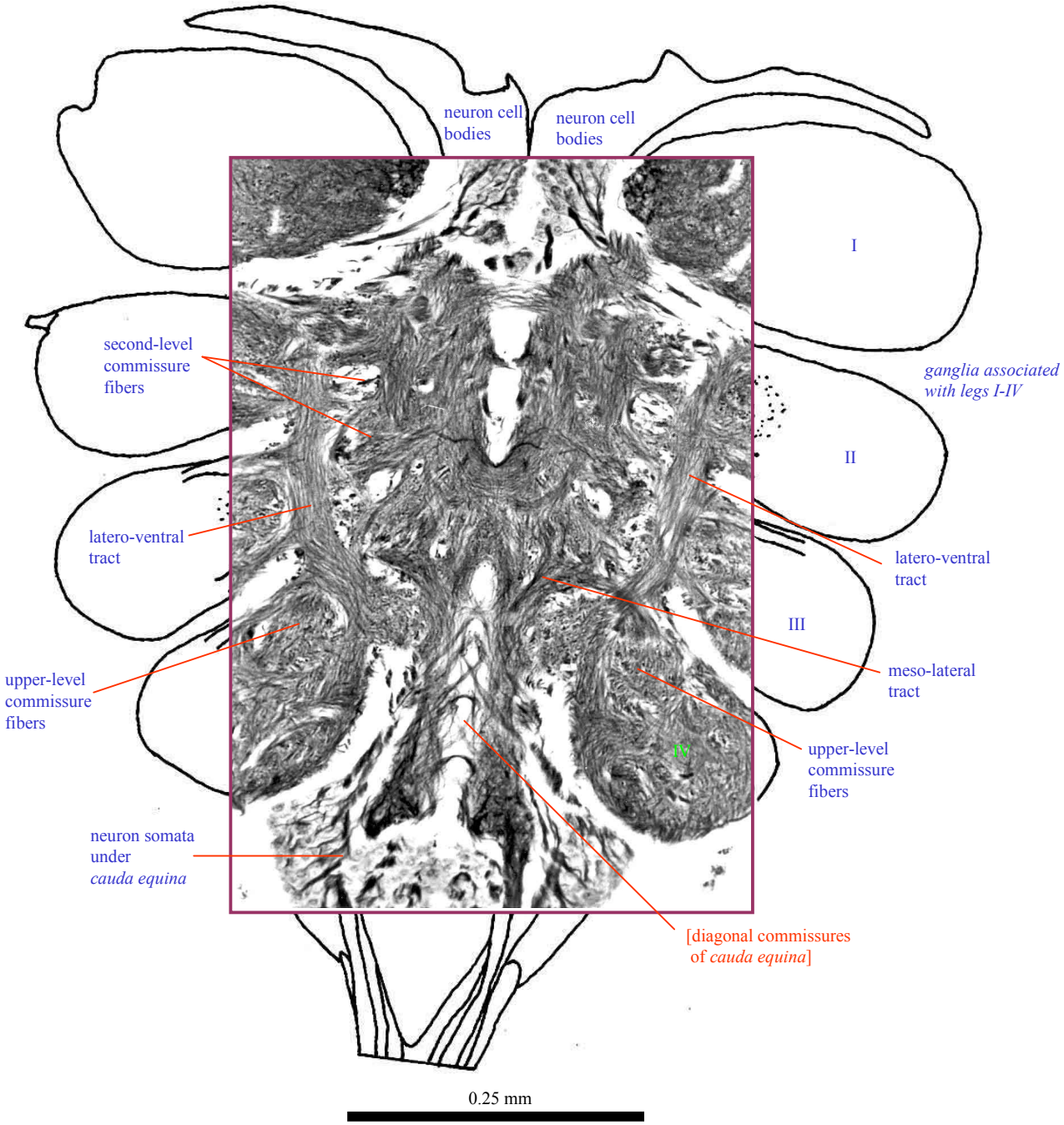

neuron cell bodies
neuron cell bodies
I
second-level commissure fibers
ganglia associated with legs I-IV
II
latero-ventral tract
latero-ventral tract
III
meso-lateral tract
upper-level commissure fibers
IV
upper-level commissure fibers
neuron somata under cauda equina
[diagonal commissures of cauda equina]
0.25 mm

Figure 53. (20)

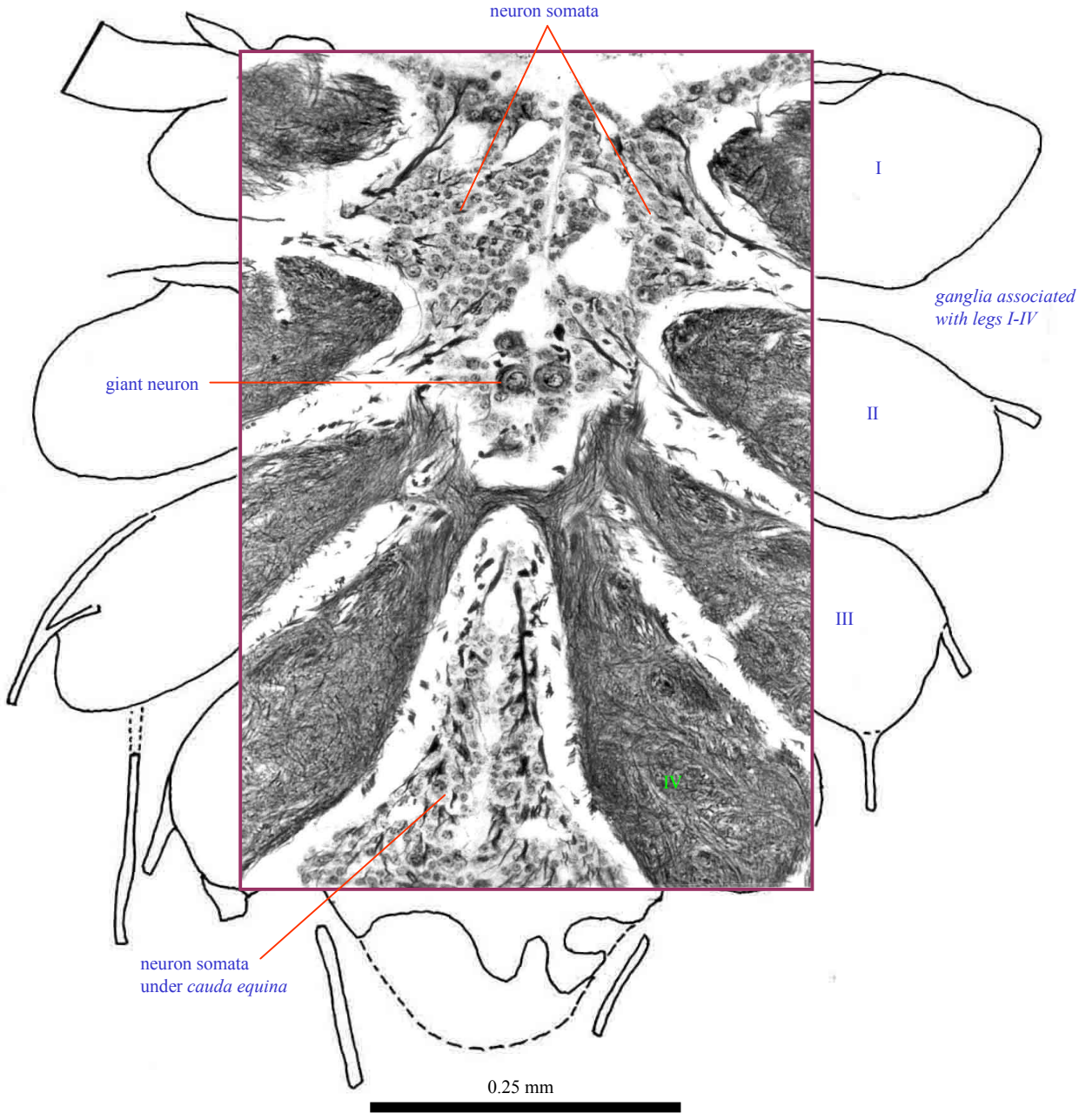


Figure 54. (27) The lower portion of each ganglion is dense neuropile.

In *Phidippus*, the *cauda equina* appears to consist of seven pairs of fused opisthosoma neuromeres, the first two of which are greatly fused (Figure 47). The actual number of neuromeres is difficult to ascertain, due to the extreme fusion of the posterior neuromeres. According to Legendre (1959), each of the neuromeres retains its original connections with the [respective] opisthosomal segment, as indicated in Table 4.

Table 4. Opisthosomal regions associated with neuromeres of the *cauda equina* (according to Legendre 1959, beginning with the most anterior pair of neuromeres)

1	pedicel
2	book lungs
3	progenital segment (epigynum)
4	gonadal segment
5-7	spinnerets [three pairs]

While Babu (1965) describes at least 11 pairs of opisthosomal ganglia in the orthognath [theraphosid] *Poecilotheria*, the seven pairs of ganglia of the *cauda equina* found in *Phidippus* correspond to those described in other labidognath spiders by Legendre (1959).

[Barth (2002, Chapters XIV, XV) provided a very comprehensive overview of the CNS of the ctenid spider *Cupiennius salei*. This included a summary of more recent work on the tracts of the subesophageal ganglia. Barth *et al* have attempted to classify many of these tracts as either motor or sensory in function, and the more detailed work related to tracing sensory axons should be studied by anyone with a serious interest in this subject. Barth rightfully referred to the structure of the subesophageal CNS as a *labyrinth*.]

[10. Discussion

Since this work was completed in 1975, many additional papers have been published on the remarkable anterior medial eyes (AME) of salticids. However, little work has appeared with respect to the other structures of the salticid CNS, with the exception of the two papers by Duelli (1978, 1980) with respect to the structure and function of the lateral eyes. More work has been done on non-salticids (e.g., work on *Cupiennius salei* reviewed by Barth 2002), and much of this work should be relevant to the Salticidae as well.

The most obviously structured or patterned neuropiles (regular synapse-fields) in the salticid CNS are:

[1] upper lobe of the central body
[2] lower lobe of the central body
[3] inner and outer lobes of the primary AME neuropile
[4] primary lateral eye (ALE, PLE) neuropiles
[5] anterior glomeruli of the pedunculate body
[6] longitudinal pedunculate body fibers (with boutons)

It is hoped that carefully study, and development of supporting theory, will allow students of the Salticidae to further understand the various functions of these regular neuropiles.]

11. Acknowledgements

I would like to sincerely thank Dr. Christopher J. Bayne of the Department of Zoology [at Oregon State University] for his continued cooperation, not only in the securing of materials for this study, but also in preparation of the final thesis. In addition, I deeply appreciate the loving devotion that my sweet and loyal wife Rose Marie has given to this endeavor.

12. Bibliography

Anderson, D. T. 1973 Embryology and phylogeny in annelids and arthropods. Oxford, Pergamon Press, 1-495.

Babu, K. Sasira 1965 Anatomy of the central nervous system of arachnids. Zoologische Jahrbucher, Abteilung fur Anatomie und Ontogenie der Tiere 82: 1-154.

Babu, K. Sasira 1969 Certain histological and anatomical features of the central nervous system of a large Indian spider, *Poecilotheria*. American Zoologist 9: 113-119.

Babu, K. Sasira 1973 Histology of the neurosecretory system and neurohemal organs of the spider *Argiope aurantia* (Lucas). Journal of Morphology 141: 77-98.

Bailey, Charles L. 1969 Life history of the spider *Phidippus audax* (Hentz), in relation to biological control of grain sorghum insects. Dissertation Abstracts 30: 1181B.

[**Barth, Friedrich G. 2002** A spider's world, senses and behavior. Springer-Verlag: i-xiv, 1-394.]

Bernstein, S., and Bernstein, R. A. 1969 Relationships between foraging efficiency and size of the head and component brain and sensory structure in the red wood ant. Brain Research 16: 85-104.

Blest, A. D. 1961 Some modifications of Holme's silver method for insect central nervous systems. Quarterly Journal of Microscopical Science 102: 413-417.

Bonnet, P. 1945-1962 *Bibliographia araneorum*, volumes I-VIII (a systematic account of all spider literature prior to 1938). Douladore, Toulouse, France.

Bristowe, W. S. 1971 The world of spiders. Collins, London: 1-304.

Bullock, Theodore Holmes, and Horridge, G. Adrian 1965 Structure and function in the nervous systems of invertebrates. W. H. Freeman and Company, San Francisco and London, volumes 1-2: 1-1719.

Bursey, Charles R. and Sherman, Robert G. 1970 Spider cardiac physiology I, structure and function of the cardiac ganglion. Comparative and General Pharmacology 1: 160-170.

Collonier, Marc 1964 The tangential organization of the visual cortex. Journal of anatomy 98: 327-344.

Crane, Jocelyn 1948 Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part II. Methods of collection, culture, observation and experiment. Zoologica 33: 139-145.

Crane, Jocelyn 1949 Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. Zoologica 34: 159-214.

Dawes, Clinton J. 1971 Biological techniques in electron microscopy. Barnes and Noble: 1-193.

Drees, O. 1952 Untersuchungen uber die angeborenen Verhaltensweisen bei Springspinnen (Salticidae). Zeitschrift fur Tierpsychologie 9: 169-206.

[**Duelli, Peter 1978** Movement detection in the posterolateral eyes of jumping spiders (*Evarcha arcuata,* Salticidae). Journal of Comparative Physiology 124, 15-26.]

[**Duelli, Peter 1980** The neuronal organization of the posterior lateral eyes of jumping spiders (Salticidae). Zoologische Jahrbuch, Abteilung Anatomie 103, 17-40.]

Dzimirsski, I. 1959 Bewegungssehen und Optomotorik bei Springspinnen (Salticidae). Zeitschrift fur Tierpsychologie 16: 385-402.

Eakin, Richard M., and Brandenburger, Jean L. 1971 Fine structure of the eyes of jumping spiders. Journal of Ultrastructure Research 37: 618-663.

[**Edwards, G. B. 2004** Revision of the jumping spiders of the genus *Phidippus* (Araneae: Salticidae). Occasional Papers of the Florida State Collection of Arthropods 11: i-viii, 1-156.]

Firstman, B. 1954 The central nervous system, musculature, and segmentation of the cephalothorax of a tarantula (*Eurypelma californicum* Ausserer.). Microentomology 19: 14-40.

Frontali, N., and Mancini, G. 1970 Studies on the neuronal organization of cockroach *corpora pedunculata*. Journal of Insect Physiology 16: 2293-2301.

Gabe, M. 1954 Emplacement et connexions des cellules neurosecretrices chez quelques araneids. Comptes Rendus hebdomadaires des Seances de l'Academie des Sciences Paris 238: 1265-1267.

Gardner, Beatrice T. 1964 Hunger and sequential responses in the hunting behavior of salticid spiders. Journal of Comparative Physiology and Psychology 58: 167-173.

Gardner, Beatrice T. 1965 Observations on three species of *Phidippus* jumping spiders (Araneae: Salticidae). Psyche, Cambridge: 72: 133-147.

Gardner, Beatrice T. 1966 Hunger and characteristics of the prey in the hunting behavior of salticid spiders. Journal of Comparative Physiology and Psychology 62: 475-478.

Gardner, Beatrice T. 1967 The life-cycle of the spider *Phidippus coccineus* (Salticidae) under laboratory conditions. Psyche, Cambridge 74: 104-106.

[**G. Giribet, G., Edgecombe, G. D., and Wheeler, W. C. 2001** Arthropod phylogeny based on eight molecular loci and morphology. Nature 413: 157-161.]

Hafner, G. S. 1973 The neural organization of the *lamina ganglionaris* in the crayfish, a Golgi and EM study. Journal of Comparative Neurology 152: 255.

Hanstrom, Bertil 1921 Uber die Histologie und vergleichende Anatomie der Sehganglien und Globuli der Araneen. Kunglica Svenska Vetenskapsakademiens Handligar 61: 1-39.

Hanstrom, Bertil 1935 Fortgesetzte Untersuchungen uber das Araneengehirn. Zoologische Jahrbucher, Abteilung fur Anatomie und Ontogenie der Tiere 59: 455-478.

Heil, K. H. 1936 Beitrage zur Physiologie und Psychologie der Springspinnen. Zeitschrift fur vergleichende Physiologie 23: 1-25.

[**Hill, D. E. 2006** Use of location (relative direction and distance) information by jumping spiders (Araneae, Salticidae, *Phidippus*) during movement toward prey and other sighted objectives. Version 2: 1-72.]

Hollis, J. H., and Branson, B. A. 1964 Laboratory observations on the behavior of the salticid spider *Phidippus audax* (Hentz). Transactions of the Kansas Academy of Science 67: 131-148.

Homann, H. 1971 Die Augen der Araneae. Anatomie, Ontogenie, und Bedeutung fur die Systematik. Zeitschrift fur Morphologie der Tiere 69: 201-272.

Horner, Norman V., and Starks, Kenneth J. 1972 Binomics of the jumping spider *Metaphidippus galathea*. Annals of the Entomological Society of America 65: 602-607.

Howse, P. E. 1975 Brain structure and behavior in insects. Annual Review of Entomology 20: 359-379.

Humason, Gretchen L. 1972 Animal Tissue Techniques, third edition. W. H. Freeman, San Francisco: 1-641.

Kaston, B. J. 1935 The slit sense organs of spiders. Journal of Morphology 58: 189-210.

Kaston, B. J. 1936 The senses involved in the courtship of some vagabond spiders. Entomologica Americana 16: 97-166.

Kaston, B. J. 1972 How to know the spiders. W. C. Brown Co., Dubuque, Iowa: 1-289.

Kuhne, H. 1959 Die neurosekretorischen Zellen und der retrocerebrale neuro-endocrine Komplex von Spinne. Zoologische Jahrbucher, Abteilung fur Anatomie und Ontogenie der Tiere 77: 527-600.

[**Halanych, K. M., and Janosik, A. M. 2006** A review of molecular markers used for annelid phylogenetics. Integrative and Comparative Biology: 1-11.]

Lahue, Robert 1973 The chelicerates. In: Invertebrate learning, Volume 2, Arthropods and gastropod mollusks, ed. W. C. Corning, J. A. Dyal, and A. O. D. Willows, Plenum Press, New York: 1-48.

Land, M. F. 1969a Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. Journal of Experimental Biology 51: 443-470.

Land, M. F. 1969b Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. Journal of Experimental Biology 51: 471-493.

Land, M. F. 1971 Orientation by jumping spiders in the absence of visual feedback. Journal of Experimental Biology 54: 119-139.

Land, M. F. 1972a Mechanisms of orientation and pattern recognition by jumping spiders (Salticidae). In: Information Processing in the Visual Systems of Arthropods, ed. R. Wehner, Springer-Verlag, Berlin: 231-247.

Land, M. F. 1972b Stepping movements made by jumping spiders during turns mediated by the lateral eyes. Journal of Experimental Biology 57: 15-40.

Legendre, Roland 1959 Contribution a l'etude du systeme nerveux des araneides. Annales des Sciences Naturelles, Zoologie et Biologie Animale 28: 343-474.

Legendre, Roland 1961 Sur deux particularities du systeme nerveux central de la mygale *Scodra calceata* Fabr. Annales des Sciences Naturelles, Zoologie et Biologie Animale 30: 767-771.

Legendre, Roland 1965 Morphologie et developpement des chelicerates: embryologie, developpement et anatomie des araneides. Fortschritte der Zoologie 17: 238-271.

Legendre, Roland 1971 Etat actuel de nos conaissances sur le developpement embryonaire et la croissance des araignees. Annales des Sciences Naturelles, Zoologie et Biologie Animale 96: 93-114.

Leguelte, L. 1969 Learning in spiders. American Zoologist 9: 145-152.

Levy, Gershom 1970 The life cycle of *Thomisus onustus* (Thomisidae: Araneae) and outlines for the classification of the life histories of spiders. Journal of Zoology, London 160: 523-536.

Luft, John H. 1961 Improvements in epoxy resin embedding methods. Journal of Biophysical and Biochemical Cytology (Journal of Cell Biology) 9: 409-414.

Meier, Franz 1967 Beitrage zur Kenntnis der postembryonalen Entwicklung der Spinnen (Araneida, Labidognatha) unter besonderer Berucksichtigung der Histogenese des Zentralnervensystems. Revue Suisse de Zoologie 74: 1-114.

Melamed, J., and Trujillo-Cenoz, O. 1966 The fine structure of the visual system of *Lycosa* (Araneae, Lycosidae). Part I. Retina and optic nerve. Zeitschrift fur Zellforschung und Mikoskopische anatomie 74: 12-31.

Millot, Jacques 1949 Ordre des araneides (Araneae). In: Traite de Zoologie, ed. P. Grasse 6: 589-743.

Parry, D. A. 1960 The small leg-nerve of spiders and a probable mechanoreceptor. Quarterly Journal of Microscopical Science 101: 1-8.

Parry, D. A., and Brown, R. H. J. 1959 The jumping mechanism of salticid spiders. Journal of Experimental Biology 36: 654-664.

Pearson, L. 1971 The *corpora pedunculata* of *Sphinx ligusti* L. and other Lepidoptera: an anatomical study. Philosophical Transactions of the Royal Society of London, Series B 259: 477-516.

Peckham, G. W., and Peckham, E. G. 1909 Revision of the Attidae of North America. Transactions of the Wisconsin Academy of Science 16: 355-644.

Peters, Hans M. 1969 Maturing and coordination of web-building activity. American Zoologist 9: 223-227.

Phanuel, G. S. 1968 Orientation and biorhythms in jumping spiders (Araneida: Salticidae). Dissertation Abstracts 29B: 1218.

Pinter, Lawrence John, and Walters, Donna M. 1971 Karyological studies I. A study of the chromosome numbers and sex-determining mechanism of three species of the genus *Phidippus* (Araneae, Salticidae, Dendryphantinae). Cytologia, Tokyo 36: 183-189.

Precht, H. 1952 Uber das angeborene Verhalten von Tieren. Versuch an Springspinnen (Salticidae). Zeitschrift fur Tierpsychologie 9: 207-230.

Precht, H., and Freytag, G. 1958 Ermudung und Hemmung angeborener Verhaltenswiesen. Behavior 13: 143-211.

Pringle, J. W. S. 1955 The function of the lyriform organs of arachnids. Journal of Experimental Biology 32: 270-278.

Rempel, J. G. 1957 The embryology of the black widow spider, *Latrodectus mactans* (Fabr.). Canadian Journal of Zoology 35: 35-74.

Russell, Findlay E. 1970 Bite by the spider *Phidippus formosus*: case history. Toxicon 8: 193-194.

Saint Remy, Georges 1890 Contribution a l'etude du cerveau chez les arthropodes tracheates. Theses a la Faculte des Sciences de Paris.

Satija, R. C., and Grewal, Harishwar K. 1970 Brain and optic lobes in a cribellate spider, *Stegodyphus pacificus* Pocock (Arachnida-Araneida). Zoologica Poloniae 20: 87-101.

Satija, R. C., Sharma, S. P., and Dhir, R. M. 1969 Brain of the web spiders, *Crossopriza lyoni* Blackwall and *Cytrophora citricola* Forskal. Zoologica Poloniae 19: 545-558.

Satija, R. C., and Sohal, R. S. 1962 The brain of *Lycosa chaperi* Simon (Arachnida-Araneida). Research Bulletin, New Series, Punjab University 13: 115-123.

Schurmann, F. W. 1973 Uber die Struktur der Pilzkorper des Insectengehirns III. Die Anatomie der Nervenfasern in den *corpora pedunculata* bei *Acheta domesticus* L. (Orthoptera): Eine Golgi-Studie. Zeitschrift fur Zellforschung und Mikroscopische Anatomie 145: 247.

Serna de Esteban, C. J. de la 1973 Histologie du systeme neuroendocrine retrocerebral de *Polybetes pythagoricus* (Holmberg 1874) (Araneae, Labidognatha). Annales des Sciences Naturelles, Zoologie, Paris 15: 595-606.

Snetsinger, R. 1966 Observation on two species of *Phidippus* (jumping spiders). Entomological News 66: 9-15.

Strausfield, N. J. 1970 Golgi studies on insects 2. The optic lobes of Diptera. Philosophical Transactions of the Royal Society of London, Series B 258: 135-223.

[**Telford, M. J., and Thomas, R. H. 1998** Expression of homeobox genes shows chelicerate arthropods retain their deutocerebral segment. Proceedings of the National Academy of Sciences 95: 10671-10675.]

Trujillo-Cenoz, O., and Melamed, J. 1964 Synapses in the visual system of *Lycosa*. Naturwissenschaften 51: 470-471.

Trujillo-Cenoz, O., and Melamed, J. 1967 The fine structure of the visual system of *Lycosa* (Araneae: Lycosidae). Part II. Primary visual centers. Zeitschrift fur Zellforschung und Mikroscopische Anatomie 76: 377-388.

Vowles, D. M. 1955 The structure and connexions of the *corpora pedunculata* in bees and ants. Quarterly Journal of Microscopical Science 96: 239-255.

Walcott, C. 1969 A spider's vibration receptor: it's anatomy and physiology. American Zoologist 9: 133-144.

Weiss, M. J. 1971 From soma to synapse. The tracings of fiber input of a complex brain center in the American Cockroach, *Perplaneta americana* (L.). American Zoologist 11: 696-697.

Weiss, M. J. 1972 A reduced silver staining method applicable to dense neuropiles, neuroendocrine organs, and other structures in insects. Brain Research 39: 268-273.

Weiss, M. J. 1974 Neural connections and the function of the *corpora pedunculata* in the brain of the American Cockroach, *Perplaneta americana* (L.). Journal of Morphology 142: 21-70.

Whitehead, W. F., and Rempel, J. G. 1959 Musculature of the black-widow. Canadian Journal of Zoology 37: 831-870.

Wilson, R. S. 1969 Control of dragline spinning in certain spiders. American Zoologist 9: 103-111.

Wilson, R. S. 1970 Some comments on the hydrostatic system of spiders (Chelicerata, Araneae). Zeitschrift fur Morphologie der Tiere 68: 308-322.

Witt, P. N., Reed, C. C., and Peakall, D. B. 1968 A spider's web: problems in regulatory biology. Springer-Verlag, New York: 1-107.

13. Appendix 1: Abbreviations used in text

The terminology for musculature is from Whitehead and Rempel (1959).

ALE	anterior lateral eye
ALE1	primary neuropile of ALE
ALEn	neuron somata of ALE
ALEon	optic nerve of ALE
ALEr	retina of ALE
AME	anterior medial eye
AME1	primary neuropile of AME
AME2	secondary neuropile of AME
AMEn	neuron somata of AME
AMEon	optic nerve of AME
AMEr	retina of AME
AO	anterior organ (Legendre 1959)
as	tracts ascending from the subesophageal ganglia to the supraesophageal ganglia
bv	blood vessel
CB	central body
CBn	intrinsic neuron somata of the central body
cbr	posterior ramification zone of dorsal CB lobe
CE	*cauda equina*
CEn	neuron somata of CE
Ch	cheliceral ganglion
Char	flexible articulation of chelicera
Chc	post-esophageal commissure of cheliceral ganglia
Chdn	dorsal cheliceral nerve
Chel	chelicera
ChN	principal cheliceral nerve
CNS	central nervous system
coxaI	coxa of first leg
coxaII	coxa of second leg
coxaIII	coxa of third leg
coxaIV	coxa of fourth leg
CO	pedunculate body (*corpora pedunculata*)
CPbr	bridge of the CP
cpnp	neuropile of CP
cpt	subesophageal tract leading from CP and Lnp
cut	cuticle
d	dendritic neuropile
dd	digestive diverticulum of midgut
dnp	dense neuropile
dSS	dorsal dilator of sucking stomach
e	esophagus
endC	endocrine cells (Legendre 1959)
ES	endosternite
exf	extrinsic fibers
GC	*globuli* cells or intrinsic neurons of CP
gi	giant neuron
gn	glomerular neuropile
hyp	hypodermis
I	first leg ganglion
i2	intrinsic neurons of AME2
Ic	commissure of the first leg ganglia
Idn	dorsal nerve of the first leg ganglion
if	intrinsic fibers
II	second leg ganglion
IIc	commissure of the second leg ganglia
IIdn	dorsal nerve of II
III	third leg ganglion
IIIc	commissure of the third leg ganglia
IIIn	principal nerve of III
IIIpd	postero-dorsal nerve of III
IIn	principal nerve of II
IIpd	postero-dorsal nerve of II
it	intrinsic tract
IN	principal nerve of first leg ganglion
inlg	interneurons connecting the primary neuropiles of lateral eyes to the *lame gomerulee*
inlt	interneurons of the lateral eye tract
Ipd	postero-dorsal nerve of first leg ganglion
IV	fourth leg ganglion
IVc	commissure of the fourth leg ganglia
IVdn	dorsal nerve of IV
IVN	principal nerve of IV
IVpd	postero-dorsal nerve of IV
Lab	labium
lc	lower level commissure of subesophageal ganglia
ldt	latero-dorsal tracts of subesophageal ganglia
led	lateral esophageal dilator muscle
lenp	lateral eye neuropile
les	lateral esophageal nerve
let	lateral eye tract to protocerebrum
lft	large fiber tract of PME1, leading to protocerebrum
lg	glomerular [synaptic] layer of CP (*lame glomerulee*)
ln	large neuron
Lnp	lateral protocerebral neuropile
lSS	lateral dilator of sucking stomach
lt	lateral tract of subesophageal ganglia
ltr	lateral tract region of CP
lvt	latero-ventral tract of subesophageal ganglia
mdt	meso-dorsal tract of subesophageal ganglia
mgt	midgut
mlt	meso-lateral tract of subesophageal ganglia
mt	major medial tract of subesophageal ganglia
n	neuron somata
nephC	nephrocytes
O1-O7	opisthosomal ganglia [telsomal ganglia, front to rear]
Oc1-Oc7	commissures of the opisthosomal [telsomal] ganglia
OSN	opisthosomal [telsomal] nerves
P	pedipalpal ganglia
PC	protocerebrum
Pdc	commissure of the pedipalpal ganglia
PdP	pedipalp
ped	pedicel
Phar	pharynx
Phpd	posterior dilator of pharynx
Phvd	ventral dilator of pharynx
PLE	posterior lateral eye
PLE1	primary neuropile of PLE
PLEn	neuron somata of PLE
PLEon	optic nerve of PLE
PLEr	retina of PLE
PME	posterior medial eye
PME1	primary neuropile of PME
PMEn	neuron somata of PME
PMEon	optic nerve of PME
PMEr	retina of PME
PN	principal pedipalpal nerve
Ppd	postero-dorsal pedipalpal nerve
R	rostral ganglion
RcN	recurrent nerve
re	ramification zone of PLE1 interneurons
RN	rostral nerve
sc	second level commissure of subesophageal ganglia
scf	fibers of sc
sES	suspensor [muscle] of endosternite
sr	small ramifications of interneurons in re
SS	sucking stomach
St	sternum
t	tracheole [or trachea]
uc	upper level commissure of subesophageal ganglia
ucf	fibers of uc
vd	venom duct
VGl	venom gland
x	small ALE neuropile

14. Appendix 2

Application of Holmes' reduced silver technique to spiders: a detailed outline of procedures. References: Weiss (1972), Blest (1961), Humason (1972).

1. Anesthesia: Place a small piece of dry ice (CO_2) into a container containing the spiders to anesthetize. Wait at least one minute after the spiders stop moving.

2. Fixation: Immerse in Bodian's fixative no. 2 (5ml formalin, 5ml glacial acetic acid, 90ml 80% ethanol) and remove opisthosoma [telsoma] and all appendages, including chelicerae, with a sharp single-edged razor blade. Fix for 18 hours.

3. Wash in three baths of 70% ethanol over 1-2 days. Store in 70% ethanol.

4. Removal of CNS from prosoma: Embed prosoma in molten wax in normal orientation. Proceed under a dissecting microscope, in 70% ethanol. Remove cuticle of optic quadrangle with a *sharp* razor. Similarly, section off the front and sides of the prosoma to sever major nerves. In doing this section, rather than tear, the eyes from the body wall and maintain the optic nerves as well as possible. Carefully tease away dorsal muscles, sucking stomach, and endosternite with fine forceps. Make certain that the anterior end of the esophagus is detached from the pharynx. Lift CNS and underlying midgut diverticula by peeling away from sternum, starting at the posterior end.

5. Dehydration and embedding: Transfer solutions rather than delicate tissue. Agitate frequently.
a. 2 minutes in 82% ethanol
b. 3 minutes in 95% ethanol
c. 4 minutes in 3 parts 95% ethanol: 1 part terpineol
d. 5 minutes in 1 part 95% ethanol: 1 part terpineol
e. 6 minutes in 1 part 95% ethanol: 3 parts terpineol
f. 30 minutes in terpineol
g. 60 minutes in terpineol
h. 30 seconds in benzene, with constant agitation. Repeat once.
i. 2 minutes in liquified 1 part benzene: 1 part *Paraplast*® (Sherwood Medical Industries, Inc.)
j. 5 minutes in *Paraplast*®, in 58-60C oven. Repeat once.
k. Orient and embed in fresh *Paraplast*®. Cool blocks in water.

6. Sectioning and mounting sections:
a. Trim blocks and mount in standard rotary microtome.
b. Section at 10µm with sharp steel knife and accumulate serial sections in box.
c. Subbed slides are prepared by dipping in the following *subbing* solution and then drying thoroughly (prepare subbing solution as follows): Dissolve 1.0g gelatin in 1.0 liter of hot distilled water. Cool, add 0.1g chromium pottassium sulfate, then store in refrigerator. A thin film of Mayer's egg albumen (Prepare as follows: Beat egg white until stiff, let stand overnight. Add equal volume of glycerol to settled liquid at bottom, then add 1 part formalin for every 100 parts of this mixture.) is then smeared over each subbed slide, and the sections are arranged in order on this thin film.
d. Float sections by adding distilled water (water standing several days to remove dissolved gases), with care to avoid dropping water on top of sections.
e. Place slides with floating sections on slide warmer, adjusted below *Paraplast*® melting point. When sections are flattened, remove excess water and dry overnight on warmer.

7. Hydration of sections on slides:
a. 2 minutes in xylene. Repeat once.
b. 2 minutes in absolute ethanol.
c. 1 minute in 95% ethanol.
d. 1 minute in 50% ethanol.
e. 2 minutes in distilled water. Repeat once.

8. Silver impregnation of sections on slides:
a. 2-3 hours in 20% silver nitrate bath, total darkness.
b. Rinse 5 minutes in distilled water.
c. Bathe in impregnating solution (27.5ml, 0.2M boric acid; 22.5ml, 0.05M borax; 10ml, 1% silver nitrate; 4ml, 2:4:6 collidine; 250ml distilled water; checked at pH 8.4 at 10C) for 18 hours in 37C oven, in total darkness.
d. Reduce in 60C reducing solution (3g hydroquinone, 30g sodium sulfite, 300ml distilled water) for 3 minutes.
e. Wash in running tap water 3 minutes; rinse in distilled water 3 minutes.
f. Tone in 1% gold chloride for 7 minutes.
g. Rinse by dipping in distilled water.
h. Reduce in 2% oxalic acid for 10 minutes.
i. Wash in distilled water for 3 minutes.
j. Fix in 5% sodium thiosulfate for 1 minute.
k. Wash thoroughly in distilled water.

9. Dehydration of sections:
a. 1 minute in 50% ethanol.
b. 1 minute in 70% ethanol
c. 2 minutes in 95% ethanol. Repeat once.
d. 2 minutes in absolute ethanol.
e. 2 minutes in xylene. Repeat once.

10. Mount with *Permount*® (Fisher Scientific Co.) and cover glass.

15. Appendix 3

Application of the Golgi-Kopsch technique described by Colonnier (1964). The following procedure was used with sixth instar spiders.

1. Spiders are anesthetized with dry ice (CO_2)
2. Remove opisthosoma [telsoma] and all appendages, including chelicerae, with a single-edge razor.
3. Quickly immerse prosoma in 1 part 25% glutaraldehyde: 4 parts 2.5% potassium dichromate. Maintain in darkness for 5-6 days.
4. Transfer to 0.75% silver nitrate. Maintain in darkness for 5-6 days.
5. Wash in distilled water several times with agitation.
6. Dehydration and embedding in *Epon*® (Luft 1961, see Appendix 4, for sixth instar spiders all infiltration times were doubled).
7. Section prosomata at 80µm with rotary microtome and hard steel knife.
8. Assemble sections on slide. Mount with *Permount*® (Fisher Scientific Co.) and cover glass.

16. Appendix 4

Fixation and epoxy embedding of second instar spiders. References: Dawes (1971), Eakin and Brandenburger (1971), Luft (1961).

1. Spiders anesthetized with dry ice (CO_2).

2. Dissection in cold fixative (2% glutaraldehyde in 0.1M cacodylate buffer at pH 7.4). Fix for 1.5 hours at room temperature.

3. Three 15 minute buffer rinses in 0.1M sodium cacodylate buffer at pH 7.4.

4. Post-fix 1.5 hours in 1% OsO_4 in 0.1M sodium cacodylate buffer.

5. Rinse in 0.1M sodium cacodylate buffer, pH 7.4, for 15 minutes.

6. Ethanol dehydration:
a. 15 minutes in 50% ethanol.
b. 15 minutes in 70% ethanol
c. 15 minutes in 95% ethanol. Repeat once (may store overnight in refrigerator).
d. Three 15 minute rinses in absolute alcohol [ethanol].

7. Transition in 1 part ethanol: 1 part propylene oxide for 20 minutes.

8. Two 20 minute rinses in propylene oxide.

Embedding by one of two sequences with occasional agitation during infiltration: [steps 9-11]

(*Araldite 502*®)

9. Infiltrate 2 hours in 1 part propylene oxide: 1 part infiltration medium. Medium consists of 27ml *Araldite 502*® (Ciba Co., Inc.), 23ml dodecenyl succinic anhydride or DDSA, 1.0ml DMP-30 or 2,4,6-tri (Dimethylaminomethyl) phenol added just before using.

10. 2-3 hours in infiltration medium [only].

11. Transfer and orient in final embedding medium (27ml *Araldite 502*®, 23ml DDSA, 0.5ml DMP-30). Incubate for 48-72 hours in 65C oven.

(Epon 812®, medium hardness)

9. Infiltrate 2 hours in 1 part propylene oxide: 1 part complete mixed resin (5ml mixture A, 5ml mixture B, 0.15ml DSP-30. Mixture A is 6.2ml *Epon 812*® (Shell Chemical Co.), 10.0ml DDSA. Mixture B is 10.0ml *Epon 812*®, 8.9ml methyl nadic anhydride or MNA).

10. 2-3 hours in complete mixed resin [only].

11. Transfer and orient in fresh complete mixed resin. Incubate in 65C oven overnight.

The Jumping Spider

A spider jumped
Upon its prey
Thus lived to leap
Another day

But for its young
A life to give
And for this end
A life to live

(An ancient story
not unlike that
given to man)

This paper is dedicated to the jumping spiders. Not only did they brighten many a sunny day (as creatures of the sunshine) but, in truth, they gave the most (unwillingly) to this enterprise.

(for Rose Marie)