

NABIL N. YOUSSEF

*Topography of the
Cephalic Musculature
and Nervous System
of the Honey Bee
Apis mellifera Linnaeus*

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Cephalic Musculature
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ABSTRACT

Youssef, Nabil N. Topography of the Cephalic Musculature and Nervous System of the Honey Bee *Apis mellifera* Linnaeus. *Smithsonian Contributions to Zoology*, number 99, 10 figures, 5 tables, 54 pages. 1971.—Fixed heads of workers, drones, and queens of *Apis mellifera* Linnaeus were dissected under distilled water for the study of two tissues: the musculature and the nerve mass.

Musculature: The movable and fixed points of muscle attachment were utilized in establishing a nomenclature for muscles to replace the systems in current usage, which depend on various combinations of topography, function, and numerical sequence. The present system proved to be consistent and useful for demonstrating the criteria of homology among muscles. Names were devised in classical Greek and Latin for international usage. For establishing muscle homology, every cephalic muscle of the three castes was compared with its homolog in other studied taxa of Hymenoptera and Neuroptera. The labial and epipharyngeal muscles are degenerate and the antennal muscles maintain primitive features. The mandibular complex consists of two well-developed muscles and a degenerate muscle which is probably modified to serve as a stretch organ. The maxillary muscles maintain the same points of attachment as in primitive insects, although the *musculus tentorio-cardinalis* has shifted its point of movable attachment to the stipes in the female bees to meet a change in function. The maxillary palpal muscles have disappeared as a result of the reduction of the palpus itself. Many of the labial muscles have shifted one or both points of attachment as a result of the specialization of the labium. The *musculus postoccipiti-prementualis* even has different points of fixed attachment among the different castes.

As a result of simplification of the "hypopharynx," many of its muscles have shifted their points of attachment. The musculature of the clypeal walls are well developed to accommodate the enlargement and specialization of the cibarium.

In this study the following undescribed muscles were found and named: *musculus tentorio-mandibularis*, *m. stipiti-maxillopalpalis*, *m. oriscuto-supensorialis*, and *m. fronto-pharyngealis III* (only in the drone).

Nerve Tissue: Existing literature indicates that only a few of the cephalic nerves have been named. Accordingly, a new system was developed under which the name of each nerve or nervule is based on the structure it innervates. Main ganglia are named according to their locations, rather than following the traditional inconsistent nomenclature. The names are in classical Greek or Latin form for international usage. Every cephalic nerve or nervule was followed to its termination. When sufficient literature was available, the criteria of nerve homology were examined. Nerve topography follows a similar plan in the gnathal segments of the three castes, except that the *Nervus Mandibularis* is degenerate in the drone. It was noted that variation in the topographical plan of a particular nerve is very small, even among members of different castes.

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Contents

	<i>Page</i>
Introduction	1
Materials and Methods	2
PART I. MUSCULATURE	
History	5
Methods of Nomenclature	8
Methods Used in Previous Studies	8
Methods Used in the Present Study	10
Topography and Homology of Musculature	10
Labral Muscles	11
Epipharyngeal Muscles	13
Antennal Muscles	13
Mandibular Muscles	14
Maxillary Muscles	15
Labial Muscles	18
Hypopharyngeal Muscles	20
Anterior Cibarial Wall Muscles	22
Pharyngeal Muscles	23
Dorsal Muscles of the Pharynx	23
Ventral Muscles of the Pharynx	24
Circular Muscles of the Pharynx	24
PART II. NERVOUS SYSTEM	
History	25
Methods of Nomenclature	25
Main Ganglia and Their Divisions	25
Nerves and Their Branches	28
Topography and Homology of the Cephalic Nerve Tissue	29
Location and Topography of the <i>Ganglion Hyperoesophagale</i>	29
<i>Ganglion Proto-Hyperoesophagale</i>	30
<i>Lobus Opticus</i>	30
<i>Nervi Optici</i>	30
<i>Nervi Ocellares</i>	31
<i>Ganglion Deuto-Hyperoesophagale</i>	31
<i>Nervus Antennalis</i>	31
<i>Ganglion Trito-Hyperoesophagale</i>	33
<i>Nervus Ganglii Pharyngealis</i>	33
<i>Nervus Labralis</i>	35
<i>Nervus Corpoallatialis</i>	36
<i>Commissura Gangliorum Trito-Hyperoesophagalium</i>	36
<i>Nervulus musculi Tentorio-oriscutarius</i>	36
Location and Topography of the <i>Ganglion Hypoesophagale</i>	36
<i>Nervus Mandibularis</i>	37
<i>Nervus Maxillaris</i>	38
<i>Nervus Labialis</i>	40
<i>Nervus Tegumentualis</i>	41
<i>Nervus Postoccipitalis</i>	42
<i>Nervus Posterior</i>	42
Acknowledgments	42
Literature Cited	42

Nabil N. Youssef

Topography of the Cephalic Musculature and Nervous System of the Honey Bee *Apis mellifera* Linnaeus

Introduction

The concept of homology, which expresses the continuity of structure in phylogeny, can be approached in many ways: comparisons of external elements, examinations of embryonic and postembryonic structures, and by following the topography and innervation of muscles. The occurrence of one of the following phenomena limits the validity of any single approach: the loss of external structures in some groups; the presence in others of secondary splits in the embryo, suggesting ancestral structures or segmentation; the tendency of some muscles to shift their points of attachment; or the innervation of a single muscle from more than one ganglion. Consequently, a valid study of homology in insect morphology requires the use of as many lines of evidence as possible.

Many morphologists and taxonomists have studied primarily the external structures, especially those tending to be the least consistent (genitalia, thoracic sclerites, mouthparts). The result is a vast amount of literature emphasizing diversity rather than homology, although the latter has not been entirely neglected.

Embryological studies have lagged for various reasons, including the following: (1) embryological stages in insects are often of such short duration that the succession of forms is hard to define, (2) larvae are generally too advanced in development to be

considered truly embryonic and can in no sense be attributed to "early hatching" of the embryo, (3) the small size of insect eggs limits flexibility in experimental methods, (4) adequate techniques for tissue culture of insect embryos have yet to be developed.

Topographical studies of insect musculature have been more numerous than those of the nervous system; however, attempts to examine the criteria of muscle homology have been made only recently. Matsuda (1965) is probably the first and only one to review this subject in detail.

The nervous systems of insects in general have been extensively and intensively studied. The gross anatomy of the "brain" and "ventral nerve cord" and the diversity exhibited by these structures have been described for many species. We have few detailed studies (Holste 1910, Denis 1928, Maki 1936, and Chaudonneret 1950-1951), however, of topographical nerve patterns and the actual innervation of muscles.

Although the honey bee, *Apis mellifera*, has had its share of morphological studies relative to external structure (Snodgrass 1910, 1925, 1956) and embryology (Nelson 1915), the study of muscle homology between its different segments and between its musculature, as a whole, and those of other insects is still in its infancy. The topography of the honey bee nervous system is in the same situation. Although there has been intensive histological work on the so-called brain of the honey bee (Kenyon 1896, Jonescu 1909, Jawlowski 1958, and Satija 1958), the

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only publication dealing with the innervation of the cephalic muscles seems to be a skimpy one by Rehm (1939) describing the innervation of the *musculus cranio-intramandibularis*.

A few workers have studied muscle-nerve patterns in insects, but attempts to compare the patterns in order to establish segmental homology or to identify segmental features common to several orders have been generally fragmentary. This is largely because of difficulties in recognizing homologous nerve groups, due in part to the current unsuitable nomenclatorial systems for insect muscles and nerves, and in part to the bundling of the proximal portion of many nerves in different ways in different segments and in different taxa.

The principal objective of the investigation reported here was to develop a complete account of the topography of nerve tissues and musculature of the honey bee head. A second objective was to determine, with a reasonable degree of accuracy, the probability of homology by comparing the topography of cephalic nerves and muscle arrangements of the honey bee with those of previously studied groups, especially the ones related and supposedly ancestral to it.

The current multifarious nomenclatorial systems for nerves and muscles create a difficult obstacle in comparative morphology. A modified system, approaching most closely that of Hannemann (1956), for naming the muscles and a new system of naming nerves were developed for this study in the hope that they would set a consistent pattern which could be used without extensive modification in future work.

In the course of the study several other members of the superfamily Apoidea, as well as the vespid *Vespula maculata* (Linnaeus), were dissected for comparison.

Materials and Methods

Adult workers, drones, and queens of the honey bee were provided by the Federal Wild Bee Pollination Investigations Laboratory at Logan, Utah. The bees were immobilized with carbon dioxide and injected with picroformalin until their abdomens expanded slightly. The injected bees were stored in picroformalin for at least 48 hours before being dissected. Eventually, it was discovered that if the injected bees were simmered in the fixative for three minutes, they could be dissected without further delay.

In the study of head muscles and nerve tissues, it was found convenient to isolate the head from the rest of the body and bisect it medially. Each half was glued (with the cut side up) to the bottom of a plastic container ($\frac{1}{2} \times 2 \times 1\frac{1}{2}$ inches), using Sticky Wax supplied by Kerr Manufacturing Company.

With the aid of a dissecting stereomicroscope ($40-120\times$), with the focusing mechanism adapted to foot manipulation, the muscles and nerves were revealed by dissecting downward, layer by layer, from the median section. To obtain a true picture of the relationships of different tissues, each muscle, nerve, and nervule was observed from various aspects and followed to its termination. For this purpose, other types of specimen orientation were used, such as: (1) embedding the head laterally and exposing one half for dissection; (2) gluing the head on its occipital aspect to present a frontal view of the nerve tissues and the prepharyngeal and pharyngeal muscles; (3) isolating the labium, antenna, and maxilla from the head to study their muscles and nerves separately; (4) embedding the head laterally to the level of the antennae for a study of the head glands and their innervation, and of the antennal muscles and their innervation.

Dissections were performed under distilled water after the specimens were washed several times with 70 percent alcohol. Bee's heads were dissected with knives made of razor blade edges, with needles made of ground-down "minuten nadeln" (Stajanovich 1945), and with ground-down jeweler's forceps. In the course of study, about 2,000 workers, 200 queens, and 500 drones were dissected.

A differential staining technique was developed for tissues found in the head (nerves, muscles, glands, etc.). After reaching a preliminary stage of dissection, the specimens were washed with 70 percent alcohol for one minute. The excess alcohol was drained and a drop of acetocarmine and another of iron hydrate (0.25 percent in 50 percent acetic acid) were applied directly to the specimens. Staining time varied from two to five minutes for different specimens, depending upon the duration of storage in the picroformalin. When necessary, the same technique was repeated for different stages of dissection.

For the preservation of dissected specimens, a mixture of one part U.S.P. glycerol and one part distilled water was found to be superior to different dilutions

of ethanol. Dissected specimens preserved in this mixture since September 1963 are still in excellent condition as this manuscript is written.

Staining with acetocarmine and iron hydrate was unsatisfactory for the study of nerve endings or receptors other than the compound eyes. Palmgren's silver pyridine technique (1955) for whole mounts

of nerve and muscle tissues proved more suitable. The staining schedule followed that already described (Youssef 1964).

Drawings for different stages of dissection were made with the aid of an ocular grid. The illustrations were designed to show the precise arrangement of nerves, muscles, and other tissues.

PART I. MUSCULATURE

History

Although the order Hymenoptera is the second largest in number of species, investigations dealing with its body musculature, in general, and its head musculature, in particular, tend to be scarce and incomplete. This review is mainly concerned with those articles investigating the cephalic musculature of Hymenoptera.

In the Symphyta the Tenthredinidae has been given more attention than other families, probably because of its primitive nature. Taylor (1931) worked on the morphology of a few species but his work is far from complete.

Matsuda (1957) studied the cephalic external and internal morphology of *Macrophya pluricincta* Norton is an attempt to correlate it with that of higher groups of Hymenoptera. He also attempted to test several theories with regard to the external morphology of the facial region. In his descriptive section, he classified the muscles into groups but gave each muscle a separate number. In the illustrations, however, he devised names for some muscles by hyphenating the two names of the structures to which they are attached. He derived the first part of the name from the point of fixed attachment (point of origin), e.g., frons-epipharynx, vertex-stomodaeum, etc. Matsuda's nomenclature, based on a different number for each muscle, was occasionally inaccurate. For example, he gave the numbers "22-23" to both flagellar muscles (p. 105, pl. III: fig. E) and mandibular muscles (p. 103, pl. II: fig. B). Although he used consecutive numbers for the most part, he skipped numbers "17" and "18" for no apparent reason. According to Matsuda, muscle "26" comes from the ventral side of the composite tentorial bar and inserts on the base of the lacinia. On page 105, plate III: figure F, he identifies this muscle as "Tentorium-Lacinia," whereas the drawing itself shows that its movable point of attachment is on the stipes rather than the lacinia. If it is assumed that this muscle shifted its movable point of attachment to the stipes (although remaining in reality a "tentorio-lacinial muscle"), there is still a contradiction with Matsuda's later work (1965:268) in

which he states that "the *tentorio-lacinial* muscle has been found in *Machilis* only." It seems strange that muscle "35" (t-s) of *Macrophya* has no homolog in the other groups of insects he studied. Matsuda's general plan for labial muscles (1965), which he based on the available literature of cephalic muscles of insects, indicates that such a muscle does not exist in insects.

In the Apocrita the cephalic muscles of four genera have been studied in detail: *Stenobracon* (Braconidae), *Lasius* (Formicidae), *Vespula* (Vespidae), and *Apis* (Apidae).

Alam (1951) studied the cephalic muscles of *Stenobracon deesae* Cameron. He followed the pattern of nomenclature used by Duncan (1939) and Snodgrass (1942) and tried to homologize many muscles with those of other Hymenoptera and with those described for *Gryllus* by Duporte (1920). Apparently Alam did not believe that muscles are plastic enough in phylogeny to shift their points of attachment or combine with other muscles. For details see his discussion on page 15 (1951) in regard to the "flexor of maxilla" (*musculi tentorio-stipitales*) and the "second flexor of lacinia" (*musculus stipiti-lacinialis*).

Janet (1905) studied the cephalic musculature of the ant *Lasius niger* Reine by means of longitudinal sections. Although this technique is practical for studying small organisms, it hinders the investigator from determining exact locations or functions of muscles. His study is nearly complete but his illustrations are difficult to follow. In some instances he described muscles in detail but in others he merely named them.

Duncan (1939) studied and illustrated the musculature of *Vespula pennsylvanica* Saussure in an essentially complete fashion. However, I discovered two pairs of muscles in the head of *Vespula maculata* which Duncan must have missed because of their smallness. Duncan adopted the nomenclatorial system proposed by Berlese (1909), Bauer (1910), and others which is based largely on function rather than exact position.

Hymenoptera	Hymenoptera	Hymenoptera	Hymenoptera	General		
<i>Apis mellifera</i> Linn.	<i>Apis mellifera</i> Linn.	<i>Apis mellifera</i> Linn.	<i>Apis mellifera</i> Linn.			
Wolff, 1875	Morison, 1927	Snodgrass, 1942	Present Study	Matauda, 1965		
Name	Abr. Name	Abr. Name	Abr. Name	Abr. Name		
	<u>levator labri</u>	adductor of labrum	1 <u>fronti-labralis</u>	<u>m. fron-labr.</u> posterior fronto-labral anterior fronto-labral labro-epipharyngeal	61 62 63	
<u>levator veli planti</u>	<u>levator veli planti</u>	retractor or levator of epipharynx	25 <u>clypeo-epipharyngealis</u>	<u>m. clyp-epiph.</u> anterior clypeo-epipharyngeal	81	
	<u>musculi antennae</u>	extrinsic muscles of antenna	2 <u>tentorio-scapularis I</u> 3 <u>tentorio-scapularis II</u> 4 <u>tentorio-scapularis III</u> 5 <u>tentorio-scapularis IV</u>	<u>m. tent-scap. I</u> <u>m. tent-scap. II</u> <u>m. tent-scap. III</u> <u>m. tent-scap. IV</u>		
	<u>abductor articuli secundi antennae</u> <u>adductor articuli secundi antennae</u>	levator of antennal flagellum depressor of antennal flagellum	6 7	<u>m. scapo-pedicularis I</u> <u>m. scapo-pedicularis II</u>		
	<u>extensor mandibulae flexor mandibulae</u>	abductor of the mandible adductor of the mandible a, b	8 9a,b	<u>m. cran-extramand.</u> <u>m. cran-intramand.</u>	tergo-mandibular tergo-mandibular	23 21
				<u>m. tent-mand.</u>	tentorio-mandibular	25
<u>protractor cardinis vel maxillae inferior externus protractor cardinis vel maxillae inferior internus</u>	<u>extensor maxillae externus</u>	promotor of the maxilla or cardinal protractor of proboscis	10	<u>geno-cardinalis</u>	<u>m. geno-card.</u> tergo-cardinal	1
	<u>extensor maxillae internus</u>	adductor of the maxilla	11	<u>tentorio-cardinalis</u>	<u>m. tent-card.</u> tentorio-cardinal	3
<u>retractor maxillae inferioris major</u> <u>retractor maxillae inferioris minor</u>	<u>flexor maxillae major</u> <u>flexor maxillae minor</u>	adductor of maxilla	12 13	<u>tentorio-stipitalis I</u> <u>tentorio-stipitalis II</u>	<u>m. tent-stip. I</u> <u>m. tent-stip. II</u> tergo-lacinal	4 5
	<u>flexor labi externi maxillaris</u>	flexor of lacinia flexor of galea	16 15	<u>stipiti-laciniaris</u> <u>stipiti-galearis</u>	<u>m. stip-lac.</u> <u>m. stip-gal.</u> stipito-lacinal stipito-galeal	6 7
				<u>stipiti-maxillopalpalis II</u>	<u>m. stip-maxpalp. II</u> antagonistic muscles of palpus from atipes	9&10
<u>spanner des segelhalters?</u>	<u>extensor labi externi maxillaris</u>	muscle of maxillary palpus	14	<u>stipiti-maxillopalpalis I</u>	<u>m. stip-maxpalp. I</u> palpus from atipes	
<u>retractor linguae longus</u>	<u>retractor lingulae superior</u>	anterior adductor of labium	17	<u>postoccipiti-prementualis</u>	<u>m. postoccip-prement.</u> postoccipito-premental	34
<u>protractor labii inferior vel menti</u>	<u>protractor labii</u>	posterior adductor of labium	18	<u>tentorio-prementualis</u>	<u>m. tent-prement.</u> tentorio-premental	35
<u>retractor linguae brevis</u>	<u>flexor palpi maxillaris</u>	prementum retractor of ligula		<u>premento-paraglossaris</u>	<u>m. prement-paragloss.</u> submento-mental premento-ligular	41 43
<u>retractor linguae biceps</u>	<u>retractor lingulae inferior</u>	flexor of the glossa		<u>premento-glossaris</u>	<u>m. prement-gloss.</u> premento-glossal submento-premental	42 38
	<u>extensor palpi secundi maxillaris</u> <u>extensor palpi maxillaris</u>	muscle of 2nd seg. of labial palpus flexor of labial palpus	22 21	<u>labiopalporum I-II</u> <u>premento-labiopalpalis</u>	<u>m. labiopalp. I-II</u> <u>m. prement-labiopalp.</u> premento-palpal tentorio-paraglossal	44&45
<u>protractor linguae</u>	<u>ampullae superior</u>	dilator of salivary syringe	23	<u>dorsopremento-salivarius</u>	<u>m. dorsoprem-saliv.</u> dorsal dilator salivarial	17
<u>retractor linguae biceps</u>	<u>dilator ampullae salival posterior</u> <u>retractor pharyngis superior</u>	compressor of salivary syringe retractor of oral plate	24 33	<u>basipremento-salivarius</u> <u>fronti-suspensorialis</u>	<u>m. basiprem-saliv.</u> <u>m. fron-susp.</u> posterior premental salivarial fronto-hypharyngeal	44 or 47 74
<u>retractor pharyngis inferior</u>	<u>protractor pharyngis</u>	protractor of oral plate	32	<u>clypeo-suspensorialis</u>	<u>m. clyp-susp.</u> clypeo-hypharyngeal	75
	lateral dilator	posterior contractor of pharynx	37	<u>tentorio-oriscutarius</u>	<u>m. tent-oriscut.</u> tentolo-oral	87
	lateral compressor	paratral contractor of pharynx	38	<u>tentorio-suspensorialis</u>	<u>m. tent-susp.</u> anterior tentorio pharyngeal	88
	<u>dilator pharyngis</u>			<u>oriscuto-suspensorialis</u>	<u>m. oriscut-susp.</u>	
	01		26			
	02		27	(5-7 muscles)		
	03	<u>dilator pharyngis</u>	28	<u>clypeo-cibarioparietalis</u>	<u>m. clyp-cibariet.</u> clypeo-dilator of the cibarium	81-82
	04		29			
	05	<u>pharyngeal compressor</u>	30			
		compressor of the suctorium	31	<u>intrasuspensorialis dorsalis</u>	<u>m. intrasusp. dors.</u> longitudinal muscle of the pharynx	91&92
	<u>dilator pharyngis</u>	precerebral dilator of pharynx	34	<u>fronti-pharyngealis I</u>	<u>m. fron-phar. I</u> precerebral dorsal dilator of the pharynx	83 84
			35	<u>fronti-pharyngealis II</u> <u>fronti-pharyngealis III</u>	<u>m. fron-phar. II</u> <u>m. fron-phar. III</u>	85
		postcerebrae of pharynx	36	<u>cranio-pharyngealis</u>	<u>m. cran-phar.</u> posterior dorsal dilator of pharynx	86
		constrictor of the pharynx	36	<u>circulopharyngealis</u>	<u>m. circ. phar.</u> ring muscle	

TABLE 1.—Cephalic musculature of some representatives of hymenopteroid and neuropteroid insects

Order	Neuroptera	Hymenoptera	Hymenoptera	Hymenoptera		
Species	<i>Corydalus cornutus</i> Linn.	<i>Macrophys pluricincta</i> Norton	<i>Stenobracon deesse</i> Cameron	<i>Vespa pensylvanica</i> Sauss.		
Author	Kelsey, 1954	Matsuda, 1957	Alam, 1951	Duncan, 1939		
Muscle	Name	Abr. Name	Abr. Name	Abr. Name		
Labral	tromal muscle of the labrum	3 frons-epipharynx	1 abductor of the labrum	1		
	retractor of the labrum	2 frons-epipharynx	2			
	compressor of the labrum	1				
Epipharyngeal	first dorsal dilator of cibarium	35 labrum-epipharynx	3&4 retractor of the epipharynx	2 clypeo-dilator of the mouth	cdmth	
Antennal	first promotor of the antenna	4	19 external depressor	7 external antennal depressor	ead	
	second promotor of the antenna	4a	20 internal depressor	8a,b internal antennal depressor	cad	
	first retractor of the antenna	6	21 external levator	6 external antennal levator	cal	
	second retractor of the antenna	6a	22 internal levator	5 internal antennal levator	ial	
	levator of flagellum	7	muscles of the flagellum	22 levator of flagellum	9	
	depressor of flagellum	8		23 depressor of flagellum	10	
Mandibular	abductor of the mandible	9 abductor of the mandibla	22 abductor of the mandibla	3 mandibular abductor	abmd	
	adductor of the mandible	10 adductor of the mandibla	23 adductor of the mandibla	4 mandibular adductor	admd	
Maxillary	abductor of the cardo	11		first protractor of the maxillae	22 product of the cardo	
	proximal adductor of cardo	12	tentorium-cardo?	25 second protractor of maxillae?	23 extensor of the maxilla?	exm
	distal adductor of cardo	13				
	compressor of the cardo	14				
	adductor of stipes	15	tentorium-lacinia	26 flexor of maxillae	24 flexor of stipes	fst
	abductor of stipes	16				
	cranial flexor or adductor of lacinia	17		second flexor of lacinia	26	
	stipital flexor of lacinia	18	stipes-lacinia	27 flexor of lacinia	25 flexor of lacinia	flc
	flexor of galea	19	stipes-galea	30 flexor of galea	27 flexor of galea	fga
	levator of maxillary palpus	20	stipes-palpus	29	28 anterior depressor of maxillary palpus	adm
	depressor of maxillary palpus	21	stipes-palpus	28	29 posterior depressor of maxillary palpus	pdm
	muscle of 1st segment of maxillary palpus	22		31 flexor of palpal segment	a	
	muscle of 2nd segment of maxillary palpus	23		32 flexor of palpal segment	b	
	muscle of 3rd segment of maxillary palpus	24	muscles of maxillary palpus	33 flexor of palpal segment	c	
	muscle of 4th segment of maxillary palpus	25		34		
Labial	levator of paraglossa	28 tentorium-prementum	36 posterior adductor	14 flexor of paraglossa	fgl	
	depressor of prementum	26 tentorium-glossa		13 posterior labial adductor	plad	
			prementum-paraglossa	39 ligular flexor	17 anterior flexor of lingula	aftl
			prementum-glossa	41&43 lingual flexor	16 posterior flexor of lingula	plf
	retractor of the mentum	34 submentum-prementum	38			
	extensor of palpiger	27 tentorium-submentum	35			
	levator of the palpus	27		04		
	abductor of labial palpus	31 prementum-palpus	42	42 flexor of the palpus	18 depressor of labial palpus	dlbp
	muscles of labial palpus	32 muscles of labial palpus	44,45	44,45 flexor of the palpus	19	
		33 palpus	46	46 flexor of the palpus	20	
Hypopharyngeal	dorsal muscle of salivary pump	29 muscles of salivary syringe	48 anterior dilator of salivarium	12 dilator of salivarium	dmsl	
	ventral muscle of salivary pump	30	48 posterior dilator of salivarium	11 posterior muscle of salivarium	pmsl	
	retractor of the mouth angle	42 frons-stomodaeum	9 frontal dilator of pharyngeal diverticula	35		
	first lateral dilator of pharynx	42 tentorium-stomodaeum	12 tentorial dilator of pharyngeal diverticula	34 lateral pharyngeal muscle	lphm	
	second lateral dilator of pharynx	44				
	ventral dilator of cibarium	43 tentorium-stomodaeum	13 second ventral dilator of anterior pharynx	37 posterior dilator of anterior pharynx	3dph	
	ventral dilator of anterior pharynx	46				
	first ventral dilator of posterior pharynx	47 tentorium-stomodaeum	14 first ventral dilator of anterior pharynx	36 ventral dilator of posterior pharynx	4dph	
	second ventral dilator of posterior pharynx	48				
	third ventral dilator of posterior pharynx	49				
	ventral constrictor of cibarium	51			posterior intrinsic pharyngeal muscle	ptim
	Anterior cibarial wall	first dorsal dilator of cibarium	35 clypeus-stomodaeum	5 clypeal dilator of anterior pharynx (one muscle)	30 dilator buccalis (one muscle)	dlbc
second dorsal dilator of cibarium		36	6			
			7			
			8			
	dorsal constrictor of cibarium	50 superficial muscle of stomodaeum	16	anterior intrinsic pharyngeal and Pharyngeal dilator of the mouth	atim pdmth	
Pharyngeal	first dorsal dilator of posterior pharynx	37 frons-stomodaeum	11 first frontal dilator of anterior pharynx	31		
	second dorsal dilator of posterior pharynx	38	10 second frontal dilator of anterior pharynx	32		
			11 third frontal dilator of anterior pharynx	33		
	dorsal dilators of anterior pharynx	39-40-41 vertex-stomodaeum	15 occipital dilator of posterior pharynx	38		
	constrictors of the pharynx	52-53			dorsal dilator of posterior pharynx intrinsic muscle of the pharyngeal diverticulum	2dph pdmth

Wolff (1875) was among the first to describe and illustrate cephalic muscles of the honey bee. These muscles were mainly those associated with what he called "the sucking organs." He also studied the pharynx and its muscles in great detail. His illustration of the muscles extending between the clypeus and the upper cibarial wall is very clear and generally more accurate than those made by later investigators.

Braints (1884) illustrated a few of the mouthpart muscles. Although he ascribed function to each muscle, he used only Arabic numbers for naming them.

Morison (1927) reviewed the fragmentary preceding work on the honey bee musculature. Following this he studied the musculature intensively and missed only several very small muscles. Although the points of attachment indicated by him are not always accurate, his study formed the basis for subsequent investigations on honey bee musculature, including those of Snodgrass (1942-1956).

Snodgrass (1942), in his study of the skeleto-musculature mechanisms of the honey bee, was the first to correlate carefully the findings on musculature with those on the endo- and exoskeletal structures. In the course of reviewing the musculature, he corrected a few errors committed by Morison and others. However, his study of the muscles attached to the upper wall of the cibarium is inaccurate. He stated that there were five pairs of cibarial muscles, but his drawing (p. 31, fig. 10c) showed only five unpaired ones. These muscles are attached to the cibarial wall in the manner described by Wolff (1875, pl. II: fig. 9) rather than Snodgrass (1942, 1956).

Since only the fragmentary investigations made by Snodgrass (1942), Alam (1951), and Matsuda (1957, 1965) have been reported, we have no complete study of muscle homology between the head of the honey bee and that of other insects.

Methods of Nomenclature

Although insect musculature has been investigated intensively, its nomenclature is still a challenge to the morphologist.

Table 1 compares nomenclatorial systems as they have been used by various authors for the cephalic muscles of a neuropteran and several species of Hymenoptera. It also indicates the different systems of nomenclature applied by different authors (Wolff,

Morison, and Snodgrass) for the cephalic muscles of the honey bee.

METHODS USED IN PREVIOUS STUDIES

Methods used in the past for naming insect muscles (Table 1) are as follows: (1) by arbitrary reference number; (2) according to function; (3) according to location on the main axis; and (4) according to the points of fixed and movable attachment. The first system is noncontroversial, but the names themselves are morphologically meaningless and hard to remember. The second system is misleading in relation to muscle homology. The traditional method of determining the function of each muscle is to use micromanipulation. The function of smaller muscles can only be determined by deduction, and this is often actually an "educated guess." Table 1 shows that different functional names have been given by different workers for the same muscles of *Apis mellifera*. Furthermore, it is difficult and often impossible to identify corresponding muscles on a functional basis. For example, a muscle may be a retractor in one species but its homolog in another may be an abductor because of a slight change in the point of fixed or movable attachment, or both. The *musculus gena-cardinalis* of the honey bee was designated by Snodgrass (1942) as "promoter of the maxilla" or "cardinal protractor of the proboscis"; whereas it is a "productor" in *Vespula*, according to Duncan (1939); and an abductor in the megalopteran, *Corydalus*, according to Kelsey (1954).

The third system is simple and precise, but unfortunately it is hard to apply to complicated structures such as the head, thorax, and genitalia. Nüesch (1953) adopted the "purely" morphological system utilized by Weber (1928, 1933) because, as he stated (p. 591), ". . . it seems to me to be more suitable than those which also consider the function, as in the case of the nomenclature of Snodgrass ('35) and Maki ('36)." Accordingly, Nüesch arranged the muscles (e.g., de_{1a} , de_{1b} , de_2 and de_3) of a location into a group named according to its placement (i.e., "dorsolongitudinal muscles").

The final system, that depending on the points of movable and fixed attachment, is flexible and makes it possible to locate quickly any muscle in a dissected specimen. It can be criticized, however, on the basis of arguments concerning the homologies of sclerites

in different orders and also because of the tendency of some muscles to shift their points of fixed or movable attachment, or both. Actually, muscles may be of more help in establishing the homology of sclerites than vice versa. There are two schools of thought regarding the value and reliability of muscles for establishing the homology of the skeletal parts to which they are attached, and contradicting claims have been made (Snodgrass 1935, 1942; Ferris 1942, 1944). If the muscles in question are serially repeated and their points of fixed and movable attachment are constant, however, their points of fixed attachment may be used with considerable assurance. Unless it is realized that musculature is a plastic system and that each muscle can shift its point of fixed attachment, as well as its movable one within certain limits, it becomes very difficult for the morphologist to establish any homology between different muscles in different segments of the same insect and between muscles in different groups of insects.

Many morphologists have attempted to name the muscles according to their points of fixed and movable attachment. Chaudonneret (1950–1951), in his study of the cephalic morphology of *Thermobia domestica* Packard, tried a combination system. He named each muscle according to its function; however, he grouped the muscles and named each group according to the points of fixed and movable attachment of its members.

Hannemann (1956), in his study of the cephalic musculature of *Micropteryx calthella* (Linnaeus), utilized the points of fixed and movable attachment in naming the muscles. The name of a given muscle was composed of the latinized name of the fixed attachment point, hyphenated to that of the movable attachment point, and followed in some instances by a general descriptive term to show the location of the muscle. This system has considerable merit, but the descriptive terms are misleading since they do not indicate the exact locations of the points of attachment. A muscle may have its point of fixed attachment in a lateral position and its point of movable attachment in a ventral position, as in the case of the *musculus fronti-labralis* in the honey bee which has a median point of fixed attachment and a lateral point of movable attachment.

Matsuda (1956:8) avoided naming the muscles according to their function on the basis "that the primary concern of the comparative morphologist

should be the morphological origin of musculature in relation to the external structure, regardless of its function." Although Matsuda made this statement at the time of his study, he failed to apply "morphological" names to every muscle. Instead, he placed the muscles into groups and gave each group a morphological name. Even so, he was inconsistent in naming the muscle groups. In some cases he named groups of muscles according to their placement (ventral muscles, spiracular muscles, etc.), and at other times according to the structures between which the muscles stretch (muscles from the notum to the lateral jugular membrane, muscles inserted on the coxal margin and on the membrane near the coxal margin, etc.).

Chadwick (1957), in his study of the intersegmental muscles of cockroaches, gave each morphologically distinct muscle a designation formed by hyphenating the accepted abbreviations for the skeletal parts between which the muscle stretches. According to this system, if an attachment is segmental, it is identified by an Arabic or Roman subscript for the thorax or abdomen, respectively. He designated the intersegmental structures by an Arabic numerical prefix beginning with "0" for the cervical intersegment. However, he used the customary abbreviations 1cv, 2cv, . . . and 1ax, 2ax, . . . for the cervical sclerites and the axillary sclerites of the wing, respectively. Cross-shaped muscles with "origin" and "insertion" on opposite sides of the longitudinal body axis were distinguished by adding "x" to the usual designation. Although Chadwick's method of naming muscles is in full agreement with that of naming them according to the points of fixed and movable attachment, it defeats its purpose by depending on morphologically meaningless abbreviations. Also, the names are difficult to follow or apply in studies dealing with homology.

Daly (1963, 1964) adapted Chadwick's system for naming the close-packed and fibrillar muscles of some representatives of Hymenoptera and also for his study on the morphogenesis of the honey bee thorax.

Matsuda (1965), in his comparative study of the musculature of the insect head, utilized extensively the points of fixed and movable attachment. Unfortunately, he did not name all the muscles of the head. Furthermore, he combined purely morphological and functional names for certain muscles ("the

posterior dorsal dilators of the pharynx, the ventral dilators of the pharynx, etc.”).

METHOD USED IN PRESENT STUDY

In this investigation every muscle is named according to its points of fixed and movable attachment. Such a system seems reasonable, especially in the light of Matsuda's study (1965), which demonstrated that (at least in the head) homology between muscles of different insects can be established. Before naming each muscle, the available literature was studied to compare the points of fixed and movable attachment of the honey bee muscles with those of the homologous muscles in other insects. Because of the tendency of some muscles to shift either their points of fixed or movable attachment, or both, generalized rather than precise topographic terminology would have, in most cases, resulted in even more cumbersome names than those chosen. For international usage, it was decided to use classical Greek and Latin forms for these names. The name of the point of fixed attachment is placed in front of that of the point of movable attachment and hyphenated with it.

A few muscles are stretched between two movable points of attachment. In such cases, points of fixed or movable attachment are not differentiated. Instead, the prefix “inter” is added to the composite word formed by the names of the two points of movable attachment. A muscle with no definite points of fixed or movable attachment (ring type) is designated as a circular muscle of the structure it ensheaths.

For the sake of brevity and clarity the segments of segmental structures are designated by the suffix “mere”¹ and are given Roman numerals to indicate their position in the series (for example, labiopalpomere II, maxillopalpomere III, etc.).

The principal value of the present nomenclatorial system is that a person can locate a particular muscle without having to read a long topographic description, interpret functions, or trace evolutionary changes. To maintain this value, it would seem advisable to base such names solely on the attachment points of the insect being studied.

The morphologist may be tempted to change the name of a muscle when it is obviously homologous

¹ The current usage of the term “mere” is incorrect, but it has become widespread and well established throughout the scientific world. Therefore, I decided not to introduce the very unfamiliar (though correct) form “mereikalis.”

with one given a different name in another insect. For example, Stajanovich (1945) found that in Anoplura the “antennal muscles” “originate” on the dorsal wall of the antennal segment instead of on the tentorium as the same muscle does in most other insects. Since the Anoplura lack a tentorium, the “antennal muscles” had to shift their points of fixed attachment. Obviously, to use a homologous term incorporating the term tentorium would only confuse someone making a dissection of an anopluran. Nevertheless, it is apparent that homology should not be ignored. To many students homology is the principal issue involved in morphological work. Originally I had hoped to set up a parallel but homologous nomenclatorial system. This was to be done by dividing all of the cephalic muscles into groups representing the main structural areas with which they were associated and giving them an anterior to posterior sequential numbering system within each group. This abbreviated name was to be used in the illustrations and supplemented with the full topographic name in the text. The advantage of such a system, besides that of brevity in illustrations, would be that the same abbreviations could presumably be used for all insects, since shifts in points of attachment would not have to be taken into account.

I finally decided that such a system, however desirable, should await a detailed study of the sclerites, muscles, and nerves of many representative insects and be based on a hypothetical “primitive” insect with a “complete” muscular system. Following this the same grouped numbering system could be followed for any insect, with changes in the names occurring only when a primitive muscle appeared to have divided (in which case letter subscripts could be added) or when fusion seemed to have occurred (in which case two or more numbers could be combined). Naturally, there would be many cases of omitted numbers. Nevertheless, mandibular muscle “5” would always be “5” in whatever insect it occurred, even if it represented the only mandibular muscle remaining in the insect in question.

Topography and Homology of Musculature

Although the musculature of the honey bee, *Apis mellifera*, exhibits sexual dimorphism, all of the muscles in the head of the male (drone) can be homologized with those in the female (worker and queen).

An intensive study of both sexes indicates that the male musculature has followed a pattern of degeneration in certain muscles and a retention of primitive features in others.

Musculature of the head in general tends to be more standardized than that of any other part of the insect body, in spite of great specialization in structure and function between different orders and families. The cephalic muscles are readily classifiable under the following groups: labral, clypeal, antennal, mandibular, maxillary, labial, hypopharyngeal, cibarial, and pharyngeal muscles.

In this study, the muscles of the three castes of the honey bee are compared with their homologs in the various groups of Hymenoptera and Neuroptera that have been studied. Table 2 gives names of major contributors, years of publication, and the insects that have been studied (in phylogenetic order). In many instances, the comparisons include other kinds of insects, especially when they deal with more generalized features. In these cases, the names of the contributors are mentioned in the text.

This study is strictly morphological, no attempt has been made to study the function of muscles except for those not previously described. Consequently, most of the functions mentioned in the text have been proposed by various authors. The points of fixed and movable attachment of the cephalic musculature in the honey bee are summarized in Table 3.

LABRAL MUSCLES

The labrum in most higher insects has three pairs of

muscles, two extrinsic and one intrinsic. The extrinsic ones are median and lateral, and the intrinsic ones are median.

The *musculus fronti-labralis* (*m. fron-labr.*) (Figure 4)

The point of fixed attachment of this muscle is located medially on the frons between the *musculi fronti-suspensoriali*. It attaches laterally on a long tendonlike apodemal growth from the base of the labrum (tromal area) which serves as a point for movable attachment. The *m. fron-labr.* is better developed in the queen than is its homolog in the worker or drone. It is absent in *Vespula pensylvanica* (Duncan 1939) and in *Vespula maculata*. In *Lasius niger* Reine (Janet 1905) it is well developed and has similar points of attachment to those of the honey bee. Alam (1951) described an "abductor" of the labrum in *Stenobracon deesae*, which he claimed served the same function as the *m. fron-labr.* in the honey bee but is probably a homolog of muscle "1" in *Macrophya pluricincta*, which Matsuda (1957) reported to have its movable attachment located submedially rather than laterally as in the honey bee. According to Snodgrass, it functions as an abductor in the honey bee, although Maki considered it to be a posterior retractor to the labrum in *Corydalus*.

It seems that in the honey bee this muscle has maintained its primitive points of attachment, whereas in *Macrophya* the movable attachment has shifted, and in *Vespa* and *Stenobracon* it has disappeared.

TABLE 2.—Major contributors to the cephalic musculature of Hymenoptera and Neuroptera

Order	Family	Species	Author	Year
Neuroptera	Corydalidae	<i>Corydalus cornutus</i> Linn.	Kelsey	1954
	Sialidae	<i>Chauliodes formosanus</i> Peterson	Maki	1936
Hymenoptera	Tenthredinidae	<i>Macrophya pluricincta</i> Norton	Matsuda	1957
	Braconidae	<i>Stenobracon deesae</i> Cameron	Alam	1951
	Formicidae	<i>Lasius niger</i> Reine	Janet	1905
	Vespidae	<i>Vespula pensylvanica</i> Sauss.	Duncan	1939
	Apidae	<i>Apis mellifera</i> Linn.	Snodgrass	1942
		<i>Apis mellifera</i> Linn.	Morison	1927

TABLE 3.—Points of fixed and movable attachment of the cephalic musculature in the honey bee

Name	Muscle	Abbreviation	Point of fixed attachment	Point of movable attachment
<u>musculus fronti-labralis</u>		m. <u>fron-labr.</u>	medially on frons	on lateral base of labrum
<u>musculus clypeo-epipharyngealis</u>		m. <u>clyp-epiph.</u>	on distal portion of clypeus	on inner wall of epipharyngeal lobe
<u>musculus tentorio-scapualis I</u>		m. <u>tent-scap. I</u>		
<u>musculus tentorio-scapualis II</u>		m. <u>tent-scap. II</u>		
<u>musculus tentorio-scapualis III</u>		m. <u>tent-scap. III</u>	dorsally on pretentorium	on base of antennal scape
<u>musculus tentorio-scapualis IV</u>		m. <u>tent-scap. IV</u>		
<u>musculus scapo-pedicularis I</u>		m. <u>scap-pedic. I</u>	on dorsal wall of antennal scape	on dorsal base of antennal pedicel
<u>musculus scapo-pedicularis II</u>		m. <u>scap-pedic. II</u>	on ventral wall on antennal scape	on ventral base of antennal pedicel
<u>musculus cranio-extramandibularis I</u>		m. <u>cran-extramand. I</u>	on gena	on outer articulating mandibular membrane
<u>musculus cranio-intramandibularis I</u>		m. <u>cran-intramand. I</u>	on post gena	on inner articulating mandibular membrane
<u>musculus cranio-intramandibularis II</u>		m. <u>cran-intramand. II</u>	on top of cranium	on inner articulating mandibular membrane
<u>musculus tentorio-mandibularis</u>		m. <u>tent-mand.</u>	on the anterior end of pretentorium	on inner articulating mandibular membrane
<u>musculus gena-cardinalis</u>		m. <u>gena-card.</u>	on inner wall of post gena	anteriorly on outer wall of cardo
<u>musculus tentorio-cardinalis</u> ^a		m. <u>tent-card.</u>	anteriorly on pretentorium	anteriorly on base of stipes
<u>musculus tentorio-stipitalis I</u>		m. <u>tent-stip. I</u>	anteriorly on pretentorium	medially on base of stipes
<u>musculus tentorio-stipitalis II</u>		m. <u>tent-stip. II</u>	anteriorly on pretentorium	medially on base of stipes
<u>musculus stipiti-laciniaris</u>		m. <u>stip-lac.</u>	on base of stipes	on base of licinia
<u>musculus stipiti-galearis</u>		m. <u>stip-gal.</u>	posteriorly on stipes	on base of galea
<u>musculus stipiti-maxillopalpualis I</u>		m. <u>stip-maxpalp. I</u>	anterio-laterally on outer wall of stipes	on base of maxillary palpus
<u>musculus stipiti-maxillopalpualis II</u>		m. <u>stip-maxpalp. II</u>	anterio-medially on outer wall	on base of maxillary palpus
<u>musculus postoccipiti-prementualis</u> ^b		m. <u>postoccip-prement.</u>	on occiput adjacent to the base of tentorium	on ligula on pretentorium
<u>musculus tentorio-prementualis</u>		m. <u>tent-prement.</u>	anteriorly on pretentorium	on base of prementum
<u>musculus premento-paraglossaris</u>		m. <u>prement-paragloss.</u>	laterally on base of prementum	on ligula of prementum
<u>musculus premento-glossaris</u>		m. <u>prement-gloss.</u>	posteriorly on base of prementum	laterally on glossal rod
<u>musculus premento-labiopalpualis</u>		m. <u>prement-labiopalp.</u>	on lateral side of prementum	posteriorly on palpiger
<u>musculus labiopalpomere I-II</u>		m. <u>labiopalp. I-II</u>	on base of first labiopalpomere	on base of second labiopalpomere
<u>musculus dorsopremento-salivarius</u>		m. <u>dorsoprement-saliv.</u>	anteriorly on edge of prementum	medially on salivary syringe
<u>musculus basipremento-salivarius</u>		m. <u>basiprement-saliv.</u>	on base of prementum	laterally on salivary syringe
<u>musculus fronti-suspensorialis</u>		m. <u>fron-susp.</u>	medially on frons	dorsally on hypopharyngeal suspensorial node
<u>musculus clypeo-suspensorialis</u>		m. <u>clyp-susp.</u>	on inner lateral side of pretentorium	ventrally on hypopharyngeal suspensorial node
<u>musculus tentorio-oriscutorius</u>		m. <u>tent-oriscut.</u>	medially on the tentorial bridge	medially on the oral plate
<u>musculus tentorio-suspensorialis</u>		m. <u>tent-susp.</u>	laterally on the tentorial bridge	ventro-laterally on hypopharyngeal suspensorium
<u>musculus oriscuto-suspensorialis</u>		m. <u>oriscut-susp.</u>	medially on the oral plate	laterally on hypopharyngeal suspensorium
<u>musculi clypeo-ciberioparietales</u>		m. <u>clyp-cibpariet.</u>	on the cranial wall of clypeus	on inner wall of clypeus
<u>musculus intersuspensorialis dorsualis</u> ^c		m. <u>intersusp. dors.</u>		
<u>musculus fronti-pharyngealis I</u>		m. <u>fron-phar. I</u>	medially on the frons	anteriorly on anterior pharynx
<u>musculus fronti-pharyngealis II</u>		m. <u>fron-phar. II</u>	on the frons, above <u>fron-phar. I</u>	posteriorly on anterior pharynx
<u>musculus fronti-pharyngealis III</u> ^d		m. <u>fron-phar. III</u>	on the frons, submedially to <u>fron-phar. II</u>	laterally on anterior pharynx
<u>musculus cranio-pharyngealis</u>		m. <u>cran-phar.</u>	submedially on the top of cranium	dorsally on posterior pharynx
<u>musculus circulo-pharyngealis</u> ^e		m. <u>circulophar.</u>		

^aIn the drone the point of movable attachment is located on the end of the cardo.^bIn the worker the point of fixed attachment is located dorsally on the cranium.^cMuscle with no definite point of attachment.^dThis muscle is found in the drone only.^eMuscle with no definite point of attachment.

EPIPHARYNGEAL MUSCLES

The term "epipharynx" is applied to the anterior wall of the preoral cavity, the inner surface of the labrum and clypeus. Consequently, this term is a misnomer since it has no relationship with the pharynx, which is a part of the stomodaeum. The term "epipharynx" is used in this investigation for lack of a substitute.²

Matsuda (1965) included the "epipharyngeal muscle" with the pharyngeal muscles. For the reasons indicated above, however, I consider it more logical to group them separately. An examination of the epipharyngeal muscles in the lower and higher insects (including Thysanura and Diptera) revealed a maximum of two muscles belonging to this group, one anterior and the other posterior. The honey bee has only one epipharyngeal muscle.

The *musculus clypeo-epipharyngealis* (*m. clyp-epiph.*) (Figures 1, 3)

This is an unpaired muscle, probably of a fusiform type. Its point of fixed attachment is located distally on the clypeus close to the margin of the clypeo-labral suture. Its point of movable attachment is on the median inner wall of the epipharynx. It is about the same size in the different castes.

Although Duncan (1939) considered *m. clyp-epiph* to be absent in *Vespula pensylvanica*, it is probably the "clypeo-dilator of the mouth" he described as "originating" on the clypeus and "inserting" on the anterior pharyngeal wall immediately above the mouth. Examination of this muscle in *Vespula maculata* revealed that its point of movable attachment is on the upper epipharyngeal wall rather than the pharyngeal wall.

Duncan made his position ambiguous by stating that the "clypeo-dilator" may be the homolog of the "dilator cibarii" of generalized insects (described by Snodgrass 1935), thus indicating that it is attached to the cibarial wall (epipharyngeal wall) which belongs to the preoral cavity rather than the true pharynx. Janet (1905) did not describe any epipharyngeal muscle in *Lasius*. According to his illustration (p. 3, fig. a) and innervation plan, however, it would seem that the *musculus clypeo-epipharyngealis* is ho-

² Perhaps the term "extra-internolabrum" or upper internal lip could be used as a substitute.

mologous to the pair of muscles he called "retractors of the buccal tube." In *Stenobracon*, this muscle is paired (Alam 1951). Matsuda (1957) considered muscles "3" and "4" in *Macrophya* to be homologs of this muscle, although their points of fixed attachment are on the upper surface of the labrum.

The *musculus clypeo-epipharyngealis* is probably the homolog of a "cibarial" muscle in *Corydalus* (the first dorsal dilator of the cibarium). According to Kelsey's description, it extends between the clypeus and the lateral portion of the epipharyngeal plate (as in *Stenobracon*). The same situation was reported for *Chauliodes*. Reports in the literature indicate that this muscle has the same points of attachment in lower and higher insects, except for *Macrophya* (described by Matsuda 1957).

Snodgrass and Alam considered *m. clyp-epiph.* to be the retractor (levator) of the epipharynx. Yet Duncan, Janet, Kelsey, and Maki stated that it is a dilator (protractor) of the cibarium.

ANTENNAL MUSCLES

This group is treated rather superficially because topographic work on antennal muscles, especially the intrinsic ones, has been fragmentary.

Imms (1939) classified antennae into two major groups: the "segmental" type in which each segment has intrinsic muscles moving the next segment, and the "annulated" type in which the muscles are located mainly in the basal segment (scape). Insects, except Diplura and Collembola, have antennae belonging to the latter type. The number of the extrinsic antennal muscles varies greatly among primitive insects. Studies of the lepidopteran *Micropteryx calthella* Hanne-mann (1956) and the thysanuran *Machilis* species (Bitsch 1963) suggest that primitive insects had four intrinsic muscles of the scape. However, according to Matsuda (1965), the typical number of intrinsic muscles is two.

The *musculus tentorio-scapualis I* (*m. tent-scap. I*) (Figure 4)

This muscle has its point of fixed attachment on the inner margin of the concave surface of the pre-tentorium (anterior tentorial arm) lateral to that of the *m. tentorio-scapualis II*. The point of movable attachment is located medially and dorsally on a

tendonlike apodemal growth of the base of the antennal scape.

The *musculus tentorio-scapualis II* (*m. tent-scap. II*) (Figure 4)

The point of fixed attachment of this muscle is on the outer posterior margin of the concave surface of the pretentorium. Its point of movable attachment is located laterally and dorsally on the apodemal growth of the base of the scape.

The *musculus tentorio-scapualis III* (*m. tent-scap. III*) (Figure 4)

This muscle has its point of fixed attachment on the inner margin of the concave surface of the pretentorium under that of *m. tent-scap. I*. Its point of movable attachment is located ventrally and laterally on the apodemal growth of the base of the scape in the opposite position to that of *m. tent-scap. II*.

The *musculus tentorio-scapualis IV* (*m. tent-scap. IV*) (Figure 4)

The fixed point of attachment of this muscle is on the outer margin of the concave surface of the pretentorium under that of *m. tent-scap. II*. Its point of movable attachment is located ventrally and medially on the apodemal growth of the base of the scape in the opposite position to that of *m. tent-scap. I*.

According to Duncan four extrinsic antennal muscles in *Vespula* are arranged in the same manner as in the honey bee. Alam found the same situation in *Stenobracon*. Matsuda found only three extrinsic antennal muscles in *Macrophya*, all of which have their fixed attachment on the "dorsal arm and upper portion of the composite tentorial bar." However, I found four extrinsic muscles in the antenna of the tenthredinid, *Tenthredo maxima* Norton. According to Maki, only three extrinsic muscles are in the antenna of *Chauliodes*. His first "levator of the antenna" and "second levator of the antenna" are probably the homologs of *m. tent-scap. I* and *m. tent-scap. II*. Unfortunately, Maki did not describe the exact location of the attachments of what he named "depressor of the antenna."

By comparing the points of movable attachments of the extrinsic antennal muscles of the honey bee

with those of the hypothetically primitive antenna as proposed by Matsuda (1965), it appears reasonable to assume that the honey bee has retained primitive features with regard to the points of movable attachment. On the other hand, it is evident that *m. tent-scap. I* and *m. tent-scap. II* have shifted their points of fixed attachment from the metatentorium (primitive feature) to the pretentorium owing to a degeneration of the metatentorium. According to the literature, *m. tent-scap. I* and *m. tent-scap. II* (dorsally located) act as levators; *m. tent-scap. III* and *m. tent-scap. IV* (ventrally located) are supposed to act as depressors.

The *musculus scapo-pedicularis I* (*m. scap-pedic. I*) (Figure 10)

This muscle's point of fixed attachment is located dorsally on the inner wall of the scape near its base. Its point of movable attachment is located on a short, dorsal apodemal growth at the base of pedicel. It is presumed to act as a levator of the flagellum.

The *musculus scapo-pedicularis II* (*m. scap-pedic. II*) (Figure 10)

This muscle has its point of fixed attachment on the inner ventral wall of the scape. Its point of movable attachment is located on a short, ventral apodemal growth at the base of the pedicel. It apparently functions as a depressor of the flagellum.

MANDIBULAR MUSCLES

Mandibular muscles of insects are classified into two groups: the dorsal (attached to the cranium and the mandible) and the ventral (attached to the tentorium and the mandible). According to Matsuda (1965), one muscle of the ventral group is generally adductor in function and the other is abductor. In higher Pterygota the dorsal group is always retained but the ventral group is often degenerated or lost.

The *musculus cranio-extramandibularis* (*m. cran-extramand.*) (Figure 2)

This muscle has its point of fixed attachment on the genal and postgenal areas of the cranium behind the compound eye in the worker and queen. In the drone the point of fixed attachment is limited to the lower

part of the gena. In all three castes, the point of movable attachment is located on a strong apodemal growth (small in the case of the drone) of the articulating membrane at the outer side of the base of the mandible between the latter's base and the malar area. The muscle is very small in the drone but well developed in both worker and queen.

The *m. cran-extramand.* is the homolog of what has been called the "abductor muscle of the mandible" in various groups of insects such as *Vespula*, *Lasius*, *Stenobracon*, *Chauliodes*, *Corydalus*, and others.

The *musculus cranio-intramandibularis* (*m. cran-intramand.*) (Figure 2)

In the worker and queen this muscle has two branches, I and II. Branch I has several groups of muscle fibers, some of which have their point of fixed attachment on the occipital area and the others on the postgena below the foramen. Branch II has its point of fixed attachment on the vertex behind the *Lobus Opticus* and next to the point of fixed attachment of the *musculus postoccipiti-prementualis*. The articulating mandibular membrane at the inner margin of the mandible (next to the mesal wall of the mandibular gland) gives rise to a very stout apodeme splitting into two apodemal growths. One is short and stout and bears the point of movable attachment of *m. cran-intramand. I*. The other is long (about four times as long) and thin on which branch *II* has its point of movable attachment.

In the drone *m. cran-intramand.* is very small in comparison to its homolog in the worker and queen. It has its point of fixed attachment only on the postgena and its point of movable attachment on a short growth arising from the same location as described for the worker and queen. Evidently branch *II* of this muscle has degenerated completely in the drone, although the apodemal growth still exists as a loose thread.

M. cran-intramand. is the homolog of what has been named the "abductor muscle of the mandible" in other insects.

The *musculus tentorio-mandibularis* (*m. tent-mand.*) (Figure 2)

This muscle has not been described before in the honey bee or any other aculeate hymenopteran. In

the honey bee it is a very small muscle consisting of one or two fibers, which I originally thought to be a nerve fiber because of its close association with the mandibular nerve. Examination under the compound microscope, however, revealed it to be composed of muscle tissue. It has its point of fixed attachment on the extreme anterior end of the outer wall of the pretentorium and extends cephalad with its movable attachment on the inner articulating membrane close to the apodemal growth associated with *m. cran-intramand.* It probably represents the remains of the ventral mandibular muscles. According to Duncan, no such muscle exists in *Vespula pennsylvanica*, but I found it even more developed in *V. maculata* than in the honey bee. In *V. maculata* it is composed of four to six muscle fibers and has its fixed attachment on the pretentorium, as does its homolog in the honey bee. On the other hand, its movable attachment is located on the inner wall of the mandible, near its base. Janet did not find it in *Lasius*, Alam in *Stenobracon*, nor did Matsuda find it in *Macrophya*. Careful examination of other Hymenoptera may be necessary to clarify its status. It is probably the homolog of the muscle described as the "tentorial adductor of the mandible" by Maki in *Chauliodes*. At any rate the points of attachment of the latter are similar to those of the honey bee.

By comparing *m. tent-mand.* of the honey bee with that of primitive insects, its point of movable attachment seems to have shifted from the inner wall of the mandible to the inner articulating membrane. Its function is supposed to be adduction of the mandible when it is well developed, as in *Chauliodes*. In *Apis* (and probably in *Vespula*), however, where the *m. tent-mand.* is reduced to only one strand of muscle fibers, it appears to be modified to function similar to a stretch organ, especially since it is innervated in much the same way as known stretch organs (Finlayson and Lowenstein 1958). These organs have been described only from the abdomen of many insects. Physiological and histological studies will be required to verify its function.

MAXILLARY MUSCLES

Generally speaking, the maxilla and its associated muscles have retained primitive features in most insect groups. The major change in many orders has been limited to reduction of the palpus. Accordingly,

many of the maxillary palpal muscles have degenerated or disappeared.

The *musculus gena-cardinalis* (*m. gena-card.*) (Figures 4, 5)

This muscle has its point of fixed attachment on the postgenal inflection adjacent to the proboscival fossa. Its point of movable attachment is located on the small arm of the cardo beyond the articulating condyle. The *m. gena-card.* is equally developed in the three castes but tends to have a wider point of fixed attachment (fan shaped) in the drone. According to Duncan, the homolog muscle in *Vespula* has similar points of attachment. Alam found that in *Stenobracon* the point of movable attachment is on the outer margin of the cardo close to its articulation with the "hypostomal rod." Matsuda (1957) did not find this muscle in *Macrophya*, but in 1965 he stated that "it may be present." Maki in *Chauliodes* and Kelsey in *Corydalus* found that *m. gena-card.* has a broad movable attachment extending along the mesal and lateral side of the "abductor" apodeme which, in turn, projects from the apex of the cardinal process. In the primitive insects studied, it has its points of fixed and movable attachment, respectively, on the side of the occipital foramen and the internal process of the cardo.

The function of this muscle varies among insects due to differences in the shape of the head (hypognathal or prognathal) and according to the location of the points of attachment. In *Corydalus* it is supposed to be an adductor of the cardo, and the same function was claimed for it by Janet in *Lasius*. Maki referred to it as a promoter of the cardo in *Chauliodes*; Alam called it a protractor of the maxilla in *Stenobracon*; Duncan termed it the producter of the cardo in *Vespula*; and Snodgrass claimed that in the honey bee it acts as a protractor of the maxilla, probably because of a shift of the point of fixed attachment from the sides of the occipital foramen to the postgenal inflection.

The *musculus tentorio-cardinalis* (*m. tent-card.*) (Figures 4, 5)

In the honey bee, this muscle has its point of fixed attachment on the anterior ventral margin of the pretentorium. According to Morison (1927) and Snodgrass (1942), the point of movable attachment

is located on the proximal end of the stipes. Careful examination of the worker and queen, however, revealed that its movable point of attachment is on both the proximal end of the stipes and the distal end of the cardo. In the drone it is only on the distal end of the cardo, close to its articulation with the stipes. Duncan stated that the homolog of *m. tent-card.* in *V. pennsylvanica* "originates" on the clypeus and "inserts" by a long tendon on the toothlike process of the cardo. I found that in *V. maculata*, however, its point of fixed attachment is on the pretentorium.

In *Lasius*, Janet found one muscle of the pair, which he named "adductrice maxillaire," to have its point of movable attachment on the area of articulation between the cardo and stipes. Also, Alam found that in *Stenobracon* this muscle attaches to the "hinge line." Matsuda found muscle "24" in *Macrophya* to have its point of movable attachment on almost the entire cardo. In *Chauliodes* and *Corydalus*, homologs of *m. tent-card.* have their points of movable attachment on the distal portion of the cardo. Accordingly, it seems that this muscle usually has its point of movable attachment on the cardo, but in *Lasius*, *Stenobracon*, and the female honey bee it has shifted to the articulation between the cardo and stipes and in *Vespula* to the apex of the stipes. In the drone honey bee this muscle has retained the primitive feature of having its point of movable attachment on the cardo. It is presumed to be the adductor of the cardo in *Corydalus* and *Chauliodes*, the protractor of the maxilla in *Stenobracon*, and the extensor of the maxilla in *Vespula*. Nevertheless, Snodgrass considers it to be one of the stipital protractors of the proboscis in the honey bee.

The *musculus tentorio-stipitalis I* (*m. tent-stip. I*) (Figure 3)

This muscle has its point of fixed attachment on the anterior ventral margin of the pretentorium under that of *m. tent-card.* Its point of movable attachment is located medially on the inner wall of the base of the stipes.

The *musculus tentorio-stipitalis II* (*m. tent-stip. II*) (Figures 3, 4)

The point of fixed attachment of this muscle is located laterally on the inner side of the pretentorium above the combined points of fixed attachment of

m. tent-card. and *m. tent-stip. I*. Its point of movable attachment is on the inner wall of the base of the stipes, just above that of *m. tent-stip. I*.

Since these two muscles have similar points of attachment, they probably serve similar functions. Accordingly, they may be named collectively as *musculi tentorio-stipitales*.

In other groups of studied Hymenoptera (*Vespula*, *Lasius*, *Stenobracon*, and *Macrophya*), the *mi. tent-stipitales* are represented by a single muscle. The same situation exists in the most primitive Lepidoptera, such as *Micropteryx calthella* (L.) (Hannemann 1956). However, in *Corydalus* there are two muscles. According to Matsuda (1965), primitive insects usually have more than one muscle belonging to this group.

Dissection of *V. maculata* indicated that the homolog of this group of muscles has its point of fixed attachment on the pretentorium and clypeus rather than only the clypeus as stated by Duncan for *V. pennsylvanica*. According to Matsuda, the group does not exist in *Macrophya*. He also indicated (1957) that muscle "26" is a "Tentorium-Lacinia" muscle. However, by examining his illustration (pl. III: fig. f) and by considering the fact that the "tentorio-lacinial" muscle "has been found in *Machilis* only" (Matsuda 1965:268), it appears that muscle "26" of *Macrophya* is the homolog of *musculi tentorio-stipitales*.

This group of muscles is supposed to function as an adductor of the stipes in *Corydalus*, *Chauliodes*, and *Lasius* and as a flexor of the maxilla in *Stenobracon* and *Vespula*. Yet Snodgrass (1942) considered it, together with *m. tent-card.*, as serving to protract the proboscis.

The *musculus stipiti-laciniaris* (*m. stip-lac.*) (Figure 5)

This muscle has its point of fixed attachment on the outer wall of the base of the stipes. The point of movable attachment is located on a small sclerite ("lever of lacinia," Snodgrass 1942) at the base of the lacinia. It functions as a flexor in the honey bee and in a majority of other insects. Although it has similar points of attachment in all groups of insects studied, it has also been reported to function as a protractor of the lacinial stylet in Psocoptera, Thysanoptera, Mallophaga, and Siphonaptera and a retractor for the maxillary stylet in Hemiptera.

The *musculus stipiti-galearis* (*m. stip-gal.*) (Figure 5)

This muscle has a broad point of fixed attachment on the anterior and lateral inner wall of the stipes. Its point of movable attachment is located on the long tendonlike apodemal growth of the base of the galea at the middle of a "leverlike" ridge. In some insects the galea has no apodemal growth, so the muscle attaches directly to the galea. In many primitive insects (*Thermobia*, *Machilis*, *Campodea*, *Periplaneta*, etc.) and in primitive members of higher orders (*Micropteryx*, *Macrophya*, etc.) this muscle has its point of fixed attachment on the stipes. In many higher groups of insects, however, it has shifted its point of fixed attachment to other areas. In higher Lepidoptera, for instance, its point of fixed attachment is on the tentorium, yet in the larvae of Trichoptera, Lepidoptera, Mecoptera, and Diptera it is on the cranium.

When *m. stip-gal.* has its point of fixed attachment on the stipes, it functions as a flexor of the galea, as in *Thermobia* and *Machilis*. In the honey bee it folds the galea because of its attachment to the "leverlike" ridge. According to Snodgrass (1942) its tension, when contracted, first depresses the galea and then turns it backward and outward. Continuous contraction finally turns the galea straight back and folds it against the stipes.

The *musculus stipiti-maxillopalpalis I* (*m. stip-max-palp. I*) (Figure 5)

The point of fixed attachment of this muscle is located anteriorly and laterally on the outer wall of the stipes. The point of movable attachment is on the ventral mesal base of the maxillary palpus. These findings with regard to the point of movable attachment agree with those of Snodgrass (1942) and disagree with those of Wolff (1875) and Morison (1927) who regarded it as a galeal muscle, based on the argument that it attaches "near" the base of the palpus. Examination under the compound microscope indicated that it attaches directly to the base of the palpus.

The *musculus stipiti-maxillopalpalis II* (*m. stip-max-palp. II*) (Figure 5)

This muscle has not previously been described in the honey bee. It is a very small muscle, a single

fiber, embedded between the fibers of *m. stip-maxpalp. I*. It was observed for the first time by following a parallel "nerve" that eventually diverges to innervate the stipital integument. Tracing this muscle fiber to its termination indicated that it (*m. stip-maxpalp. II*) attaches separately but close to *m. stip-maxpalp. I*, where its points of fixed and movable attachment are on the base of the stipes (dorsally and medially over *m. stip-maxpalp. I*) and the base of the maxillary palpus, respectively. The pattern of its innervation, the way it extends, and its being a single fiber suggest that it may act in a fashion similar to that of a "stretch organ." These two, *m. stip-maxpalp. I* and *m. stip-maxpalp. II*, can be grouped as *musculi stipiti-maxillopalpales*.

Two muscles belonging to the above group are found in *Vespula*, *Macrophya*, *Chauliodes*, and *Corydalus*. In the first two genera, these muscles have their points of movable attachment on the ventral side of the maxillary palpus, but in the last two, the point of movable attachment of one muscle is dorsal and the other is ventral, as in primitive insects. Consequently, in the cases of *Macrophya*, *Vespula*, and *Apis*, *m. stip-maxpalp. II* is believed to have shifted its point of movable attachment from a dorsal to a ventral location on the base of the maxillary palpus.

These muscles act as depressors of the maxillary palpus when their points of fixed attachment are on the ventral side of the base of the maxillary palpus, as in *Macrophya*.

LABIAL MUSCLES

Probably the labium is the most specialized gnathal segment. Hence, labial muscles have tended to change the location of their points of attachment more than the other gnathal segments. This tendency can be seen even between members of primitive orders; for example, the labial muscles of Machilidae are apparently more specialized than those of Lepismatidae (both belong to Thysanura). Many labial muscles found in primitive orders or in primitive groups of higher orders have not been found in the honey bee (Table 1). Some labial muscles have been treated as hypopharyngeal muscles because they are closely associated with the hypopharynx, which is a union of several sclerites of more than one gnathal segment.

The *musculus postoccipiti-prementualis* (*m. postoccip-prement.*) (Figures 3, 6)

This muscle, the longest in the head of the worker honey bee, has its point of fixed attachment on the dorsal wall of the cranium next to branch II of *m. cran-intramand.* In the drone and queen, however, its point of fixed attachment is on the occiput adjacent to the posterior end of the tentorial body. In all three castes, its point of movable attachment is located on a long tendonlike apodemal growth arising on the so-called ligular arm of the prementum. In *Vespula* and *Lasius* the point of fixed attachment is located on the tentorial body; in *Stenobracon* it is on the clypeus. Matsuda (1957) regarded muscle "36," which "arises" from the hindmost end of the tentorium and "inserts" on the posterolateral angle of the prementum, to be a homolog of this muscle. However, when one compares the point of attachment of muscle "37" in *Macrophya* with *m. postoccip-prement.* in the honey bee, these two appear to be homologs. In *Chauliodes* and in *Corydalus* this muscle has its point of fixed attachment on the posterior tentorial arm and on the postgena, respectively, yet in generalized insects its point of fixed attachment is on the postoccipital phragma. Apparently this muscle has retained the primitive point of fixed attachment in the drone and the queen honey bee but has shifted it to the top of the cranial wall in the worker honey bee, to the clypeus in *Stenobracon*, and to the posterior part of the tentorium in *Macrophya* and *Chauliodes*.

The *m. postoccip-prement.* functions as a levator of the paraglossa in *Corydalus*, a retractor of the hypopharynx in *Chauliodes*, and a retractor or adductor of the labium in *Lasius* and *Apis*.

The *musculus tentorio-prementualis* (*m. tent-prement.*) (Figure 3)

The point of fixed attachment of this muscle is on the anterior end of the pretentorium adjacent and dorsal to that of *m. tent-stip. II*. Ahead of its point of movable attachment it converges with its homolog from the opposite side of the head and the two attach to a single tendonlike apodemal growth arising medially from the proximal end of the prementum. According to Duncan, the homolog of this muscle in

Vespula has its point of fixed attachment on the clypeus and remains paired. Accordingly, the points of movable attachment of the pair are on separate apodemal growths. In *Lasius* its point of fixed attachment is on the posterior end of the pretentorium but its movable attachment is like that of the honey bee. *Stenobracon* has almost the same attachment points for this muscle as *Apis*. In *Macrophya*, *Chauliodes*, *Corydalus*, and also primitive insects like *Thermobia*, its fixed attachment is on the metatentorium. Apparently in *Apis*, *Vespula*, and *Stenobracon*, the fixed attachment shifted to the pretentorium as the metatentorium was being lost. The *m. tent-prement.* acts as a protractor of the labium in *Vespula*, *Lasius*, *Macrophya*, *Chauliodes*, and *Corydalus*.

The *musculus premento-paraglossaris* (*m. prement-paragloss.*) (Figures 6, 7)

This muscle has its point of fixed attachment on the lateral base of the prementum. Its point of movable attachment is on an apodemal growth arising from the ligular arm of the prementum, just lateral to that of *m. postoccip-prement.* In *Vespula* and *Stenobracon*, the points of movable attachment are on the lingual plate and the basal sclerite of the paraglossa, respectively. According to Maki and Kelsey, there is no homolog of this muscle in *Chauliodes* or *Corydalus*, although it is rather commonly found in lower pterygote insects. In the honey bee the points of attachment seem not to have changed from those found in generalized insects. The muscle acts as a flexor of the entire ligula in *Stenobracon* and *Vespula*. In the honey bee it was considered by Morison to be a "*flexor palpi maxillari*," but Snodgrass (1942) referred to it as a retractor of the labium.

The *musculus premento-glossaris* (*m. prement-gloss.*) (Figures 6, 7)

The point of fixed attachment is on the submedian base of the prementum under that of the *musculus basi-premento-salivarius*. The point of movable attachment is on a long apodemal growth close to the sides of the recurved basal part of the glossal rod. In *Vespula* the same muscle is fused medially with its homolog from the other side of the midline. The

points of fixed and movable attachment of the fused structure are, respectively, on the base of the prementum and the posterior lingual plate. In *Stenobracon* this muscle is unfused and is attached as in the honey bee. Matsuda (1957) stated that muscles "41" and "43" of *Macrophya* are homologous to this muscle, although he did not describe their points of attachment. The *m. prement-gloss.* has not been found in *Chauliodes* and *Corydalus*, but in several primitive insects it attaches to the prementum and the glossa. It appears that this muscle has shifted its point of movable attachment from the glossa to the side of its rods. In the honey bee, it is considered to be a flexor of the glossa (retractor of the tongue) as in other insects.

The *musculus premento-labiopalpalis* (*m. prement-labiopalp.*) (Figure 6)

This muscle has its point of fixed attachment about midway along the side of the prementum. The point of movable attachment is located on a long tendon-like apodemal growth arising on a rod within the basal lobe of the labial palpus (the palpiger). In *Vespula* and *Stenobracon* the point of fixed attachment is located on the spatulate process of the prementum. *Macrophya* has two muscles that could be designated as *musculi premento-labiopalpales*. Their points of fixed attachment are on the ventral side of the base of the labial palpus. *Chauliodes* and *Corydalus* also have two muscles, differing from those of *Macrophya* in being attached to the base of the labial palpus on its ventral and dorsal sides. Primitive insects also have two muscles attached in the same manner as in *Chauliodes*. It appears that in *Macrophya* one of these muscles has shifted its point of movable attachment from the dorsal side of the base of the labial palpus to the ventral side, yet it has disappeared completely in *Stenobracon*, *Vespula*, and *Apis*.

This muscle is considered to be a flexor of the palpus when its point of movable attachment is on the ventral side of the base of the labial palpus. But when this point is located dorsally on the base of the palpus, the *m. prement-labiopalp.* is considered to be a levator of the palpus.

The *musculus labiopalpomere I-II* (*labiopalp. I-II*) (Figure 6)

The intrinsic labial muscles have not been as well studied as other groups of muscles; consequently, they will be treated rather superficially here.

Labipalp. I-II has its point of fixed attachment on the middle of the base of labiopalpomere I (first segment of the labial palpus). The point of movable attachment is located on an apodemal growth arising from the base of labiopalpomere II. In *Stenobracon*, *Macrophya*, and *Corydalus* there are two muscles in labiopalpomere I. Matsuda (1957) found one muscle in each of labiopalpomeres II and III in *Macrophya*.

The function of *labipalp. I-II* apparently differs among insects. For instance, in *Grylloblatta* the muscles of labiopalpomere I are extensors of labiopalpomere II (Walker 1931). On the other hand, Snodgrass considered it to be a flexor of the palpus in the honey bee.

HYPOPHARYNGEAL MUSCLES

In generalized insects the hypopharynx forms the ventral wall of the cibarium. The term "hypopharynx" is misleading since the structure itself is not related to the pharynx. It is a preoral structure, embryologically of composite origin. According to Matsuda (1965), it is produced by the union of sclerites of more than one gnathal segment. The term "lingue" has been suggested as a replacement but such a term is properly inter-oral. In the present investigation, the term hypopharynx is used because no proper substitute is available.³

Some of the muscles classified under this section were formerly classified as labial. Their close association with the hypopharynx, however, makes it less confusing to consider them as hypopharyngeal.

The *musculus dorsopremento-salivarius* (*m. dorsopremment-sal.*) (Figure 6)

This muscle has its point of fixed attachment on the anterior edge of the prementum and converges toward the salivary syringe (a specialized salivarium). The broad zone of its point of fixed attachment is located

³ The term "inner internal lip" or "intra-internobialum" is suggested in this study as a replacement.

medially on the upper wall of the salivarium. In *Vespula*, *Stenobracon*, and *Macrophya* it has the same areas of attachment described for the honey bee; however, in *Chauliodes* and *Corydalus* its point of fixed attachment is on the mentum and the pharyngeal plate, respectively. In more primitive insects (*Thermobia*, *Periplaneta*, *Grylloblataria*, and others) it is located on the loral arm of the pharynx. With the loss of the loral arm in various groups of insects, this muscle had to shift its point of fixed attachment to other skeletal areas, such as the "ovoidal" sclerite in Psocoptera, the hind part of the hypopharynx in Thysanoptera, or the anterior lateral sides of the prementum in Hymenoptera. The *m. dorsopremment-sal.* probably acts as a dilator of the salivary syringe. According to Snodgrass (1942) it is effective in the honey bee only when the proboscis is in the protracted position.

The *musculus basipremento-salivarius* (*m. basipremment-sal.*) (Figure 6)

The point of fixed attachment is on the base of the prementum above that of *m. prement-gloss*. The point of movable attachment is located distally on the lateral margin of the salivary syringe. *Stenobracon*, *Macrophya*, and *Chauliodes* have approximately the same points of attachment as the honey bee; however, in *Vespula* the point of fixed attachment is within the inflected apex of the lateral "spatulate process" of the prementum, and that of the movable attachment is located partly on the proximolateral lobe of the anterior lingual plate and partly on the margin of the salivarium. *Corydalus* differs from other groups studied by having its point of fixed attachment on the ventromesal base of the palpiger. Although this muscle is found in many groups of insects (Blattaria, Isoptera, Orthoptera, Phasmida, Dermaptera, Ephemeroptera, and others), the primitive areas of attachment are difficult to determine because of their variability from group to group.

In *Stenobracon* and *Vespula*, *m. basipremment-sal.* functions as a posterior dilator of the salivarium, but in *Corydalus* it is considered to be a ventral dilator of the salivary duct. Snodgrass suggested that it acts as an expulsor of saliva by flattening the dilator chamber. Apparently, in the honey bee it is effective only when the proboscis is extended.

The *musculus fronti-suspensorialis* (*m. fron-susp.*) (Figures 1, 3)

This muscle has its point of fixed attachment submedially on the frons below the median ocellus and above *m. front-labr.* The point of movable attachment is located dorsally on the nodelike process of the upper portion of the hypopharyngeal suspensorium (pharyngeal arm of the oral plate). It is absent in *Vespula*.

In *Stenobracon*, *Macrophya*, *Chauliodes*, and *Corydalus*, and also in more primitive insects, *m. fron-susp.* has almost the same points of attachment. Its function reportedly differs—it is a retractor of the hypopharynx in *Thermobia*, *Corydalus*, and *Apis* but a protractor in *Periplaneta*. Snodgrass considered it to be a retractor of the oral plate, a part of the hypopharynx.

The *musculus tentorio-suspensorialis* (*m. tent-susp.*) (Figure 3)

This muscle has its point of fixed attachment on the inner lateral side of the pretentorium. It is directed toward the hypopharyngeal suspensorium and has its point of movable attachment on the nodelike process, opposite that of *m. fron-susp.* In both *V. pennsylvanica* and *V. maculata* this muscle has its point of fixed attachment on a peglike process alongside the ventrolateral angle of the clypeus. In *Stenobracon* and *Macrophya* it has the same points of attachment as in the honey bee. In *Chauliodes* and *Corydalus* the point of fixed attachment is on the metatentorium and that of the movable attachment is on the posterior lateral portion of the anterior pharynx. This is probably due to the undeveloped condition of the hypopharyngeal suspensorium. In many orders this muscle has its point of fixed attachment on the clypeus, rather than the tentorium. It even varies in this regard between families of the same order. Accordingly, the name *m. clypleo-suspensorialis* has been suggested. It functions as a suspensor in *Thermobia* and *Corydalus* but as a retractor in *Periplaneta*. According to Snodgrass it is a protractor of the oral plate in the honey bee.

The *musculus tentorio-oriscutarius* (*m. tent-oriscut.*) (Figure 3)

This has been classified by many authors (Janet, Duncan, Alam, Matsuda) as a stomodaeal muscle, prob-

ably on the assumption that the “functional mouth” is a part of the stomodaeum. Since the basal part of the anterior wall of the hypopharynx furnishes the posterior wall of the cibarium, the oral plate in the honey bee belongs to the hypopharynx and not to the pharynx, as has commonly been thought. Consequently, the muscle that has its point of movable attachment on the oral plate is actually hypopharyngeal.

The *m. tent-oriscut.* is an unpaired muscle probably resulting from fusion of an originally bilateral pair. Its point of fixed attachment is on a tendonlike apodemal growth arising from the median process of the tentorial bridge. The broad point of movable attachment is located medially on the oral plate. *Vespula*, *Lasius*, *Macrophya*, and *Chauliodes* also have this muscle unpaired and the points of attachment are similar to those of the honey bee. *Stenobracon* and *Corydalus* have it paired and attached to the sides of the oral plate. The available literature is fragmentary and misleading, owing to the misconception that the muscle is pharyngeal. Maki and Kelsey, who classified it as belonging to the cibarium or buccal cavity, considered it to be a dilator of the cibarium. According to Duncan, Snodgrass, and Alam, the *m. tent-oriscut* acts as a dilator of the pharynx. Actually, when contracted, it pulls the oral plate, which indirectly pulls the pharyngeal wall posteriorly, thus opening the mouth.

The *musculus tentorio-suspensorialis* (*m. tent-susp.*) (Figure 3)

Since early entomologists usually considered the suspensorium and oral plate to be part of the pharynx, I first devised the term “*musculus tentorio-hypopharyngeosuspensorialis*.” For convenient usage, however, it is probably better to limit the name of the movable attachment to “suspensorium,” especially since it has been proved that the only suspensorium in the head is of hypopharyngeal origin⁴ (Snodgrass 1956; Matsuda 1965).

This muscle has its points of fixed attachment on the tentorial bridge, adjacent to *m. tent-oriscut.* It spreads over the lateral and posterior walls of the pharynx and runs beneath the *musculus circulopha-*

⁴ Even as late as 1952, Alam used the term “pharyngeal diverticulum” and “pharyngeal plate” for the hypopharyngeal suspensorium and the hypopharyngeal oral plate.

ryngealis until it reaches the hypopharyngeal suspensorium on which it has its point of movable attachment. According to Duncan, its homolog in *V. pennsylvanica* is composed of short fibers which "insert on the under side of the pharynx." In *V. maculata*, I was able to trace a few muscle fibers to their attachment on the hypopharyngeal suspensorium. Matsuda (1957) claimed that the homolog of this muscle is absent in *Macrophya* but his muscle "14" which inserts on the "oesophageal" region, fits the description. In *Stenobracon* it has the same points of attachment as in the honey bee. The *m. tent-susp.* is probably homologous to the "first ventral dilator of anterior pharynx" in *Chauliodes* and *Corydalus*, which has its point of movable attachment on the ventral wall of the "anterior pharynx." In general this muscle has been poorly studied. Consequently, I am unable to determine whether the primitive point of movable attachment is on the pharynx or hypopharynx. If it proves to be the pharynx, the name should be changed to "*musculus tentorio-pharyngealis*." On such a basis the assumption would be that its movable attachment was shifted to the suspensorium as a later development.

According to Snodgrass, *m. tent-susp.* functions in the honey bee as a contractor of the pharynx. But, judging from its action of pulling the suspensorium backward, I suggest that it acts as indirect dilator of the pharynx.

The *musculus oriscuto-suspensorialis* (*m. oriscut-susp.*) (Figure 3)

This fan-shaped muscle has not been previously described or illustrated in the honey bee. Its point of fixed attachment is on the middle of the oral plate. The *m. oriscut-susp.* lies adjacent to the anterior wall of the pharynx and extends laterally toward the suspensorium, on which it has its broad point of movable attachment. It is probably the homolog of the "posterior intrinsic muscle of the pharyngeal diverticulum" in *Vespula*, which extends transversely on the upper half of the anterior pharynx, and is homologous to the "ventral constrictor of the cibarium" in *Corydalus*. These are the only descriptions in the literature that seem to pertain to this muscle. Accordingly, for the time being, a sound homology is impossible.

The *m. oriscut-susp.* may function as an indirect

dilator of the pharyngeal wall since it exerts direct pull on the hypopharyngeal suspensoria.

ANTERIOR CIBARIAL WALL MUSCLES

These muscles are attached to the anterior cibarial wall (the inner clypeal wall). Entomologists have usually classified them as pharyngeal, but since they are attached to preoral structures rather than the pharynx, the traditional classification seems to be improper. Kelsey (1954) classified them as cibarial. The term "cibarium" refers to the preoral food-receiving pocket formed between the inner clypeal wall and the base of the hypopharynx, but not to the wall itself. Accordingly, the expression "muscles of the cibarium" is not precisely accurate. My first thought was to group these muscles as "inner clypeal wall muscles," but in many insects the inner clypeal wall also enters into the formation of the epipharynx. Consequently, the expression "anterior cibarial wall muscles" is coined as a replacement.

The *musculi clypeo-cibarioparietales* (*m. clyp-cibpariet.*) (Figure 1)

The number of these muscles in the honey bee varies from five to seven pairs; the usual number is six pairs. Their points of fixed attachment are on the cranial wall of the clypeus, parallel to the epistomal sulcus. They diverge internally toward the inner wall of the clypeus (anterior cibarial wall), where they have their points of movable attachment between the bundles of the *musculus intrasuspensorialis dorsualis*. Snodgrass (1942) stated that "the lower part of the organ [the sucking pump] has five pairs of large bundles of dilator muscle fibers attached on its anterior wall . . ." Yet his illustration (p. 31, fig. 10c) shows only five bundles of muscle fibers. Also, his illustration of the points of movable attachment are not accurate (fig. 10d). Duncan stated that *V. pennsylvanica* has only one muscle pair, but I found two pairs in *V. maculata*. This group of muscles is represented by two pairs in *Lasius* and *Corydalus*, one pair in *Stenobracon*, and four pairs in *Macrophya* and *Chauliodes*. In primitive insects, the number of these muscle bundles varies greatly. In all cases, however, they have the same areas of attachment⁵ as in the honey bee.

⁵ Unfortunately, the earlier entomologists gave the name pharynx to the cibarium and consequently many authors believed the cibarial muscles to be attached to the pharynx. Their drawings, however, showed them attached to the anterior cibarial wall.

The *musculus intersuspensorialis dorsualis* (*m. intersusp-dors.*) (Figure 1)

This muscle consists of many bundles, each extending between the two suspensoria. The different bundles can be classified into three groups: (1) those running transversely just above the epipharynx, (2) those running obliquely between the bundles of the *m. clyp-cibpariet.* to form a net, and (3) those running transversely in the area between the level of the *Ganglion Pharyngeale* and the first pair of *m. clyp-cibpariet.* Snodgrass (1942:103) made the following statement with regard to this muscle: "Five thick bundles of fibers on the anterior wall of cibarial region of sucking pump. The first transverse over the mouth, the others oblique between the dilators, attached laterally on the oral plate." The findings of the present study agree with those of Snodgrass with regard to the first muscle bundle but not the other four bundles. At least thirteen muscle bundles extend obliquely to form a net, and they are attached to the hypopharyngeal suspensoria rather than the oral plate. Snodgrass did not describe the third kind of bundle, although he illustrated it (p. 31, fig. 10c). The "upper longitudinal muscle of the pharyngeal suspensorium" of *Lasius* may be the homolog of the second and third groups of muscle bundles in the honey bee. Also, these two groups of muscle bundles are probably the homologs of the "anterior intrinsic pharyngeal muscle" and the "pharyngeal dilator of the mouth" in *Vespula*. Matsuda (1957) stated that there is no homolog of this muscle in *Macrophya*. An examination of his drawings (p. 103, pl. IIA, B) however, indicates that muscle "16" may be its homolog. According to Kelsey, the only bundles represented in *Corydalus* could be homologous to the third group described above. Since descriptions are scarce, no practical homology could be established for this composite muscle. The *m. intersusp-dors.* probably acts as a constrictor of the anterior cibarial wall.

PHARYNGEAL MUSCLES

Matsuda (1965) classified all the muscles attached to the cibarial wall, oral plate (of hypopharyngeal origin), and the pharynx as pharyngeal muscles. In this study, only the muscles attached to the stomodaeum (the true pharynx) are considered as pharyngeal. The pharyngeal muscles can be classified under three subgroups: dorsal, ventral, and circular.

Dorsal Muscles of the Pharynx

The *musculus fronti-pharyngealis I* (*m. fron-phar. I*) (Figures 1, 3)

This muscle has its point of fixed attachment submedially on the frons below that of the *musculus fronti-pharyngealis II*. The point of movable attachment is located on the pharynx beyond the *Ganglion Pharyngeale* and in front of the movable attachment of *musculus fronti-pharyngealis II*.

The *musculus fronti-pharyngealis II* (*m. fron-phar. II*) (Figures 1, 3)

The point of fixed attachment is on the frons, just above that of the *m. fron-phar. I* and below the median ocellus. The broad point of movable attachment is located on the pharynx posterior to that of the *m. fron-phar. I*.

The *musculus fronti-pharyngealis III* (*m. fron-phar. III*)

Although this muscle has not been described or illustrated for any of the three castes of the honey bee, I found it in the drone. It is a very small muscle, about one tenth to one fifth the size of *m. fron-phar. II*. It often extends over the pharynx, making it hard to distinguish. Its point of fixed attachment is located submedially on the frons, dorsad to that of *m. fron-phar. II*. Its point of movable attachment is on the anterior portion of the pharynx, laterad and posterior to that of *m. fron-phar. II*. In many instances, it was found to be loose from its point of fixed attachment, suggesting that it is degenerating.

For convenience, these last three muscles are classified under a subgroup with the name *musculi fronti-pharyngeales*. They have been found on all groups of insects studied. Matsuda (1965) classified them in primitive insects as anterior, posterior, and lateral. In many cases each one is represented by more than one bundle. The number of these muscles varies among insects. As a general rule, they have their points of fixed and movable attachment on the frons and on the pharynx in front of the *Ganglion Hyperoesophagale*, respectively. In *Stenopsocus* (Psocoptera), however, the fixed attachment is on the clypeus (Matsuda 1965). In *V. pennsylvanica*

this group is represented by a single muscle; in *V. maculata*, I found two, the posterolateral one is very small and degenerate. In *Lasius* there are three well-developed muscles belonging to this group. *Stenobracon* has only one, but *Macrophya*, *Chaoliodes*, and *Corydalus* have two.

All authors agree that the *musculi fronti-pharyngeales* act as dilators of the anterior part of the pharynx.

The *musculus cranio-pharyngealis* (*m. cran-phar.*) (Figure 3)

In the worker and queen, this muscle has its point of fixed attachment on the vertex. In the drone, it is attached submedially on the inner lamella of the compound eye.⁶ In all three castes, the point of movable attachment is on the posterior portion of the pharynx in front of the *corpus cardiacum*. In the majority of the drones dissected in the course of this study, this muscle was loose from its point of fixed attachment or was attached with two to four extremely small fibers. In other Hymenoptera and Neuroptera, the *m. cran-phar.* has the same points of attachment as that of the worker honey bee. In a few insects, however, its fixed attachment has shifted to the postoccipital area or vertex. In the drone honey bee, the shift was probably necessitated

⁶Snodgrass (1956) only illustrated these lamellae and named them the "midcranial ridge," on the assumption that they comprise a single structure. Dissection, however, revealed that the inner margin of each compound eye is surrounded by a separate lamella. Because of the closeness of the compound eyes at the top of the head in the drone, these lamellae are approximate and appear as one ridge.

by the large compound eyes and their expansion onto the postoccipital area. In all insects studied, this muscle functions as a dilator of the posterior pharynx.

Ventral Muscles of the Pharynx

These muscles have their points of fixed attachment on the tentorium and their points of movable attachment on the pharynx. In the honey bee there is no unequivocal ventral muscle, although the *m. tentorio suspensorialis* (classified in the present investigation as a hypopharyngeal muscle) may belong to this group. More research is needed, however, to determine the primitive areas of movable attachment before a definite assignment can be made.

Circular Muscles of the Pharynx

The *musculus, circulo-pharyngealis* (*m. circulo-phar.*) (Figure 3)

This muscle is composed of ring-shaped bundles that ensheath the entire pharynx posterior to the hypopharyngeal suspensoria and cover the *musculus tentorio-suspensorialis*. Homologous muscles in other insects are usually identified as ring or circular muscles. In some insects (Psocoptera) the *m. circulo-phar.* is reduced to a series of transverse bundles between the suspensoria. In larval Diptera, it is well developed even though it is absent in the adults. There is general agreement that it functions as a constrictor of the pharyngeal walls.

PART II. NERVOUS SYSTEM

History

Nervous systems may be studied from various viewpoints. The basic questions, however, are always those of homology and of the relationships between nerve-structure, physiological, and behavioral patterns. Despite intensive histological studies, there is still a surprising lack of information about both functional nerve anatomy and nerve homology. To some degree this is because of an insufficient knowledge of the detailed topography of the whole system.

Table 4 presents an annotated list of the more important topographical and histological studies on the nervous systems of insects. In the subsequent text, references are made to nervous tissues of insects included in this table. The reader can refer to the table to find the authors and dates and then to the Literature Cited for complete citations. Physiological studies are not included in the table since, for the most part, they are not germane to this investigation. Articles dealing with each cephalic ganglion and the main nerves emanating from them for insects in general, and Hymenoptera in particular, are reviewed and comparisons are made with comparable structures in the topography section.

Methods of Nomenclature

MAIN GANGLIA AND THEIR DIVISIONS

Nomenclature for the insect nervous system has lagged behind that of other systems. As Snodgrass stated (1931:31), "The basic plan is found to be simple; but, as so often occurs in insect morphology, more difficulties are encountered in finding suitable terms to express the facts than in discovering the facts themselves." Some of the reasons for the difficulties are: (1) the belief that nerve homology is not practically possible because of the diversity of patterns in different insects; (2) a standard terminology would imply homology that often does not exist because of differing degrees of bundling of nerve axons; and (3) detailed topographical studies

of the cephalic nervous system of insects are scarce (Table 4).

In spite of the extensive morphological, histological, and physiological investigations of the so-called brain (Bullock and Horridge 1965), the study of nerve topography in the insect head and its relationship with other tissues is still fragmentary. Even so, the nomenclature of the "brain" and its different divisions is misleading and sometimes inaccurate.

Table 5, an analysis of the literature, shows the different systems of nomenclature devised by different authors (and followed by others) for the various nerves and divisions of the "brain."

The term "brain," according to the current usage for insects, means "the cephalic nerve mass situated above the stomodaeum, including the primitively postoral second antennal ganglia" (Snodgrass 1935: 507). This belief probably dates back to the time of the discovery of the microscope. Some authors, however, have questioned which parts of the nerve mass should be included under the "brain." Binet (1894) and Kenyon (1896) applied the term "brain" to the whole neural mass found within the head except for what they called the "stomogastric ganglia."

Others have avoided using the term "brain" by using noncommittal expressions. Crauss, as early as 1884, used the term supraoesophageal ganglia. Kenyon (1896) designated nerve tissues above the stomodaeum as "the superintestinal portion or dorso-cerebron." Jonescu (1909) considered the nerve mass above the oesophagus as a single ganglion, which he named "the supraoesophageal ganglion."

In the present investigation the term "*Ganglion Hyperoesophagale*" is used for the following reasons: (1) it does not infer a close homology or analogy with the "brain" as found in vertebrates, (2) it does not indicate any function and is strictly morphological, (3) the prefix "hyper" (of Greek origin) fits better than "supra" (of Latin origin) for usage with the Greek term oesophagus, and (4) the term ganglion refers to a composite structure and does not need a plural ending even though more than one neural

TABLE 4.—Major investigations on the cephalic nerve tissues of insects

Author	Year	Order	Family	Species	Major contribution in relation to present study
Newton	1879	Orthoptera	Blattidae	<u>Blatta orientalis</u> Linn.	Gross anatomy of main nerves, general histological studies on the adult
Packard	1880	Orthoptera	Acrididae	<u>Melanoplus femurrubrum</u> DeGeer	Gross anatomy of main nerves of Ganglia Hyper- ¹ and Hypoesophagalia ² in the adult
Craus	1884	Neuroptera	Corydalidae	<u>Corydalus cornutus</u> Linn.	Gross anatomy of the main nerves of Ganglia Hyper- and Hypoesophagalia in the larvae
Vallianes	1887 ^{a,b}	General	—	General	Histology of the Ganglia Hyper- and Hypoesophagalia of the adults
Kenyon	1896	Hymenoptera	Apidae	<u>Apis mellifera</u> Linn.	Mainly gross anatomy of the nerves of Ganglia Hyper- and Hypoesophagalia in the adult
Janet	1905	Hymenoptera	Formicidae	<u>Lasius niger</u> Reine.	Topography of the main nerve tissues found in the head, innervation of some muscles in the adult worker
Hammar	1909	Neuroptera	Corydalidae	<u>Corydalus cornutus</u> Linn.	Incomplete topography of the nerve tissue found in the head, innervation of a few muscles in the larva
Jonescu	1909	Hymenoptera	Apidae	<u>Apis mellifera</u> Linn.	Detailed histological studies of the Ganglion Hyperoesophagale in the adult (three castes)
Holste	1910	Coleoptera	Dytiscidae	<u>Dytiscus marginalis</u> Linn.	Nearly complete topography of the cephalic nerve tissues and innervation of its muscles in the adult
Peterson	1912	Lepidoptera	Sphingidae	<u>Protoparce sexta</u> Johan.	Gross anatomy of the main nerves of the Ganglia Hyper- and Hypoesophagalia in the larva
McIndoo	1914 ^a	Hymenoptera	Apidae	<u>Apis mellifera</u> Linn.	Sense organs associated with the mouthparts in the adult (worker)
Swaine	1920	Lepidoptera	Hepialidae	<u>Sthenopsis thule</u> Strecker	Gross anatomy of the main nerves of the Ganglia Hyper- and Hypoesophagalia in the larva
Nelson	1924	Hymenoptera	Apidae	<u>Apis mellifera</u> Linn.	Gross anatomy of the Ganglia Hyper- and Hypoesophagalia in the larva
James	1926	Hymenoptera	Eurytomidae	<u>Harmolita graminicola</u> Giraud.	Gross anatomy and rather incomplete histology of the Ganglia Hyper- and Hypoesophagalia in the adult
Denis	1928	Collembola	—	Various species	Topography of the cephalic nerve tissues and innervation of other tissues found in the head of the adults
Hilleman	1933	Lepidoptera	Papilionidae	<u>Papilio polyxenes</u> Fab.	Gross anatomy of the Ganglia Hyper- and Hypoesophagalia in the adult
Hanna	1935	Hymenoptera	Chalcididae	<u>Euchalcidia caryobori</u> Hanna	Gross anatomy of the Ganglia Hyper- and Hypoesophagalia in the adult
Snodgrass	1935	Orthoptera	Acrididae	<u>Dissosteira carolina</u> Linn.	Gross anatomy of the Ganglia Hyper- and Hypoesophagalia and their main nerves in the adult
Graichen	1936	Hemiptera	Nepidae	<u>Nepa cinerea</u>	Detailed histological study of the Ganglion Hyperoesophagale in the adult
Maki	1936	Neuroptera	Sialidae	<u>Chauliodes formosanus</u> Peterson	Topography of the cephalic nerve tissue, innervation of some muscles found in the adult
Marquadrat	1939	Phasmida	Lonchodidae	<u>Carausius (Dixippus) morosus</u> Br.	Incomplete topography of the cephalic nerve tissue, innervation of some muscles found in the adult head
Rehm	1939	Hymenoptera	Apidae	<u>Apis mellifera</u> Linn.	Study of muscles innervated by Nervus Mandibularis and Nervus Posterior in the adult (worker)
Nesbitt	1941	Orthoptera	—	Various species	Gross anatomy of the Ganglia Hyper- and Hypoesophagalia of the adults
Power	1943	Diptera	Drosophilidae	<u>Drosophila melanogaster</u> Meigen	Detailed histological study of the Ganglion Hyperoesophagale of the adult
Bucher	1948	Hymenoptera	Torymidae	<u>Monodontomerus dentipes</u> Boh.	Gross anatomy and histology of the Ganglia Hyper- and Hypoesophagalia in the adult
Chaudenreter	1950-51	Thysanura	Lepismatidae	<u>Thermobia domestica</u> Packard	Rather complete topography of the cephalic nerve tissues, following each nerve to its termination
Snodgrass	1956	Hymenoptera	Apidae	<u>Apis mellifera</u> Linn.	Gross anatomy and histology of the Ganglia Hyper- and Hypoesophagalia in the adult (general)
Jawlowski	1958	Hymenoptera	Apidae	<u>Apis mellifera</u> Linn.	Detailed histological study of the Ganglion Hyperoesophagale in the adult (worker)
Satija	1958	Hymenoptera	Apidae	<u>Apis mellifera</u> Linn.	Detailed histological study of the Ganglion Hyperoesophagale in the adult (worker)
Buckup	1959	Mallophaga	Amblycera	<u>Myrsidea cornicis</u> Degeer	Gross anatomy of the Ganglia Hyper- and Hypoesophagalia and their main nerves in the adult

¹—"Brain" of other authors²—"Suboesophageal ganglion" of other authors

mass may be included. Vallianes (1884), independently of embryological data, divided the *Ganglion Hyperoesophagale* into three regions: "protocerebrum," "deutocerebrum," and "tritocerebrum" which he later (1893) found to correspond with the three "primitive elements of neuromeres." Since that time morphologists have used these terms or modifications of them. For the reasons given previously, these terms are respectively changed to *Ganglion Proto-hyper-*

oesophagale, *Ganglion Deuto-hyperoesophagale*, and *Ganglion Trito-hyperoesophagale*.

The nerve mass usually found beneath the stomodaeum in the head is generally known as the "suboesophageal ganglion" (the cerebellum of Craus 1884; the ventrocerebrum of Kenyon 1896). According to Snodgrass (1935) the so-called suboesophageal ganglion is a composite of three ganglia of the ventral nerve cord belonging to those segments

TABLE 5.—Nomenclature of cephalic nerve tissues used by different authors

Order	Orthoptera	Megaloptera	Hymenoptera	Hymenoptera	Megaloptera	Orthoptera	Hymenoptera
Insect	<i>Melanoplus femur-rubrun</i>	<i>Corydalus cornutus</i> L.	<i>Apis mellifera</i> L.	<i>Lasius niger</i> Reine	<i>Corydalus cornutus</i> L.	<i>Discoptera carolina</i> L.	<i>Apis mellifera</i> L.
Nerve tissue/Author	Packard (1880)	Crausa (1884)	Kenyon (1896)	Janet (1905)	Hammar (1908)	Snodgrass (1935)	Present study
	Optic lobe	Caudal Tract	Optic lobe	Protocerebrum	---	Protocerebrum	Ganglion Proto-Hyperoesophagale
	Optic ganglion	---	---	Ocular nerve	---	Nervus opticus	Nervus Opticus
	Ocellar nerve	Optic nerve	Ganglion of the ocellus	Ocellar nerve	Optic nerve	Nervus ocellaris	Nervus Ocellaris
	Antennal olfactory lobe	Cephalad tract	Antennal lobe	Deutocerebrum	---	Deutocerebrum	Ganglion Deuto-Hyperoesophagale
	Antennal nerve	Antennal nerve	Antennal nerve	Antennal nerve	---	Nervus antennalis	Nervus Antennalis
Ganglion Hyperoesophagale (Brain)	Oesophageal lobe	---	Tritocerebrum	Tritocerebrum	---	Tritocerebrum	Ganglion Trito-Hyperoesophagale
	---	---	---	---	---	Nervus labro-frontalis	
	Viseral or frontal nerve	Vagus nerve	---	Connective of the frontal ganglion	Arched nerve	Frontal ganglion connective	Nervus Gangli-Pharyngealis
	Nerve to the labrum	Clypeo-labral nerve	Labral nerve	Sensory nerve of the labrum	Clypeo-labral nerve	Labral nerve	Nervus Labrualis
	Commissure between the two hemispheres	Cross-nerve of the commissure	---	Transverse commissure of the oesophagus	Suboesophageal commissure	Suboesophageal commissure or tritocerebral commissure	Commissura Gangliorum Trito-Hyperoesophagalium
	Oesophageal commissure to the suboesophageal ganglion	Crura cerebri	Oesophageal commissure	Cerebro-gnathal connective	Crura cerebri	Circumoesophageal connective	Connectivi Gangliorum Hyper-Hypo-oesophagalium
	Nerve to the mandible	Mandibular nerve	Mandibular nerve	Nerve to the mandibular metamere	Mandibular nerve	Mandibular nerve	Nervus Mandibularis
Ganglion Hypoesophagale (Suboesophageal ganglion)	---	Gustatory nerve	---	---	Gustatory nerve	Hypopharyngeal nerve	---
	Maxillary nerve	Maxillary nerve	Maxillary nerve	Nerve of the maxillary metamere	Maxillary nerve	Maxillary nerve	Nervus Maxillaris
	Labial nerve	Labial nerve	Labial nerve	Nerve of the labial metamere	Labial nerve	Labial nerve	Nervus Labrualis
	Salivary nerve?	Salivary nerve	Salivary nerve	Nerve of the labial gland	Salivary nerve	Salivary nerve	Nervulus Glandulae Thoracicalis

that became the gnathal region of the insect head. For these two reasons the name *Ganglion Hypoesophagale* is used as a replacement.

The commissure that extends between the pair of *Ganglia Trito-hyperoesophagale* has been given several names (Table 5): "commissure between the two hemispheres," "transverse commissure of the oesophagus," "suboesophageal commissure," and "tritocerebral commissure." Unfortunately, these names (except the last, coined by Snodgrass 1935) are misleading because they do not accurately describe either the function or the position of this commissure. The last name (tritocerebral commissure) is accurate, but the term "cerebral" is questionable for reasons already given. Accordingly, the term *Commissura Gangliorum Trito-hyperoesophagalium* is used here as a replacement.

Nerve cords connecting the *Ganglion Hyperoesophagale* to the *Ganglion Hypoesophagale* have

been variously named as follows (Table 5): (1) "oesophageal commissures to the suboesophageal ganglion," (2) "oesophageal commissures," (3) "circumoesophageal connectives," (4) "*crura cerebri*," and (5) "cerebrognathal connectives." The first name does not indicate what is connected to the "suboesophageal ganglion." The second and third are incomplete, and they emphasize the oesophagus rather than nerve tissues. The fourth name is misleading since the word "crura" is derived from the Latin word "crus" or "cruris" which means leg. The fifth name (proposed by Janet 1905) is more descriptive than the others. However, it does not indicate to which gnathal nerve tissue the "cerebrum" is connected. Following the same pattern used by Janet, the term *Connectivi Gangliorum Hypo-hyperoesophagalium* is proposed as a replacement.

NERVES AND THEIR BRANCHES

Earlier authors investigating main nerves innervating the gnathal segments of the head have named each nerve according to the segment it innervates, e.g., "mandibular nerve," "maxillary nerve," etc. Some investigators put the names in their native languages and others combined Latin and the native language. In the present investigation terms based on classical Greek or Latin are used.

Studies of the topography of the branch nerves, which eventually subdivide into nervules innervating the cephalic tissues, have been infrequent and usually fragmentary. The paucity of published information and questions concerning the homology of this branching make it inadvisable to attempt a homologous system for these branches at this time. Bullock and Horridge (1965:869), after reviewing almost all of the available literature, concluded that "a standard terminology which suggests that a nerve of one species is the same as a nerve in another species is in detail misleading because the axon constituents are almost certainly different." Their statement refers particularly to the main- and branch-nerve level rather than the nervule (innervation) level. The principal problem with the nerves seems to be the coalescence or the bundling of axons that has taken place to varying degrees in different orders. However, as Bullock and Horridge (p. 876) admitted, "the physical condition that governs the growth of axons and their grouping into nerve bundles is believed to be of similar pattern in a large range of insects."

According to my observations in the Hymenoptera, good homology can be ascertained at the branch level by working carefully from one related group to the next. Where large evolutionary gaps are unavoidable, probably histological and physiological studies could be required.

Homology is easier to establish for the terminal branches that actually innervate the tissues than for the more proximal branches or the main nerves. Reasons for this will be presented later. Although Janet (1905) did not study innervation of muscles or follow each nerve to its termination, he named three "nerves" according to the muscles they innervate (nerf du muscle dilatateur inferieur du pharynx, nerf moteur des muscles clypeopharyngiens, and nerf moteur du muscle adducteur du labre). Hammar

(1908), in his fragmentary work in *Corydalus*, designated the branches of each main nerve with Arabic numerals, i.e., branch 1, branch 2, etc. Holste (1910) modified this system by adding the abbreviated form for a main nerve (maxillary nerve equals nm_x) to an Arabic numeral, i.e., nm_x1, nm_x2, etc.

According to the available literature, Denis (1928), Maki (1936), and Chaudonneret (1950-1951) are probably the only morphologists who followed each nerve, branch, or subbranch to its termination. Unfortunately, their systems for nerve nomenclature (combinations of letters and numbers) are difficult to follow, morphologically meaningless, and are not adaptable for studies of nerve homology.

In the present investigation, nerves leaving the *Ganglion Hyperoesophagale* and the *Ganglion Hypoesophagale* are named according to the segment or major area they innervate (ocular, ocellar, mandibular, maxillary). If only one pair of lateral nerves⁷ innervates a certain segment or area, each lateral nerve is recognized as a *Nervus*. If one of the pair branches, however, it is designated as a *Nervus* and each branch as a *Nervus Lateralis*. If a *Nervus Lateralis* branches, each branch is recognized as a *Nervus Sublateralis* provided it does not innervate any tissue before dividing. The portion of the neural mass that innervates a muscle or other type of tissue is designated as a *Nervulus*, which may be a branch of a nerve, a lateral nerve, or a sub-lateral nerve. Each *Nervulus* is named after the tissue it innervates for the following reasons:

1. No standardized system is in use, and the systems that have been used are generally composed of meaningless letters and numbers arbitrarily chosen for each insect studied.

2. As stated previously, homology usually is not difficult to perceive at the nervule level. This is because each nervule supplying a tissue has a limited number of axons (usually two or three per muscle [Bullock and Horridge 1965]), whereas the more proximal nerves have variable and larger numbers of axons, depending upon the number of structures innervated. Unless a structure is innervated from more than one source, its neural supply will be es-

⁷ In some insects nerves innervating the mouthparts are not exactly lateral in position. This can be explained, however, by the assumption that the ancestral insect was annelidlike with no head appendages and with circular segmental muscles innervated by lateral nerves. (Snodgrass 1935:475).

sentially the same as that of its homolog in other insects. In a few cases a single muscle in the head is innervated by more than one nervule arising from the same ganglion. Assuming that the homolog muscle in some other insect has only one nervule, it is not possible to establish a clear homology without histological work. In such cases these nervules are given a collective term, *Nervuli*.

3. In the thorax a muscle appearing to be an integral part of one segment may be innervated by two coalesced *Nervuli*, one arising from its segmental ganglion and the other from a different ganglion. This has been shown experimentally by Nüesch (1954) in the thorax of *Telea polyphemus* Cr. (Saturniidae) and histologically by Pipa and Cook (1959) in the thorax of *Periplaneta americana* Linnaeus (Blattidae). In such situations, more comparative investigations on muscle and nerve homologies between closely related genera, rather than orders, should clarify the problem to some extent. Histological and electrostimulation techniques may also become necessary. Despite the above problems, the proposed system of nomenclature can be a useful tool for understanding muscle homology and the shifting of either the point of fixed or of movable attachment, or both. The ability of the imaginal buds of holometabolous insects (at least in Lepidoptera) to develop muscles depends on the presence of their nerve supply (Kopec 1918, 1922; Richards and Miller 1937). Nüesch (1952) and Williams and Schneiderman (1952) demonstrated that the extirpation of a ganglion or cutting off a single nerve in the thorax of a diapausing pupa of *Telea polyphemus* results in an adult lacking the group of muscles normally innervated by the eliminated ganglion or nerve. Their facts indicate that the muscle anlagen of the pupa requires innervation in order to develop normally during the formation of the adult. Accordingly a nervule of a hypothetical "muscle X" is essential for the development of this muscle, whether the gross anatomy shows that this nerve arises from the first or second ganglion. If the investigator suspects that "muscle X" is homologous in the various species under study, he can verify his suspicion by histological studies of the nerve tissues involved.

4. Comparative studies of the cephalic musculature in insects (Matsuda 1965) revealed that homology can be established between muscles of differ-

ent species. This seems to indicate that homology can be reached between *Nervuli* of different muscles, when complete data on the innervation of the muscles are available.

Topography and Homology of the Cephalic Nerve Tissue

In this investigation, the cephalic nerve tissue is described with regard to its gross anatomy and topography and to its relationships with other tissues (muscular, glandular, integumental, and stomodaeal) in adult queen, worker, and drone honey bees. It also includes a comparison between the nerve patterns of honey bees and those of related pterygotes.

The following are the principal cephalic nerves listed under the ganglia with which they are associated:

Ganglion Hyperoesophagale
Nervi Optici and *Nervi Ocellares*
Nervus Antennalis
Nervus Ganglii Pharyngealis
Nervus Labralis
Nervus Musculi Tentorio-oriscutarius
Nervus Corpoallatialis
Ganglion Hypoesophagale
Nervus Mandibularis
Nervus Maxillaris
Nervus Labialis
Nervus Tegumentalis
Nervus Postoccipitalis
Nervus Posterior

LOCATION AND TOPOGRAPHY OF THE *Ganglion Hyperoesophagale*

Many early investigators studied this structure with the assumption that it is similar to the brain of vertebrates, but more recent physiological as well as morphological studies have shown that it is only crudely analogous at most.

Its principal nerves are essentially the same among different insects, but some obvious differences are related to the shape of the head, the position of the eyes, and the arrangement of such internal structures as the tentorium, muscles, glands, and stomodaeum.

In the honey bee the *Ganglion Hyperoesophagale* is a composite nerve mass occupying almost the entire upper portion of the head cavity. It is surrounded by muscles beneath, glands above and at the sides, and fat bodies and tracheae in between. The position

of this nerve mass varies among the three castes as dictated by differences in the shape of the head, the size of the compound eyes, and the location of the simple eyes. The *Ganglion Hyperoesophagale* in the honey bee occupies a location similar to that in *Lasius*, as shown in Janet's drawings (figs. F, G, H, I) and in *Vespula maculata*.

In the worker honey bee the *Ganglion Hyperoesophagale* (Figure 1) lies directly against branches I and II of the *m. cranio-intramandibularis*, the *m. postoccipiti-prementualis*, and parts of the salivary gland. Between the frontal surface of this nerve mass and frons is an area as broad as the nerve mass itself, which is occupied by the pharyngeal gland. The anterior and posterior surfaces of the ganglionic mass are parallel to each other. The ocelli are arranged in a triangle at the vertex of the worker's head, causing their field of vision to be directed vertically upward. Accordingly, the median part of the *Ganglion Hyperoesophagale* is at a higher level than the dorsal part of the compound eyes (frontal view, Figure 1). In sagittal view, the ganglion follows a vertical axis which is at a 90-degree angle to that of the ventral nerve cord (Figures 2, 3).

In the queen this ganglionic mass occupies a more central position than in the worker, and the anterior surface of the *Lobus Opticus* is nearly covered with the enlarged mandibular glands. The mass is similar in shape to that of the worker but is somewhat wider. The ocelli, forming a triangle, are located on the slope of the vertex, causing their field of vision to be directed upward at an angle of approximately 45 degrees. Consequently, the median part of the ganglionic mass is at the same level as the dorsal part of the compound eyes. Its inclination (using the same axis as that of the worker) is approximately 110 degrees. The queen's *Lobus Opticus* is smaller than in the other castes, but its shape and orientation are similar to those of the worker.

In the drone the *Ganglion Hyperoesophagale* is almost adjacent to the frons. This location may be dictated by the highly developed compound eyes. The area between the posterior surfaces of the median part of this ganglion is tightly packed with tracheae. The ocelli are in completely different locations from those of the queen or worker. According to Jonescu (1909), however, the *Nervi Ocellares*

have the same origin in the *Ganglion Hyperoesophagale* in the three castes. The ocelli of the drone are arranged in a triangle, but on the frontal side of the head, causing the field of vision to be directed forward. Accordingly, the median part of the *Ganglion Hyperoesophagale* is lower than the tips of the compound eyes and inclined about 130 degrees, which is greater than in the other castes. The drone's *Lobus Opticus* is strikingly the largest of the three castes, due without doubt to its exceptionally large compound eyes. This lobe differs in the drone from its homolog in the worker and queen by being bent apically toward the rear.

The *Ganglion Hyperoesophagale* of insects can be divided into three portions: *Ganglion Proto-Hyperoesophagale*, *Ganglion Deuto-Hyperoesophagale*, and *Ganglion Trito-Hyperoesophagale*. Each of these ganglia gives rise to several nerves.

Ganglion Proto-Hyperoesophagale

Lobus Opticus.—Leydig (1864) probably was the first author to use "sehappen" (optic lobe) for the lobes that represent lateral elongations of the "protocerebrum" in which the optic centers are located.

The size of the *Lobus Opticus* differs among insects. In many cases, as in *Corydalus* (Crauss 1884), it is rudimentary. Its size and shape sometimes differ between the sexes, as in the honey bee (Jonescu 1909). Ehnborn (1948) found that the exterior structure of the "cerebrum" varies considerably in different lepidopterous groups depending upon the development of the *Lobus Opticus*. He classified this structure in Lepidoptera into four types: (1) Rhopalocera types, with a square cross section; (2) Macrofrenatae type, constricted into two distinct parts; (3) Tineoidea type, separated ventrally from the "protocerebrum" but merging dorsally with the protocerebral lobe; and (4) Micropterygidae type, essentially like that of a Trichoptera.

In the honey bee worker the *Lobus Opticus*, which constitutes a great portion of the *Ganglion Hyperoesophagale*, is intermediate in size between that of the drone and queen. A horizontal section indicates that in the worker this lobe is in the same plane as the *Ganglion Proto-Hyperoesophagale*.

Nervi Optici.—These are the retinal neurites of the compound or simple lateral eyes and are received in the outer end of the optic lobes (*Lobi Optici*).

Therefore, the *Nervi Optici* are generally very short. The *Nervi Optici* differ, however, in caterpillars which have rudimentary optic centers.

Crauss (1884) and Hammar (1908) observed the *Nervi Optici* in *Corydalus*. Both authors stated that the main "optic nerve" is divided into seven branches even though the larva has six ocelli.

Viallanes (1887a) described the *Nervi Optici* in *Vespa crabro* Linnaeus and called them "la couch post-retinienne" (the postretinal layer).

Jonescu (1909), in his histological study of the drone honey bee, followed the terminology proposed by Viallanes and stated that the structure of the *Nervus Opticus* layer is the same as in the other two castes.

According to Holste (1910), *Dytiscus marginalis* Linnaeus has a single *Nervus Opticus*, which he described (p. 424) as "Dieser ist bei weitem der starkste allen Nerven" (This is by far the strongest of all nerves). Peterson (1912) stated that the "optic nerve" in the larva of *Protoparce sexta* is very small and extends laterally without branching until it reaches the area where the lateral simple eyes are located. Swaine (1920) and Hilleman (1933) found almost the same situation in the larvae of *Sthenopas thule* and *Papilio polyxenes*, respectively. According to Ehnborn's histological studies (1948), Trichoptera larvae have no *Nervus Opticus*.

Nervi Ocellares.—According to Snodgrass (1935: 479) "the slender ocellar pedicels uniting the facial ocelli with the brain are commonly called the ocellar nerves." Cajal (1918), however, has shown that the primary ocellar center is located in an enlarged outer end of what has been called the "ocellar nerve." Therefore, *Nervi Ocellares* are those groups of "retinal fibers" that terminate in the distal ends of the so-called ocellar stalks.

The available literature on ocellar nerves is very meager. However, a few authors have described the "ocellar pedicel" corresponding to the *Lobus Opticus* in many insects (Maki 1936; Ehnborn 1948).

In the honey bee the ocellar nerves have their centers in the *Ganglion Proto-Hyperoesophagale*, which is the most anterior structure of the composite *Ganglion Hyperoesophagale* as in other studied groups of insects. Since the gross anatomy and histology of the *Nervi Optici* and the *Nervi Ocellares* have been studied extensively in the honey bee, there is no need for a detailed description at this time. The

reader is referred to the works of Kenyon (1896), Jonescu (1909), Snodgrass (1956), Jawlowski (1958), and Satija (1958).

Ganglion Deuto-Hyperoesophagale

Nervus Antennalis (N. Anten.) (Figures 2, 4, 10)

The *Nervus Antennalis* innervates the extrinsic and intrinsic antennal muscles and the various sense organs found in the antenna. Newton (1879) was the first to observe a fine branch arising from the antennal nerve and innervating the antennal muscles within the head of the cockroach. Crauss (1884) reported that this nerve in *Corydalus* divides into two branches, the cephalic entering the antenna and the caudal innervating the antennal muscles in the head. However, he did not mention which nerve innervates the intrinsic muscles of the antenna. He also stated that the "antennal nerve" gives rise to a small branch which bifurcates and innervates the area near the eyes.

Viallanes (1887a) found a "branch" leaving the "antennal nerve" in *Vespa crabro* which he named "nerf antennaire accelsoire" and correlated it with that described by Newton for *Blatta*, although he did not trace it to its termination in the muscles. In the honey bee worker, Kenyon (1896) stated that a nerve innervating the extrinsic antennal muscles arises from the lower surface of the "antennal nerve." He named this nerve the "*antenna motor internus*" and considered it as a part of the "trito-cerebron." He also gave the name "*antenna motor externus*" to the main nerve, although he did not trace it to its termination.

Janet (1905) was the first author to study the topography of the *Nervus Antennalis*. He stated that in *Lasius niger* it gives rise to five branch nerves: (1) a small motor nerve dividing into four branches, one for each of the four intrinsic muscles of the antenna; (2) a small motor nerve innervating the extrinsic muscles of the antenna; (3 and 4) two big nerves entering the antenna; and (5) a "chordotonal nerve" terminating in the integument. Jonescu (1909) found the same nerves in the honey bee except for the "chordotonal nerve." Swaine (1920) stated that the *Nervus Antennalis* appears to be united at its base with the "fronto labral" nerve. According to Maki (1936) the "common root of

the antennal nerves" gives rise to three nerves, two (Ad and Al) to the extrinsic, and one (Af) to the intrinsic muscles of the antenna. He also stated that the common root divided at the scape into two main branches (Ai and Aii). Chaudonneret (1950-1951) described the topography of the *Nervus Antennalis* in great detail. His drawings, however, do not show innervation or relation to other tissues found in the head. He used a combination of letters and numbers to designate "nerves" (t42, t47, Naa, etc.). Backup (1959) in his study of the mallophagan *Myrsidea* showed that the antennal nerve gives rise to three "nerves" before entering the scape. Two of these "nerves" (NAnt1 and NAnt2) innervate what he called the "*Musc. scape anterior*" and the "*Musc. scape posterior*." The third one (NAnt3) innervates the "*Musc. pedicelli anterior*" and the "*Musc. pedicelli posterior*."

From the above review, it appears that no one has attempted to name the branches or subbranches of the main nerves. Maki, Chaudonneret, and Backup, however, used letters and combinations of letters and numbers for most of the nervules innervating the muscles.

In the honey bee the *Nervus Antennalis* appears to be an extension of a small lobe, the *Lobus Antennalis* (*Lob. Ant.*), located anteriorly on the lower part of the *Ganglion Hyperoesophagale* and surrounds the top part of the pharynx (Figure 2). This lobe was called the olfactory lobe by Viallanes (1887a), whose lead was followed by others. Actually, the roots of the *Nervus Antennalis* come in part from the *Ganglion Deuto-Hyperoesophagale* (*Gang. Deut-Hyperoesoph.*), and in part from the *Lobus Antennalis* (Jonescu 1909 and Jawlowski 1958). The *Nervus Antennalis* extends forward and passes through the neural mass of the *Lobus Antennalis*. In the worker and queen, after leaving the lobe, this nerve angles anteriorly and cephalad until it enters the antennal scape; however, in the drone it runs anteriorly only to the base of the scape. This extrinsic part of the *Nervus Antennalis* is longest in the worker; in the queen it is about two thirds as long, and in the drone about one fifth as long as in the worker. The extrinsic part of the *Nervus Antennalis* in all castes of *Vespula maculata* is similar to that found in the drone honey bee, but in *Lasius* (workers) it is similar to that in the worker honey bee.

In the worker and queen a short motor branch, the *Nervus Antennalis Lateralis I* (*N. Ant. Lat. I*), emerges from the cephalad side of the *Lobus Antennalis* and runs downward toward the extrinsic muscles of the antennae. It subdivides into four small branches, each of which innervates one of the extrinsic muscles of the antenna. These branches, designated as nervules, are named the *Nervulus musculi Tentorio-scapualis I* (*Nl. m. Tent-scap. I*), *Nervulus musculi Tentorio-scapualis II* (*Nl. m. Tent-scap. II*), the *Nervulus musculi Tentorio-scapualis III* (*Nl. m. Tent-scap. III*), and the *Nervulus musculi Tentorio-scapualis IV* (*Nl. m. Tent-scap. IV*). In the drone, the *Nervus Antennalis Lateralis I* appears to emerge from the base instead of the distal tip of the *Lobus Antennalis*. Also, the degree of bundling of the nervules of the extrinsic antennal muscles differs among individual drones. In some cases, each of two sublateral nerves divides into two nervules, and in other cases there are four nervules, each serving one extrinsic antennal muscle and leaving the *Lobus Antennalis* without bundling into sublateral nerves. This last situation is similar to that found in *Vespula maculata*.

The *Nervus Antennalis Lateralis I* in the honey bee appears to be the "accessory nerve of the antenna" described for *Caloptenus* and *Oedaleus* (Acrididae) by Viallanes (1887b). In *Lasius* it resembles that in the worker honey bee, but in *Vespula maculata* it resembles that in the drone since it has separate nervules for each muscle.

In drone honey bees that have two sublateral nerves for the extrinsic antennal muscles, it was found that one nerve divides into two nervules that go to the *m. tentorio-scapualis I* and the *m. tentorio-scapualis II* (dorsal muscles acting as levators). The other nerve divides into two nervules that innervate the *m. tentorio-scapualis III* and the *m. tentorio-scapualis IV* (ventral muscles acting as depressors). This situation is found also in *Chauliodes* which, however, has only one "levator" muscle.

After leaving the *Lobus Antennalis*, the *Nervus Antennalis* gives off a sensory branch that extends dorsally and anteriorly until it reaches the integument above the area of articulation of the antenna. There it gives rise to several small branches innervating the integument of the frontal area. In the area of branching, it is attached to a sense organ located at the outer end of the upper area of the

articulating membrane between the scape and the frons. This nerve is named *Nervus Antennalis Tegumentualis*. It may be the same as a nerve in *Corydalus* described by Crauss (p. 180) as a "small branch which divides in small branches and innervates the area near the eye." This "chordotonal nerve" described in *Lasius* by Janet (1905) is probably another homolog even though Jonescu (1909) was not able to see it in the honey bee.

A short distance from the divergence of the *Nervus Antennalis Tegumentualis*, the *Nervus Antennalis* gives off from its dorsal side another branch, the *Nervus Antennalis Lateralis II* (*N. Ant. Lat. II*). This branch extends dorsally, lying against the *Nervus Antennalis* until it enters the scape, and starts diverging to the outer side of the antenna where it divides into two branches. The first branch, the *Nervulus Scapo-tegmentualis* (*Nl. Scap-tegum.*), is small and sensory, directed dorsally and laterally and attached to a sense organ located on the outer dorsolateral corner of the scapal base. Janet named the homolog of this sense organ in *Lasius* the "sensitif tactile ganglia." The second branch, the *Nervulus muscoli Scapo-pedicularis I* (*Nl. m. Scap-pedic. I*), is a motor nervulus, and extends dorsally and medially in the scape until it meets with and innervates the *m. scapo-pedicularis I*.

From the ventral side of the *Nervus Antennalis*, a short distance anterior to the point of divergence of *N. Ant. Lat. II*, the *Nervus Antennalis Lateralis III* (*N. Ant. Lat. III*) separates. It extends ventrally and parallels the main nerve until it reaches the scape, where it bends toward the inner lateral side of the scape. It divides into two branches, the first being sensory and connecting with a sense organ located on the lateral ventral corner of the scapal base, and the second, the *Nervulus muscoli Scapo-pedicularis II* (*Nl. m. Scap-pedic. II*), extending ventrally and laterally until it innervates the *m. scapo-pedicularis II*. In *Lasius*, however, the homologs of the intrinsic antennal muscles are innervated by two subbranches of a nerve that arises ventrally from the *Nervus Antennalis*. Maki (1936) and Buckup (1959) found the same situation to occur in *Chauliodes* and *Myrsidea cornicis*, respectively. In a few drones the intrinsic muscles of the antenna are innervated by subbranches of a nerve arising ventrally. Such drones had only one, relatively large,

sense organ in the dorsolateral corner of the scapal base, as in *Lasius*.

Prior to entering the scape, the *Nervus Antennalis* divides into two main sensory nerves extending to the tip of the antenna. These nerves are the *Nervus Antennalis Lateralis IV* (*N. Ant. Lat. IV*) and the *Nervus Antennalis Lateralis V* (*N. Ant. Lat. V*). Each of these sensory nerves, just before entering the pedicel, gives rise to a short sensory branch terminating in the so-called Johnson organ.

The topography of the *Nervus Antennalis* in the honey bee, especially the drone, is similar to that in *Vespula maculata*. It has the same number of branches and nervules arising from homologous locations and innervating homologous muscles.

Ganglion Trito-hyperoesophagale

Nervus Ganglii Pharyngealis (*N. Gang. Phar.*) (Figures 1, 3, 10)

Janet (1905) proposed the name "connective of the frontal ganglion" for this nerve. Hammar (1908) named it the "arched nerve." Jonescu, one year later, named it the "frontal ganglionic nerve." This name has been universally accepted and applies to the inner nerve of the *Nervus Pharyngeo-labralis* (*N. Phar-labr.*) which is connected to the "frontal ganglion."

In the honey bee this nerve leaves the *Ganglion Hyperoesophagale* in the area behind the *Lobus Antennalis*, adjacent to the pharynx. However, its center is in the *Ganglion Trito-hyperoesophagale*. In other insects this nerve and the *Nervus Labralis* are bundled together for a short distance forming the so-called "fronto-labral" nerve. This situation is demonstrated clearly in *Vespula maculata*. The *Nervus Ganglii Pharyngealis* runs cephalad against the walls of the pharynx and curves anteriorly, until it meets the *Ganglion Pharyngeale* (*Gang. Phar.*), which is located medially between the clypeus and frons. This ganglion has been known as the "frontal ganglion" in the works of Leydig (1864), Janet (1905), and others. The term is misleading, although some authors think it is useful in designating the structure as a landmark separating the preoral clypeus from the oral frons. This is questionable, as suggested by the work of Pesson (1944) on coccids and Dupor:é (1956) on adult monarch butterflies, since both

these investigations found this ganglion to be much more posterior than in more generalized insects. Actually, its nerves innervate muscles belonging to the pharynx and the anterior cibarial wall rather than the frons. Snodgrass (1947) stated that the "frontal ganglion" always lies near the distal end of the pharynx behind the mouth. For the above reasons, the term *Ganglion Pharyngeale* appears to be a logical designation.

The *Nervus Ganglii Pharyngealis* gives rise dorsally to a small motor branch immediately after it curves toward the anterior wall of the pharynx. This branch, designated as the *Nervule musculi Fronti-suspensorialis* (Nl. m. *Fron-susp.*), innervates the *m. fronti-suspensorialis*. In the same area, but from its ventral side, the *Nervus Ganglii Pharyngealis* gives off two small nervules. One angles anterolaterally until it reaches and innervates the *m. tentorio-suspensorialis*. This nervule is named the *Nervulus musculi Tentorio-suspensorialis* (Nl. m. *Tent-susp.*). The other nervule extends posteriorly and innervates the *m. fronti-labralis* and is consequently named the *Nervulus musculi Fronti-labralis* (Nl. m. *Fron-labr.*). *N. Gang. Phar.* also gives off another motor branch just before entering the *Ganglion Pharyngeale*. This branch, named the *Nervus musculorum Fronti-pharyngealium* (N. m. *Fron-phar.*), extends dorsally and subdivides into two nervules innervating the *m. fronti-pharyngealis I* and the *m. fronti-pharyngealis II*. Consequently, they are named the *Nervulus musculi Fronti-pharyngealis* (Nl. m. *Fron-phar. I*) and the *Nervulus musculi Fronti-pharyngealis II* (Nl. m. *Fron-phar. II*), respectively. Although the drone has three muscles belonging to the *musculi fronti-pharyngeales* group, no third nervule has been found for the third muscle. This may explain why this muscle appears to be degenerating in the drone.

From the *Ganglion Pharyngeale*, two main nerves leave in opposite directions. One extends anteriorly and medially over the cibarium and the other extends posteriorly and medially over the pharynx. The first one is named the *Nervus Ganglii Pharyngealis Anterior* (N. *Gang. Phar. Ant.*). It gives rise to a variable number of small lateral branches innervating the different bundles of the *m. clypeo-cibarioparietalis*. Each nervule is named according to the bundle it innervates. For convenience, they are given a collective term, *Nervuli musculorum*

clypeo-cibarioparietalium (Nl. m. *Clyp-cibar.*). The most anterior part of the *Nervus Ganglii Pharyngealis Anterior* (the part that follows the nervule going to the most ventral bundle of the *m. clypeo-epipharyngealis*) innervates the *m. clypeo-epipharyngealis* and is named, accordingly, the *Nervulus musculi Clypeo-epipharyngealis* (Nl. m. *Clyp-epi-phar.*). Since the *Nervus Ganglii Pharyngealis Anterior* has not been studied in detail in pterygote insects, a sound homology for it cannot be reached. In *Vespula maculata*, however, I found that it divides into a pair of nerves, each innervating the muscles lateral to it. Since in *Vespula* each member of the pair innervates the series of muscles on its own side of the head, it appears that in the honey bee the main nerve is bundled. Surprisingly, it is not involved in the innervation of the *m. intrasuspensorialis dorsualis*.

The second nerve is named the *Nervus Ganglii Pharyngealis Posterior* (N. *Gang. Phar. Post.*). It extends mediodorsally and posteriorly over the pharynx. Before passing under the *Ganglion Hyperoesophagale*, it gives rise to a lateral branch extending ventrally, paralleling the hypopharyngeal suspensorium and innervating the *m. oriscuto-suspensorialis*. Accordingly, this branch is named the *Nervulus musculi Oriscuto-suspensorialis* (Nl. m. *Orisc-susp.*). It passes under the *Ganglion Hyperoesophagale* and the most anterior part of the so-called aorta. Before passing between the points of movable attachment of the *m. cranio-pharyngealis*, it gives off laterally two small nervules, both innervating the *m. cranio-pharyngealis*. Consequently, they are given the name *Nervuli musculi Cranio-pharyngealis* (Nl. m. *Cran-phar.*). The *Nervus Ganglii Pharyngealis Posterior* continues posteriorly until it reaches the level of the "dorsal paracardial commissure" where it divides into two branches. Each member of the pair curves around ventrally and posteriorly until it is on the lateral side of the oesophagus, where it continues without subbranching until it reaches the crop. At that point each branch divides and subdivides into many nervules that innervate the walls of the crop. It was noted that before dividing into a pair, the *Nervus Ganglii Pharyngealis Posterior* gives off laterally numerous nervules, the *Nervuli musculi Circulopharyngealis* (Nl. m. *Circulphar.*) which innervate the *musculus circulopharyngealis*. This nerve has not yet been described in detail in other insects.

In *Vespula* the homologous nerve follows the same topographic pattern.

Nervus Labrualis (*N. Labr.*) (Figures 1, 3)

The name "clypeo-labral" was proposed for this nerve by Crauss (1884). He wrote that it arises from each "crus" and gives rise to three small branches innervating the clypeus, while the main nerve extends cephalad into the labrum. Hammar (1908) disagreed with Crauss about its origin and indicated that it arises from the tritocerebrum. Janet (1905) was the first to associate it with muscles and sense organs found on the margins (*les cotes*) of the pharynx. He also stated that it innervates the various structures belonging to the "post cerebral segment" such as the labrum and the muscles of the upper parts of the pharynx. Consequently, he designated it as the "proto-cerebral nerve."

Jonescu (1909) considered it to be situated behind the "deuto-cerebrum," but did not indicate from which segment it arises. Instead, he stated that it should be included within the "suboesophageal ganglion," especially since it shows a close connection with the latter.

Holste (1910) found that the labral nerve gives rise to a small branch passing transversely over the "oesophagus" to join with the "prefrontal plexus" of the sympathetic nervous system. He found the main nerve splitting into two branches, the "upper" innervating the clypeus and the "lower" innervating the labrum ("*musculus dilator pharyngis primus*" and "*musculus compressor pharyngis*"), respectively. Peterson's (1912) and Swaine's (1920) studies on *Protoparce* and *Sthenopus* (Lepidoptera), respectively, indicate that the topography of the "labral nerve" is similar to that described by Holste for *Dytiscus*. Maki (1936) found almost the same pattern to exist in the neuropteroid, *Chauliodes*. Chaudonneret (1950-1951) illustrated and described in great detail the topography of the "clypeo-labral" nerve in *Thermobia*. He found the plan to be very complicated and quite different from those described for Pterygota. As might be expected, his findings on the topography of this nerve are similar to those of Denis (1928) for *Anurida* (Collembola).

In the honey bee this nerve is separate from and directly behind the *Nervus Ganglii Pharyngealis*. In other insects, however, such as *Corydalus*, *Chauliodes*,

Lasius, and *Vespula*, both nerves are joined for a short distance.

The *Nervus Labrualis* extends anteriorly and ventrally, parallel to the *m. tentorio-oriscutarius*. About midway and before crossing over the hypopharyngeal suspensorium, it gives rise to a sensory branch directed backward and connecting with a sense organ on the oral plate. This branch is called the *Nervulus Tegumenti Labrualis I* (*Nl. Tegum. Labr. I*). McIndoo (1914a) considered this sense organ to be for taste. Unfortunately, no complete histological or physiological study has been made to determine its function. The *Nervus Labrualis* then passes over the hypopharyngeal suspensorium at the level of the fixed attachment of the *m. tentorio-suspensorialis*. In the above area, it gives rise to a sensory branch that extends anteriorly until it reaches and innervates the cranial wall of the clypeus. This branch is named the *Nervulus Tegumenti Labrualis II* (*Nl. Tegum. Labr. II*). A short distance ventral to the last branching, the *Nervus Labrualis* gives rise to a nervule that is directed medially toward the midline of the anterior cibarial wall. Since this nervule innervates the *m. intrasuspensorialis dorsualis*, it is named the *Nervulus musculi Intrasuspensorialis Dorsualis* (*Nl. m. Intrasusp. Dors.*).

The *Nervus Labrualis* then parallels the suspensorium and at the level of the basal part of the oral plate it gives rise to a branch directed horizontally and posteriorly. This branch, designated as the *Nervulus Tegumenti Labrualis III* (*Nl. Tegum. Labr. III*), enters the epipharynx and connects with the sense organ located laterally on the inner wall of the epipharynx. The remaining portion of the *Nervus Labrualis* extends ventrally and enters the labrum, innervating its anterior and posterior walls with several subbranches. This terminal portion of the main nerve is called the *Nervulus Tegumenti Labrualis II* (*Nl. Tegum. Labr. II*) indicating that it innervates the labrum proper.

In *Vespula maculata* the topography of the *Nervus Labrualis* is similar to that in the honey bee, thus indicating that criteria of homology can be established between distantly related genera. Unfortunately, no complete studies of this nerve have been made. Fragmentary works on *Dytiscus* (Coleoptera), *Protoparce*, *Sthenopsis* (Lepidoptera), and *Chauliodes* (Neuroptera), however, indicate that the *Nervus Labrualis* has quite a different topographic

pattern in these insects, largely because they have two additional pairs of labral muscles. In these insects the *Nervus Labrualis* is connected to the *Nervus Ganglii Pharyngealis Anterior*.

Nervus Corpoallatialis (*N. Corpoallat.*) (Figures 3, 8)

In the honey bee this nerve leaves from the lower posterior end of the *Ganglion Hyperoesophagale*, just above the level of the oesophagus. It extends backward for a short distance and is attached medially to the anterior side of the *corpus allatum*. Hanan (1955), in a detailed study of the relations between the *corpora cardiaca* and the *corpora allata* in the honey bee, discovered the ring of "neural and aortal tissue" surrounding the oesophagus and connecting each *corpus cardiacum* with its homolog on the other side by what he called the "dorsal paracardial commissure" and the "ventral paracardial commissure." He also indicated that each *corpus allatum* connected to the *corpus cardiacum* by a very short, almost indistinguishable, connective. My findings disagree with those of Hanan in the following particulars: (1) A distinct and complete ring, probably of neural tissue, surrounds the oesophagus and connects to the *corpora cardiaca* with a membranous tissue. (2) A separate connective of neural tissue connects the two *corpora allata* ventrally. (3) Another connective of neural tissue ventrally connects the ventral parts of the *corpora cardiaca* (Figure 8). According to Hanan, the connectives he discovered had not been described in other insects. The same holds true for the connectives I found between the *corpora cardiaca* and between the *corpora allata*. These connectives are named the *Commissura Corporum Cardiacorum* (*Com. Corp. Card.*) and *Commissura Corporum Allatorum* (*Com. Corp. Allat.*), respectively.

Commissura Gangliorum Trito-Hyperoesophagalium

Table 5 shows the different names that have been applied to this commissure. It is distinguishable in *Corydalus*, *Melanoplus*, *Dytiscus*, *Protoparce*, and others, but it is indistinguishable in *Lasius* and *Apis*. According to Snodgrass (1956), it is embedded in the "suboesophagial" ganglion in the adult honey bee, although free in the larva (Nelson 1924).

Nervulus musculi Tentorio-oriscutarius (*Nl. m. Tent.-orisc.*) (Figure 3)

The nerve arises from the median line on the dorsal side of the *Ganglion Hypoesophagale* of the honey bee, but, according to the histological studies of Jonescu (1909), its group of motor cells is located on the side of the labral ganglion. Consequently, it is described under the *Ganglion Hyperoesophagale* rather than under the *Ganglion Hypoesophagale*. Jonescu also stated that this "nerve" has a pair of roots, thus indicating a type of bundling resulting from the fusion of the two innervated muscles.

The *Nervulus musculi Tentorio-oriscutarius* extends ventrally and anteriorly adjacent to the *musculus tentorio-oriscutarius* which it innervates. A corresponding nervule is in *Lasius* and two in *Vespula maculata*.

LOCATION AND TOPOGRAPHY OF THE *Ganglion Hypoesophagale*

Contradictory opinions exist concerning the placement of this neural mass and whether it is a part of the so-called brain. However, it is now believed to be a part of the ventral nerve cord. Even from the histological aspects, only limited investigations have been carried out on this ganglionic mass or its main nerves. The more important works dealing entirely or in part with this nerve mass are those of Crauss (1884), Bauer (1904), Hammar (1908), Holste* (1910), Swaine (1920), Denis* (1928), Maki* (1936), Marquardt (1939), and Chaudonneret* (1950-1951). (Asterisk indicates a detailed study of the "suboesophagial ganglion.")

In the honey bee the main nerves arising from the *Ganglion Hypoesophagale* are the *Nervus Mandibularis*, the *Nervus Maxillaris*, the *Nervus Labialis*, the *Nervus Postoccipitalis*, and the *Nervus Posterior*.

In the honey bee this ganglion appears to be connected directly to *Ganglion Trito-hyperoesophagale* because of the shortness of the *Connectivi Gangliorum Hyper-hypoesophagalium*. It is located directly beneath the stomodaeum and above the level of the point of fixed attachment of the extrinsic muscles of the antenna. The *Ganglion Hypoesophagale* has almost the same location in the three castes. The connectives are also short in *Vespula maculata* and *Lasius niger*.

Nervus Mandibularis (N. Mand.) (Figures 2, 4)

Crauss probably was the first morphologist to study the "mandibular nerve" and its branches in *Corydalus*. His study was fragmentary, however, and did not deal with innervation. Hammar found the mandibular nerve in *Corydalus* to have three branches: branch 1 bending caudad and innervating the "large mandibular muscle" (probably the homolog of the *musculus cranio-intramandibularis*), branch 2 connecting to "ganglion g" (a part of what he called the sympathetic nervous system), and branch 3 entering the mandible and also innervating some muscles (not identified). Holste likewise found that the "mandibular nerve" in *Dytiscus* divides into three branches: branch "nfmnd" innervating the "*musculus flexor mandibularis*" (*cranio-intramandibularis*), the second branch innervating both integument and the "extensor muscle of the mandible" (*cranio-extramandibularis*), and the third branch entering the mandible. His investigation showed that the "mandibular nerve" does not give rise to any branches connecting to the "sympathetic nervous system," thus differing from the situation in *Corydalus*. According to Swaine, the general topography of the mandibular nerve in *Sthenopsis* is almost the same as it is in *Dytiscus*, except that the "mandibular nerve" gives rise to a small branch that fuses with its homolog from the opposite side and continues cephalad as a double nerve serving the hypopharynx. Owing to a "tentorial adductor of the mandible" in *Chauliodes*, Maki found the mandibular nerve to have four branches that "enter the lateral portion of the clypeus." Chaudonneret found that the topography of the "mandibular nerve" in *Thermobia* differed between specimens. He stated also that such a difference could exist even between the two mandibles of the same specimen. In general, however, he found that the mandibular segment is innervated by four "main nerves" and their branches. The topography of these nerves (thysanuroid-type mandible) differs greatly from those of other groups studied (orthopteroid-type mandible). Consequently, there is no need to review it in detail here. It is notable, however, that Chaudonneret was probably the first to study the innervation of the mandibular gland.

The *N. Mand.* was described by Rehm (1939) for the worker honey bee. Unfortunately, his description

contains many errors as evidenced in his Figure 1 on page 92.

In the worker honey bee the *Nervus Mandibularis* is the most anterior nerve attached to the *Ganglion Hypoesophagale*. It passes anteriorly and ventrally under the pharynx and laterally to the fixed point of attachment of the intrinsic antennal muscles, the pretentorium, the *m. gena-cardinalis*, and the *m. tentorio-stipitalis I*. It then angles laterally and anteriorly toward the points of fixed attachment of the *m. tentorio-cardinalis* and the *m. tentorio-stipitalis II*, curves under them, and divides into three branches.

The first, the *Nervus Mandibularis Lateralis I*, extends laterally over the *m. tentorio-mandibularis* and posteriorly under the mandibular gland. After passing under half of this gland, it gives rise to a small branch, the *Nervulus Glanduli Mandibularis*, (*Nl. Gland-Mand.*) which innervates it. After passing under the mandibular gland, the *Nervus Mandibularis Lateralis I* forks into two subbranches. The branches of this fork extend laterally and upward until they reach and innervate the *m. cranio-extramandibularis*. This part of the *Nervus Mandibularis Lateralis I* is named the *Nervulus musculi Cranio-extramandibularis* (*Nl. m. Cran-extramand.*).

The second branch, the *Nervus Mandibularis Lateralis II* (*N. Mand. Lat. II*), is very short and almost indistinguishable. It connects directly to the lateral corner of a diamond-shaped neural mass lying against the *m. tentorio-mandibularis*. The ventral corner is extended as a long threadlike branch connecting with the *Nervus Mandibularis* before the latter enters the mandible. The other lateral corner of the neural mass gives rise to a very thin branch, the *Nervulus musculi Cranio-intramandibularis II* (*Nl. m. Cran-intramand. II*), which curves upward and passes posteriorly between the two nodes of the cranial articulation of the cardo. It passes posteriorly and dorsally over the *m. gena-cardinalis*, where it parallels the inner side of the long tendonlike apodemal growth on which the *m. cranio-intramandibularis II* has its point of movable attachment. Eventually it reaches this muscle and innervates it.

The third and last branch extends dorsally and passes between the two nodes of the cranial articulation of the cardo on the outer side of the *Nervus musculi Cranio-intramandibularis II*. It continues dorsally, passing across the *m. gena-cardinalis* until

it reaches and innervates branch I of the *m. cranio-intramandibularis*. Accordingly, it is named the *Nervulus musculi Cranio-intramandibularis I* (*Nl. m. Cran-intramand. I*).

After giving off the aforementioned three lateral nerves, the *Nervus Mandibularis* curves downward and passes under the *m. tentorio-mandibularis*. In this area it gives rise to a sensory nervule that reaches the inner articulating membrane of the mandible, and then extends cephalad, parallel to the inner side of the *m. tentorio-mandibularis*. After passing under the anterior portion of the mandibular gland, the nervule enters the mandible and innervates its integumental walls. Accordingly, this nervule is named *Nervulus Tegumenti Mandibularis* (*Nl. Tegum. Mand.*).

Establishing homology for the *Nervus Mandibularis* among insects is rather difficult because of the fragmentary work that has been done. For example, only Chaudonneret (1950-1951) has even mentioned the innervation of the mandibular gland (in *Thermobia*). However, by comparing the topography of the *Nervus Mandibularis* of the honey bee with other groups studied, a general plan may be reached. All authors agree that it divides into several branches, each of which is responsible for innervating a single mandibular muscle, or the mandible proper. Accordingly, the branches may be considered as homologs whenever they innervate homologous muscles.

In the drone honey bee the topography of the *Nervus Mandibularis* is similar to that of the worker and queen (described above), with minor differences resulting from a reduction of the mandibular muscles. For instance, since branch II of the *m. cranio-intramandibularis* is absent, there is no homolog of the nervule innervating it. Accordingly, the "diamond-shaped nerve mass" (found in the worker) is rather triangular in the drone. Also, the male appears to have no *Nervulus Glanduli Mandibularis*, because its mandibular gland is greatly reduced in size.

Nervus Maxillaris (*N. Max.*) (Figures 3, 4, 5)

According to Craus, the "maxillary nerve" divides into four branches: branch "a" entering the maxillary palpus, branch "b" innervating the integument, and branches "c" and "d" innervating the extrinsic and intrinsic muscles of the maxilla, respectively.

Hammar (1908) and Swaine (1920) made only incomplete statements concerning the topography of this nerve. According to Holste (1910), all the branches innervating the maxillary muscles arise from the maxillary nerve directly after it emerges from the "suboesophageal ganglion." He also stated that this nerve gives rise to two lateral branches other than the main branch which enters the maxilla. Holste did not describe the movable and fixed attachments of the muscles. Instead he described the muscles according to their function, thus making it impossible to homologize them with those of other groups of insects. For this reason I am not reviewing his study in detail. However, he found that one of the maxillary branches attached to the nerve of what he called "dorsal-blood-vessel ganglion." Holste also noted that the "*flexor maxillae anterior*" has double innervation.

Maki (1936), however, studied the topography of the maxillary nerve in great detail. He found that it divides into three main branches. One branch (Mai) divides and subdivides into four nerves, three of which innervate the "adductors of the cardo" (*m. pretentorio-stipitalis I*) and the "levator of the maxillary palpus" (*m. stipiti-maxillopalpalis I*), while the fourth nerve subdivides and innervates the "flexor of the stipes" (*m. pretentorio-stipitalis II*). The second main branch (Maii) divides and subdivides to innervate the "stipital flexor of the lacinia" (*m. stipiti-laciniaris*), the "stipital flexor of the galea" (*m. stipiti-galearis*), and the "levator of the maxillary palpus" (*m. stipiti-maxillopalpalis II*). The third main branch (Maiii) gives rise to three subbranches; (Maiiil) serving the lacinial wall, (Maiiig) the galeal wall, and (Maiiip) the maxillary palpus. He further states that the "levator of the maxillary palpus" (*m. stipiti-maxillopalpalis I*) is the only maxillary muscle to receive double innervation from "the maxillary nerve," in *Thermobia*. This muscle (*m. stipiti-galearis*) he referred to as the "muscle flexor de la galea maxillaire." He also found that a mandibular nerve and four maxillary nerves enter what he called the "corps jugul."⁸

In the honey bee *Nervus Maxillaris* is located be-

⁸ This gland was first described by Chaudonneret (1946 and 1950-1951) in *Thermobia*. According to him it is a neuroendocrine gland, which is simply a *corpus allatum* still preserving the embryological condition. It results from the fusion and the functional modification of the maxillary and mandibular ganglia of the sympathetic nervous system.

hind the *Nervus Mandibularis*. It extends ventrally and medially under the stomodaeum and laterally over the points of fixed attachment of the extrinsic muscles of the antenna and the pretenorium. Just behind this point it gives rise to a branch designated as the *Nervulus musculi Gena-cardinalis* (Nl. m. *Gen-Card.*). This nervule angles away from the main nerve in an anterior and ventral direction and passes adjacently by the inner side of the *m. tentorio-prementualis*, the *m. tentorio-stipitalis I*, *m. tentorio-cardinalis*, and the *m. tentorio-stipitalis II*. After passing over the last-named muscle, it curves, turns under the muscle, twists, and passes dorsally over its outer side. The nervule then extends between the nodes of the cranial articulation of the cardo where it turns posteriorly over the *m. gena-cardinalis* and innervates it medially. This nervule connects with a loose aggregation of neurons before it contacts the *m. gena-cardinalis*.

After giving off the aforementioned nervule, the *Nervus Maxillaris* passes medially and laterally over the *m. tentorio-prementualis* and gives off a branch termed the *Nervus Maxillaris Lateralis I* (N. Max. Lat. I). This branch extends anteriorly and laterally over the *m. tentorio-stipitalis*, where it divides into three nervules: the *Nervulus musculi Tentorio-stipitalis I* (Nl. m. *Tent-stip. I*), the *Nervulus musculi Tentorio-cardinalis* (Nl. m. *Tent-card.*), and the *Nervulus musculi Tentorio-stipitalis II* (Nl. m. *Tent-stip. II*). The first-mentioned nervule twists dorsally and anteriorly to contact and innervate the *m. tentorio-stipitalis I*. The second one extends anteriorly and innervates the *m. tentorio-cardinalis*. The third runs cephalad, parallel to the main nerve, until it reaches and innervates the *m. tentorio-stipitalis II*.

The *Nervus Maxillaris* continues to extend cephalad and mediad, passing laterally over the *m. tentorio-stipitalis I* and the *m. tentorio-stipitalis II*, where it gives rise to the *Nervus Maxillaris Lateralis II* (N. Max. Lat. II) and to a sensory branch, the *Nervulus Tegumenti Galearis* (Nl. Tegum. Gal.). The first of these two lateral nerves is directed posteriorly with respect to the second one. After separating from the main nerve, it gives rise to two small "ganglia" connected directly to it. The *Nervus Maxillaris Lateralis II* then passes medially over the *m. stipiti-laciniaris* and divides into three branches. The first, the *Nervus Maxillaris Sublateralis I* (N. Max. Sublat. I), diverges upward toward the *m.*

stipiti-laciniaris, where it forks into two nervules. One of these enters the *m. stipiti-laciniaris* and is consequently named the *Nervulus musculi Stipiti-laciniaris* (Nl. m. *Stip-lacin.*). The second is sensory, passing horizontally and posteriorly under the *m. stipiti-laciniaris* and over the *m. stipiti-maxillopalpalis* until it reaches the corner of the articulation between the cardo and the stipes. It turns under the *m. stipiti-maxillopalpalis* and innervates the basal part of the stipital integument. Accordingly, it is named the *Nervulus Tegumenti Stipitalis I* (Nl. Tegum. Stipiti I). The second branch, the *Nervus Maxillaris Sublateralis II* (N. Max. Sublat. II), turns dorsally toward the *m. stipiti-galearis*, where it divides into two nervules. The first, the *Nervulus musculi Stipiti-galearis* (Nl. m. *Stip-gal.*) enters the *m. stipiti-galearis* and the lacinial sclerite, where it diverges toward the distal portion of the stipes and innervates it.

The third branch of the main nerve, the *Nervus Maxillaris Sublateralis III* (N. Max. Sublat. III), extends ventrally, parallel to the main nerve for a short distance and then divides into two nervules. The first one passes horizontally over the *m. stipiti-galearis* and then turns under it, passing over the *m. stipiti-maxillopalpalis* and innervating it. Consequently, this nervule is named the *Nervulus musculi Stipiti-maxillopalpalis* (Nl. m. *Stip-maxpalp.*). The other nervule extends ventrally and passes over the tendonlike apodeme on which the *m. stipiti-galearis* is attached and enters the maxillary palp. This nervule is named the *Nervulus Maxillopalpalis* (Nl. *Maxpalp.*).

The *Nervulus Tegumenti galearis* extends submedially and ventrally between the lacinia and stipes. It enters the galea, passes between its walls, and gives rise to several nervules innervating it.

The nervules innervating the extrinsic muscles in *Corydalus* (Crauss 1884), and *Chauliodes* (Maki 1936) are bundled together as in the honey bee. However, the honey bee differs in having the *Nervulus Maxillopalpalis* bundled with the nerve innervating *m. stipiti-galearis* and *m. stipiti-maxillopalpalis*, rather than with the Nl. Tegum. Gal. (which innervates the galea) as in *Corydalus* or *Chauliodes*. In *Thermobia*, the *Nervus Mandibularis* connects with the *Nervus Maxillaris* through a "jugal body," whereas *Apis*, *Vespula*, *Chauliodes*, and *Corydalus* have no such connection.

Nervus Labialis (*N. Lab.*) (Figures 3, 6, 7)

The investigations of Crauss (1884) and Hammar (1908) on the "labial nerve" of *Corydalus* were incomplete. Holste (1910) also failed to study the topography of this nerve in detail; he merely mentioned that the "labial nerve" gives rise to two nerves, one innervating the gula, mentum, and various labial muscles and the other passing by means of two branches into the "*palparium*" and the labial palpus. According to Maki (1936), the labial nerve in *Chauliodes* is divided into two main branches, the first (*Lba*) of which divides into two subbranches (*Lba1*) and (*Lba2*) that innervate the "median retractor of the mentum" (*m. postoccipiti-prementualis*) and the "median retractor of the prementum" (*m. tentorio-prementualis*), respectively. The second main branch gives off four branches: the first three innervating, respectively, the "lateral retractor of the mentum" (*m. tentorio-paraglossaris*), the "dorsal dilator of the common salivary duct" (*m. dorsopremento-salivarius*), and the labial palpus muscles, while the fourth innervates the walls of the ligula.

Chaudonneret (1950-1951) found great variability in the topography of the labial nerve of *Thermobia* between individuals and even between the right and left half of a labium of one individual. Consequently, he described a "median" type and then discussed the great variation in the specimens studied. He found the following muscles to receive double innervation: "cranial-fulcral," "levator of external labial lobe," "cranial flexors of the internal labial lobe," and "cranial flexors of the external labial lobe." By contrast, he found that the "anterior depressor of the labium," the "ventral dilator of the labial salivary orifice," and the "fulcro-postmental muscle" receive no innervation as a consequence of their degenerate condition.

In the honey bee the labial nerve arises directly behind the *Nervus Maxillaris*. It is directed ventrally toward the labium. While passing over the extrinsic muscles of the antenna, it gives rise to a small "threadlike" branch that turns backward and upward, lying parallel and lateral to the common duct of the thoracic glands. Where the common duct forks beneath the ventral nerve cord and extends parallel to it in the thorax, the nerve branch also forks into two subbranches, each extending laterally adjacent

to a fork of the thoracic gland. In the area of the reservoir, each subbranch divides and subdivides to innervate the gland. Accordingly, this branch is named the *Nervulus Glanduli Thoracicalis*.

The *Nervus Labialis* then passes laterally over the pretentorium toward the *musculus tentorio-prementualis*, which is provided with a nervule, the *Nervulus musculi Tentorio-prementualis* (*Nl. m. Tent-prement.*). A short distance more distally the *N. Lab.* gives rise to another nervule, which is directed laterally and posteriorly and innervates the *musculus postoccipiti-prementualis* in several points by means of several subbranches. This nervule is designated as the *Nervulus musculi Postoccipiti-prementualis I* (*Nl. m. Postoccip-prement. I*). The *Nervus Labialis* then extends posteriorly and ventrally and passes medially between the closely approximated pair of *musculi postoccipiti-prementualis*. Each nerve of the pair then diverges underneath the corresponding member of the muscle pair. Before the area of divergence, it gives rise to a second nervule that leads to the *m. postoccipiti-prementualis* and innervates it ventrally. This nervule is named the *Nervulus musculi Postoccipiti-prementualis II* (*Nl. m. Postoccip-prement. II*).

The *Nervus Labialis* continues distally, passing submedially between the *m. postoccipiti-prementualis* and *m. basipremento-salivarius*. Before it starts paralleling the salivary duct, it gives rise laterally, on the outer side, to a branch designated as the *Nervus Labialis Lateralis I* (*N. Lab. Lat. I*). This lateral nerve is divided into two nervules, *Nervulus musculi Basipremento-salivarius* (*Nl. m. Basiprement-saliv. I*) and the *Nervulus Tegumenti Prementualis I* (*Nl. Tegum. Prement. I*). The first nervule extends posteriorly and innervates the *m. basipremento-salivarius*. The second one extends laterally over the *m. basipremento-salivarius*, then penetrates posteriorly between the latter muscle and the *m. premento-paraglossaris*, until it reaches and innervates the integument. In the same area, but from the inner lateral side, the *Nervus Labialis* gives rise to a nervule that passes forward over the salivary duct until it reaches and innervates the *m. dorsopremento-salivarius*. It is named the *Nervulus musculi Dorsopremento-salivarius* (*Nl. m. Dorsoprement-saliv.*).

The *N. Lab.* continues to extend distally and while passing over the *m. basipremento-salivarius*, it gives rise to the *Nervus Labialis II*. This lateral nerve

divides into three nervules: the *Nervulus musculi Premento-glossarius* (Nl. *m. Prement-Gloss.*), the *Nervulus Tegumenti Prementualis II* (Nl. *Tegum. Prement. II*), and the *Nervulus musculi Premento-labiopalpualis* (Nl. *m. Prement-labiopalp.*). The first nervule passes under the *m. basipremento-salivarius* then twists around it and innervates the *musculus premento-glossaris*. The second nervule penetrates between the *m. tentorio-glossaris* and the *m. tentorio-paraglossaris*, then passes laterally under the latter muscle until it reaches the lateral wall of the prementum, where it subbranches and innervates the integument. It was also noted that this nervule is connected to a chordotonal sense organ that extends from the base of the labial palpus. The third nervule extends laterally over the *m. premento-paraglossaris* and innervates the *m. premento-labiopalpualis*. Before diverging toward the labial palpus, the *Nervus Labialis* gives rise to the *Nervulus musculi Premento-paraglossaris* (Nl. *m. Prement-paragloss.*), which extends laterally to innervate the *m. premento-paraglossaris*.

In the course of its divergence, the main labial nerve passes under the *m. postoccipiti-prementualis* and the *m. premento-paraglossaris*, above the *m. basipremento-salivarius* and parallel laterally to the *m. premento-labiopalpualis*. In the area of the "palpiger," this main nerve gives off three branches. The first branch, the *Nervulus Tegumenti Paraglossaris* (Nl. *Tegum. Paragloss.*), extends toward the paraglossa, enters it, and innervates its integumental walls. The second branch, the *Nervulus Tegumenti Glossaris* (Nl. *Tegum. Gloss.*), extends laterally and ventrally. It then passes over the tendonlike apodemal growth to which the *m. premento-paraglossaris* is attached, reaches the lateral side of the glossal rod, and stays adjacent to the rod until it terminates. This nervule probably innervates the labellum, but only detailed histological studies could prove this point. The third branch, the *Nervus Labialis Sublateralis III* (N. *Lab. Sublat.*), extends medially through the labial palpus to its termination. While running through the first segment of the maxillary palp, this lateral nerve passes under the *m. labiopalpomere I-II*, to which it gives off a nervule designated as the *Nervulus musculi Labiopalpomere I-II* (Nl. *m. Labiopalp. I-II*). The part of the *Nervus Labialis Sublateralis III* that passes through the labial palpus gives rise to several

branches innervating the integument. Accordingly, this portion is named *Nervulus Tegumenti Labiopalpualis* (Nl. *Tegum. Labiopalp.*).

Nervus Tegumentualis (N. *Tegum.*) (Figures 1-10)

In the honey bee, this nerve is a separate structure on the posterior face of the *Ganglion Hyperoesophagale*. According to Jonescu (1909), however, this nerve has its center in the *Ganglion Hypoesophagale*. Jonescu also states that "according to Kenyon, the 'salivary gland' nerve arises on the side of tritocerebrum." Yet examination of Kenyon's original publication revealed that Jonescu misinterpreted Kenyon's statement with regard to this nerve. Actually, Kenyon indicated that it arises from the side of "ventrocerebrum." According to Chaudonneret (1950-1951), nerves innervating the cephalic integument are of "protocerebral" origin. Consequently, he named these nerves as the anterior and posterior tegumentary nerves of the protocerebrum. Jonescu (1909) agreed with Kenyon's findings and regarded the "nerf tegumentaire" of Viallanes as a "motor salivary gland nerve." Hanstrom (1928) stated that it arises from the "tritocerebrum" but is entirely tegumentary. Snodgrass (1935) found the same situation in *Dissosteira carolina* Linnaeus. Accordingly, in the present study, this nerve is described under the *Ganglion Hypoesophagale* rather than the *Ganglion Hyperoesophagale*.

In the honey bee the *Nervus Tegumentualis* extends dorsally adjacent to the *Ganglion Hyperoesophagale*. When it reaches approximately the level of the movable attachment of branch II of the *m. cranio-intermandibularis*, it divides into three main branches. Two of these branches form a fork and extend dorsally until they reach and innervate the integument on each side of branch II of *m. cranio-intermandibularis*. In their course, they extend over parts of the salivary gland. The third branch angles laterally toward the compound eye, then turns ventrally, passing over parts of the hypopharyngeal gland until it reaches the level of the lower part of the compound eye. At this point it angles laterally and innervates the adjacent integument. This nerve is more conspicuous and has more branches in the drone than in the worker or queen.

A homolog of the *Nervus Tegumentualis* was found in the acridid *Oedipoda coerulescence* by

Viallanes (1887b). Kenyon (1896) was the first to find this nerve in the honey bee, but he disputed Viallanes' idea that it is a sensory nerve and innervates the integument. He stated that in the honey bee it is a "nerve to the salivary gland." Jonescu (1909) agreed with Kenyon with regard to its nature. My findings agree with those of Viallanes and contradict those of Kenyon and Jonescu. Usually this nerve passes over the salivary gland but does not innervate it. Also, its termination (which both Kenyon and Jonescu were unable to locate) was found on the integument in several places. Superficially, the salivary gland seems to be innervated by the *N. Tegumentalis*, but examination under the compound microscope indicated that what appears to be a structure of neural origin is in fact a small trachea. Probable homologs of this nerve are found in *Vespula*, (Hymenoptera), *Dytiscus* (Coleoptera), *Dissosteira* (Orthoptera), *Thermobia* (Thysanura), and others. Workers are, however, in disagreement as to the origin of this nerve and the major ganglion to which it belongs.

Nervus Postoccipitalis (*N. Postoccipit.*) (Figure 9)

Viallanes (1887a) and Kenyon (1896) were the first authors to observe this nerve in the wasp and the honey bee, respectively. Since they were unable to follow it to its termination, however, they did not name it. Jonescu (1909) termed it nerve "X" but did not investigate its origin or topography.

In the honey bee it arises from the posterior side of the *Ganglion Hypoesophagale*, close to the lateral side of the ventral nerve cord. It angles posteriorly and ventrally toward the postoccipital sulcus, where it attaches to a very small ganglion located under a previously undescribed bridgelike structure which is formed by an arm extending transversely from the base of the tentorium, parallels the tentorial bridge and attaches medially to the ventral lobe of the postocciput. The two ganglia (one on each side of the occipital foramen) are connected to each other by a nerve embedded in a furrow found on the posterior part of the postocciput. A very thin nerve connects this small ganglion with the *Nervus Prothoracicalis Anterior* (*N. Prothorac. Ant.*) which enters the thorax, passes under the occipital process of the episternum, over the cervical apodeme of the episternum and over the *m. episterno-endosternalis*,

where it meets with the *Nervus Prothoracicalis Anterior*.

Nervus Posterior (*N. Post.*) (Figure 9)

Holste (1910) designated this nerve as "*nervus jugularis primus*." He found that in *Dytiscus* it leaves the "suboesophageal ganglion" and enters the prothorax, shortly after which it gives rise to two small branches that innervate the foramen integument and then extend farther into the thorax to innervate the "rotator capitis superior."

Rehm (1939) described the *Nervus Posterior* in the honey bee as a lateral dorsal nerve leaving the connective union between the suboesophageal and prothoracic ganglia. He named it the "dorsal connective nerve" but did not name its two branches. In this study, these branches are named as follows: the *Nervulus musculi Episterno-endosternalis* (*Nl. m. Epister.-endoster.*), which innervates the *m. episterno-endosternalis*, and the *Nervulus musculi Endosterno-postoccipitalis* (*Nl. m. Endostern-postoccip.*), which innervates the *m. endosterno-postoccipitalis*. A sound homology for this nerve is impossible for the time being, since the only complete study was made by Holste (1910), using *Dytiscus*. Unfortunately, he named the muscles according to their function and did not describe their points of attachment.

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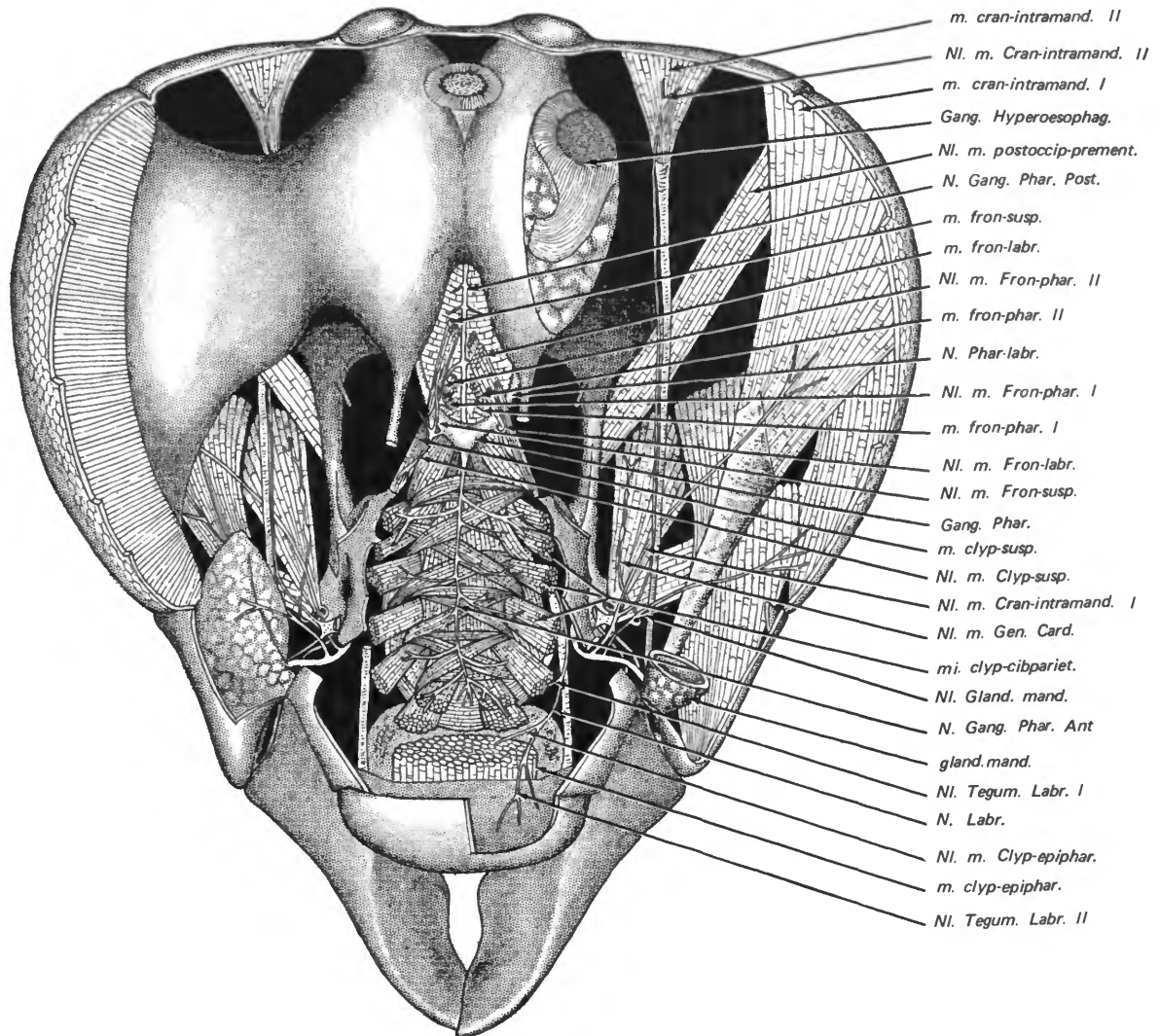


FIGURE 1.—Dissection of head of the worker (frontal view).

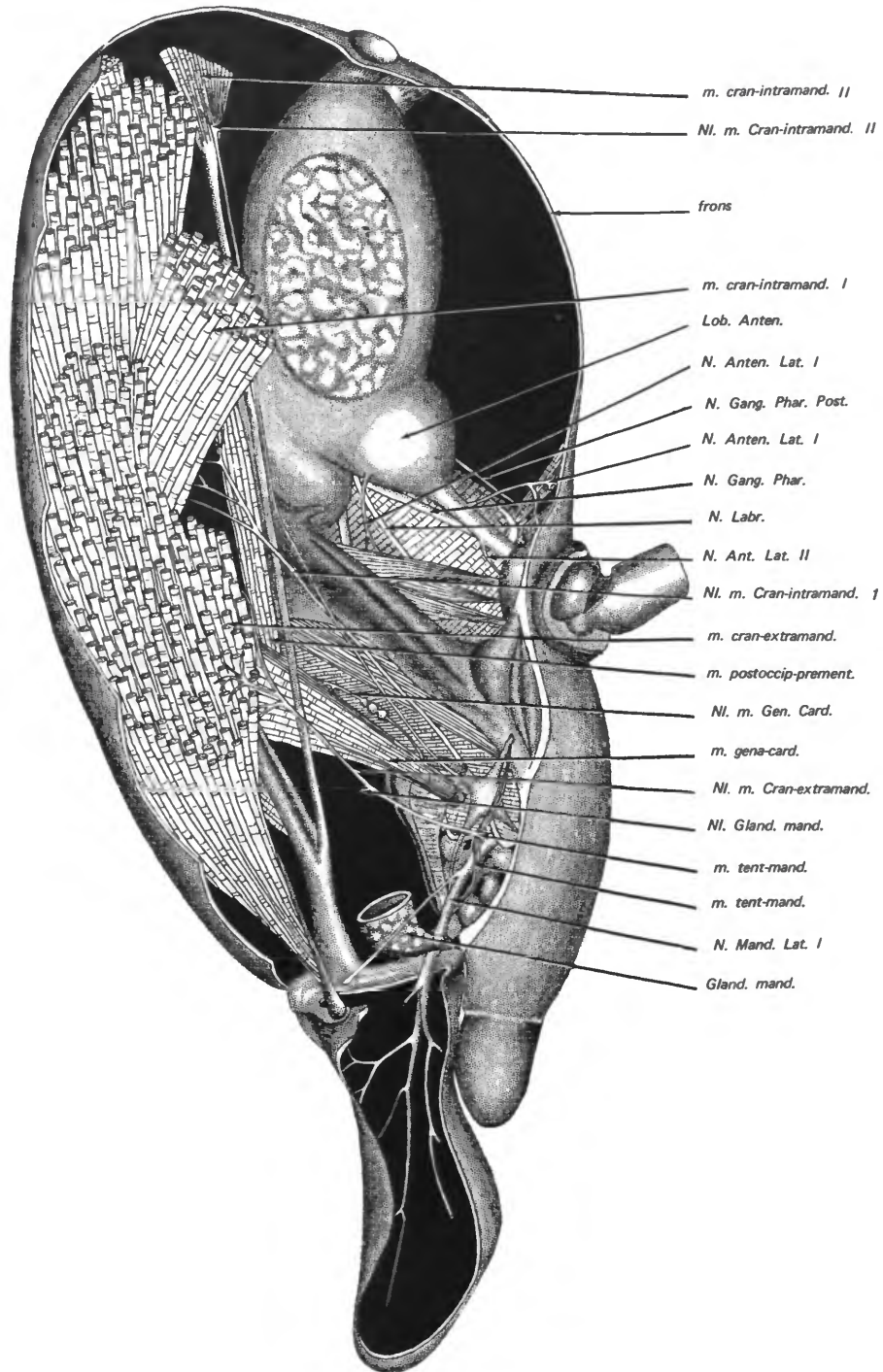


FIGURE 2.—First stage of dissection of the head of the worker (sagittal aspect).

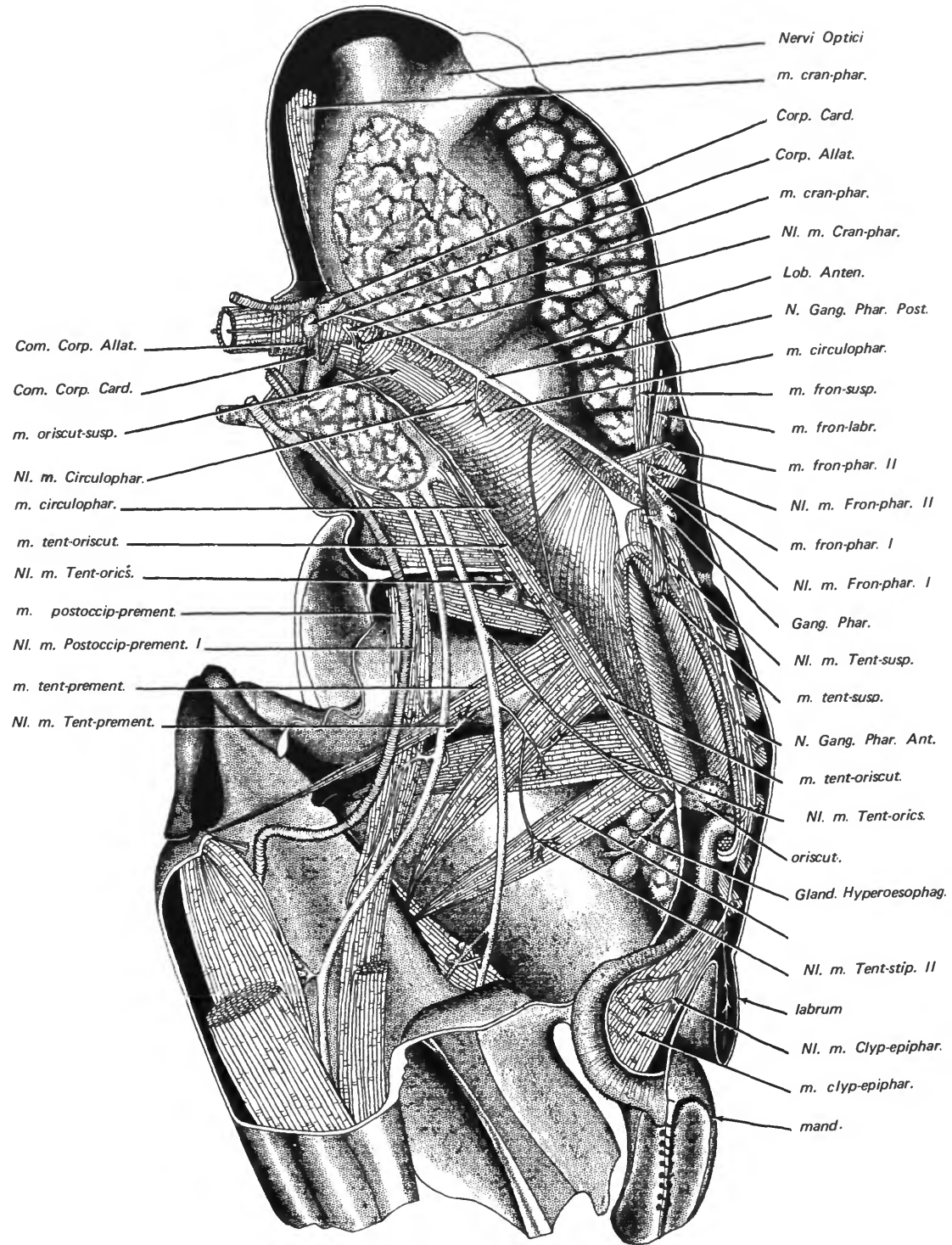


FIGURE 3.—Second stage of dissection of the head of the worker (sagittal aspect).

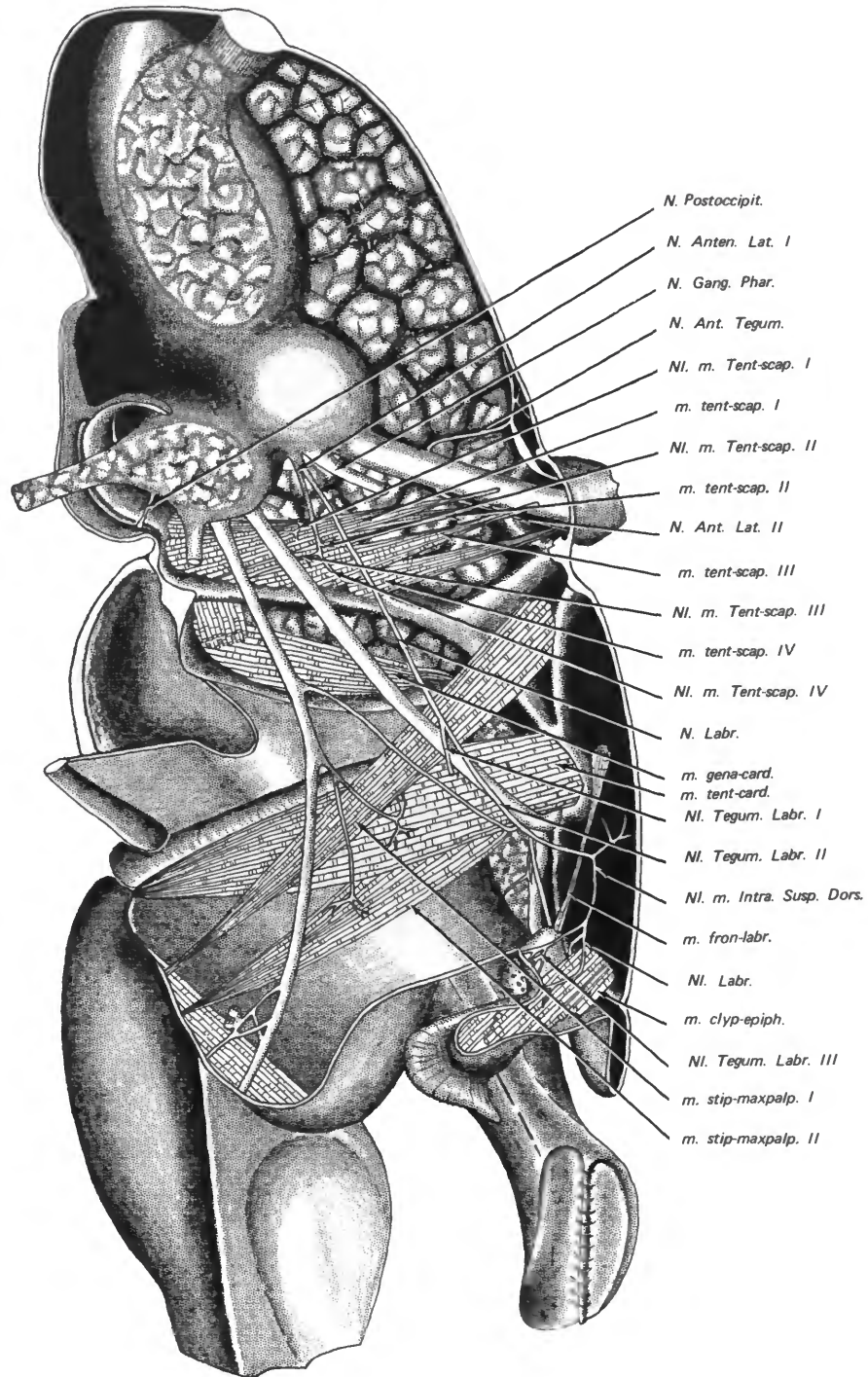


FIGURE 4.—Third stage of dissection of the head of the worker (sagittal aspect).

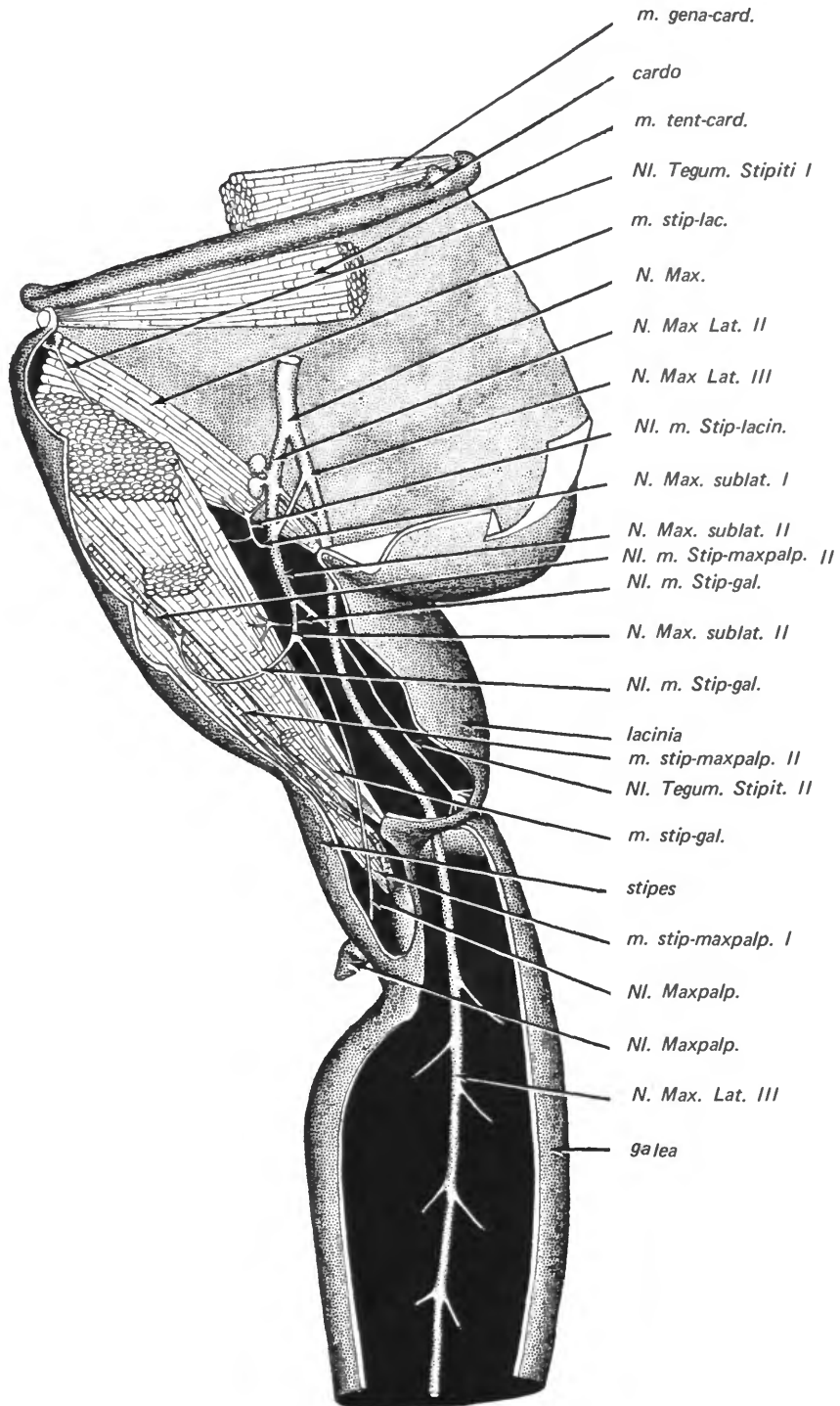


FIGURE 5.—Dissection of the maxilla of the worker (lateral aspect).

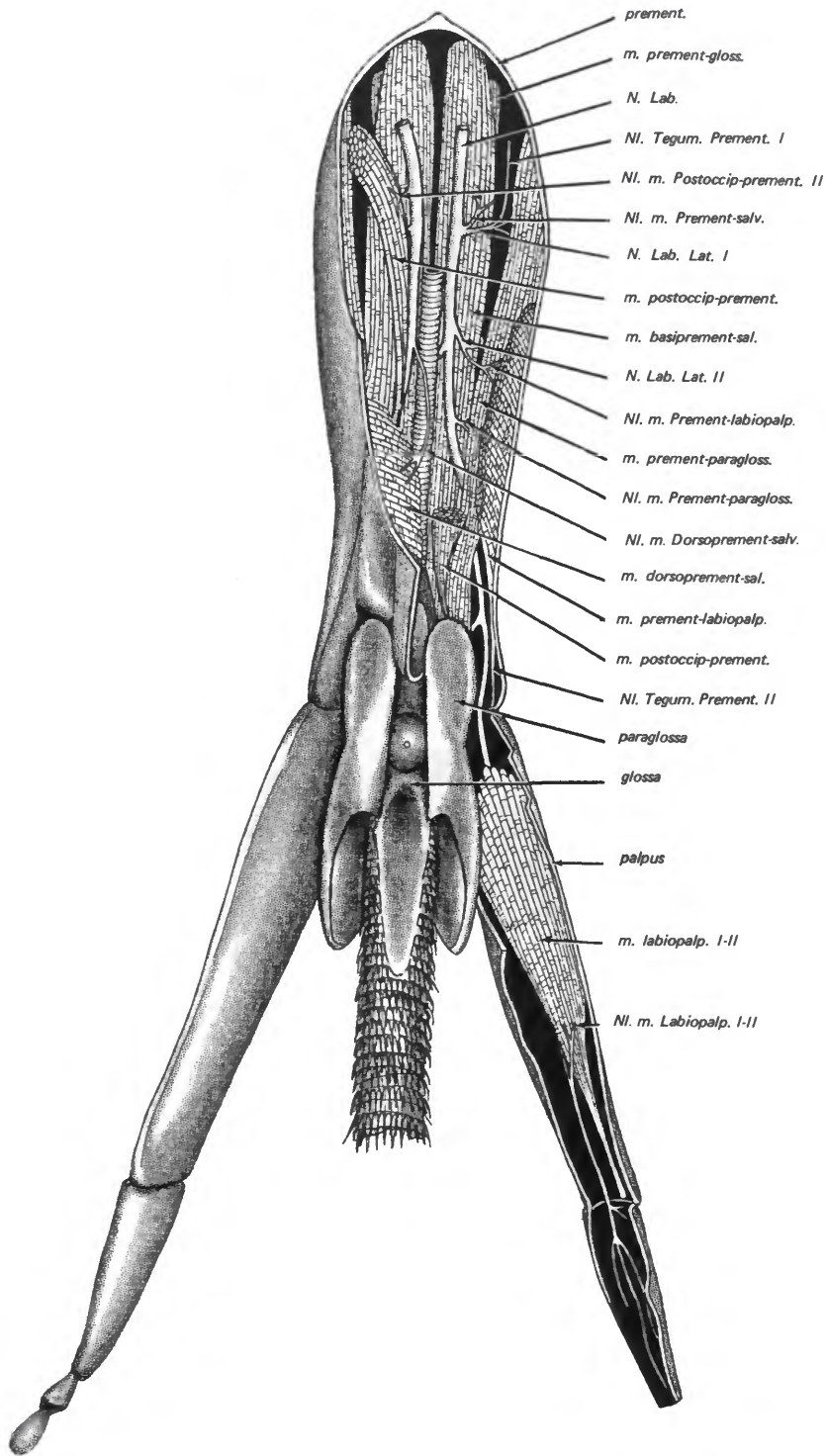


FIGURE 6.—First stage of dissection of the labium of the worker (frontal aspect).

FIGURE 7.—Second stage of dissection of the labium of the worker (frontal aspect).

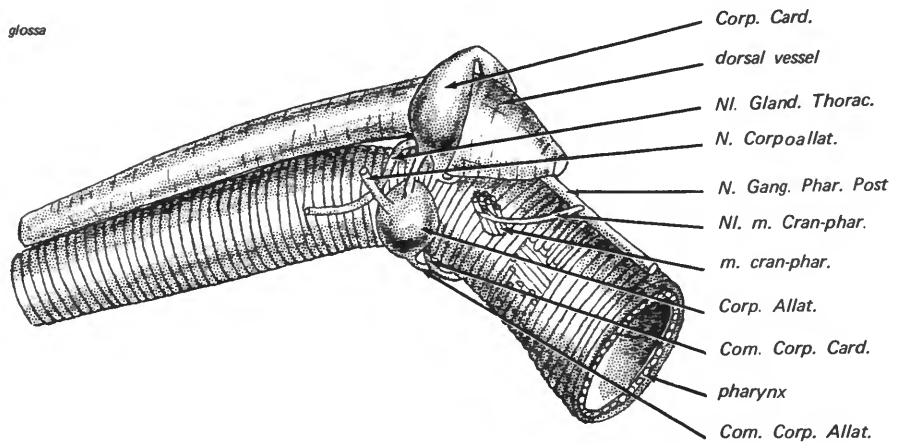
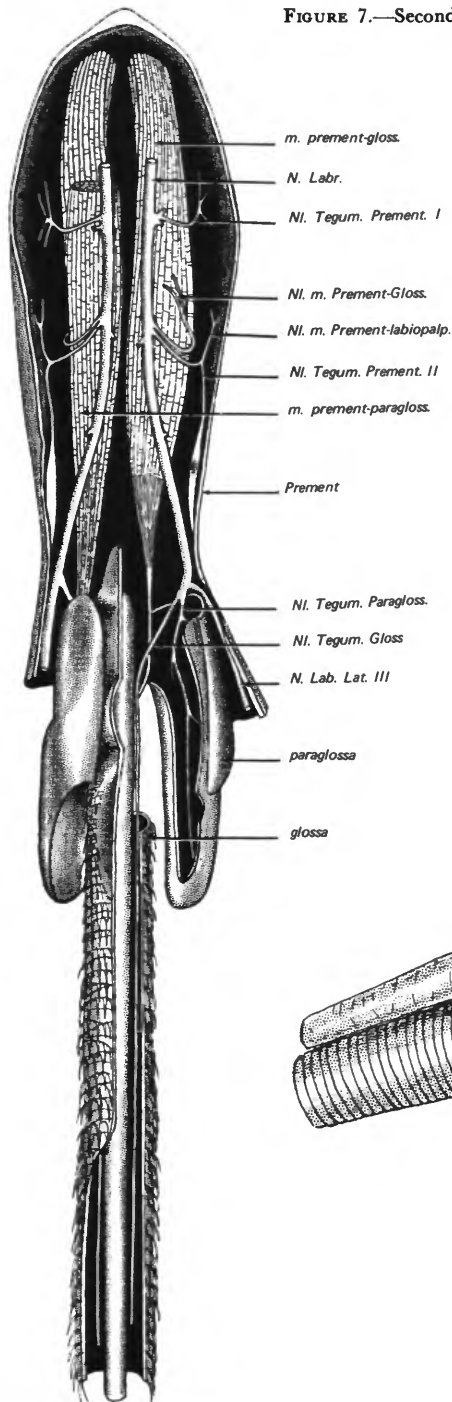


FIGURE 8.—The retrocerebral complex in the honey bee.

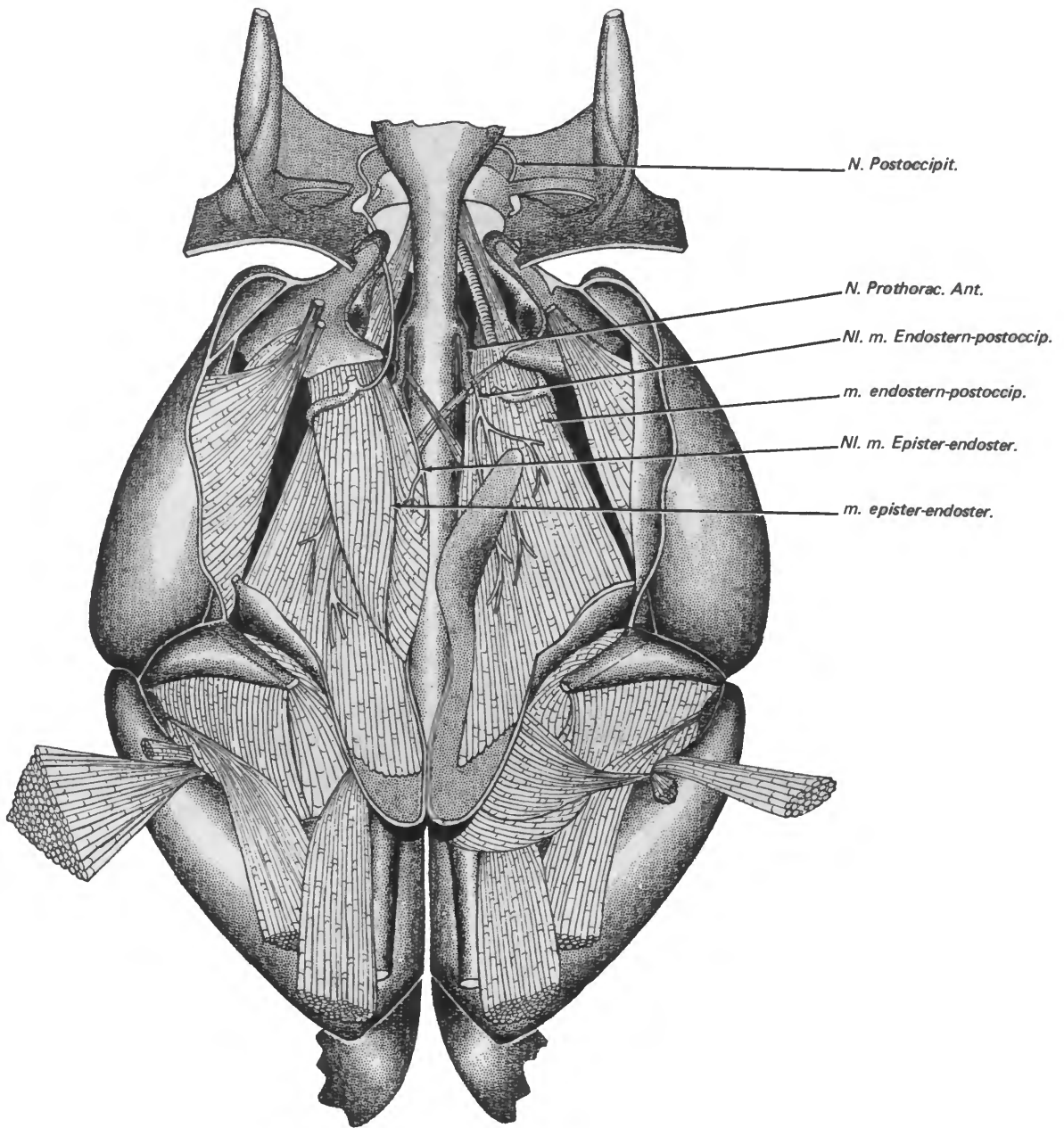


FIGURE 9.—Dissection of the cervical area of the worker showing the topography of *Nervus Posterior*.

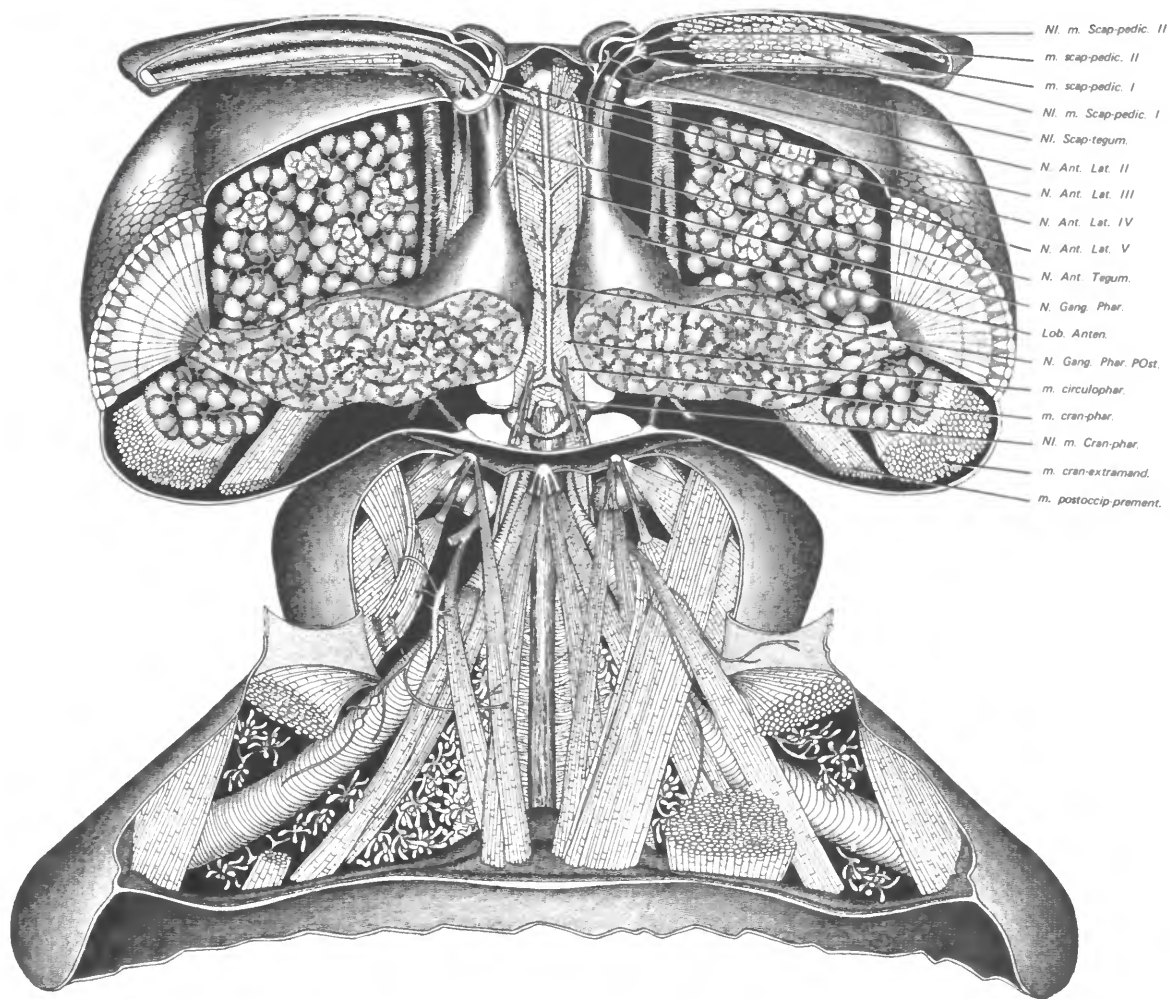


FIGURE 10.—Dissection of the head and cervical area of the worker (dorsal aspect).

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