

THE CRANIAL MORPHOLOGY OF THE FRUIT-PIERCING
MOTH, SERRODES PARTITA (FABR.), WITH SPECIAL
REFERENCE TO THE FEEDING MECHANISM

by



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CONTENTS

I.	INTRODUCTION	1
II.	LITERATURE REVIEW	4
	A. Cranial Morphology	4
	B. Extension and Coiling of the Proboscis	6
III.	MATERIAL AND TECHNIQUE	8
IV.	EXTERNAL AND INTERNAL STRUCTURE OF THE CRANIUM AND ITS APPENDAGES	10
	A. Cranial Capsule	10
	1. Compound eyes	10
	2. Genae, ocular diaphragms and ocular foramina	12
	3. Frontoclypeus, anterior tentorial pits, clypeolabral sulcus, laterofacial sulci and transfrontal suture	16
	4. Antennal sockets, circumantennal sclerites, antennifers and antennal membranes	27
	5. Vertex, ocelli, occiput, occipital suture, postoccipital suture, posterior tentorial pits and postantennal sulci	28
	6. Occipital foramen, tentorial bridge and occipital condyles	33
	7. Postgenae, postgenal sutures, hypostomata and hypostomal sutures	34
	8. Ventral cranial membranes	38
	9. Tentorium	39
	B. Cranial Appendages	40
	1. Antennae	40
	2. Trophi	41
	a. Labrum	41
	b. Mandibles	43

c. Maxillae	43
(i) Cardines	44
(ii) Stipites	44
(iii) Galeae	47
Proximal region of the galea	49
Intermediate or coilable region of the galea	51
Apical region of the galea	56
Linking mechanisms of the galea	61
Galeal septum	64
Galeal trachea	65
Galeal nerve	66
Trichoid sensilla of the galea	67
d. Labium and labial palps	67
V. MUSCULATURE OF THE CRANIUM AND ITS APPENDAGES	70
A. Antennal Muscles	70
a. Extrinsic antennal muscles	70
(i) Anterior tentorio-antennal depressor muscle	70
(ii) Posterior tentorio-antennal depressor muscle	70
(iii) Anterior tentorio-antennal levator muscle	71
(iv) Posterior tentorio-antennal levator muscle	71
b. Intrinsic antennal muscles	71
(i) Scape-pedicel depressor muscle	71
(ii) Scape-pedicel levator muscle	72
B. Trophial Muscles	72
1. Maxillary muscles	72

a.	Extrinsic maxillary muscles	72
(i)	Geno-stipital adductor muscle	72
(ii)	Anterior tentorio-stipital adductor muscle	73
(iii)	Posterior tentorio-stipital adductor muscle	74
(iv)	Tentorio-galeal retractor muscle	75
b.	Intrinsic maxillary muscles	76
(i)	Posterior basal galeal levator muscle	77
(ii)	Anterior basal galeal levator muscle	77
(iii)	Proximal galeal levator muscle	79
(iv)	Primary oblique galeal muscle	80
(v)	Secondary oblique galeal muscle	86
2.	Labial palp muscles	88
a.	Extrinsic labial palp muscle	88
(i)	Labial palp abductor muscle	88
b.	Intrinsic labial palp muscle	89
(i)	Labial palp depressor muscle	89
VI.	SUCKING PUMP	91
A.	Structure of the Sucking Pump	91
B.	Regions of the Sucking Pump	94
C.	Musculature of the Sucking Pump	100
a.	Extrinsic muscles of the sucking pump	100
(i)	Anterior frontoclypeus-cibarial dilator muscle	100
(ii)	Posterior frontoclypeus-cibarial dilator muscles	101
(iii)	Lateral frontoclypeus-buccal dilator muscles	102

(iv)	Frontoclypeus-pharyngeal dilator muscles	103
b.	Intrinsic muscles of the sucking pump	104
(i)	Cibarial compressor muscle	104
(ii)	Ventral buccal compressor muscle	105
(iii)	Lateral buccal compressor muscles	106
(iv)	Cruciform buccal compressor muscles	106
(v)	Pharyngeal compressor muscle	107
D.	Mechanism of the Sucking Pump	107
E.	Innervation of the Sucking Pump	109
VII.	MECHANISM OF EXTENSION AND COILING OF THE PROBOSCIS AND THE MANNER OF ITS INSERTION INTO AND EXTRACTION FROM FRUIT	110
A.	Review of Theories and Opinions on the Mechanism of Extension and Coiling of the Lepidopterous Proboscis	110
B.	Observations and Experiments to Test the Different Theories and Opinions on the Mechanism of Extension and Coiling of the Lepidopterous Proboscis	114
C.	Mechanism of Extension and Coiling of the Proboscis	121
D.	Movements of the Proboscis in Feeding and the Manner of its Insertion into and Extraction from Fruit	133
VIII.	SUMMARY	136
A.	Cranial Areas	136
B.	Cranial Sulci and Sutures	137
C.	Tentorium	139
D.	Cranial Appendages	139
E.	Musculature of the Cranium and its Appendages	144
F.	Sucking Pump	146
G.	Extension and Coiling of the Proboscis	149

H.	Insertion and Extraction of the Proboscis	150
I.	Laceration of Fruit Flesh Cells	150
IX.	ACKNOWLEDGEMENTS	151
X.	REFERENCES	152
XI.	FIGURES	159
XII.	ABBREVIATIONS	164

I. INTRODUCTION

Serrododes partita (Fabr.) (Serrododes inara (Cram.), erroneously Serrododes inara Dist.) is one of a complex of so-called fruit-piercing or fruit-sucking moths of the subfamilies Catocalinae and Noctuinae of the Noctuidae, S. partita belonging to the latter subfamily. These fruit-piercing or fruit-sucking moths attack many stone, deciduous and tropical fruit by inserting their proboscides into the flesh and sucking out the juices. They are an important pest in some parts of the world such as Africa, Australia and India, and they have also been reported from Ceylon, Fiji, Indonesia, Indo-China, Japan, Malaya, Samoa and South America (Hargreaves, 1936).

Aspects of the bionomics of S. partita, or of the fruit-piercing or fruit-sucking moth complex including S. partita, were studied or reported by Jack (1922), Gunn (1929), Hargreaves (1936), Ramakrishna Ayyar (1944), Kriegler (1958), Myburgh (1963a, 1963b, 1966), Myburgh and Rust (1963), Neubecker (1966), Whitehead and Rust (1967) and others.

In the Republic of South Africa S. partita is the most destructive of a complex of more than twenty known species of fruit-piercing or fruit-sucking moths. They are economically important as agricultural pests on canning peaches and apricots, causing in epidemic seasons losses of more than R250,000 in the canning peach industry alone. Normally S. partita occurs in pest proportions only in the Little Karroo and Langkloof which fall in or are adjacent to the areas of distribution of its main larval host plant, the wild plum, Pappea capensis E.Z. In epidemic seasons, which may occur every five or ten years,

S. partita moths, however, migrate to the South-Western Districts and to all fruit growing areas of the Western Cape, apparently flying or being "air-lifted" a hundred miles or more from their breeding grounds (Myburgh, 1963a).

Primary damage to fruit by the feeding of the moth of S. partita is indicated by pin-prick holes in the skin of fruit where the proboscis has penetrated. The proboscis is further inserted into the flesh of the fruit and the cells are lacerated. Fruit juice so released is sucked up, and the fruit flesh around the zone of penetration becomes dry and spongy in an area of more than a centimeter in diameter and a centimeter in depth. The feeding holes also allow the passage of air, thus causing fermentation by oxidation, and secondary rotting organisms, which gain entrance, cause a browning and softening of these and adjacent parts of the fruit. Attacked fruit decay further and drop from the trees.

As the moths of S. partita do not feed on superficial fluids or juices, as does the butterfly Pieris brassicae L. which was studied extensively by Eastham and Eassa (1955), it was initially thought that the study of the functioning of the feeding mechanism of S. partita might provide additional evidence for testing the validity of the theory of extension and coiling of the lepidopterous proboscis, advocated, qualitatively analyzed and experimentally proved by Eastham and Eassa (1955). A study of the literature, however, revealed differences in opinion about the homology of the different cranial areas, sulci and sutures, as well as uncertainty as to what parts of the cephalic

stomodaeum contribute to the formation of the sucking pump in adult Lepidoptera. The scope of the present study was therefore broadened to include an investigation of the anatomic and histologic structure of the cranium, the cranial appendages and the sucking pump. An additional attempt of the present study was to elucidate the manner of penetration of the fruit skin by the proboscis, and the insertion into and extraction of the latter from the flesh of the fruit. The process by which fruit juice is made available to the moth, i.e. how the cells of the fruit flesh are lacerated for the release of their fluid contents, was also studied.

II. LITERATURE REVIEW

A. Cranial Morphology

The cranial morphology of adult Lepidoptera has received relatively little attention, yet the limited number of existing publications already reveals a considerable and confusing difference of opinion. This is mainly due to the fact that the exact homologies of the sclerites, sulci and sutures are still uncertain.

Burgess was among the earlier authors to describe briefly the galea and its intrinsic musculature (1880a), the anatomy of the cranium and the musculature and mechanism of the sucking pump (1880b) in Danaus plexippus L. (= Danais archippus (Fabr.)). The extensive study of Kirbach (1884) on the lepidopterous galea and its musculature, and on the sucking pump and its musculature and mechanism, however, surpasses the works of earlier authors on these aspects. Among the earlier authors Kellogg (1893) made a valuable contribution with the first intensive study of the cranial sclerites and some of the mouthparts in adult Danaus plexippus L. (= Danais archippus (Fabr.)) and a number of other Lepidoptera. He found that the mandibles, where present, are always articulated on or fused with the genae. The comparative studies of Kellogg (1895) and Tillyard (1923) on the mouthparts of the Lepidoptera are also important. Kellogg established that the maxilla consists of the cardo, stipes, galea, and in some instances also of the lacinia, and Tillyard produced conclusive evidence that the proboscis is formed by the galeae.

Schmitt (1938) comparatively studied the feeding mechanism of

adult Lepidoptera and found that the stipes is so constructed as to have a valve which can be closed by muscle contraction. He also showed that the cibarium is included in the sucking pump. Srivastava (1956) also found evidence that the cibarium is included in the sucking pump.

Pradhan and Aren (1941) described in some detail the structure and musculature of the mouthparts in Scirpophaga nivella (Fabr.) and a number of other adult Lepidoptera. They could, however, not establish a stipital valve arrangement. The most complete and important work on the structure of the mouthparts and the sucking pump, its musculature and functioning, is undoubtedly the study of Eastham and Eassa (1955) on Pieris brassicae L. in which they accurately describe its feeding mechanism, and critically review and correct certain ideas expressed by earlier authors. Eassa later (1963a) published a full account of the musculature of the cranial appendages and the structure, musculature and mechanism of the sucking pump in Pieris brassicae L. He (1963b) also contributed considerably to our knowledge of the homologies of certain cranial areas in adult Lepidoptera by an investigation of the development of the cranial capsule and its appendages in the same pierid.

Other informative studies on the morphology of the adult lepidopterous cranial capsule, its appendages and musculature, and the sucking pump and its musculature are those of Madden (1944) on Protoparce sexta (Johan.), Short (1951) on Dilina tiliae (L.), Michener (1952) on Eacles imperialis (Drury) and Srivastava (1957) and Vasudeva (1957) on Papilio demoleus L. Ehrlich (1958a, 1960) also gives noteworthy

accounts of the cranial capsules of Danaus plexippus L. and Epargyreus clarus Cramer.

Jack (1922), Taylor (1957) and Neubecker (1966) all comment on the modified and strengthened galeae in Serrodes partita (Fabr.).

The publications of Snodgrass (1935, 1947), Ferris (1942, 1943) and DuPorte (1946, 1956), on the general morphology of the insect head, were useful in determining certain cranial structures. The more recent works of DuPorte (1957, 1959), Snodgrass (1960, 1961, 1963) and Matsuda (1965) summarize the findings of earlier authors, but contain no additional information on the morphology of the adult lepidopterous cranium.

B. Extension and Coiling of the Proboscis

Opinions or theories on the mechanism of extension and coiling of the lepidopterous proboscis were expressed or formulated by Burgess (1880a), Kirbach (1884), Snodgrass (1935), Schmitt (1938), Pradhan and Aren (1941), Imms (1942), Portier (1949), Bourgogne (1951) and Eastham and Eassa (1955).

Burgess (1880a), Snodgrass (1935), Schmitt (1938), Imms (1942) and Bourgogne (1951) propound that the proboscis is coiled by muscle contraction, whereas Kirbach (1884) and Pradhan and Aren (1941) attribute extension of the proboscis to muscle contraction. Portier (1949) believes that the contraction of some muscles causes coiling of the proboscis and that the contraction of others, antagonistic to them, is responsible for proboscis extension. Snodgrass (1935), Schmitt (1938) and Imms (1942), however, advance the theory that the proboscis is

extended by means of blood pressure (inflation).

Burgess (1880a) and Bourgogne (1951), on the other hand, regard elasticity as the cause of extension of the proboscis, but Kirbach (1884) believes, and Pradhan and Aren (1941) and Eastham and Eassa (1955) showed experimentally that the proboscis is coiled by virtue of elasticity. Eastham and Eassa determined that in Pieris brassicae L. the elastic properties lie in so-called dorsal bars in the galeae. They also proved experimentally that extension of the proboscis is neither caused by inflation, nor by direct muscle action, and offer a qualitatively analyzed, new theory on the mechanism of extension of the proboscis, as will be discussed later on.

III. MATERIAL AND TECHNIQUE

S. partita moths were readily obtained from the Fruit and Food Technology Research Institute, Stellenbosch.

For studying the anatomic structure of the cranial capsule and cranial appendages, heads of etherized moths were detached from the bodies and cleared overnight in 10% potassium hydroxide at a temperature of 60°C. They were then washed in distilled water and subsequently bleached for approximately 10 to 15 minutes with hydrogen peroxide, to which some drops of ammonia had been added, according to the method described by Rees (1938). This method ensures that improved staining is obtained. After bleaching, the heads were transferred to boiling 10% potassium hydroxide, for a short time, to permit the escape of all air bubbles caused by the bleaching process. Afterwards the heads were prepared for microscopical examination according to the method originally used by Theron (1958) for male coccids, and later by Swart (1966) for both the male and female external reproductive organs in a lepidopteron. Thus the heads were washed in distilled water and subsequently dehydrated by passing them through a series of graded alcohols. From absolute ethyl alcohol they were transferred to a saturated solution of Chlorazol Black E (Azo Black) in absolute methyl alcohol, and stained for 5 seconds. Excess stain was removed by leaving them overnight in absolute ethyl alcohol, to which a few drops of pyridine had been added. The alcohol was gradually replaced by terpeneol, by means of the flotation method described by Gray (1958). Temporary whole mounts of the heads were then made in terpeneol in cavity slides.

The musculature of the cranium, cranial appendages and sucking pump was studied by dissecting, in 70% alcohol, heads which had been preserved in Bouin's fixative. Serial transverse, sagittal and frontal sections of the heads were also examined.

Material intended for microtomy was fixed in Bouin's fixative for at least 5 days, the heads having been detached from the body to enable rapid penetration of the fixative. The heads were then transferred to Mukerji's fluid, as recommended by Sinha (1953), and left for softening for at least one week. Subsequent dehydration was achieved by several changes of dioxane. The usual method of paraffin embedding was employed and several series of transverse, sagittal and frontal sections of the heads were cut at a thickness of 7.0 microns and 10.0 microns. Sections were stained with Heidenhain's Azan stain which stains exocuticle red to brown and endocuticle blue.

Anatomic illustrations were drawn to scale on graph paper by using a squared eyepiece micrometer in a stereoscopic microscope, whereas histologic illustrations were drawn by means of a projecting apparatus. In the anatomic illustrations membranous areas are stippled and sclerotized areas are left blank or are coloured in, while in the histologic illustrations exocuticular areas are coloured in and endocuticular areas are stippled.

Live moths were etherized prior to carrying out experimental operations involving perforation of the galeal and stipital haemocoels and cranial cavity, and in severing of the galeal nerves.



IV. EXTERNAL AND INTERNAL STRUCTURE OF THE CRANIUM AND ITS APPENDAGES

In S. partita the unsegmented, subglobular, hypognathous cranium and its appendages are heavily sclerotized, except for the ventral cranial and antennal membranes. Scales and hairs densely cover the greater part of the cranial areas and some of the appendages; they are, however, omitted from the illustrations.

In the present study the term sulcus is used exclusively for all external grooves representing lines of cuticular inflection and forming internal ridges, whereas the term suture is used for all other superficial lines of demarcation.

A. Cranial Capsule

A perusal of the existing literature on the anatomy of the cranial capsule in adult Lepidoptera reveals a considerable diversity of opinion on the homology of the different cranial areas, sulci and sutures.

1. Compound eyes

In S. partita the paired, prominently enlarged, hemispherical, hairless compound eyes (figs. 1-5, cpd.e), each situated laterally on either side of the cranial capsule, occupy the greater part of the genal areas and project somewhat beyond the ventral limits of the cranial capsule. The optic lobes (figs. 14-16, opt.lob) of the compound eyes extend laterally from the brain (figs. 14-16, brn) and pass through the ocular foramina.

Ocular or circumocular sclerites and ocular or circumocular sutures are absent in S. partita. Similarly Kellogg (1893), Schmitt (1938), Michener (1952), Ehrlich (1958a, 1960) and Eassa (1963b) do not describe ocular sclerites or ocular sutures for the Lepidoptera studied by them. Portier (1949), Bourgogne (1951) and Imms (1960) also do not mention such sclerites or sutures in the order Lepidoptera. Short (1951) also does not describe ocular sclerites in Dilina in the text, but denotes ocular sulci in his illustrations. Similarly Eassa (1963b) figures narrow circumocular areas which he does not describe or name in the text, but which apparently show agreement with the ocular sclerites described by others.

Madden (1944) definitely describes ocular sclerites in Protoparce. These separate the eyes from the frontoclypeus and terminate dorsally at the antennal sockets, merging ventrally with the subgenal areas of the head. He further found that the ocular sclerites are demarcated from the frontoclypeus by ocular sutures which extend from the antennal sockets ventrally to the subgenal sutures. Srivastava (1957) describes similar sclerites in Papilio. Here they merge posteriorly into the postgenae and, being very narrow ventrally, are present between the compound eyes and the so-called epistoma from which they are demarcated by the ocular sulci. The upper three-fourths of the latter merge with the subantennal sulci and are termed the "oculo-subantennal sulci" by Srivastava. Vasudeva (1957) also found ocular sclerites in the same papilionid, but describes them as "narrow bands encircling the compound eyes." They are separated from the rest of the cranial area by ocular sutures. The areas regarded by Srivastava (1957) as the

ocular sclerites in Papilio is believed by Vasudeva (1957) to be the parietals.

The cranial areas regarded by Madden (1944) and Srivastava (1957) as the ocular sclerites in Protoparce and Papilio, respectively, apparently correspond to those areas regarded as the facial parts of the genae in S. partita, as will be discussed presently.

2. Genae, ocular diaphragms and ocular foramina

In S. partita the compound eyes are basally surrounded by cranial areas which are here regarded as the genae (figs. 1-5 & 19-21, ge). They form sharp angles with the postgenae and hypostomata in the posterior and ventral cranial regions, respectively, and are densely covered dorsally and posteriorly with long, slender scales, but are bare in the ventral region. The genae vary in width, being very narrow in the region of the ocelli, then widening in the vicinity of the antennal sockets and having a narrow, more or less even width in the facial region. Ventrally, where the vestigial mandibles are fused to them, the genae are triangularly expanded, reaching the anterior tentorial pits, but from here their width along the ventral and posterior borders of the compound eyes is fairly even. Genae, like those of S. partita, which completely surround the compound eyes have apparently never been described before in an adult lepidopteron.

The narrow ridges which circumscribe the eyes in Danaus were termed "orbits" by Burgess (1880b). Kellogg (1893) later concluded that the front portion and parts of the upper and lower portions of the "orbits" of the eyes are composed of the genae, which he then describes

in the same danaïd as "extending up and back between the clypeus and eyes to the postgenae, bounding the antennary fossae outwardly." Eassa (1963b) found that in Pieris the genae form "two narrow strands running between the border of the eyes and the clypeus" and he established, by means of developmental studies, that these are the only parts of the larval genae remaining in the adult Pieris. Srivastava (1957) names paired, triangular sclerites lying between the eyes and the lower portions of the so-called epistoma in Papilio, the genae, whereas Vasudeva (1957) regards these areas in the same species as the subgenae. The latter author regards the genae in this lepidopteron as "the lateral areas of the parietals beneath and behind the eyes." Bourgogne (1951) and Imms (1960) regard the narrow areas between the eyes and the median facial area as the genae, while Portier (1949) names small areas at the ventrolateral corners of the median facial area, the genae.

The small triangular areas "on either side, and below the face" which are called the genae or "cheeks" in Danaus by Burgess (1880b), obviously represent vestigial mandibles and are also named thus by Ehrlich (1958a). Burgess mistook the pilifers for the mandibles, as was already pointed out by Kellogg (1893).

The cranial areas occupying the same positions as the genae of Pieris (Eassa, 1963b) and the facial parts of the genae in Danaus (Kellogg, 1893) and S. partita are designated as the ocular sclerites in Protoparce and Papilio by Madden (1944) and Srivastava (1957) respectively. Corresponding areas are regarded as parts of the parietal regions by Schmitt (1938) and Vasudeva (1957) in the Lepidoptera stu-

died by them. Ehrlich (1958a) denotes similar areas in Danaus as "paraocular areas", and in a more recent publication (1960) he figures, but does not name, similar areas in Epargyreus. Short (1951) similarly does not name identical areas figured in Dilina. Eassa (1963b), however, ascertained that Madden (1944) mistook the genae in Protoparce for ocular sclerites by showing that the two narrow extensions between the eyes and the clypeus in adult Pieris are remnants of the larval genae. In the same study Eassa also established that the only parts of the larval parietals which are retained in the imago are the areas occupied by the antennal sockets. The views of Madden (1944) and Srivastava (1957) that the corresponding areas in Protoparce and Papilio, respectively, represent ocular sclerites, and those of Schmitt (1938) and Vasudeva (1957) that they represent parts of the parietal regions, therefore appear to be erroneous. Ehrlich's (1958a) designation of corresponding areas in Danaus as "paraocular areas" also seems inappropriate.

Incidentally, if the genae of S. partita, being continuous around the compound eyes, were to be regarded as ocular sclerites, it would imply that the vestigial mandibles are fused to the ocular sclerites in this moth. The present author would find such a condition unacceptable, more so since Kellogg (1893) already observed that the mandibles, where present in Lepidoptera, are articulated on or fused with the genae. It would further imply that the geno-stipital adductor muscles (figs. 14, 17 & 13, ge.st.add.m) have their origin on the ocular sclerites, instead of on the genae. Schmitt (1938), Eastham and Eassa (1955), Srivastava (1957), Ehrlich and Davidson (1961), Ehrlich and

Ehrlich (1962) and Eassa (1963a) found that muscles which, according to the present author, correspond to the geno-stipital adductor muscles of S. partita, originate either entirely or partly on the genae in the Lepidoptera studied by them.

In S. partita the genae are produced into narrow rims which border on the compound eyes and simulate separate band-like sclerites (figs. 19-21). The present author believes that these rims probably correspond to the "slightly elevated rims" which Ferris (1942) considers to be commonly present "about the eye" in insects. It is also thought that Vasudeva (1957) mistook similar bands or rims in Papilio for ocular sclerites. From the base of these rims the genae in S. partita project internally, forming broad, disk-like, weakly sclerotized ocular diaphragms (figs. 6, 19-21, oc.dph) which support the ommatidia of the compound eyes. Internally the ocular diaphragms form the central, relatively large, oval-shaped ocular foramina (fig. 6, oc.for) through which the optic lobes pass. Michener (1952) and Ehrlich (1958a, 1960) are apparently the only other authors to describe and figure ocular diaphragms in adult Lepidoptera. The term "ocular diaphragm" was introduced by Ferris (1942) for the usually deeply pigmented area of the head wall beneath the bulging eyes in many insects. He points out that the ocular diaphragm is not a separate sclerite and states that although it is especially well developed in the Neuropteroid orders, morphologists seem quite generally to have ignored it. Short's (1951) and Srivastava's (1957) assumption that the ocular ridges in Dilina and Papilio, respectively, probably represent the ocular diaphragms of Ferris (1942), is quite possibly erroneous. Being internal

invaginations of the ocular sulci, the ocular ridges by definition (Snodgrass, 1935) separate the ocular sclerites from the mesal cranial areas and not from the eyes. Ocular ridges therefore cannot, like ocular diaphragms, be in direct contact with the compound eyes.

3. Frontoclypeus, anterior tentorial pits, clypeolabral sulcus, laterofacial sulci and transfrontal suture

In S. partita the relatively large, bulging, rectangular frontoclypeus (figs. 1-4, frclp), which completely lacks a sutural division into a frons and clypeus, constitutes the median facial area of the cranium.

Since by definition (Snodgrass, 1935) the anterior tentorial pits are located in the subgenal sutures or usually in the epistomal suture, they may provide an external means of determining the point of division between the frons and clypeus in instances where a frontoclypeal or an epistomal suture is lacking.

Snodgrass (1935), however, regards the origin of the cranial muscles as the definite basis for the identification of the clypeal and frontal areas. According to him the clypeus is the area upon which arise the dilator muscles of the cibarium and the dorsal muscles of the buccal cavity. These muscles lie anterior to the frontal ganglion. The frons gives attachment to the stomadaeal dilators, lying posterior to the frontal ganglion. Ferris (1943) is in general agreement with Snodgrass (1935) as far as this criterion for identifying the clypeal area is concerned.

DuPorte (1946), in tracing the evolution of the pterygote cranium,

concludes that the anterior tentorial pits are located primitively at the level of the mouth in the ventral ends of the frontogenal sutures and that the anterior mandibular articulation lies immediately ventral to the anterior tentorial pits. According to him the anterior tentorial pits may, however, migrate into the frontoclypeal suture. He then regards that portion of the face dorsal to the anterior mandibular articulation as the frontal area, and that portion ventral to and including the articulation as the clypeal area. When a transfrontal suture is present between the antennal sockets, DuPorte names the area dorsal to it and typically bearing the antennae and ocelli, the postfrons. The area ventral to it, which is bounded ventrally by what he regards as the frontoclypeal sulcus (actually the clypeolabral sulcus) and which bears no organs, he terms the antefrons. This interpretation of DuPorte caused him to misidentify the area ventral to the sulcus as the clypeus, instead of the labrum, in the Lepidoptera included in his study. The actual clypeus is in fact part of his antefrons. DuPorte also believes, in contrast to Snodgrass (1935), that muscle origins can hardly be regarded as a sufficient criterion for determining the homologies of the facial sclerites, since according to him muscles do not only shift their origins, but new muscles arise and other atrophy to meet the needs of the insect.

In a later publication Snodgrass (1947) again points out that the clypeal and frontal areas are to be identified by the muscles attached on them in instances where an epistomal or a frontoclypeal sulcus is absent. He shows that the clypeal muscles (cibarial and buccal dilators, which are inserted on the foregut, ventral or anterior to the

frontal ganglion) and the frontal muscles (pharyngeal dilators, which are inserted on the pharynx, posterior to the frontal ganglion within the loops formed by its connectives) can be determined by the position of the frontal ganglion and its brain connectives which invariably separate these two sets of muscles. According to him the frontal ganglion retains its primitive position just posterior to the edge of the mouth, regardless of the changes that might take place in the structure of the insect head. Snodgrass therefore presents a criterion for recognizing the position of the primary mouth and, thus, for distinguishing between the buccal cavity and the pharynx. By definition (Snodgrass, 1935) the buccal cavity lies just within the mouth and the pharynx lies posterior to the buccal cavity or the mouth. As may now be concluded from Snodgrass' (1947) findings, the buccal cavity lies just anterior to the frontal ganglion, while the pharynx lies posterior to it. It is therefore possible to distinguish between the clypeal and frontal muscles, and so to determine the approximate limits of the clypeal and frontal areas. The former area is essentially preoral, while the latter area forms part of the postoral anterior cranial wall. Snodgrass (1947) also draws attention to the fact that, because of the correlation between the size of the clypeus and the development of the cibarial muscles and the cibarium, the clypeal area usually is relatively large (being extended upward or posteriorly at the expense of the frons) in liquid-feeding insects where the cibarium forms the principal sucking pump. He concludes that in such insects the proper clypeal area "is always to be identified by the origins of the dilator muscles of the sucking pump, and in no such case is it necessary to

suppose that the clypeus in its upward or posterior extension has taken over the muscles of the invaded frons."

DuPorte (1956), in studying the median facial sclerite in larval and adult Lepidoptera, ascertained that a frontoclypeal suture is absent and that in the larva of Protoparce and in the adult of Danaus the frontal ganglion lies at approximately the same level as the anterior tentorial pits. He therefore believes that the position of the anterior tentorial pits may also mark the level at which the primary mouth is located. According to him a line drawn between the anterior tentorial pits would then indicate the position of a frontoclypeal suture and divide the median facial sclerite into a dorsal postoral frontal region, on which the pharyngeal dilators originate, and a ventral preoral clypeal region, on which the cibarial dilators originate. He then regards the median facial sclerite, which he previously (1946) named the antefrons, as the complete frontoclypeus in the larvae and adults of Protoparce and Danaus. DuPorte (1956) is thus now apparently in some agreement with Snodgrass (1935, 1947) in as far as the value of the origins of the clypeal and frontal muscles in indicating the clypeal and frontal regions is concerned, but he states that "muscles are purely functional units and their mechanical efficiency depends in large part on their point of origin in the skeleton" and that "with changes in the form or in the direction of growth of the organs they move, they must often shift their origins, even if this involves crossing a secondary inflection." Therefore, when he found that in adult Danaus one pair of muscles, regarded by him as cibarial dilator muscles, but which may according to the present author probably repre-

sent buccal dilator muscles, arise on the facial area immediately dorsal to the anterior tentorial pits, DuPorte presumes that these muscles may have shifted their origins to the frontal region to increase their mechanical efficiency. However, he does not rule out the possibility of a ventral positional shift of the anterior tentorial arms. In adult Protoparce where two pairs of muscles, which are regarded by him as cibarial dilator muscles, arise on the facial area above the anterior tentorial pits, he definitely assumes a ventral migration of these pits in the clypeogenal sutures and accepts that they no longer mark the dividing line between the clypeus and frons. Ehrlich (1958a) claims to have confirmed the anatomical relationships presented by DuPorte (1956) for Danaus.

Eassa (1963b), however, established in his developmental studies of Pieris that the adult tentorium develops continuously from that of the larva, but that the new shape of the adult head gives the misimpression that the anterior tentorial arms have shifted their origins. He (1963a) found that the cibarial dilator muscles, the posterior pair of which the present author believes may be regarded as buccal dilators, arise in larval Pieris on the clypeus, ventral to the anterior tentorial pits (as DuPorte (1956) found in larval Protoparce), while in the adult Pieris they arise dorsal to these pits (as DuPorte (1956) found in adult Protoparce), but still on the clypeus. Eassa (1963b) believes that the imaginal clypeal area is increased (to provide more space for the more extensive adult cibarial dilator muscles) by the development of a "pupal crest" from which the greatest part of the adult clypeus is derived.

If these observations of Eassa (1963a, 1963b) are correct, then neither do the anterior tentorial pits migrate ventrally, nor do the cibarial and/or buccal dilator muscles shift their origins when the larval Lepidoptera changes to the adult, as DuPorte (1956) claims for Protoparce and Danaus. The clypeal area is, however, expanded dorsally, extending upward, even beyond the anterior tentorial pits in adult Lepidoptera, as Snodgrass (1935, 1947) alleges to be the case in liquid-feeding insects. It can therefore be concluded that the level at which the anterior tentorial pits occur in adult Lepidoptera is an unreliable indication of the line of demarcation between the clypeal and frontal areas. The present author therefore follows Snodgrass (1935, 1947) and determines the approximate boundary between these two areas in S. partita according to the origins of the cibarial, buccal and pharyngeal dilator muscles of the sucking pump on the frontoclypeus.

In S. partita the anterior tentorial pits (figs. 1, 2 & 4, a.tnt.pt) or frontal pits, which are discernable as elongated, vertical depressions, are present in the ventrofacial region at the junctions of the clypeolabral sulcus with the laterofacial sulci, dorsomedial to the mandibles. The cibarial dilator muscles originate on the frontoclypeus, both ventral and dorsal to the level at which the anterior tentorial pits occur. The buccal dilator muscles originate dorsal to this level, above the origins of those cibarial dilator muscles which arise dorsal to the anterior tentorial pits. As may be deduced from figures 13 and 16, the clypeal area, as is indicated by the origins of the cibarial dilators (termed the anterior and posterior fronto-

clypeus-cibarial dilator muscles, a.frclp.cib.dil.m and p.frclp.cib.dil.m) and buccal dilators (termed the lateral frontoclypeus-buccal dilator muscles, l.frclp.buc.dil.m), forms a larger portion, in fact, approximately the ventral three-quarters, of the frontoclypeus in S. partita than is indicated by the position of the anterior tentorial pits. The frontal area, which is indicated by the origin of the pharyngeal dilators (termed the frontoclypeus-pharyngeal dilator muscles, frclp.ph.dil.m), actually forms only approximately the dorsal quarter of the frontoclypeus.

In general, similar conditions regarding the origins of the cibarial and/or buccal dilator muscles, dorsal to the level at which the anterior tentorial pits occur, were found in Protoparce by Madden (1944), in Danaus and Protoparce by DuPorte (1956) and in Pieris by Eassa (1963b). The former two authors regard the median facial sclerite up to the level of the antennal sockets as the clypeus, and the small area between and just posterior to the sockets as the frons. Ehrlich (1958a, 1960) regards the median facial sclerite in Danaus and Epargyreus as the frontoclypeal sclerite. Michener (1952), however, calls a similar sclerite in Eacles, the frontal area and, in accepting DuPorte's (1946) interpretation, misidentifies the labrum as the clypeus in Eacles and Rhescyntis. Schmitt (1938) mentions for the Lepidoptera studied by him that the clypeus forms an elongate anterior area which is not marked off from the frons. Burgess (1880b) regards the median facial sclerite in Danaus as the "face", being "formed chiefly by the large, vaulted clypeus", while Kellogg (1893) terms the entire median facial sclerite up to its dorsal demarcating suture be-

tween the antennal sockets, the clypeus. Portier (1949) and Bourgonne (1951) also call the median facial sclerite the clypeus, while Imms (1960) regards it as either the clypeus or clypeus and frons. Short (1951) and Vasudeva (1957) base their interpretations of the median facial sclerite in Dilina and Papilio, respectively, on muscle origins. They found that the pharyngeal dilators apparently arise posterior to the dorsal demarcating suture of the median facial sclerite which extends between the antennal sockets. They therefore term the entire median facial sclerite anterior (or ventral) to this suture, the clypeus, and the area posterior (or dorsal) to it, on which the pharyngeal dilators originate, the frons. Srivastava (1957), however, found, in contrast to the findings of Vasudeva (1957), that the frons, clypeus and labrum are completely fused with each other in Papilio and terms this compound median facial sclerite, the epistoma. He then applies DuPorte's (1946) criterion that the anterior mandibular articulation, in lying immediately ventral to the anterior tentorial pits, denotes the limit between the clypeus and frons. However, since mandibles are absent in this papilionid, Srivastava believes that the area below a line drawn between the anterior tentorial pits represents the clypeus, and that the comparatively larger area above this line represents the frons. He finds support for his basis of demarcation in the fact that the cibarial dilators originate within the level of the anterior tentorial pits and that the pharyngeal dilators originate above this level. However, the muscles denoted by him as the "sub-antenna-buccal muscles" originate on what he terms the "oculo-subantennal ridges", therefore far dorsal to the anterior tentorial pits

and between the origins of the cibarial and pharyngeal dilators. When Snodgrass' (1935, 1947) criterion that the cibarial and buccal dilators arise on the clypeal area is taken into account, Srivastava's assumption that the level of the anterior tentorial pits shows the limit between the clypeus and frons in Papilio, may be incorrect, since these muscles apparently do not shift their origins as he, following DuPorte (1946, 1956), believes. From the foregoing it is therefore evident that the clypeus actually frons a greater part of the epistoma in Papilio than is indicated by the level at which the anterior tentorial pits occur.

In designating the bordering sulci and suture of the frontoclypeus in S. partita the terminology of DuPorte (1956) is used.

In S. partita the frontoclypeus is bounded ventrally by the slightly ventrally curving, transverse clypeolabral sulcus (figs. 1 & 2, clplbr.su) which separates the frontoclypeus from the labrum. Internally this sulcus frons for its entire length a slight clypeolabral ridge (fig. 17, clplbr.rdg) which joins the anterior tentorial arms at the anterior tentorial pits.

Similar sulci or sutures are also described as clypeolabral sutures in Danaus and Protoparce by DuPorte (1956) and in Danaus and Eupargyreus by Ehrlich (1958a, 1960). It may be noted that this is the sulcus which DuPorte (1946) regarded as the frontoclypeal inflection. Burgess (1880b), Kellogg (1893), Schmitt (1938), Madden (1944), Short (1951), Michener (1952), Srivastava (1957) and Vasudeva (1957) do not mention such sutures or sulci for the Lepidoptera studied by them, while Eassa (1963b) states that in Pieris the clypeus is ventrally se-

parated by a "furrow" which, according to him, develops from the larval conjunctiva between the labrum and cranium.

In S. partita the clypeolabral sulcus terminates in the anterior tentorial pits from which the mesally curving, ventral extensions of the vertical, relatively long laterofacial sulci (figs. 1-4, 1fc.su) also arise. These sulci separate the frontoclypeus laterally and ventrolaterally from the facial parts of the genae. Internally they form for their entire lengths strong, well-developed laterofacial ridges (figs. 13, 15 & 17, 1fc.rdg) and extend dorsally to the ventrolateral angles of the antennal sockets, fusing with the circumantennal sclerites of the latter.

The lateral, vertical borders of the median facial region in insects were previously designated as the frontogenal sulci by DuPorte (1946), who emphasised the importance of these sulci in defining the lateral limits of the frons. He, however, subsequently (1956) modified his views, stating that the ventral descent of the genal regions in Lepidoptera beyond the level of the mouth (as is the case in S. partita), results in the formation of clypeogenal sutures. Therefore, what he previously (1946) regarded as the frontogenal sulci are in fact composite laterofacial sulci formed by the union of the frontogenal and clypeogenal sulci, as described by him (1956) in Danaus and Protoparce. Ehrlich (1958a, 1960) also names the sutures bounding the frontoclypeus laterally in Danaus and Epargyreus, the laterofacial sutures, but Michener (1952) terms similar sutures in Rhescyntis and Hemileuca, the laterofrontal sutures. Corresponding sutures or sulci are regarded as ocular sutures by Madden (1944) in Protoparce, parts

of the epistomal suture by Short (1951) in Dilina, "lateral arms of the epistomal suture" by Vasudeva (1957) in Papilio, and as consisting of the pleurostomal sutures, subantennal sulci and "oculo-subantennal sulci" by Srivastava (1957) in Papilio. Burgess (1880b), Kellogg (1893) and Schmitt (1938) do not name comparable sutures in the Lepidoptera studied by them, while Eassa (1963b) does not describe these sutures in Pieris, and Michener (1952) found that in Eacles the median facial sclerite extends to the eyes, leaving no bordering vertical, lateral sutures.

In S. partita the dorsolateral angles of the frontoclypeus is flanked by the antennal sockets. Dorsally this sclerite is separated from the vertex by an oblique, dorsally arched transfrontal suture (figs. 1 & 3, tfr.s) which extends between the ventral rims of the antennal sockets.

DuPorte (1946, 1956) apparently was the first to name the suture extending between the antennal sockets in the majority of the Lepidoptera, the transfrontal suture, and Michener (1952) and Ehrlich (1958a, 1960) followed suit. Madden (1944) names a corresponding suture in Protoparce, the frontal suture. Short (1951) regards a comparable suture in Dilina as part of the epistomal suture, while Vasudeva (1957) designates a similar suture in Papilio as the "median arm of the epistomal suture." Kellogg (1893) describes a corresponding suture in Danaus and the other Lepidoptera included in his study as the "suture between epicranium and clypeus", and Bourgonne (1951) actually terms a similar suture, the "suture clypéo-epicraniale." Burgess (1880b), Schmitt (1938) and Srivastava (1957) do not mention similar sutures in

the Lepidoptera studied by them, and neither do Portier (1949) and Imms (1960). According to Eassa (1963b) the frons in Pieris is demarcated dorsally by a "transverse ridge" which passes between the eyes, dorsal to the antennal sockets. He believes that this ridge marks the point from which the adult epicranium began its growth.

4. Antennal sockets, circumantennal sclerites, antennifers and antennal membranes

The nearly circular antennal sockets (figs. 1 & 3, ant.soc), antennal fossae or antennal foramina are situated in S. partita at the dorsolateral corners of the frontoclypeus and at the ventrolateral corners of the vertex. The rims of the antennal sockets are strongly inflected to form circumantennal sclerites (figs. 1, 3 & 15, cant.scl) which are very broad laterally where they are produced into small, recurved, heavily sclerotized antennifers (figs. 1 & 3, anf). The circumantennal sclerites are overlain by the bases of the scapes which articulate with the antennifers. The bases of the scapes are connected to the rims of the circumantennal sclerites by elastic antennal membranes (figs. 1 & 3, ant.mem) or antacoria which facilitate the movements of the antennae. Distinct circumantennal ridges could not be discerned.

The circumantennal sclerites of S. partita apparently correspond to the antennal sclerites described by Madden (1944) in Protoparce, to the antennal ridges illustrated by Short (1951) in Dilina, and to the antennal sclerites or to the antennal ridges described by Vasudeva (1957) in Papilio. They may also correspond to the structures which

Srivastava (1957) terms the "antero-lateral and antero-mesal inflections of the rims of the antennal sockets" in Papilio.

5. Vertex, ocelli, occiput, occipital suture, postoccipital suture, posterior tentorial pits and postantennal sulci

In S. partita the median dorsofacial region of the cranium, which is separated from the frontoclypeus by the antennal sockets and the transfrontal suture, is a relatively large, transverse, sub-oblongate, convex area, here regarded as the vertex (figs. 1-3, vx). It is densely covered with long, slender scales.

Corresponding central areas on the dorsum of the cranium are also regarded as the vertex by Madden (1944), Michener (1952) and Ehrlich (1958a, 1960) in the Lepidoptera studied by them. Srivastava (1957) applies the term vertex in Papilio to "the narrow area between the two antennal bases formed by the frontal and the occipital portions", while Vasudeva (1957) regards the "dorsal surface of the parietals that forms the top of the head" as the vertex in the same papilionid. Burgess (1880b), however, regards the "roof of the head" in Danaus as the epicranium, the posterior part of which he calls the occiput, while he believes that the region immediately above and between the antennae is the front. Kellogg (1893) also terms the "dorsal aspect" and "the middle upper part of the hind aspect" of the head, the epicranium in Danaus. Bourgonne (1951) uses the term epicranium for the top of the cranium, as does Eassa (1963b) for adult Pieris. According to Eassa the epicranium in the adult Pieris is a new formation which does not correspond to any part of the larval or pupal head and which is formed

by growth of the hypodermis posterior to the pupal frons. It is uncertain what Schmitt (1938) regards as the corresponding cranial area in the Lepidoptera studied by him, but Short (1951) regards part of a similar area in the head of Dilina as the frons and another part probably as the occipital region.

The terms "vertex" and "epicranium" are therefore loosely used for the same general cranial area in Lepidoptera. The present author, however, prefers the term "vertex" for the said cranial area in S. partita, not only because it is used in the majority of works consulted, but because it is a more restricted term. According to Imms (1960) it is "that portion of the epicranium which lies immediately behind the frons, and between the compound eyes" and according to Snodgrass (1935) it is "the top of the cranium between and behind the compound eyes." The epicranium, itself, is defined by Snodgrass (1935) as "a term variously applied to the entire cranium, to the cranium exclusive of the frons, or preferably to the upper part of the cranium."

The two small, lateral, dome-shaped ocelli (figs. 1-3 & 5, o) of S. partita are situated on the vertex, well behind the antennae and adjacent to the postantennal sulci. The ocelli are each provided with a relatively thick ocellar nerve (figs. 14-16, o.n) which arises from the dorsal surface of the brain (figs. 14-16, brn), posterior to an antennal nerve.

Posteriorly or dorsally, at the top of the cranium where the latter is sharply angled in S. partita, the vertex is separated from a smaller, convex, elongated, transverse, median posterodorsal area, here regarded as the occiput (figs. 2, 3 & 5, occ), by a faint, slight-

ly dorsally curving occipital suture (figs. 1-3 & 5, occ.s). The occiput is densely covered with long, slender scales, as well as with short, flabilliform scales. The occipital suture runs along a low "crest" between the postantennal sulci, meeting the latter at their points of junction with the postgenal sutures.

Madden (1944) denotes, but does not describe, a corresponding cranial area in Protoparce as the occiput, and Bourgogne (1951) regards a similar area accordingly. Burgess (1880b) calls the posterior aspect of the roof of the head in Danaus, the occiput, but, since he includes no illustration of this area, it is uncertain whether it may correspond to the occiput or to the postgenae, or perhaps to both of these cranial areas in S. partita. Occipital areas are also designated by Kellogg (1893), Srivastava (1957) and Vasudeva (1957) in the Lepidoptera studied by them, but these occupy somewhat different positions from that of S. partita. Schmitt (1938) mentions, but does not illustrate, an occiput for the Lepidoptera studied by him. Short (1951) illustrates an occipital region in Dilina which apparently occupies the same position as the occiput in S. partita. Eassa (1963b) does not mention an occiput for Pieris. The cranial areas denoted as the occipital area by Michener (1952) in Eacles, and as the occiput by Ehrlich (1958a, 1960) in Danaus and Epargyreus, largely correspond to the areas designated as the postgenae by Kellogg (1893), Madden (1944), Srivastava (1957), Eassa (1963b) and the present author. The occiput in S. partita apparently occupies an area corresponding to the posterior half of the vertex in Eacles, Danaus and Epargyreus. No reference to an occipital suture like that of S. partita could be

found in the literature consulted.

In S. partita the occiput is posteriorly limited by the postoccipital suture (fig. 5, pocc.s) which borders the upper half (so-called alaforamen, afor) of the occipital foramen dorsally and laterally. This suture ends on either side of the occipital foramen in the open, oval-shaped posterior tentorial pits (fig. 5, p.tnt.pt) or gular pits which are present in the postgenae at the ventrolateral corners of the so-called alaforamen. A definite postocciput is absent in S. partita, but the presence of occipital condyles (occ.con) on the tentorial bridge (tnt.brg) indicate that vestiges of the postocciput are still present, since Snodgrass (1935) defines the occipital condyles as "processes on the margin of the postocciput." A narrow integumental area posterior to the postoccipital suture is inflected along the lateral edges of the so-called alaforamen, forming submarginal postoccipital inflections (fig. 5, pocc.inf) which afford attachment for neck and prothoracic muscles. The ventral parts of the postoccipital inflections join the posterior tentorial arms at the posterior tentorial pits.

Srivastava (1957) observed a well-marked postoccipital sulcus in Papilio, but found that "the postocciput has been reduced to a mere thickened line which gives attachment to the neck membrane." In the other literature consulted, except in the papers of Burgess (1880b) and Kellogg (1893), a postoccipital suture and a rather narrow or reduced postocciput are described or illustrated in the Lepidoptera studied.

Both the vertex and occiput are in S. partita laterally bounded

by sulci which, in conformity with Short's (1951) terminology of corresponding sulci in Dilina, are here regarded as the postantennal sulci (figs. 1-3 & 5, pant.su). These sulci originate in the postoccipital suture, immediately ventral to the dorsolateral corners of the so-called alaforamen and extend anteriorly over the cranium. They then run immediately lateral to the ocelli and curve sharply mesally, posterior to the antennal sockets, and end in the dorsolateral angles of the latter. The postantennal sulci therefore separate the vertex and occiput laterally from the dorsofacial parts of the genae and from the dorsal parts of the postgenae respectively. Internally the postantennal sulci form for their entire lengths strong, well-developed postantennal ridges (figs. 14-17, pant.rdg). Their anterior parts are fused with the circumantennal sclerites of the antennal sockets and their posterior parts with the postoccipital inflections.

Madden (1944) and Vasudeva (1957) denote corresponding sutures in Protoparce and Papilio, respectively, as postgenal sutures, while Srivastava (1957) terms similar sulci in Papilio, the "occipito-postgenal sulci." Michener (1952) and Ehrlich (1958a, 1960) designate comparable sutures in the Lepidoptera studied by them as the temporal sutures, after Ferris (1942). Kellogg (1893) describes corresponding sutures in some of the Lepidoptera included in his study as the "sutures between epicranium and postgena", but comparable sutures are not mentioned by Burgess (1880b) and Eassa (1963b) for Danaus and Pieris, respectively, while it is impossible to determine if Schmitt (1938) refers to any similar sutures in his study.

The appropriate designation "postantennal sulci" of Short (1951)

is, however, preferred for these sulci in S. partita, because if they were to be regarded as the postgenal sulci, it would imply that the vertex is separated from the dorsal genal portions by parts of the postgenal sulci, a condition which the present author finds unacceptable. Further, the term "postgenal sutures" is applied in the present study for the demarcating lines between the genae and postgenae, and will be described subsequently. Ferris' (1942) terminology of cranial sutures and sclerites is not used.

6. Occipital foramen, tentorial bridge and occipital condyles

The posterior cranial surface in S. partita is centrally perforated by the large occipital foramen or foramen magnum. It is bordered dorsally and dorsolaterally by the postoccipital suture, laterally by the postgenae and ventrally by the posterior (or dorsal) margin of the transverse "beam" of the T-shaped labium. Approximately across its middle the occipital foramen is transversally bisected by the short, hollow tentorial bridge (fig. 5, tnt.brg). An upper so-called alaforamen (fig. 5, afor) (MacGillivray, 1923; Srivastava, 1957) through which the oesophagus passes, and a lower so-called neuraforamen (fig. 5, nfor) through which the salivary ducts and nerve cord pass, are thus formed.

Immediately dorsomesal to the posterior tentorial pits the occipital condyles (fig. 5, occ.con), which articulate with the lateral cervical sclerites, occur as elevated discs on the tentorial bridge, itself, and obviously represent vestiges of the ventral extremities of the postocciput.

7. Postgenae, postgenal sutures, hypostomata and hypostomal sutures

The large meniscate areas in the posterior cranial region, which adjoin the occipital foramen and the transverse "beam" of the T-shaped labium on either side, are regarded as the postgenae (figs. 2-5, pge) in S. partita. Next to the so-called alaforamen they are densely covered with short, flabilliform scales and next to the so-called neuraforamen with long, slender scales.

Corresponding cranial areas are similarly regarded as the postgenae by Kellogg (1893), Madden (1944), Bourgonne (1951), Srivastava (1957) and Eassa (1963b) in the Lepidoptera studied by them. Vasudeva (1957) apparently also describes similar areas as the postgenae in Papilio, but the areas which he labels accordingly, differ in two consecutive figures. Schmitt (1938) believes similar areas to represent the parietals in the Lepidoptera studied by him, while Short (1951) regards comparable areas in Dilina as part of the "parietal and occipital regions." Eassa (1963b), however, points out that Schmitt (1938), and therefore also Short (1951), mistakenly named the postgenae of the adult, the parietals, when he in fact established that in Pieris "the only parts of the parietals that remain in the imago are the areas occupied by the antennal sockets." Burgess (1880b) does not describe or illustrate similar areas in Danaus, but it may be that he regards these areas as part of his occiput. Corresponding cranial areas are designated as the occipital area by Michener (1952) in Eacles, and as the occiput by Ehrlich (1958a, 1960) in Danaus and Epargyreus. By definition (Snodgrass, 1935), however, the lateral and ventral parts

of the occipital arch, or areas of the cranium posterior to the genae, are named the postgenae. As the relevant areas in S. partita are in this way related to the occiput and genae, they can be regarded as the postgenae.

At the lateral edges of the so-called neuroforamen the postgenae in S. partita are inflected to form strong, well-developed postgenal inflections (figs. 14-16, pge.inf) which are dorsally fused with the anterior tentorial arms and tentorial bridge. They extend internally in the posteroventral cranial region where they are fused with the posterior margins of the cardines and so-called verastipites. Along the lateral sides of the so-called alaforamen the postgenae are bordered by parts of the postoccipital suture, while they are dorsally separated from the occiput by the postantennal sulci. Laterally the postgenae are separated from the posterior parts of the genae, with which they form sharp angles, by definite sutures, here regarded as the postgenal sutures (figs. 1-5, pge.s). These sutures originate in the postantennal sulci at the points where the latter join the occipital suture, and are then continued in the ventral cranial region as the hypostomal sutures, which will be described subsequently. The postgenal sutures in S. partita may be compared to the lateral, ventrally extending parts of the occipital suture in the typical insect which, according to Snodgrass (1935), usually end in the subgenal sutures. But, as the postgenal sutures are not continuous with the occipital suture and separate the genae from the postgenae in S. partita, they are regarded as separate sutures and named accordingly.

It should be noted that the postgenal sutures in S. partita do

not correspond to the sutures similarly named by Madden (1944) and Vasudeva (1957) in Protoparce and Papilio, respectively, nor to the sulci termed the "occipito-postgenal sulci" by Srivastava (1957) in Papilio. The sulci in S. partita which correspond to the former two authors' postgenal sutures and to the latter author's "occipito-postgenal sulci" are the postantennal sulci, which have already been described. It is probable that the postgenal sutures in S. partita may correspond in some degree to what Ehrlich (1960) in Epargyreus terms the "transoccipital bands", which "occur at a sharp angling of the occiput" (=postgenae in S. partita). Kellogg (1893) terms a certain suture observed by him in some Lepidoptera, the "suture between gena and postgena." It is possible that the most dorsal part of a postgenal suture in S. partita may correspond to this suture. No reference to similar sutures could be found in the other literature consulted.

In S. partita the narrow, vertical parts of the postgenae in the ventral cranial region are regarded as the hypostomata (figs. 4, 5, 18 & 19-22, hps), in conformity with Eassa's (1963b) terminology of corresponding cranial areas in Pieris. The latter author established in adult Pieris that the narrow extensions of the postgenae which run forward represent the hypostomata. In S. partita the hypostomata are partly concealed in ventral view by the compound eyes (fig. 4), only the most anterior hypostomal parts being visible.

Michener (1952) and Ehrlich (1958a) also regard corresponding areas in Eacles and Danaus, respectively, as the hypostomata, which in these instances, however, are continuous posteriorly with what they regard as the occipital areas. Areas occupying rather similar posi-

tions as the hypostomata in S. partita are regarded as parts of the postgenae by Madden (1944) in Protoparce, probably as parts of the parietals or hypostomata by Schmitt (1938) in the Lepidoptera studied by him, probably as parts of the parietal region by Short (1951) in Dilina, and as the subgenae by Srivastava (1957) and Vasudeva (1957) in Papilio. It is uncertain what Kellogg (1893) regards as corresponding areas in the Lepidoptera studied by him, but it could either be part of the postgenae or the genae. Burgess (1880b) does not name corresponding areas in Danaus.

In S. partita the hypostomata are, as in Papilio (Vasudeva, 1957), Danaus and Epargyreus (Ehrlich, 1958a; 1960) and Pieris (Eassa, 1963b), not united behind the posterior (or dorsal) margin of the transverse "beam" of the T-shaped labium to form a "hypostomal bridge." A hypostomal bridge, posterior to the labium and bordering the occipital foramen ventrally, is, however, described by Madden (1944) in Protoparce and by Srivastava (1957) in Papilio. It is also illustrated by Schmitt (1938) in some Lepidoptera studied by him and by Short (1951) in Dilina, whilst Snodgrass (1935) states that in all adult Lepidoptera the labium is "supported posteriorly on a hypostomal bar, uniting the postgenae of the epicranium." Michener (1952) regards an area posterior to the hind edge of the labium in Eacles as the "post-occipital bridge", while Kellogg (1893) denotes generally corresponding areas in some of the Lepidoptera studied by him as the gula. Burgess (1880b) does not name corresponding areas in Danaus.

Mesally the hypostomata are in S. partita fused with the lateral margins of the cardines (fig. 4) and palpifers (figs. 19-22), while

posterior to the mandibles they are connected to the anterolateral hypopharyngeal extensions (figs. 11, 18 & 42) of the floor of the sucking pump. Laterally they are separated from the ventral parts of the genae by sutures, here regarded as the hypostomal sutures (figs. 2, 4, 10 & 18, hps.s). These sutures are continuous with the postgenal sutures at the posteroventral angle of the cranium and extend anteriorly into the ventral region, being sharply curved mesally, posterior to the mandibles. The hypostomal sutures therefore also separate the hypostomata from the mandibles, and end at the most anterior fusion of the hypostomata with the anterolateral hypopharyngeal extensions. The interpretation of the hypostomal sutures in S. partita is partly based on Snodgrass' (1935) definition that in the typical insect those parts of the subgenal sutures posterior to the mandibles are the hypostomal sutures.

Schmitt (1938) mentions hypostomal sutures for the Lepidoptera studied by him, but it is uncertain whether they may correspond to that in S. partita. Srivastava (1957) describes subgenal sutures in Papilio which he divides into pleurostomal and hypostomal sutures and states that each of the latter sutures "runs on the outer margin of the subgenal area." It is probable that the hypostomal sutures in S. partita may in part correspond to these hypostomal sutures in Papilio. Similar sutures are not mentioned for Lepidoptera in the other literature consulted.

8. Ventral cranial membranes

In S. partita the labium is separated from the cardines and sti-

pites by a pair of relatively large, trough-shaped, roughly square ventral cranial membranes (figs. 14, 19-22, 29-31, 41 & 42, v.cr.mem). Laterally they are attached to the cardines and the so-called verastipites, and anteriorly to the so-called juxtastipites, as well as to portions of the proximal parts of the galeal bases. Mesally they are attached to the lateral margins of the longitudinal "stem" of the T-shaped labium, while posteriorly they are joined to the anterior margins of the transverse "beam" of the labium. These membranes form part of the ventral cranial floor, are externally covered with minute setae (figs. 19-22, 29-31, 41 & 42, se), and support the tentorio-galeal retractor muscles ventrally.

Eastham and Eassa (1955) term similar membranes in Pieris, the "ventral membranes." Kellogg (1893), Madden (1944), Srivastava (1957), Vasudeva (1957), Ehrlich (1958a, 1960) and Eassa (1963b) illustrate or mention, but do not name, comparable structures in the Lepidoptera studied by them.

9. Tentorium

In S. partita the tentorium is pi-shaped and in general similar to that of other adult Lepidoptera. It gives rigidity to the cranial capsule, provides a basis for the attachment of cephalic muscles, lends support to the brain, the sucking pump and the alimentary canal, and consists of the paired anterior tentorial arms and the tentorial bridge.

The broad, elongated, laterally compressed, hollow anterior tentorial arms (figs. 5, 14, 15, 17 & 18, a.tnt.am), each giving attach-

ment to four extrinsic antennal muscles and three extrinsic maxillary muscles, arise from the anterior tentorial pits and are fused with the clypeolabral ridge and the laterofacial ridges. The arms then extend horizontally through the cranial cavity, passing lateral to the sucking pump. Behind the latter they converge strongly and terminate in cup-shaped extremities which are fused with the tentorial bridge and the postgenal inflections, and which partially occlude the so-called neuroforamen. Next to the sucking pump the anterior tentorial arms are dorsally produced into enlarged, shell-like dorsal flanges (figs. 13, 15 & 17, d.fg) on which inter alia originate some of the extrinsic antennal muscles. These flanges may therefore represent dorsal tentorial arms, since according to Snodgrass (1935) the tentorium secondarily gives attachment to the antennal muscles on a pair of dorsal arms.

The short, hollow tentorial bridge (figs. 5 & 18, tnt.brg), representing the medially fused posterior tentorial arms which arise from the posterior tentorial pits, divides the occipital foramen into an upper so-called alaforamen and a lower so-called neuroforamen, as has already been described. With the posterior tentorial arms are fused the postoccipital inflections, the anterior tentorial arms and the postgenal inflections.

B. Cranial Appendages

The homologies of the cranial appendages present no difficulties.

1. Antennae

In S. partita the antennae are setaceous in both sexes and vary

in length from 15.0 mm. to 16.0 mm. The scape (figs. 1-3, scp) of the antenna is cylindrical at its base, but bulbous distally and considerably larger than the pedicel (figs. 1-3 & 5, pde). The remaining segments of the antenna constitute the flagellum (figs. 1-3, 5 & 12, flg) and vary in number from 95 to 97 among individuals. Very short, narrow scales densely cover the outer sides of the antennal segments and on the distal margins of the flagellar segments a few short, thin setae (figs. 1-3, 5 & 12, se) are present.

The antennae are each provided with a thick antennal nerve (fig. 16, ant.n) which arises from the anterodorsal surface of the brain (figs. 14-16, brn), anterior to an ocellar nerve.

2. Trophi

Although the hypopharynx forms part of the trophi, it constitutes the anterior part of the floor of the sucking pump and its structure will therefore be discussed when the latter organ is described.

a. Labrum

As in other adult Lepidoptera, the narrow, transverse labrum (figs. 1 & 2, lbr) is in S. partita really a fixed part of the cranium. DuPorte (1946) erroneously described the labrum as the clypeus in the Lepidoptera included in his study, and therefore believed the pilifers to be protuberances of the clypeus. Michener (1952), following DuPorte (1946), makes the same error in Eacles and Rhescyntis.

The labrum is present in the ventrofacial region of the cranium, being separated from the frontoclypeus by the clypeolabral sulcus,

which has already been described. On its ventrolateral extremities the labrum is produced into two cylindroconical, sharply pointed, ventrally projecting structures for which the term pilifers (figs. 1, 2 & 4, pf) was coined by Kellogg (1893) in Danaus. They bear straight, stiff bristles (figs. 1, 2 & 4, br) of varying lengths on their inner surfaces. It may be mentioned that the pilifers have frequently been misinterpreted as the mandibles by lepidopterists.

Ventromedially the labrum is expanded into a broad, rounded labral lobe (fig. 1, lbr.lob), similar to that termed the "median labral extension" by Eastham and Eassa (1955) and Eassa (1963b) in Pieris. Madden (1944) describes the small mesal lobe of the labrum in Proto-parce as the "epipharynx in part", and Vasudeva (1957) names a similar structure, the epipharynx in Papilio. Portier (1949) and Bourgonne (1951) also regard a similar labral extension in Lepidoptera as the epipharynx. Eassa (1963b), however, points out that Lang (1891)*, who also terms a similar median labral lobe, the epipharynx in Lepidoptera, failed to observe the true epipharynx beneath this median labral extension.

Ventrally the labrum and labral lobe are folded back into the cranial capsule and are joined to the epipharynx which is continued posteriorly as the roof of the sucking pump. The labrum and labral lobe form the roof of the food channel proximally where the latter is shaped like a dorsally open gutter between the galeal bases, as will be described subsequently in detail.

*Not seen in the original.

b. Mandibles

The paired, vestigial, non-functional mandibles (figs. 1, 2 & 4, md) are in S. partita immovably fused to the genae, ventrolateral to the anterior tentorial pits and are partly concealed by the pilifers. They have the appearance of small, tooth-like elevations, showing no articulatory points or demarcating sutures.

Posteroventrally the mandibles are separated from the hypostomata by the hypostomal sutures and mesally they extend to the galeal bases and are continuous with the invaginations of the integument at the anterior tentorial pits.

c. Maxillae

As in the majority of adult Lepidoptera, the paired maxillae, lacking laciniae, are the largest, most important and most complicated of the mouthparts in S. partita. They are situated in the so-called proboscidial fossa. Michener (1952) and Ehrlich (1958a) regard the broad depression which occupies the entire ventral surface of the head between the eyes as the proboscidial fossa in Eacles and Danaus respectively. In S. partita this fossa therefore enclose the hypostomata, cardines, stipites, ventral cranial membranes and T-shaped labium.

Burgess (1880a, 1880b) did not distinguish between the different parts of the maxillae in Danaus. Kellogg (1893) originally also did not name the different parts of the maxillae in Danaus and the other Lepidoptera included in his study, but he later (1895) established that in Lepidoptera the maxillae consist of the cardines, stipites, galeae, and in some instances also of the laciniae. However, he ap-

parently believes that the proboscis is formed either by the galeae, or by the laciniae. Tillyard (1923), however, produced conclusive evidence that in the Micropterygoidea the proboscis is formed by the galeae.

(i) Cardines

The paired, relatively large, approximately quadrangular, slightly convex cardines (figs. 4, 7 & 8, cd) are bordered posteriorly by the postgenae, laterally by the hypostomata and mesally by the ventral cranial membranes. Their posteromesal angles are in contact with the anterolateral angles of the transverse "beam" of the T-shaped labium, while their anterolateral and anterior margins are attached to the posterior margins of the so-called verastipites.

(ii) Stipites

Anteriorly to the cardines are fused the paired, elongated, tubular, heavily sclerotized (preponderantly exocuticular) stipites. They lie in recesses or fossae, formed by the dorsally displaced hypostomata and ventral cranial membranes. The anterior parts of the stipites converge, but do not meet. Mesally they are connected to the ventral cranial membranes, laterally to the hypostomata and anteriorly they are fused with the galeal bases. Each stipes is tripartite, and Srivastava's (1957) terminology for these three stipital parts in Papilio will be employed in the present study.

The so-called juxtastipes (figs. 4, 7, 8, 20 & 21, jxst) forms the small, flat, exocuticular, mesal stipital part of the anterior

half of each stipes and to its mesal border is attached a ventral cranial membrane. It is anterolaterally continuous with an exocuticular, middle stipital part, the so-called verastipes (figs. 4, 7, 8 & 19-21, *vrst*), from which it is internally demarcated by an exocuticular, dorsomesally projecting stipital apodeme (figs. 20 & 21, *st.apd*) or stipital ridge on which the geno-stipital adductor muscle and the anterior and posterior tentorio-stipital adductor muscles are inserted. The verastipes is gutter-shaped, broad anteriorly, but narrower posteriorly where it is connected to a cardo. From the stipital apodeme the wall of the verastipes curves in transverse section sharply ventrolaterally and then dorsally (figs. 20 & 21). Here the stipital wall is indented to form a stipital groove (figs. 19-21, *st.grv*) or stipital furrow which consists mainly of flexible endocuticle. This groove runs obliquely across the stipital wall (figs. 19-21). It is to be expected that the stipital grooves are capable of accommodating themselves to changes in the haemolymph pressure within the stipital and galeal haemocoel, as is also assumed by Eastham and Eassa (1955) for similar grooves in Pieris. The stipital groove separates the verastipes from an exocuticular, lateral stipital part, the palpifer (figs. 4, 7, 8 & 19-21, *plf*), whose wall in transverse section extends from the stipital groove consecutively in a lateral, dorsal (where it is joined by the hypostoma), mesal and ventrolateral direction (figs. 19-21). The ventrolaterally projecting part of the wall of the palpifer forms a flap-like stipital valve (figs. 19-21, *st.vlv*) which forms the lateral wall of the slit-like stipital aperture (figs. 19-21, *st.ap*). The mesal wall of the stipital aperture is formed by

the stipital apodeme and by part of the verastipes (figs. 20 & 21), except posteriorly where the stipital apodeme is not developed and where the aperture is mesally bounded only by part of the verastipes (fig. 19).

From the foregoing description it is evident that the palpifer and the verastipes enclose a stipital haemocoel (figs. 19-21, st.hmc) which is broader anteriorly than posteriorly and which is partly divided into two compartments by the stipital groove. The stipital haemocoels contain cephalic haemolymph and are continuous anteriorly with the galeal haemocoels, while they are dorsally in communication with the cranial cavity by means of the slit-like stipital apertures.

The exact manner in which a stipes is joined to a galeal base is extremely difficult to detect and describe. This is also evident from the works of other authors who state rather vaguely that "The distal end of each stipes bears one half of the proboscis" (Pradhan & Aren, 1941; Vasudeva, 1957), or "a stipes bearing at its apex the short, curled galea" (Michener, 1952), or "The stipes is a complex sclerite. To its anterior border is fitted the galea base" (Eastham & Eassa, 1955), or "Attached to the anterior border of the stipes is the very much elongated galea" (Eassa, 1963b). In S. partita the anterior margins of the palpifer, the verastipes and the juxtastipes are apparently inseparably fused with the posterolateral angles of the galeal base (figs. 7 & 8), but leaves a faint line of demarcation externally. Immediately anterior to the point of fusion of the juxtastipes with part of the ventral wall of the galeal base, the maxilla becomes a complete tube. As is evident from figure 22, this condition

is brought about by the fact that the hindmost part of the dorsal wall of the galeal base (fig. 22, gl.b) is here fused with the anteromesal margin of the palpifer (fig. 22, plf) at the point where the latter is joined by the hypostoma. The palpifer is here not reflected to form a stipital valve. Furthermore, the hindmost part of the ventromesal wall of the galeal base is here fused with the verastipes (fig. 22, vrst) at the mesal side of the base of the stipital apodeme, before the most anterior part of the palpifer and the verastipes are connected to the galeal base. At this point (fig. 22) the stipital apodeme (st.apd) has become twisted to the other side and projects laterally, supporting both the galeal trachea (fig. 22, gl.tr) and the galeal nerve (fig. 22, gl.n) (which here enter the maxilla), and projecting them against compression during movement of the proboscis. Further forward the most anterior margins of the palpifer is fused with the lateral wall and part of the dorsal and ventral wall of the galeal base, while the verastipes is fused with part of the ventral and mesal walls of the galeal base. The cylindrical galeal haemocoelae can therefore communicate with the cranial cavity only by means of the stipital apertures.

Anterolaterally, near its point of attachment to a galeal base, each palpifer bears a vestigial, one-segmented maxillary palp (figs. 2, 4, 7 & 8, mx.plp) which is covered with a tuft of short hair.

(iii) Galeae

The strong, paired, much elongated, tubular, distally tapering, terminally closed and sharply pointed galeae (figs. 1 & 2, gl) are

fused at their posterolateral angles with the anterior margins of the stipites (figs. 7 & 8), as has already been described in detail. Their haemocoelae contain cephalic haemolymph and are continuous posteriorly with the stipital haemocoelae. They are firmly linked together by a dorsal and a ventral linking mechanism to form the suctorial proboscis which constitutes the greater part of the maxillae.

In S. partita the length of the galeae vary among individuals from 12.4 mm. to 13.2 mm. One of them, usually the left one, is up to 0.02 mm. shorter than the other one. When coiled, their greatest dorsoventral and lateromesal diameters diminish from approximately 275μ and 594μ , respectively, at their bases, to approximately 2μ and 3μ , respectively, at their tips. Their mesal (inner) walls are concave and, in opposing each other, form between them a much elongated, cylindrical food channel (figs. 24-28 & 42, f.ch1), food canal, food tube or sucking tube. Through the food channel the fruit juice on which S. partita feeds is imbibed by means of a suction power which is created within the sucking pump. This suction power is produced by the action of the extrinsic and intrinsic sucking pump muscles which causes the enlargement of the sucking pump cavity and leads to a reduction of the air pressure within the cavity, as will be explained in detail when the sucking pump is described. The dorsoventral and lateromesal diameters of the food channel gradually decrease from approximately 92μ to 97μ , respectively, proximally, to approximately 35μ and 38μ , respectively, distally. Proximally, where the galeae fail to meet dorsally, the food channel is shaped like a dorsally open gutter between the galeal bases (fig. 42) and is overhung by the la-

brum and labral lobe which here form its roof. The posterior portion of this part of the food channel is dorsally in communication with the cibarial region (figs. 30 & 31, cib.rgn) of the sucking pump by means of the functional mouth (figs. 30 & 31, func.mth) via the food meatus (figs. 30 & 31, f.mts), as will be noted in detail when the sucking pump is described. Distally, at the extreme apex of the proboscis, the food channel is also dorsally open, thus providing for the greater intake of fruit juice.

At rest the proboscis is tightly coiled in a vertical plane underneath the head and between the labial palps. Normally it forms about two coils.

In S. partita each galea is divided into three regions, a proximal, an intermediate or coilable and an apical region. Eastham and Eassa (1955) and Vasudeva (1957) divide the galeae in Pieris and Papilio, respectively, into two regions, viz. a proximal and a distal or coilable region. The intermediate plus apical region of a galea in S. partita correspond to the distal regions of the galeae in Pieris and Papilio.

Proximal region of the galea

This region, the galeal base (figs. 7 & 8, gl.b), which is dorso-ventrally compressed and therefore somewhat oval-shaped in transverse section (fig. 23), constitutes the very short, basal portion of the galea and differs from the proboscis proper in that it does not take part in the coiling process. Proximally, at its posterolateral angle, it is inseparably fused with the anterior margin of a stipes (figs. 7

& 8), as has already been described, while distally it is continuous with the intermediate region of the galea. The galeal base is anteriorly not demarcated from the intermediate region of the galea by a dorsal, transverse cuticular inflection or apodeme, as Eastham and Eassa (1955) and Vasudeva (1957) found in Pieris and Papilio respectively. Its distal limits are indicated externally to some extent by the onset of the exocuticular ribs (exc.rb), occurring on the outer wall of the intermediate region of the galea, and by the onset of the exocuticular bars (exc.bar), occurring in the mesal wall of the same region. Internally its distal limits are marked by the insertion of the anterior basal galeal levator muscle (a.bs.gl.lev.m) on the dorsal wall of the galeal base, by the beginning of the galeal septum (gl.spt), occurring in the haemocoel of the intermediate region of the galea, and by the beginning of the dorsal bar (d.bar), occurring in the mesal wall of the same region.

The walls of the galeal base vary in thickness from approximately 22 μ to 118 μ . Its outer wall lacks the exocuticular ribs (exc.rb) which are present in the outer wall of the intermediate region of the galea, and its mesal wall lacks the exocuticular bars (exc.bar) which are present in the mesal wall of the same region. The proximal part of the galeal base consists of rigid exocuticle (figs. 29-31 & 41, exc), being separated from a similar distal part by an intermediate zone of flexible endocuticle (figs. 29-31 & 41, enc₁). The endocuticle is thrown into more or less transverse folds and permits the elevation and the lowering of the galeal base, as will be discussed subsequently in detail when the musculature is described.

At the junction of a galeal base with a stipes the galeal trachea (figs. 22 & 29, gl.tr) and galeal nerve (figs. 22 & 29, gl.n) enter the galeal haemocoele (fig. 23, gl.hmc). Their passage into the galea is shielded by an exocuticular valvular fold (fig. 29, vlv.fld) in the galeal base and they are here protected against compression, during movement of the proboscis, by the stipital apodeme (fig. 22, st.apd) which supports them. It may be assumed that the valvular folds of the galeal bases effectively prevent the passage of haemolymph from the galeal haemocoeles to the cranial cavity, should any haemolymph pressure be set up within the galeae. This function is also assumed by Eastham and Eassa (1955) for similar folds in Pieris.

Intermediate or coilable region of the galea

This region is continuous proximally with the galeal base, as has already been described, and distally it merges with the apical region of the galea. It is very long and fairly uniform in structure, tapering distally and in repose presenting a nearly circular outline in transverse section (fig. 26), except distally where its lateral wall is indented (fig. 28) like that of the apical region of the galea.

Its outer wall (anterodorsal, lateral and posteroventral) varies in thickness from approximately 6μ to 35μ basally, at its junction with the galeal base, and from approximately 15μ to 25μ distally, at its junction with the apical region of the galea. This wall consists of flexible, laminated endocuticle (figs. 24-33, 36, 37 & 41, enc) in which transversely arranged exocuticular ribs (figs. 36, 37, 1, 2, 4, 5, 7-9, 24-33 & 41, exc.rb), exocuticular annulations, sclerotic arches,

sclerotic rings, "chitinous bands" or "chitinous annuli", strengthening the galea and imparting an annulated appearance to the proboscis, are embedded at fairly regular intervals. These exocuticular ribs vary in width from approximately $5/\mu$ to $8/\mu$ and in thickness from approximately $14/\mu$ to $20/\mu$. They therefore occupy approximately three-quarters of the thickness of the cuticle where they occur, being separated from each other by endocuticle of a width about equal to their own. That the regions intervening between the exocuticular ribs is endocuticular in nature, is in agreement with the findings of Eastham and Eassa (1955) and Eassa (1963b) in Pieris and Vasudeva (1957) in Papilio, but differs from the views of Burgess (1880a, 1880b), Snodgrass (1935), Schmitt (1938), Portier (1949) and Bourgogne (1951) who regard these regions of the lepidopterous galea as being membranous. As in other Lepidoptera, the irregularly-shaped exocuticular ribs, which in places are incomplete or coalescent or forked (figs. 7, 8 & 36), are not present over the entire surface of the outer wall — they are not developed in the dorsal and ventral areas adjacent to the mesal wall (figs. 24-28).

This particular cuticular composition of the outer walls of the intermediate regions of the galeae permits changes in shape to take place during coiling and extension of the proboscis. As in Pieris (Eastham & Eassa, 1955), the flexibility of the endocuticle permits these changes in shape. Burgess (1880a, 1880b), Snodgrass (1935), Schmitt (1938), Portier (1949) and Bourgogne (1951) similarly regard the "membranes" in the proboscis of Lepidoptera as providing suppleness and allowing coiling. The flexibility of the endocuticle, espe-

cially between the exocuticular ribs, is well seen when sagittal sections of the galeae in the coiled and extended conditions are compared. In the coiled position of the proboscis the endocuticle is reflected inward into transverse endocuticular folds (fig. 32A, enc.fld) between the exocuticular ribs, especially on the posteroventral walls of the intermediate regions of the galeae. These folds are smoothed out when the proboscis is fully uncoiled (fig. 33A), thus demonstrating the ability of the cuticle to accommodate itself to movements of the proboscis in the vertical plane, as was already pointed out by Eastham and Eassa (1955) in Pieris.

Some exocuticular ribs superficially bear spherical, exocuticular galeal sensilla (fig. 36, gl.sens) which are each provided with a very short, central, spine-like sensory seta (figs. 24-33, 37 & 41, sens.se) whose function may be tactile, as it is always brought in direct contact with any food source. Burgess (1880b), Kirbach (1884), Eastham and Eassa (1955) and Srivastava (1957) report similar sensilla for the Lepidoptera studied by them. In Pieris, however, Eastham and Eassa (1955) depict these sensilla as occurring in the endocuticle between the exocuticular ribs, while in Papilio (Srivastava, 1957) these sensilla are unsclerotized.

The concave mesal (inner) wall of the intermediate region of the galea varies in thickness from approximately 15μ to 41μ and is therefore in general more rigid than the outer wall. It is, like the mesal wall of the apical region of the galea, composed of a large series of regularly arranged, nearly contiguous, rigid, transverse exocuticular bars (figs. 37-39, 7, 17, 24-28 & 41, exc.bar) which impart a ribbed

appearance to the walls of the food channel. Each exocuticular bar is always more or less directly opposite a counterpart in the other galea. In thickness and width the exocuticular bars vary only from approximately $12/\mu$ to $18/\mu$ and from approximately $2/\mu$ to $3/\mu$, respectively, being therefore fairly uniform in structure. Internally they are underlain by an uninterrupted layer of endocuticle of varying thickness which is dorsally and ventrally continuous with the endocuticle of the outer wall (figs. 24-28).

Under high magnification and with the aid of phase contrast microscopy it is possible to ascertain that these exocuticular bars consist of regularly arranged, closely packed laminae (figs. 37A & 37-39, 1am), similar to those described by Eastham and Eassa (1955) in Pieris. The long axes of the laminae are parallel to those of the exocuticular bars. Neighbouring exocuticular bars (fig. 37A, exc.bar) are intermittently connected by laminae which extend obliquely forward from one bar to the other (figs. 37A & 37-39).

The ability of the walls of the food channel to adapt themselves to the changes undergone during coiling and extension of the proboscis, and the fact that the proboscis is only capable of vertical displacement during these movements, are attributable to the absolutely regular arrangement of the laminae, as Eastham and Eassa (1955) also pointed out in Pieris. In agreement with them, the present author believes that an attempted lateral bending of the proboscis to one side will put the laminae of the galea on that side into a state of compression, and those of the galea on the opposite side into a state of tension. The latter therefore resist and even prevent such a lateral bending

force and tend to keep the proboscis in the vertical plane. The ribbed structure of the mesal walls of the intermediate and apical regions of the galeae therefore allows, but restricts, free coiling and extension movements of the proboscis to the vertical plane and ensures that a circular transverse section of the food channel is maintained in both the coiled and extended conditions of the proboscis.

The exocuticular bars are associated dorsally and ventrally with the structures which link the two galeae together. Dorsally each bar is continued (fig. 38) to form a plate (plt), while ventrally every three bars apparently become fused (fig. 39) to form a process which bears an upper tooth (th) and a lower hook (hk), as will be described subsequently in detail. In this respect S. partita differs from Pieris (Eastham & Eassa, 1955) and Papilio (Vasudeva, 1957) where the structures forming the dorsal linking mechanism are attached to the dorsal bars and where alternate exocuticular bars end ventrally in a swelling, to which a toothed hook of the ventral linking mechanism is articulated. At the galeal bases and galeal tips of S. partita, where the food channel is shaped like a dorsally open gutter, only the ventral linking structures are present and the exocuticular bars are incomplete, being only evident at the bases of these structures (figs. 22 & 23).

Dorsally, before the point where the structures forming the dorsal linking mechanism arise, the exocuticular bars of a galea in S. partita apparently all independently become partly fused to form a continuous elastic, exocuticular, longitudinal, rod-like dorsal bar (figs. 24-28 & 37, d.bar). These dorsal bars are basally fused with

the exocuticular dorsomesal walls of the galeal bases and are continued distally into the apical regions of the galeae to the point where the dorsal linking ends and where they are fused with the exocuticle of the outer walls of these regions. The specific manner in which the dorsal bars are formed in S. partita by the partial and independent fusion of the exocuticular bars, differs from that in Pieris where Eastham and Eassa (1955) found that the exocuticular bars "become fused in pairs, neighbouring larger sections again fusing together so as to form themselves eventually into the dorsal continuous bar." Eastham and Eassa (1955) established that in Pieris the elastic properties on which the ability of the proboscis to come to the coiled position of rest depends, rest in these dorsal bars. This fact is confirmed by the results obtained in the present study, as will be described subsequently when the mechanism of extension and coiling of the proboscis is discussed. Although Kirbach (1884) and Pradhan and Aren (1941) attribute coiling of the lepidopterous proboscis partly to elasticity, while Burgess (1880a) and Bourgogne (1951) incorrectly attribute extension of the lepidopterous proboscis to elasticity, none of these authors attempted to discover in which part of the proboscis the elastic properties reside.

Apical region of the galea

This region is proximally continuous with the intermediate region of the galea and constitutes the short, most distal portion of the galea which tapers to a closed, sharply pointed tip.

As in the case of the galeal base, the outer wall of the apical

region of the galea also lacks the exocuticular ribs (exc.rb) which are characteristic of the outer wall of the intermediate region. Externally the apical region can be distinguished from the intermediate region by the absence of the exocuticular ribs and the presence of modified galeal blades (gl.bld) and galeal spines (gl.sp), whereas internally the galeal septum (gl.spt) ends at the boundary between these two regions. The outer wall of the apical region of the galea is indented and is composed of an external layer of exocuticle (figs. 34 & 35, exc), underlain internally by a layer of endocuticle (figs. 34 & 35, enc) which varies in thickness from approximately 5μ to 11μ . The exocuticle varies in thickness from approximately 3μ , at the bases of the galeal spines, to approximately 95μ , at the extreme, strongly reinforced tips (fig. 35) of the apical region where endocuticle is absent.

The concave mesal wall of this region of the galea is similar to that of the intermediate region, being composed internally of endocuticle (enc) and externally of exocuticular bars (exc.bar), except for their extreme tips where the structures forming the dorsal and ventral linking mechanisms are also absent.

Lateral to the dorsal linking mechanism the outer wall of the apical region of the galea is covered externally with relatively long galeal hairs (figs. 2 & 9, gl.hr). Externally the proximal half of the outer wall bears an apparently even number of from 40 to 60 irregularly spaced, involuntarily moveable, hollow, exocuticular, lanceolate galeal blades (figs. 9, 34 & 2, gl.bld) which vary in length from 70μ to 160μ . On its distal half the outer wall externally bears an

apparently even number of from 26 to 30 sturdy, regularly placed, solid, exocuticular, thorn-like, proximally directed galeal spines (figs. 9, 34, 35 & 2, gl.sp) which impart a barbed appearance to the apex. These galeal spines vary in length from 30μ to 48μ and are situated in oval indentations of the outer wall of the apical region. As will be described in more detail later on, the galeal spines are utilised for the laceration of the cells of the fruit flesh for releasing the fruit juice on which S. partita feeds — a function which they can accomplish only when they are in an elevated position. Although they are not voluntarily moveable, being devoid of muscles, and are held flush against the outer walls of the apical regions when the proboscis is in the coiled position of rest, it was experimentally established that they are definitely elevated during feeding when the proboscis is in the extended position. When pressure is experimentally exerted on a galea at the proximal end of its apical region, by means of a pair of forceps, a haemolymph pressure is produced within the haemocoeles of the apical region which causes the evagination of the oval indentations and a subsequent elevation of the galeal spines. As will be shown when the mechanism of extension and coiling of the proboscis is described, a haemolymph pressure prevails within the galeal haemocoeles when the proboscis is in the extended position of feeding and it may therefore be inferred that the galeal spines are then definitely in the elevated position.

The modified, strongly reinforced and sharply pointed tips of the apical regions of the galeae doubtlessly enable S. partita to pierce the intact skin and flesh of many sound stone, deciduous and tropical

fruit, especially canning peaches and apricots on which this moth is a pest of economic importance in the Republic of South Africa. The cells of the fruit flesh are definitely lacerated by means of the galeal spines and to some extent by means of the galeal blades. The sturdy galeal spines are, however, the principal lacerating agents of the intact cells of the sound fruit flesh because they are rigid and elevated when the proboscis is in the extended position of feeding. They are therefore more efficient than the galeal blades, which are more mobile and which are apparently only capable of further breaking up of cells already damaged by the galeal spines. To effect the process of laceration, after insertion of the proboscis into the fruit flesh, intermittent poking movements of the proboscis are performed during the entire process of feeding. Fruit juice, and perhaps minute cell-particles, so released are then imbibed through the food channel by means of a suction power which is created within the sucking pump, as will be discussed in detail when the sucking pump is described.

Although Jack (1922) published photographs of the galeae of several fruit-piercing or fruit-sucking noctuid species, including S. partita which according to him possesses a "modified" proboscis, he does not elaborate on the structure of the galeae. Taylor (1957) notes "bristle-like setae" and stouter "teeth" on the strong and pointed tip of the proboscis in S. partita. He did not illustrate the proboscis, but the "bristle-like setae" probably represent the galeal blades of the present author and the "teeth" probably represent the galeal spines. Neubecker (1966) also published a photograph of the apical part of a galea of S. partita, possessing what he regards as a

"verstärkte Rüsselspitze." The "Widerhaken" mentioned by him definitely represent the galeal spines of the present author.

Comparative anatomical studies were also undertaken by the present author on the proboscides of other species of the fruit-piercing or fruit-sucking moth complex possessing "modified" (or "strengthened") proboscides and on some possessing "unmodified" (or "unstrengthened") proboscides (as they were classified by Jack (1922)). It was found that the only anatomical differences between these two groups are that the galeal apices of species with modified proboscides bear galeal spines and galeal blades and have strong, sharply pointed tips, whereas the galeal apices of species with "unmodified" proboscides lack galeal spines, but bear galeal blades and have weaker, more rounded tips.

Bot (1967) suggests that the term "fruit-sucking moths" should be used for and restricted to those species which are responsible for secondary fruit damage. For the other species which are responsible for primary fruit damage, he proposes the term "fruit-piercing moths." It would be logical to infer that those species responsible for secondary fruit damage (i.e. species which should only be able to attack damaged fruit and which should only be capable of piercing fruit of which the skin and flesh are already broken) should be those with "unmodified" proboscides. They possess galeal blades for further breaking up of already damaged fruit cells and have weak, rounded galeal tips which render them incapable of piercing hard tissue. Those species responsible for primary fruit damage (i.e. species which are able to attack sound fruit and which are capable of piercing the intact skin

and flesh of fruit) should be those with "modified" proboscides. They possess galeal spines for initially lacerating the intact fruit cells, in addition to the galeal blades which are capable of further breaking up of cells already damaged by the galeal spines. Their proboscides also have strong, sharply pointed tips which enable them to pierce harder tissues. Personally communicated information, however, suggests that certain species which the present author found to have "unmodified" proboscides are also capable of causing primary damage. If this information is correct, it may then be assumed that some of the species with "unmodified" proboscides would be capable of causing primary damage on certain fruit, depending probably on the penetrability of the fruit skin and flesh, which may be determined by the ripeness of the fruit. Classifying these moths into a "fruit-sucking moth" group which is responsible for secondary fruit damage and a "fruit-piercing moth" group which is responsible for primary fruit damage as Bot (1967) proposes, will thus be of little value. The term "fruit-sucking moths" also seems inappropriate as these moths do not suck the fruit, but only the fruit juice! However, all of them pierce the skin and flesh of the fruit which they attack, and the present author therefore feels that the term "fruit-sucking moths" should be discarded in favour of the term "fruit-piercing moths", which should then include all the species of the complex. The only satisfactory classification of the fruit-piercing moth complex would seem to be a division into species with "modified" proboscides and species with "unmodified" proboscides.

Linking mechanisms of the galea

The two galeae are firmly linked together, to form the suctorial

proboscis, by a dorsal and a ventral linking mechanism.

The dorsal linkage is uncomplicated, less firm and less rigid than the ventral linkage. It is brought about by a series of narrow, oblique, distally directed, contiguous, exocuticular plates (figs. 38, 24-28, 7 & 8, plt). Each plate apparently is a continuation of an exocuticular bar (figs. 24-28) of the median wall of the galea, as has already been described. The arrangement of the plates in the galea of S. partita differs from that described in Pieris by Eastham and Eassa (1955) in that they do not partly "overlap each other like the tiles on a roof", but are only flush against each other along their sides (fig. 38). In the proboscis the plates of one galea overlap those of the other galea (figs. 38 & 24-28), and in doing so they effectively close the food channel dorsally, except in the proximal parts of the galeal bases and extreme distal parts of the apical regions of the galeae. Here the plates are absent because the exocuticular bars are incomplete, as has already been described, and the food channel in these parts is shaped like a dorsally open gutter. As may be seen in figure 38, the plates of S. partita are directed obliquely forward in such a way that every plate of one galea overlap, or are overlapped by, three plates of the other galea.

The ventral linkage is more complicated, firmer and more rigid than the dorsal linkage. It is brought about by a series of very rigid, oblique, distally directed, contiguous, exocuticular processes which each bears a curved upper tooth (figs. 39, 22-28, 8 & 42, th) and a larger, curved, lower hook (figs. 39, 22-28, 7, 8 & 42, hk). In the proboscis the teeth and hooks ventrally close the entire food

channel, except at the extreme tip of the proboscis. The teeth and hooks of the two galeae closely interlock in such a way that the free ends of the teeth of one galea fit into the recesses between the teeth and the hooks of the other galea, whereas the free ends of the hooks of the latter galea again fit into the recesses between the teeth and hooks of the former galea (figs. 24-28). As may be seen in figure 39, the tooth and hook bearing processes, forming the ventral linking structures, are directed obliquely forward in such a way that every process of one galea interlocks with three processes of the other galea. The ventral interlocking mechanism is then such that every tooth of a galea is associated with a tooth directly opposite it on the other galea, but the free end of every hook of a galea is associated with the base of a hook immediately anterior to it in the other galea.

It is evident from the foregoing that the two galeae are kept in relatively rigid adherence because of the interlocking of the teeth and hooks. The firmness of the ventral linkage is doubtlessly also augmented by the rigidity of the exocuticular bars of the mesal walls of the galeae. The dorsal linkage is not of an interlocking nature and is much looser than the ventral linkage. However, the overlapping of the plates of one galea with those of the other, and the fact that the teeth and hooks of the two galeae always remain interlocked, ensure that the roof of the food channel stays closed during all changes in attitude of the proboscis.

Because the overlapping plates and interlocking teeth and hooks are directed obliquely forward, the sliding movements of the proboscis as a whole are permitted, without the food channel being unsealed. As

the proboscis is coiled when at rest, its posteroventral (concave when coiled) surface is stretched, while its anterodorsal (convex when coiled) surface is compressed when it is extended. When the proboscis is again being coiled, the reverse processes take place. The difference in the structure of the dorsal and ventral linking mechanisms of the lepidopterous proboscis partly depends on these facts, as were already pointed out by Eastham and Eassa (1955) in Pieris.

Galeal septum

In S. partita the haemocoel of the intermediate region of the galea is divided by a vertical, longitudinal galeal septum (figs. 24-28, gl.spt), which obviously corresponds to the ventral longitudinal septum described by Eastham and Eassa (1955) in Pieris, into a large outer galeal chamber (figs. 24-28, ot.gl.chm) and a smaller inner galeal chamber (figs. 24-28, in.gl.chm). This septum, which bears the galeal trachea, is a continuation of the hypodermis (the latter is not illustrated because of its scantiness). Towards the distal ends of the intermediate regions of the galeae the galeal septa become narrower, and the inner galeal chambers smaller.

The galeal septa apparently retain constant dimensions, regardless of whether the proboscis is coiled or extended. It may therefore be assumed fairly certainly that the galeal septa to some extent control the movements and determine the shape of the flexible outer walls of the intermediate regions of the galeae, relatively to the fixed mesal walls. These movements are brought about by the action of the primary oblique galeal muscles (prm.obl.gl.m), as will be described

when the mechanism of extension and coiling of the proboscis is discussed. Eastham and Eassa (1955) came to similar conclusions regarding the internal galeal septa in Pieris which they, however, probably erroneously describe as consisting of "thin inturnings of the cuticular walls of the galea."

In Pieris Eastham and Eassa (1955) also found a dorsal longitudinal septum which bears the galeal trachea, but a corresponding septum is completely absent in S. partita. Vasudeva (1957), but not Srivastava (1957), illustrates and describes, but does not name, similar septa in the galea of Papilio.

Galeal trachea

The galeal trachea (figs. 21-31, 41 & 42, gl.tr) enters the maxilla at the fusion of the posterolateral angle of the galeal base with the anterior margin of the stipes. Its passage is shielded by the valvular fold (fig. 29, vlv.fld) of the galeal base and it is here protected against compression, during movement of the proboscis, by the stipital apodeme (fig. 22, st.apd) which here partially embraces it, as has already been described.

The galeal trachea is continued in the galeal haemocoel almost up to its tip and gradually diminishes in diameter. In the galeal base it lies free in the galeal haemocoel (fig. 23, gl.hmc), but in the intermediate region of the galea it lies within the galeal septum (figs. 24-28, gl.spt). In the apical region of the galea it again lies free in the haemocoel.

As will become clear later, the extension of the proboscis, for

which the contraction of the primary oblique galeal muscles is a necessity, implies a condition of tension across the vertical axis of the galeal septa. The cuticular walls of the galeal tracheae, embedded in the galeal septa, are exceptionally thick and probably resist the external pressure to which they are subjected during contraction of the primary oblique galeal muscles. Eastham and Eassa (1955) ascribe a similar function to the thick walls of the galeal tracheae in Pieris.

Galeal nerve

The galeal nerve (figs. 16, 21-31, 41 & 42, gl.n), which innervates the extrinsic and intrinsic maxillary muscles, arises from the anteroventral surface of the suboesophageal ganglion (fig. 16, soes.gng), anterodorsal to a labial nerve. It runs forward and passes into the maxilla at the point where the posterolateral angle of the galeal base is fused to the anterior margin of the stipes. As with the galeal trachea, its entrance into the galeal haemocoel is shielded by the valvular fold (fig. 29, vlv.fld) of the galeal base and it is here protected against compression, during movement of the proboscis, by the stipital apodeme (fig. 22, st.apd) which here supports it, as has already been described.

The nerve is continued into the galeal haemocoel, but terminates before the galeal trachea. In the galeal base (fig. 23) it is situated lateral to the galeal trachea, but in the intermediate region of the galea it gradually shifts to the ventral side of the galeal trachea and is then located in the outer galeal chamber (figs. 24-28, ot.

gl.chm).

Trichoid sensilla of the galea

From four to seven modified trichoid sensilla (fig. 40) are present on the mesal wall of the intermediate region of each galea. Two sensilla normally occur fairly close together on the proximal part of the intermediate region of the galea, while the remaining sensilla are irregularly spaced on the distal part of this region. Similar sensilla were observed by Kirbach (1884) in the Lepidoptera studied by him, and Eastham and Eassa (1955) found two on each galea in Pieris.

These trichoid sensilla are located at the junction of the galeal septum (fig. 40, gl.spt) with the mesal wall of the intermediate region of the galea. Each consists of a central sense cell extension (fig. 40, sn.cl.ext) which is surrounded by a cylindrical hypodermal sheath (fig. 40, hpd.sht) which perforates the exocuticular bars (fig. 40, exc.bar) of the mesal wall of the intermediate region of the galea. The sense cell within the hypodermal sheath is connected to a trichium (fig. 40, trhm) which projects into the food channel. Eastham and Eassa (1955) state that these sensilla are apparently not concerned with proboscis movements in Pieris and that their function is uncertain. The present author, however, believes that in S. partita they may serve as chemoreceptors, and are perhaps gustatory in function, as they definitely come in contact with all imbibed food.

d. Labium and labial palps

In S. partita the labium (figs. 4, 5, 10, 30, 31 & 42, 1b) is T-

shaped and can be distinguished from bordering cranial areas by its degree of sclerotization. It is immovably fixed in the ventral cranial region with its "stem" directed anteroposteriorly and its "beam" transversely. The narrow, elongated, trough-shaped (in transverse section, fig. 42) "stem" is anteriorly triangularly broadened (fig. 10) and is here attached to the anterior margin of the hypopharyngeal part of the floor of the sucking pump by means of flexible endocuticle. The lateral margins of the "stem" and the anterior margins of the relatively broad "beam" are connected to the ventral cranial membranes which separate the labium from the stipites and cardines. The anterolateral angles of the "beam" are in contact with the posteromesal angles of the cardines, while its lateral margins are connected to the posteroventral parts of the postgenae. Its posterior edge borders on the neuraforamen as a "hypostomal bridge" is absent in S. partita, as has already been described.

The large, three-segmented labial palps (figs. 1, 2, 5 & 10, 1b. plp) are similar in both sexes, being membranously attached (fig. 4, att.1b.plp) to the "beam" of the labium near its anterior margin. From here they project forward and upward, being normally applied closely to the anterior surface of the head on either side of the proboscis. All the segments of the labial palps are cylindrical and are connected to each other by membrane. The well-developed, thick basal segment of each palpus is ovally compressed basally. The second segment is larger and longer than the basal segment, while the much more slender terminal segment is shorter than the second segment, but longer than the basal segment. Internally on its distal end the terminal

segment bears an apical sensory pit (figs. 1 & 2, sens.pt), similar to that described by Madden (1944) in Protoparce and by Vasudeva (1957) in Papilio. Philpott (1926) erroneously describes apparently similar organs in the terminal segment in Trichophysetis as "Johnston's organs." Medium-length, narrow scales densely cover the first and second labial palp segments in S. partita, the third being sparsely covered with thin, medium-length hairs.

The labial palps are each provided with a labial nerve (fig. 16, lb.n) which arises from the ventral surface of the suboesophageal ganglion (fig. 16, soes.gng), posteroventral to a galeal nerve.

V. MUSCULATURE OF THE CRANIUM AND ITS APPENDAGES

In the present study a positional and functional nomenclature for the muscles was adopted, i.e. they were named according to their origins and insertions, combined wherever possible or ascertainable, with a reference to their functions. This involved partial adoption of some terminologies used by Schmitt (1938), Short (1951), Eastham and Eassa (1955), Srivastava (1957), Vasudeva (1957) and Eassa (1963a), or combinations or modifications thereof. Some are newly introduced.

A. Antennal Muscles

a. Extrinsic antennal muscles

In S. partita the antennae are each provided with four, relatively long extrinsic muscles. The same number was found in Papilio by Srivastava (1957) and Vasudeva (1957), and in Danaus by Ehrlich and Davidson (1961). These muscles are spindle-shaped, being greater in diameter at their origins than at their insertions where they are tendonous.

(i) Anterior tentorio-antennal depressor muscle (figs. 14-17, a.tnt. ant.dep.m). This muscle originates dorsally on the posterior slope of the dorsal flange of the anterior tentorial arm, anterior to the posterior tentorio-antennal depressor muscle. It extends anterodorsally and is inserted on the anterior aspect of the base of the scape. By its contraction the antenna is depressed in the vertical plane.

(ii) Posterior tentorio-antennal depressor muscle (figs. 14-17, p.tnt.

ant.dep.m). It originates dorsally on the anterior tentorial arm, posterior to the anterior tentorio-antennal depressor muscle. It extends anterodorsally and mesally and is inserted on the anteromesal aspect of the base of the scape. By its contraction the antenna is primarily depressed, but towards the median line.

(iii) Anterior tentorio-antennal levator muscle (figs. 14-17, a.tnt. ant.lev.m). It originates dorsally on the anterior tentorial arm, posterolateral to the posterior tentorio-antennal depressor muscle. It extends anterodorsally and laterally and is inserted on the posterolateral aspect of the base of the scape. By its contraction the antenna is primarily elevated, but in an outward direction.

(iv) Posterior tentorio-antennal levator muscle (figs. 14-17, p.tnt. ant.lev.m). This muscle originates dorsally on the anterior tentorial arm, posteromesal to the anterior tentorio-antennal levator muscle. It extends anterodorsally and is inserted on the posterior aspect of the base of the scape. By its contraction the antenna is elevated in the vertical plane.

b. Intrinsic antennal muscles

In S. partita the scape is virtually filled with muscle fibres and the two separate muscles, the fibres of which converge from their origins to their insertions, can barely be discerned.

(i) Scape-pedicel depressor muscle (fig. 17, scp.pde.dep.m). Originating on the anterolateral, anterior and anteromesal wall of the scape,

this muscle is inserted on the anterior and anteromesal aspect of the base of the pedicel. By its contraction the pedicel and flagellum are depressed.

(ii) Scape-pedicel levator muscle (fig. 17, scp.pde.lev.m). It is smaller than the scape-pedicel depressor muscle and, originating on the posterolateral, posterior and posteromesal wall of the scape, it is inserted on the posterior and posterolateral aspect of the base of the pedicel. By its contraction the pedicel and flagellum are elevated.

B. Trophial Muscles

1. Maxillary muscles

a. Extrinsic maxillary muscles

In S. partita the maxillae are each provided with four extrinsic muscles.

(i) Geno-stipital adductor muscle (figs. 14, 17 & 13, ge.st.add.m). This muscle is very large and fan-shaped. Schmitt (1938) drew attention to the remarkable size of the corresponding muscle in the noctuid Catocala nubilis and pointed out that this is interesting in view of the fact that this is the muscle most frequently absent in instances where there is not a full compliment of maxillary muscles. Originating on the facial part of the gena along the laterofacial ridge, and occupying a narrow area between the mandible and the antennal socket, this muscle runs laterally of the anterior part of the anterior tento-

rial arm and is inserted on the stipital apodeme.

The geno-stipital adductor muscle of S. partita corresponds to that muscle termed the "cranial adductor muscle of the stipes" by Eastham and Eassa (1955) and Eassa (1963a) in Pieris, the "cranial adductor" by Vasudeva (1957) in Papilio, and the "cranial proboscis extensor" by Schmitt (1938) in the Lepidoptera studied by him. It apparently also corresponds to the "geno-stipital muscle" described by Srivastava (1957) in Papilio, and to that muscle numbered 5 by Ehrlich and Davidson (1961) and Ehrlich and Ehrlich (1962) in the Lepidoptera studied by them.

(ii) Anterior tentorio-stipital adductor muscle (figs. 15, 17 & 13, a.tnt.st.add.m). This broad, flat muscle originates mesally on the anterior half of the anterior tentorial arm and also on the dorsal flange of the latter. It then extends ventroposteriorly and is inserted lateral to the posterior tentorio-stipital adductor muscle on the stipital apodeme.

The anterior tentorio-stipital adductor muscle of S. partita corresponds to that muscle termed the "anterior tentorial stipital adductor muscle" by Eastham and Eassa (1955) in Pieris, the "anterior tentorial adductor of the stipes" by Eassa (1963a) in the same insect, the "anterior tentorial stipital adductor" by Vasudeva (1957) in Papilio, and the "anterior tentorial proboscis extensor" by Schmitt (1938) in the Lepidoptera studied by him. It apparently also corresponds to the "tentorio-juxtastipital muscle" described by Srivastava (1957) in Papilio, and to that muscle numbered 3 by Ehrlich and Davidson (1961)

and Ehrlich and Ehrlich (1962) in the Lepidoptera studied by them. It is, however, by no means certain which muscle of Scirpophaga (Pradhan & Aren, 1941) corresponds to the anterior tentorio-stipital adductor muscle of S. partita.

(iii) Posterior tentorio-stipital adductor muscle (figs. 14, 15 & 17, p.tnt.st.add.m). This broad, flat muscle originates mesally on the posterior half of the anterior tentorial arm. It extends anteroventrally and is inserted mesal to the anterior tentorio-stipital adductor muscle on the stipital apodeme and therefore crosses this muscle.

The posterior tentorio-stipital adductor muscle of S. partita corresponds to that muscle termed the "posterior tentorial stipital adductor muscle" by Eastham and Eassa (1955) in Pieris, the "posterior tentorial adductor of the stipes" by Eassa (1963a) in the same pierid, the "posterior tentorial stipital adductor" by Vasudeva (1955) in Papilio, and the "posterior tentorial proboscis extensor" by Schmitt (1938) in the Lepidoptera studied by him. This muscle apparently also corresponds to the "dilateurs du pharynx 3" described by Portier (1949), the "tentorio-cardinal muscle" described by Srivastava (1957) in Papilio, and to that muscle numbered 4 by Ehrlich and Davidson (1961) and Ehrlich and Ehrlich (1962) in the Lepidoptera studied by them. It is not certain what muscle in the Scirpophaga sp. studied by Pradhan and Aren (1941) corresponds to the posterior tentorio-stipital adductor muscle of S. partita.

By their contraction the geno-stipital adductor muscles and anterior and posterior tentorio-stipital adductor muscles draw the stipital

apodemes and parts of the so-called verastipites against the stipital valves, thus closing the stipital apertures between the stipital haemocoels and cranial cavity and disrupting the connection between the haemolymph contained in the stipital and the galeal haemocoels and that contained in the cranial cavity, as may be visualised from figures 20 and 21. This action is permitted by the flexible endocuticular stipital grooves (st.grv) between the so-called verastipites and palpi. Eastham and Eassa (1955) attribute a similar function to the contraction of corresponding muscles in Pieris. Schmitt (1938) also believes that contraction of corresponding muscles in the Lepidoptera studied by him closes the stipital valves, but that by their further contraction the volumes of the stipital haemocoels are reduced and haemolymph is then forced from the stipital haemocoels into the galeal haemocoels, thus causing extension of the proboscis by inflation. Imms (1942) again believes that contraction of corresponding muscles reduces the volume of the cranial cavity, thus forcing haemolymph from the latter through the stipital valves, via the stipital haemocoels, into the galeal haemocoels and in this way effect proboscis extension by inflation. It will later be shown that the views of Schmitt (1938) and Imms (1942) are incorrect.

(iv) Tentorio-galeal retractor muscle (figs. 16, 17, 19-21, 29-31 & 41, tnt.gl.ret.m). This strongly developed muscle extends horizontally in the anteroposterior cranial axis alongside its opposite number and is supported ventrally by the ventral cranial membrane. It originates on the posterior cup-shaped termination of the anterior tentorial

arm and is inserted on the galeal base, mesal to the junction of the latter with the stipes.

As in the case of corresponding muscles in Pieris (Eastham & Eassa, 1955), the tentorio-galeal retractor muscles by their contraction draw the bases of the galeae backward and upward as a preliminary to feeding. Thus the food channel, which is shaped like a dorsally open gutter between the galeal bases, is brought into effective relation with the functional mouth (func.mth), anteriorly in the cibarial region of the sucking pump. The size of the food meatus (f.mts) is therefore in effect reduced, as is evident from a comparison between figures 30 and 31. When these muscles are contracted, alternate partial relaxation causes the slight sideways movements executed by the extended proboscis in the horizontal plane when S. partita senses a food source.

The tentorio-galeal retractor muscle of S. partita corresponds to that muscle termed the "retractor muscle of the galea" by Eastham and Eassa (1955) in Pieris, and the "retractor of the galea" by Vasudeva (1957) in Papilio. It may also correspond to the "first tentorio-stipital muscle" described by Srivastava (1957) in Papilio and to the "compresseurs 1" described by Portier (1949). In other works consulted a similar muscle is not mentioned or named, or it is uncertain to which of the muscles described the tentorio-galeal retractor muscle of S. partita corresponds, or the extrinsic muscles of the maxillae are treated collectively.

b. Intrinsic maxillary muscles

Five separate intrinsic muscles are present in each galea in S.

partita.

(i) Posterior basal galeal levator muscle (figs. 23, 29-31, 41 & 42, p.bs.gl.lev.m). This muscle is confined, together with the anterior basal galeal levator muscle, to the haemocoele of the galeal base. Originating lateral to the anterior basal galeal levator muscle on the posterior wall of the galeal base, mesal and anterior to the latter's junction with the stipes, this muscle extends anterodorsally and is inserted on the dorsal wall of the galeal base near its distal end, posterior to the anterior basal galeal levator muscle.

The posterior basal galeal levator muscle of S. partita corresponds to that muscle termed the "dorsal or proximal elevator muscle of the galea base" by Eastham and Eassa (1955) in Pieris, and the "dorsal levator of the galea base" by Vasudeva (1957) in Papilio. It may also correspond to the muscle named the "stipito-galeal muscle" by Srivastava (1957) in Papilio, although the function ascribed to this muscle in Papilio is performed by the tentorio-galeal retractor muscle in S. partita.

(ii) Anterior basal galeal levator muscle (figs. 23, 29-31, 41 & 42, a.bs.gl.lev.m). This muscle is confined, together with the posterior basal galeal levator muscle, to the haemocoele of the galeal base. Originating mesal to the posterior basal galeal levator muscle on the posterior wall of the galeal base, mesal and anterior to the latter's junction with the stipes, this muscle extends anterodorsally and is inserted on the dorsal wall of the galeal base at its distal end, anterior to the posterior basal galeal levator muscle. As has already been

noted, the insertions of the anterior basal galeal levator muscles to some extent indicate internally the distal limits of the galeal bases.

The anterior basal galeal levator muscle of S. partita corresponds to that muscle termed the "ventral or distal elevator muscle of the galea base" by Eastham and Eassa (1955) in Pieris, and the "ventral levator of the galea base" by Vasudeva (1957) in Papilio.

By contraction of the posterior and anterior basal galeal levator muscles the proximal regions of the galeae are elevated as a preliminary to proboscis extension. The action of these muscles is permitted by the intermediate zone of flexible endocuticle (enc_1) of the walls of the galeal bases and by their particular disposition in the galeal bases. As may be seen in figure 30, which depicts a sagittal section through the cranium with the proboscis in the coiled position of rest and with relaxed posterior and anterior basal galeal levator muscles, the ventral wall of the zone of endocuticle of the galeal base is more folded transversely than the dorsal wall. When these muscles are, however, contracted and the proboscis is in the extended position of feeding, the dorsal wall of the zone of endocuticle of the galeal base is now more folded transversely than the ventral wall (fig. 31). The elevation of the galeal bases are therefore dependent upon the fact that their dorsal walls are pulled backward and their ventral walls are pushed forward by the contraction of the posterior and anterior basal galeal levator muscles. Eastham and Eassa (1955) ascribe a similar function to the contraction of corresponding muscles in Pieris.

Muscles apparently corresponding to either or both the posterior and anterior basal galeal levator muscles of S. partita is described

by Burgess (1880a) in Danaus, but he believes that by their contraction the entire proboscis is pulled closely up under the head. Schmitt (1938) is of the same opinion. These views of Burgess and Schmitt, however, embody a physical impossibility, viz. that these muscles are in a state of contraction when the proboscis is in the coiled position of rest. Kirbach (1884) describes muscles in the bases of the galeae in Vanessa as the "Basalmuskeln" and he apparently partly attributes the uncoiling of the proboscis to the contraction of these muscles. Pradhan and Aren (1941) and Eassa (1963a) also collectively name the muscles in the bases of the galeae in Scirpophaga and Pieris, respectively, the "basal muscles." According to Pradhan and Aren (1941) contraction of these muscles bring about the uncoiling of the very short proboscis in Scirpophaga.

(iii) Proximal galeal levator muscle (figs. 24, 29-34 & 41, px.gl.lev. m). This muscle is present in the most proximal part of the outer galeal chamber of the intermediate or coilable region of the galea, distal to the anterior basal galeal levator muscle. Originating on the ventral wall of the distal end of the galeal base, this muscle extends somewhat anterolaterally towards the dorsolateral wall of the proximal end of the intermediate region of the galea where it is inserted.

By their contraction the proximal galeal levator muscles elevate the most proximal parts of the intermediate regions of the galeae by pulling the hindmost parts of the dorsal walls of these regions backward. Their action is also responsible for the small movements made by the proboscis when it is beginning to be elevated or coiled. East-

ham and Eassa (1955) ascribe a similar function to the contraction of corresponding muscles in Pieris.

The proximal galeal levator muscle of S. partita corresponds to that muscle termed the "proximal elevator muscle of the proboscis" by Eastham and Eassa (1955) in Pieris, and the "proximal levator of the proboscis" by Vasudeva (1957) in Papilio. It is not certain whether the proximal galeal levator muscle of S. partita corresponds to the "intra-galeal muscle" described by Srivastava (1957) in Papilio as his illustration is indistinct.

(iv) Primary oblique galeal muscle (figs. 25-34 & 41, prm.obl.gl.m). The fibres of this muscle (oblique or diagonal intrinsic galeal muscles of authors) are present as a series in the galea, occupying the outer galeal chamber of the intermediate or coilable region, and are continued into the haemocoel of the apical region nearly to its tip. The fibres are not all contiguous with one another (figs. 32 & 33) and taper to their insertions which are always distal, ventral and mesal to their origins.

In the proximal half of the intermediate region of the galea the primary oblique galeal muscle fibres are longer, more numerous (fig. 25) and run a more longitudinal course (fig. 29). They originate here on the dorsal, dorsolateral and lateral parts of the outer wall and are respectively inserted distally on the ventromesal, ventral and ventrolateral parts of the outer wall. In the distal half of the intermediate region the muscle fibres become fewer (figs. 26 & 27) and shorter because their origins are more lateral and their insertions

further ventrolateral. They therefore have a more vertical course (fig. 28), becoming again more numerous in the apical region of the galea where the galeal septum is absent and where some fibres become transversely arranged so that the primary oblique galeal muscle fibres here run in both the dorsomesal and lateromesal directions.

When the proboscis is in the coiled position of rest the primary oblique galeal muscles are relaxed, each fibre roughly conforming to the curvature of the galeae (fig. 32). In the coiled position the intermediate and apical regions of the two galeae are nearly circular in transverse section (fig. 26) and for the entire length of these regions fit together in such a way that the dorsal surface of the proboscis is almost level (figs. 26 & 28). Ventrally, along the median line, there is, however, a deep, narrow groove where the ventral linkage between the two galeae occurs (figs. 26 & 28). When the proboscis is, however, in the extended position of feeding the primary oblique galeal muscles are contracted and the fibres straight (fig. 33). The intermediate and apical regions of the two galeae are now dorsoventrally flattened and for the entire length of these regions fit together in such a way that the dorsal surface of the proboscis is convex (figs. 25 & 27). The ventral groove is shallower and wider (figs. 25 & 27).

As Eastham and Eassa (1955) indicated for corresponding muscles in Pieris, the result of the contraction of the primary oblique galeal muscles in S. partita is therefore to pull the dorsal and ventral walls of the intermediate and apical regions of the galeae towards each other. In doing so they effect a change of form in the intermediate and apical regions of the galeae which is indicated by the transverse

dorsal convexity of the proboscis in its extended position of feeding. The outer walls of the intermediate and apical regions of the galeae are thrust outward, beyond the confines of the curvature which they assume in the coiled position of rest. This is clear when figure 26 is compared with figures 25 and 27.

It can be noted, as Eastham and Eassa (1955) showed for corresponding muscles in Pieris, that the primary oblique galeal muscles in S. partita exert, because of their particular dispositions (insertions of the fibres distal, ventral and mesal to their origins), three components of force at their insertions when they contract. These components are firstly, a horizontal longitudinal component of force (fig. 44, a1) which is directed along the length of the galeae towards the cranium and which tends to coil the galeae on the fixed point of the cranium. Secondly, a horizontal transverse component of force (fig. 44, b1) which is directed outward and which pulls across the proboscis against the fixed part of the ventral linkage of the two galeae. Thirdly, a vertical transverse component of force (fig. 44, c1) which is directed upward and which, by pulling upward on the ventromesal, ventral and ventrolateral parts of the outer walls of the intermediate and apical regions of the galeae, must pull the dorsal and ventral walls of these regions towards each other. In doing so the vertical transverse component of force (c1) operates counter to the horizontal longitudinal component of force (a1) which tends to coil the galeae. That this is so is because of the fact that the former component of force's effect (as will be shown when the mechanism of extension and coiling of the proboscis is described) is to bring about the change

of form in the proboscis which is responsible for its extension under conditions of haemocoelic turgidity, as Eastham and Eassa (1955) also found in Pieris.

In accordance with the assumption of Eastham and Eassa (1955) for corresponding muscles in Pieris, it is clear that by the contraction of the primary oblique galeal muscles in S. partita the outer walls of the intermediate and apical regions of the galeae are moved at both the points of insertion and origin of these muscles. Components of force corresponding to those at their insertions therefore exist at the origins of the primary oblique galeal muscles when they contract, but are directed oppositely. The components of force exerted at the origins are then firstly, a horizontal longitudinal component of force (fig. 44, a2) which is directed along the length of the galeae away from the cranium. It assists the corresponding component of force (a1) at the insertions in coiling the galeae by thrusting along the length of the elastic, exocuticular, longitudinal dorsal bars (in which lies the ability of the proboscis to come to the coiled position of rest), in the mesal walls of the intermediate or coilable and posterior parts of the apical regions of the galeae, already coiled when at rest. Secondly, a horizontal transverse component of force (fig. 44, b2) which is directed inward and which neutralizes the corresponding component of force (b1) at the insertions. Thirdly, a vertical transverse component of force (fig. 44, c2) which is directed downward and which, by pulling downward on the dorsal, dorsolateral and lateral parts of the outer walls of the intermediate and apical regions of the galeae, reinforces the effect of the corresponding component of force (c1) at

the insertions by pulling the dorsal and ventral walls of these regions towards each other.

The rigid form of the mesal walls of the intermediate and apical regions of the galeae (i.e. the greater part of the walls of the food channel) provides the fulcrum on which the horizontal transverse component of force (b1) at the insertions of the primary oblique galeal muscles can work. The dorsal bars, in the mesal walls of the intermediate and posterior parts of the apical regions of the galeae, assist the horizontal longitudinal components of force (a1 & a2) of the primary oblique galeal muscles at their insertions and origins in maintaining the coiled condition of the galeae. The exocuticular ribs in the outer walls of the intermediate regions of the galeae, being more or less circular when the proboscis is in the coiled position of rest, resist the vertical transverse components of force (c1 & c2) of the primary oblique galeal muscles at their insertions and origins. But, as Eastham and Eassa (1955) note in Pieris, the flexible endocuticle (in which the exocuticular ribs are embedded) of the intermediate regions of the galeae provides the means by which the galeae can accommodate themselves to those forces which tend to bend the exocuticular ribs and to bring the dorsal and ventral walls of these regions closer to each other. That the proboscis during extension undergoes this change of form, which is indicated by the transverse dorsal convexity of the intermediate and apical regions of the galeae, is clearly observable. It is also clear that this change is coupled with contraction of the primary oblique galeal muscles. The predominant effect of the described conflicting components of force, in relation to the pe-

culiar properties of the walls of the intermediate and apical regions of the galeae, is such that the vertical transverse components of force (c_1 & c_2), aided by the horizontal transverse components of force (b_1 & b_2), have a stronger effect than the resisting horizontal longitudinal components of force (a_1 & a_2). The formerly described change of form in the intermediate and apical regions of the galeae, when the proboscis is in the extended position of feeding, is therefore brought about by the contraction of the primary oblique galeal muscles, thus confirming the conclusions of Eastham and Eassa (1955) regarding the effect of the contraction of the corresponding muscles in Pieris.

The phenomenon that the primary oblique galeal muscle fibres are more numerous in the apical regions of the galeae, where some are almost directly dorsoventrally arranged, can be ascribed to the tapering of the galeae to strongly reinforced, exocuticular tips. Here the energy required to bring about the change of form in the galeae is relatively much greater. Eastham and Eassa (1955) account in a similar way for the increased strength of corresponding muscles in the galeal tips in Pieris.

When S. partita senses a food source, slight but rapid sideways and upward and downward twitching and searching movements of the apical regions of the galeae of the extended proboscis are executed in the horizontal and vertical planes. These movements of the proboscis apex are made possible by the discontinuity of the galeal septa in the haemocoel of the apical regions of the galeae, and in part also by the almost direct transverse and vertical directions in which the primary oblique galeal muscle fibres run. As the galeal septa are absent

they have no controlling influence on proboscis movement in these regions. Partial relaxation of the primary oblique galeal muscle fibres in the apical region of one galea, rapidly alternated by a similar relaxation in the other galea, may cause the above movements. Eastham and Eassa (1955) also attribute the upward coiling of the proboscis tip in Pieris, during feeding, to the discontinuity of the internal galeal septa and to the dorsoventral disposition of the primary oblique intrinsic muscles in the galeal tips.

The oblique or diagonal intrinsic galeal muscles are described by most authors, but the function of these muscles has not always been interpreted correctly, as will be described in detail when the mechanism of extension and coiling of the proboscis is discussed.

(v) Secondary oblique galeal muscle (fig. 26, sec.obl.gl.m). When S. partita extends its proboscis a dorsal curvature of about 110° to 150° is always maintained in the intermediate or coilable regions of the galeae at a point approximately one-third of the latter's length from the bases. This curvature represents the so-called "knee-bend" (figs. 46 & 47, k.b), a term introduced by Eastham and Eassa (1955) for a similar angle in the extended proboscis of Pieris.

The "knee-bend" covers a length of approximately 1.5 mm. in the extended proboscis and it is here that the short, slender secondary oblique galeal muscle fibres are found in the inner galeal chamber of the intermediate region of the galea. The exact number of the fibres could not be ascertained, but five to seven may be present in each galea. Eastham and Eassa (1955) found nine to ten similar muscles in each ga-

lea in Pieris. The secondary oblique galeal muscle fibres originate on the mesal wall of the intermediate region of the galea, immediately lateral to the ventral linkage at the junction between the outer and mesal (inner) walls of this region. The fibres extend distally and laterally from their origins and are inserted on the ventromesal part of the outer wall of the intermediate region of the galea, close to the galeal septum. The secondary oblique galeal muscle fibres are therefore arranged horizontally, forming "overlapping V's" with the primary oblique galeal muscle fibres.

By the contraction of the secondary oblique galeal muscles components of force are exerted at their insertions and origins which correspond to those forces exerted by the primary oblique galeal muscles at their insertions and origins. As Eastham and Eassa (1955) pointed out for corresponding muscles in Pieris, the forces of contraction of the secondary oblique galeal muscles will act diagonally and antagonistically to those of the primary oblique galeal muscles. Because of the horizontal disposition of the secondary oblique galeal muscles in the galeae, it is evident that their vertical transverse components of force (fig. 45, c3 & c4) are negligible at both their insertions and origins. Furthermore, the horizontal transverse components of force (fig. 45, b3 & b4) at their insertions and origins are directed inward and outward, respectively, i.e. being directed oppositely to the corresponding components of force (fig. 44, b1 & b2) of the primary oblique galeal muscles at their insertions and origins respectively. These components of force therefore neutralize each other. The horizontal longitudinal components of force (fig. 45, a3 & a4) at the insertions

and origins of the secondary oblique galeal muscles are therefore, as Eastham and Eassa (1955) indicated for corresponding muscles in Pieris, the only effective components of force left. As has been noted previously in the case of the primary oblique galeal muscles, the horizontal longitudinal components of force (fig. 44, a1 & a2) tend to coil the galeae. In the intermediate regions of the galeae where the secondary oblique galeal muscles are present the horizontal longitudinal components of force (a3 & a4) of these muscles therefore reinforce the corresponding components of force (a1 & a2) of the primary oblique galeal muscles. These tend to coil the galeae, thus resisting and preventing full extension of the galeae at this point in the extended proboscis, resulting in a dorsal curvature, the "knee-bend."

Muscles to which the secondary oblique galeal muscles of S. partita correspond are described in Pieris by Eastham and Eassa (1955).

2. Labial palp muscles

In S. partita the labial palps are each provided with one extrinsic and one intrinsic muscle.

a. Extrinsic labial palp muscle

(i) Labial palp abductor muscle (fig. 10, 1b.plp.abd.m). This is a small, flat muscle which originates on the dorsal surface of the transverse "beam" of the T-shaped labium, lateral to its median line. It is inserted basally on the anterior edge of the first segment of the labial palp. By contraction of the labial palp abductor muscles the labial palps are abducted when the proboscis is being extended or coil-

ed.

The labial palp abductor muscles of S. partita correspond to the "labial palp muscles" of Pieris which, according to Eassa (1963a), by their contraction move the palps apart. They may also correspond to the muscles numbered 12 by Ehrlich and Davidson (1961) in Danaus. Schmitt (1938) and Pradhan and Aren (1941) name extrinsic muscles in the palps of the Lepidoptera studied by them, "levators of the palps." Srivastava (1957) terms similar muscles in Papilio, the "intra labial muscles" and he believes that the palps are elevated by their contraction. The muscles described by the previous four authors apparently occupy the same positions as the labial palp abductor muscles of S. partita, although a different function is ascribed to them. However, as the labial palps of Lepidoptera are in repose closely applied to the facial region of the head, being actually in an elevated position when at rest, it would imply that the muscles to which Schmitt (1938), Pradhan and Aren (1941) and Srivastava (1957) attribute the elevation of the palps are in a state of tension when the palps are in their normal position.

b. Intrinsic labial palp muscle

(i) Labial palp depressor muscle (figs. 10 & 17, 1b.plp.dep.m). This muscle is wedge-shaped and originates with a broad base on the dorsal wall of the basal palp segment, some distance from the latter's connection with the second segment. It is inserted on the ventral edge of the base of the second palp segment. By its contraction the second and terminal palp segments are depressed and drawn away from the facial

region of the head to which they are closely applied when this muscle is relaxed. The depression of the second and terminal palp segments are probably correlated with the functioning of the apical sensory pit (figs. 1 & 2, sens.pt) on the terminal segment, which has already been described.

Pradhan and Aren (1941) describe intrinsic muscles in the labial palps of Scirpophaga and term them the "segmental muscles of the palps." These muscles, however, originate on the posterior (ventral) walls of the basal palp segments and are inserted on the proximal margins of the second palp segments. It is therefore uncertain if the intrinsic labial palp depressor muscles of S. partita correspond to these muscles.

VI. SUCKING PUMP

A. Structure of the Sucking Pump

In S. partita the sucking pump, which is entirely enclosed by muscles, is a complex, well-developed, globular structure which is laterally flanked by the bulging anterior tentorial arms. Anteriorly it communicates by means of a transverse, slit-like aperture, the functional mouth (figs. 18, 30 & 31, func.mth), with the food channel via the food meatus (figs. 30 & 31, f.mts). Posteriorly it narrows to merge with and to open into the oesophagus (figs. 16, 18, 30 & 31, oes).

In S. partita the floor of the sucking pump (figs. 11, 30, 31 & 42, flr.sck.pmp) forms a fixed, exocuticular, concave, somewhat triangular plate which is medially depressed along its longitudinal axis (fig. 42). Burgess (1880b) terms the floor of the sucking pump in Danaus, the "hypopharynx." Schmitt (1938), however, points out that only the anterior part of the floor of the lepidopterous sucking pump is derived from the hypopharynx. According to him this is indicated by the fact that muscles corresponding to the dorsal pair of salivary duct muscles, which in insects originate on the hypopharynx (Snodgrass, 1935), originate on the anterior part of the floor of the sucking pump in Lepidoptera. Srivastava (1957) provides additional evidence that in Papilio the anterior part of the floor of the sucking pump is formed by the hypopharynx. He points out that the opening of the common salivary duct, which in insects opens between the hypopharynx and labium (Snodgrass, 1935), is situated at the junction of the ventral wall of

the sucking pump and the labium, and that suspensorial sclerites (hypopharyngeal suspensoria), which in insects flank the adoral area of the hypopharynx (Snodgrass, 1935), are present on the anterior part of the floor of the sucking pump. Eassa (1963a) also states that in Pieris the hypopharynx in reality comprises only the anterior part of the floor of the sucking pump. In S. partita the floor of the sucking pump forms a continuous, exocuticular plate which even remains intact in dissections and in which a separate hypopharynx cannot be discerned. That the anterior part of the sucking pump floor is hypopharyngeal in origin is, however, indicated by the position of the salivary duct aperture, by the origins of the salivary duct dilator muscles and by the location of the hypopharyngeal suspensoria. To regard the entire floor of the sucking pump in S. partita as the hypopharynx, like Burgess (1880b) and others did in Lepidoptera studied by them, would imply that the floors or ventral walls of both the buccal and pharyngeal regions are hypopharyngeal.

At its anterolateral angles the hypopharyngeal part of the floor of the sucking pump is laterally produced into short arms, here named the anterolateral hypopharyngeal extensions (figs. 11, 18 & 42, al.hyp. ext). These extensions represent transformed hypopharyngeal suspensoria by means of which the floor of the sucking pump is connected laterally to the most anterior parts of the hypostomata, immediately posterior to the mandibles (figs. 11 & 18). The anterolateral hypopharyngeal extensions are ridge-like on their ventral aspects, and these ridge-like structures probably correspond to the "hypopharyngeal ridges" on the floor of the sucking pump which are described by Schmitt (1938)

in some Lepidoptera, by Eastham and Eassa (1955) and Eassa (1963a) in Pieris and by Vasudeva (1957) in Papilio. They apparently also correspond to the structure which Kirbach (1884) names the "Criste" in Vanessa.

The anterior margin of the hypopharyngeal part of the floor of the sucking pump is connected to the anterior margin of the longitudinal "stem" of the T-shaped labium by means of flexible endocuticle. Medially, at this junction, the salivary duct (figs. 16, 18, 30, 31, 41 & 42, slv.dct) opens into the cibarial region of the sucking pump (figs. 30 & 31). At its aperture the ventral wall of the salivary duct is sclerotized and immediately posterior to this aperture a pair of small hypopharyngeal-salivary duct dilator muscles (figs. 18, 30 & 31, hyp. slv.dct.dil.m) is inserted on the dorsal wall of the salivary duct. These muscles originate on the hypopharyngeal part of the floor of the sucking pump, lateral to its median line and mesal to the anterolateral hypopharyngeal extensions. By their contraction the aperture of the salivary duct is opened.

In S. partita the flexible roof of the sucking pump (figs. 30, 31 & 42, rf.sck.pmp), which is the internal continuation of the epipharynx, is endocuticular and not membranous as in Pieris (Eastham and Eassa, 1955; Eassa, 1963a) and Papilio (Srivastava, 1957). In the epipharyngeal part of the roof of the sucking pump (in the generalized insect the roof of the cibarium is formed by the epipharynx (Snodgrass, 1935)), immediately posterior to the functional mouth, approximately 30 peculiar, circular organs are embedded. They consist of rings of exocuticle (fig. 43, exc) which encircle a granular contents (fig. 43, grn.

ent). The function of these organs is still in doubt, but as all imbibed fruit juices are brought into contact with them they may serve as chemoreceptors and are perhaps gustatory in function. Apparently similar organs, though on the floor of the sucking pump, is reported by Kirbach (1884) in the so-called "Papillenfild der Schlundplatte" of Saturnia.

B. Regions of the Sucking Pump

According to Snodgrass (1935) the buccal cavity lies just within the mouth and on its walls the dorsal buccal dilator muscles are inserted, anterior to the frontal ganglion. Following posteriorly on the mouth or the buccal cavity is the pharynx, and on its walls the dorsal pharyngeal dilator muscles are inserted, posterior to the frontal ganglion, within the loops formed by its connectives. He further points out that the functional lepidopterous sucking pump includes the buccopharyngeal region of the stomadaeum, "since the frontal ganglion lies on its dorsal wall, and the dorsal dilator muscles are inserted before and behind the connectives of the ganglion." He also states that "it is to be suspected that the anterior part of the region may be formed by the cibarium." The cibarium of course is situated anterior to the mouth or the buccal cavity and on its walls the cibarial dilator muscles are inserted, anterior to the buccal dilator muscles.

Schmitt (1938) accepts Snodgrass' (1935) views and established that the cibarium necessarily forms the anterior section of the lepidopterous sucking pump. He found in the Lepidoptera studied by him that (i) muscles which correspond to the labral compressor muscles (regarded

as a cibarial dilator muscles in S. partita) of orthopteroid insects and which originate on the labrum and are inserted on the epipharyngeal wall, i.e. the roof of the cibarium in insects (Snodgrass, 1935), exist in Lepidoptera and (ii) muscles corresponding to the dorsal pair of salivary duct muscles (termed the hypopharyngeal-salivary duct dilator muscles in S. partita), which in insects originate on the hypopharynx, i.e. the floor of the cibarium (Snodgrass, 1935), originate on the anterior part of the floor of the sucking pump in Lepidoptera. This shows that the anterior part of the floor of the lepidopterous sucking pump is derived from the hypopharynx, and this portion of the sucking pump therefore belongs to the cibarium. Schmitt, however, could find no criterion whereby muscles which might be dilators of the buccal cavity could be distinguished from dilators of the cibarium. He therefore could not distinguish between the buccal and cibarial regions in the sucking pump of the Lepidoptera studied by him and regards all muscles inserted on the foregut, anterior to the frontal ganglion, as the dilators of the cibarium. Those muscles inserted on the foregut posterior to the frontal ganglion, he regards as the dilators of the pharynx.

Snodgrass (1947) shows, on good evidence, that the frontal ganglion retains its primitive position just posterior to the edge of the mouth, regardless of the changes that might take place in the structure of the insect head. He therefore presents a criterion for recognizing the primary mouth and, thus, for distinguishing between the buccal cavity and the pharynx. According to him (1935) the buccal cavity lies just within the mouth and the pharynx lies posterior to the buccal ca-

vity or the mouth. It may now be concluded from Snodgrass' (1947) findings that the buccal cavity lies just anterior to the frontal ganglion, while the pharynx lies posterior to it. Snodgrass (1947) also stresses that the frontal ganglion invariably separates the clypeal muscles, i.e. the cibarial and buccal dilators, from the frontal muscles, i.e. the pharyngeal dilators.

DuPorte (1956) regards that part of the sucking pump in Danaus and Protoparce posterior to the frontal ganglion as the pharynx, and that part anterior to the frontal ganglion as the cibarium. He distinguishes only between pharyngeal and cibarial dilators, as does Madden (1944) in Protoparce. Both Portier (1949) and Bourgogne (1951), however, regard all extrinsic muscles of the lepidopterous sucking pump as "muscles dilateurs du pharynx." They therefore believe that the sucking pump is composed only of the pharynx, as does Burgess (1880a, 1880b) in Danaus.

Short (1951), Eastham and Eassa (1955), Srivastava (1956, 1957), Vasudeva (1957) and Eassa (1963a) all regard the sucking pump in the Lepidoptera studied by them as consisting of the cibarial and buccopharyngeal regions. Short (1951) maintains that in Dilina the precise contribution of the buccal cavity to the formation of the sucking pump cannot be ascertained. He distinguishes between pharyngeal and cibarial dilators, inserted on the roof of the sucking pump, posterior and anterior to the frontal ganglion, respectively, and he therefore regards that part of the sucking pump anterior to the frontal ganglion as the pharynx. Eastham and Eassa (1955) distinguish between a buccopharynx and a cibarium in the sucking pump of Pieris. They recognize

pharyngeal dilators, inserted on the roof of the buccopharynx, posterior to the frontal ganglion, as well as cibarial dilators, inserted on the roof of the buccopharynx, anterior to the frontal ganglion.

What Eastham and Eassa (1955), however, regard as the cibarium in this pierid is, according to their illustration, in fact the so-called food meatus, as it occurs anterior to what is evidently the functional mouth. The latter is, according to Snodgrass (1935), the distal opening by means of which the transformed cibarium opens into the food meatus in sucking insects. What Eastham and Eassa (1955) therefore regard as the buccopharynx in Pieris in reality then includes not only the pharynx and buccal cavity, but also the cibarium. Eassa (1963a), however, divides the sucking pump in Pieris into a cibario-buccal cavity, anterior to the frontal ganglion, and a pharynx, posterior to the frontal ganglion. He also distinguishes only between cibarial dilators, inserted on the roof of the cibario-buccal cavity, and pharyngeal dilators, inserted on the roof of the pharynx. Vasudeva (1957) distinguishes between a cibarium and a buccopharyngeal region in the sucking pump in Papilio, recognizing dilators of the pharynx which are inserted on the roof of the sucking pump, posterior to the frontal ganglion, as well as clypeal dilators of the buccal region which are inserted on the roof of the sucking pump, anterior to the frontal ganglion. Srivastava (1957) provides evidence in Papilio that the cibarium is included in the sucking pump by pointing out that the anterior part of the roof of the sucking pump is doubtlessly formed by the ventral wall of the clypeo-labrum, i.e. the epipharynx, which forms the roof of the cibarium in insects (Snodgrass, 1935). He also shows that, in addition to the

reason furnished by Schmitt (1938), the hypopharynx, which in insects forms the floor of the cibarium (Snodgrass, 1935), constitutes the anterior part of the floor of the sucking pump, as (i) the opening of the common salivary duct, which in insects opens between the labium and hypopharynx (Snodgrass, 1935), is situated at the junction of the labium and the ventral wall of the sucking pump and (ii) a suspensorial sclerite (hypopharyngeal suspensorium), which flanks the adoral area of the hypopharynx on each side in insects (Snodgrass, 1935), is present on each side of the anterior part of the floor of the pump. He (1957) further points out that the suspensorial sclerites determine the posterior limits of the floor of the cibarium. Srivastava (1956, 1957) then divides the sucking pump in Papilio into a cibarium (indicated by the epipharynx and by the hypopharyngeal part of the floor of the sucking pump), a buccal cavity and a pharynx. On the roof of the cibarium cibarial dilators are inserted, on the roof of the buccal cavity buccal dilators are inserted, posterior to the cibarium and anterior to the frontal ganglion, and on the roof of the pharynx pharyngeal dilators are inserted, posterior to the frontal ganglion.

In consequence of the foregoing discussion, the present author will now attempt to identify the pharyngeal, buccal and cibarial regions of the sucking pump in S. partita. As is evident from Snodgrass' (1935, 1947) works, the pharynx lies posterior to the mouth, the buccal cavity and the frontal ganglion. On its walls the pharyngeal dilators are inserted, posterior to the frontal ganglion and within the loops formed by the latter's brain connectives. In S. partita the relatively short part of the sucking pump posterior to the frontal ganglion (figs.

30 & 31, fr.gng) is then the pharyngeal region (figs. 30 & 31, ph.rgn), on the roof of which the frontoclypeus-pharyngeal dilator muscles (figs. 13 & 16, frclp.ph.dil.m) are inserted. It is also clear from Snodgrass' (1935, 1947) publications that the buccal cavity, in lying just within the mouth, lies anterior to the frontal ganglion. On its walls the buccal dilators are inserted, anterior to the frontal ganglion. In S. partita the first set of dilator muscles inserted on the roof of the sucking pump, anterior to the frontal ganglion (figs. 13, 16, 30 & 31, fr.gng), is here regarded as the buccal dilators. They are termed the lateral frontoclypeus-buccal dilator muscles (figs. 13 & 16, l.frclp.buc.dil.m) and indicate the approximate anterior limits of the larger intermediate buccal region (figs. 30 & 31, buc.rgn) of the sucking pump. Following anteriorly on the buccal cavity, in the generalized insect, is the cibarium which is part of the intergnathal preoral cavity and which bears the cibarial dilators (Snodgrass, 1935). Snodgrass (1935) further states that in most sucking insects where the cibarium is converted into part of the sucking pump of the feeding mechanism "the cibarium becomes a chamber partly or entirely enclosed within the head cavity" and "its distal opening into the food meatus is then the functional mouth." In S. partita that part of the sucking pump following anteriorly on the presumed buccal region is here then regarded as the cibarial region (figs. 30 & 31, cib.rgn), on the roof (epipharynx) of which are inserted the cibarial dilators, termed the anterior frontoclypeus-cibarial dilator muscle (figs. 13, 16, 30 & 31, a.frclp.cib.dil.m) and posterior frontoclypeus-cibarial dilator muscles (figs. 13, 16, 30 & 31, p.frclp.cib.dil.m). The floor of this region is formed

by the hypopharyngeal part of the sucking pump, as is indicated by the origins of the hypopharyngeal-salivary duct dilator muscles and the presence of the anterolateral hypopharyngeal extensions. The cibarial region of the sucking pump communicates anteriorly with the food channel, between the galeae, by means of the transverse, slit-like functional mouth (figs. 18, 30 & 31, func.mth) via the food meatus (figs. 30 & 31, f.mts).

C. Musculature of the Sucking Pump

The muscles of the sucking pump will again be named with reference to their origins, insertions and functions.

a. Extrinsic muscles of the sucking pump

As in other adult Lepidoptera, the extrinsic muscles of the sucking pump in S. partita act as dorsal dilators. Their fibres penetrate between the fibres of the intrinsic muscles, becoming inserted on the sucking pump roof.

(i) Anterior frontoclypeus-cibarial dilator muscle (figs. 13, 16, 30 & 31, a.frclp.cib.dil.m). This small, transverse, fan-shaped, unpaired muscle originates partly on the clypeolabral ridge and partly dorsal to this ridge on the most ventral part of the clypeal area of the frontoclypeus, ventral to the level of the anterior tentorial pits. It is inserted on the most anterior part of the roof of the cibarial region of the sucking pump. By its contraction, and provided that the cibarial compressor muscle is relaxed, the most anterior part of the roof of the cibarial region of the sucking pump, i.e. the epipharynx, is

displaced and the functional mouth (func.mth) is opened, as is shown in figure 31.

The anterior frontoclypeus-cibarial dilator muscle of S. partita corresponds to the labral compressor muscle in orthopteroid insects, and a similar muscle is then also termed the "labral compressor muscle" by Eastham and Eassa (1955) and Eassa (1963a) in Pieris. As this muscle, however, originates partly on the clypeolabral ridge and partly on the rigid, sclerotized clypeus in S. partita and is inserted on the anterior part of the flexible, endocuticular roof of the cibarial region of the sucking pump, i.e. on the epipharynx, its contraction results in the movement of this part of the sucking pump roof. The present author therefore prefers to regard it as a cibarial dilator muscle. This muscle also corresponds to the muscle regarded as the "first dilator of the cibarium" by Short (1951) in Dilina, the "first anterior cibarial dilator" or "anterior cibarial muscle" by Srivastava (1956, 1957) and the "clypeal dilator of the mouth" by Vasudeva (1957) in Papilio, and to the muscle numbered 13 by Ehrlich and Davidson (1961) and Ehrlich and Ehrlich (1962) in the Lepidoptera studied by them. It apparently also corresponds to that muscle termed the "Hebemuskeln der Mundklappen" in the Lepidoptera studied by Kirbach (1884).

(ii) Posterior frontoclypeus-cibarial dilator muscles (figs. 13, 16, 30 & 31, p.frclp.cib.dil.m). These short, thick muscles are paired, as e.g. in Dilina, studied by Short (1951), and in Papilio, studied by Srivastava (1957) and Vasudeva (1957), but they are contiguous mesally. They originate on the clypeal area of the frontoclypeus next to each other, dorsal to the origin of the anterior frontoclypeus-cibarial di-

lator muscle and also dorsal to the level of the anterior tentorial pits. They are inserted close together, medially on the most posterior part of the roof of the cibarial region of the sucking pump and posterior (or dorsal) to the insertion of the anterior frontoclypeus-cibarial dilator muscle.

The posterior frontoclypeus-cibarial dilator muscles of S. partita correspond to those muscles termed the "second dilators of the cium" by Short (1951) in Dilina, the "second anterior cibarial dilators" or "posterior clypeo-cibarial muscles" by Srivastava (1956, 1957) and the "dilators of the buccal regions" by Vasudeva (1957) in Papilio, the "anterior cibarial dilator muscle" by Eastham and Eassa (1955) and the "first cibarial dilator" by Eassa (1963a) in Pieris, and to the muscles numbered 14 by Ehrlich and Davidson (1961) and Ehrlich and Ehrlich (1962) in the Lepidoptera studied by them. They apparently also correspond to those muscles regarded as the "frontal muscles" by Burgess (1880a, 1880b) in Danaus, and to the muscles termed the "Stirn-muskeln" in the Lepidoptera studied by Kirbach (1884).

(iii) Lateral frontoclypeus-buccal dilator muscles (figs. 13 & 16, 1. frclp.buc.dil.m). These paired, very large, strongly-developed, broad muscles are the principal dilators of the sucking pump roof and originate on the dorsal part of the clypeal area of the frontoclypeus, mesal to and partly on the laterofacial ridges and dorsal to the origins of the posterior frontoclypeus-cibarial dilator muscles. From their origins these muscles extend obliquely mesally and are inserted dorso-laterally on the roof of the buccal region of the sucking pump, anterior to the frontal ganglion and its connectives and posterior (or dor-

sal) to the insertions of the posterior frontoclypeus-cibarial dilator muscles.

The lateral frontoclypeus-buccal dilator muscles of S. partita correspond to those muscles termed the "buccal dilators" or "subantennobuccal muscles" by Srivastava (1956, 1957) and the "clypeal dilators" by Vasudeva (1957) in Papilio, the "lateral cibarial dilator muscles" by Eastham and Eassa (1955) and the "second cibarial dilators" by Eassa (1963a) in Pieris. They also correspond to the muscles numbered 15 by Ehrlich and Davidson (1961) and Ehrlich and Ehrlich (1962) in the Lepidoptera studied by them, to the muscles regarded as the "lateral muscles" by Burgess (1880a, 1880b) in Danaus, and to the muscles termed the "Seitenmuskeln" in the Lepidoptera studied by Kirbach (1884). Apparently they also agree with the muscles named the "third dilators of the cibarium" by Short (1951) in Dilina.

(iv) Frontoclypeus-pharyngeal dilator muscles (figs. 13 & 16, frc1p.ph.dil.m). These are paired, slender muscles, each of which is composed of two contiguous bundles as in the papilionid Battus philenor, described by Ehrlich and Ehrlich (1962). They originate on the small frontal area of the frontoclypeus, immediately anterior (or ventral) to the transfrontal suture. Extending obliquely ventrally, they are inserted dorsolaterally on the roof of the pharyngeal region of the sucking pump, posterior to the frontal ganglion and within the loops formed by its connectives.

Muscles to which the frontoclypeus-pharyngeal dilator muscles of S. partita correspond are described by Short (1951) in Dilina, Eastham and Eassa (1955) and Eassa (1963a) in Pieris, and Srivastava (1956,

1957) and Vasudeva (1957) in Papilio. The frontoclypeus-pharyngeal dilator muscles also correspond to those muscles numbered 16 by Ehrlich and Davidson (1961) and Ehrlich and Ehrlich (1962) in the Lepidoptera studied by them, to those muscles regarded as the "dorsal muscles" by Burgess (1880a, 1880b) in Danaus, and to those muscles named the "Rückenmuskeln" in the Lepidoptera studied by Kirbach (1884).

b. Intrinsic muscles of the sucking pump

As in other adult Lepidoptera, the intrinsic muscles of the sucking pump in S. partita act as compressors.

Schmitt (1938) distinguishes between "transverse and lateral pump muscles" in the Lepidoptera studied by him, and Vasudeva (1957) regards all intrinsic sucking pump muscles in Papilio as the "intrinsic cibarial muscles." Kirbach (1884) recognizes "Längsmuskeln seiner Decke" and "Quermuskeln seiner Decke" in the intrinsic sucking pump muscles of Vanessa, but Burgess (1880a, 1880b) does not distinguish between different intrinsic muscles of the sucking pump in Danaus. Portier (1949), Bourgonne (1951) and Short (1951) do not describe the intrinsic muscles of the sucking pump in the Lepidoptera studied by them.

Although the intrinsic muscles of the sucking pump are intricately interwoven in S. partita, the following separate muscles can be discerned.

(i) Cibarial compressor muscle (figs. 13, 16, 18, 30 & 31, cib.comp. m). The fibres of this muscle are attached along either side of the median line of the floor of the cibarial region of the sucking pump and pass transversely over the roof of the cibarial region, between

the insertions of the anterior frontoclypeus-cibarial dilator muscle and the posterior frontoclypeus-cibarial dilator muscles. It acts as a sphincter, and is termed the "oral valve" by Burgess (1880a, 1880b) in Danaus. By its contraction, and provided that the anterior frontoclypeus-cibarial dilator muscle is relaxed, the functional mouth (mouth) is closed, as is shown in figure 30.

The cibarial compressor muscle of S. partita corresponds to the muscle named the "oral valve muscle" by Schmitt (1938) in the Lepidoptera studied by him, the "cibarial compressor" by Srivastava (1957) in Papilio, and the "anterior sphincter" by Eastham and Eassa (1955) in Pieris. A similar muscle is also described by Eassa (1963a) in Pieris.

(ii) Ventral buccal compressor muscle (figs. 13, 16, 18, 30, 31 & 42, v.buc.comp.m). This thick layer of muscle fibres is attached along either side of the median line of the floor of the buccal region of the sucking pump, between the attachments of the cibarial compressor muscle and the pharyngeal compressor muscle. Its fibres are interstitial with the fibres of the lateral frontoclypeus-buccal dilator muscles and extend transversely over the roof of the buccal region underneath the lateral buccal compressor muscles and cruciform buccal compressor muscles, between the insertions of the posterior frontoclypeus-cibarial dilator muscles and the frontoclypeus-pharyngeal dilator muscles.

The ventral buccal compressor muscle of S. partita corresponds to the muscle fibres termed the "ventral sheath of buccal compressors" by Srivastava (1957) in Papilio, the "first layer of fibres" by East-

ham and Eassa (1955) and the "innermost layer of fibres" by Eassa (1963a) in Pieris.

(iii) Lateral buccal compressor muscles (figs. 13, 16, 18 & 42, 1.buc.comp.m). These muscles are paired and occur dorsal to the ventral buccal compressor muscle. Their anterior and posterior attachments are on the same side along the median line of the floor of the buccal region of the sucking pump. Anteriorly they are attached posterior to the anterior attachments of the cruciform compressor muscles, while posteriorly they are attached anterior to the attachments of the pharyngeal compressor muscle. From their anterior attachments they extend longitudinally over the roof of the buccal region, mesal to the lateral frontoclypeus-buccal dilator muscles.

The lateral buccal compressor muscles of S. partita correspond to those muscles termed the "lateral compressors" by Eastham and Eassa (1955) and the "first set of the second layer of longitudinal muscles" by Eassa (1963a) in Pieris.

(iv) Cruciform buccal compressor muscles (figs. 13, 18, 30, 31 & 42, crcf.buc.comp.m). These two muscle bands are present between the lateral buccal compressor muscles and on top of the ventral buccal compressor muscle. Their anterior attachments are on the anterior part of the floor of the buccal region of the sucking pump, lateral to the median line and posterior to the attachments of the cibarial compressor muscle. From their anterior attachments they extend diagonally over the roof of the buccal region, thus crossing one another and becoming attached on the posterior part of the floor of the buccal re-

gion, anterior to the attachments of the pharyngeal compressor muscle. At the point of crossing their fibres are somewhat interwoven.

The cruciform buccal compressor muscles of S. partita correspond to those muscles termed the "cruciform compressors" by Eastham and Eassa (1955) and the muscles regarded as the "second set of the second layer of longitudinal muscles" by Eassa (1963a) in Pieris. They also correspond to those muscles regarded as the "dorsal sheath of buccal compressors" by Srivastava (1957) in Papilio.

(v) Pharyngeal compressor muscle (figs. 16, 18, 30 & 31, ph.comp.m). The fibres of this muscle extend transversely over the roof of the pharyngeal region of the sucking pump, posterior to the insertions of the frontoclypeus-pharyngeal dilator muscles. It is attached to the floor of this region on either side of the median line, posterior to the attachments of the lateral buccal compressor muscles. By its contraction the opening of the sucking pump into the oesophagus is closed, and it therefore acts as a posterior sphincter.

Muscles which correspond to the pharyngeal compressor muscle in S. partita are described by Eastham and Eassa (1955) and Eassa (1963a) in Pieris, and by Srivastava (1957) in Papilio.

D. Mechanism of the Sucking Pump

The sucking pump, by means of which fruit juice is imbibed, comes into operation when S. partita feeds, i.e. when the proboscis is in the extended position and inserted into the flesh of a fruit.

To imbibe fruit juice all the intrinsic compressor muscles must be relaxed, except the pharyngeal compressor muscle which must be con-

tracted to ensure that the opening of the sucking pump into the oesophagus is closed. This is a necessary prerequisite for the subsequent creation of a suction power within the cavity of the sucking pump. By now contracting the anterior frontoclypeus-cibarial dilator muscle the functional mouth is opened (fig. 31). When the posterior frontoclypeus-cibarial dilator muscles, lateral frontoclypeus-buccal dilator muscles and frontoclypeus-pharyngeal dilator muscles then contract the flexible, endocuticular roof of the sucking pump is raised and the sucking pump cavity dilated. The volume of the cavity is thus enlarged and the air pressure within reduced. A suction power is so created and fruit juice is drawn through the food channel, via the food meatus and functional mouth, into the zone of negative pressure in the sucking pump.

When the enlarged cavity of the sucking pump is filled with juice, the simultaneous contraction of the cibarial compressor muscle and relaxation of the anterior frontoclypeus-cibarial dilator muscle cause the closure of the functional mouth (fig. 30). By the subsequent relaxation of the pharyngeal compressor muscle the exit of the sucking pump into the oesophagus is opened. When the ventral buccal compressor muscle, lateral buccal compressor muscles and cruciform buccal compressor muscles then contract, and the posterior frontoclypeus-cibarial dilator muscles, lateral frontoclypeus-buccal dilator muscles and frontoclypeus-pharyngeal dilator muscles relax, the volume of the sucking pump cavity is reduced and the imbibed fruit juice is forced backward into the oesophagus.

E. Innervation of the Sucking Pump

Two pairs of nerves arise from the anterior surface of the sub-oesophageal ganglion (fig. 16, soes.gng), one pair above the other, anterodorsal to the galeal nerves. The ventral and larger of these, here termed the sucking pump nerves (fig. 16, sck.pmp.n), pass dorsal to the galeal nerves and, in embracing the sucking pump laterally, innervate the muscles of this organ. The more dorsal nerves, the frontal ganglion connectives (fig. 16, fr.gng.conn), pass directly over the posterodorsal wall of the sucking pump to innervate the muscles of this region. They then unite with the frontal ganglion (figs. 13 & 16, fr.gng) which lies dorsally on the sucking pump, just anterior to the insertions of the frontoclypeus-pharyngeal dilator muscles.

VII. MECHANISM OF EXTENSION AND COILING OF THE PROBOSCIS
AND THE MANNER OF ITS INSERTION INTO AND EXTRACTION
FROM FRUIT

A. Review of Theories and Opinions on the Mechanism of Extension
and Coiling of the Lepidopterous Proboscis

Snodgrass (1935) assumes that the lepidopterous proboscis is extended by blood pressure in the same way as a toy paper "snake" is unrolled by inflation. He stresses, however, that although the natural uncoiling of the proboscis, beginning at the base and progressing towards the tip, strikingly resembles the uncoiling of the inflated "snake", the mechanism for creating the assumed blood pressure is not evident. He attributes coiling of the proboscis to the contraction of the oblique (or diagonal) intrinsic maxillary muscles which run distally in the galeae. Pradhan and Aren (1941), however, pointed out that Snodgrass (1935) "does not take into consideration the important fact that, whereas the tube of the paper "snake" is definitely deflated during the coiled condition and becomes fully inflated in the uncoiled state, there is no such alteration in girth in the case of the lepidopterous proboscis." They also established and noted in the Lepidoptera studied by them that the proboscis resembles the toy paper "snake" in its coiling (being coiled by its own elastic properties), but not in its uncoiling mechanism.

Schmitt (1938) believes that the extrinsic maxillary muscles, inserted on the stipital apodemes, by their contraction draw the stipites upward, forcing them against the recurved flanges of the genae. Hereby the stipital valves are closed, with the result that the stipital

haemocoeles become closed cylinders. Therefore pressure is exerted on the blood within the stipital haemocoeles and as the pressure continues, by further contraction of the extrinsic maxillary muscles, the blood moves outward into the galeal haemocoeles and causes extension of the coiled proboscis by inflation. He attributes coiling of the lepidopterous proboscis to the contraction of the oblique (or diagonal) intrinsic maxillary muscles in the galeae.

Imms (1942) also believes that the lepidopterous proboscis is extended by means of inflation. He postulates that contraction of the extrinsic maxillary muscles, inserted on the stipital apodemes, leads to the reduction of the volume of the cranial cavity whereby pressure is exerted on the blood within it. Blood from the cranial cavity is then forced through the stipital valves, via the stipital haemocoeles, into the galeal haemocoeles, and in this manner causes extension of the proboscis by inflation. He also attributes coiling of the proboscis to the contraction of the oblique (or diagonal) intrinsic maxillary muscles in the galeae.

Both Burgess (1880a) and Bourgogne (1951), however, attribute extension of the proboscis in Lepidoptera to elasticity of the galeal walls, and claim that contraction of the diagonal (or oblique) intrinsic maxillary muscles in the galeae is responsible for the coiling of the proboscis.

Kirbach (1884) again believes that the proboscis in Lepidoptera is coiled by its own elasticity and that contraction of each diagonal (or oblique) intrinsic maxillary muscle fibre brings about local elevation, the total effect of their contraction leading to the extension

of the proboscis.

Pradhan and Aren (1941) to some extent accepted the earlier work of Kirbach (1884). As a result of their experiments they conclude that extension of the proboscis is effected by the oblique (or diagonal) intrinsic maxillary muscles which, by their contraction, act as a "mechanical couple", except in Scirpophaga which, according to them, is an exceptional case. The efficacy of this theory depends in their view on the greater thickness and strength of the posterior walls of the galeae, as compared with the anterior walls. Eastham and Eassa (1955), however, pointed out that such a difference may well have arisen from a little obliquity in the cutting of their sections and may be insignificant. Pradhan and Aren describe those muscles corresponding to the extrinsic maxillary muscles, which e.g. Schmitt (1938), Eastham and Eassa (1955), Vasudeva (1957), Eassa (1963a) and the present author found to be inserted on the stipital apodemes, as being inserted within the stipital cavities in the Lepidoptera studied by them. They could therefore not establish a stipital valve arrangement which could be closed by the contraction of these muscles. They further proved experimentally that the proboscis is coiled by means of its own elasticity. They also found that, instead of the oblique (or diagonal) intrinsic maxillary muscles, the galeae of Scirpophaga possess so-called "longitudinal proboscis muscles" and to the contraction of these muscles they partly attribute coiling of the proboscis in this moth. They believe that extension of the proboscis is here effected by the contraction of "basal muscles" in the galeae. The present author, however, has doubts about the convergent development of more than one intricate type of me-

chanism of proboscis extension and coiling in the order Lepidoptera.

Portier (1949), on the other hand, regards the contraction of some intrinsic maxillary muscles in the galeae as the cause of extension of the proboscis and the contraction of others, supposedly antagonistic to them, as the cause of coiling.

Eastham and Eassa (1955) offer a new theory on the mechanism of extension of the proboscis in Pieris — a theory for which the senior author alone is actually responsible and a theory which is supported by the findings of the present author in S. partita. Eastham and Eassa conclude, as a result of a detailed examination of the maxillary structure, musculature and proboscis movements, and after performing numerous operations involving neurotomy, perforation and artificial inflation of the cranial, stipital and galeal haemocoels, that extension of the proboscis is neither caused by inflation, nor by direct muscle action, nor by elasticity of the galeal walls. They found that contraction of the extrinsic maxillary muscles, inserted on the stipital apodemes, closes the stipital valves, and thus also the galeal haemocoels which are filled with haemolymph. They further found that by contraction of the oblique (or diagonal) intrinsic maxillary muscles in the galeae the dorsal and ventral galeal walls are drawn towards each other. In the closed galeal haemocoels this results in an internal pressure being set up in the contained haemolymph whereby conditions of haemocoelic turgidity are induced within the closed galeal haemocoels. This condition is maintained by the closed stipital valves and a change in the shape of the galeae is produced, being expressed in the form of a transverse dorsal convexity of the proboscis. They

then show that in Pieris the extension of the proboscis is a consequence of this dorsal convexity, under conditions of haemocoelic turgidity in an elastic system (as the galeae are), and only indirectly of the contraction of the oblique intrinsic maxillary muscles in the galeae. Eastham and Eassa also ascertained that the longitudinal internal septa in the galeae, which control the degree of movement of the galeal walls, and the strong walls of the food channel, which act as bases for the movement of the outer galeal walls, assist in the production of the changed shape of the extended proboscis, as is seen in transverse section. They also established experimentally in Pieris that coiling of the proboscis is due to the elasticity of the exocuticular, longitudinal dorsal bars which lie in the mesal walls of the coilable regions of the galeae.

B. Observations and Experiments to Test the Different Theories and Opinions on the Mechanism of Extension and Coiling of the Lepidopterous Proboscis

The same experiments done by Pradhan and Aren (1941) on a number of Lepidoptera and by Eastham and Eassa (1955) on Pieris were carried out on S. partita. In general, the results obtained essentially agree with the findings of the latter two authors.

1. In view of the theories or opinions of Snodgrass (1935), Schmitt (1938) and Imms (1942), the proboscides of several etherized S. partita moths were punctured, without injuring the galeal nerves. On recovering from anaesthesia, the proximal region of the proboscis could be elevated as a preliminary to feeding, but extension of the entire proboscis seemed impossible, as Eastham and Eassa (1955) also found in

Pieris. A considerable degree of muscular twitching, as evinced by the movements of the stipites, took place, and coupled with these movements, haemolymph was seen to emit from the puncture, thus agreeing with the observations of Eastham and Eassa (1955) in Pieris. Their conclusion that closed galeal haemocoels are a prerequisite for full extension of the proboscis, whether or not haemolymph is pumped into the galeae, therefore seems justified. The power to elevate the proboscis is, however, not impaired by the puncturing of the galeal walls. The elevation of the proximal region may therefore, as Eastham and Eassa (1955) pointed out, be attributed to muscle action alone, which is effected in S. partita by the contraction of the posterior and anterior basal galeal levator muscles and proximal galeal levator muscles.

When the ventral cranial membranes of etherised S. partita moths were perforated alongside the "stem" of the T-shaped labium, without injury to any other structures, these moths were still able to extend their proboscides, as Eastham and Eassa (1955) also found in Pieris. As such perforations would render ineffective any mechanism for forcing haemolymph from the cranial cavity into the galeal haemocoels, there would seem, in the absence of any visible mechanism for the movement of haemolymph to the galeae, no reason for accepting Imms' (1942) view on proboscis extension.

It should be noted here that Eastham and Eassa (1955) incorrectly assume that Schmitt (1938) believes extension of the lepidopterous proboscis to be caused by haemolymph forced from the cranial cavity into the galeal haemocoels via the stipital valves — a view in fact held by Imms (1942). Schmitt, however, clearly states that the proboscis

"is extended by means of blood pressure created in the stipes of each maxilla." The experiments conducted by Eastham and Eassa, on the results of which they reject Schmitt's theory regarding extension, is therefore in fact a rejection of Imms' view. The present author, however, infers from the structure and musculature of the maxillae that the extrinsic maxillary muscles, inserted on the stipital apodemes, can by contraction only effect the closing of the stipital valves. They cannot contract further and so diminish the stipital haemocoelae to such an extent as to exert appreciable extra pressure on the relatively small amount of haemolymph contained within the stipital haemocoelae to effect extension of the proboscis in the way Schmitt describes.

To put Imms' (1942) theory to a further test, a fine injection needle was inserted into the cranial cavity of an etherized S. partita moth through one of the ventral cranial membranes and by means of gentle pressure on the syringe, fluid was forced into the cranial cavity. No extension of the proboscis occurred, but the introduced fluid was forced into the thorax, causing the wings to be depressed as a result of the arching of the thoracic terga — a phenomenon also observed by Eastham and Eassa (1955) in Pieris.

By inserting the needle into the stipital haemocoelae of an etherized S. partita moth, of which the galeae were separated from one another previously (by inserting a fine needle between the two galeae at their bases and working towards their apices), it was, however, possible to inflate the galea of this particular stipes. This shows, as Eastham and Eassa (1955) observed in Pieris, that the stipital valves serve for the prevention of haemolymph back-flow from the galeal hae-

mocoeles into the cranial cavity. It may be assumed therefore, as Eastham and Eassa (1955) did in Pieris, that the stipital valves are so constructed that by their closure they shut off the stipital and galeal haemocoeles from the cranial cavity, rather than serving as passages for haemolymph under pressure from the cranial cavity, and that closed galeal haemocoeles are necessary for proboscis extension.

To test this assumption further, the stipital haemocoeles of S. partita moths were perforated after anaesthesia. On recovering, only partial extension of the proboscis occurred when the moths sensed a provided food source, even though they had been kept without food for 24 hours. Eastham and Eassa (1955) obtained similar results in Pieris. That the proboscides did not uncoil fully under these circumstances is no proof that they could not do so, as Eastham and Eassa (1955) correctly remarked. But when these perforations were again closed, by covering them with celloidin, the proboscides did in fact become fully extended when the moths sensed a provided food source, as Eastham and Eassa (1955) also found in Pieris. It may therefore be inferred that perforation of the stipital haemocoeles prevents full extension of the proboscis.

After separating the galeae of an etherized S. partita moth from one another, the right stipital haemocoele was perforated. After recovery, the moth, having been kept without food for 24 hours, extended its left (unoperated) galea as in feeding, on sensing a provided food source. The right (operated) galea, however, remained coiled and, except for slight lifting movements at the base, was motionless, as Eastham and Eassa (1955) found in Pieris. On closing the wound in the

right stipes with celloidin, the right galea regained its power of extension and the two galeae could then be extended as in feeding, except that they remained separate and tended to diverge, as Eastham and Eassa (1955) also observed in Pieris. A similar experiment was carried out on another moth, perforating and closing in this instance the left stipes and leaving the right stipes intact, with corresponding results.

From the results obtained in the described experiments the "inflation" theories of Snodgrass (1935), Schmitt (1938) and Imms (1942) must be rejected. There is, however, definite confirmation, as Eastham and Eassa (1955) pointed out, that for full extension of the proboscis the formation and ~~maintenance~~ of closed galeal haemocoel is a prerequisite. This can be effected only by the closing of the stipital valves and resultant closing of the stipital haemocoel, which is brought about in S. partita by the contraction of the geno-stipital adductor muscles and anterior and posterior tentorio-stipital adductor muscles.

2. After dissolving the intrinsic maxillary muscles in the galeae of S. partita, by boiling a proboscis in 10% KOH, the proboscis remained coiled. When the coils were mechanically opened and then released the proboscis returned to the coiled condition, as Pradhan and Aren (1941) found in proboscides similarly treated. When the proboscis was removed from a living S. partita moth and the two galeae then separated from one another and cut along the line of the food channel, thus dividing each galea into dorsal and ventral halves, the dorsal halves, which contain the exocuticular, longitudinal, dorsal bars in the intermediate regions of the galeae, returned to the coiled state. The ventral halves remained loosely outstretched, as Eastham and Eassa (1955) also

observed in Pieris. The proboscis is therefore brought to the coiled position of rest by its own elastic properties. These elastic properties must be situated in the exocuticular, longitudinal dorsal bars of the galeae, as Eastham and Eassa (1955) pointed out, because these bars constitute the only structural difference between dorsal and ventral halves of the galeae. The views of Kirbach (1884), Pradhan and Aren (1941) and Eastham and Eassa (1955), as well as those of Savigny (1816)*, Hering (1926)* and Weber (1933)*, are therefore correct, while the views of Burgess (1880a) and Bourgogne (1951), and that of Lameere (1938)*, must be rejected.

3. After etherizing a S. partita moth, the two galeae were separated from one another. By means of a fine scalpel, inserted through one of the ventral cranial membranes and between the two tentorio-galeal retractor muscles, the right galeal nerve was severed between its exit from the suboesophageal ganglion and its entrance into the right galea. The left galeal nerve was left intact. When the moth, which had been kept without food for 24 hours, recovered, the two galeae remained separate. When the moth sensed a provided food source the galea on the left (unoperated) side became extended, with a slight turning to the left side, while on the right (operated) side the galea remained loosely coiled, as Eastham and Eassa (1955) also found in Pieris. Another moth was treated similarly, but in this instance the right side was left intact, the left galeal nerve having been severed. In this case the right galea was extended as in feeding, though with a slight turn-

*Not seen in the original

ing to the right side, while the left galea remained loosely coiled, thus again agreeing with a similar experiment carried out by Eastham and Eassa (1955) on Pieris.

To prove that in each case the specific galeal nerve had in fact been cut, the heads of the operated moths were afterwards injected with Bouin's fluid and dissected.

In view of the results obtained from all the described experiments on S. partita it is evident that extension of the proboscis can only take place when the primary oblique galeal muscles contract, on being stimulated by the galeal nerves, and then only on condition that the galeal haemocoelae form closed systems, filled with haemolymph. This condition can again only be brought about by the closure of the stipital valves, which is effected by the contraction of the extrinsic maxillary muscles inserted on the stipital apodemes. This finding confirms the view of Eastham and Eassa (1955) that proboscis extension is caused by the contraction of the oblique intrinsic maxillary muscles in the galeae, stimulated by the galeal nerves, under conditions where the haemocoelae of each galea form a closed system, i.e. a closed fluid-filled tube. The views of Kirbach (1884), Pradhan and Aren (1941) and Portier (1949), as well as those of Reaumur (1734)*, Burmeister (1832)*, Hering (1926)* and Weber (1933)*, are therefore unsatisfactory as they claim that contraction of the oblique (or diagonal) intrinsic maxillary muscles in the galeae, irrespective of maintained haemocoelic turgidity, alone causes extension of the lepidopte-

*Not seen in the original

rous proboscis. The views of Burgess (1880a), Snodgrass (1935), Schmitt (1938), Imms (1942), Portier (1949) and Bourgogne (1951), as well as those of Burmeister (1832)*, Eltringham (1923)* and Lameere (1938)*, that contraction of the oblique (or diagonal) intrinsic maxillary muscles in the galeae causes coiling of the lepidopterous proboscis are rejected. The views of these authors would also imply that the oblique (or diagonal) intrinsic maxillary muscles in the galeae are in a state of tension when the lepidopterous proboscis is in its coiled position of rest.

C. Mechanism of Extension and Coiling of the Proboscis

As the anatomical and histological structure of the maxillae and the results obtained by experimentation in S. partita in all respects correspond to that described by Eastham and Eassa (1955) in Pieris, the present author must conclude that the mechanism of extension and coiling of the proboscis in S. partita is essentially similar to that of Pieris.

The change of form in the transverse sectional configuration of the proboscis, i.e. the transverse dorsal convexity of the proboscis in the intermediate and apical regions of the galeae which is brought about by the contraction of the primary oblique galeal muscles when the dorsal and ventral walls of these galeal regions are drawn towards each other, is in itself responsible for extension of the proboscis, as Eastham and Eassa (1955) believe in Pieris.

*Not seen in the original

The relative effects of the components of force exerted by the contraction of the primary oblique galeal muscles are partly determined by the particular characteristics of the walls of the intermediate or coilable and apical regions of the galeae on which they operate. As Eastham and Eassa (1955) pointed out in Pieris, these characteristics are:

1. The presence of the ventral linking mechanism of the galeae which permits no lateral movement of the linked parts on each other.
2. The presence of elastic, exocuticular, longitudinal dorsal bars in the mesal walls of the intermediate regions of the galeae.
3. The presence of exocuticular ribs which are transversely positioned in the outer walls of the intermediate regions of the galeae, being separated from each other by flexible, laminated endocuticle.
4. The fact that dorsal and ventral flexible endocuticular parts in the outer walls of the intermediate regions of the galeae separate the exocuticular ribs from the mesal walls of these galeal regions.
5. As the flexible dorsal endocuticular part, just mentioned, is more extensive than the ventral endocuticular part (figs. 25-28), the dorsal walls of the intermediate and apical regions of the galeae are pulled further downward than the ventral walls are pulled upward when the primary oblique galeal muscles contract. This largely accounts for the transverse dorsal convexity of the proboscis in the intermediate and apical regions of the galeae when these muscles are contracted (figs. 25 & 27).
6. The fact that the mesal walls of the intermediate and posterior parts of the apical regions of the galeae contain the laminated, exocuticular bars which are so constructed as to permit little (or no) lateral bending of the proboscis and preserve a circular out-

line in the food channel in both the coiled and extended conditions of the proboscis.

The regularity of the change of form in the transverse sectional configuration of the proboscis in the intermediate regions of the galeae, which is brought about by the contraction of the primary oblique galeal muscles, is to some extent determined by the galeal septa which pass from one end to the other in the haemocoels of the intermediate regions of the galeae.

As is evident from the experiments described previously, extension of the proboscis is, however, only possible when the stipital valves are closed, i.e. when the galeal and stipital haemocoels form closed systems, filled with haemolymph. Extension of the proboscis is therefore only possible under conditions of haemocoelic turgidity in the galeae and stipites as contraction of the primary oblique galeal muscles, whereby the dorsal and ventral walls of the intermediate and apical regions of the galeae are drawn towards each other, leads to the reduction of the volumes of the galeal haemocoels. In the closed galeal and stipital haemocoels the contained haemolymph is therefore put under compression, with the result that internal pressure is produced in the contained haemolymph and conditions of haemocoelic turgidity, permitted and maintained by closed stipital valves, are thus induced.

The reason why maintained conditions of haemocoelic turgidity (internal haemolymph pressure) are needed in the galeal haemocoels for extension of the proboscis is explained by Eastham and Eassa (1955) by means of the following analogy. Lateral pressure applied to the walls of a closed rubber tube only partly filled with fluid has little or no

effect, except on the place where it is applied. However, by imparting greater initial turgidity to the tube by adding more fluid, pressure applied at any part of its walls becomes effective on the other parts of the tube walls distant from the place of pressure application, the effect being transmitted along the tube under these turgid conditions by the compressed, contained fluid.

In cases where the galeal or stipital haemocoels have been punctured, haemocoelic turgidity cannot be induced, or is lost, in the galeal haemocoels when the primary oblique galeal muscles contract, even though the extrinsic maxillary muscles, inserted on the stipital apodemes, are contracted and the stipital valves are closed. Contraction of the primary oblique galeal muscles now only results in driving haemolymph out of the galeal or stipital haemocoels, with little or no uniform effect on the outer walls of the intermediate and apical regions of the galeae. In the intact maxillae the closure of the stipital valves by the contraction of the extrinsic maxillary muscles prevents loss of haemolymph from the closed galeal and stipital haemocoels when the primary oblique galeal muscles by their contraction draw the dorsal and ventral walls of the intermediate and apical regions of the galeae towards each other. The galeal haemocoels thus receive the necessary haemocoelic turgidity which now allows the primary oblique galeal muscles to produce, by their contraction, a uniform effect on the walls of the intermediate and apical regions of the galeae. This effect is manifested in the change of form in the transverse sectional configuration of the proboscis, i.e. by the transverse dorsal convexity of the proboscis, in its extended condition in the

intermediate and apical regions of the galeae.

That the change of form in the sectional configuration of the proboscis, which is brought about by the contraction of the primary oblique galeal muscles, is in itself responsible for extension of the proboscis, is fittingly explained by Eastham and Eassa (1955). According to them a coiled steel measuring-tape is flat in transverse section when coiled in its case, but when it is drawn out it assumes a curved transverse section, convex on one side and concave on the other, and in this state attains the condition of extension. In this instance the rule has to be forced into its case and it can only be bent when its transverse sectional curvature is flattened out. In contrast to the lepidopterous proboscis, its condition of rest is, however, attained when it is extended, and force has to be applied to coil it up, the measuring-tape having been manufactured with these properties.

The lepidopterous proboscis therefore resembles an elastic, coiled strip with the intrinsic property of being coiled when at rest and showing a flat transverse section in this condition. Eastham and Eassa (1955) then point out that when the lateral borders of such a strip are pressed down the coil begins to straighten out, and the upper-surface is put into a state of tension from side to side and the under-surface into a state of compression. Taking into account the elastic properties of the material of which this strip is composed, the lateral tension imposed on its upper-surface increases its lateral dimension, an increase which takes effect at the expense of its longitudinal dimension. The longitudinal axis of the strip therefore diminishes sufficiently to convert its coiled or curved condition into the straight or

extended condition. As Eastham and Eassa (1955) emphasize, lateral tension, brought about by transverse curvature, thus results in extension.

Herein lies, according to Eastham and Eassa (1955), the explanation of the extension of the lepidopterous proboscis. When coiled, the proboscis has a flat dorsal surface, and an "equatorial" line drawn across it divides it transversely into upper and lower halves, more or less similar to each other. When extended, the dorsal surface of the proboscis becomes transversely arched, as the dorsal and ventral walls of the galeae become pulled towards each other because of the contraction of the oblique (or diagonal) intrinsic maxillary muscles in the galeae. Contraction of these muscles, in bringing about the change of form in the transverse sectional configuration of the proboscis, subjects the entire dorsal surface of the proboscis to transverse tension. As in the analogous case of the elastic strip, this results in a shortening of the whole of the dorsal longitudinal axis of the proboscis. This shortening of the dorsal surface of the proboscis must have as its further result the straightening out of the hitherto coiled proboscis. But this can only be achieved under conditions of haemocoelic turgidity in the closed galeal and stipital haemocoelae (as in the analogy of the closed, fluid-filled rubber tube) so that the effect can be transmitted along the galeae under these turgid conditions by the compressed, contained haemolymph in the galeae and stipites.

As Eastham and Eassa (1955) assume, it appears probable that in this straightening of the proboscis the elastic, exocuticular, longitudinal dorsal bars in the galeae play an important part in responding to

the effects of lateral tension formerly described. Furthermore, the forces which bring about these changes in form would also seem to put the dorsal linking mechanism of the galeae under some stress, tending to pull the two galeae away from each other in the dorsal line. That this in fact does not occur is undoubtedly due to the firmness of the ventral linking mechanism and to the ability of the mesal walls of the intermediate regions of the galeae to maintain the food channel in its circular shape in both the coiled and extended positions of the proboscis. The circular shape of the food channel, even when the proboscis is coiled in repose, is not correlated with feeding, but is due to the inherent rigidity of its walls. Rigidity in the walls is essential, as they accommodate the dorsal bars by virtue of which alone the proboscis is coiled, without expenditure of energy, when the muscles of all the systems involved in the extension of the proboscis relax. They also provide the strong fulcrum on which the outer walls of the galeae can be flexed by the contraction of the oblique (or diagonal) intrinsic maxillary muscles in the galeae.

Eastham and Eassa (1955) further assume that some slight withdrawal of the overlapping plates of the dorsal linking mechanism of the galeae from each other takes place in the extended proboscis in Pieris. They then also believe that in so far as it happens at all, the food channel will leak along this line during feeding — a leak which they distinctly observed in Pieris, as did the present author in S. partita. Eastham and Eassa (1955) found about 150 large, roughly pear-shaped, unicellular and uninucleate gland cells in the haemocoel of each galea in Pieris. They found that these gland cells open by means of fine

ducts which pass through the cuticular walls of the galeae between the overlapping dorsal plates by which the two galeae are joined dorsally. They therefore suggest that, as these gland cells open into the dorsal juncture of the two galeae, their secretion serves to seal the gaps between the plates of the dorsal linking mechanism at times when the galeae tend to be drawn apart. They furthermore believe that the gland cells also serve to lubricate the dorsal plates as they slide over each other during coiling and extension of the proboscis, because movement is here of a greater magnitude than at the ventral linkage. They draw attention to the fact that, from the mechanical point of view, the compression of the galeal haemocoel by the contraction of the oblique (or diagonal) intrinsic maxillary muscles might well cause the gland cells to pour out their secretion onto the dorsal linkage. This occurs at the moment of extension when their secretion would serve to seal up the gaps in this region and would facilitate the sliding of the dorsal plates. Although the present author also observed a leakage in the food channel along the line of dorsal linkage when S. partita feeds, the absence of gland cells, similar to those of Pieris, leads him to believe that the galeae of this moth is not drawn apart to such an extent during feeding that a secretional sealing is needed for the plates. It may also be that this particular function ascribed to the secretion of the gland cells in Pieris is incorrect. Furthermore, in view of the lubricational function ascribed to the secretion of the gland cells in Pieris and granted that movement during extension and coiling of the proboscis is greater along the dorsal linkage, the present author still finds it incongruous that only the dorsal linking

structures would need lubrication in performing their sliding movements and not also the ventral linking structures which must also move in respect to each other during proboscis extension and coiling. It may be that if sealing and lubrication is really necessary, fruit juice, leaking from the food channel along the line of dorsal linkage during feeding, in itself acts as a sealing and lubrication agent in S. partita. Lubrication would then also be provided for the teeth and hooks of the ventral linkage.

That the galeae in fact tend to be drawn apart during extension of the proboscis was indeed established in S. partita, as Eastham and Eassa (1955) also did in Pieris, because when the two galeae were artificially separated from one another they diverged on being extended. The fact that a single galea can be fully extended may at first seem to involve a different principle from that involved when the two galeae are linked together. However, a comparison of transverse sections through the intermediate regions of the galeae of a proboscis in the coiled condition (fig. 26) and a proboscis in the extended condition (figs. 25 & 27) shows that each galea is separately endowed with a curvature which is dorsally of a greater magnitude when the proboscis is extended, than when it is coiled. A single galea therefore employs similar forces for its extension as those operating for the proboscis as a whole (Eastham & Eassa, 1955).

Full extension of the proboscis is, however, impossible at the "knee-bend", about one-third from the base of the proboscis in the intermediate regions of the galeae in S. partita where the secondary oblique galeal muscles are present in the inner galeal chambers. As has

already been described in detail, contraction of these muscles acts diagonally and antagonistically to the contraction of the primary oblique galeal muscles and results, at this point, in a dorsal curvature of the extended proboscis.

An indirect confirmation of the validity of the theory offered by Eastham and Eassa (1955) on the mechanism of extension of the proboscis in Pieris is furnished by the galeal spines which are externally present on the outer walls of the apical regions of the galeae in S. partita. As has already been described, these galeal spines are utilized for the laceration of the cells of the fruit flesh for releasing the juice on which S. partita feeds. They can, however accomplish this function only when they are in an elevated position. As they are, however, devoid of muscles and are held flush against the outer walls of the apical regions when the proboscis is in the coiled condition, they cannot come to the elevated position of their own accord and they therefore must have some other means of elevation. As has also already been described, pressure experimentally exerted on the galeae at the proximal ends of their apical regions produces a haemolymph pressure within the haemocoel of the apical regions. This causes the evagination of the oval indentations of the outer walls of the apical regions in which the galeal spines are situated, and thus the subsequent elevation of the latter. It is therefore necessary that the haemolymph contained in the galeal haemocoel must be under compression when the proboscis is in the extended position of feeding for the galeal spines to perform their function. From the previous description of the mechanism of extension of the proboscis it is evident that when the probos-

cis is in the extended position, internal haemolymph pressure prevails in the closed galeal and stipital haemocoelae. The necessary means for the elevation of the galeal spines is thus provided, and they remain in the elevated position as long as the proboscis is in the extended condition.

From the preceding descriptions the sequence of actions in S. partita which leads to the extension of the proboscis in preparation for feeding may then be summarized as follows: The tentorio-galeal retractor muscles contract and pull the galeal bases backward and upward under the cranium. By this means the galeal bases (between which the food channel is shaped like a dorsally open gutter) are made to press against the ventral walls of the labrum and labral lobe which here form the roof of the food channel. This act also brings the food channel into effective relation with the functional mouth anteriorly in the cibarial region of the sucking pump. The functional mouth is opened when the anterior frontoclypeus-cibarial dilator muscle by its contraction raise the anterior part of the roof of the cibarial region of the sucking pump.

At the same time the posterior and anterior basal galeal levator muscles and proximal galeal levator muscles contract. Hereby the galeal bases and proximal parts of the intermediate regions of the galeae are elevated because, as a preliminary to proboscis extension, the dorsal walls of the galeal bases are pulled backward in relation to the ventral walls.

By contraction of the geno-stipital adductor muscles and anterior and posterior tentorio-stipital adductor muscles, which pull the stipi-

tal apodemes and parts of the verastipites against the stipital valves, the stipital apertures, and so the stipital and galeal haemocoeles, are closed. Within the closed galeal haemocoeles the primary oblique galeal muscles now contract, pulling the dorsal and ventral walls of the intermediate and apical regions of the galeae towards each other.

Hereby the volumes of the galeal haemocoeles are reduced and internal haemolymph pressure is produced in the galeae and stipites. Conditions of haemocoelic turgidity are so induced in the closed galeal and stipital haemocoeles and a uniform change of form is brought about in the transverse sectional configuration of the proboscis, manifested by a transverse dorsal convexity of the proboscis — in the intermediate and apical regions of the galeae — which is necessary for the extension of the proboscis.

The proboscis now uncoils and becomes rapidly extended, except at the "knee-bend" about one third of its length from the base in the intermediate regions of the galeae. Full extension is here prevented by the contraction of the secondary oblique galeal muscles which acts diagonally and antagonistically to the contraction of the primary oblique galeal muscles, effecting a dorsal curvature in the extended proboscis at this point.

When all the muscle systems involved in the extension of the proboscis relax, pressure on the haemolymph contained in the galeal and stipital haemocoeles are released, the conditions of haemocoelic turgidity within the galeae and stipites are lost, the stipital valves are opened and the haemolymph can now flow freely between the cranial cavity and the galeal haemocoeles. The galeal bases and proximal parts of the intermediate regions of the galeae then move forward and down-

ward, out of effective relation with the now closed functional mouth. By virtue of the elastic properties of the exocuticular, longitudinal dorsal bars, in the mesal walls of the intermediate regions of the galeae, the proboscis now returns to the tightly coiled position of rest underneath the head and between the labial palps.

D. Movements of the Proboscis in Feeding and the Manner of its Insertion into and Extraction from Fruit

After S. partita has discovered and settled on a fruit it extends the proboscis and touches the fruit with the tip of the latter at a point between and slightly behind the fore legs (fig. 46, position A). To move the tip of the proboscis forward (fig. 46, position B) the proximal third of the proboscis, up to the "knee-bend", is elevated and/or the front part of the body is raised. Elevation of the proximal third of the proboscis is effected by the further contraction of the posterior and anterior basal galeal levator muscles and the proximal galeal levator muscles. By straightening the fore legs the front part of the body is raised and this, together with the elevation of the proximal third of the proboscis, causes the proboscis to straighten out completely, and its remaining two-thirds, distal to the "knee-bend", to move forward. Coupled with these movements there are also slight sideways movements of the entire proboscis which are effected by the action of the tentorio-galeal retractor muscles. Very slight but rapid sideways and upward and downward twitching movements are also executed by the apex of the proboscis and are brought about by the action of the primary oblique galeal muscles. All these movements, especially the fact that the angle of the "knee-bend" can be varied, enable the moth

to explore the fruit and find the best place to insert the proboscis.

The actual penetration of the fruit skin and the insertion of the proboscis into the fruit flesh is effected by a straightening of the hind legs and a bending of the fore legs which results in a forward movement of the body and transfer of the body weight onto the extended proboscis. Penetration and insertion is facilitated by the acuteness of the heavily sclerotized galeal tips, as well as by the fact that the one galea is shorter than the other, thus rendering the proboscis tip still more acute. The twitching movements of the proboscis apex may also be of importance in the rupturing of the skin. After the fruit skin has been penetrated, insertion of the proboscis into the flesh is promoted by a rhythmic, sideways rocking movement of the head. This movement of the head results in a barely perceptible waggle of the proboscis which further facilitates its insertion.

The fruit skin is sometimes penetrated while the proboscis tip is in position A (fig. 46), and the proboscis is then inserted for some distance immediately underneath the fruit skin. However, the moth then invariably withdraws the proboscis and moves backward a little so that the terminal part of the proboscis is redirected more vertically downward. Usually, however, penetration and insertion takes place when the proboscis tip is in position B (fig. 46). Insertion of the proboscis is often only partial, in which case the proboscis is then arched forward (fig. 47). At other times insertion is deeper (fig. 48) and occasionally it is so deep that the head nearly touches the fruit surface.

After insertion, intermittent poking movements of the proboscis

at different depths and in slightly different directions in the fruit flesh cause the galeal spines and galeal blades to lacerate the fruit cells for releasing the fruit juice, as has already been described in detail. Partial extraction of the proboscis from the fruit during feeding is effected by the elevation of the proximal third of the proboscis and/or by straightening the fore legs and bending the hind legs. Subsequent straightening of the hind legs and bending of the fore legs again causes insertion of the proboscis. Intake of fruit juice occurs simultaneously with laceration, and continues as long as fruit juice is released. During the period of feeding the proboscis may be inserted at several places in the same fruit.

Feeding may continue for as long as two hours and the proboscis is afterwards returned to its coiled position of rest underneath the head.

VIII. SUMMARYA. Cranial Areas

1. The compound eyes occupy the greater part of the genal areas, laterally on either side of the cranium.
2. The cranial areas surrounding the compound eyes basally are regarded as the genae. They are produced into narrow rims which border on the compound eyes. From the base of these rims the genae project internally, forming the ocular diaphragms which support the ommatidia of the compound eyes. Internally the ocular diaphragms form the central ocular foramina through which the optic lobes pass.
3. The median facial cranial area is regarded as the frontoclypeus as a sutural division into a frons and clypeus is completely absent. The approximate boundary between the clypeal and frontal areas is indicated by the origins of the cibarial, buccal and pharyngeal dilator muscles of the sucking pump on the frontoclypeus.
4. The antennal sockets are situated at the dorsolateral corners of the frontoclypeus and the ventrolateral corners of the vertex. The rims of the antennal sockets are inflected to form circumantennal sclerites which bear the antennifers. The bases of the scapes are connected to the rims of the circumantennal sclerites by antennal membranes. Circumantennal ridges could not be discerned.

5. The median dorsofacial cranial area is regarded as the vertex, which bears the two lateral ocelli. The latter are each provided with an ocellar nerve.
6. The median posterodorsal cranial area is regarded as the occiput.
7. A definite postocciput is absent.
8. The occipital foramen perforates the posterior cranial surface centrally. Approximately across its middle the occipital foramen is bisected by the tentorial bridge. An upper so-called alaforamen through which the oesophagus passes, and a lower so-called neuraforamen through which the salivary ducts and nerve cord pass, are thus formed.
9. The posterior cranial areas which adjoin the occipital foramen and the transverse "beam" of the T-shaped labium on either side are regarded as the postgenae. Their narrow continuations in the ventral cranial region are regarded as the hypostomata which are mesally fused with the cardines and palpifers.
10. The membranous areas in the ventral cranial region, bordered by the labium, cardines, stipites and galeal bases, are termed the ventral cranial membranes.

B. Cranial Sulci and Sutures

1. A clypeolabral sulcus, terminating in the anterior tentorial pits, separates the frontoclypeus from the labrum.

2. Laterofacial sulci, extending between the anterior tentorial pits and the ventrolateral angles of the antennal sockets, separate the frontoclypeus from the facial parts of the genae.
3. A transfrontal suture, extending between the ventral rims of the antennal sockets, separates the vertex from the occiput.
4. An occipital suture, running between the postantennal sulci, separates the vertex from the occiput.
5. A postoccipital suture, terminating in the posterior tentorial pits and bordering the so-called alaforamen dorsally and laterally, limits the occiput posteriorly.
6. The sulci which run between the postoccipital sutures and the dorsolateral angles of the antennal sockets, and which separate the vertex from the dorsofacial parts of the genae and the occiput from the postgenae, are regarded as the postantennal sulci.
7. Definite sutures, extending between the postantennal sulci and the anterior fusion of the hypostomata with the anterolateral hypopharyngeal extensions, limit the postgenae and hypostomata laterally. Those parts of the sutures which separate the postgenae from the posterior parts of the genae are regarded as the postgenal sutures. The continuations of these sutures in the ventral cranial region, which separate the hypostomata from the ventral parts of the genae and from the mandibles, are regarded as the hypostomal sutures.

C. Tentorium

1. The tentorium is pi-shaped and consists of the paired anterior tentorial arms and the tentorial bridge.
2. The anterior tentorial arms arise from the anterior tentorial pits in the ventrofacial region at the junctions of the clypeolabral sulcus with the laterofacial sulci, dorsomedial to the mandibles. Next to the sucking pump they are dorsally expanded into flanges.
3. Each anterior tentorial arm gives attachment to four extrinsic antennal muscles and three extrinsic maxillary muscles.
4. The tentorial bridge, representing the medially fused posterior tentorial arms which arise from the posterior tentorial pits in the postgenae at the ventrolateral corners of the so-called alaforamen, divides the occipital foramen transversely.
5. On the tentorial bridge occur the occipital condyles, immediately dorsomesal to the posterior tentorial pits.

D. Cranial Appendages

1. The antennae are setaceous in both sexes, and among individuals the flagellar segments vary in number from 95 to 97. The antennae are each provided with an antennal nerve.
2. The labrum is present in the ventrofacial region as a fixed part of the cranium and is dorsally separated from the frontoclypeus by the clypeolabral sulcus. On its ventrolateral extremities it

is produced into bristled pilifers, and ventromedially it is expanded into a rounded labral lobe. Ventrally the labrum and labral lobe is folded back into the cranial capsule and is joined to the epipharynx which is continued posteriorly as the roof of the sucking pump.

3. The vestigial mandibles are non-functional. They are immovably fused to the genae, ventrolateral to the anterior tentorial pits and appear as small, tooth-like elevations.
4. The maxillae consist of the paired cardines, stipites and galeae. The cardines are simple, quadrangular plates, whereas the stipites are elongated, tubular and tripartite. Each stipite consists of a flat, exocuticular, mesal juxtastipes which is internally demarcated by an exocuticular stipital apodeme from a gutter-shaped, exocuticular verastipes. The latter is separated by a flexible endocuticular stipital groove from the reflected, exocuticular, lateral palpifer. The ventrolaterally projecting part of the wall of the palpifer forms the stipital valve. The stipital valve forms the lateral wall of the stipital aperture, whose mesal wall is formed by the stipital apodeme and by part of the verastipes. Anterolaterally each palpifer bears a vestigial, one-segmented, pubescent maxillary palp.
5. The strong, much elongated, tubular, distally tapering, terminally closed and sharply pointed galeae vary in length from 12.4 mm. to 13.2 mm. among individuals and are firmly linked together to form the suctorial proboscis. Each galea is provided with a ga-

leal nerve, the latter which innervates the extrinsic and intrinsic maxillary muscles.

6. Between them the linked galeae form the cylindrical food channel through which fruit juice is imbibed. Proximally the food channel is shaped like a dorsally open gutter, overhung by the labrum and labral lobe which here form its roof.
7. Each galea is divided into three regions, a proximal, an intermediate or coilable and an apical region.
8. The proximal region of the galea, the galeal base, does not take part in the coiling process. Its proximal part consists of exocuticle, being separated from a similar distal part by an intermediate zone of flexible endocuticle which permits the elevation and the lowering of the galeal base.
9. The outer (anterodorsal, lateral and posteroventral) wall of the intermediate or coilable region of the galea consists of flexible endocuticle in which transversely arranged, sensilla bearing exocuticular ribs are embedded. This particular cuticular composition of the outer walls of the intermediate regions of the galeae permits changes in shape to take place during coiling and extension of the proboscis. The concave mesal (inner) walls of the intermediate and apical regions of the galea are composed of a series of regularly arranged, nearly contiguous, transverse exocuticular bars which impart a ribbed appearance to the walls of the food channel. The exocuticular bars are underlain internally

by endocuticle which is continuous with that of the outer walls. The exocuticular bars consist of regularly arranged, closely packed laminae to which the walls of the food channel owe the ability to adapt themselves to changes undergone during coiling and extension of the proboscis. The ribbed structure of the mesal walls of the intermediate and apical regions of the galeae also restricts free coiling and extension movements of the proboscis to the vertical plane, and ensures that a circular transverse section of the food channel is maintained in both the coiled and extended conditions of the proboscis.

10. The exocuticular bars of the mesal walls of the intermediate and apical regions of the galeae are associated with the structures which form the dorsal and ventral linking mechanisms of the galeae. Dorsally each exocuticular bar is continued to form an oblique, distally directed, exocuticular plate, and ventrally every three exocuticular bars apparently become fused to form an oblique, distally directed, exocuticular process which bears an upper tooth and a lower hook. The contiguous plates of one galea overlap those of the other galea, whereas the contiguous teeth and hooks of one galea interlock with those of the other galea. The dorsal and ventral linking structures ensure that the food channel always stays closed dorsally and ventrally during all changes in attitude of the proboscis, and because the linking structures are directed obliquely forward, the sliding movements which they must perform during movement of the proboscis are permitted.

11. Dorsally, before the point where the structures forming the dorsal linking mechanism arise, the exocuticular bars of the mesal wall of the intermediate region of the galea apparently all independently become partly fused to form an elastic, exocuticular, longitudinal dorsal bar. In these dorsal bars of the galeae rest the elastic properties on which the ability of the proboscis to come to rest in the coiled position depends.
12. The outer walls and extreme distal part of the mesal wall of the apical region of the galea are strongly reinforced, being composed of exocuticle externally and endocuticle internally. It tapers to a closed, sharply pointed tip which enables S. partita to pierce the intact skin and flesh of sound fruit. This region of the galea is modified and bears externally on its outer wall 40 to 60 galeal blades and 26 to 30 galeal spines by means of which the cells of the fruit flesh are lacerated for releasing the fruit juice. The sturdy galeal spines, which are rigid and elevated when the proboscis is in the extended position of feeding, are the principal lacerating agents of the intact cells of the sound fruit flesh, whereas the more mobile galeal blades are apparently only capable of further breaking up of cells already damaged by the galeal spines.
13. The haemocoele of the intermediate region of the galea is divided into an outer and inner galeal chamber by a vertical, longitudinal galeal septum. The galeal septa to some extent control the movements and determine the shape of the outer walls of the interme-

mediate regions of the galeae in the coiled and extended conditions of the proboscis.

14. From four to seven trichoid sensilla, which are perhaps gustatory in function, are present in the mesal wall of the intermediate region of each galea and project into the food channel.
15. The labium, which is immovably fixed in the ventral cranial region, is T-shaped and can be distinguished from bordering cranial areas by its degree of sclerotization. Its longitudinal "stem" is anteriorly attached to the anterior margin of the hypopharyngeal part of the floor of the sucking pump. The lateral margins of its "stem" and the anterior margins of its transverse "beam" are connected to the ventral cranial membranes. The anterolateral angles of the "beam" are in contact with the posteromesal angles of the cardines, while its lateral margins are connected to the postgenae. Its posterior edge borders on the neuroforamen, a "hypostomal bridge" being absent. The "beam" bears two, three-segmented labial palps which are normally applied closely to the anterior surface of the head. Each labial palp is provided with a labial nerve and the terminal segment bears an internal, apical sensory pit.

E. Musculature of the Cranium and its Appendages

1. The antennae are each provided with two extrinsic depressor and two extrinsic levator muscles which by their action move the entire antenna. Each antenna is also provided with one intrinsic

depressor and one intrinsic levator muscle which by their action move the pedicel and flagellum.

2. The stipites are each provided with three extrinsic adductor maxillary muscles. By contraction these muscles close the stipital valves and disrupt the connection between the haemolymph contained in the stipital and galeal haemocoelae and that contained in the cranial cavity.
3. The galeae are each provided with one extrinsic retractor maxillary muscle. By contraction these muscles draw the bases of the galeae backward and upward as a preliminary to feeding. Their action is also responsible for the slight sideways movements executed by the proboscis in the horizontal plane when S. partita senses a food source.
4. Five separate intrinsic maxillary muscles are present in each galea. Two are levator muscles in the galeal base, and by their contraction the proximal regions of the galeae are elevated. A third is a levator muscle present in the most proximal part of the intermediate region of the galea. By their contraction the most proximal parts of the intermediate regions of the galeae are elevated. The fourth is the oblique or diagonal muscle, the primary oblique galeal muscle, whose fibres are present as a series in the galea, occupying the outer galeal chamber of the intermediate region and the haemocoelae of the apical region. By their contraction the dorsal and ventral walls of the intermediate and

apical regions of the galeae are pulled towards each other. The action of the fibres in the apical regions of the galeae is also responsible for the slight sideways and upward and downward twitching and searching movements of the apex of the extended proboscis when S. partita senses a food source. The fifth is the secondary oblique galeal muscle in the inner galeal chamber of the intermediate region of the galea at a point about one-third of the latter's length from the base. The forces of contraction of these muscles act diagonally and antagonistically to those of the primary oblique galeal muscles, having in effect a dorsal curvature, the "knee-bend", at this point in the extended proboscis. The angle of the "knee-bend" is variable and the moth is by this means enabled to explore the fruit and find the best place to insert the proboscis.

5. The labial palps are each provided with one extrinsic abductor and one intrinsic depressor muscle. By contraction of the abductor muscles the labial palps are abducted when the proboscis is being extended or coiled, and by contraction of the depressor muscles the second and terminal palp segments are depressed and drawn away from the facial region of the head.

F. Sucking Pump

1. Anteriorly the sucking pump communicates by means of the functional mouth with the food channel via the food meatus. Posteriorly it narrows to merge with and to open into the oesophagus.

2. The floor of the sucking pump is in the form of a fixed, exocuticular plate. That the anterior part of the sucking pump floor is hypopharyngeal in origin, is indicated by the position of the salivary duct aperture, by the origin of the salivary duct dilator muscles and by the location of the hypopharyngeal suspensoria.
3. By means of the anterolateral hypopharyngeal extensions, which represent transformed hypopharyngeal suspensoria, the floor of the sucking pump is connected to the hypostomata. The anterior margin of the hypopharyngeal part of the floor of the sucking pump is connected to the anterior margin of the "stem" of the T-shaped labium by means of endocuticle. Medially, at this junction, the salivary duct opens into the cibarial region of the sucking pump.
4. The roof of the sucking pump consists of flexible endocuticle and is the internal continuation of the epipharynx.
5. The sucking pump is comprised of three different regions, viz., an anterior cibarial region, an intermediate buccal region and a posterior pharyngeal region. The identification of these different regions of the sucking pump is based on the location of the frontal ganglion and on the identification of the extrinsic dilator muscles inserted on its roof.
6. The extrinsic muscles of the sucking pump act as dorsal dilators. They consist of unpaired and paired cibarial dilator muscles, paired buccal dilator muscles and paired, double bundled pharyngeal dilator muscles.

7. The intrinsic muscles of the sucking pump act as compressors. They consist of an unpaired cibarial compressor muscle, an unpaired and two paired buccal compressor muscles and an unpaired pharyngeal compressor muscle.
8. By means of the sucking pump fruit juice is imbibed. Contraction of the pharyngeal compressor muscle closes the opening of the sucking pump into the oesophagus. By the subsequent contraction of all the extrinsic dilator muscles the functional mouth is opened and the roof of the sucking pump is raised. The volume of the sucking pump cavity is thus enlarged, the air pressure within reduced and a suction power created. Fruit juice is then drawn through the food channel, via the food meatus and functional mouth, into the zone of negative pressure in the sucking pump. When the pump cavity is filled with juice all the extrinsic dilator muscles relax and the cibarial compressor muscle by its contraction closes the functional mouth. By the subsequent relaxation of the pharyngeal compressor muscle the exit of the sucking pump into the oesophagus is opened. Contraction of the rest of the intrinsic compressor muscles then reduces the volume of the sucking pump cavity, forcing the imbibed fruit juice backward into the oesophagus.
9. The muscles of the sucking pump is innervated by two pairs of nerves. A ventral pair of sucking pump nerves embrace the sucking pump laterally. A dorsal pair of frontal ganglion connectives unite with the frontal ganglion dorsally on the sucking pump.

G. Extension and Coiling of the Proboscis

1. Extension of the proboscis is the consequence of a change of form in its transverse sectional configuration, manifested by a transverse dorsal convexity in the intermediate and apical regions of the galeae. It is brought about by the contraction of the oblique (or diagonal) intrinsic maxillary muscles in the galeae which draw the dorsal and ventral walls of the intermediate and apical regions of the galeae towards each other. This change of form in the proboscis is, however, possible and will lead to the straightening out of the coiled proboscis, only under conditions of haemocoelic turgidity in the closed galeal and stipital haemocoeles. Conditions of haemocoelic turgidity are induced by an internal pressure which is produced in the haemolymph contained in the galeae and stipites, because when the oblique intrinsic maxillary muscles by their contraction draw the dorsal and ventral walls of the intermediate and apical regions of the galeae towards each other, the volumes of the galeal haemocoeles are reduced and the contained haemolymph is put under compression. The formation of conditions of haemocoelic turgidity is permitted and maintained in the closed galeal and stipital haemocoeles by the closed stipital valves. Closure of the stipital valves is brought about by the contraction of the extrinsic maxillary muscles which are inserted on the stipital apodemes.
2. The proboscis is coiled by virtue of the elastic properties of the exocuticular, longitudinal dorsal bars, in the mesal walls of

the intermediate regions of the galeae, when the muscle systems involved in the extension of the proboscis relax.

H. Insertion and Extraction of the Proboscis

1. The penetration of fruit skin and the insertion of the proboscis into fruit flesh is effected by a straightening of the hind legs and a bending of the fore legs whereby the body weight is transferred onto the extended proboscis. Penetration and insertion is facilitated by the acuteness and unequal length of the heavily sclerotized galeal tips. Insertion is further promoted by a rhythmic sideways rocking movement of the head.
2. Extraction of the proboscis from fruit is effected by the elevation of the proximal third of the proboscis and/or by straightening the fore legs and bending the hind legs.

I. Laceration of Fruit Flesh Cells

1. The cells of fruit flesh are lacerated, for releasing the fruit juice on which S. partita feeds, by means of the sturdy galeal spines (which are rigid and elevated when the proboscis is in the extended position of feeding) and to some extent by means of the more mobile galeal blades (which are apparently only capable of further breaking up of cells already damaged by the galeal spines), externally on the apical regions of the galeae. To effect the process of laceration, after insertion of the proboscis into the fruit flesh, intermittent poking movements of the proboscis are performed during the entire process of feeding.

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XI. FIGURES

- 1 - Frontal view of the cranium with the left antenna removed.
- 2 - Lateral view of the cranium with the proboscis coils slightly opened.
- 3 - Dorsal view of the cranium with the left antenna removed.
- 4 - Ventral view of the cranium with the labial palps removed.
- 5 - Posterior view of the cranium.
- 6 - Lateral view of the cranium with the left compound eye removed.
- 7 - Ventral (external) view of the right cardo, stipes, galeal base and proximal part of the intermediate region of the galea; A-A indicates the position where the transverse section illustrated in figure 22 was cut.
- 8 - Dorsal (internal) view of the right cardo, stipes, galeal base and proximal part of the intermediate region of the galea; A-A indicates the position where the transverse section illustrated in figure 22 was cut.
- 9 - Lateral view of the apical region and distal part of the intermediate region of the left galea and the mesal aspect of the extreme tip of the apical region of the right galea.
- 10 - Dorsal (internal) view of the labium and basal labial palp segments.
- 11 - Dorsal (internal) view of the floor of the sucking pump.
- 12 - Lateral view of the apical flagellar segments of an antenna.
- 13 - Frontal view of the cranium with the facial parts of the genae and the greater part of the frontoclypeus removed.

- 14 - Lateral view of the cranium with the left compound eye, ocular diaphragm and part of the optic lobe removed.
- 15 - Lateral aspect of the cranium with the left compound eye, ocular diaphragm, part of the optic lobe and the geno-stipital adductor muscle removed.
- 16 - Interior view of the right side of the cranium (cranial capsule having been cut through in the sagittal plane, lateral to the left maxilla).
- 17 - Interior view of the right half of the cranium, right scape and part of the right basal labial palp segment (cranial capsule having been cut through along the median sagittal line with the sucking pump, oesophagus, salivary duct and brain removed).
- 18 - Ventral view of the cranium with the maxillae, labium, ventral cranial membranes and extrinsic maxillary muscles removed.
- 19 - Transverse section through the posterior part of the left stipes, near its fusion with the cardo.
- 20 - Transverse section through the middle of the left stipes.
- 21 - Transverse section through the anterior part of the left stipes, near its fusion with the galeal base.
- 22 - Transverse section through the left stipes and left galeal base at their point of fusion (section cut at position A-A shown in figures 7 and 8).
- 23 - Transverse section through the middle of the left galeal base.
- 24 - Transverse section of the proboscis through the proximal parts of the intermediate regions of the galeae.
- 25 - Transverse section of the extended proboscis through the intermediate regions of the galeae, posterior to the "knee-bend".

- 26 - Transverse section of the coiled proboscis through the intermediate regions of the galeae at the "knee-bend".
- 27 - Transverse section of the extended proboscis through the intermediate regions of the galeae, anterior to the "knee-bend".
- 28 - Transverse section of the coiled proboscis through the distal parts of the intermediate regions of the galeae.
- 29 - Sagittal section through the base and proximal part of the intermediate region of a galea at the point where the galeal trachea and galeal nerve pass into the galeal haemocoel.
- 30 - Median sagittal section through the cranium and the base and proximal part of the intermediate region of a galea in the coiled position of rest with a relaxed proximal galeal levator muscle, anterior and posterior basal galeal levator muscles and a folded ventral wall of the zone of endocuticle of the galeal base, a relaxed tentorio-galeal retractor muscle and a large food meatus, a relaxed anterior frontoclypeus-cibarial dilator muscle, a contracted cibarial compressor muscle and a closed functional mouth.
- 31 - Median sagittal section through the cranium and the base and proximal part of the intermediate region of a galea in the extended position of feeding with a contracted proximal galeal levator muscle, anterior and posterior basal galeal levator muscles and a folded dorsal wall of the zone of endocuticle of the galeal base, a contracted tentorio-galeal retractor muscle and a small food meatus, a relaxed cibarial compressor muscle, a contracted anterior frontoclypeus-cibarial dilator muscle and a fully opened functional mouth.
- 32 - Sagittal section through part of the intermediate region of a galea in the coiled position of rest with relaxed primary oblique galeal muscle fibres.

- 32A - Sagittal section through part of the outer posteroventral wall of the intermediate region of a galea in the coiled position of rest.
- 33 - Sagittal section through part of the intermediate region of a galea in the extended position of feeding with contracted primary oblique galeal muscle fibres.
- 33A - Sagittal section through part of the outer posteroventral wall of the intermediate region of a galea in the extended position of feeding.
- 34 - Sagittal section through part of the apical region of a galea.
- 35 - Sagittal section through the tip of the apical region of a galea.
- 36 - Tangential section through the outer lateral wall of part of the intermediate region of a galea.
- 37 - Tangential section through the mesal wall of part of the intermediate region of a galea.
- 37A - Diagrammatic representation of a tangential section through the exocuticular bars of the mesal wall of part of the intermediate region of a galea.
- 38 - Composite frontal section for a short length of the intermediate regions of the galeae through the structures of the dorsal linking mechanism.
- 39 - Composite frontal section for a short length of the intermediate regions of the galeae through the structures of the ventral linking mechanism.
- 40 - Transverse section of part of the mesal wall of the intermediate region of a galea through a trichoid sensillum.
- 41 - Frontal section through part of the cranium, galeal bases and

proximal parts of the intermediate regions of the cranium.

- 42 - Transverse section of the cranium through the middle of the cibarial region of the sucking pump and posterior parts of the galeal bases.
- 43 - Frontal section through the organs in the roof of the cibarial region of the sucking pump.
- 44 - Diagram of part of the coiled proboscis to show the components of force exerted by the primary oblique galeal muscles when they contract.
- 45 - Diagram of part of the coiled proboscis to show the components of force exerted by the secondary oblique galeal muscles when they contract.
- 46 - S. partita reposing on a fruit with the proboscis extended and illustrated in the approximate extreme posterior position (A) (the point where the proboscis tip touches the fruit surface after uncoiling) and anterior position (B) (the point to which the proboscis tip can be moved after uncoiling, from position A, without a positional movement of the body), prior to insertion into the fruit flesh.
- 47 - S. partita reposing on a fruit with the proboscis partly inserted.
- 48 - S. partita reposing on a fruit with the proboscis nearly completely inserted.

XII. ABBREVIATIONS

- a1 - horizontal longitudinal component of force exerted at the insertions of the primary oblique galeal muscles when they contract
- a2 - horizontal longitudinal component of force exerted at the origins of the primary oblique galeal muscles when they contract
- a3 - horizontal longitudinal component of force exerted at the insertions of the secondary oblique galeal muscles when they contract
- a4 - horizontal longitudinal component of force exerted at the origins of the secondary oblique galeal muscles when they contract
- a.bs.gl.lev.m - anterior basal galeal levator muscle
- afor - alafortamen
- a.frclp.cib.dil.m - anterior frontoclypeus-cibarial dilator muscle
- al.hyp.ext - anterolateral hypopharyngeal extension
- anf - antennifer
- ant.mem - antennal membrane
- ant.n - antennal nerve
- ant.soc - antennal socket
- a.tnt.am - anterior tentorial arm
- a.tnt.ant.dep.m - anterior tentorio-antennal depressor muscle
- a.tnt.ant.lev.m - anterior tentorio-antennal levator muscle
- a.tnt.pt - anterior tentorial pit
- a.tnt.st.add.m - anterior tentorio-stipital adductor muscle
- att.lb.plp - attachment of labial palp
- b1 - horizontal transverse component of force exerted at the insertions of the primary oblique galeal muscles when they contract
- b2 - horizontal transverse component of force exerted at the origins of the primary oblique galeal muscles when they contract

- b3 - horizontal transverse component of force exerted at the insertions of the secondary oblique galeal muscles when they contract
- b4 - horizontal transverse component of force exerted at the origins of the secondary oblique galeal muscles when they contract
- br - bristle
- brn - brain
- buc.rgn - buccal region
- c1 - vertical transverse component of force exerted at the insertions of the primary oblique galeal muscles when they contract
- c2 - vertical transverse component of force exerted at the origins of the primary oblique galeal muscles when they contract
- c3 - vertical transverse component of force exerted at the insertions of the secondary oblique galeal muscles when they contract (negligible)
- c4 - vertical transverse component of force exerted at the origins of the secondary oblique galeal muscles when they contract (negligible)
- cant.scl - circumantennal sclerite
- cd - cardo
- cib.comp.m - cibarial compressor muscle
- cib.rgn - cibarial region
- clplbr.rdg - clypeolabral ridge
- clplbr.su - clypeolabral sulcus
- cpd.e - compound eye
- crcf.buc.comp.m - cruciform buccal compressor muscle
- d.bar - dorsal bar
- d.fg - dorsal flange
- enc - endocuticle

enc₁ - intermediate zone of endocuticle in the galeal base
enc.fld - endocuticular fold
exc - exocuticle
exc.bar - exocuticular bar
exc.rb - exocuticular rib
f.chl - food channel
flg - flagellum
flr.sck.pmp - floor of sucking pump
f.mts - food meatus
frclp - frontoclypeus
frclp.ph.dil.m - frontoclypeus-pharyngeal dilator muscle
fr.gng - frontal ganglion
fr.gng.conn - frontal ganglion connective
frt - fruit
func.mth - functional mouth
ge - gena
ge.st.add.m - geno-stipital adductor muscle
gl - galea
gl.b - galeal base
gl.bld - galeal blade
gl.hmc - galeal haemocoele
gl.hr - galeal hair
gl.n - galeal nerve
gl.sens - galeal sensillum
gl.sp - galeal spine
gl.spt - galeal septum

gl.tr - galeal trachea
grn.cnt - granular contents
hk - hook
hpd - hypodermis
hpd.sht - hypodermal sheath
hps - hypostoma
hps.s - hypostomal suture
hyp.slv.dct.dil.m - hypopharyngeal-salivary duct dilator muscle
in.gl.chm - inner galeal chamber
jxst - juxtastipes
k.b - "knee-bend"
lam - lamina
lb - labium
lb.n - labial nerve
lb.plp - labial palp
lb.plp.abd.m - labial palp abductor muscle
lb.plp.dep.m - labial palp depressor muscle
lbr - labrum
lbr.lob - labral lobe
l.buc.comp.m - lateral buccal compressor muscle
lfc.rdg - laterofacial ridge
lfc.su - laterofacial sulcus
l.frclp.buc.dil.m - lateral frontoclypeus-buccal dilator muscle
md - mandible
mx.plp - maxillary palp
nfor - neuroforamen

o - ocellus
occ - occiput
occ.con - occipital condyle
occ.s - occipital suture
oc.dph - ocular diaphragm
oc.for - ocular foramen
oes - oesophagus
o.n - ocellar nerve
opt.lob - optic lobe
ot.gl.chm - outer galeal chamber
pant.rdg - postantennal ridge
pant.su - postantennal sulcus
p.bs.gl.lev.m - posterior basal galeal levator muscle
pde - pedicel
pf - pilifer
p.frclp.cib.dil.m - posterior frontoclypeus-cibarial dilator muscle
pge - postgena
pge.inf - postgenal inflection
pge.s - postgenal suture
ph.comp.m - pharyngeal compressor muscle
ph.rgn - pharyngeal region
plf - palpifer
plt - plate
pocc.inf - postoccipital inflection
pocc.s - postoccipital suture
prm.obl.gl.m - primary oblique galeal muscle

p.tnt.ant.dep.m - posterior tentorio-antennal depressor muscle
p.tnt.ant.lev.m - posterior tentorio-antennal levator muscle
p.tnt.pt - posterior tentorial pit
p.tnt.st.add.m - posterior tentorio-stipital adductor muscle
px - proximal
px.gl.lev.m - proximal galeal levator muscle
rf.sck.pmp - roof of sucking pump
sck.pmp.n - sucking pump nerve
scp - scape
scp.pde.dep.m - scape-pedicel depressor muscle
scp.pde.lev.m - scape-pedicel levator muscle
se - seta
sec.obl.gl.m - secondary oblique galeal muscle
sens.pt - sensory pit
sens.se - sensory seta
slv.dct - salivary duct
sn.cl.ext - sense cell extension
soes.gng - suboesophageal ganglion
st - stipes
st.apd - stipital apodeme
st.apd - stipital aperture
st.grv - stipital groove
st.hmc - stipital haemocoele
st.vlv - stipital valve
tfr.s - transfrontal suture
th - tooth

tnt.brg - tentorial bridge

tnt.gl.ret.m - tentorio-galeal retractor muscle

trhm - trichium

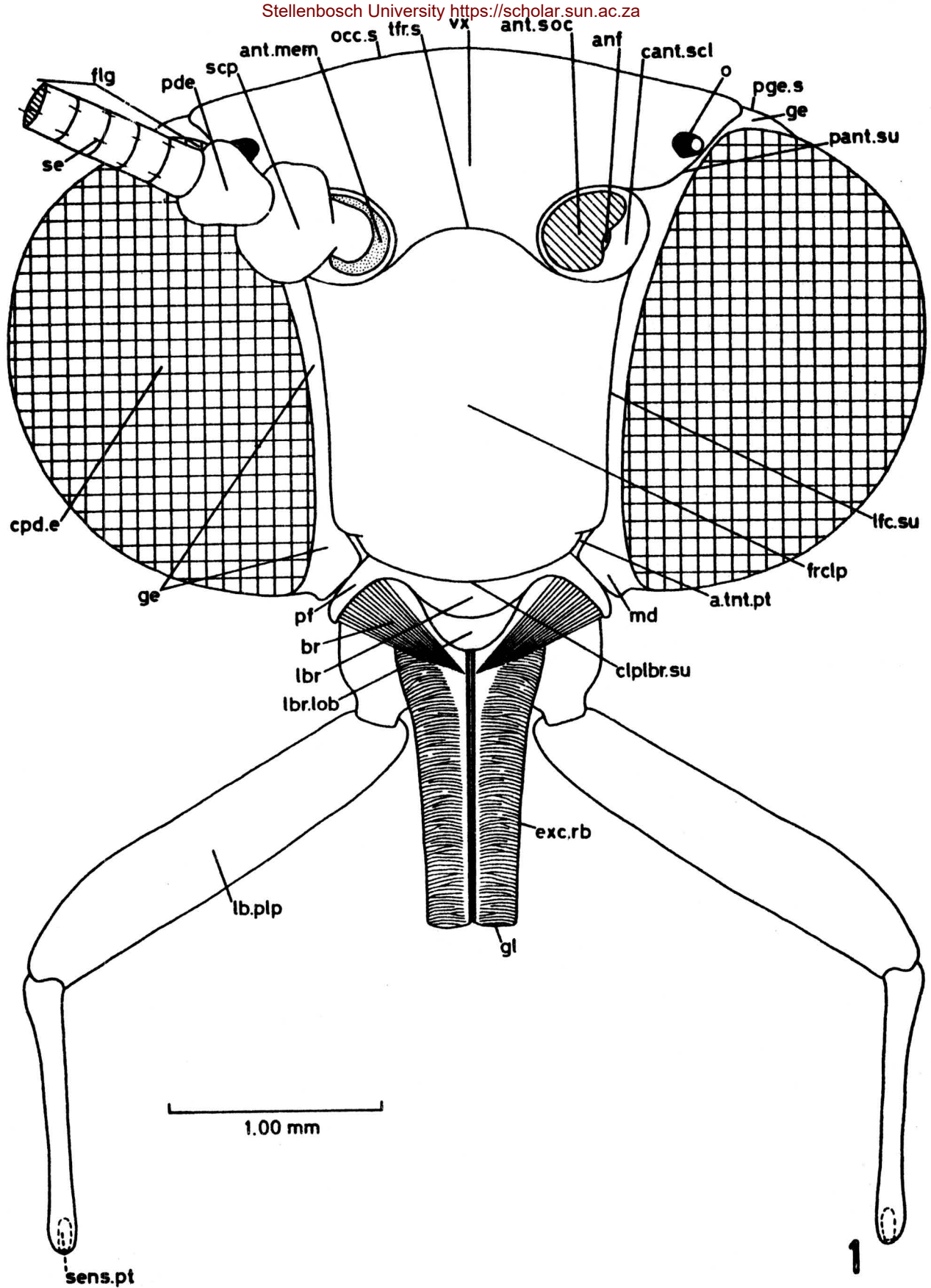
v.buc.comp.m - ventral buccal compressor muscle

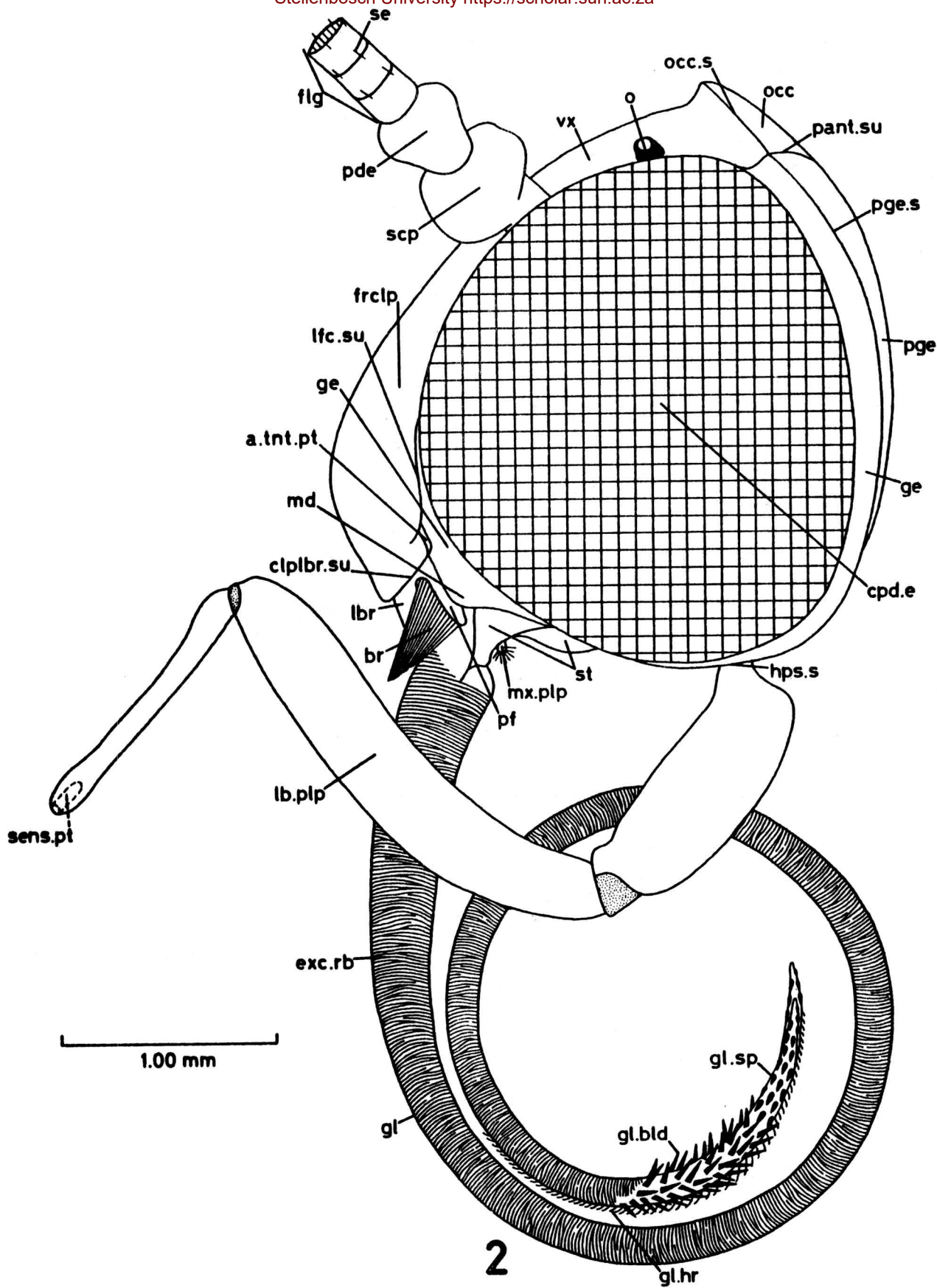
v.cr.mem - ventral cranial membrane

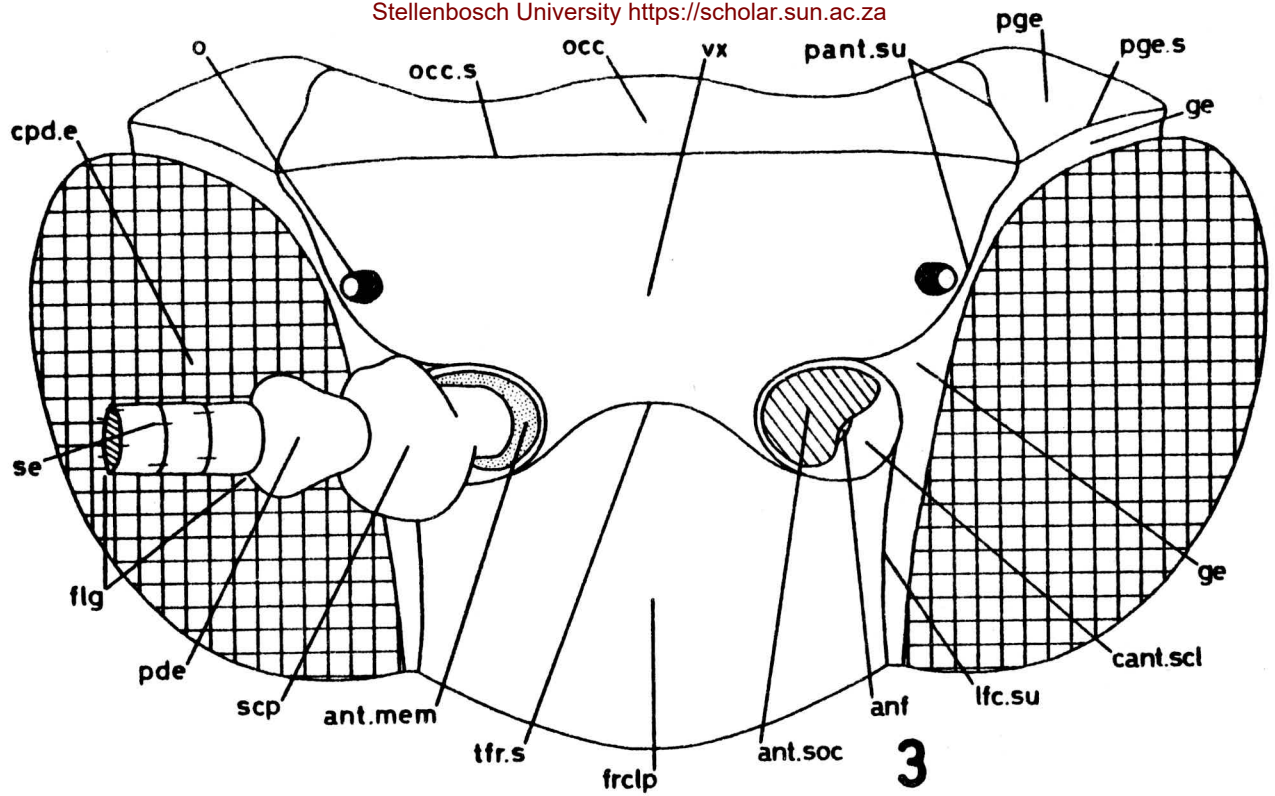
vlv.fld - valvular fold

vrst - verastipes

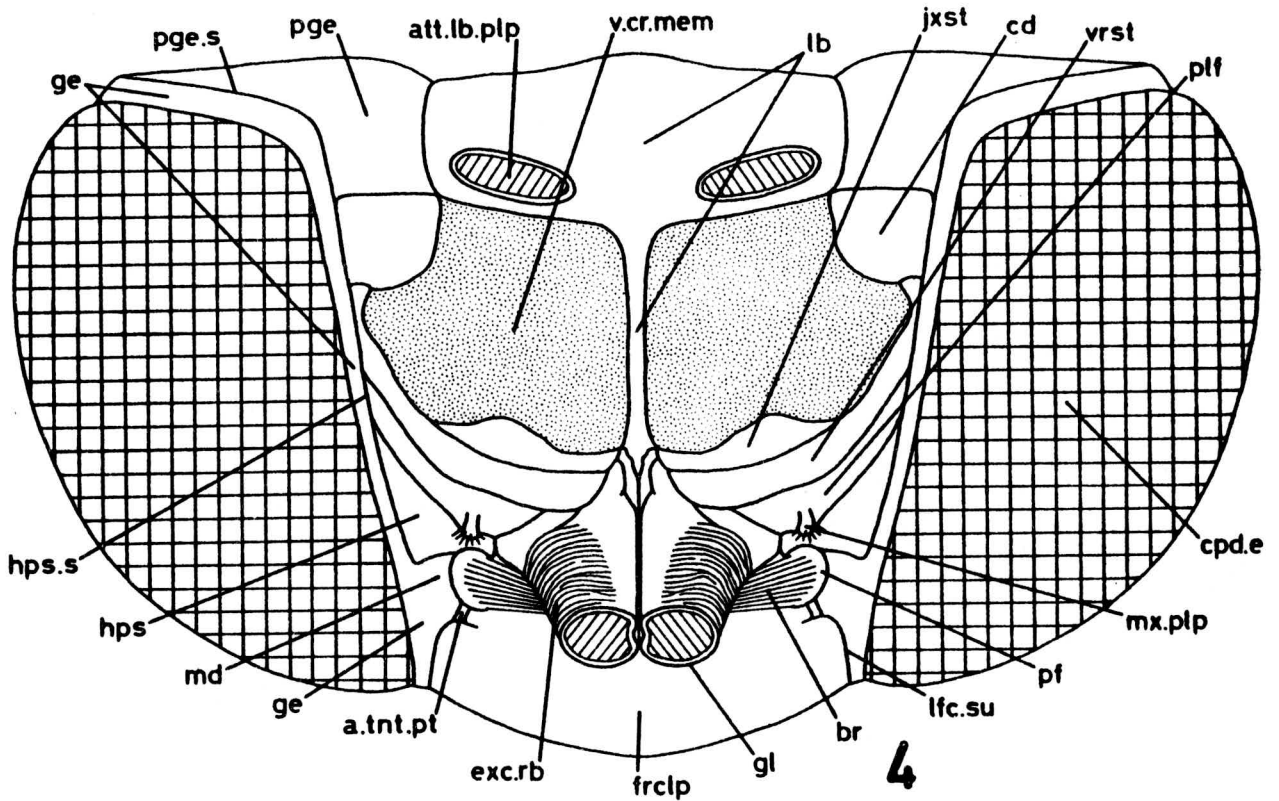
vx - vertex

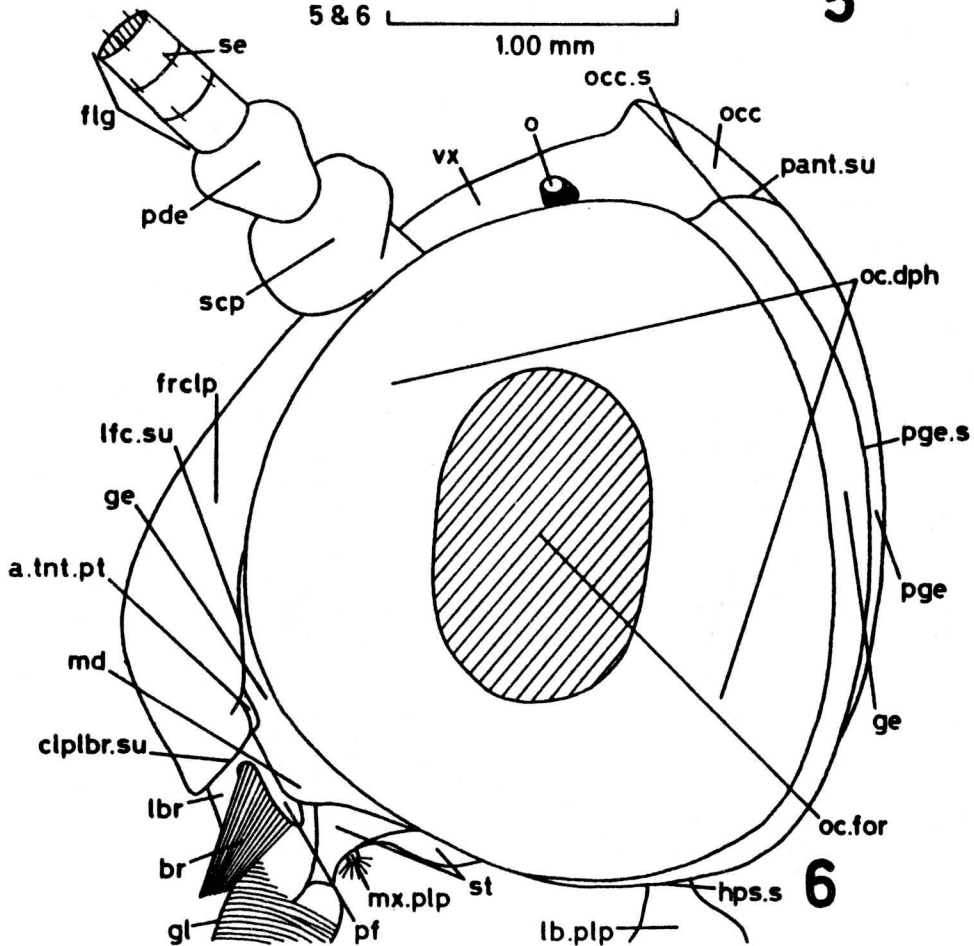
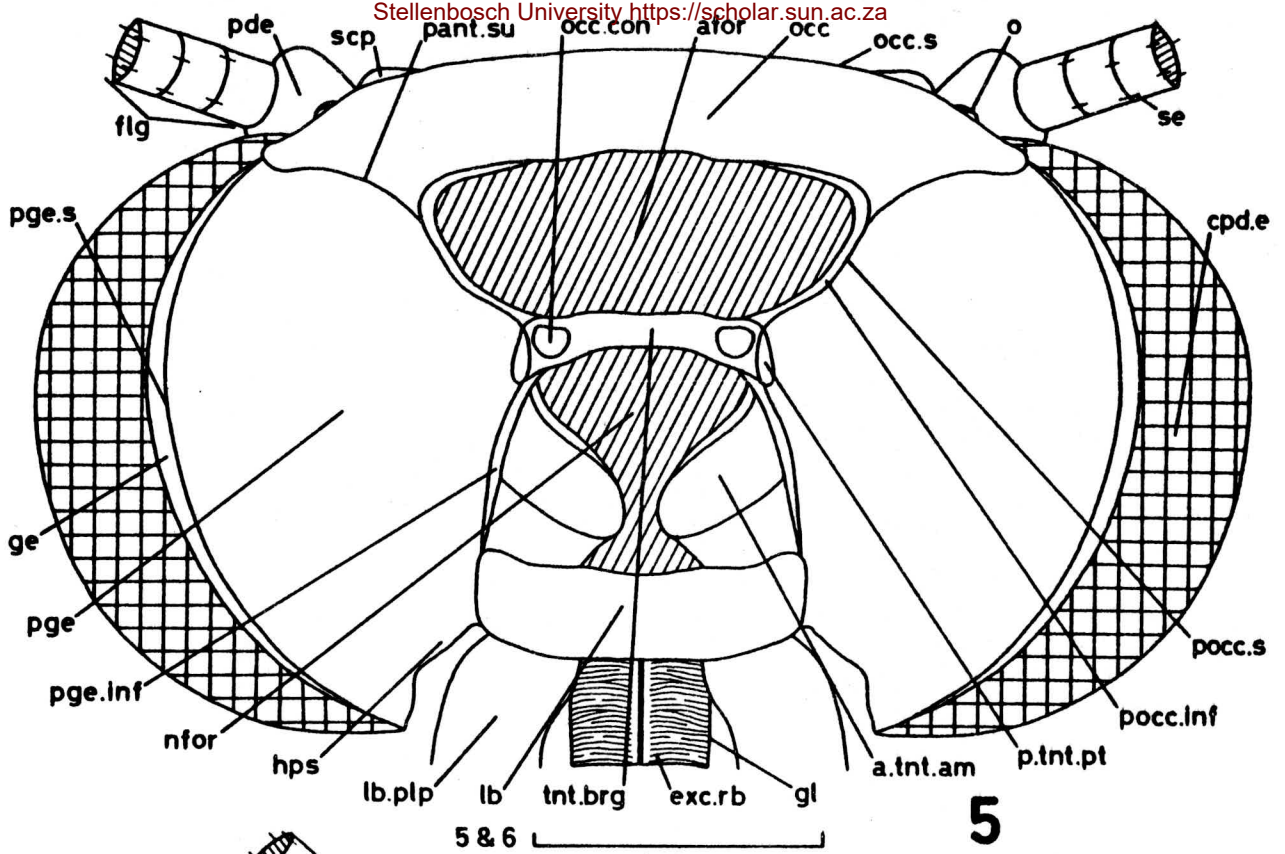


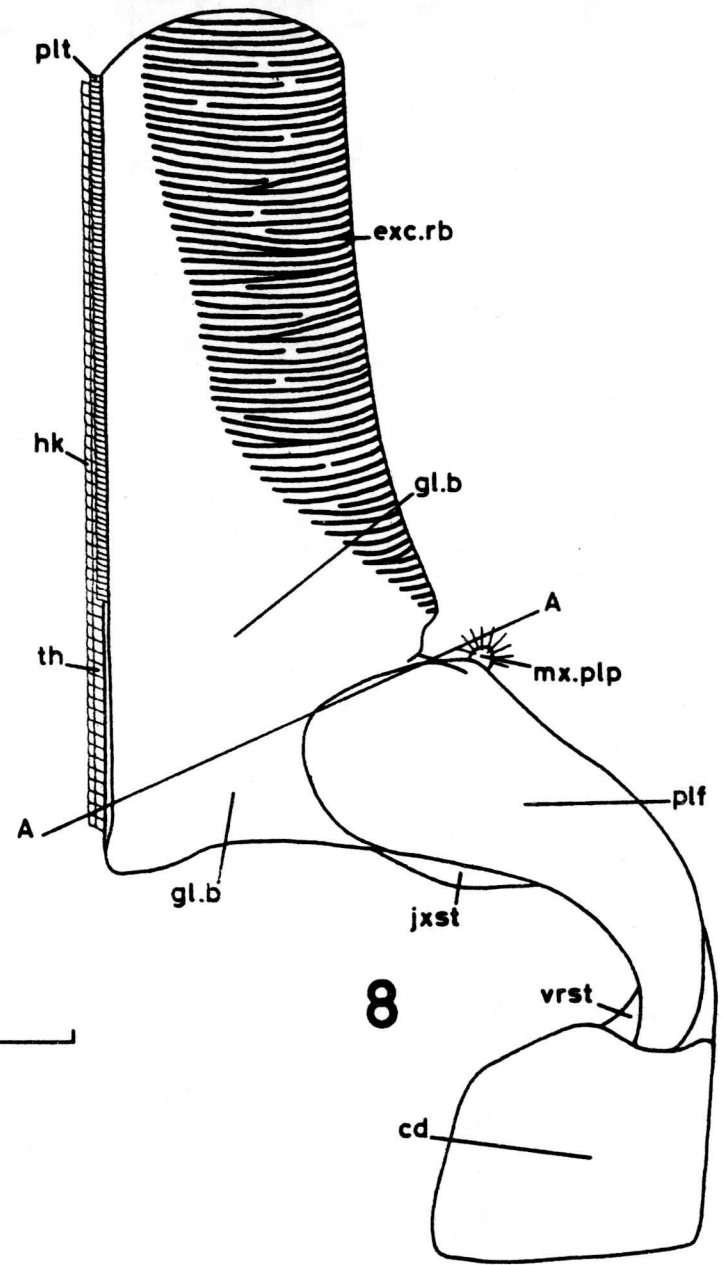
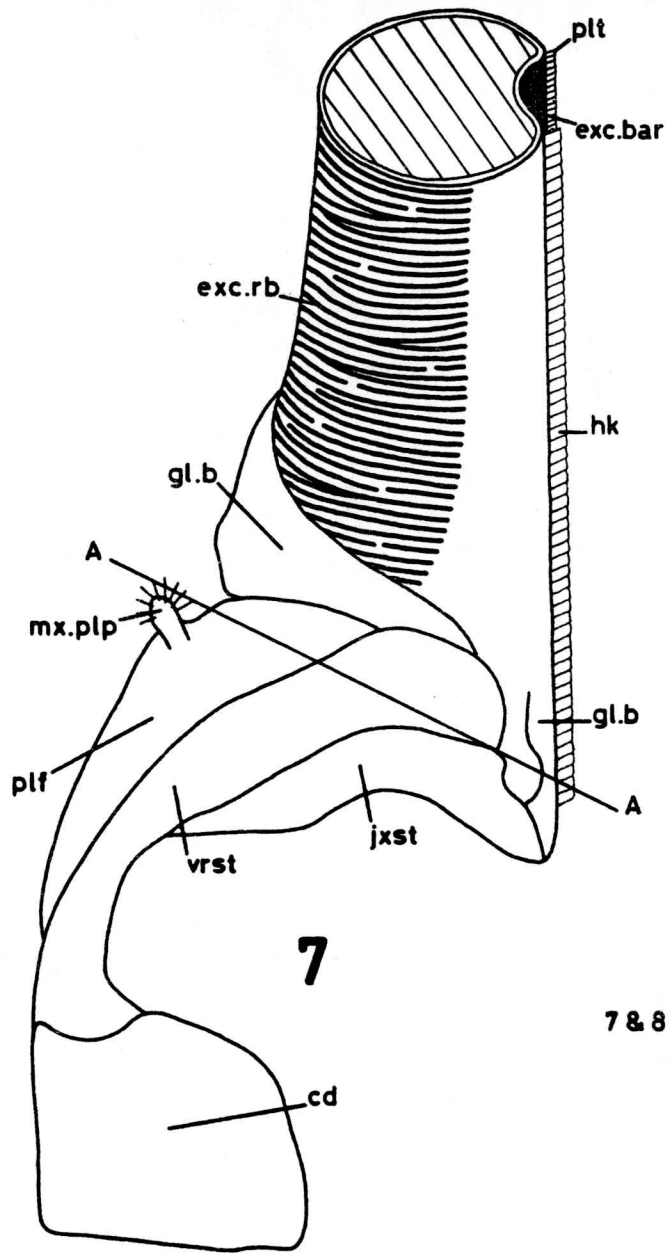




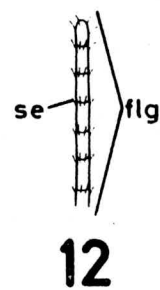
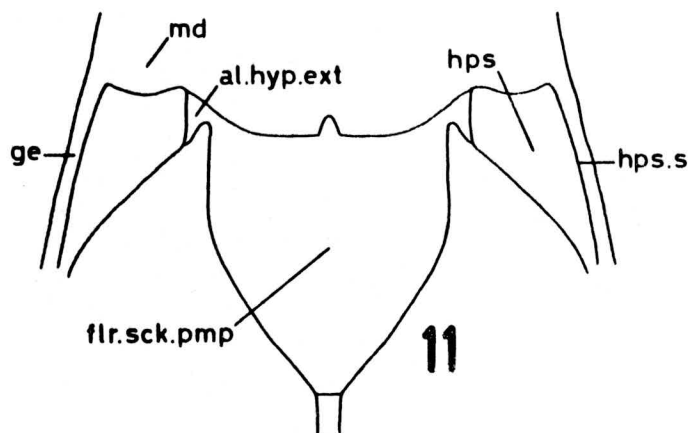
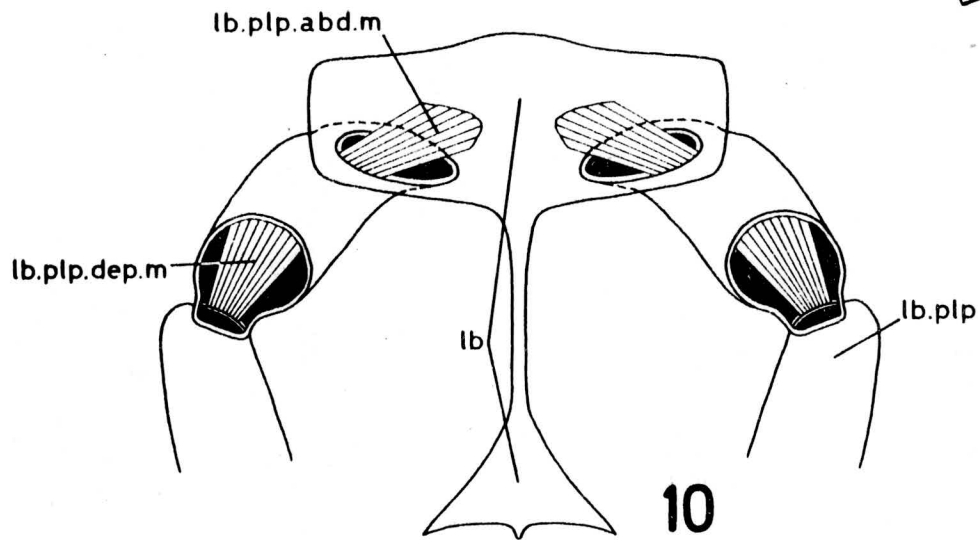
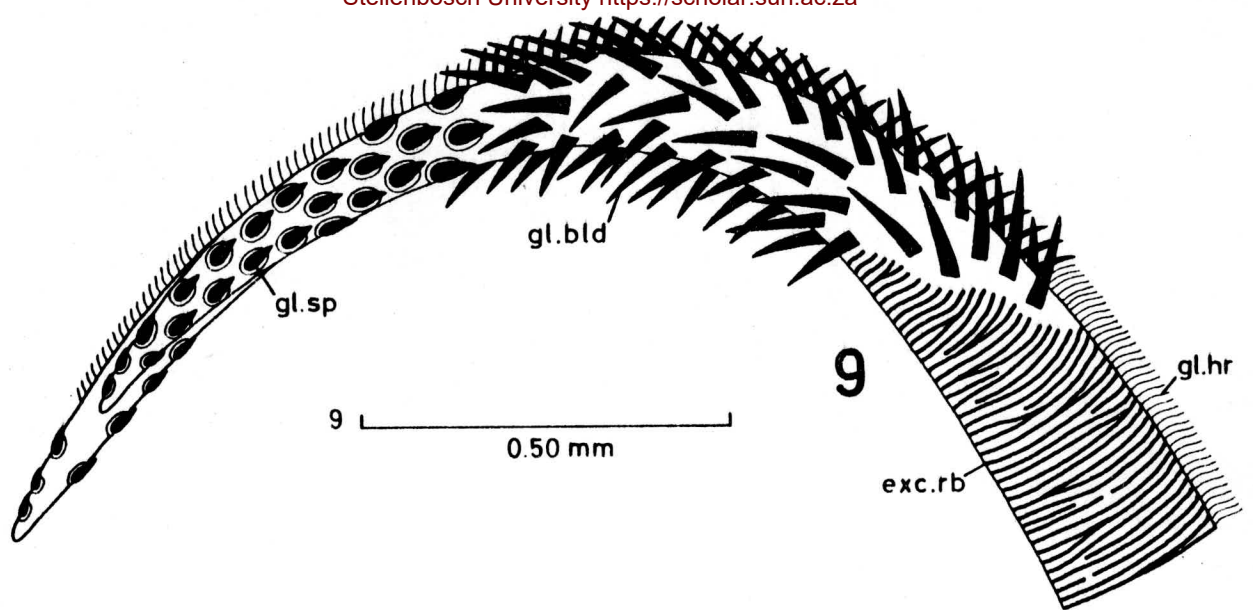
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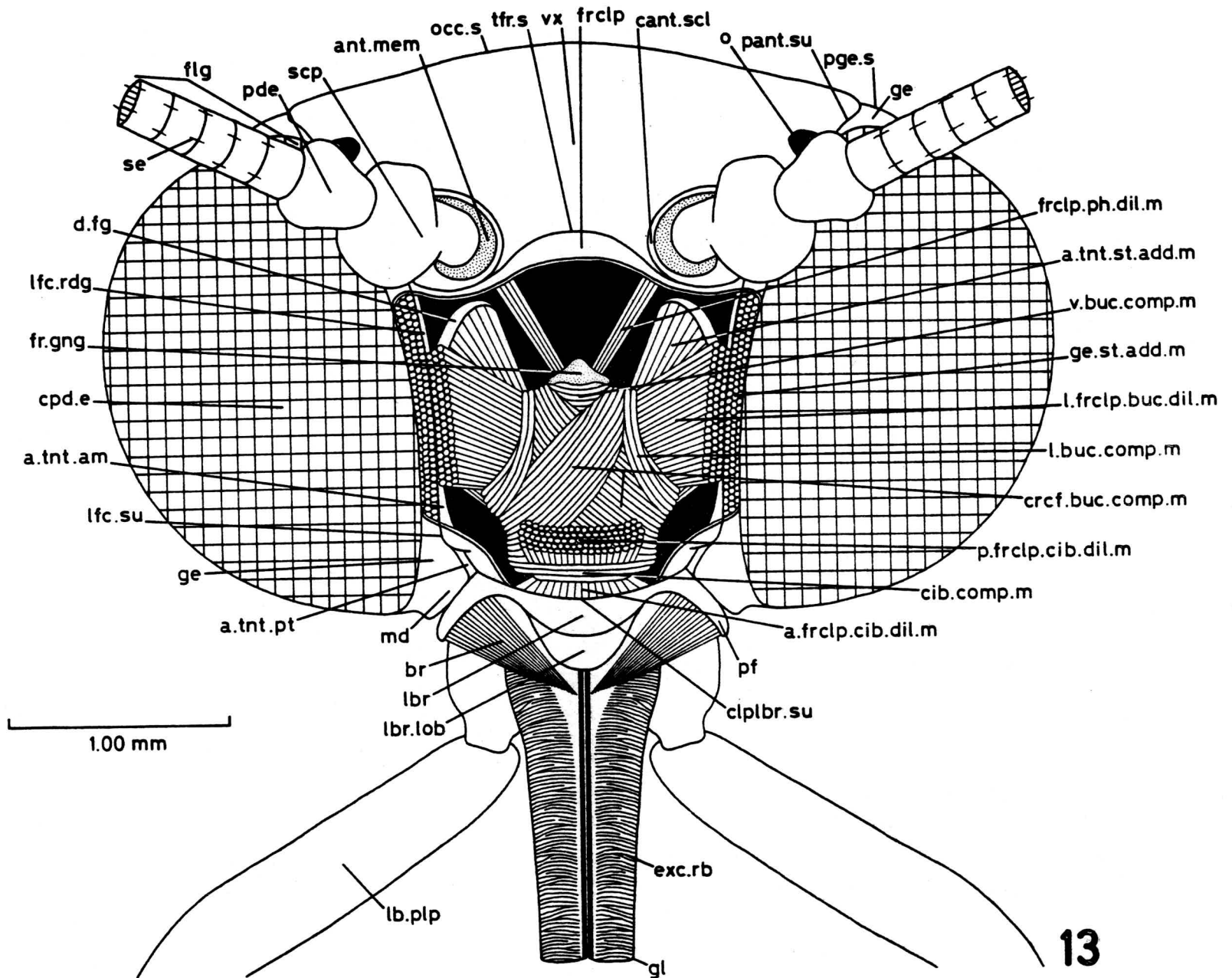


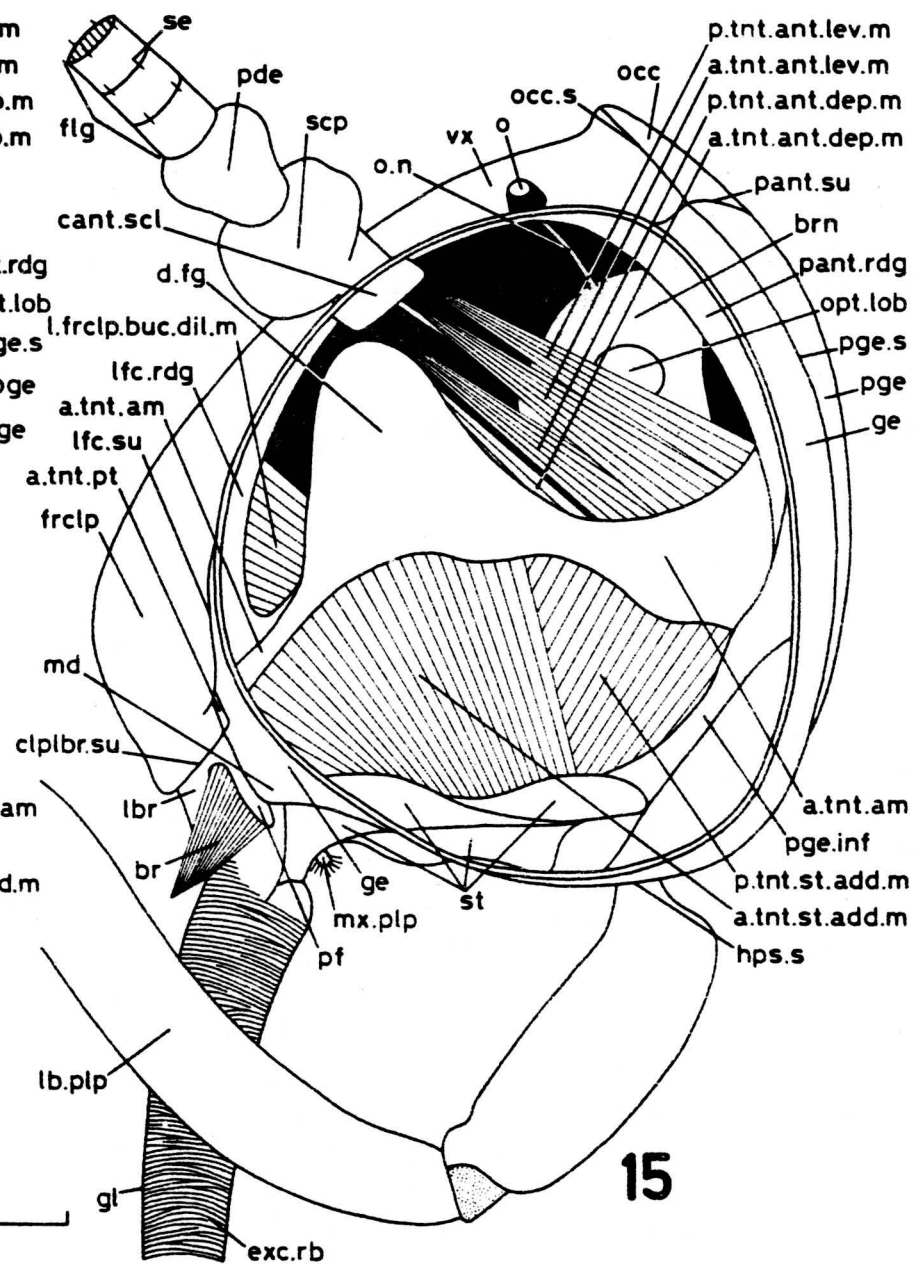
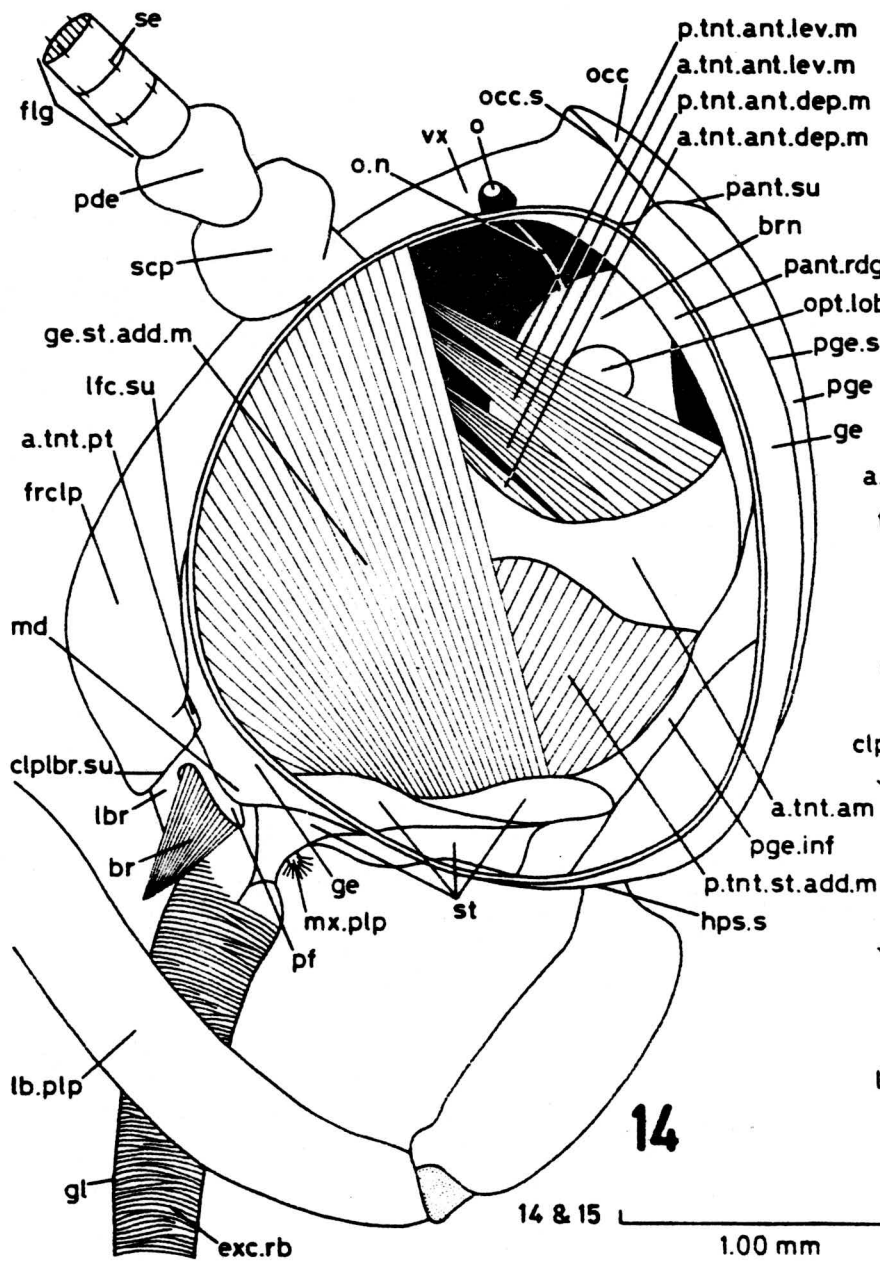




7 & 8 0.50 mm

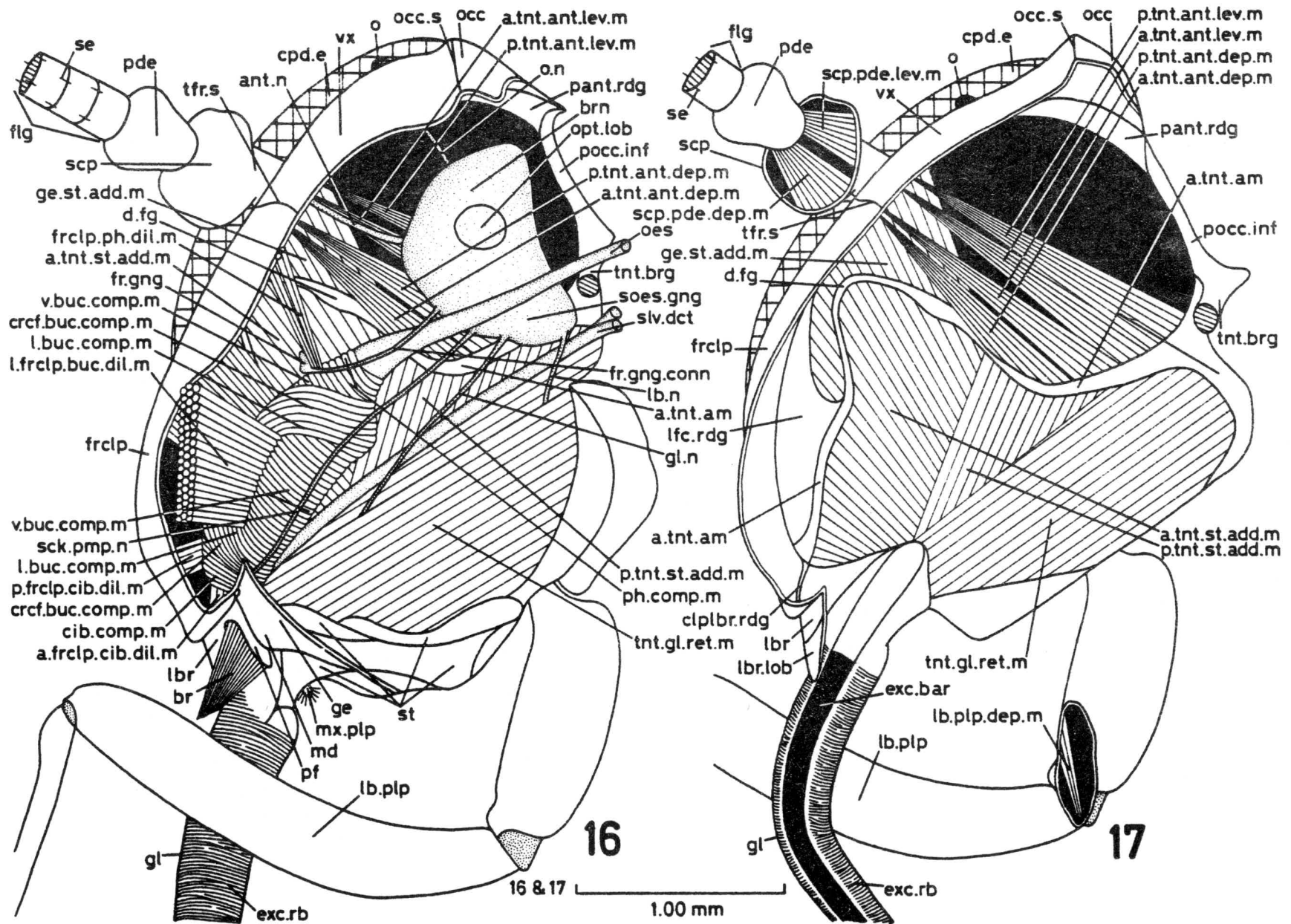


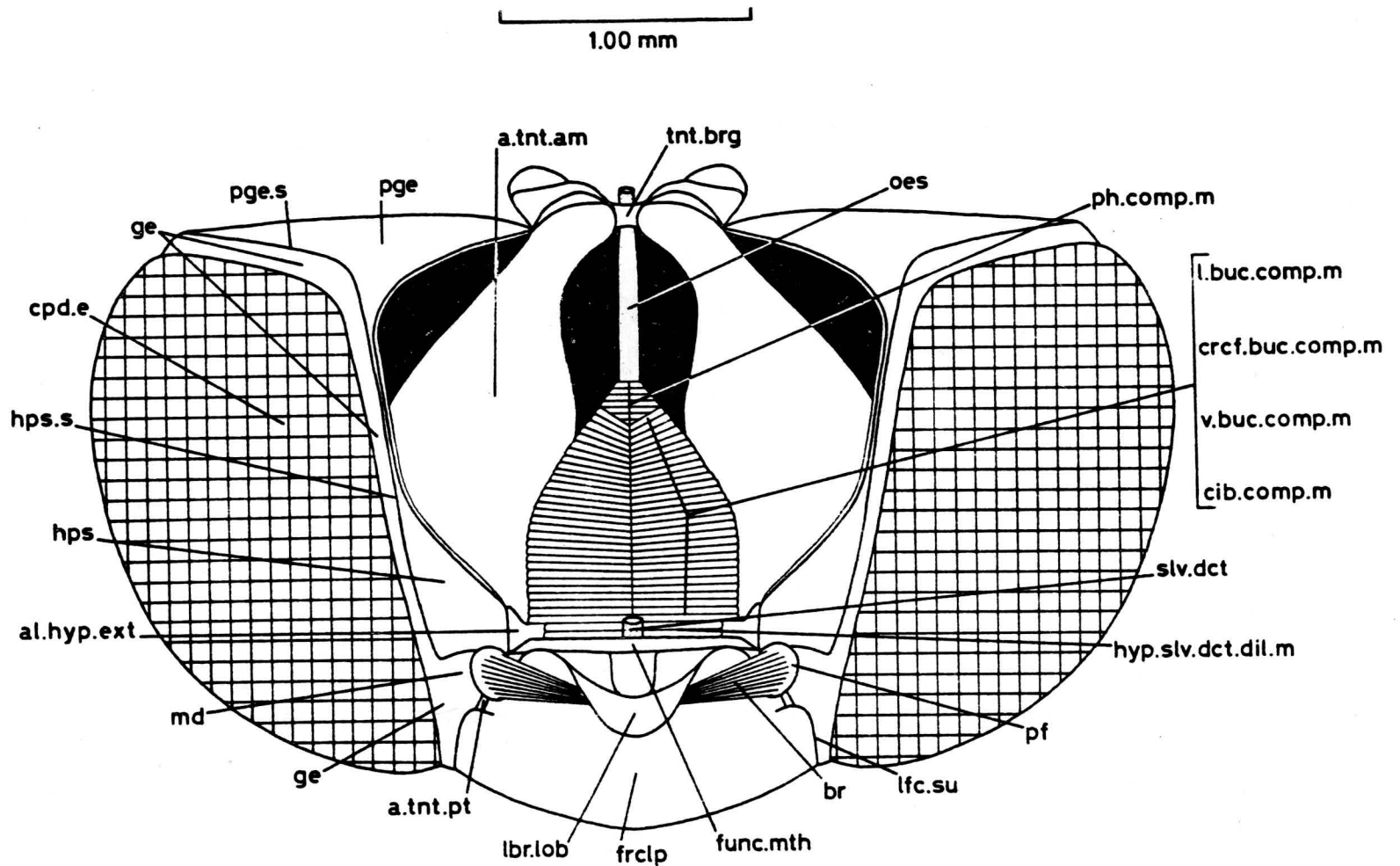


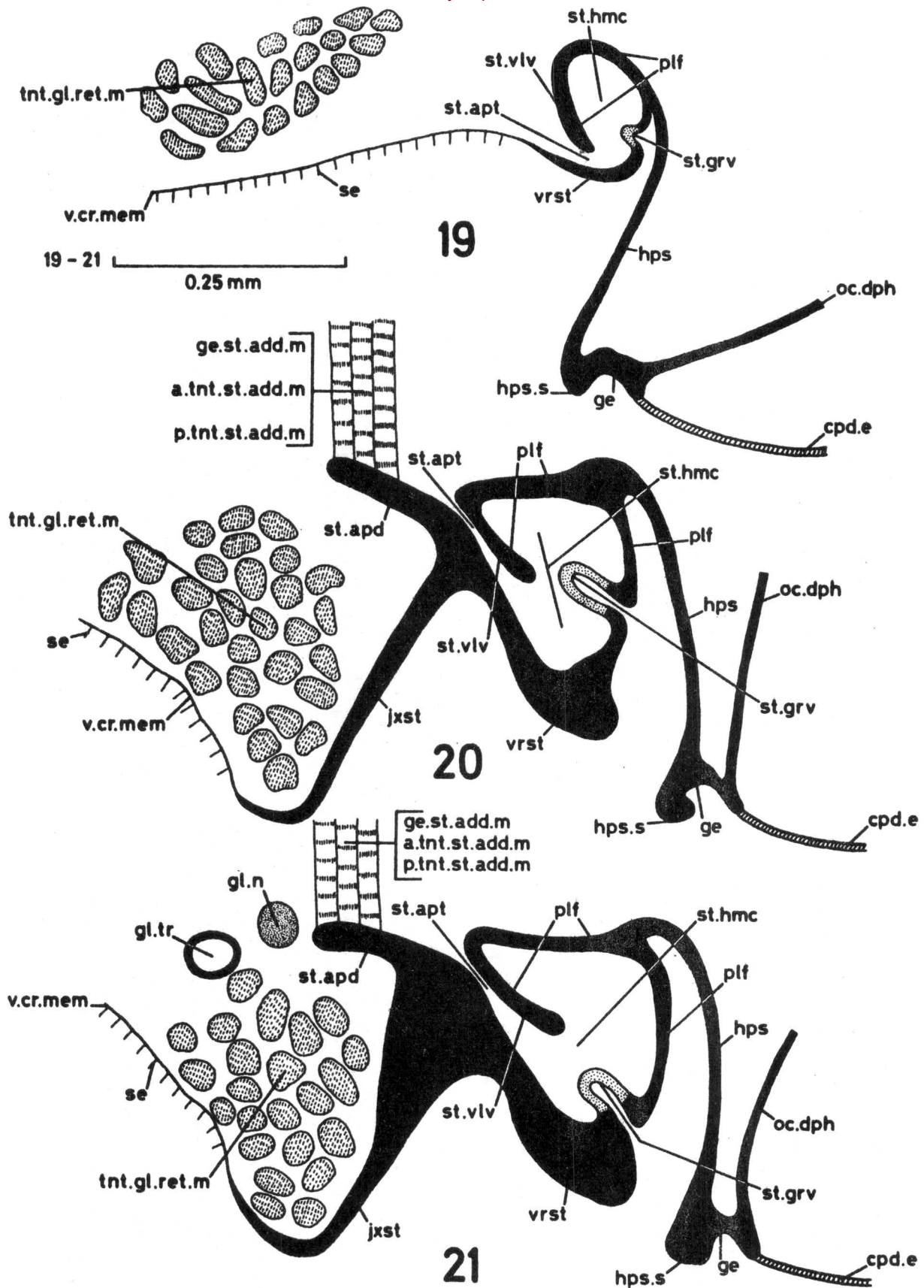


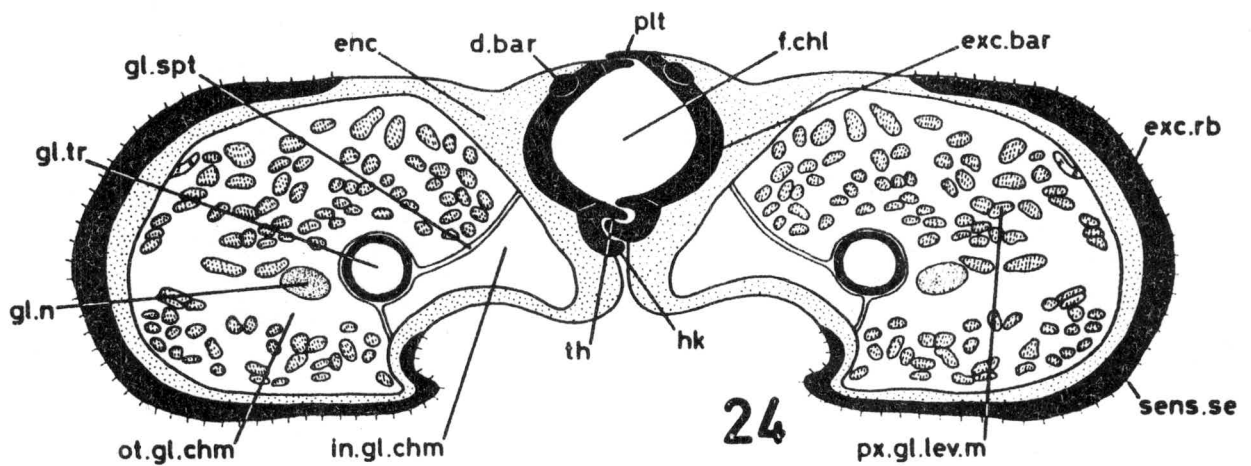
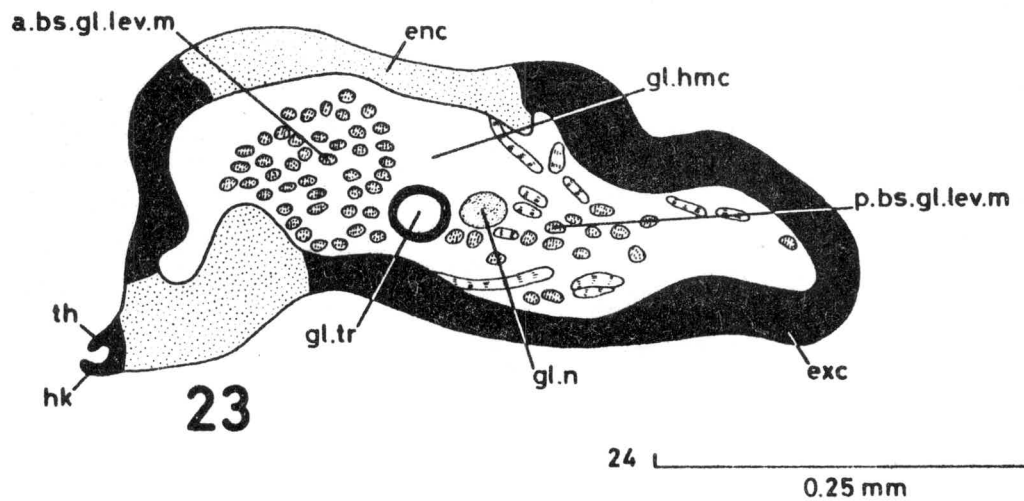
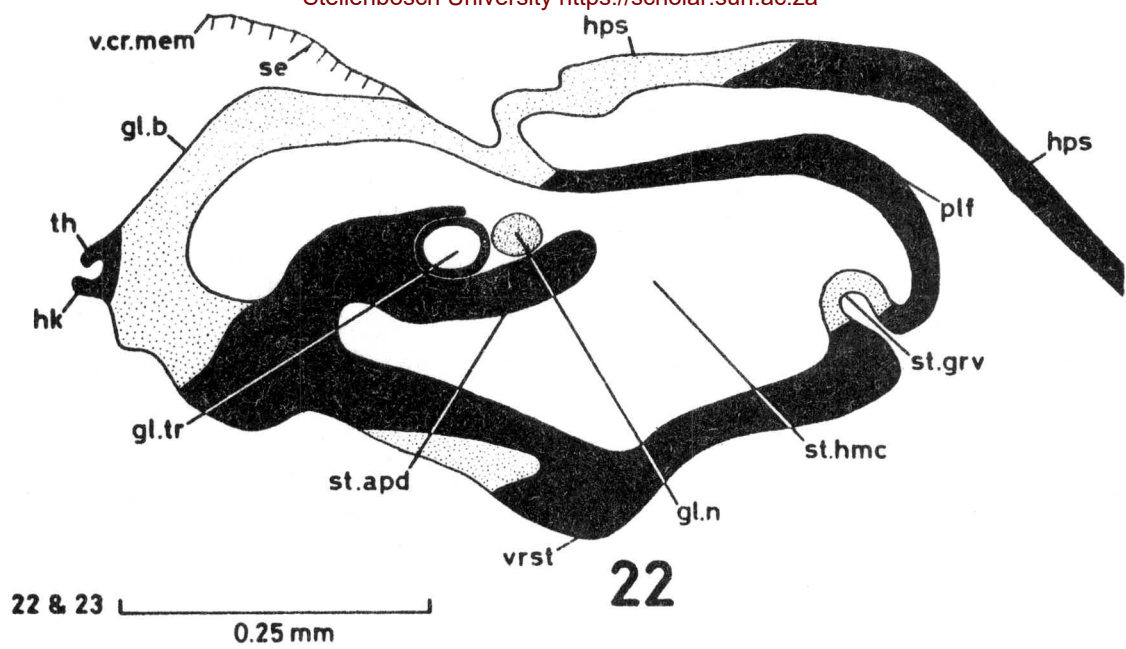
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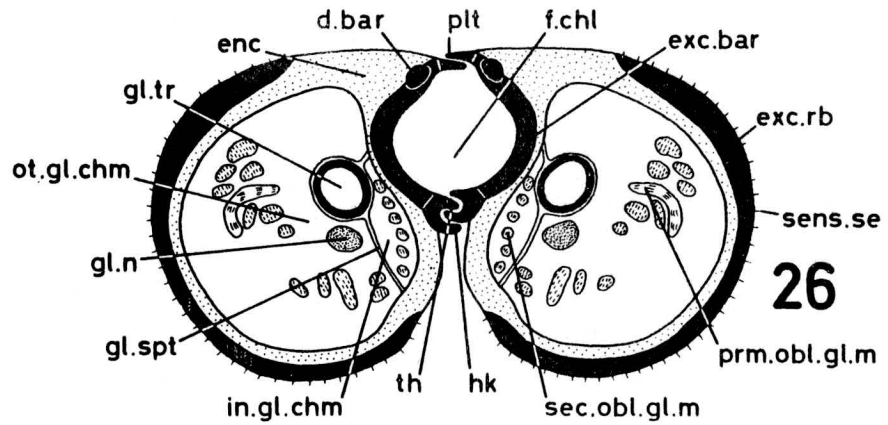
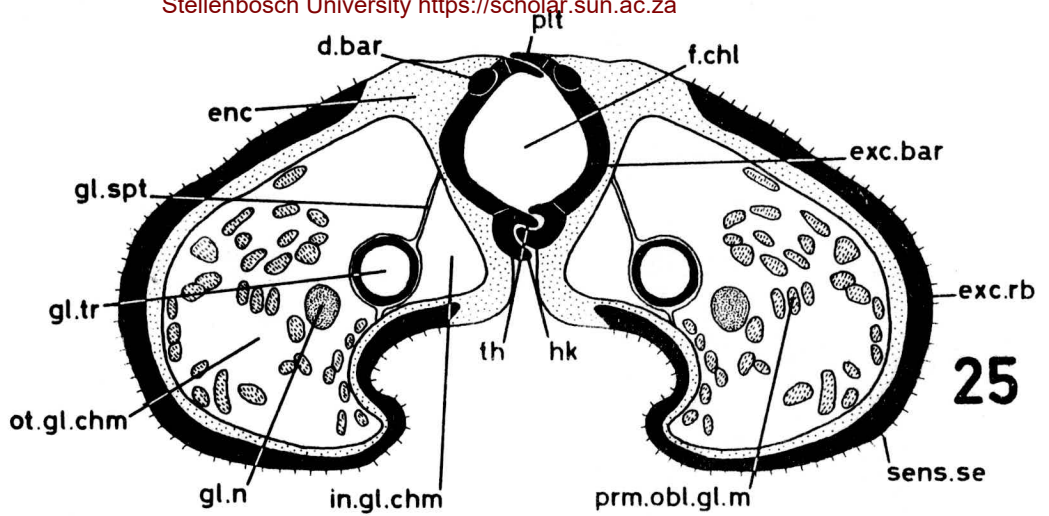
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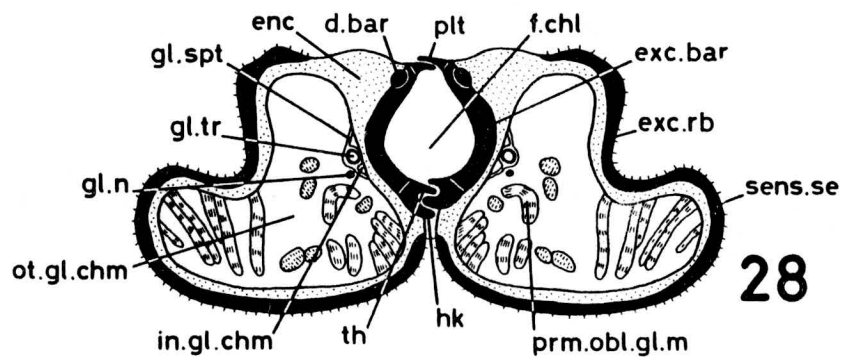
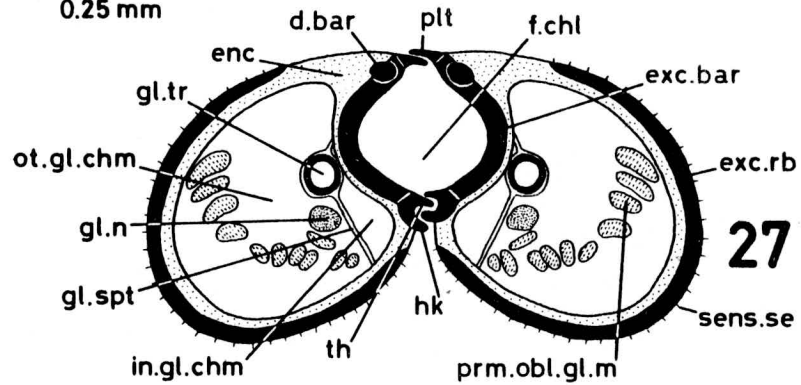


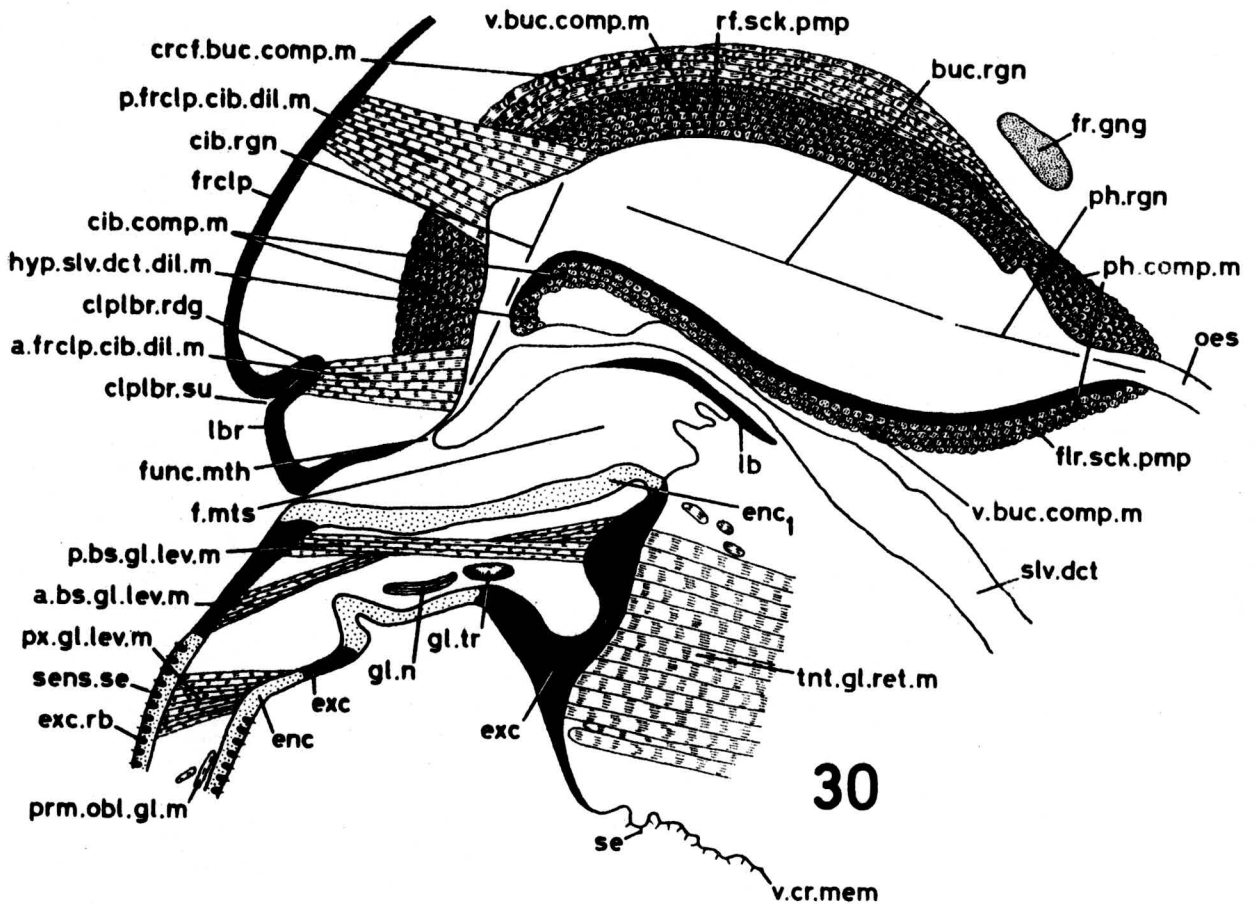
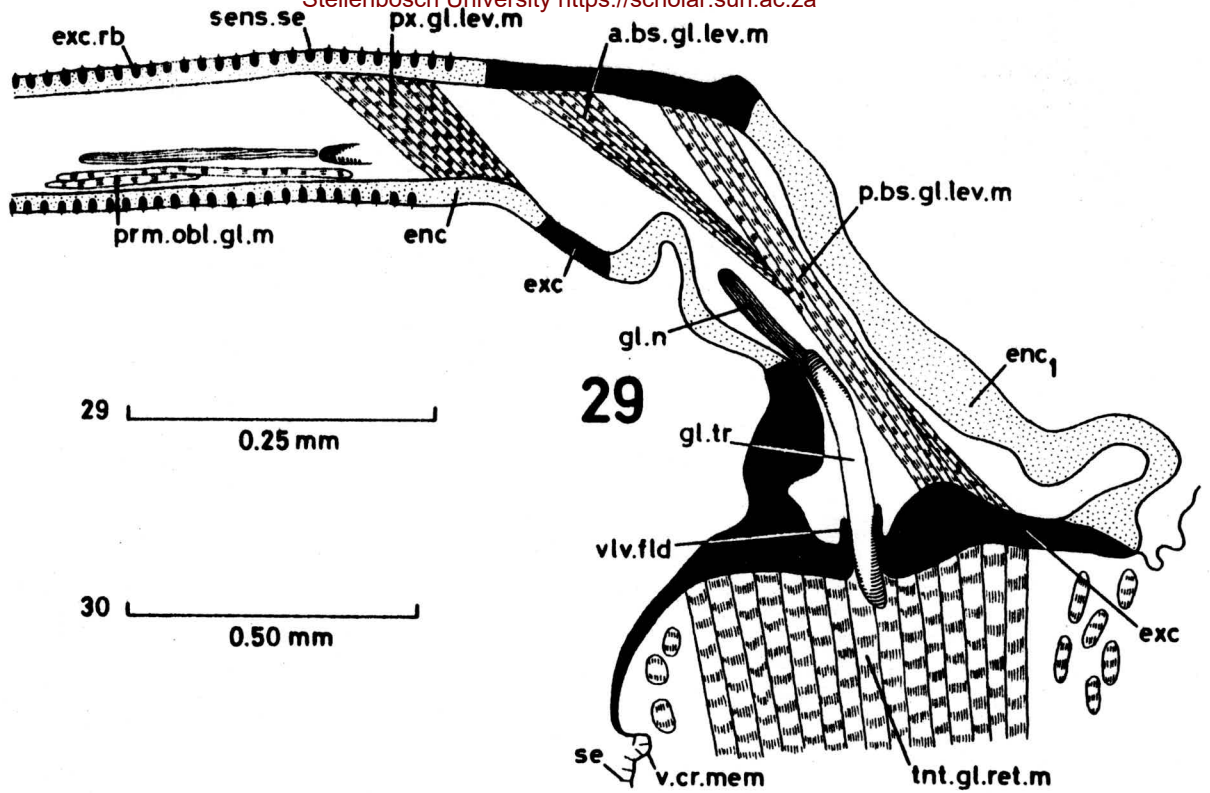


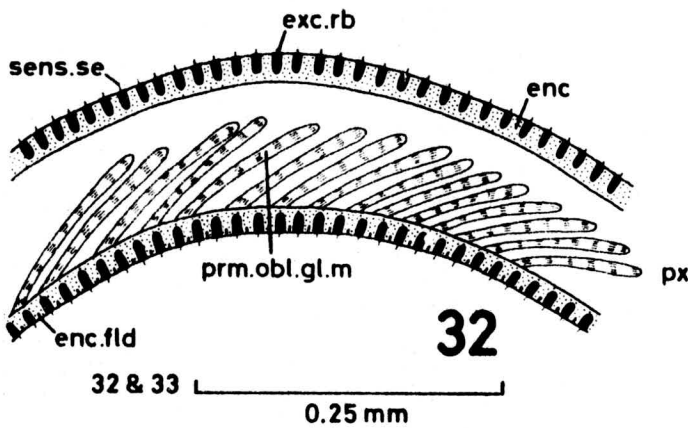
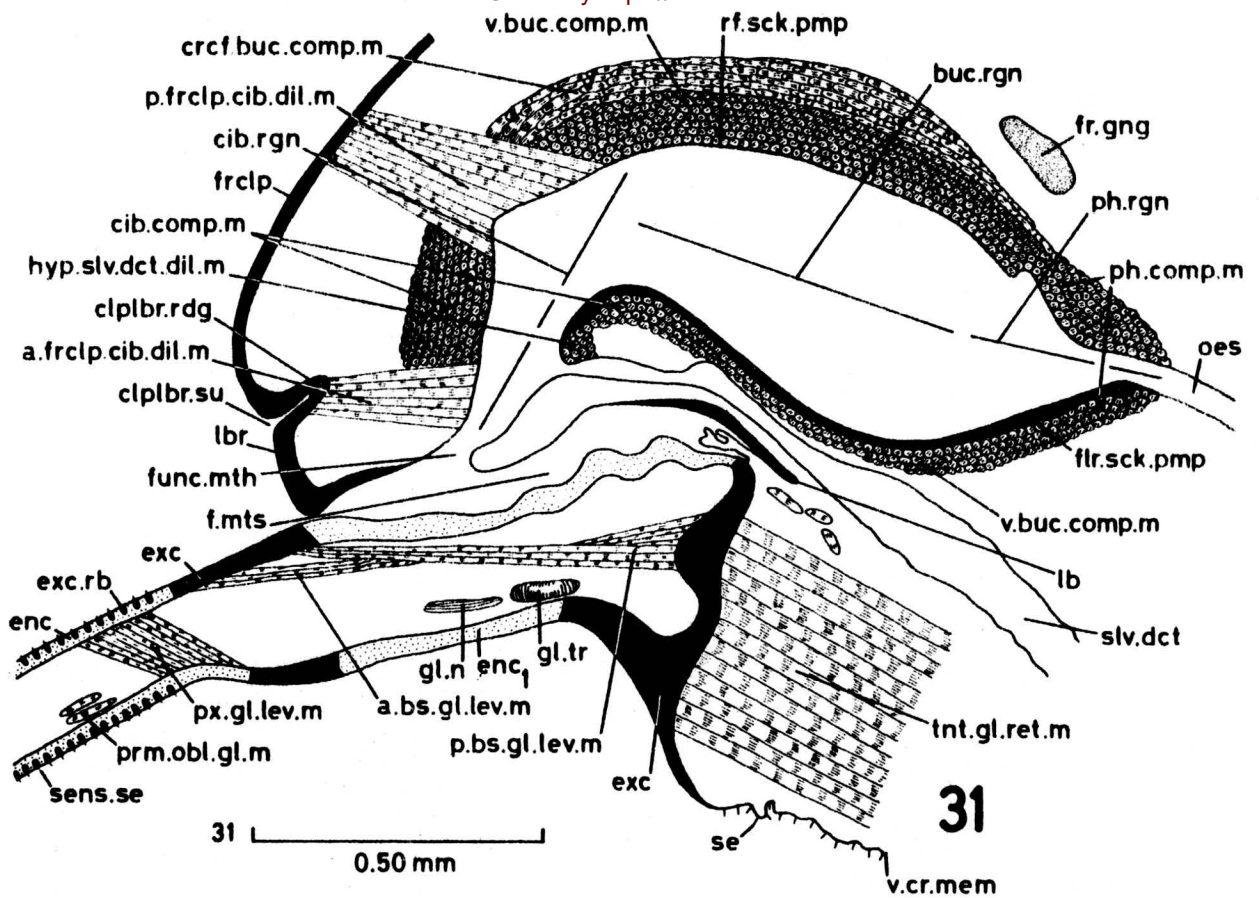




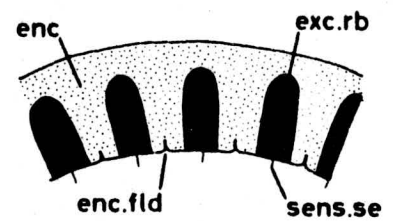
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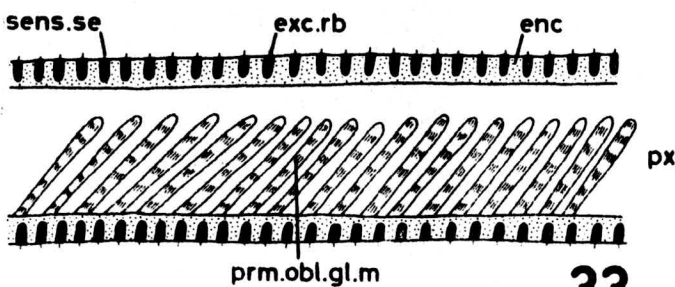




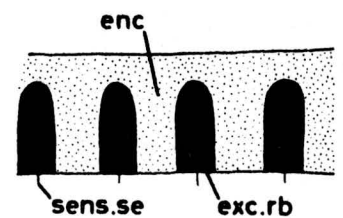
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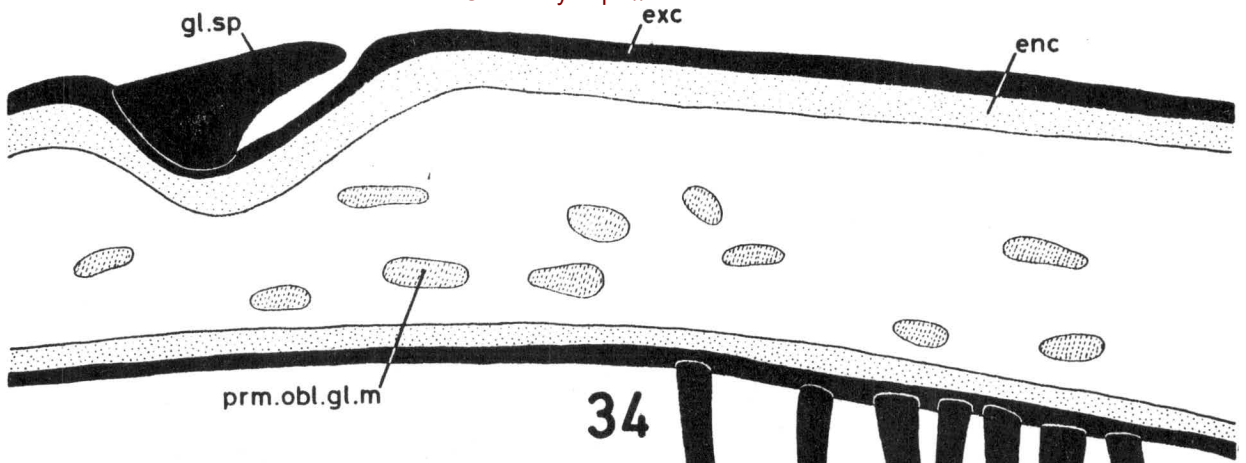
32A



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33A

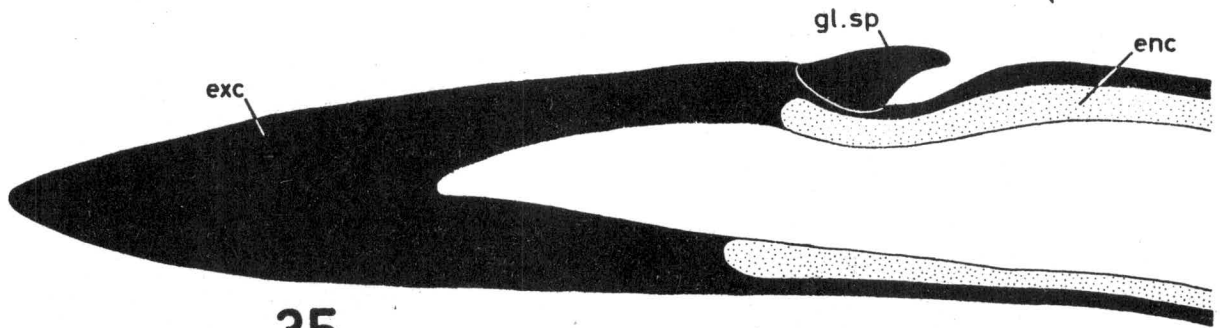


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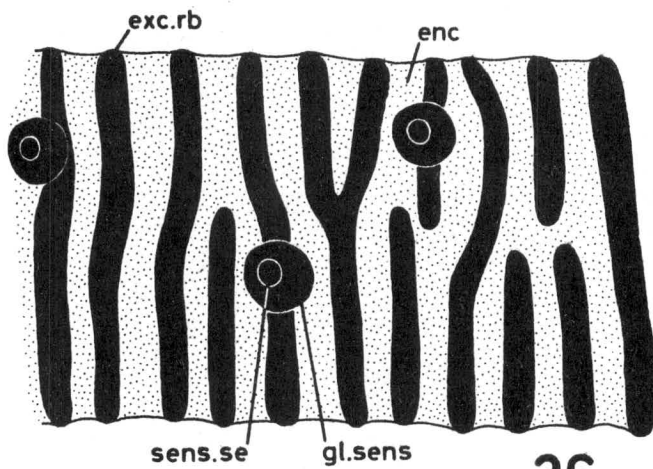
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36 & 37 0.05 mm

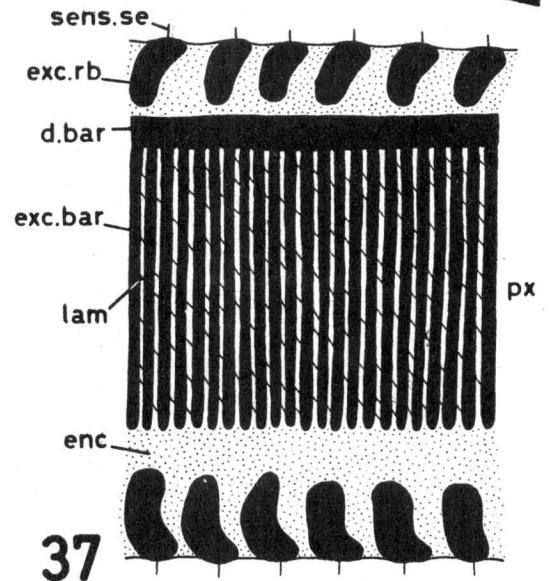
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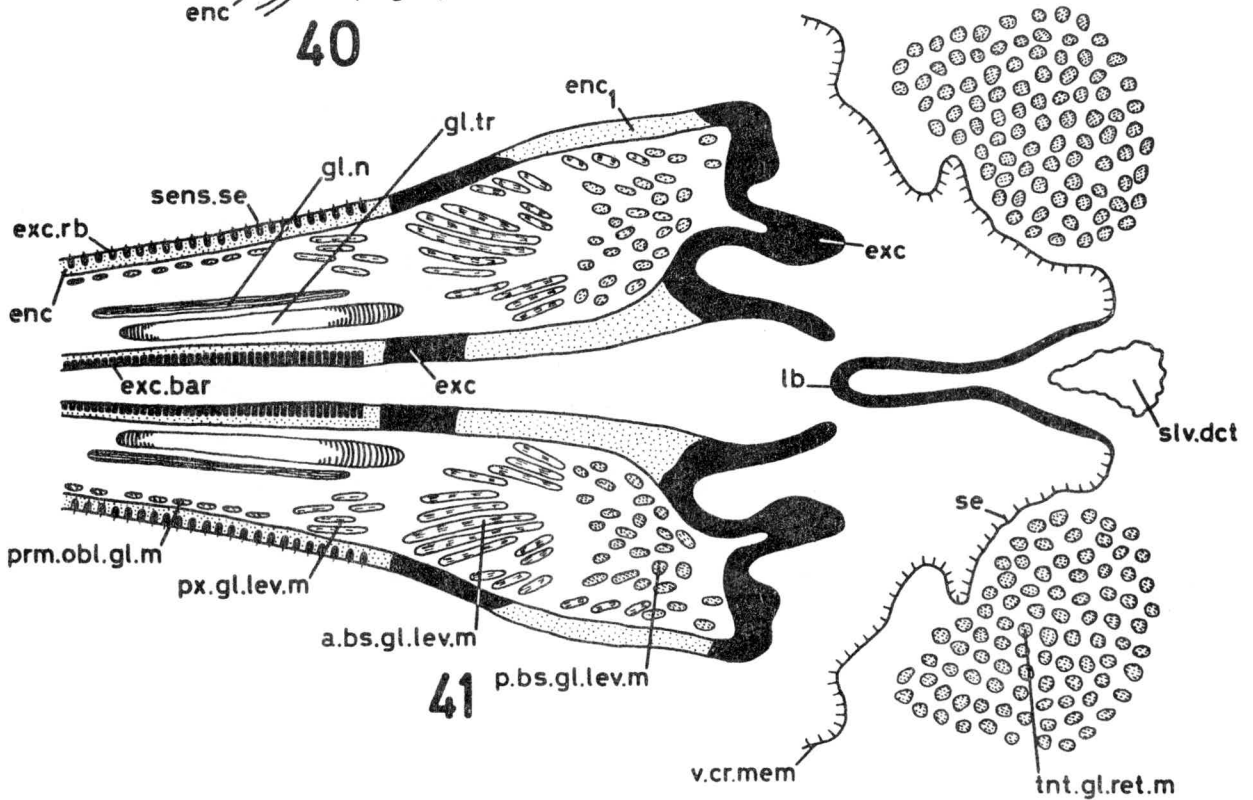
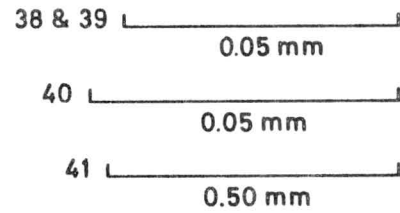
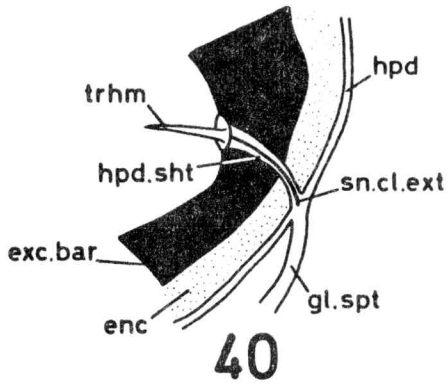
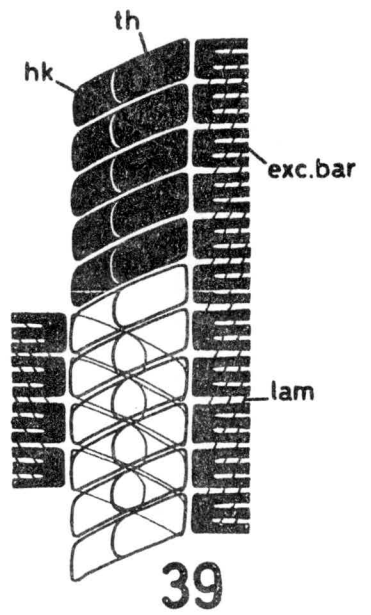
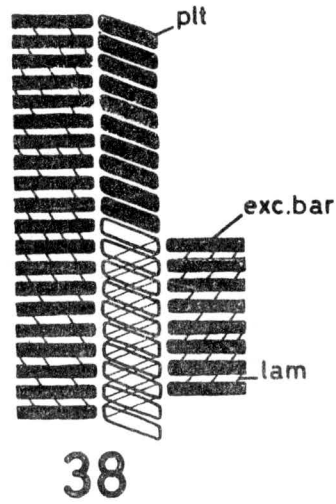
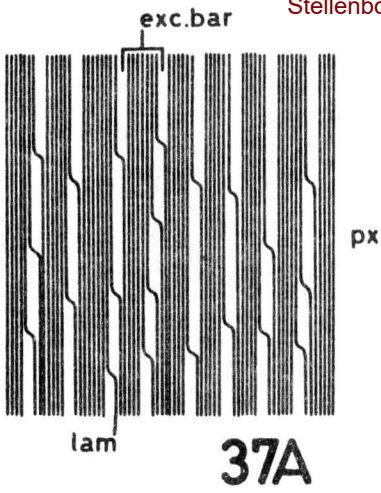
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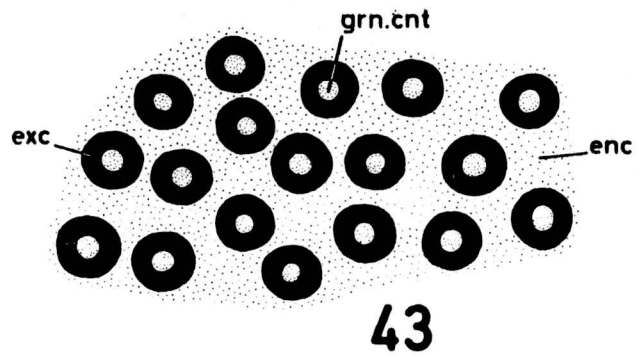
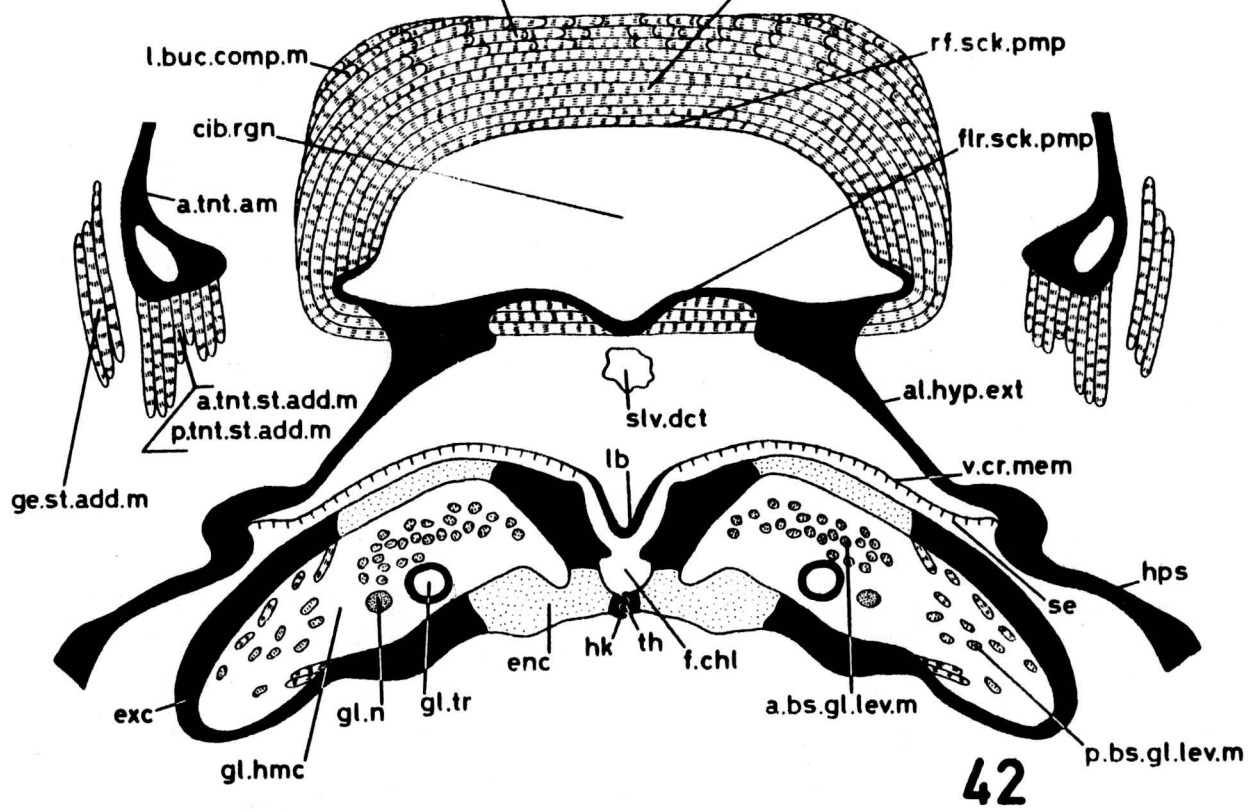


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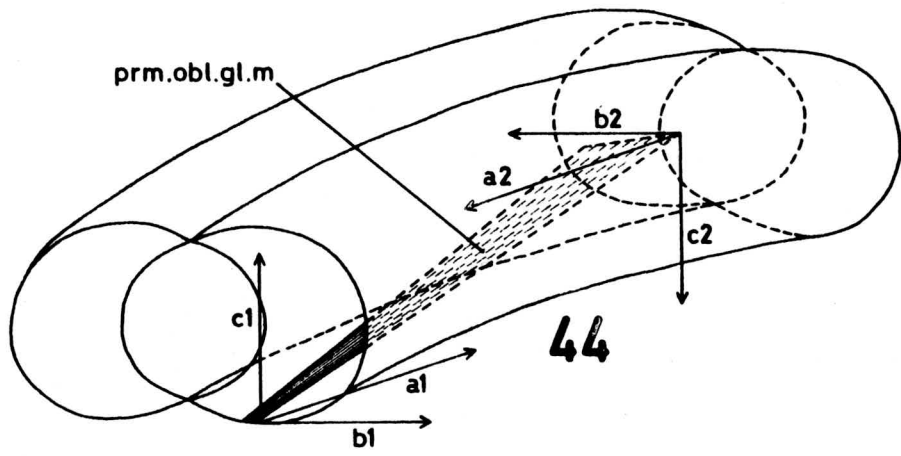
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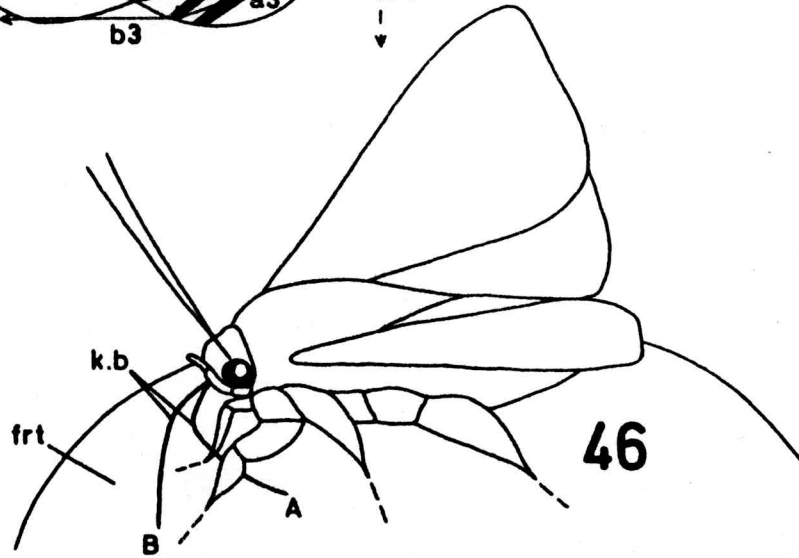
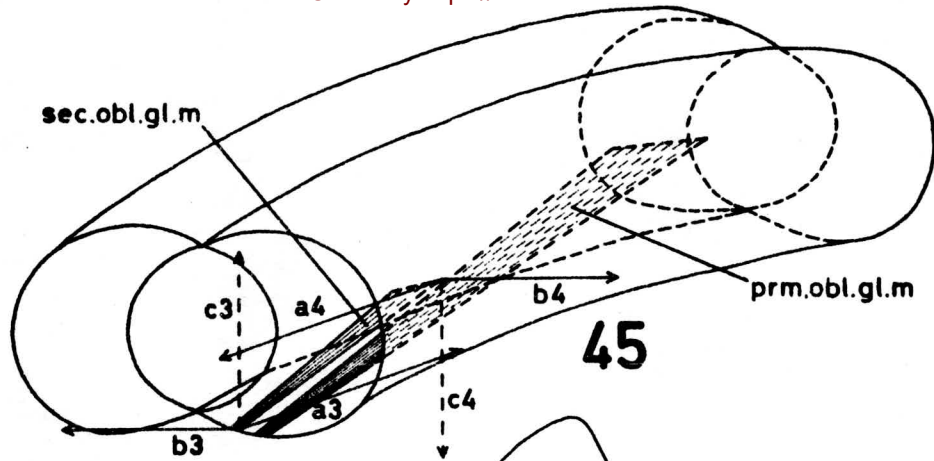




42 0.50 mm

43 0.05 mm





46 - 48 | 10.00 mm

