MORPHOLOGY OF THE BRAIN AND SUBOESOPHAGEAL GANGLION OF THE ADULT MALE OF *CHORISTONEURA FUMIFERANA* (CLEMENS) (LEPIDOPTERA: TORTRICIDAE)

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ABSTRACT

The neuromorphology of the brain and suboesophageal ganglion (SOG) of the adult male spruce budworm, *Choristoneura fumiferana* (Clemens), is described and compared with information in the existing literature on adult Lepidoptera. The brain, SOG, and connecting nerves are illustrated. Protocerebral nerves include two pairs to the corpora cardiaca as well as optic nerves and ocellar pedicels. One pair of antennal nerves innervate the deuto-cerebrum and the tritocerebrum is innervated by one pair of labrofontalis nerves. Five pairs of nerves arise from the SOG: the mandibular, maxillary, labial, and two pairs of cervical nerves.

Key Words: *Choristoneura fumiferana,* morphology, brain, suboesophageal ganglion, nerves.

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INTRODUCTION

Although some aspects of the neuromorphology of *Choristoneura fumiferana* (Clemens), have been studied in the past (Mitchell and Seabrook 1973), the morphology of the brain and suboesophageal ganglion (SOG) has been neglected. This study describes the neuromorphology of the brain and SOG with their associated nerves in the adult male spruce budworm. Various aspects of the neuromorphology of the head region have been studied in over 160 species of adult Lepidoptera. Ehnbom's (1948) work involved a comparison of brain neuromorphology among 155 species of Lepidoptera including three species in the same family as *C. fumiferana* (*Tortrix viridana* (B. and Bsk.), *Epiblema pandaevana,* and *Pandemis rebeana* (Hon.). He classified lepidopteran brains into four types and also examined the nerves of the brain. Eaton (1974) reported on the nerves associated with the brain and SOG in *Manduca sexta* (L.). Chauthani and Callahan (1967) looked at the entire nervous system of *Heliothis zea* (Boddie) including the brain and SOG, and compared it to Nuesch's (1957) work on *Antherea polyphemus* (Cr.) Nordlander and Edwards' (1968) study of the anatomy of the brain of *Danaus plexippus* (L.) focussed on the internal anatomy of the brain, but briefly mentioned the peripheral nerves. A study by Ehrlich and Davidson (1961) described the entire internal anatomy of *D. plexippus* adults. Included in this study are figures illustrating the nerves of the brain although these nerves are not described in the text of the paper. Schroen et al.'s (1978) study of larval *C. occidentalis* (Freeman) examined the entire nervous system. The morphology of the adult male brain and SOG of *C. fumiferana* is compared to the existing literature. This study serves as a basis for an ongoing neurophysiological study of the central nervous system of the adult spruce budworm.

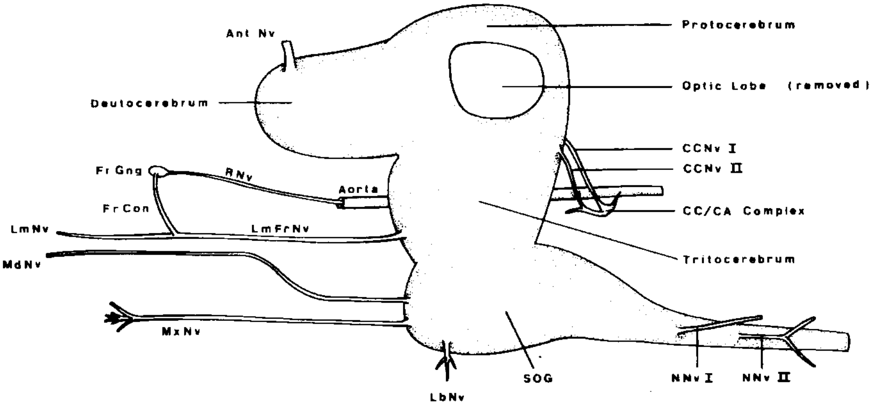
METHODS AND MATERIALS

Individuals of *C. fumiferana* were obtained as second instar larvae, from the Insect Rearing Section of the Forest Pest Management Institute, Sault Ste. Marie, Ontario. They were reared to pupation on synthetic diet (McMorran 1965) as modified by Harvey (1974), following the technique of Grisdale (1970). Wild moths from New Brunswick, collected as pupae, were also used. Males and females were separated as pupae. Two hundred adult male budworm moths, aged one to four days, were used in this study. Specimens were fixed in alcoholic Bouin's solution (Brasil 1904 in Gray 1954) for several hours and then placed in a 5% sodium thiosulphate solution for one hour. This removed any yellow coloration due to picric acid present in the fixative. The brain, SOG, and associated nerves were exposed by removal of the cuticle of the head, the compound eyes, and muscles in the anterior portion of the head capsule. Luxol fast blue stain (Lockhard and Reers 1965) was then applied topically when necessary, to demonstrate very fine peripheral nerves.

We use the nerve terminology of Snodgrass (1935) and the muscle terminology of Albert and Seabrook (1970).

RESULTS

The brain and suboesophageal ganglion in *C. fumiferana* are fused into a single ganglionic mass (Fig. 1). They are located in the head capsule dorsad and



AnNv = Antennal nerve
CCNvI = Corpus cardiacum nerve I
CCNvII = Corpus cardiacum nerve II
FrCon = Frontal ganglion connective
LbNv = Labial nerve
LmFrNv = Labrofrontalis nerve
LmNv = Labral nerve
MdNv = Mandibular nerve
MxNv = Maxillary nerve
NNvI = Cervical nerve I
NNvII = Cervical nerve II
RNv = Recurrent nerve

Fig. 1. Lateral aspect of the brain, suboesophageal ganglion and associated nerves of adult male *Choristoneura fumiferana.*

posteriad of the mouthparts, the sucking pump, and their associated muscles. The brain is positioned on a dorsal-ventral axis. The protocerebral lobes of the brain appear to be fused into a protocerebral mass which is located dorsad and posteriad of the other lobes. Large optic lobes project ventrally and anteriorly from the lateral surfaces of the protocerebrum.

The brain of the male spruce budworm is reflected dorsally so that the deutocerebral lobes are the most anterior parts of the brain (Fig. 1). The tritocerebrum is composed of two small lobes and constitutes the ventral surface of the brain (Fig. 1).

The SOG (Fig. 1) is located ventral to the brain and projects posteriorly. It is positioned on an anteior-posterior axis and appears to be fused to the tritocerebrum. Circumoesophageal connectives are not apparent and the oesophageal canal, although much reduced, permits passage of the recurrent nerve, the aorta and the oesophagus.

Nerves of the Brain

Two ocellar pedicels arise from the dorsal surface of the protocerebral lobes. The optic nerves are located within the optic lobes. Other nerves arising from the protocerebrum include two pairs of corpora cardiaca nerves (Fig. 2). Corpus cardiacum nerve I (CCNvI) exits from the postero-medial face of the protocerebrum and CCNvII from a more lateral position on the posterior face. CCNvI proceeds posteriad to the medial anterior corner of the triangular shaped corpus cardiacum and corpus allatum (CC/CA) complex. CCNvII proceeds posteriad and mesad to

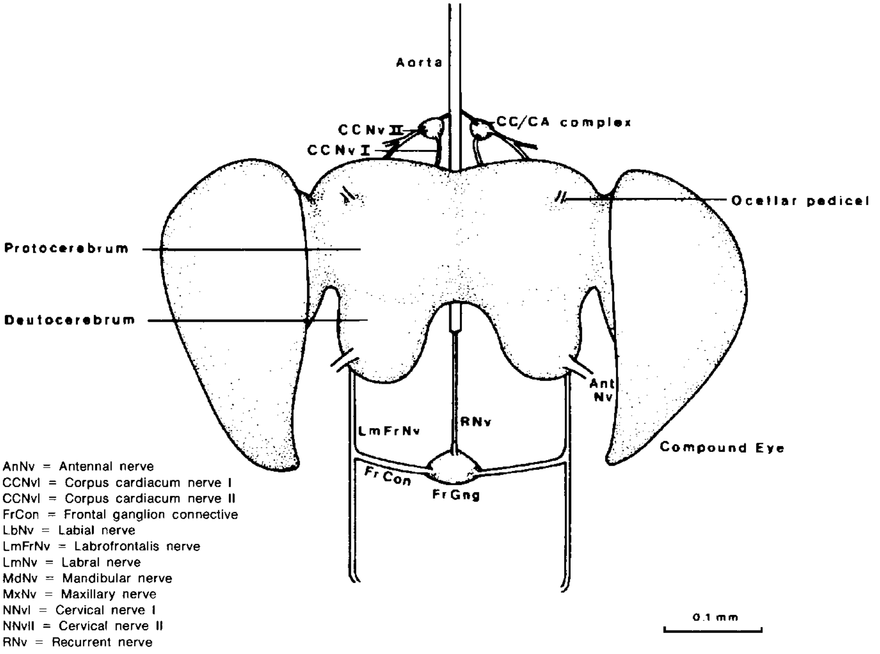


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Fig. 2. Dorsal aspect of the nerves associated with the brain of adult male *Choristoneura fumiferana*.

the lateral anterior corner of the CC/CA complex. CCNvII A, a branch of CCNvII thought to be associated with the CC/CA complex, branches off close to the complex and extends laterad and anterad alongside the anterior tentorial arm between the optic lobe and the rest of the brain.

The large, paired antennal nerves, containing both sensory and motor fibers, arise from the antero-lateral margins of the dorsal face of the deutocerebrum (Fig. 1). The motor fibers do not branch off until the antennal nerve is inside the antenna. These fibers innervate the seven pairs of antennal muscles that either insert on the antennal scape or pedicel. The remaining branch extends the length of the antenna innervating its sensory hairs (Albert and Seabrook 1973).

The paired labrofontalis (LmFrNv) nerves arise from the lower region of the anterior surface of the tritocerebrum (Fig. 1) and innervate segment 1 of the insect (Snodgrass 1935). Midway between the tritocerebrum and the labrum this nerve divides into the frontal ganglion connective (FrCon) and the labral nerve (LmNv). The frontal ganglion connective, passes dorsad and mesad to enter the frontal ganglion (FrGng). The labral nerve continues anteriad towards the cuticle where it turns ventrad and mesad to enter the labral pilifer. There is variability in this system on the point of branching in the labrofrontalis nerve. Very infrequently the labral nerve and the frontal ganglion connective will arise separately from the face of the tritocerebrum.

The recurrent nerve (RNv) exits the posterior corner of the triangular-shaped frontal ganglion and proceeds posteriad. Immediately in front of the oesophageal canal, the recurrent nerve enters the aorta (Figs. 1 and 2) and passes through the oesophageal canal inside this structure. A pair of very fine nerves branch laterally off the recurrent nerve and innervate the posterior corners of the CC/CA complex. The CC/CA complex lies on either side of the aorta.

Nerves of the Suboesophageal Ganglion (SOG)

Five pairs of nerves exit from SOG and innervate segments 2, 3, 4, and 5 of the insect.

The mandibular nerve (MdNv) is small and exhibits considerable variability in its site of origin from the SOG, and in its course to the mandible. Most often it arises from the lower, anterior face of the SOG within the same sheath as the maxillary nerve (MxNv). When this occurs, the mandibular nerve separates from the maxillary nerve as the latter proceeds anteriad towards the surface of the head capsule. The mandibular nerve continues anteriad and dorsad and near the cuticle, turns laterad to innervate the mandibular muscle close to its point of insertion on the mandible. Less frequently, the mandibular nerve may arise separately from the maxillary nerve. When this occurs, it arises immediately above the maxillary nerve from the anterior surface of the SOG. It should be noted that occasionally the mandibular nerve may anastomose with the labral nerve (LmNv). When this occurs, the two bifurcate just before reaching the cuticle, the labral nerve extending into the pilifer, and the mandibular nerve turning laterad to innervate the mandibular muscle.

The maxillary nerve (MxNv) arises from the lower anterior surface of the SOG and proceeds anteriad. At the point of insertion of the maxillary muscles on the stipes, this nerve divides into several small branches. One of these turns mesad and enters the galea, and another extends laterad and anteriad to enter the maxillary palp. The remaining branches of the maxillary (MxNv) nerve innervate four pairs of maxillary muscles.

The labial nerve (LbNv) arises from the lateral margin of the ventral surface of the SOG. Two minor branches arise close to the ganglion. One turns mesad and ventrad to innervate muscle 10, a labial muscle. The other branch turns laterad and ventrad to innervate muscle 11, another labial muscle. The major branch enters the labial palp.

Two pairs of nerves innervating the cervical muscles of *C. fumiferana* leave the ventral nerve cord immediately posterad of the SOG (Fig. 1). Cervical nerve I (NNvI) arises from the lateral surface of the ventral nerve cord (VNC). It proceeds posteriad, running parallel to the VNC until it passes through the occipital foramen at which point it proceeds dorsad to innervate muscle 18, a depressor muscle of the neck. Cervical nerve II (NNvII) arises from the lateral surface of the VNC at the occiptal foramen. It extends posteriad, running parallel to the VNC and ventral to NNvI for a short distance. It then turns laterad and bifurcates. The dorsal branch, NNvII A, innervates neck muscle 24, a depressor/retractor muscle. NNvII B, the ventral branch, turns postero-lateral to innervate muscle 19, a depressor muscle of the neck.

DISCUSSION

The neuromorphology of the brain and SOG in the adult male spruce budworm follows the general plan seen in other adult Lepidoptera (Ehnbom 1948; Eaton 1974). Variations most commonly occur in the location and in the frequency of branching of the nerves, and in the route followed to their target organs.

The degree of fusion between brain and SOG in *C. fumiferana* is characteristic of other Lepidoptera (Ehnbom 1948). Members of the Tortricidae are classified as having Type III brains, by Ehnbom (1948). In this category the optic lobes and the brain extend primarily in a dorsal-ventral direction, a feature which *C. fumiferana's* brain does possess. *Choristoneura fumiferana,* however, also possesses such features as the deutocerebrum being visible from the dorsal aspect, long labrofrontalis nerves and a frontal ganglion which is situated anterior to the brain; these are features of a Type II brain (Ehnbom 1948).

Nerves of the Brain

Two pairs of corpora cardiaca nerves arise from the posterior face of the brain of *C. fumiferana* and innervate the paired CC/CA complexes. These nerves are present in all other Lepidoptera studied with the CCNvII arising lateral to CCNvI in all cases. The deutocerebral nerves of all Lepidoptera studied consist of one pair of antennal nerves. As in *C. fumiferana,* the motor nerve fibers do not branch off the main nerve until it is inside the scape of the antenna in *H. zea* (Chauthani and Callahan 1967) and in *A. polyphemus* (Nuesch 1957). In *M. sexta* (Eaton 1974) and in *D. plexippus* (Ehrlich and Davidson 1961), the motor nerve fibers branch off from the antennal nerve before the antennal nerve enters the scape.

The tritocerebral nerves of Lepidoptera may include a labral nerve, frontal ganglion connective, and tegumentary nerve. However, all three nerves are not always present. A pair of labrofrontal nerves are present in *C. fumiferana* which bifurcate into the lateral nerves and the frontal ganglion connectives.

There was no evidence of a tegumentary nerve in *C. fumiferana*. This nerve, or variation of it, is mentioned by Ehnbom (1948) and is present in adults of *M. sexta* (Eaton 1974) and *D. plexippus* (Norlander and Edwards 1968), but not of *H. zea* (Chauthani and Callahan 1967).

Ehnbom (1948) claims that a labrofrontalis nerve is rare in Lepidoptera and is not found among more primitive species. In the over 155 species of Lepidoptera which Ehnbom (1948) looked at, a labrofrontalis nerve was observed only in one Noctuid moth, *Hyphilare lithargyria* (Esp.). The three species of tortricids examined in Ehnbom's study did not possess this nerve. As a rule, the frontal ganglion connectives and labral nerves are separate. Schroen et al. (1978) reported a clypeo-labral nerve as a branch off the frontal ganglion connectives in the 6th instar larva of *C. occidentalis*. Unfortunately, the adult state of *C. occidentalis* was not studied. Most recent papers on the various lepidopterans not covered by Ehnbom do not mention a labral nerve. Eaton's (1974) paper on *M. sexta* describes the frontal connective and tegumentary nerves as the only tritocerebral nerves. *Antherea polyphemus* also possesses frontal connectives. *Heliothis zea* has a tritocerebral nerve which innervates the proboscis, the maxillary palp and the frontal ganglion (Chauthani and Callahan 1967). Nordlander and Edwards's (1968) study on *D. plexippus* briefly mentions the presence of a labral nerve, which along with frontal connectives and tegumentary nerves constitute the nerves of the tritocerebrum.

Nerves of the SOG

Five pairs of nerves arise from the SOG in adult male *C. fumiferana*. *Choristoneura fumiferana* possess a mandibular nerve which often arises within the same sheath as the maxillary nerve. A short distance from the ganglion this common nerve bifurcates. Occasionally the mandibular nerve will anastomose with the labral nerve and pass for a short distance before dividing. This condition is unique to *C. fumiferana*. In *M. sexta* (Eaton 1974), the mandibular nerve arises separately from the maxillary nerve and its main branch innervates the mandibular muscle giving rise to branches which combine with the procurrent nerve from the frontal ganglion. The mandibular nerve in *D. plexippus* arises immediately above the maxillary nerve and bifurcates, with one branch running parallel to the frontal ganglion connective and eventually anastomosing with the procurrent nerve (Ehrlich and Davidson 1961). The other branch extends to the front of the head capsule where it appears to innervate a muscle and a pilifer. *Choristoneura occidentalis* larvae possess a mandibulo-lateral nerve while the major branch innervates the abductor muscle of the mandible and gives rise to a smaller nerve which anastomoses with the clypeo-labral nerve. Neither *A. polyphemus* (Neusch 1957) nor *H. zea* (Chauthani and Callahan 1967) possess a mandibular nerve.

In *C. fumiferana*, the maxillary nerve arises from the anterior surface of the SOG and innervates the maxillary muscles, the galea, and the maxillary palp. This nerve in *M. sexta* arises from the same area and branches of it innervate the maxillary muscles and proboscis. One branch connects this nerve to the corpora cardiaca (Eaton 1974). The maxillary nerves in both *D. plexippus* (Ehrlich and Davidson 1961) and *A. polyphemus* (Neusch 1957) also innervate the proboscis and maxillary muscles. The labial-maxillary nerve found in larvae of *C. occidentalis* runs forward to the base of the maxilla where it innervates muscles of the 'silk gland complex' (Schroen et al. 1978).

The labial nerve in *C. fumiferana* is short and originates from the ventral surface of the SOG. Two small branches of this nerve innervate labial muscles while its main branch extends into the labial palpus. A similar condition occurs in *D. plexippus* (Ehrlich and Davidson 1961) and *A. polyphemus* (Neusch 1957). Eaton (1974) indicated that two labial nerves are present in *M. sexta*. One of these has an innervation field similar to the labial nerve in *C. fumiferana*; the other innervates a hair plate.

Various depressor muscles in the neck and prothorax of *C. fumiferana* are innervated by two pairs of cervical nerve arising from the VNC immediately posterior to the SOG. This is similar to that found in *D. plexippus* (Ehrlich and Davidson 1961), *A. polyphemus* (Neusch 1957), *M. sexta* (Eaton 1974), and larval *C. occidentalis* (Schroen et al. 1978) which also have two pairs of cervical nerves. In addition, in all species reported above, the second nerve divides into a dorsal and a ventral branch as in *C. fumiferana*. These nerves innervate muscles in the neck and prothoracic regions, and in *D. plexippus*, one small branch innervates a sensory area in the vertex of the head capsule (Ehrlich and Davidson 1961). Based on site of origin, branching patterns and innervation, NNvI in *C. fumiferana* appears to be homologous to ON5 in *M. sexta* and ON3 in *A. polyphemus*, and likewise NNvVII in *C. fumiferana* is homologous to ON6 in *M. sexta* and ON4 in *A. polyphemus*.

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