"MORPHOLOGICAL AND BEHAVIOURAL STUDIES ON RESTING POSITION IN LEPIDOPTERA"

by

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ABSTRACT

The literature on resting habits in Lepidoptera is reviewed. An account of the higher classification of the Lepidoptera is given. Earlier descriptions of the lepidopterous wing base are reviewed and tables of comparative nomenclature are given for the wing base sclerites and the flight muscles.

Microscopical preparations of wing bases were made and the cuticular elements were differentiated with Mallory's triple stain. It was found that a specialized type of cuticle was present wherever the sclerotized parts of the wing base were distorted during flight or wing folding. This was called "bending cuticle".

Dissections of the thoracic musculature were made and some electrophysiological experiments were conducted to find out which muscles were involved in wing folding.

Wing folding in living insects was observed and some operations were performed on live insects to determine how the wing was folded.

The wing base morphology was found to have undergone considerable changes in the Lepidoptera from the more primitive to the most advanced forms. These structural modifications were associated with changes in the resting attitude.

The thigmotactic and phototactic responses of some Noctuoids were investigated by means of choice chambers. The interactions between these two factors and hydrotaxis and geotaxis were studied in Operophtera brumata.

It was concluded that behaviour patterns have been evolved in nocturnal moths which enable them to settle in a suitable place of concealment at dawn. The resting attitude was found to be adapted to this choice of resting site.

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Introduction

Most species of Lepidoptera have a characteristic resting attitude and settle in an equally characteristic resting site. The resting attitudes of Lepidoptera have been described by Oudemans (1903) and Graham (1950). The resting attitude is largely determined by the posture of the wings. No attempt has previously been made to discuss the morphology of the thorax and the wing base in relation to the position of the wings at rest. Wing folding includes the movement of the whole wing to the resting position and in many cases pleating. The resting sites of many species of Lepidoptera have been recorded, but the relationship between the attitude of a moth and the place in which it is found has not been investigated by previous workers. The morphological and behavioural aspects of wing folding are considered in separate sections.

Part I.

Wing folding and the morphology of the Lepidopterous Wing Base

Most major groups of Lepidoptera have a typical resting attitude. Primitive Lepidoptera hold the wings in a tectiform position, which is similar to the resting position of Trichoptera. The various attitudes characteristic of the higher Ditrysia differ greatly from the primitive type.

This part of the thesis is an attempt to study the mechanics of wing folding in Lepidoptera. It will be

shown that there is an evolutionary trend in the wing base associated with changes in the method of wing folding.

Review of Literature

Snodgrass (1909, 1927, 1935) proposed the first satisfactory plan for the generalized insect wing base. He retained the name "axillaries" for the wing base sclerites, which was first used by Straus-Dürckheim (1828). The axillary sclerites were defined and numbered by Snodgrass, according to their position and relation to the wing veins. This was possible because a consistent system of nomenclature for the venation of all insect orders had been developed by Comstock and Needham (1898-9).

The first axillary sclerite was defined by Snodgrass as a detached piece of the notum, with which it articulates proximally. Distally the first axillary articulates with the second, and anteriorly it is associated with the subcostal vein. The second axillary sclerite is always attached to the radial vein and Snodgrass concluded that it was probably derived from the radius. The second axillary is always present on both upper and lower surfaces of the wing, and it articulates ventrally with the pleural wing process. The third axillary sclerite is associated with the bases of the anal veins, and was described by Snodgrass as the "Posterior hinge plate of the wing base and the active sclerite of the flexor mechanism". The same author considered that the fourth axillary sclerite, sometimes present in Orthoptera,

Hemiptera and Hymenoptera, was a detached piece of the posterior notal wing process.

Snodgrass was the first to recognise the importance of the median plates in wing folding, and to notice that they form a convex fold when the wing is flexed. In his description of the lepidopterous thorax, Snodgrass (1909) describes a large anterior arm of the pleural wing process of the mesopleuron serving as a "Prop for the tegular plate of the notum".

Ligamentous thickenings of the wing base membrane were described by Snodgrass (1929). The structure and properties of these ligaments have been studied by Weis-Fogh (1959) who has found that their positions are often useful in tracing the homologies of the axillary sclerites (pers. com.).

The nomenclature of Snodgrass is used in this thesis for all external morphology. The term "Notal incision" was restricted to that part of the lateral emargination which is continued into the line of weakness in the notum. It was found necessary to invent the name "Radial plate" for a structure lying between the second axillary and the main part of the radial vein.

The lepidopterous wing base has been described by several authors. A summary of their nomenclature is given in table I (p. 4). These descriptions tend to be inaccurate because the material was examined in surface view only, and preparations of individual sclerites were not made. Onesto

TABLE I

AUTHOR	FIRST AXILLARY SCLERITE	ANTERIOR ARM OF FIRST AXILLARY
ONESTO, 1959. (*Anthocaris cardamines*)	1 Ascellare	Iobo anteriore 1 Asc. collo 1 Ascellare
EHRLICH, 1958. (*Danaus plexippus*)	First Axillary	Anterior arm
NÜESCH, 1953. (*Telea polyphemus*)	First Axillary	
BOURGOGNE, 1951. (*Hepialus*, *Papilio*)	1er Sclérite axillaire	
FREEMAN, 1947 (*Choristoneura fumiferana*)	First Axillary sclerite	
MADDEN, 1944. (*Protoparce sexta*)	First Axillary	
SNODGRASS, 1935, 1930, 1928, 1927, 1906	First Axillary sclerite	
CRAMPTON, 1928. (*Ctenocha virginica*). 1920. (*Mnemonica auricyanca*)	Notal ossicle (Notale)	
JORDAN, 1928. (*Chrysophanus dispar*.)	Mediobasale=Condylophore	Anterobasale
WEBER, 1928, 1924. (18 species).	Vorderes Tergalgelenkstück = Axillare 1.	
BERLESE, 1909. (*Sphinx convolvuli*.)	Mesoptero.	Proptero esterno

DORSAL SECOND AXILLARY SCLERITE	VENTRAL SECOND AXILLARY	THIRD AXILLARY SCLERITE
II Ascellare 2Axa	II Ascellare 2Axb	III Ascellare
Second Axillary	Second Axillary	Third Axillary
Second Axillary	Second Axillary	Third Axillary
2e sclérite axillaire	Praeparaptère	3e sclérite axillaire
Second Axillary sclerite		Third Axillary sclerite
Second Axillary		Third Axillary
Second Axillary sclerite	Second Axillary Sclerite	Third Axillary sclerite
Median ossicle (Medialia)		Median ossicle (Medialia)
Submediocentrale=acetabular	Mediocentrale = Tylophore	Posteroneurale = Zygellum
Mittelgelenkstück=Axillare 2		Analgelenkstück=Axillare 3
Proptero	Endoptero.	Pezzo articolare

FOURTH AXILLARY SCLERITE	ANTERIOR NOTAL WING PROCESS	MEDIAN NOTAL WING PROCESS	POSTERIOR N
	Processo notale anteriore and Processo notale medio.	Lobo scrutale (sic.)	IV Ascellare &
Third Axillary	Suralare, anterior notal wing process	Adnotale	Posterior notal axillary
Fourth Axillary	Anterior notal wing process	Median notal wing process	Posterior notal
	Apophyse notale alaire antérieure		Apophyse notale
Third Axillary sclerite	Suralare	Adnotale	Adanale
Fourth axillary	Suralare	Adnotale	Adanale
Third Axillary sclerite Fourth Axillary sclerite	Anterior notal wing process		Posterior notal
Basanal sclerite (Basanale)	Suralar sclerite (Suralare)	Adnotal sclerite (Adnotale)	Adanal sclerite
Posterocentrale			Posterobasale
Hinteres Tergalgelenkstück	Vorderer Tergalhebel	Hinterer Tergalhebel	Hinterer Gelenk
Metaptero	Procondilo	Mesocondilo	Condilo

OTAL WING PROCESS

rocesso notale posteriore

wing process and Fourth

wing process

alaire postérieure

wing process

(Adanale)

fortsatz

LATERAL EMARGINATION	AXILLARY CORD	FIRST MEDIAN PLATE	SECOND MEDIAN PLATE
Emarginazione		III Ascellare.Lamina prossimale	Lamina prossimale. Lamina distale
	Axillary cord		
tergal fissure	Axillary cord	Median plate	Median plate
	Axillary cord		
Notal incision	Axillary cord	Proximal Median Plate	
Lateral notal emargination		Median plate M	Median plate M′
		Median ossicle (Medialia)	
Tergalspalt	Flügelligament	Vermittlungsstück	Vermittlungsstück
	Ligamento	Capo delle nervature della preala	

RADIAL PLATE	HUMERAL PLATE	BASE OF SUBCOSTA	BASE OF SECOND CUBITUS	SUBTEGULA
Lamina distale	Basi nervature dorsale	Uncino subcostale		Sclerite accessorio
Second axillary		Basal process of subcosta		Tegular arm
				Tegular arm
Radius		Subcosta		Sclerite prolongeant l'apophyse pleurale alaire
	Humeral plate	Humeral plate		Subtegula
	Humeral plate	Subcosta	Distal median plate	Subtegula
Radius	Humeral plate	Subcosta		(Prescutal Apodeme -Weis-Fogh)
	Parategula or Basicosta	Subcostal head	Basosinus or Marsupium	Subtegula
Mediocentrale=Mesum	Anterocentrale=claviform		Medioneurale	
Radius		Subcosta		Tegulararm
Subcostale & Radiale	Vena costale l'interna	Vena costale l'interna	Cubitale(Cu_1)	Clavicola

TERGOPLEURAL APODEME	PLEURAL WING PROCESS	PREALARE	POSTALARE	FIRST BASALAR	SECOND BASALAR	SUBALARE
Braccio tegulare	Processo alifero	Prescuto	Postalare	Apodeme	Basalare 1	Subalare
Tegular arm	Pleural wing process	Prealare	Postalar portion of Epimeron	Preepisternum	Basalare	Subalare
Tegular arm	Pleural wing process	Prealar arm	Postalar bridge & laterophragma	Tendon cap of Basalare	Basalare	Subalare
	Apophyse pleurale ailaire	Bras prealaire				Postparaptère
	Pleural wing process		Postadanale		Pleural wing process Basalar	Subalare
Subtegula	Pleural wing process	Prealar	Postadanale			Subalare
Tegular arm	Pleural wing process	Prealare	Postalare of Acrotergite	First and second paraptera preparaptera or Basalar sclerites		Epimeral parapterum Postparapterum. Subalare
Prealar Bridge		Prealar sclerite Prealare	Postadanal sclerite (Postadanale.)			Subalare
Tegulararm	Pleuraler [redacted] Flügelgelenkkopf	Tergalarm	Postnotalhaken	Episternalgelenkstück or Basalare		Epimeralgelenkstück Subalare
Clavicola	Processo alifero o fulcro	Preclavicola	Preclavicola del Metanoto	due metà dell' acrosterno o Prefulcro		Paraptero.

BASALAR SCALE PLATE

Parategula

Anepisternum

Basalar pad

(1959) studied the wing base of a Pierid in great detail, giving new names to every thickening and projection on each sclerite, but some of the basic homologies were incorrectly interpreted.

Weber (1924) compared the thoracic morphology of primitive and advanced Lepidoptera with that of one example from each of the orders Neuroptera, Mecoptera and Trichoptera. He described the development of large notal wing processes in Lepidoptera, and the most obvious changes in the shape of the thorax, but his observations were not correlated with function. Weber concluded that the hind wing base in Lepidoptera is more primitive than the fore wing base.

The musculature of the thorax has been studied by several authors. Table II (p. 6) gives the equivalent nomenclature for the "Direct" and "Indirect" flight muscles. These authors disagree on the homologies of the anterior tergopleural muscles. The origin - insertion nomenclature of Snodgrass was followed in this thesis, and those names indicating function were avoided.

The only author to describe wing folding in detail was Voss (1905) who gave a description of the flexed wing in Orthoptera. Vogel (1912) and Mc.Indoo (1917) described the campaniform sensilla in the lepidopterous wing base.

Axillary characters of the wings have not been used in the systematics of Lepidoptera. In contrast venation is very important in classification, (Comstock, 1918; Tillyard,

TABLE II

	"Direct Flight" Muscles							
NAME USED IN PRESENT WORK	First Tergopleural Muscle	Second Tergopleural Muscle	Third Tergopleural Muscle	Fourth Tergopleural Muscle	Fifth Tergopleural Muscle	Sixth Tergopleural Muscle	Seventh Tergopleural Muscle
ABBREVIATION	1 t-p. Mu	2 t-p. Mu.	3 t-p Mu.	4 t-p Mu.	5 t-p Mu.	6 t-p Mu.	7 t-p. Mu
ORIGIN	First Basalar Sclerite	First Basalar Sclerite	Pleural Wing Process	Pleural Ridge	Pleural Ridge	Pleural Ridge	Pleural Ridge
INSERTION	Prescutum, Prelare	Anterior lateral Scutum	Suptegula, Presecutal Apodeme	Posterior lateral Scutum	First Axillary sclerite	Median Notal Wing Process	Third Axillary Sclerite
SNODGRASS (1935,1929,1927)	1b. Tergopleural Muscle	Tergopleural Mu.2B	Tergopleural Mu.3B	Tergopleural Mu.4B	Axillary Muscle	-	Flexor of the Wing
KELER 1955 II	Musculus 106 praealaromesepis-ternalis	Mu.Mesonotobasalaris 107	-	-	Mu.Mesopleuroendoj-teralis III	-	Mu.Mesopleuro-mesopteralis 112.
III	-	-	-	-	Mu.Metapleuro-propteralis 144	-	Mu.Metapleuro-mesopteralis 146
NUESH 1953 II	Pleurodorsal 1	Pleurodorsal 5	Pleurodorsal 4	-	Pleurodorsal 3	-	Pleurodorsal 2
III	-	Spiracular dilator	Pleural 2	-	"	-	"
MAKI 1938 II	Ordinary tergopleural Muscle	Ordinary tergopleural Mu.	Ordinary tergopleural Mu	-	-	Ordinary tergopleural Muscle	Pleuro-axillary Mu.
III	-	-	" "	" -	-	" "	"
WEBER 1928 II	Musculus pleuralis tertius mesothoracis	-	-	-	Mu.pleuralis quintus mesothoracis	-	Mu.pleuralis quartus Mesothoracis
III		-	-	-	Mu.pleuralis tertius metathoracis	-	Mu.pleuralis sextus metathoracis
BERLESE 1909 II	Musculo laterale decimo 87	Mu.laterale decimoquinto XCl	Mu.interclavicolare LXXVI	-	-	-	Mu.laterale settimo 85 Mu.laterale decimosesto XCII
III	-	-	-	-	-	-	Mu.laterale nono 56

	"Direct Flight" Muscles						
Sternobasalar Muscle	Coxobasalar Muscle	Trochanterobasalar Muscle	Coxosubalar Muscle	Pleurosubalar Muscle	Pleurofurcal Muscle	Median dorsal Longitudinal Muscle
s -ba.Mu.	cx-ba. Mu	tn.-ba. Mu	cx-sa Mu.	p.sa Mu.	p.fs.Mu	lg.d. Mu
Sternum	Coxa	Apodeme of Trochanter	Meron	Epimeron	Pleural Ridge	Prescutum and Scutum
First Basalar	First Basalar	First Basalar	Subalare	Subalare	Mesofurca	Posthpragma
First promator-extensor of Wing, Epipleural Mu. 28	Second promator-extensor Epipleural Mu. 38	Depressor of Trochanter	Depressor-extensor Coxosubalar Mu.	Pleuro-subalar Mu.	Pleuro-sternal Mu.	Longitudinal dorsal Muscle
Mu.Praecoxbasalaris mesothoracis 115	Mu.Mesepisternobasi-coxalis Superior 117.	Mu trochantinobasalaris mesothoracis 116	Mu Merocoxamesepimeralis 122	Mu Mesepimerosubalaris 123	Mu.Mesapodemafurcalis 124	Mu.Mesophragma-prsephragmalis 95
-	Mu.Metepisternobasicoxalis Superior 151	-	M.Merocoxametepimeralis 153	-	-	Mu.Metaphragmamiso-phragmalis 131.
Pleuroventral 1	Pleuroventral 2	Pleuroventral 3	Pleuroventral 4 + 5	Pleural 1	Pleuroventral 7	Dorsolongitudinal 1
"	"	"	"	"	"	"
Sterno-basalar Mu	Coxo-basalar Mu	Trochanterobasalar Mu	Coxo-subalar Mu	Pleuro-subalar Mu	Furco-entopleural Mu	Median longitudinal Dorsal Mu
"	"	"	"	"	"	"
Mu-Pleuralis primus mesothoracis	Mu.Pleuralis secundus mesothoracis	-	Mu.pleuralis septimus mesothoracis	Mu.pleuralis nonus (adductor alae)	-	II dlm$_1$
-	Mu.Pleuralis primus metathoracis	Mu Pleuralis secundus Metathoracis	Mu.pleuralis quartus and quintus metathoracis	-	-	III dlm$_1$
Mu.laterale decimequarto 91	Mu.laterale quarto 82.	Mu. laterale terzo del mesotorace	Mu. laterale sesto	M. Pterosternale	Mu.laterale del forca del Mesotorace 100.	Mu.primo del mesonoto Mu.secondodel mesonoto 69 + 70
-	Mu.lungo laterale pleuropedale del metatorace XLVII	-	Mu. laterale endopterocoxale.	-	Mu.pleurosternali 65.	Mu. primo del metanoto 37

	"Indirect Flight" Muscles						
Lateral Oblique Dorsal Muscle	Median External Dorsal Muscle	Anterior Tergocoxal Muscle	Posterior Tergocoxal Muscle	Tergotrochanteral Muscle	Tergosternal Muscle	Intersegmental Muscle
l.Obl. Mu	ex.d. Mu	a.t.-ex.Mu	po.t-cx.Mu	t-tn. Mu	t-s. Mu	interseg. Mu.
Scutum	Scutellum	Scutum	Scutum	Scutum	Scutum	First Basalar III
Postalar apodeme	Postnotum	Coxa	Meron	Apodeme of Trochanter	Sternum	Post Coxal Bridge II
Oblique dorsal Muscle	-	Tergal Promotor of Coxa	Tergal remotor of Coxa	Tergal depressor of Trochanter	First and Second tergosternal Mu's.	-
Mu.Mesophragmamesonotalis 96	-	Mu.Basicoxamesonotalis 103	Mu.Merocoxamesonotalis 105	Mu.Mesonototrochanteralis 104	Mu.basisternomesonotalis 100 Mu.latersternomesono-talis 101	Mu. (intersegmentalis) Mesophragmamesofurcalis 125
-	-	Mu. 138 Basicoxametanotalis.	Mu.Merocoxametanotalis	Mu.Metanototrochanteralis 139	Mu.basisternometanotalis 135	
Dorsolongitudinal$_2$	Dorsolongitudinal$_3$	Dorsoventral$_2$	Dorsoventral$_{4+5}$	Dorsoventral$_3$	Dorsoventral 1a & b	pleuroventral 8
"	"	"	"	"	"	
Lateral Oblique dorsal Mu.	Median External Dorsal Muscle	Tergal Promotor of Coxa	Tergal Remotor of Coxa	Tergal depressor of trochanter	Anterior tergo-sternal Mu.	Sternobasalar
"	"	"	"	"	"	
II dlm$_2$	-	Mu.dorsoventralistertius und sextus mesothoracis	Mu.dorsoventralis octavus mesothoracis	Mu.dorsoventralis quartusund. Septimus	Mu.dorsoventralis primus, Secundus,quintus mesothoracis	Mu. dorsoventralis intersegmentalis mesothoracis
III dlm$_2$	-	Mu.dorsoventralis secundus metathoracis.	Mu.dorsoventralis quartus meta thoracis	Mu.dorsoventralis tertius metathoracis	Mu.dorsoventralis primus metathoracis	
Mu.terzo del Mesonoto 71	-	Mu.dorsoventrale primo del mesotorace 74	Mu.dorsoventrale Secondo 75	Mu.dorsoventrale quinto, sesto. 76 + 77	Mu.tergosternale primo del mesotorace LXXVIII	Mu. intersegmentale primo del mesotorace 73.
Mu. del metanoto secondo 38	-	Mu.dorsoventrale primo del metatorace 42	Mu. dorsoventrale Secondo 43	Mu.dorsoventrale quinto. 46	Mu.tergosternale primo XXXVI	

1919a, 1919b; Turner, 1947, 1918.) Turner divided the Lepidoptera into Homoneura and Heteroneura largely on characters of the hind wing veins. The method of wing coupling has also been used in taxonomy, (Braun, 1919, 1924; Tillyard, 1918.) The suborders Jugatae and Frenatae of Comstock were based on wing coupling apparatus. The presence of aculei between the wing scales of primitive Lepidoptera, similar to those of Trichoptera, has been used by Busck (1914) in his classification of the Microlepidoptera.

Chapman (1916) suggested that Micropteryx should be placed in a new order called the Zeugloptera on the strength of the fact that the female has 10 abdominal segments and a single genital opening. Crampton (1920) did not agree that the Micropterygidae should be a distinct order. He suggested that the extent of division of the mesothoracic coxa into a eucoxa and a meron might be used as a criterion for separating the adults of Lepidoptera and Trichoptera. In his opinion the Micropterygidae are Lepidoptera. Martynova (1950), states that in spite of the significant resemblance to the Trichoptera, the Micropterygidae, together with the two nearly related families, Eriocraniidae and Mnesarchaeidae, undoubtedly belong in the order Lepidoptera, in which they are not completely isolated, since in the adult structure it is possible to observe a transition to the higher forms of the order. Martynova found that the first instar larva of Micropteryx calthella had more characters in common

with the larvae of Mecoptera than with Trichopterous or Lepidopterous larvae. Hinton (1946) used wing characters, female genitalia, adult mouthparts, larval and pupal morphology, in his reclassification. He agrees with Chapman (1916) in raising the Micropterygidae to ordinal rank. Hinton created three suborders; the Dacnonypha (Eriocraniidae), Monotrysia (Hepialoidea, Nepticuloidea, and Incurvarioidea), and the Ditrysia which contains all the higher Lepidoptera. Richards and Davies, (Imms, 1957) combined the Dacnonypha in their Monotrysia and preserved Hinton's suborder Ditrysia. The classification used in this present work follows Imms. (See table III, p. 9).

Another current classification is that of Kloet and Hincks (1945) which contains three suborders: the Zeugloptera including the Eriocraniidae and the Micropterygidae; the Homoneura with the single family Hepialidae, and the Heteroneura containing all the other families. Although their classification is not followed, the specific names used in this thesis are those given by Kloet and Hincks. It was found convenient to call the superfamilies Pyraloidea, Tortricoidea and Tineoidea the Microditrysia. Busck (1914) stated that this grouping, which was used by the older German lepidopterists, is an unnatural one, because the Pyraloidea, in his opinion, form a distinct group. Busck says that the Sesiidae and Cossidae have affinities with the "Microlepidotera". Chapman (1894) related <u>Micropteryx</u> to the Psychoidea

T A B L E III

ORDER LEPIDOPTERA

SUBORDER ZEUGLOPTERA

FAMILY MICROPTERYGIDAE

Micropteryx calthella (Linnaeus)

SUBORDER MONOTRYSIA

SUPERFAMILY ERIOCRANIOIDEA

FAMILY ERIOCRANIIDAE

Mnemonica subpurpurella (Haworth)

SUPERFAMILY HEPIALOIDEA

FAMILY HEPIALIDAE

Hepialus lupulinus (Linnaeus)

SUPERFAMILY STIGMELLOIDEA

FAMILY STIGMELLIDAE

Stigmella basalella (Herrich-Schaeffer)

SUPERFAMILY INCURVARIOIDEA

FAMILY INCURVARIIDAE

Adela reaumurella (Linnaeus)

SUBORDER DITRYSIA

SUPERFAMILY PSYCHOIDEA

FAMILY ZYGAENIDAE

Zygaena filipendulae (Linnaeus)

SUPERFAMILY COSSOIDEA

FAMILY COSSIDAE

Zeuzera pyrina (Linnaeus)

Cossus cossus (Linnaeus)

MICRODITRYSIA

SUPERFAMILY TINAEOIDEA

FAMILY TINAEIDAE

Tinecla bisselliella (Hummel)

FAMILY GELECHIIDAE

Sitotroga cerealella (Olivier)

SUPERFAMILY TORTRICOIDEA

FAMILY EUCOSMIDAE

Evetria buoliana (Schiffermueller)

FAMILY TORTRICIDAE

Tortrix viridana (Linnaeus)

SUPERFAMILY PYRALOIDEA

FAMILY CRAMBIDAE

Crambus hortuellus (Huebner)

FAMILY PYRAUSTIDAE

Scoparia ambigualis (Treitschke)

FAMILY PHYCITIDAE

Plodia interpunctella (Huebner)

FAMILY PTEROPHORIDAE

Stenoptilia pterodactyla (Linnaeus)

MACRODITRYSIA

SUPERFAMILY BOMBYCOIDEA

FAMILY LASIOCAMPIDAE

Poecilocampa populi (Linnaeus)

FAMILY SATURNIIDAE

Saturnia pavonia (Linnaeus)

SUPERFAMILY SPHINGOIDEA

FAMILY SPHINGIDAE

Deilephila elpenor (Linnaeus)

Laothoe populi (Linnaeus)

Dilina tiliae (Linnaeus)

SUPERFAMILY GEOMETROIDEA

FAMILY GEOMETRIDAE

Biston betularia (Linnaeus)

Operophtera brumata (Linnaeus)

Colotois pennaria (Linnaeus)

Selenia tetralunaria (Hufnagel)

Deuteronomos alniaria (Linnaeus)

FAMILY DREPANIDAE

Drepana binaria (Hufnagel)

FAMILY CYMATOPHORIDAE

Asphalia diluta (Schiffermueller)

SUPERFAMILY NOCTUOIDEA.

FAMILY NOCTUIDAE.

Plusia gamma (Linnaeus)

Orthosia gothica (Linnaeus)

Agrotis ypsilon (von Rottenburg)

Agrotis exclamationis (Linnaeus)

Agrochola lychnidis (Schiffermueller)

Agrochola macilenta (Huebner)

Allophyes oxyacanthae (Linnaeus)

Amathes xanthographa (Schiffermueller)

Amathes umbrosa (Huebner)

Amathes c-nigrum (Linnaeus)

Amphipyra pyramidea (Linnaeus)

Amphipyra tragopoginis (Linnaeus)

Anchoscelis lunosa (Haworth)

Apatele psi (Schiffermueller)

Aporophyla lutulenta (Schiffermueller)

Ceramica pisi (Linnaeus)

Charadrina morpheus (Hufnagel)

Charadrina alsines (Brahm)

Charmeas graminis (Linnaeus)

Cirrhia fulvago (Linnaeus)

Colocasia coryli (Linnaeus)

Cosmia trapezina (Linnaeus)

Conistra vaccinii (Linnaeus)

Eupsilia transversa (Hufnagel)

Hydraecia micacea (Esper)

Hydraecia oculea (Linnaeus)

Lampra fimbriata (von Schreber)

Leucania comma (Linnaeus)

Leucania pallens (Linnaeus)

Leucania lythargyria (Esper)

Luperina testacea (Schiffermueller)

Lycophotia porphyrea (Schiffermueller)

Meristis trigrammica (Hufnagel)

Ochropleura plecta (Linnaeus)

Orthosia gothica (Linnaeus)

Phlogophora meticulosa (Linnaeus)

Plusia chrysitis (Linnaeus)

Rhizedra lutosa (Huebner)

Rusina umbratica (Goeze)

Thalpophila matura (Hufnagel)

Tholera cespitis (Schiffermueller)

Tholera popularis (Fabricius)

Triphaena interjecta (Huebner)

Triphaena janthina (Schiffermueller)

Triphaena pronuba (Linnaeus)

Xylophasia monoglypha (Hufnagel)

Xylophasia rurea (Huebner)

FAMILY NOTODONTIDAE

Lophopteryx capucina (Linnaeus)

Phalera bucephala (Linnaeus)

FAMILY ARCTIIDAE

Spilosoma lubricipeda (Linnaeus)

Spilosoma lutea (Hufnagel)

Eilema lurideola (Zincken)

Paragmatobia fuliginosa (Linnaeus)

FAMILY LYMANTRIIDAE

Euproctis chrysorrhoea (Linnaeus)

SUPERFAMILY HESPERIOIDEA

FAMILY HESPERIIDAE

Augiades sylvanus (Esper)

SUPERFAMILY PAPILIONOIDEA

FAMILY PIERIDAE

Pieris brassicae (Linnaeus)

FAMILY LYCAENIDAE

Polyommatus icarus (von Rottenburg)

FAMILY NYMPHALIDAE

Aglais urticae (Linnaeus)

Polygonia c-album (Linnaeus)

(Zygaena and Limacodes) on the basis of larval and pupal characters.

Recent work on the phylogeny of the Papilionoidea, which was of use in the choice of species for this study, is that of Ehrlich (1957). He compared the morphology of all parts except the axillary sclerites and the female genitalia, which he described separately (Ehrlich 1958), and concluded that the Papilionidae and Pieridae form a group distinct from the Lycaenidae. The Nymphalidae and Libytheidae form a third group intermediate between them.

The theory of Chapman (1917, 1918) that the attitude assumed by Lepidoptera during the hardening of the wings may be an example of recapitulation in habit, is not generally accepted. Cottrell (pers. com.) has studied wing expansion in Pieris.

Colouration in Lepidoptera has attracted a large number of workers. Schwanwitsch (1924, 1926, 1935, 1943, 1949) describes the evolution of colour patterns in butterflies. O'Byrne (1933), Jones (1933) and Blest (1957) studied colouration in relation to predation, and numerous papers have been written on melanic forms, (summarised by Kettlewell, 1956). Carpenter (1947) gave some examples of the relation between colour pattern and attitude. Oudemans (1903) made accurate drawings of the resting attitudes of a large number of macrolepidoptera, and related colour pattern with resting position. He concluded that the colour patterns

on exposed parts of the body are different from those on areas hidden at rest. Hodgson (1909) also notices the sharp demarcation between hidden and exposed areas in the wings of butterflies and named these "Phaneron" and "Crypton" respectively

Chapman (1906) and Russel (1938) both distinguished between the "Just settled", initial resting attitude, and the "Definite" or "Permanent" final resting attitude. Graham (1950) related colour pattern with attitude and attempted to derive all Lepidopterous postures from the primitive stegopterous (tectiform) position. He did not distinguish between initial and final resting position; in butterflies he described these as the "Polygonia" and "Argynnis" types respectively. Graham's main conclusions support and augment those of Oudemans.

Materials and Methods

The Lepidoptera listed in table IV (p. 13) were studied in detail. A wide variety of other species were also examined to determine how generally the results could be applied. The insects were drawn in the resting attitude and then killed with ethyl acetate. The scales were removed with a stiff pencil brush. To get an indication of shape, measurements of the thorax and wing base sclerites of ten specimens of each species were taken.

The tegulae of living insects were removed and the method of wing folding was watched under a stereoscopic microscope. The wing was also forcibly protracted and retracted and the effect on the wing base sclerites was observed.

Dissected pieces of fresh wing base were stained for 24 hours in newly made up very dilute methylene blue; one drop of saturated aqueous dye solution in 10ccs. of a mixture of 50% glycerine and 50% distilled water. The ligaments stained deep blue. This method of demonstrating ligaments was discovered by Weis-Fogh.

Some specimens were fixed in aqueous Bouin's fixative for 24 hours and then stored in 70% alcohol. The thoracic musculature was dissected and drawn. The thoraces of fresh or alcohol-preserved specimens were warmed in 2% KOH for about $\frac{3}{4}$ of an hour. The upper and lower membranes of the wing base were dissected apart and

TABLE IV

SPECIES	WING COUPLING					MEDIA	SECOND CUBITUS			ACULEI	RESTING ATTITUDE			FOLDS IN HIND WING		
	Fore Wing Apparatus		Hind Wing Apparatus		Type	Fore Wing	Hind Wing	Fore Wing	Hind Wing		Fore Wings	Hind Wings	Type	Anal	Cubital	Medial
Micropteryx calthella	Fibula or Jugum		Costal spines		Jugo-Frenate	Present	Present	Present	Present	Present	Small overlap-in	Meet in mid-line; hidden under Fore	Tectiform or Stegopterous	-	-	-
Mnemonica subpurpurella	Fibula or Jugum		Costal spines		Jugo-Frenate	Present	Present	Present	Present	Present	Small overlap	Small overlap;hidden under Fore	Tectiform or Stegopterous	Posterior to vein 2A	-	-
Hepialus lupulinus	Jugum		-		Jugate	Present	Present	Vestigial	Vestigial	Present	Small overlap	Small overlap; hidden under Fore	Lateral Tectiform	-	-	-
Stigmella basalella	Male-Jugum & Subcostal scales	Female-Jugum & Cubital spines	Male-Frenulum.	Female-Costal spines	Jugo-Frenate	-	-	-	-	Present	Small overlap	Apart; hidden under Fore	Flattened Tectiform	Posterior to anal vein	-	-
Adela reaumurella	Male-Jugum & Subcostal retinaculum	Female-Jugum & Cubital bristles	Male-Frenulum & Costal spines	Female-Costal spines	Frenate	Present	Present	Vestigial	Vestigial	Present	Small overlap	Medium overlap; hidden under Fore	Flattened Tectiform	Posterior to 2A	-	-
Sitotroga cerealella	Male-Subcostal retinaculum & Radial scales.	Female-Subcostal scales & Radial scales	Male-Frenulum	Female-Frenular bristles	Frenate	-	Vestigial	Vestigial	Present	-	Small overlap	Apart; hidden under Fore	Flattened Tectiform	Posterior to 2A	Present	Present
Tineola bisselliella	Male-Subcostal retinaculum	Female-Cubital spines	Male-Frenulum	Female-Frenular bristles	Frenate	Vestigial	Vestigial	Present	Present	-	Small overlap	Small overlap; hidden under Fore	Tectiform	Posterior to 2A	-	-
Zygaena filipendulae	Male-Subcostal retinaculum	Female-weak Cubital & Anal bristles	Male-Frenulum	Female-Frenular bristles	Frenate	Vestigial	Vestigial	Present	Present	-	Medium overlap	Small overlap; hidden under Fore	Tectiform	Posterior to 2A	-	-
Zeuzera pyrina	Male-Subcostal retinaculum	Female-few hairs	Male-Frenulum	Female-Frenular bristles	Frenate	Present	Present	Present	Present	-	Medium overlap	Meet in mid-line;hidden under Fore	Tectiform	Posterior to 1 + 2A	-	-
Evetria buoliana	Male-Subcostal retinaculum & Cubital Scales	Female-Subcostal scales & Cubital scales	Male-Frenulum	Female-Frenular bristles	Frenate	-	Vestigial	Vestigial	Vestigial	-	Medium overlap	Large overlap; Hidden under Fore	Tectiform	Posterior to 1 + 2A	Present	Present
Tortrix viridana	Male-Subcostal retinaculum & Cubital scales	Female-Subcostalscales & Cubital scales	Male-Frenulum	Female-Frenular bristles	Frenate	Vestigial	Present	Vestigial	Vestigial	-	Medium overlap	Large overlap; Hidden under Fore	Flattened Tectiform	Posterior to 1 + 2A	Present	Present
Plodia interpunctella	Male-Cubital scales & Costal fold	Female-Cubital scales	Male-Frenulum	Female-Frenulum	Frenate	-	-	-	Present	-	Medium overlap	No overlap; hidden under Fore	Tectiform	Posterior to 2A	Present	-
Crambus hortvellus	Subcostal and Cubital spines		Male-Frenulum	Female-Frenular bristles	Frenate	-	-	-	Present	-	Large overlap	No overlap; hidden under Fore	Lateral Linear	Posterior to 2A	Present	Present
Scoparia ambigualis	Subcostal and Cubital spines		Male-Frenulum	Female-Frenular bristles	Frenate	-	-	-	Present	-	Large overlap	No overlap; hidden under Fore	Flat narrow	Posterior to 2A	Present	Present
Stenoptilia pterodactyla	Male-Subcostal retinaculum	Female-Cubital scales	Male-Frenulum	Female-Frenulum	Frenate	-	-	Vestigial	-	-	Foreward,Apart	Foreward; anal angle exposed	Flat or slightly raised	-	Present	Present
Poecilocampa populi	—		Large Humeral lobe & Reduced Frenular bristles		Amplexiform	-	-	-	-	-	Meet in mid-line	Apart; hidden under Fore	Flat wide	Posterior to 2A	Present	Absent
Saturnia pavonia	—		Large Humeral Lobe		Amplexiform	-	-	-	-	-	Slightly apart	Medium overlap; Costal and anal margins exposed	Flat wide	Posterior to 2A	Absent	Absent
Deilephila elpenor	Male-Subcostal retinaculum	Female-Cubital hairs	Male-Frenulum	Female-Frenular bristles	Frenate	-	-	-	-	-	Apart	Apart; Anal angle exposed	Flat wide	Posterior to 2A	Present	Absent
Lophopteryx capucina	Male-Subcostal retinaculum		Male-Frenulum		Frenate	-	-	-	Vestigial	-	Meet in mid-line	Meet in mid-line; Anal angle exposed	Lateral	Posterior to 2A	Present	Absent
Euproctis chrysorrhoea	Male-Subcostal retinaculum, Cubital & Anal hairs	Female-Cubital and Anal hairs	Male-Frenulum	Female-Frenular bristles	Frenate	-	-	-	Vestigial	-	Meet in mid-line	Meet in mid-line; Anal angle exposed	Declivous Wide	Posterior to 2A	Present	Absent
Spilosoma lubricipeda	Male-Subcostal retinaculum & Cubital hairs		Male-Frenulum		Frenate	-	-	-	Vestigial	-	Small overlap	Meet in mid-line; Hidden under Fore	Declivous Wide	Posterior to 2A	Present	Absent
Plusia gamma	Male-Subcostal retinaculum & Cubital scales	Female-Subcostal hairs & Cubital hairs	Male-Frenulum	Female-Frenular bristles	Frenate	-	-	-	-	-	Meet in mid-line	Meet in mid-line; hidden under Fore	Declivous Wide	Posterior to 2A	Present	Absent
Orthosia gothica	Male-Subcostal retinaculum & Cubital hairs	Female-Subcostal hairs & Cubital hairs	Male-Frenulum	Female-Frenular bristles	Frenate	-	-	-	-	-	Large overlap	Small overlap; hidden under Fore	Flat Narrow	Posterior to 2A	Present	Present
Drepana binaria	Male-Subcostal retinaculum		Male-Frenulum		Frenate	-	-	-	-	-	Apart	Medium overlap; Anal margin exposed	Flat Wide	-	Present	Absent
Biston betularia	Male-Subcostal retinaculum	Female-Cubital scales	Male-Frenulum	Female-Frenular bristles	Frenate	-	Vestigial	Vestigial	Present	-	Apart	Apart; Anal margin exposed	Flat Wide	Posterior to 2A	Present	Absent
Operophtera brumata	—		Male-Large humeral lobe & Frenulum		Freno-amplexiform	Vestigial	-	-	Vestigial	-	Raised touching	Small overlap when flat; anal angle exposed Ventral surface exposed when up	Flat or Up	Posterior to 2A	Absent	Absent
Pieris brassicae	—		Humeral lobe		Amplexiform	-	-	-	-	-	Raised touching	Ventral surface exposed	Up	-	Absent	Absent
Polyommatus icarus	—		Humeral lobe		Amplexiform	-	Vestigial	-	-	-	Raised touching	Ventral surface exposed	Up	-	Absent	Absent
Augiades sylvanus	Cubital hairs		Hairy Humeral lobe		Amplexiform	-	-	-	-	-	Raised touching or Apart	Ventral surface exposed	Up	Half fold posterior to 2A	Half fold	Absent

mounted separately in Hoyer's medium (Beirne 1955). Similarly treated wing bases were stained in Mallory's triple stain, made up according to the formula given by Pantin (1948). Both the acid fuchsin and analine blue/orange G were used at one quarter strength. The staining time varied from 5-45 minutes according to the thickness of the cuticle. Preparations of individual sclerites were also made. Sections of parts of the wing base embedded by Peterfi's collodion paraffin method (Lee 1950) were made. These were also stained with Mallory's triple stain. An attempt was made to find out something about the composition of the different types of cuticle shown up by Mallory's triple stain in the wing base. The physical properties of the two main types of cuticle were compared using the torsion apparatus described on p. 29.

Experimental work was carried out on some of the larger species. A pair of watchmaker's forceps were ground down and the tips were hooked inwards so that they overlapped. These were used to cut the muscles individually; they were inserted through the membrane wherever possible. When it was necessary to damage sclerotized parts the hole was sealed with wax (Wooten and Sawyer 1954).

Fine probe electrodes were made by drawing out 1mm. bore pyrex glass capillary tubes in a small flame. Each tube contained two smaller capillary tubes threaded with 48 gauge Nichrome wires. In about one case out of ten these

wires broke off evenly when the glass was pulled out to give satisfactory electrodes, which could be used to stimulate individual muscles, (photograph Fig. 122). A single channel electrophysiological stimulator with independently variable frequency, output and pulse width, was used in series with a variable 173-25000 ohm resistance. The voltage when the electrode was in the tissue was of the order of 1 volt. The moths were pinned onto a plastacine cone in the centre of a large protractor, and the movements of the wings were measured. This experiment was unsatisfactory and the results are not reported in full. It was not possible to put the "indirect" flight muscles into tetanus. A satisfactory strong movement was obtained only in about 1 in 5 specimens in which the "direct" flight muscles were stimulated.

All diagrams given in this thesis were drawn from one specimen, using a squared eyepiece, and then altered where necessary after reference to other specimens had been made.

Cuticle

General Observations

It was clear from observations on living insects that some parts of the wing base cuticle are more flexible than others. Differences in rigidity are not always due to variations in the thickness of the cuticle. It was necessary to investigate some of the properties of the different types of cuticle, before the mechanics of the wing base could be related to morphology.

Sections of normal cuticle were taken from the mesonotum of Laothoe populi and Spilosoma lubricipeda. A pale brown exocuticle and a thicker, colourless endocuticle were seen in unstained sections. Three layers of procuticle were visible after staining with Mallory's triple stain: a non-staining exocuticle, a red outer endocuticle (mesocuticle of Schatz, 1952) and a thin inner endocuticle which stained deep blue. These observations were in agreement with those Ito (1954) who used Mallory's triple stain on the cuticle of Bombyx mori. Lower (1957) describes a thin exocuticle, a thicker mesocuticle and a thin endocuticle, in a Noctuid moth. Cuticle from the nota of the same insects was treated with two percent KOH solution, sectioned and stained. The exocuticle, which was no longer refractory, stained deep red and all the endocuticle stained a deep blue. It was found that in fresh tissue the endocuticle gave a positive reaction to Millon's reagent, but after treatment with KOH, it was negative. The

exocuticle gave a positive Millon reaction only after warming in 2% KOH solution, being refractory to this reagent as well as to Mallory's stain in fresh tissue. Kennaugh (1959) reports that tanned exocuticle is refractory to Mallory's stain in scorpions. Kuwana (1940) found that the primary (pre-exuvial) cuticle of Bombyx mori was acidiphilous and Millon positive; the secondary (post-exuvial) cuticle was basiphilous and Millon negative.

Clear differentiation of the cuticular elements was obtained, when whole wing base dissections were stained in Mallory's triple stain or Lower's trichrome (1955). Combination stains are generally considered unsatisfactory for preparations of whole tissue, but it was found that satisfactory results were obtained with thick material if the dyes were sufficiently dilute. The specimens were examined at intervals during staining because the staining time varied from species to species.

The inner endocuticle is the only layer of the procuticle present in the wing base membrane which, therefore, stains dark blue in fresh tissue. Dennell and Malek (1954) found that the arthrodial membrane of Periplaneta Americana consisted only of epicuticle and post-exuvial endocuticle. Outer endocuticle occurs in scattered patches on the upper wing membrane especially around the veins; exocuticle is present in the wing veins themselves.

Colours seen in surface view of whole mounts, stained in Mallory's triple stain after 2% KOH treatment, and their representation on the diagrams.

Cuticular type	Colour	Diagram
Exocuticle Outer Endocuticle Inner Endocuticle	Thick: Dark Red Thin: Mauve	Thick: Black Thin: Cross Hatched
Outer Endocuticle Inner Endocuticle	Dark Blue	Irregular white spots on black
Inner Endocuticle	Blue	Widely spaced black spots on white
Inner Endocuticle with scattered patches of Outer Endocuticle	Shades of Blue	Medium spaced black spots on white
Bending cuticle	Purple spots on Red	Close black spots on white

Differentiation of Cuticle following KOH treatment

One hind wing base (upper membrane) and one fore wing base (lower membrane) of S. lubricipeda were subjected, prior to staining in Mallory's triple stain, to each of the following treatments: distilled water, Ringer's solution (see appendix 1), half percent aqueons KOH solution and unit

concentrations of KOH from 1% - 10%, for 90 minutes at 90°C. These were stained simultaneously with a fresh, fourteenth pair as controls. After staining the sclerites of the controls and those pieces heated in water or Ringer, appeared orange-yellow in surface view. Specimens subjected to concentrations of KOH below 4% gave very good separation into red and blue areas after staining. Unspecialised cuticle appeared red or purple in surface view depending on the thickness of the red - staining exocuticle. This cuticle was thick in most places in the wing base and is shown plain black in all diagrams of wing bases. Cross-hatching indicates thin "normal" cuticle. Exocuticle was absent in part of the posterior notal wing process, and second median plate of the fore wing in some species, and the base of the radius in the hind wing, the blue staining outer endocuticle being visible in surface view. Similar patches of blue-staining cuticle are present in the base of the subcosta of the hind wing, the anterior notal, and pleural wing processes of the fore wing. In these places the endocuticle is invaginated so that the exocuticle of the surrounding parts appears to be continuous. These invaginations consist mainly of outer endocuticle, which is seen in blue-staining patches in surface view, extending underneath the surface membrane and parallel to it. The invaginations can be opened out in cuticle which has been treated with 10% KOH. Cuticle staining blue in Mallory after 2% KOH treatment is

indicated by irregular white spots on a black background in diagrams. Exocuticle begins to loose its red-staining properties after treatment with 4% KOH and after 6% KOH all normal wing base cuticle is non-fuchsinophil. Isolated patches of "red" cuticle do remain in positions where the cuticle was observed to bend during wing movements. This cuticle was called "Bending cuticle" (see p. 24). Its position is best demonstrated by fuchsinophil staining after warming with 6-8% KOH, all the rest of the cuticle being pale blue. Bending exocuticle is the only Millon positive element remaining in the wing bases so treated. All the Millon-positive protein was removed from wing base cuticle by 10% KOH, and homogeneous light blue staining was then given with Mallory's stain.

Protein Tests.

Fresh, scraped nota from a large number of Noctuids were heated for 90 minutes, at 90°c. in 2% KOH solution. The solution was a light brown colour, and became opalescent when ethyl alcohol was added to it. Ten percent trichloracetic acid gave a cloudiness that disappeared on heating. It was assumed that arthropodin (Fraenkel and Rudall 1947) was removed from the cuticle by the KOH. The exocuticle remained Millon and Xanthoprotein positive but all protein had been removed from the endocuticle. Richards (1951) states that the sclerotin group of proteins (Pryor 1940) are removed by 5% KOH, which coincides with the time of loss of red-staining

properties, and Millon positivity from the exocuticle. Blower (1951) thought that fuchsin-staining with Mallory was a property of the cuticular proteins. Krishnan (1953) found that the entire endocuticle of a scorpion was impregnated with protein and stained blue with Mallory's triple stain. Inner endocuticle of Lepidoptera is Millon-positive and stains deep blue with Mallory. Dennell and Malek (1956) concluded that quinone-containing cuticular proteins are fuchsinophil.

Ligaments

Ligaments are largely dissolved by 2% KOH solution, and skrink to a bundle of wavy fibres that run from origin to insertion of the ligament. These fibres gave a positive chitosan-iodine reaction after heating in KOH solution, saturated at room temperature, for 20 minutes at 160°c. They stain pale blue with Mallory's triple stain after KOH treatment. and it is this basis of chitin fibres that was used to identify ligament insertions on some sclerites. In fresh tissue the ligaments stain very deep blue with Mallory's stain and often have an imprecise outline. This type of ligament is called a tension ligament by Weis-Fogh (pers. com.), who has found that they are tough when stretched in the direction of the fibres. Tension ligaments were found between all the sclerites of the wing base. Only those which were of significance in comparative morphology are described in this thesis.

Carbohydrate tests

Wigglesworth (1956, 1957) showed that the flexible membrane of the neck and legs of Rhodnius prolixus gave a positive PA/S reaction, whereas the rest of the endocuticle was negative. The axillary cord and wing base membrane of Lepidoptera stain pink with this test. The ligaments of the wing base are intensely PA/S positive, staining deep pink (almost magenta) with this reagent. They also stain very strongly in cold Millon's reagent (Ryder 1959) in three to four hours, under these conditions the cuticular proteins do not react. This was found to be the best method of showing up ligaments. The ligaments were PA/S negative after incubation with Protease at 30°c for 48 hours. Incubation with diastase, ptyalin or chloroform ethanol did not affect the positive reaction to the PA/S test, which was probably not due to the presence of polysaccharide or some unsaturated lipid which also may be PA/S positive, (Schmidt 1956). Fresh ligaments stained dark purple in 0.5% toluidine blue after a few hours; the other wing base tissues stained blue. This may be β-metachromasia (Pearse 1960), which is given by some mucoproteins, (Day 1949). Acid mucopolysaccharides give a red Y - metachromasia with this stain. Ligaments are also stained by bismark brown; this reaction is given by mucoproteins (Leach 1947).

Schmidt (1956) describes a "subcuticle" in Cecropia pupa, lying between the epidermis and the endocuticle. This

contained thickly packed fibres in some areas. The subcuticular layer was thickest in the places where the dorsoventral muscles were attached and in the intersegmental membranes. This gave a positive reaction to the PA/S and aldehyde-fuchsin tests, and was stained heavily by bromophenol blue. It stained orthochromatically with toluidine blue and gave no reaction with sudan black or ammoniacal silver nitrate. Schmidt concluded that a mucoprotein or a glycoprotein was present. Lepidopteran wing base ligaments differ from "subcuticle" only in their staining with toluidine blue. Although the ligaments are stained with aldehyde-fuchsin (Halmi and Davies 1953; Scott and Clayton 1953) the pink colour is easily washed out in alcohol. Clark and Clark (1960) are of the opinion that the irregular, crystalline attachment nodes of the ligaments in a Polychaete worm, Nephtys, are probably composed of glycoprotein.

The epidermis can be stained with aceto-carmine, and is seen to lie underneath the ligaments in the lepidopteran wing base. Histochemical tests on accurate sections of ligaments were not performed and are necessary to show whether ligaments are endocuticle, "subcuticle", or a separate cuticular layer of a different composition.

Rubber-like Cuticle

Two thick patches of rubber-like cuticle are present in the mesothorax, (labelled Subtg.- N. Li and Subtg.- Psc. Li in figures 101 and 102.) These stain heavily with methylene

blue, as do the tension ligaments. A very intense reaction is given to Millon's reagent, but staining with toluidine blue is orthochromatic. Rubber-like ligaments stain unevenly with Mallory's triple stain in whole mounts and red in sections; they are PA/S negative. The chemical and physical properties of the rubber-like protein of which they are composed, have been investigated by Weis-Fogh (in press.) He calls this resilin; it has an unusual amino acid composition. Weis-Fogh has located other rubber-like ligaments in the wing base of a Sphingid, but I have been unable to find them.

Bending Cuticle

Bending cuticle from Laothoe populi, Spilosoma lubricipeda, Scoparia ambigualis and Tortrix viridana was sectioned. The exocuticle was refractory to Mallory's stain in fresh tissue, and was red-staining in sections of bending cuticle which had been treated in 2% KOH. It differs from normal exocuticle in being more resistant to KOH (see page 20). The outer endocuticle is not a continuous layer, but consists of a series of red cones embedded apex downwards in blue-staining inner endocuticle. (Figs. 25 & 35).

The whole of the endocuticle is Millon-positive. The inner endocuticle is PA/S positive; the cones resemble normal outer endocuticle in being negative. The cones of outer endocuticle are more strongly ninhydrin positive than

is the inner endocuticle. (Schatz, 1952, records that mesocuticle is ninhydrin positive).

Inner and outer endocuticle are indistinguishable in sections of undifferentiated cuticle after KOH treatment. The bending cuticle cones differ from normal outer exocuticle in staining a darker blue than the inner endocuticle, which may be the same as normal inner endocuticle.

The endocuticular lamellae are very pronounced in bending cuticle and probably glide over one another to give increased flexibility, (Wigglesworth 1948). These horizontal lamellae can be seen to be continuous in both the cones and the inner endocuticle in KOH-treated tissue. (Fig. 24, p. 153)

Bending cuticle appears in surface view to be dark blue with orange spots in Mallory stained fresh tissue. The standard wing base preparations of all species were made from tissue treated with 2% KOH and in these the bending cuticle was red with purple spots. It is represented in diagrams by close black spots on white. The cones are very difficult to detect in unstained tissue because they are almost colourless. They have different optical properties from the inner endocuticle; Figure 36 is a photograph taken by polarized light of a hand cut section distorted inside a glass capillary tube. The inner endocuticle stretches when the cones move apart, and can be seen to bulge inwards when the cones close together.

Dark, sclerotized, exocuticular cones have been described by Plotnikow (1904) and Hass (1916) in insect

intersegmental membranes. These cones are easily visible in surface view, and do not extend downwards to the inner margin of the endocuticle (see fig. 31, p./57). Blower (1951) describes similar, dark cone-shaped structures in Myriapod cuticle. These appeared to be formed partly from exocuticle and partly from outer endocuticle, the inner endocuticle being undifferentiated. C.T. Lewis (pers. com.) has found that the sclerotized bars described by Eastham and Eassa (1955) in the butterfly proboscis are broken internally in Aglais urticae into cones (Fig. 32, p./57). These are dark in colour, but resemble the cones of wing base bending cuticle in reaching to the inner margin of the endocuticle. The exocuticle is produced externally above each cone into a rounded hump or a seta. Way (1950) describes the formation of exocuticular cones around the pore canals during the development of the cuticle of a Noctuid larva.

The cones of wing base bending cuticle appear to be entirely endocuticular. The exocuticle is not thinner than that of adjacent normal cuticle (Fig. 28, p./55), and is quite smooth on its outer surface. Manton (1958) commented on the staining reactions of fresh cuticle with Mallory's triple stain. She concluded that sclerotized non-staining exocuticle is unstretchable when it is thick, and that the red staining cuticle is less fully sclerotized, less rigid and more elastic than the non-staining cuticle, whereas cuticle staining pale blue is flexible but not elastic. Manton suggested that

cuticle staining dark blue is intermediate between the red-staining and pale blue staining types. Bending cuticle in living Lepidoptera is usually distorted in such a way that it bulges outwards; the endocuticle being compressed and the exocuticle stretched. The bending exocuticle is as thick as it is in some areas of normal cuticle which are markedly more rigid. It therefore seems that refractory exocuticle may be stretchable in specialized areas.

The bending exocuticle is penetrated by red-staining canals seen in Mallory-stained sections to extend upwards from the inner endocuticle between the cones. (Fig. 26, p./54). These may be pore canals, which are described by Way (1950) in Diataraxia larva, or the ducts of dermal glands, which are described by Blower (1951) between the cones of Haplophilus and by Malek (1958) between the scale like sculpture on the surface of Schistocerca cuticle. The true nature of these canals was not investigated. An air sac is always present immediately beneath bending cuticle, and very little of the hypodermis remains. Studies on the development of bending cuticle were outside the scope of this work. There are no scales on bending cuticle.

Types of Bending Cuticle

Three types of bending cuticle were found in the species studied: In Micropteryx calthella, Monotrysia, the Microditrysia and Zygaena filipendulae the cones are small and irregular, often being clumped together in small groups.

The cones of Z. filipendulae (Fig. 34, p./58) are the largest in this type and there are about 320 cones or clumps per millimeter. In Hepialus lupulinus this type of bending cuticle, which is probably primitive, is present in the humeral split of the fore wing. Elsewhere large irregularly shaped cones are present, evenly spaced as in the next type, but between these numerous small cones occur.

All higher Lepidoptera have larger cones which are almost always distinct entities. They may be fused together in clumps near the junction of normal cuticle and bending cuticle. In Noctuoidea and Geometroidea the cones are extremely regular in shape and constant in size, within each species. The shape of the cones may, when seen in surface view, appear very different in closely related species. (Fig. 27, p./55). The cones of Bombycoidea and Sphingoidea are round in section but differ in basal diameter within one species. Cossus cossus, Zeuzera pyrina and all the butterflies studied have smaller cones than the other macrolepidoptera, and these are a little irregular in size and spacing. Augiades sylvanus possesses the smallest cones of the advanced type. These vary from 107-256 per millimeter. The normal exocuticle of Papilionoidea is pigmented. The exocuticle of the bending cuticle is much paler, making the flexible parts of the cuticle easy to detect in these species. Bending cuticle is superficially indistinguishable from normal cuticle in most Lepidoptera.

Preparations of Mallory-stained Limephilus lunatus wing bases were unsatisfactory because the stain which proved so reliable for lepidopterous cuticle, produced uneven colouring in Trichoptera. The presence of bending cuticle was suspected from superficial examination, but surface microtrichia made its detection uncertain from this badly stained material. No sections of Trichopterous cuticle were taken to decide this point.

Torsion of bending cuticle.

Bending cuticle is usually not bent in one direction only, but is seen to be buckled and twisted in the living insect. A torsion apparatus (figure 38) was constructed by Mr. J.W. Siddorn to demonstrate that bending cuticle was more easily twisted than normal cuticle.

A strip of bending cuticle approximately 1 mm. long and $\frac{1}{2}$ mm. wide was cut from each mesothoracic posterior notal wing process of 5 Laothoe populi. Small lumps of sealing wax were attached to tags of normal cuticle which were left on each end of the strips. The length (L), width (b) and thickness (C) of the strips were measured, and they were kept in Ringer's solution until they were used. One strip of normal cuticle was taken from each side of the mesonotum of the same 5 moths. These were waxed and measured in the same way as the strips of bending cuticle.

Each strip was removed from Ringer's solution and quickly waxed onto a short length of glass capillary

tubing on the bottom of a glass torsion fibre. The cuticle was observed with a micro-telescope and when it was quite straight, it was waxed onto the bottom of a glass dish above the centre of a rotating stage (fig. 40, p./62). The glass dish was filled with Ringer's solution. The torsion fibre was 25 cm. long and of the order of 0.05 mm. thick; a counterbalanced pointed was attached to the bottom of the fibre and was in line with the zero mark on the base of the apparatus when the fibre was not twisted.

The stage was rotated so that the endocuticle was on the inside of the curve as the cuticle was twisted. It was observed that bending cuticle was buckled upwards in life. The angle of the pointer was recorded for every 15° rotation of the stage. The force exerted by the torsion fibre on the top of the cuticle was directly proportional to the angle through which the fibre is twisted, (β° in fig. 39, p. /62). The amount of twisting produced in the cuticle by this force is given by the difference between the angle of rotation of the stage (i.e. bottom of cuticle) and the pointer (i.e. top of cuticle) $= \alpha - \beta^{\circ}$.

The formula applicable to twisted strips is:-

$$\theta = \frac{T}{1/3\ bc3G}$$ (P.P. Benham, pers. com.)

Where θ = the angle of twist per unit length, T is the applied force, and G is the tension modulus in units of stress ($gm./cm^2$.

$$(\alpha^{o} - \beta^{o}) \propto \frac{b}{L} = \frac{\beta^{o} x}{\frac{1}{3} C^{3} G}$$ where x is a constant

A correction for thickness could not be applied because the cuticle was not homogeneous. (The average thickness of the notal strips was 0·0445 mm. and that of the bending cuticle 0·0253 mm. This being largely due to the differences in thickness of the endocuticle.

The angle of twist of the cuticle, corrected for length and width was plotted against the force in degrees which produced that amount of twisting. The results for a rotation of the stage from 0-180° are shown in graph (Fig. 41, p./63). It was found that the strips of cuticle did not always return to their original shape after being twisted more than 180°, and the stage, when released did not always return to the zero mark.

It was concluded that bending cuticle is more easily twisted than normal cuticle. It was not clear how much of this difference was due to the endocuticle being thinner, or differentiated into cones or due to differences in the composition of the exocuticle. In the notal incision the bending cuticle is bounded by normal cuticle and the exocuticle is the same thickness throughout. If however, the results of the torsion experiment are corrected for thickness the bending cuticle seems to be more rigid than normal cuticle.

Fore Wing

First Axillary Sclerite - 1 Ax.

In all higher Lepidoptera there are three ligaments between the notum and the first axillary sclerite. One is in front of the lateral emargination and the other two are behind it. In locusts there are two ligaments anterior and one posterior to the line of weakness in the notum. (Weis-Fogh pers. com.) It would seem at first sight that the lateral emargination and line of weakness, along which the notum bends when the dorsal longitudinal muscles contract, are in a different position relative to the 1Ax. in Lepidoptera. In some primitive Lepidoptera, however, a small ligament is present running from the anterior notal wing process to the base of the first axillary. This is probably the true second noto-axillary ligament, and is found in Mnemonica subpurpurella, Stigmella basalella and Zeuzera pyrina (Figs. 43, 45, p. 164 48, p. 165).

There is a patch of bending cuticle in the anterior arm of the first axillary sclerite which is strongly arched upwards (Fig. 51b, p. 165). Sometimes the first noto-axillary ligament is split into two parts, one inserting anterior and one posterior to this patch of bending cuticle. (Figs. 50, 51a, 52).

Both ligaments posterior to the lateral emargination in Lepidoptera are probably homologous with the third noto-axillary ligament of locusts. This ligament in Locusta

migratoria does appear to have two thickenings in it. In Monotrysia and Micropteryx calthella the origins of the two halves of this ligament are wide apart on the notum (Figs 43-47), but in higher Ditrysia they approximate and are close together on the enlarged median notal wing process. (Fig. 52, p. 166).

The anterior proximal corner of the first axillary sclerite, which bears the insertion of the anterior half of the third noto-axillary ligament, is invaginated in life underneath the median notal wing process. It consists of a flap of cuticle which is softer than the rest of the 1Ax., and stains blue with Mallory's triple stain. The fifth tergopleural muscle, when present, inserts on this anterior corner which is therefore called the apodeme of the 1Ax. This apodeme is large in Monotrysia and only that part of the 1Ax. distal to the insertion of the posterior half of the third noto-axillary ligament projects beyond the median notal wing process. In Ditrysia the apodeme is small or absent, and the main part of the first axillary sclerite is longer, projecting well out from the notum.

It is seen from Fig. 57 that the whole mesothorax tends to become longer in proportion to its width from the more primitive to the most advanced Lepidoptera, and that this parallels the change in shape of the 1Ax. This could be connected with flight, or resting position or merely represent an orthogenetic trend. The positions of most

species on this graph agree with their classification. Stenoptilia pterodactyla (25) however, is close to the other species that can sit with their wings up and is not near the other Ditrysian microlepidoptera, which form a discrete group. Five Noctuids that sit with their wings closely folded over the abdomen (Fig. 57, nos. 7, 17, 24, 35, 36.) were found to have a narrower thorax than another five which sit with their wings more spread out, (fig. 57, nos. 14, 31, 32, 34, 38.)

In spite of this evidence it was thought that these changes in shape were more likely to be adaptations for better flight because the first axillary sclerite is not directly concerned in wing folding.

The distortions of the thorax produced by the indirect flight muscles act directly on the 1Ax. (Fig. 59, p./69). In Lepidoptera, when the dorsolongitudinal muscles contract the median notal wing process and the proximal end of the first axillary are raised and the wing moves downwards. Clearly the greater the effective length of the first axillary sclerite the greater the mechanical advantage to lever the wing up and down, and the further median notal wing process will have to move at each stroke to produce a wing movement of the same amplitude as before. This could account for the fact that a large median notal wing process, a long lateral emargination, and a notal incision joined to the line of weakness in the notum by bending cuticle, are present in

all higher Lepidoptera which have a long 1Ax.

It was assumed that the movability of the median notal wing process depended on its free length X, which was proportional to the amplitude of movement of the median notal wing process. If the amplitude of movement of the wing is approximately the same in all Lepidoptera, then the length of 1Ax. (excluding apodeme) divided by wing length, when plotted against the free length of the median notal wing process also divided by wing length to correct for size differences between species, should give a straight line. Representatives of 14 superfamilies were found to give a good straight line (Fig. 58), but two species in the Papilionoidea did not fit on this graph. These two, Pieris brassicae (15) and Polyommatus icarus (20) were found to have the lateral emargination produced into the notum by a strip of bending cuticle to form a secondary line of weakness. (Fig. 52, p.166) It was concluded that the evolution of a large median notal wing process and a long first axillary sclerite was an improvement for flight.

Weber (1924) states that the distance between the anterior notal wing process and the median notal wing process is reduced as the median notal wing process grows forward in higher Lepidoptera. This distance is relatively constant in all Lepidoptera, being about 1/100th. of the wing length. The median notal wing process appears to have been enlarged by an extension of the lateral emargination into the notum.

The first axillary sclerite always has a positive slope away from the body when the insect is not flying, and therefore its angle with the horizontal is not the same as that of the wing at rest. The angle of 1Ax. is however broadly correlated with resting position and is also correlated with the overlap of the pleuron and the notum: that is the vertical distance between the pleural wing process and the anterior notal wing process. The scatter diagram (Fig. 60, p.170) shows this correlation, which is inexact because it was not possible to allow for the angle of the second axillary sclerite when the wing is at rest. The joint between 1Ax. and 2Ax. allows 60° play of movement. It is clear however, that those Lepidoptera which can hold their wings upwards at rest, have a large overlap between the pleuron and the notum.

In general the longer the 1Ax. the greater the horizontal distance between the pleuron and the notum. The narrower the notum is the more it has to bulge upwards, otherwise the volume of flight muscle would be reduced. This general correlation is demonstrated when the vertical distance between the pleural wing process and the top of the notum, divided by the vertical height of the pleuron, from coxa to pleural wing process, is plotted against the horizontal distance between the anterior notal and pleural wing processes, divided by the width of the notum (Fig. 61, p.171). The Papilionoidea have the widest "pleural shelves" and the

narrowest, most bulging nota (Fig. 56, p.167). It therefore seems that a hypothetical primitive moth with a flattish notum could be converted into a butterfly by squeezing the notum inwards at the sides and pushing it downwards into the pleuron, so that the wings rest on the shelf between the pleuron and the notum, supported on the outside by the projecting pleural wing process (Fig. 62, p.171).

Third and Fourth Axillary sclerites.

The third axillary sclerite is associated with the vannal area of the wing. It articulates with the posterior notal wing process either directly or through a fourth axillary sclerite which originates as that part of the third axillary associated with the jugum. The posterior notal wing process is a part of the scutum which has been cut off from the notum by a patch of bending cuticle and appears to be associated with the scutellum in higher Lepidoptera. (Weber 1924)

Monotrysian Lepidoptera and Micropteryx calthella have a jugum, sometimes called a fibula, which is a small flap from the vannal area of the wing which is folded forwards under the wing at rest. In Micropteryx calthella, Mnemonica subpurpurella and Stigmella basalella the posterior part is joined by a ligament to the jugal lobe (figs. 63, 64, 65, p.172). In all Lepidoptera the anterior part of the third axillary is attached to the first median plate. In Stigmella basalella this posterior part of the third axillary

sclerite is produced into a flap of bending cuticle towards the posterior edge of the jugum and axillary cord (Fig.65). The third axillary sclerite of Hepialus lupulinus and Adela reaumurella is divided into two by a thin strip of bending cuticle (Fig. 66, p.173). The anterior part articulates with the first median plate and bears the insertion of the seventh tergopleural muscle; the posterior part articulates with the posterior notal wing process, and is connected to the jugum by an anterior ligament in Hepialus lupulinus and posterior bending cuticle in Adela reaumurella.

Ditrysia lack a jugum projecting from the anal margin of the wing. The anal corner of the wing is, however, folded underneath the wing at rest in Zygaena filipendulae (Fig. 68, p.173), Zeuzera pyrina (fig. 67.) and all the Microditrysia examined (fig. 69, p.174). This jugal area is associated with the posterior part of the third axillary sclerite in the same way as is the Monotrysian jugum. All Macroditrysia lack a jugal area (fig. 70). The posterior part of the third axillary is attached to the underside of the anterior part by bending cuticle which acts as a hinge. It appears in surface view to be a distinct sclerite and is called the fourth axillary sclerite. (Fig. 75, p.176).

On contraction of the seventh tergo-pleural muscles, the third axillary sclerite rotates inwards and forwards over its articulation with the posterior notal wing process. When a fourth axillary sclerite is present a second fold occurs between the third and fourth axillaries so that these two

sclerites form a Z-bend with the posterior notal wing process. The posterior notal wing process bends downwards at its bending cuticle hinge with the notum until it rests on the subalare which is often grooved for its reception. In Zeuzera pyrina and Sitotroga cerealella a soft patch of Mallory blue-staining cuticle is present in the posterior notal wing process allowing the distal end to bend downwards when the third and fourth axillaries are folded on top of it.

The third axillary sclerite remains simple in shape in all Lepidoptera. It is a narrow, hard plate in Pieris brassicae and is much wider in Deilephila elpenor consisting largely of bending cuticle. Spilosoma lubricipeda and Euproctis chrysorrhoea also have a large part of the simple plate of the third axillary composed of bending cuticle. The insertion of the seventh tergopleural muscle appears to be attached to the fourth axillary sclerite in Drepana binaria (fig. 71, p. 174) and Asphalia diluta, being separated from the rest of the third axillary plate by a secondary strip of bending cuticle. When this muscle contracts the wing is not drawn back as far in this species as in other Lepidoptera, because the insertion of the seventh tergopleural muscle is near the first axillary. (See p. 54).

The insertion of this muscle is further from the junction of the third axillary and first median plate in Ditrysia than in Monotrysia. This means that the muscle has to shorten more but apply less force to pull the wing

back. Third third axillary sclerite of Augiades sylvanus articulates with the first median plate by a ball and socket joint, which allows these two sclerites to move freely on one another (fig. 72, p.175).

Second Axillary Complex

The second axillary sclerite and the base of the radial vein form a complex in Lepidoptera consisting of several distinct parts, which connect the distal end of the first axillary sclerite, on the dorsal wing membrane and with the pleural wing process on the ventral wing membrane.

The dorsal half of the second axillary sclerite (d2Ax.) articulates proximally with the first axillary sclerite and distally with the first median plate. The dorsal second axillary has a peg of cuticle (fig. 84, p.179) projecting downwards from its underside which does not reach the ventral wing membrane but fits into a depression in the ventral second axillary. The main part of the ventral second axillary consists of a sclerotization on the ventral wing membrane (fig. 76, p.176), which is connected by ligaments to the subalare and the pleural wing process (figs. 80 - 83). A vertical bar extends upwards through the wing base and joins the ventral second axillary to the radial plate, on the dorsal surface. In all higher Lepidoptera the dorsal and ventral parts of the second axillary sclerite are joined together by bending cuticle, and the radial plate is joined to the radius by a narrow arch of bending cuticle. The

radius is produced, under the radial plate, into a process on the ventral wing membrane, which is connected to the pleural wing process by a ligament. The pleural wing process projects upwards between the ventral radius and ventral second axillary, articulating distally with the postero-lateral radius and the vertical bar of the ventral second axillary. The ligaments between the pleural wing process and the ventral radius and ventral second axillary are long in moths and in some species allow the pleural wing process to articulate with the underside of the anterior half of the dorsal second axillary (fig. 103, p./89). These ligaments are straight when the wing is horizontal and twisted when the wing is up or down. In butterflies these ligaments are shorter, not allowing the pleural wing process to reach the dorsal second axillary, and are straight when the wing is upwards in the resting position.

The dorsal second axillary probably represents the primitive second axillary sclerite, which articulates with the first axillary, pleural wing process and first median plate. It appears to be homologous with the second axillary of Panorpa communis (fig. 79.)

A small plate of thin cuticle lies between the dorsal second axillary and the radial plate in most species. It bears a tuft of long scales and is therefore called the scale plate (figs. 85, p./86, and 94, p./94).

The second axillary sclerite of Limnephilus lunatus

is very similar to that of Lepidoptera. The ventral second axillary is connected to the first median plate, part of which is on the ventral wing membrane, by a strip of cuticle. Bending cuticle is present in this position in Micropteryx calthella, Mnemonica subpurpurella and Hepialus lupulinus (fig. 82, p./79). All other species studied have a ligament between the ventral second axillary and the first median plate. Another ligament joins the ventral second axillary and the fourth axillary which usually breaks the surface of the lower wing membrane near its junction with the posterior notal wing process. The upper and lower wing membranes which are wide apart in the region of the second axillary, are close together around the median plates and third and fourth axillaries. The radial plate is higher than the dorsal second axillary and overlies it when the wing is folded. (Figs. 80, 84, 93, 94).

In Monotrysia the subcosta is continuous in the wing base, but in Ditrysia it is broken either by bending cuticle (fig. 91, p./83) or by a membranous enlargement of the humeral split (fig. 92.). In the absence of any rigid structure anterior to the bending cuticle joint between radius and radial plate, the radius is free to rotate backwards on the radial plate. A similar bending cuticle folding point is present on the ventral surface. (Fig. 103, p./89).

Median Plates

The junction of the first and second median plates is always lifted when the wing is folded. The first median plate is V-shaded in section. The bottom of the V reaches the ventral wing membrane and is connected to the ventral second axillary by bending cuticle or a ligament as mentioned previously. The proximal part consists of normal cuticle, and slopes downwards away from the body, it articulates with the dorsal second axillary sclerite, and has a broad junction with the third axillary sclerite. The distal part of the first median plate slopes upwards away from the proximal part and consists of bending cuticle (Figs. 78, p. /77), 91, p. /83). The second Median plate consists of normal cuticle in Micropteryx and Monotrysia and is exposed on the surface of the wing membrane where it joins the base of the media (figs. 85, 88). In Ditrysia the second median plate consists of outer endocuticle and appears to be connected to the radial vein in higher Lepidoptera (figs. 91, 94). The second median plate of Zygaena filipendulae is connected to the remains of the base of the media which is joined to the radial plate by a loop of bending cuticle (figs. 89, 90, p./82).

The base of the second cubitus projects over the second median plate and becomes fused with the bending cuticle junction of the media and the radial plate. Although the vein is absent in the wing of all higher Lepidoptera, the base of the second cubitus has a bending cuticle joint with

the radial plate in all the Ditrysia studied except Pieris brassicae (figs. 91, 92, p./83, 94, p./84). Stigmella basalella (fig. 86, p./80) and Adela reaumurella (fig. 88, p./81) show intermediate stages in the growth of the second cubitus over the second median plate.

The base of the second cubital vein of Hepialus lupulinus is fused with the second median plate, and is detached from the rest of the vein in the wing itself (fig. 87, p./81).

The second median plate may penetrate the upper wing membrane in some species but it is usually invaginated under the second cubitus in a pocket of membrane (Fig. 78, p.///).

Direct flight muscles

The first tergopleural muscle was found in all Lepidoptera. It originates on the first basalar sclerite and inserts on the antero-lateral prescutum, the prealare (Figs. 104, p./90, 107, p./91).

The second tergopleural muscle was absent in butterflies but present in all the moths dissected. It also originates on the first basalar sclerite, but inserts on the scutum in front of the anterior notal wing process (fig. 104).

The third tergopleural muscle originates on an apodeme arising from the pleural wing process and inserts on the subtegula. The subtegula is thought to be prescutal in origin because the third tergopleural muscle inserts on a

projection of the posterior prescutum in locusts. It is called the prescutal apodeme by Weis-Fogh. In Limnephilus lunatus the third tergopleural muscle inserts on the pleural ridge directly (fig. 106, p. 191); the presence of a well developed tergopleural apodeme may be characteristic of the order Lepidoptera. (Figs. 99, p. 187, 101, p. 188, 108, p. 192). In Micropteryx and Monotrysia the tergopleural and prescutal apodemes are separate (fig. 97, p. 186), although they are closely associated in Adela reaumurella; these two apodemes are, however, joined in Ditrysia, sometimes by bending cuticle, but more usually by a thin plate of very springy cuticle which stains bright red in Mallory's triple stain. The prescutal apodeme is connected to the prealare and the notum by thick rubber-like cuticle. No evidence was found to support the idea that the third tergopleural muscle (tegular muscle) moves the tegulae. The tegulae probably act as a protection for the fore wing base when the insect is not flying, this would enable a moth to "shoulder" its way into debris without injuring the soft anterior membrane of the wing base.

The fourth tergopleural muscle is absent in the lepidopterous fore wing. The fifth tergopleural muscle, inserting on the first axillary sclerite, is sometimes present (see table V, figs. 104, 105, p. 190, 107, p. 191). In some species it is present only in one sex, and in Plodia interpunctella it was found in one culture but not in another. It is sometimes present in Pieris brassicae, having apparently

T A B L E V

	FORE WING								HIND WING							
	1t-p.Mu	2t-p.Mu	3t-p.Mu	4t-p.Mu	5t-p.Mu	6t-p Mu.	7t-p.Mu	p-sa.Mu	1t-p.Mu	2t-p.Mu	3t-p.Mu	4t-p.Mu	5t-p.Mu	6t-p.Mu	7t-p.Mu	p-sa.Mu
Micropteryx calthella	P	P	P	A	A	A	2 fasciculi	P Large	P	P	P	A	P	P	2	P
Mnemonica subpurpurella	P	P	P	A	A	at	2	P Large	P	P	P	A	P	A	2	P
Hepialus lupulinus	P	P	P	A	at	P	2	P	A	P	P	A	P	P	2	P
Stigmella basalella	P	P	P	A	A	P	3	P	P	P	P	A	P	A	3	at.
Adela reaumurella	P	P	P	A	P	at	3	P	A	P	P	P	P	P	2	A
Zygaena filipendulae	P	P	P	A	Male-A Female-at	A	3	P	A	A	P	A	P	P	2	A
Sitotroga cerealella	P	P	P	A	P	P	3	P	A	A	P	P	P	P	3	A
Tincola bisselliella	P	P	P	A	P	P	3	P	A	P	P	P	P	P	3	A
Tortrix viridana	P	P	P	A	A	A	3	P	A	A	P	A	P	A	3	A
Evetria buoliana	P	P	P	A	Male-A Female-at	Male-A Female-at	3	P	A	A	P	at	P	P	3	A
Plodia interpunctella	P	P	P	A	P or A in different cultures	P or A in different cultures	3	P	A	A	P	P	P	A	3	A
Crambus hortuellus	P	P	P	A	A or at	A or at	3	P	A	A	P	A	P	A	3	A
Scoparia ambigualis	P	P	P	A	A or at	A or at	3	P	A	A	P	A	P	A	3	A
Stenoptila pterodactyla	P	P	P	A	A	A	3	P	A	A	P	A	P	A	3	A
Zeuzera pyrina	P	P	P	A	A	A	2	P	A	P	P	at.	P	P	3	A
Poecilocampa populi	P	P	P	A	P	A	3	P	A	P	P	at	P	P	3	A
Saturnia pavonia	P	P	P	A	P	A	3	P	A	P	P	A	P	A	3	A
Drepana binaria	P	P	P	A	P	at.	3	P	A	A	P	A	P	A	3	A
Biston betularia	P	P	P	A	P	at.	3	P	A	A	P	P	P	A	3	A
Operophtera brumata	P	P	P	A	P or A	at.	3	P	A	A	P	A	P	A	3	A
Deilephila elpenor	P	P	P	A	P	P	3	P	A	A	P	A	P	A	3	A
Lophopteryx capucina	P	P	P	A	at.	at.	3	P	A	A	P	A	P	A	3	A
Spilosoma lubricipeda	P	P	P	A	P	P	3	P	A	A	P	A or P	P	P	3	A
Euproctis chrysorrhoea	P	P	P	A	at.	at.	3	P	A	A	P	P	P	A	3	A
Plusa gamma	P	P	P	A	at.	at.	3	P	A	A	P	A	P	A	3	A
Orthosia gothica	P	P	P	A	at.	at	3	P	A	A	P	A	P	A	3	A
Augiades sylvanus	P	A	P	A	at.	at.	3	P	A	A	P	A	P	A	3	A
Pieris brassicae	P	A	P	A	P or at.	A	3	P	A	A	P	A	P	A	3	A
Polyommatus icarus	P	A	P	A	at.	A	3	P	A	A	P	A	P	A	3	A

P = Present
A = Absent
at.= Atrophied

normal fibres which are loose and wavy in appearance when the wings are raised. Presumably this muscle can only function at the beginning of the upstroke when the notum is raised and the muscle is straightened out. The fifth tergopleural muscle is frequently atrophied in P. brassicae. The sixth tergopleural muscle is probably part of the fifth. Its origin is on the pleural ridge very close to that of the fifth tergopleural muscle, but its insertion on the median notal wing process may be distinctly separate from that of the fifth, or these two muscles may appear as a continuous sheet of fibres. (Figs. 104, 105).

The seventh tergopleural muscle is always present, inserting on the third axillary sclerite. It is split into two parts by the pleural ridge, one originating on the episternum and the other on the epimeron. In all higher Lepidoptera there are two fasciculi originating on the epimeron (see table V).

The basalar and subalar muscles were well developed in all the species examined. The first basalar is completely fused to the episternum in Micropteryx calthella. In most Lepidoptera, however it is partly separate and in Pieris brassicae it is secondarily free. (figs. 97, 98, p./86, 99, 100, p./87).

Folding of the Fore Wing

Two wing positions were defined which could be applied to all species irrespective of the attitude of the

wings at rest:-

The final resting position is considered to be the position in which the wings are fully folded, and the third axillary sclerite is lying next to the first axillary, the jugal lobe being folded under the wing. (Figs. 115b, p.196, 117, p.197).

The free resting position is that position in which all muscles are relaxed and the wing is not under any tension. It is the position taken up by the wings when a live insect is decapitated and the central nervous system of the thorax is picked out with forceps. The wings in this position are always much further back than they are during flight. Some species naturally use this position when walking just before or after flight (fig. 10, p.149).

The seventh tergopleural muscle is the wing folding muscle in all insects. The following experiment was conducted to make sure that it is the only wing retractor in Lepidoptera:-

Ten Plodia interpunctella, 10 Pieris brassicae and 5 Dilina tiliae were anaesthetized individually with carbon dioxide and immediately one muscle on the right side of the thorax was cut. A series of operations was performed in this way for each of the direct flight muscles. The only operation which affected the resting position was that in which the seventh tergopleural muscle was cut. This muscle was severed at its insertion on the third axillary sclerite,

and the only subsidiary damage was a slight tear in the dorsal wing membrane. The result was that the right wing was in the free resting position, while the left wing was in the final resting position.

The third axillary muscles (7t-p.Mu.) of Triphaena pronuba and Pieris brassicae were stimulated electrically through a small hole in the membrane between the subalare and the pleural ridge. The wing was only drawn back in T. pronuba, but was remoted and then jerked upwards in P. brassicae. This muscle is very large in P. brassicae even although the remotion of the wing into the resting position is a small movement; it could act as an upstroke muscle when the wing is above the horizontal.

To find out whether the third axillary muscle (7t-p.Mu.) is contracted all the time that the wing is folded, 10 moths of each of the following species were placed in a refrigerator at 5°c.

Deuteronomos alniaria - Geometridae
Cirrhia fulvago - Noctuidae
Anchoscelis lunosa - "
Amathes c-nigrum - "
Aporophyla lutulenta - "

The moths were removed from the refrigerator individually and the right seventh tergopleural muscle was cut through the membrane posterior to the pleural ridge, without opening the wings from the resting position. The moths were allowed

to warm up at room temperature and it was found that the wings remained in the resting position until the moths had flown. After flight the left wing was folded normally, but the right wing remained in the free resting position. The anal margin of the wing is approximately at the level of the side of the abdomen in the free resting position of Noctuids. It appears that the wing is stable in the final resting position once it has been folded by the third axillary muscle (7t-p. Mu.). When this muscle contracts the third axillary sclerite is pulled over the fourth axillary and comes to lie next to the first axillary, where it is in many species caught underneath the posterior distal corner of the first axillary, and is prevented from opening up and outwards again (fig. 117).

The movement of the third axillary is communicated to the rest of the wing through the median plates which connect the third axillary sclerite to the radius and media. The first axillary sclerite and dorsal second axillary are not involved in the antero-postero wing movements. The first median plate can rotate about its articulation on the postero-distal dorsal second axillary. The radial plate and ventral second axillary can rotate around their bending cuticle junction (or bridge) with the antero-proximal dorsal second axillary. When the radial plate rotates backwards, the humeral plate moves further away from the first axillary allowing the arched anterior arm of the first axillary to

flatten a little.

A diagram (figs. 112, 113, p.195) demonstrates the action of the median plates in Tortrix viridana. In the final resting position the proximal margin of the first median plate and the third axillary sclerite (YU) lies along the line YU'. The angle U'YU is 80°, i.e. in T. viridana the angle between the position of the third axillary when the wing is extended and at rest is 80°.

The proximal end of the first median plate rotates around its articulation with the second median plate at Y. The distal end of the second median plate is attached to the radius and rotates around X. At the extended and folded positions the posterior margin of the median plates is straight and the wing is stable. Between these two positions the posterior margin is bent backwards, the first median plate slopes upwards distally, and the second median plate slopes downwards away from the first. In the extended position the anterior margin of the median plates is straight, but in the final resting position it is strongly arched. The bending cuticle of the first median plate allows the twisting, necessary when the wing is folded, to occur. Although the median plates can be distorted they cannot elongate appreciably. This sets the limit to the backward rotation of the wing about these two folding points (X and Y). Z' is the most posterior point that the second median plate can reach, because if it were to continue along the arc ZZ' about X, it

would have to be stretched. Further backward movement is achieved in many higher Lepidoptera by the rotation of the radius and second cubitus about the radial plate.

The radial plate, radius and second cubitus are much higher than are the dorsal second axillary, median plates and the third axillary. The radial plate is thus able to slide over the dorsal second axillary into the resting position. The bending cuticle between the second axillary and the radial plate takes up the distortion due to the rotation of the radial plate. (G-G').

The mechanism of the wing folding follows this pattern in all Lepidoptera. There is always a membranous gap between the tough base of the anal lobe and the second cubitus to allow for the distortion caused by the lifting of the median plates. In Ditrysian Lepidoptera the second median plate consists of soft Mallory-blue-staining cuticle which can be twisted more easily than the Monotrysian median plate.

The folding of the fore wing in Monotrysia is proximal (fig. 116, p.97). Rotation occurs between the second axillary and the radius. The distal folding points of the radius, media and second cubitus with the radial plate are poorly developed and are not concerned in backward wing movement. The fore wing of Micropteryx calthella folds downwards along the line JK which is a forward continuation of the fold along the second cubitus. This 'cubital' fold is caused by the arching of the median plates. Anterior to

the second cubitus the wing slopes downwards at the side of the body; posterior to the cubital fold the wing overlies the abdomen. The tectiform position is produced by the action of the median plates alone.

There is very little backward rotation at the distal folding point (between the radial plate and veins R and Cu 2) in Zygaena filipendulae, Zeuzera pyrina and the Microditrysia. The humeral split is completely or partly filled with bending cuticle (fig. 89, p./82) which enables downward folding to occur, but does not allow the split to widen appreciably. In both distal and proximal folding the maximum retraction of the wing depends on the distance UU'. This distance is large in all Lepidoptera which cross the wings in the mid-dorsal line at rest. The membrane between the first and third axillary sclerites is narrow in Saturnia pavonia and those Geometroids which hold the wings apart at rest, (cf. Drepana binaria). All the Geometroidea, Sphingoidea and Bombycoidea studied showed predominantly proximal rotation. Some distal movement does occur at the bases of the radius and cubitus, the humeral split either being only partly filled with bending cuticle or composed of thick membrane. A patch of very thin membrane is present in the humeral split of Noctuids. It is wrinkled when the wing is forward and stretched when the wing is folded. The distal folding points are well developed and the proximal bridge between the second axillary and the radial plate is narrow and flexible.

The essential difference between 'narrow' and 'wide' Noctuids (figs. 15-24, pages 151/3) is in the shape of the third axillary sclerite. The insertion of the seventh tergopleural muscle lies above the fourth axillary in 'wide' Noctuids. The 'narrow' Noctuid has an arm which carries this insertion postero-distally. The third axillary can therefore move through about 90° when the wing is folded. (Figs. 117, 118, 119, p. 197). The folding points of the radius and cubitus with the radial plate allow these veins to parallel the movement of the third axillary, thus bringing the forewing back in line with the body.

Retraction of the wing in Augiades sylvanus is similar in mechanism to that of Noctuids, but the amplitude of movement is smaller. This is due to the fact that the third axillary is joined to the first median plate by a ball and socket joint. (Fig. 72, p.175). Much of the movement of the third axillary is lost in this joint and not communicated to the rest of the wing. Wing folding was entirely distal in the other butterflies examined. The radial plate is small and the bridge to the second axillary is much reduced. The well developed distal folding points are in line with the humeral split which is completely membranous (Fig, 92. p.183).

As already mentioned in the section on first axillary sclerite, the dorso-ventral position of the wing depends on the angle of the first axillary above the horizontal, the vertical overlap of the pleuron and the notum and the

horizontal distance between them. If these three values are small the long axis of the second axillary sclerite which is at right angles to the plane of the wing, slopes outwards, and the wing slopes downwards. If the wings are held flat over the abdomen, it is necessary for the radial plate to slide over the dorsal second axillary. In many species which hold the fore wings laterally at rest there is insufficient clearance to allow this and the fore wing therefore slopes downwards, e.g. Lophopteryx capucina

The frenulum of each hind wing and the tegulae were removed from 100 Amathes xanthographa. The following operations were performed on the right fore wing in batches of 20. The anterior arm of the first axillary sclerite, the 2Ax.-r.Pl. bridge, humeral split, distal folding points (r.Pl.-R.&Cu2), median plates, were waxed with beeswax filled with talc, until it had the consistence of sealing wax. The right wing was held forward and a small piece of wax was placed on the part to be immobilized. A hot needle was brought near the wax which was watched under a binocular microscope until it melted. The wing was held in position until the wax was solid. The moths were released into a cage and after one hour the angle of the costa with the long axis of the body was measured on both sides. As expected, the 20 moths which had the median plates waxed were the most asymmetrical.

Right - average $74{\cdot}7^{\circ}$, range 60° - 90°.

Left - average 13·25°, range 5° - 20°.

Variation was assumed to be due to the CO2, operation shock and variation in the amount of wax applied.

No definite wing base mechanism is present in those moths whose fore wings overlap the abdomen to determine whether the anal margins will meet in the mid-line and then be lifted upwards, or overlap one another. This depends on the stiffness of the anal lobe, the number of scales on the margin and whether these project to catch on the opposite wing, or lie flat.

The fore wings of Lepidoptera can be crossed right over left or left over right. 10 specimens of Crambus tristellus, 10 Thalpophila matura, 10 Leucanis impura, 10 Eilema lurideola, 30 Anchoscelis lunosa and 13 Agrotis ypsilon were used in the following way. The moths were confined individually in large, transparent cages and were stimulated to fly at intervals. The positions of rest were recorded when the moths settled after each of 15 flights. There was no significant tendency for any species to cross the wings preferentially in one direction. Fresh individuals with unt**a**ttered wings crossed them either way with equal facility. Some specimens with frayed edges to the wings persisted in crossing them in the same direction.

It was noticed that when the muscles on the third axillary were cut, the moth could still fly but the wing was not folded. The wing did not remain in the flight position

but was in the free resting position already described (about 45° back for most species). A wing cut free from the body will fold to this extent at the base; the mechanism must therefore be non-muscular. The anterior arm of the first axillary sclerite is arched more strongly when the wing is foreward than it is when the wing is folded. It pushes on the subcosta all the time the wing is forward and is the main cause of spontaneous wing folding. When the anterior arm of the first axillary sclerite is cut and the wing is pulled forward, the other elements of the wing show a tendency to fold. Presumably they are under least tension when the wing is in the free resting position.

The first stage in wing folding must therefore be the relaxation of the mechanism which moves the wing forward into the flight position.

When indian ink is introduced into the wing base it circulates in very narrow channels (Portier, 1932; Brocher, 1919, 1920).

There are no large blood spaces, and it was therefore considered unlikely that blood pressure could open the wings. A large part of the interior of the wing base was found to be filled with air sacs. This was demonstrated by the cobalt naphthenate method. (Wigglesworth, 1950). Many moths can, however, vibrate the wings in the flight position at a pressure of 15 mm. of mercury in a jar attached to a filter pump. It was therefore concluded that air pressure in the

air sacs of the wing base was not important in the opening of the wings.

It was thought that the anterior direct flight muscles might pull the wings forward for flight. 50 Phalera bucephala, 100 Pieris brassicae and 30 Adela reaumurella were used for a muscle-cutting series of experiments in which the basalar muscles, first, second and third tergopleural muscles were cut singly and in combinations. All these insects could still fly after the operation with the wings forward in the normal position. The basalar muscles of Triphaena pronuba and Phlogophora meticulosa were stimulated electrically and it was found that the costal margin of the wing was pulled downwards, but the wing was not protracted (figs. 120, 121, p. /98). The basalar muscles of Pieris brassicae and Aglais urticae were also stimulated. In this case the wing was pulled down from the vertical to the horizontal position, again without forward movement. Stimulation of the other groups of muscles was also tried in these four species. The only time when the wings were protracted in these experiments was during the stimulation of the indirect flight muscles, which could not be put into tetanus. While the wings were vibrating they sometimes moved forwards. These indirect flight muscles were examined more carefully and it was found that the wing of T. pronuba opened when the insertion of the oblique dorsal muscle on the postalare (postalar apodeme) was pressed. The postalar apodeme is hidden between the

mesothorax and the metathorax lateral to the phragma. The postalare connects this apodeme to the posterior notal wing process half way down its length. (Figs. 123, 124, 125, p. 199). When this muscle contracts the posterior notal wing process is lifted and the third axillary sclerite is forced outwards. If the fore wing is protracted in an isolated mesothorax movement of this apodeme can be observed under a binocular microscope. It was therefore assumed that when the oblique dorsal muscle and the seventh tergopleural muscle are both relaxed the wing is in the free resting position. When the seventh tergopleural muscle contracts the wing is folded.

As already explained the wings of headless moths remain horizontal when the central nervous system is removed from the thorax. The wings of butterflies which have been similarly treated, will only remain in the extreme up or down positions, and if forced into the horizontal position they return immediately either to the upstroke or downstroke position. This is a bistable state similar to the condition of flies treated with carbon tetrachloride, which was attributable to increased lateral stiffness caused by the contraction of the pleurosternal muscle. (Boettiger and Furshpan, 1952). The wing is unstable in the horizontal position because the pleural wing process is pushed outwards. As the wing moves up or down away from the horizontal, the second axillary sclerite slopes inwards or outwards respectively and the pleural wing process is allowed to return

inwards to its original position. The pleuro-furcal muscle (IIp-fs. Mu.) is very much reduced in Lepidoptera. It is possible that the third tergopleural muscle pulls the pleural wing process inwards as the wing passes the horizontal. This muscle was observed to be contracted on the downstroke when the notum is further backward than on the upstroke. (Figs. 126, 129, p. 200).

Presumably when a butterfly lands the last stroke is an upstroke. Usually the wings are in the upward free resting position when walking and the wings are drawn back at rest. The downward position is seen in the female during mating. Many nymphalids sun themselves with the wings horizontal. I think this is achieved by balancing the upstroke and downstroke muscles and does not indicate that the wings are stable in this position. The wings are often seen to make small amplitude up and down movements about the horizontal during sunning. These movements were thought by Krogh and Zeuthin (1941) to be pumping movements to generate heat.

The wings of all moths are stable in the horizontal position. The wings of decapitated Operophtera brumata will remain horizontal or vertically up when the central nervous system of the thorax is removed.

Mesophragma

Hepialus lupulinus, Adela reaumurella, Zygaena filipendulae, Zeuzera pyrina and all the Microditrysia

studied have a forward extension of the acrotergite which is fused to the scutellum (fig. 124, p.199). This extension reaches the anterior margin of the scutellum in all Macroditrysia except butterflies (fig. 125.). It is fused to the base of the median notal wing process in Augiades sylvanus. In Pieris brassicae, Polyommatus icarus and Polygonia c-album it forms a wide, hollow support for the median notal wing process (fig. 126, p.200). It acts as a lever, lifting the median notal wing process when the dorsolongitudinal muscles contract. The phragma is very large in all higher Lepidoptera. The oblique dorsal longitudinal muscle appears to act in the same way in butterflies as it does in moths, but it has a second antagonist, the pleural-subalar muscle. This is inserted on the posterior arm of the subalare which is connected to the main part by bending cuticle only (fig. 126).

HIND WING

First Axillary Sclerite

The first axillary sclerite and notal wing processes of the hind wing are similar to those of the fore wing in Micropteryx calthella and Mnemonica subpurpurella (Figs. 43, 44, p.164). The three noto-axillary ligaments are arranged in the same way as in the forewing of M. subpurpurella (fig. 128, p.201). In all other Lepidoptera the second noto-axillary ligament is absent. The gap between the first and third noto-axillary ligaments does not widen to give a lateral emargination homologous with that of the fore wing. A shallow emargination is present between the anterior and posterior halves of the third noto-axillary ligament; a patch of bending cuticle is present in the emarginated notum of most species, but a distinct notal incision is absent. (Fig. 131, p.201).

The first axillary sclerite does not elongate proximo-distally as it does in the fore wing of higher Lepidoptera, and a median notal lever is never developed. (Contrast Fig. 52, p.166 with Fig. 132, p.201). During flight the notum appears to bend along a line of weakness between the two halves of the third noto-axillary ligament: this movement is small and difficult to observe, the "indirect" flight muscles of the hind wing being very much reduced in all higher Lepidoptera. The mesoscutellum and large mesopostphragma of Ditrysian macrolepidoptera extend backwards

to the narrow metascutellum, and divide the metascutum into two lateral halves. (Fig. 54, p. 167). A long, endocuticular apodeme is present on the first axillary sclerite in Stigmella basalella hind wing (fig. 129, p. 201). Traces of this apodeme are seen in all Lepidoptera. The anterior arm is strongly fused to the first axillary in all lepidopterous hind wings. It is not arched upwards and very little bending cuticle is present, in contrast to the anterior arm of the first axillary in the fore wing.

The first axillary sclerite of Hepialus lupulinus is horizontal, but the first axillary selerite of all other species slopes upwards away from the body at an angle greater than 20°. The vertical overlap between the pleural and anterior notal wing processes was larger in the hind wing than in the fore wing. This was thought to be correlated with the steeper slope of the first axillary sclerite.

e.g: Averages of 10 Evetria buoliana

Fore wing, overlap 0; slope of 1Ax = 3.6°

Hind wing, overlap 0·0786mm; slope of 1Ax = 72.0°

The modifications of the first axillary sclerite of the hind wing are small compared with those of the fore wing.

Third axillary sclerite.

The third axillary sclerite of the hind wing is closely associated with the proximal part of the first median plate, which consists of normal cuticle. The distal part of the first median plate is composed of bending cuticle as it

is in the fore wing. The third axillary and first median plate can be seen as distinct sclerites in Mnemonica subpurpurella (fig. 134, p.203), but in most other Lepidoptera the suture between them is not distinguishable. The first median plate is connected to the second axillary sclerite by a broad strip of bending cuticle on the ventral wing membrane, in all the species studied except Stigmella basalella. (Fig. 143, p.207).

The third axillary sclerite of Micropteryx calthella, Monotrysia, Tortricoidea, Tineoidea, Zygaena filipendulae and Zeuzera pyrina has two arms on the dorsal wing membrane (figs. 144, 145, p.207). The proximal arm bears the insertion of the seventh tergopleural muscle, but the distal arm projects downwards and can only be seen in postero-lateral view; it is sometimes connected to the proximal arm by bending cuticle and appears to be homologous with the fourth axillary sclerite of the fore wing (fig. 145). The fourth axillary sclerite is never as well developed as it is in the fore wing. In the Pyraloidea and the higher Ditrysia the distal arm is joined to the proximal arm of the third axillary sclerite by solid cuticle and no distinct fourth axillary is present. The posterior notal wing process, therefore, articulates with the reflexed postero-distal corner of the third axillary sclerite (fig. 146.).

When the wing is folded the postero-proximal angle of the third axillary sclerite is pulled inwards and downwards

by the seventh tergopleural muscle, and the whole third axillary rotates inwards over its articulation with the posterior notal wing process, which curves downwards a little. The posterior notal wing process is a straight rod, often partially composed of blue-staining outer endocuticle; it always joins the scutum through a patch of bending cuticle. An anal plate is present between the posterior notal wing process and the axillary cord in all species which have the primitive type of third axillary sclerite, except Zeuzera pyrina. (Fig. 133, p. 202an.Pl.) An anal plate is also found in Plodia interpunctella, in which species the distal (fourth axillary) arm of the third axillary is almost completely fused with the rest of the sclerite. It is probable that the anal plate is lost in higher Lepidoptera and does not become fused with the third axillary sclerite. The anal plate lies above the posterior notal wing process but below the third axillary sclerite and third anal vein when the wing is folded (fig. 159, p. 214).

Second Axillary Complex and Median Plates.

The second axillary sclerite of the hind wing is not composed of two halves; a single bar of solid cuticle joins the sclerotizations of the upper and lower membranes. Ventrally the second axillary is joined to the subalare and the pleural wing process by ligaments, and to the first median plate by bending cuticle (fig. 143, p. 207).

All Ditrysian macrolepidoptera have a patch of long

backwardly directed scales on the second axillary sclerite. This is probably not homologous with the scale plate of the fore wing, but it is similar in appearance. The function of these scales was not investigated; they may be proprioreceptors. The second axillary sclerite is joined to the radius by a strip of bending cuticle on the upper membrane. The radius is fused with the subcosta, which articulates with the anterior arm of the first axillary sclerite at its base. (See figs. 133 - 142, pages 202/6). The centre part of the fused subcosta and radius is seen in Hepialus lupulinus (fig. 136). to consists of blue-staining outer endocuticle. This softer area is invaginated in Ditrysian Lepidoptera, and in the macrolepidoptera this invagination often extends posteriorly under the bending cuticle between the radius and the second axillary sclerite (fig. 139, p.205 and 155, p.212).

The proximal end of the fused media and first cubitus in Micropteryx calthella is a thin strip of bending cuticle which joins the radius as a patch of blue staining cuticle which extends underneath the bending cuticle connection between the second axillary and the radius. (Fig. 133).

In all other Lepidoptera the base of the fused media plus first cubitus is discontinuous, consisting of the "Median arm" projecting postero-distally from the radius to the second cubitus, and a bar of cuticle or thick membrane connecting the first cubitus with the base of the second. The base of the second cubitus is detached from the rest of

the vein (when this is present) in all species except Cossus cossus where the cubitus can be traced from the wing to its junction with the median arm in the wing base. In Micropteryx calthella and Mnemonica subpurpurella (fig. 134) the two median plates are distinguishable and hinge downwards upon each other when the wing is folded as in the fore wing. In all other Lepidoptera the median plates are reduced and their function is taken over by the base of the second cubitus and the base of the media and first cubitus. The distal end of the second median plate articulates with the end of the second cubitus and the median arm. (Fig. 138, p.205). In Crambus hortuellus the median arm and second median plate are fused (fig. 144, p.207). The median arm is reduced and no longer reaches the median plates in the Geometridae (fig. 141, p.206) and the Papilionoidea (fig. 142). It is fully developed in Augiades sylvanus, Drepana binaria (Fig. 139) and Asphalia diluta. In the fore wing of Stigmella basalella (fig. 86. p./80) there is a structure which is apparently homologous with the median arm of the hind wing. This has either been lost in all the other Lepidopterous fore wings which were examined, or incorporated into the radial plate. The "radial" plate of the fore wing may, therefore, be composed of the radius, media and first cubitus.

"Direct Flight Muscles"

The first tergopleural muscle was only found in Micropteryx calthella, Mnemonica subpurpurella and Stigmella

basalella. It is a small muscle running from the first basalar sclerite to the anterior prescutum (fig. 147, p.208). The second tergopleural muscle is present in the Monotrysia and a few Ditrysia (see table V, p. 46). It inserts on the anterior edge of the first basalar sclerite very near the second spiracle (fig. 153, p.211). Nüesch (1953) calls the second tergopleural muscle the "spiracular dilator" muscle.

The third tergopleural muscle is present in all the species studied. It is smaller than its equivalent in the fore wing, and its insertion on the pleural ridge never forms a long apodeme. In Micropteryx calthella and Mnemonica subpurpurella the third tergopleural muscle arises on the prescutal apodeme which is joined to the prescutum by a short ligament (fig. 147.) The prescutal apodeme bears a long prescutal arm, which is attached by a ligament to a projection on the first basalar sclerite in M. calthella and to the second basalare in M. subpurpurella (fig. 143). The prescutal arm of Hepialus lupulinus is hinged half way along its length, and its lower end is fused with both the first and second basalar sclerites. (Fig. 148, p.209). It is connected to the prescutum by ligament and bending cuticle. The prescutal apodeme and prescutal arm are absent in Stigmella basalella and Adela reaumurella and the third tergopleural muscle originates on the anterior prescutum. In all Ditrysia the prescutal apodeme is associated with the postalar apodeme of the mesothorax, to which it is attached by a short thick

ligament. The prescutal apodeme is linked to the prescutum by a ligament in Zeuzera pyrina and the Noctuoidea; in the other Ditrysia studied no trace of its prescutal origin remains. (see figs. 149, 150, 151.).

The second basalar sclerite of the Monotrysian hind wing is fused with the episternum and is similar in shape to the second basalar of a primitive fore wing (fig. 97, p.186). The second basalar sclerite is detached from the episternum in all the Ditrysia; It is connected to the pleural ridge, ventral subcosta, ventral radius and first basalar sclerite by ligaments. It is probable that the prescutal arm and the projection on the first basalar to which it was attached in the Monotrysia are fused with the Ditrysian second basalar. (Figs. 150, 151). A thin patch of cuticle bearing long scales lies underneath the second basalar in Hepialus lupulinus. This basalar "scale plate" is more prominent in Ditrysia and bulges over the first basalar sclerite, which like the second basalar loses its connection with the episternum. The first basalar sclerite of higher Ditrysia consists of an apodeme, on which the basalar muscles originate, hidden beneath the basalar scale plate. The sternobasalar muscle is small in the hind wing, but the other basalar muscles are well developed (figs. 150-152, p.210).

A fourth tergopleural muscle was found in several species (Table V, p. 46). It arises on the notum posterior to the lateral emargination. The fifth tergopleural muscle

was found in all species studied. A sixth tergopleural muscle was present in a few species, arising on the notum anterior to the lateral emargination (figs. 152, 156, p.210/212).

As in the fore wing, the seventh tergopleural muscle consists of three fasciculi in higher Lepidoptera, and only two in the more primitive species. The Geometridae are unusual in that one fasciculus of the seventh tergopleural muscle arises on the pleural wing process. (Fig. 154, p.211). Drepana binaria and Asphalia diluta have the normal arrangement of this muscle, in which one bundle of fibres arises on the episternum and two on the epimeral side of the pleural ridge.

A pleurosubalar muscle is absent in Adela reaumurella and in all the Ditrysia, but it is present in the other Monotrysia. The coxosubalar muscles are well developed in the Metathorax.

Folding of the Hind Wing.

The free resting position and final resting position of the hind wing are very similar. The seventh tergopleural muscle is the wing folding muscle as in the fore wing. The hind wings of decapitated moths always spring backwards against the abdomen when they are pulled forward and released, even when the seventh tergopleural muscles have been cut and the central nervous system of the thorax removed. The folds are present in the hind wing in the free resting position, but these are usually not as sharp as in the final resting position.

The right seventh tergopleural muscle was cut in 20 Plodia interpunctella, 20 Anchoscelis lunosa, 10 Triphaena pronuba and 10 Dilina tiliae. It was found that the resting position was unaffected unless the right frenulum was also removed, because the hind wing was pushed backwards by the fore wing. When the right frenulum was removed the right hind wing, which was operated on, did not overlap the abdomen as far as the left wing. In many individuals of these four species the right hind wing projected in front of the fore wing. Stimulation of the seventh tergopleural muscle in Phlogophora meticulosa and Triphaena pronuba hind wings caused a backward deflection of the wing. In Pieris brassicae the hind wing was jerked upwards and backwards when the muscle was stimulated. The seventh tergopleural muscle is well developed in P. brassicae hind wing although the final and free resting positions are identical. It is possible that this muscle is an upstroke muscle.

The folds present in the hind wings of the species studied are given in table IV (p. 13). The anal fold is formed between the second and third anal veins. It is present in all the species studied except Micropteryx calthella, Hepialus Lupulinus, Drepana binaria, Stenoptilia pterodactyla and the Papilionoidea. The anal lobe is folded ventrally and is always associated with the distal arm of the third axillary sclerite. In this respect the anal lobe resembles the jugal lobe of the fore wing which is associated with the

fourth axillary sclerite. When the seventh tergopleural muscle contracts, the third axillary sclerite rotates inwards, forwards and downwards over the posterior notal wing process and the anal veins are lifted a distance equal to the width of the third axillary sclerite. In all higher Lepidoptera the third anal vein is associated with the distal arm of the third axillary sclerite. When the seventh tergopleural muscle contracts the third axillary sclerite pulls the second anal vein up and over the third anal vein which is turned under at the same time. The anal lobe is pressed underneath the wing as the wing slides over the abdomen; this helps to make the anal fold (fig. 160, p.214). When there is neither an anal vein nor stiff vannal membrane in association with the postero-distal third axillary sclerite there is no anal fold, (figs. 139, 142.). In "narrow" Noctuids and Pyralids the anal fold is large and a correspondingly large area of vannus is associated with the distal third axillary sclerite.

In the Monotrysia there is no cubital fold. The median plates of Microteryx calthella and Mnemonica subpurpurella are functional and the median arm is brought close to the second axillary sclerite when the wing is folded. In the hind wing of Hepialus lupulinus the tuck in the wing base membrane is between the median arm and the second axillary sclerite, although the median plates are reduced. The median arm is closer to the second axillary sclerite than to the

radius in Stigmella basalella, Adela reaumurella, Zeuzera pyrina, Zygaena filipendulae and Tineola bisselliella when the wing is outstretched; the median plates are almost functionless. The base of the second cubitus and the base of the first cubitus plus media form a V-shaped fold when the wing is flexed. In these species this does not produce a fold in the wing itself because the two sclerites are surrounded by a large patch of thin membrane. A cubital fold was found in all the Ditrysia except the above mentioned and Saturnia pavonia, Operophtera brumata, Polyommatus icarus, and Pieris brassicae. The cubital fold occurs posterior to the first cubital vein, and is formed by the bases of the second cubitus and first cubitus plus media. The base of the second cubitus slopes antero-ventrally and the base of the first cubitus plus media slopes postero-ventrally often passing the vertical and coming to lie on top of the base of the second cubitus. It is seen from the diagram (fig. 157, p.213) that the radius and first cubitus which rotate about X, cannot be pulled backwards (1 - 1') by the third axillary sclerite, acting through the bases of the second cubitus and the first cubitus plus media, without distortion of these parts because the third axillary sclerite rotates about Y. Arcs drawn around X and Y from points 1 - 5 diverge widely. The third axillary sclerite comes to lie next to the second when the wing is folded (6 - 6'). Slight distortions in the median arm and median plates compensate

for the slight difference between the arcs around X and around Y through point 6. Papilionoidea and Operophtera brumata lack this mechanism and there is no cubital fold (figs. 141, 142, p.206). The base of the first cubitus plus media is reduced in Saturnia pavonia which also lacks a cubital fold. It would seem that the evolution of large "cubital plates" to replace the median plates led to the formation of the cubital fold in higher Lepidoptera. The bases of the second cubitus and first cubitus plus media form a single fold in Augiades sylvanus which, with the anal fold, forms one small pleat in the wing membrane.

"Narrow" Noctuoids and other Ditrysia which fold the wings close to the body at rest have a large distance between the radius and the median arm and a well developed second cubitus/first cubitus plus media mechanism. The bases of the right second cubitus and first cubitus plus media of Amathes xanthographa were covered in wax when the wing was unfolded, (p.55). The fore wings were cut off and the average angle of the right wing of 10 successfully waxed specimens was 58° with the long axis of the body; The left wing was folded at an angle of 18.5° from thelongitudinal line.

A median fold occurs in all the Noctuoids placed in category "narrow" and in several other species. It is formed in the wing membrane between the radius and the cubitus. This fold can be straightened out by pulling forwards on the frenulum which in turn pulls the radius away from the

cubitus and stretches the membrane between these two veins.

The lateral oblique dorsal muscle is well developed in the hind wing, especially in primitive moths. It is not connected to the posterior notal wing process directly, as is its counterpart in the fore wing, and no wing extending action could be demonstrated with this muscle. (Fig. 111, p. 194). When the basalar muscles of Phlophora meticulosa were stimulated electrically only a downward component of wing movement was observed. The hind wing can be moved forward beyond the free resting position, without being pulled by the fore wing, even in higher Ditrysia, where the metathorax is small compared with the mesothorax. The fore wings of 10 Rhizedra lutosa were cut off distal to the retinaculum, and the fore wings of another 10 were removed at the base, proximal to the retinaculum. The moths were suspended above a protractor and the greatest forward angle which the hind wings made with the longitudinal axis of the body, while the moths were flapping was measured. When the fore wing was attached to the hind wing by the frenulum the average forward angle of the hind wing was 82° (range 75°-90°). The unattached hind wing moved forward to 68°(60°-75°). It appears that the fore wing helps to pull the hind wing forward in flight and also unfolds the median area of the wing. The mechanism in the metathorax which protracts the hind wing was not discovered. It is more difficult to experiment with the reduced metathorax in higher Lepidoptera

than with the large mesothorax.

The way in which the hind wings were crossed over one another was investigated in 54 Eilema lurideola (fig. 23, p.153). The moths were seized when they were sitting in the resting attitude before they could attempt to fly away; the fore wings were pulled off to reveal the hind wings. It was found that the hind wings were crossed beneath both fore wings in 28 individuals. Fifteen of these had the hind wings crossed the same way as the fore wings and the other thirteen crossed them the opposite way. In 26 individuals each hind wing lay underneath the fore wing of the same side. It has already been shown that the forewings can be crossed right over left or left over right with equal facility (p.56). The crossing of the hind wings also depends on the way in which the anal margins chance to meet in the mid-line.

DISCUSSION

The proportions of the wing base elements and their positions relative to one another are critical. If flight is to be maintained efficiently, changes in the wing base from a primitive to a more advanced type, must take place slowly by a series of small stages. It follows, therefore, that two groups of Lepidoptera with markedly different wing bases are unlikely to have diverged recently. Positive wing base characters are therefore possible criteria for assessing evolutionary relationships. This aspect of wing base morphology has been neglected in the past.

In the species studied the degree of specialization of the wing base was in keeping with their generally accepted systematic position. Many features of the thorax and wing bases of Lepidoptera form a continuous series from the more primitive to the most advanced species. This evolutionary line appears to run from Micropteryx calthella through Mnemonica subpurpurella, Adela reaumurella, Zygaena filipendulae, the Microditrysia and Zeugera pyrina to the Macroditrysia.

Hepialus lupulinus shows the following differences from the other lepidopterous species that were examined:-

1) The bending cuticle has both large and small cones.

2) The dorsal and ventral halves of the mesothoracic second axillary sclerite are fused together (fig. 82, p.179).

3) The base of the second cubitus in the fore wing is apparently fused with the second median plate (fig. 87, p.181).

4) The prescutal arm in the hind wing is of an unusual conformation (fig. 148, p.209).

This evidence may indicate that the Hepialidae are an offshoot of the main lepidopterous line.

Stigmella basalella, and other species of the genus Stigmella, also have four unusual wing base characters:-

1) The base of the subcosta in the fore wing is strongly curved (fig. 86, p.180).

2) A structure is present in the fore wing base which is probably homologous with the median arm of the hind wing base (fig. 86).

3) The subalare of the fore wing has a spike like that of the hind wing (fig. 81, p.178).

4) The arrangement of the median plates and bases of the first and second cubital veins is slightly abnormal in the hind wing (fig. 135, p.203). If these characters are shared by the Opostegidae and Tischeriidae, the Stigmelloidea may be an isolated group.

Although the differences mentioned above are probably important, they do not represent major divergencies from the general scheme of the lepidopterous wing base. The axillary region of Lepidoptera is thick and the bases of the veins are swollen and indefinite, giving the lepidopterous wing base a very different appearance from those of the other members of the Panorpoid complex and the Neuroptera.

Certain characters of the wing base elements afford data of possible taxonomic importance. These are listed in table VI, p.79 . Micropteryx calthella (suborder Zeugloptera) is unique among the species studied in having the median arm of the hind wing connected to the base of the media and first cubitus (fig. 133, p.202). In all other respects Micropteryx calthella and Mnemonica subpurpurella are closely similar.

Type of Bending Cuticle	Jugum	Tergopleural Apodeme and Prescutal Apodeme Fore Wing	Cu 2 - r. Pl. Folding point - Fore Wing	v. 2 Ax. - v. 1 m. Pl. Bending Cuticle Fore Wing.	Media and Median arm - Hind Wing.	Median Plates - Hind Wing.	Anal plate - Hind Wing	Spike on Subalare - Hind Wing.	Second Basalar attached to episternum in Hind Wing	Prescutum and Prescutal Apodeme of Hind Wing	Prescutal Arm of Hind Wing
Primitive	Present	Separate	Absent	Present	Joined	Functional	Present	Absent	Attached	Attached	Present
"	"	"	"	"	Separate	"	"	"	"	"	"
" (and a specialized type)	"	"	"	"	"	Non-functional	"	"	"	"	"
Primitive	"	"	"	Absent	"	"	"	Present	"	"	Absent
"	"	Touching	"	"	"	"	"	"	"	"	"
"	Vestigial	Fused	Present	"	"	"	"	"	Detached	Detached	"
"	"	"	"	"	"	"	"	"	"	"	"
"	"	"	"	"	"	"	"	"	"	"	"
"	"	"	"	"	"	"	Present or absent	"	"	"	"
Advanced	"	"	"	"	"	"	Absent	Small	"	"	"
"	Absent	"	"	"	"	"	"	Absent	"	"	"
"	"	"	"	"	"	"	"	Present or Absent	"	"	"
"	"	"	"	"	"	"	"	Absent	"	"	"
"	"	"	"	"	"	"	"	Small	"	"	"
"	"	"	"	"	"	"	"	Absent	"	"	"
"	"	"	"	"	"	"	"	"	"	"	"

(Secondarily lost in Pieris)

The suborder Monotrysia and Ditrysia differ in several wing base characters:-

1) The jugum projects from the anal margin of the wing in Monotrysia, but not in Ditrysia.

2) The tergopleural and prescutal apodemes are fused in Ditrysia, free in Monotrysia.

3) The third tergopleural muscle of the hind wing inserts on the metaprescutum in Monotrysia and on the mesopostcoxal bridge in Ditrysia.

4) The second basalar sclerite of the hind wing is connected to the episternum in Monotrysia, but not in Ditrysia.

5) The second cubitus of the fore wing is fused to the radial plate in Ditrysia but not in Monotrysia. (Zygaena filipendulae is intermediate in this character, figs. 89, 90, p./82).

Micropteryx calthella, Mnemonica subpurpurella and Hepialus lupulinus are distinguished from Adela reaumurella, Stigmella basalella and the lower Ditrysia by three wing base characters:-

1) There is a prescutal arm in the hind wing.

2) They do not possess a spike on the subalare of the hind wing.

3) The ventral second axillary sclerite and the first median plate are connected by bending cuticle in the fore wing.

Micropteryx calthella, the Monotrysia, Zygaena filipendulae and the Microditrysia have the following characters in common:-

1) Bending cuticle with small, irregular cones.

2) An anal plate present in the hind wing.

3) A jugal folding mechanism present in the fore wing.

Zeuzera pyrina has a jugal lobe, but in all other respects this species resembles the Macroditrysia.

The Macroditrysia can be divided into three groups on wing base characters. The moths from one group (Bombycoidea, Spingoidea, Geometroidea and Noctuoidea); of the four superfamilies the Noctuoids have retained the most complete wing bases associated with a fully developed wing folding mechanism. In the other three superfamilies of moths the wings are not closely folded and wing bases show some reductions. The wing bases of Augiades sylvanus are similar to those of moths. The third axillary sclerite of the fore wing is joined to the first median plate by a joint which was not found in any other species (fig. 72, p.175). The shape of the thorax is different from that of most moths due to the resting position of the wing (attitude).

The wing bases of the Papilionoidea show many differences from those of the rest of the Macrolepidoptera. No evidence was found from wing base morphology to indicate whether they evolved from the same stock as the other Macroditrysia or along a different line.

Drepana binaria (Drepanidae) and Asphalia diluta (Cymatophoridae) have a modified third axillary sclerite in the fore wing; unlike the condition in Geometridae, no part of the seventh tergopleural muscle arises on the pleural wing process in the hind wing (fig. 154, p.211); they also differ from Geometridae in having a well-developed median arm in the hind wing (fig. 139, p.205). It is possible that the Drepanidae and Cymatophoridae are more nearly related to each other than to the Geometridae. No characters of possible taxonomic interest were found within the other superfamilies.

CONCLUSIONS

In primitive Lepidoptera backward movement of the fore wing occurs at the wing base, proximal to the bases of all the veins. A secondary folding point is developed in the subcosta and the radius of higher Lepidoptera which cuts off a "radial plate" proximally. Backward movement takes place mainly around this point in the Macroditrysia; in the Papilionoidea the retraction of the wing is entirely of this distal type.

There is also a tendency towards distal hind wing folding, but the main change from a primitive to an advanced Lepidopteran hind wing is the loss of the median plates and their functional replacement by the bases of the first and second cubital veins and the media.

It was concluded that the wing base morphology of a superfamily is related to the basic resting attitude and the phylogenetic position of that group. No aberrant wing folding mechanisms were found; major changes in resting attitude are achieved by small changes in the spatial relations of the parts of the wing base. It is possible to deduce the resting attitude of a species from the morphology of its wing bases only by comparing these with related species whose attitude is known.

Wing base morphology may prove to be of value in the systematics of the major groups of Lepidoptera. The wing bases of related families are too similar to provide taxonomic characters at this level. The presence of a tergopleural apodeme in the mesothorax is probably one of the best characters for a definition of the order Lepidoptera.

PART II

Wing folding and choice of resting site in Lepidoptera

Introduction.

It is well known that many Lepidoptera rely on their colouration and posture to protect them from enemies when they are at rest. Most procryptic moths hide during the day in dark crannies or under vegetation; some rest inconspicuously on tree trunks or in other exposed places. It has been assumed that behaviour patterns have evolved to enable nocturnal moths to "choose" a daytime resting site appropriate to their morphological adaptations. Kettlewell (1959) showed that an accurate choice of background is sometimes made, although he commented that the complicated pattern of the typical cryptic insect melts into a surprising number of backgrounds, (Kettlewell 1955). Very little experimental work has previously been done on the mechanism or extent of this choice of resting site.

Review of Literature

Collins (1934) showed that the codling moth was only active when the pigment in the eye was migrating. When completely light adapted the moth was passive, when completely dark adapted it was positively phototactic, (Collins and Machado 1935). Phototaxis in dark adapted moths has been studied by Longstaff (1906, 1909) and Winn (1916). Collins found no trace of a diurnal rhythm in the codling moth, but Horstman (1935), Larsen (1943) and Colguhoun (1939) have found

a rhythm independent of light. Larsen found that Noctuids which were normally nocturnal would fly during the day in search of food if they were very hungry. The inhibiting factors of light and low himidity during the daytime being overcome by hunger.

Colour sense in Lepidoptera has been investigated by several workers. Knoll (1921, 1926) found that Deilephila can recognise colours at very low light intensities. Mc.Indoo (1929) demonstrated that violet, blue and blue-green are more attractive to moths than green, yellow or red. Robinson (1951) concluded that night flying Lepidoptera are red blind. Butterflies have been shown to respond to all colours including red, by Stride (1956), Tinbergen et al. (1942), Ilse (1928) and Eltringham (1919).

Kettlewell (1955) left Biston betularia overnight in a black and white striped barrel. In the morning he found that significantly more f. carbonaria than f. typica were sitting on the black stripes. Grison and Silvestre de Sacy (1955) found that winter moth females, when placed in a similar situation, collected on the vertical black bands in preference to the white ones.

It is not known how moths find their hiding places after the night activity is over. Tonge (1909) observed that moths settled in exposed places drop to the ground when the sun shines on them in the morning. The resting sites of some Lepidoptera are described by Hamm, (1904, 1906a, 1906b). The

daytime habitat of most nocturnal moths is unknown. Porritt (1913) and Tonge (1909) record finding some species among fallen leaves. Poulton (1890) said that Triphaena pronuba hides deeply among thick foliage or dead leaves on the ground and is extremely difficult to detect at rest.

Wood (1913) suggested, that the compact resting attitude of some Noctuids, Microlepidoptera and butterflies enables them to creep into small chinks in rubbish to shelter when hibernating. Geometrids and other moths which rest with their wings spread out cannot do this without damaging the wings.

The effect of various meterological factors on the night activity of nocturnal moths has been studied by many authors. (Williams 1940, Hosny 1955, and El-Zaidy 1954.) The following facts taken from other contexts could be important in the choice of resting site:- Some Lepidoptera show a response to gravity (Makings, 1957; Briggs, 1956). Makings also found that female moths were sensitive to the surface texture of the substratum and were able to select cracks of certain widths in which to lay their eggs. There are contact chemoreceptors on all the walking legs of some Lepidoptera (Minnich 1921, 1924), and others are known to find their host plant by smell (Cripps, 1947 and Thorsteinson 1953).

Materials and Methods

Several species of Noctuoid moth and one Geometrid Operophtera brumata were used. The Noctuoids were caught in a light trap, which was kept running from May until October 1959. The moths caught one night were put in a cage with some grass and leaves the next morning, and were kept outside in the shade all day. Swabs of cotton wool soaked in sugar solution scented with fruit joice, were left in the cage so that the normal behaviour pattern would not be upset by hunger. Many of the moths were seen to feed from these. Next evening, at dusk, as they became active, the moths were transferred to test cages where a restricted choice of resting site was available.

The males of O. brumata were caught by hand while they were active in the evening and put directly into "choice chambers". The positions of the moths were noted at about 9 a.m. the following morning, (except on sunny days when it was found necessary to record them earlier). It was hoped that any diurnal rhythm of activity in the moths would not be upset by this method of conducting the experiment. Except in those species which hibernate as adults, male moths only were used, so that oviposition behaviour did not interfere with the results. Occasionally when fresh material was scarce the same moths were used on two consecutive nights, in different choice chambers. Sometimes when the light trap catch was very good, excess moths were kept in the feeding

cage for several days before being used. Between 10 and 20 moths were used per night in each choice chamber.

The choice chambers were kept outside on the ground under a glass roof to keep off the rain. They are described in detail in the experimental section. The following general rules were observed in making the choice chambers. They were made of glass, "Windowlite", or cellulose acetate so that they were transparent on all sides, except where painted black for the purposes of the experiment. The lids were of muslin or polythene sheeting punched with holes. It was assumed that the temperature and humidity inside the choice chamber were nearly the same as outside, and under the influence of these factors the experimental moths became active and settled down to rest at the same time as unconfined moths.

Experimental

Thigmotaxis in Noctuoids

Forty-nine species were used in this experiment; forty-seven of these were classified into one of the following categories:-

Procryptic linear - fig. 19 (One species only)

Procryptic narrow - figs. 20, 21 p. 152

Procryptic medium - fig. 15, p. 151

Procryptic flat - fig. 22.

Procryptic wide - fig. 16.

Aposematic narrow - fig. 23 (One species only)

Aposematic wide - fig. 17

Approximately 10 different individuals were left in the choice chamber shown in figure 161, (p. 215) every night for six months. Each moth was given a score between 1 and 4 according to its position in the morning.

1 - touching the cage on one side only

2 - touching on two sides

3 - touching on three sides (fig. 162b, p. 215)

4 - touching on four sides (fig. 162a).

The opportunity for a moth to score 1 point was very much greater than that of scoring 2 points. There was even less opportunity for a score of 3 points, and the maximum score of 4 could only be obtained in 24 positions in the chamber. As fewer than 24 moths were used at once, it was possible for every moth to gain the maximum score.

The results are given in table VII (p. 90) and figure 163. The data from the cryptic moths were analized by a X^2 - test, to see if there was any correlation between the degree of thigmotaxis and the resting attitude. The results were statistically significant. The categories, into which the moths were divided, contain unequal numbers of species and different numbers of individuals from the various species were used in this experiment. A t-test was performed on the categories "medium" and "narrow" because their behaviour was similar (figure 163). Morphologically these two categories grade into one another; Anchoscelis lunosa (fig. 21) was the widest of the moths classed as "narrow". A score of 3 or 4 was counted as positively thigmotactic, and a species was only used in the t-test if more than 20 individuals were employed in the experiment. The percentage positive thigmotaxis was taken to ensure that the behaviour of one or two more numerous species was not attributed to the whole category. The results are given in table VIII, p. 91; they were statistically significant.

This experiment indicates that those procryptic moths which fold their wings closely to the body at rest have the strongest thigmotactic reponses. The aposematic moths behaved in the same way as the "wide" procryptic moths. The majority of these sat with only one surface touching the substratum and were considered not to show a thigmotactic response. Plusia chrysitis, which is shiny, and Phlogophora

T A B L E VII

CRYPTIC	Number of Moths scoring 1	2	3	4	Total Number Moths
Linear					
Agrotis ypsilon	8	18	35	73	134
Narrow					
Amathes xanthographa	21	49	30	20	120
Anchoscelis lunosa	10	28	30	8	76
Amathes umbrosa	4	9	11	1	25
Charadrina morpheus	1	10	1	0	12
Amathes c-nigrum	15	25	33	20	93
Chara drina alsines	9	35	8	1	53
Lycophotia porphyrea	2	5	5	0	12
Orthosia gothica	0	7	0	0	7
Triphaena pronuba	6	31	42	26	105
Agrotis exclamationis	7	26	22	12	67
Ochropleura plecta	6	10	12	4	32
Lampra fimbriata	1	1	3	2	7
* Conistra vaccinii	6	36	57	23	122
* Eupsilia transversa	1	4	19	4	28
Totals	89	276	273	121	759
Mean score	6.36	19.71	19.5	8.64	
Medium					
* Agrochola lychnidis	5	16	11	0	32
Agrochola macilenta	0	10	9	2	21
Hydraecia micacea	8	37	17	0	62
Rhizedra lutosa	16	26	3	0	45
Leucania comma	9	30	8	1	48
Leucania pallens	16	26	12	1	55
Leucania lythargyria	5	10	5	0	20
Hydraecia oculea	10	28	6	0	44
Apor ophyla lutulenta	11	17	14	0	42
Cirrhia fulvago	12	27	12	0	51
Xylophasia remissa	5	8	3	0	16
Cosmia trapezina	1	8	0	1	10
Charaeas graminis	13	8	0	1	22
Totals	111	251	100	6	468
Mean Score	8.54	19.31	7.69	0.461	
Flat					
* Amphipyra pyramidea	0	1	6	8	15
Amphipyra tragopoginis	0	0	2	2	4
Triphaena janthina	0	1	2	2	5
Triphaena interjecta	0	0	1	1	2
Totals	0	2	11	13	26
Mean score	0	0.5	2.75	3.25	
Wide					
Tholera cespitis	6	10	2	0	18
Tholera popularis	5	2	3	0	10
Thalpophila matura	42	31	5	0	78
Meristis trigrammica	10	4	2	0	16
Colocasia coryli	15	2	1	0	18
Ceramica pisi	1	8	2	0	11
Rusina umbratica	7	9	1	0	17
Luperina testacea	3	6	2	1	12
Apatele psi	8	2	1	0	11
Xylophasia monoglypha	3	6	2	0	11
Totals	100	80	21	1	202
Mean score	10	8	2.1	0.1	
APOSEMATIC					
Narrow					
Eilema lurideola	51	29	2	0	82
Wide					
Euproctis chrysorrhoea	8	2	0	0	10
Spilosoma lutea	27	15	0	0	42
Spilosoma lubricipeda	12	7	1	0	20
Phragmatobia fuliginosa	14	4	0	0	18
Totals	61	28	1	0	90
Mean Score	15.25	7	0.25	0	
OTHERS					
Plusia chrysitis	22	8	0	0	30
Phlogophora meticulosa	13	12	3	0	28

* = females as well as males used

OBSERVED

Cryptic Score	Category Linear	Flat	Narr.	Med.	Wide	Total
1	8	0	89	111	99	307
2	18	2	276	251	81	628
3	35	11	273	90	21	430
4	73	13	121	6	1	214
Totals	134	26	759	458	202	1579

Expected

Score	L.	F.	N.	M.	W.	Total
1	26.05	5.055	147.57	89.05	39.27	307
2	53.30	10.34	301.87	182.156	80.34	628
3	36.49	7.08	206.7	124.72	55.01	430
4	18.16	3.5	102.86	62.07	27.38	214
Total	134	26	759	458	202	1579

$$\sum \frac{\Delta^2}{e} = \chi^2_{12} = 499.02 \quad p < 0.001$$

T A B L E VLLL

Narrow

Species	Number of Moths Scoring 1 or 2	Number of Moths Scoring 3 or 4	% in 3&4	Angular Transformation of % in 3&4	Square of Ang. Trans.
A. xanthographa	70	50	42	40.2	1616.04
A. lunosa	38	38	50	45	2025.00
A. umbrosa	13	12	48	43.9	1927.21
A. c-nigrum	40	53	57	49	2401.00
C. alsines	44	9	17	24.4	595.36
T. promuba	37	68	64.8	55.5	3080.25
A. exclamationis	33	34	50.7	45.45	2065.70
O. plecta	16	16	50	45	2025.00
C. vaccinii	42	80	65.6	54.04	2920.32
E. transversa	5	23	82.2	65	4225.00
				Σ 457.49	Σ 22880.88

n = 10

$\bar{x}$ = 46.749

d. of f. = 9

Medium

Species	1 or 2	3 or 4	3&4	Transformation	Square
H. micacea	45	17	27.4	31.55	995.40
R. lutosa	42	3	6.7	14.9	222.01
L. comma	39	9	18.7	25.6	655.36
L. pallens	42	13	23.6	29.04	843.32
L. lythargyria	15	5	25	30	900.00
H. oculea	38	6	134	21. 43	459.245
A. lutulenta	28	14	33.3	35.2	1239.04
C. fulvago	39	12	23.5	29.5	851.47
A. lychnidis	21	11	34.4	35.92	1290.606
A. nagilenta	10	11	52.4	46.23	2137.21
C. graminis	21	1	4.5	12.36	150.38
				Σ 311.35	Σ 9744.044

t_{19} = 3.963 p = 0.001

n = 11

$\bar{x}$ = 28.299

d. of f. = 10

meticulosa (fig. 18 p. /5/) which is thought to resemble a dead leaf, were also "non-thigmotactic" in their behaviour.

Phototaxis in Noctuoids.

A glass trough, 11½ inches in diameter and 5½ inches high was lined with windowlite painted in black and white quarters with cellulose paint as in fig. 164, (p.217). In the morning the numbers of moths sitting on the white quarters, black quarters or the junctions between the two, were counted. The results are given in tables IX, X and XI (p's 93 & 94). No tendency to sit on the junction of black and white was observed; no species with disruptive colouration were used. Most of the moths classified as procryptic were found to settle more frequently on the two black quarters of the chamber than on the white ones. Three pale coloured species, Rhizedra lutosa, Cirrhia fulvago, and Meristis trigrammica were found to settle more often on the light side; as was Eupsilia transversa, a reddish brown moth with one white spot on each fore wing. Two other species which chose the light side were Apatele psi and Colocasia coryli which were observed sitting on tree trunks in the field. Xylophasia monoglypha which was found frequently on tree trunks seemed to "prefer" the black quarters. The aposematic moths settled in almost equal numbers on both black and white surfaces, Table XI.

Phototaxis and Thigmotaxis in Noctuoids

Some of the procryptic species used in the last

T A B L E IX

Procryptic Positively Thigmotactic		BLACK AND WHITE QUATERS CHOICE CHAMBER							DARK AND LIGHT CRACKS CHOICE CHAMBER					
		Black	Junction of B.& W	White	Total	%age Black	Angular Trans.	Square of Ang.Trans.	Dark Cracks	Light Cracks	Total	%age in Dark	Angular Transform.	Square of Ang.Trans
Linear														
	A. ypsilon	101	1	31	133	76.3	60.9	3708.81	124	17	141	87.9	69.7	4858.09
Narrow														
	A. xanthographa	96	6	33	135	73.3	58.9	3469.21	110	8	118	93.2	75.0	5625.00
	A. lunosa	42	2	23	67	64.2	53.3	2840.89	65	14	79	82.3	61.1	3733.21
	A. umbrosa	9	0	5	14	64.2	53.3	2840.89	18	3	21	85.7	67.8	4596.84
	A. c-nigrum	40	1	11	52	77.9	61.9	3831.61	26	4	30	86.7	68.5	4692.25
	T. pronuba	74	4	20	98	77.5	61.7	3806.89	88	8	96	91.7	73.1	5343.61
	O. plecta	19	0	9	28	65.5	54.0	2916.00	19	9	28	65.5	54.0	2916.00
	C. vaccinii	73	0	24	97	75.3	60.2	3624.24	82	27	109	75.23	60.1	3612.01
	E. transversa	9	0	21	30	30.0	33.2	1102.24	7	13	20	35.0	36.3	1317.69
	L. fimbriata	5	2	1	8				5	3	8			
	C. alsines	12	0	7	19									
	L. porphyrea	3	0	2	5									
	O. gothica	11	0	2	13									
	A. exclamationis	42	0	16	58									
Medium														
	A. lychnidis	23	1	6	30	76.7	61.1	3733.21	38	4	42	90.5	73.1	5198.41
	A. macilenta	12	0	7	19	63.2	52.6	2766.76	25	0	25	100	90	8100.00
	H. micacea	42	3	23	68	63.9	53.1	2819.61	65	4	69	94.2	76.1	5791.21
	R. lutosa	43	2	68	113	38.9	38.6	1489.96	50	13	63	79.4	62.9	3956.41
	H. oculea	36	4	6	46	82.6	65.3	4264.09	27	7	34	79.4	63.0	3969.00
	A. lutulenta	43	2	5	50	86.0	68.0	4624.00	40	3	43	93.0	74.7	5580.09
	C. fulvago	18	2	32	52	36.5	37.2	1383.84	33	19	52	63.5	53.0	2809.00
	C. trapezina	1	0	2	3				3	0	3			
	C. graminis	5	1	1	7				6	5	11			
	L. comma	20	0	8	28									
	L. pallens	31	3	19	53									
	L. lythargyria	5	0	1	6									
Flat														
	A. pyramidea	16	0	0	16	100	90	8100.00	14	0	14	100	90	8100.00
	A. tragopoginis	2	0	0	2									
	T. janthina	3	0	0	3									

$\Sigma x = 963.3$ 57322.05
$n_x = 17$ = sum of squares
$\bar{x} = 56.665$ x
dof. = 16

$t_{32} = 2.376$
$t_{30} = 2.042$ at 5% level
p = 0.05

$\Sigma y = 1146.6$ 80198.82
$n_y = 17$ = sum of squares
$\bar{y} = 67.447$ y.
dof = 16

T A B L E X

PROCRYPTIC "WIDE" Not Positively Thigmotactic	BLACK and WHITE CHOICE CHAMBER					DARK and LIGHT CHOICE CHAMBER			
	BLACK	JUNCTION	WHITE	TOTAL	% age BLACK	DARK	LIGHT	TOTAL	% age DARK
L. testacea	11	0	3	14	78.6	13	7	20	65.0
X. monoglypha	8	0	2	10	80.0	7	2	9	77.8
T. cespitis	9	1	2	12	75.0	20	6	26	76.9
T. matura	25	1	11	37	67.6	21	8	29	72.4
Allophyes oxyacanthae (Linnaeus)	9	0	3	12	75.0	13	2	15	86.7
A. psi	0	0	6	6		4	1	5	
T. popularis	3	0	2	5		4	5	9	
C. pisi	4	0	2	6					
R. umbratica	13	0	4	17					
M. trigrammica	1	0	3	4					
C. Coryli	5	0	14	19					
	Average percent on Black				75.3	Average % dark cracks			75.8%

T A B L E XI

NON - CRYPTIC	BLACK and WHITE CHOICE CHAMBER				
Aposematic	BLACK	JUNCTION	WHITE	TOTAL	% BLACK
S. lubricipeda	6	0	8	14	42.9
S. lutea	15	0	10	25	60.0
P. fuliginosa	3	2	2	7	57.1
E. chrysorrhoea	3	1	2	6	58.3
E. lurideola	12	2	11	25	52.0
	Average % on Black =				54.06
Shining					
P. chrysitis	7	0	4	11	63.6
Leaf Mimic					
P. meticulosa	17	2	13	32	53.1

experiment were also tested in the apparatus shown in figure 165. The numbers of moths settling in the two identical sets of cracks, one in the dark half and the other in the light half of the tank, were counted.

The results were compared with those obtained in the last experiment. The "wide" moths, which have already been shown to be non-thigmotactic, did not tend to sit on a dark surface more often when cracks were available. The other categories of cryptic moths showed a slightly higher proportion of moths settling in the dark cracks than on the black surface, table IX. This increase was shown by means of a t-test to be significant at the 5% level.

It was concluded from these experiments that those Noctuoids which hold their wings close to the body at rest, are concealed in dark crannies during the day, in which they are trapped because they are positively thigmotactic and negatively phototactic in daylight. An attempt to verify this conclusion by field observations failed because very few moths were found in more than 60 hours searching. This was considered to be negative evidence of their efficient concealment. The only species found sitting exposed on tree trunks which was thought to be positively thigmotactic was Cosmia trapezina. Two females of Amphipyra pyramidea and four A. tragopoginis females were found under bands of sacking around tree trunks. Noctuoids were more frequently found in the grass and litter underneath trees than in the intervening

areas, but only occasional specimens of any one species were found.

General Observations on Operophtera brumata

It has already been mentioned that the males of O. brumata have two resting positions; one in which the wings are held up, and the other with the wings down in the characteristic Geometrid position. It was noticed that in the laboratory the same individual was capable of sitting in either position for long periods. (Fig. 9, p./49).

The adult winter moths were watched in the field in Autumn 1957. During the period of activity in the evening the males walk up the trunks of oak and apple trees with the wings raised when they are not flying. An extensive search of an infested apple orchard was made during daylight. A ladder was used to reach the upper branches of the trees but no moths were found; a few were resting on the tree trunks in the down position, but most moths were found in the grass beneath the trees with their wings up. They were down among the dead grass blades and the undersides of the wings matched these closely.

Phototonus in Operophtera brumata

Because it was observed that the moths mostly held their wings up at night and that those hidden in comparative darkness among the dead grasses also sat with their wings raised, while moths sitting exposed on tree trunks in daylight held the wings down, it was thought that the light intensity

might affect wing attitude.

Two large batches of moths were kept overnight in identical glass jars, and their attitudes were recorded in the morning. One jar was then moved to a dark cupboard, and the other was put in a dark refrigerator. The resulting change in wing attitude, which was recorded one hour later, was the same in spite of differences in temperature and humidity.

Result:-

Original Attitude				Final Attitude	
Down	Up			Down	Up
98	34	-	Refrigerator at 3°c. -	26	95
97	32	-	Cupboard at 17·5°c. -	28	100

Winter moths with the wings in the up position hold the body raised higher on the legs than when the wings are in the down position. In some insects the balance of muscle tonus is altered when part of each eye is covered, and the stance is affected. (Wigglesworth 1953). The eyes of O. brumata were painted in three different ways with black cellulose paint, while the moths were anaesthetized with carbon dioxide. Each group of moths was left outside in a glass jar. Two groups of controls were included; both having the eyes unpainted, but one group being in a jar painted black on the outside.

Results:-

Treatment	Up	Down	Dead	Total	% Up
Upper halves of eyes painted -	54	89	13	156	34.6
Lower halves of eyes painted -	60	70	26	156	38.5
Whole of eyes painted -	82	54	20	156	52.6
Outside of jar painted -	100	44	12	156	64.1
Unpainted Controls -	69	221	23	313	22.0

There was no difference in attitude between moths with the tops of the eyes painted, and those with the bottoms of the eyes painted. It seems that the greater the surface of the eye covered, the greater is the tendency to sit with the wings up.

Although it is important, the effect of light on wing attitude is not the only factor concerned in deciding whether a moth will sit with its wings up or down. Caged moths will often sit with their wings up in strong illumination, especially if they are resting on vegetation. In order to find out more about these two resting positions a programme

of field work and behaviour experiments was conducted in 1958 and 1959.

Field Observations on Operophtera brumata

Adult male winter moths can live about a fortnight. The last of five males in a muslin cage, put among the grass and leaves in an orchard on Nov. 18th 1958, died on Dec. 3rd; five moths left out on Nov. 24th. were all dead by Dec. 10th. The adults emerge from pupae in the soil during the daytime (Briggs 1956) and remain in the grass until the evening flight. To make sure that all the moths found in the grass were not newly emerged, the following experiment was conducted:-

On December the 7th 1958, 50 males were caught during the evening flight activity and marked with a spot of cellulose paint on the ventral side of the abdomen. These moths were released on an apple tree the same evening; they were placed on the trunk evenly distributed around the circumference. At 9 a.m. the next day the ground within a foot of the trunk was searched with a vacuum sampler (Johnson et al. 1955). Additional areas of 1 sqr. ft. were searched on the north, south, east and west sides of the trunk. Live, marked moths were found. This experiment was repeated on the next four nights using four different trees;

Results:-

Date	Recoveries out of 50		Temperature on Trunk	
7 - 8 Dec.	25 in Grass	0 on Trunk	+1°c at 5 pm	-1°c at 7 pm

8 - 9	Dec.	2	in Grass	2	on Trunk	+7°c	at 5 pm	+6°c	at 7 pm
9 -10	"	9	"	0	"	+2.5°c	"	+1°c	"
10 -11	"	5	"	0	"	+2.5°c	"	+2.5°c	"
11 -12	"	10	"	0	"	+4°c	"	+4°c	"

The numbers of moths caught between six inches and a foot from the trunk were kept separate from those caught within six inches of the trunk. The catches from different sides of the tree were also kept separate (fig. 166). The wind direction in the orchard on these nights was recorded; most moths were found on the leeward side of the tree.

It was concluded that many winter moth males return to the grass after the night activity to "hide" there during the day.

On two occasions O. brumata were watched all night. The numbers on a tree were counted at hourly intervals. After 6.30 p.m. it was noticed that the moths began to drop off the tree. They fell from the trunk and branches, very few were seen to fly away. No morning flight was observed but some walking and fluttering was seen at dawn.

Results:-

Dec.12th-13th 1958 Apple tree

Dry clear night. Rel. Humidity 96% all night.

Time	Temp°c	Up	Down
4.30 pm	7.5°	9	0
5.0 "	7°	164	0

Dec.19th-20th 1959. Oak tree

Wind and Rain R.H. Varied between 80% and 90%

Time	Temp°c	Up	Down
4.3o pm	11°	4	0
4.45 "	11°	23	0

5.30 pm	6.5°	208	1	5.0 pm	11°	50	0
6.30 "	5.5°	155	0	5.30 "	11°	38	0
7.30	4.75°	99	5	6.0 "	11°	26	0
8.30 "	5°	77	5	7.0 "	10.75°	23	0
9.30 "	5°	69	5	8.0 "	11.5°	20	1
10.30 "	5°	62	4	9.0 "	10.25°	15	0
11.30 "	4.5°	42	4	10.0 "	10°	17	0
12.30 am	3.5°	34	7	11.0 "	10°	13	0
1.30 "	2.5°	34	6	12.0	10°	10	0
2.30 "	2°	27	8	1.0 am	10°	9	0
3.30 "	-1°	14	5	2.0 "	10°	14	0
4.30 "	-1.5°	13	5	3.0 "	10°	11	0
5.30 "	-2°	9	4	4.0 "	10°	11	0
6.30 "	-1.5°	5	4	5.0 "	10°	7	1
7.30 "	-1°	0	2	6.0 "	10°	5	0
8.30 "	-.5°	0	1	7.0 "	10°	3	0
9.30 "	+1°	0	0	7.30 "	10°	0	0
				8.0 "	10°	0	0

If the males of O. brumata drop passively from the trees, as is indicated by these observations, and remain in the grass until the next evening without flying further, the distribution of the moths in the grass during the day should reflect this behaviour. On the mornings of the 9th - 12th Dec. 1958 inclusive, the area within 10 ft. of several apple trees was searched carefully by hand and the

distance from each moth which was found to the trunk was measured in inches. As the tree canopy is thickest above the ground near the trunk it was expected that the frequency of moths would decrease from the trunk to the edge of the canopy. The results (see appendix 3) indicate that the number of moths decreased with the square of the distance from the tree trunk. Five inch running means are plotted in the graph (fig. 167 p.219) and the regression line for this "inverse square" relationship is drawn in fig. 168. The regression coefficient is significant.

Results:-

Distance = X	Frequency. F.	$\sqrt{\frac{1}{F}}$ = Y
0	19	0.22942
1	13	0.27735
2	4	0.5
3	8	0.35355
4	6	0.40743
5	8	0.35355
6	4	0.5
7	2	0.70711
8	4	0.5
9	5	0.44721
10	4	0.5
11	5	0.44721
12	4	0.5

Distance = X	Frequency. F.	$\sqrt{\frac{I}{F}} = Y$
13	3	0.57706
14	5	0.44721
15	2	0.70711
16	4	0.5
17	2	0.70711
18	1	1.0
19	2	0.70711
20	2	0.70711
$\bar{X}$ = 10		$\bar{Y}$ = 0.5274

Items	Degrees of freedom	Sums of Squares	Mean Square
Regression of Y on X	1	0.476	0.476
Residual	19	0.1512	0.007958
Totals	20	0.62793	

$F_{1, 19} = \frac{0.476}{0.007958} = 59.8.$ Significant $p < 0.01$

Hydrotaxis in Operophtera brumata

It was noticed that wet patches of bark were avoided by the moths during rain on the night of Dec. 19-20 1959. In Autumn the grass under trees is almost always wet and many winter moths were seen helplessly stuck to wet grass blades. This must be a major hazard to the moths resting in the grass during the day and the following experiments were tried to find out if behaviour patterns enabling the moths to avoid free water were present.

Two tins were buried in plaster of paris in a large

biscuit tin. Each small tin was filled with plaster and had muslin-covered microscope slides projecting from it, as in figure 170 (p.220). One tin was filled with water so that the plaster and muslin were wet; the other tin was dry. The attitudes of the moths sitting on each set of slides were recorded. The results are given in the table below. Significantly more of the moths sitting on the wet surfaces held their wings up than those sitting on the dry ones.

Observed

	Up	Down	
Wet	53	26	79
Dry	31	59	90
	84	85	169

Expected

	Up	Down	
	39.27	39.73	79
	44.73	45.27	90
	84	85	169

$$X^2_1 = \underline{17.91} \qquad p = 0.001$$

The difference in the number of moths choosing to sit on the wet and dry was not significant; a second choice chamber of a different type was used to clarify this point. A green-painted, baking tin, lined with muslin, was divided into two halves by a half-inch high partition of cellulose acetate in the bottom. The tin was lined with green foam plastic sponge half an inch thick; one half of the sponge was wet and the other half was dry. The muslin on the wet half was kept wet by capillary action and the water was prevented from spreading to the dry half by a line of "Durofix" which continued the partition up the walls. (Fig.169,

p.220). A polythene lid was used to prevent evaporation. The whole cage was dried out in an oven every third day, and the wet side was redampened to preserve the demarcation between wet and dry halves.

Result:-

	Up	Down	Total	% Up
Wet	17	49	66	25.76
Dry	12	295	307	3.91

During the night moths crossing the border from dry to wet halves, were observed to turn round and go quickly back again, so that most moths were always on the dry half. This effect was not due to humidity differences, which were found in preliminary epxeriments to have no effect on attitude.

Geotaxis in Operophtera brumata

Experiments in which moths were confined overnight in tall narrow cages of "Windowlite" or muslin, gave no indication that the moths become positively geotactic in daylight; they did not drop to the bottom of the cage. There was no difference in attitude between moths sitting on the roof, floor or sides of these cages, provided that these were made of the same material.

Thigmotaxis in Operophtera brumata

The apparatus shown in figure 161 was used, and the method of scoring was the same as for Noctuids (page 88.).

Result:-

	Position	
Score	Up	Down
1	68	121
2	67	147
3	27	64
4	0	2

This result indicates that the thigmotactic response was weak, but this conclusion was suspect because the cracks were too large in relation to the size of these moths. Many moths in the cracks only scored 1 or 2 points.

A large series of preliminary experiments was tried, to find the best arrangement of cracks for experiments with this species. It was found that a range of widths from 5 to 20 mm. was most appropriate. Glass microscope slides covered in tightly stretched muslin were found to give a good grip for the tarsi. A high proportion of O.brumata sat with their wings down on this substratum. It was found that the moths would enter cracks more readily in a completely transparent choice chamber than in one with opaque walls. It is probable that the moths "settle down" more quickly when the light intensity is low.

The choice chamber shown in Figs. 172 & 173 (p.211), which incorporates the above useful features, was used in the final experiments. Ten to twenty moths were put in the cage each night, and the numbers sitting on the cracks and

the muslin wall were counted each morning. The moths on the lid or floor were not recorded. The result was as follows:-

Number of moths in cracks = 396

" " " on flat muslin = 11

Total surface area of cracks = 360 sqr. ins.

" " " " flat muslin = 75 sqr. ins.

Surface area of cage covered by cracks but not muslin = 75 sqr. ins.

	Observed	Expected
Flat	11	$407 \times \frac{75}{510} = 59.853$
Cracks	396	$407 \times \frac{435}{510} = 347.147$

$X^2_1 = 222.93$ p 0.001

Thigmotaxis is stronger than this result suggests because over much of the crack range it was not possible for two moths to sit opposite one another in the same crack - a factor which could not be considered in the area correction.

A second choice chamber was made, similar to the one used in the above experiment, but having the cracks at the top of the cage and the flat muslin below. It was used on the same nights and the results were similar to those obtained in the above expt. An analysis of these two sets of results showed that roofed cracks were "preferred" to open cracks, or trapped the moths more efficiently because they could not walk out of the top.

	Number of Moths in cracks	On Flat
CRACKS AT BOTTOM OF CAGE	396	11
CRACKS AT TOP OF CAGE	393	29

CRACKS AT BOTTOM OF CAGE

		Observed	Expected
Open	⩗	142	198
Closed	⩓	254	198

$X^2_1 = 36.677 \quad p < 0.001$

CRACKS AT TOP OF CAGE

		Observed	Expected
Open	$\overline{\wedge}$	185	196.5
Closed	$\overline{\vee}$	208	196.5

$X^2_1 = 1.350$ Non-significant.

Thigmotaxis and Surface Water

A second choice chamber similar to the one shown in figs. 172 & 173 was made, and the inside was kept wet. It was used on the same nights as the "dry" chamber, and also on extra nights to collect more data. The following things were noted about the position of each moth:-

a) Resting attitude - wings up or down

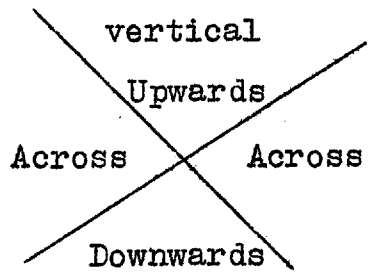
b) The maximum width in millimetres of the opening of the crack it was in (fig. 172)

c) The actual width of the crack where the moth was

sitting, measured in mm. across the thorax

d) Whether the crack was roofed or open above

e) The way the moth was facing in the crack — upwards, downwards or across:-



There was very little difference in the number of moths entering the cracks in the wet and dry chambers:-

	FLAT	CRACKS	TOTAL	%age FLAT
DRY	11	396	407	2.7%
WET	30	525	555	5.4%

The presence of water did, however, affect the position of the moths within the cracks (See table XII, p. 110)

As in the last experiment more moths held their wings up in the wet cracks than in the dry ones:-

OBSERVED

	UP	DOWN	TOTAL	% UP
WET	97	428	525	18.47
DRY	13	383	396	3.28
TOTAL	110	811	931	

EXPECTED.

	U	D	
W	62.03	462.97	525
D	47.97	348.03	396
	110	811	931

$X^2 = 51.363$ $p. < 0.001$

T A B L E XII

Crack Width Range	Available length of Width L	No. in that Crack Width in Dry D	No. in that Crack Width in Wet W.	No. Moths UP in Wet U	$\frac{D}{L}$ x 100	$\frac{W}{L}$ x 100	$\frac{U}{L}$ x 100	$\frac{W-U}{L}$ x 100
0- 1½ mm	207.534	0	0	0	0	0	0	0
1½- 2½ mm	207.534	41	10	0	19.76	4.8185	0	4.8185
2½- 3½ mm	207.534	69	33	3	33.25	15.9	1.45	14.45
3½- 4½ mm	207.534	54	44	3	26.02	21.2	1.45	19.75
4½- 5½ mm	200.034	38	58	6	19.0	29.0	3.0	26.0
5½- 6½ mm	185.284	32	61	5	17.27	32.9	2.7	30.2
6½- 7½ mm	173.909	29	49	9	16.67	28.176	5.175	23.001
7½- 8½ mm	164.0965	18	36	4	10.97	21.94	2.44	19.50
8½-10½ mm	218.866	29	78	18	13.25	35.64	8.23	27.41
10½-12½ mm	178.648	26	64	18	14.55	35.825	10.1	25.725
12½-15½ mm	192.140	28	58	20	14.57	30.186	10.4	19.786
15½-18½ mm	99.20	20	20	5	20.16	20.16	5.04	15.12
18½-20 mm	11.45	9	8	2	78.6	69.87	17.5	52.37
Totals *		393	519	93				

* These totals are smaller than mass totals because moths sitting on the cellulose acetate wall in the cracks and not on the muslin covered slides were discounted.

These figures are graphed in Fig. 174, p.222

This difference was even more marked at dawn. In the wet chamber many moths were observed to choose their resting site with the wings raised up and to lower the wings during the early morning. This behaviour is reflected in the graph (fig.174, p. 222) where there is a peak at 10 mm. This is as far as a moth with raised wings can push itself into a crack, without leaning sideways. In the curve for the dry chamber this second peak if present, is very small. The moths were observed to shuffle into their final position with their wings down, causing a definite peak at 3 mm. The width of the thorax where measurements were taken is 2 - 3 mm. The first peak on the wet graph is at 6 mm, indicating that even those moths which sit with their wings down on the wet surface, do not push as far into the cracks as those on a dry surface.

It is possible for a moth to sit on the floor of the cage as in Fig. 171a (p. 220) in cracks wider than 9 mm. Very few moths will sit facing downwards, but some individuals were found in position b. Position c is the most usual one in all cracks except the widest. In cracks of maximum width 18-20 mm. a large proportion of the moths are in positions a or b in the second crack formed between the slides and the floor of the cage. This produces an artificial peak in this range in the graph (fig.174), in which the crack widths where the moths were actually sitting are

plotted against the number of moths sitting there corrected for the amount of that crack width available (see table XII, p. 110).

In the graph shown in figure 175, the number of moths in each crack, divided by the maximum width of that crack in millimetres (because there is a greater chance of a moth walking about inside the cage at random entering the widest cracks) is plotted against the maximum crack width. There is a peak at 16 mm. in the curves. showing the results of both wet and dry chambers. This is probably because the moths walk into both wet and dry cracks with their wings vibrating. A crack with a 16 mm. opening will just allow a moth with its wings half lowered to walk in along the floor of the cage, without having room to turn round and walk out again. (See table XIII)

In both wet and dry chambers most moths sat facing upwards. Of the moths which were facing downwards, the majority were in cracks open above and tapering downwards. Less than 3% of all the moths tested faced downwards in cracks roofed in above (fig. 171b, p. 220)

	WET		DRY	
	Roofed ∧	Open ∨	Roofed ∧	Open ∨
UPWARDS	183 50.275%	100 27.45%	128 44.29%	45 15.57%
DOWNWARDS	3 00.824%	26 7.143%	7 2.422%	32 11.073%
ACROSS	19 5.22%	33 8.92%	40 13.84%	37 12.8%
TOTALS	364		289	

TABLE XIII

Maximum Width mm	Total Width mm	No. moths WET	No. moths DRY	Moths per mm.WET	Moths per mm.DRY
5	5	1	0	0.2	0.0
6	12	3	2	0.25	0.167
7	14	6	5	0.428	0.357
8	16	5	6	0.3125	0.375
9	18	11	8	0.6111	0.444
10	20	16	5	0.80	0.25
11	22	31	28	1.41	1.273
12	24	46	31	1.917	1.29
13	26	40	30	1.54	1.154
14	28	53	37	1.893	1.32
15	30	53	28	1.767	0.933
16	32	79	63	2.469	1.9687
17	34	63	46	1.853	1.353
18	36	51	43	1.4167	1.194
19	38	51	47	1.342	1.237
20	20	16	18	0.8	0.9
	Totals	525	396		

Graph figure 175, p. 222

Phototaxis in Operophtera brumata

O.brumata males were tested in the apparatus shown in figure 165 (p. 217); their position and attitude were recorded:-

Result:

	UP	DOWN	TOTAL	%UP
Dark cracks	46	265	311	17.35
Light cracks	16	79	95	20.253

More moths settled in the dark half of the chamber. There appears to be no difference in phototactic response between moths with their wings up and those with them down. The dark half was probably not dark enough for the effects described on page 92 to be apparent.

The chamber used for Noctuoids (fig.164 p. 217) was modified. One of the white quarters was painted grass green and one of the black quarters grey, with cellulose paint. The grey and the green were of approximately the same luminosity (although the grey was brighter than the green when they were compared with an optical photometer and duller when the comparison was made with a photoelectric cell).

Result:

	UP	DOWN	TOTAL	%UP
Black	12	148	160	7.5
Green	15	98	113	13.274
Grey	5	75	80	6.25
White	2	84	86	2.326

Nearly twice as many moths settled on the black quarter as

on the white. The difference between green and grey was significant when analysed by a X^2 test.

COLOUR	OBSERVED	EXPECTED
Green	113	96.5
Grey	80	96.5

$X^2_1 = 5.81$ $p = 0.02$

The difference in attitude between black and green (7.5 :13.3%) was not significant.

Effect of Surface Texture on Resting Attitude in Operophtera brumeta

Bamboo leaves were fastened with elastic bands longitudinally, over opposite quarters of the bark of three logs, 1ft. long and 4 - 6ins. in diameter. The leaves were put ventral side outwards so that the longitudinal veins ran from top to bottom of the logs, which were placed upright in large glass tanks.

No. of Moths on	BARK	BAMBOO	TOTAL
OAK, 1958 (Rough with longitudinal cracks)	22 (25.3%)	65	87
APPLE, 1959 (Flaky bark)	58 (25.7%)	168	226
HORNBEAM, 1959 (Smooth bark)	213 (36.9%)	364	577

Bamboo leaves are preferred to bark for settling on. All three logs were darker in colour than the green leaves. Hornbeam, which was the lightest in colour was avoided less than the other two, which were rougher. The surface texture

of these was thought to be unacceptable.

In an attempt to make a surface which was "uncomfortable" for the moths to sit on, one half of an 8 inch diameter tin was lined with resinated honeycomb mesh - "polygonal paper". The hexagons were half an inch in diameter. The whole of the bottom of the tin was filled with plaster of paris, so that one half was smooth and the other covered in hexagons, projecting 1/10 inch above the plaster. The whole of the inside of the tin was painted black with cellulose paint. The number of moths in each side and their attitude was recorded.

Result

	UP	DOWN	TOTAL	% UP
Honeycomb	19	26	45	42.22%
Flat	29	105	134	21.642%

Many more of the moths settled on the flat half than on the other half with hexagonal irregularities too small to accommodate the body of a winter moth.

Sixty flowering stalks of grass were cut to 9ins. long and wedged between two sides of a tin box, 9" x 9" x 5". Twenty moths were put in the box each night for 4 nights, with the stalks vertical. On alternate nights the stalks were horizontal. The number of moths on the stalks was counted.

Result.

	No. Moths on Stalks	Total No. Moths.
Horizontal	4	80
	2	80

It was concluded that winter moths do not readily sit on narrow surfaces, especially if these are horizontal.

In order to induce the moths to sit balanced on narrow edges, a box was made, two opposite sides of which consisted of flat glass. Glass microscope slides were placed vertically with their flat surfaces at right angles to the other two sides, so that they presented a row of vertical glass edges to the lumen of the box. Gaps of two tenths of an inch were left between the slides; each side of the box measured 3 inches by 3½ inches internally. The areas of flat glass and glass edges available to the moths inside the box were equal. The attitudes of the moths sitting on these were recorded. The large numbers of moths settling on the muslin top or the bottom of the box were disregarded.

OBSERVED

	UP	DOWN	TOTAL
EDGES	35	10	45
FLAT	9	55	64
	44	65	109

EXPECTED

EDGES	18.165	26.835	45
FLAT	25.835	38.165	64
	44	65	

X^2, = 44.56 p 0.001

There was a greater tendency to hold the wings up when the moths were balancing on edges then when sitting on the flat.

Tarsal contact in Operophtera brumata

The results of the last experiment indicate that the wing position might be controlled by the area of the tarsi touching the substratum. The following experiment was an attempt to test this theory. Tarsi were cut off or covered in wax, (Wootten and Sawyer, 1954). The resulting attitudes were recorded.

Results

	DOWN	UP	DEAD	Significance of X^2 Control = expected
Control (anaesthetized with CO_2 only	16	4	0	
Fore tarsi cut off	5	11	4	P = 0.001
Hind " " "	8	8	4	P = 0.01
Mid " " "	9	9	2	P = 0.01
Fore tarsi waxed	6	13	1	P = 0.001
Hind " "	5	12	3	P = 0.001
Mid " "	5	14	1	P = 0.001
F + H waxed	6	12	2	P = 0.001
M + H waxed	2	16	2	P = 0.001
F + M waxed	5	11	4	P = 0.001
ALL waxed	2	17	1	P = 0.001

Cutting off or waxing the tarsi significantly reduces the number of moths that sit flat. This was in spite of the fact that moths without tarsi cannot sit up properly. There is no way of ensuring that this was a genuine effect. The shock of the operation, or the enforced abnormal attitude of the legs may be the real factors causing the wings to be held upwards.

DISCUSSION.

It is accepted by most field entomologists that Lepidoptera which rest with their wings spread out sit exposed on flat surfaces such as rocks or tree trunks, while other species with compact resting attitudes are to be found amongst litter or vegetation. "Choice chamber" experiments using Noctuoids with a variety of resting attitudes support this idea (pages 88/92. It was found that those species which fold the wings close to the body showed stronger positive thigmotaxis than others with less compact wing folding.

Almost all the cryptic Noctuoids which were tested settled on dark surfaces in preference to lighter coloured ones. Warningly coloured species exhibited no thigmotactic or phototactic responses. It is thought that they rely on their unpleasant taste to protect them from predators and have no need to conceal themselves.

It has been said that Lepidoptera which rest with their wings spread out do not creep into crevaces in vegetation because the vulnerable wings would be damaged, (Wood, 1913). This idea implies that the choice of resting site is restricted by the resting attitude. Operophtera brumata males are more likely to hold their wings up when they are sitting on a dark, wet, irregular surface such as a clump of grass, than when they are resting on an expanse of dry tree trunk, exposed to the light. The experiments previously recorded indicate that resting attitude may be dependent on resting site (pages 96/118. Nocturnal moths with no special means of protection must have an efficient method of hiding themselves from enemies during daylight. It is reasonable to suppose that the choice of resting site, the resting attitude and the cryptic colour pattern are closely inter-related and of great survival value, having evolved in harmony with one another.

CONCLUSION

There is correlation between the resting attitude of a cryptic moth and some of the behaviour patterns involved in the choice of its resting site. The morphology of the thorax and wing bases is therefore also correlated with the resting habits of the insect.

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APPENDIX 1.

"Ephestia" Ringer solution (N. Waloff pers. com.)

7.0 g. Na Cl
0.2 g. KCl
0.2 g. $Ca\ Cl_2$
0.04 g. $Na\ H\ Co_3$
Distilled water to 1 litre.

APPENDIX 2.

Number (figs. 57-61)	Species	Length of Fore Wing (L) in mm.	Length of 1 Ax (A) in mm.	Length of "Notal Lever" (x) in mm.	A/L	X/L	Slope of 1 Ax.	Vertical overlap of pleuron and Notum.	Overlap L X 1000	Length 1Ax / Width	Length Notum / Width	Horizontal Distance between Pleuron and Notum D	N Notal Width	D/N x 1100	H Thoracic Height	P Pleural Height	H - P	H - P / P x 100
1	Adela reaumurella	7.25	0.1	0.071	0.014	0.00985	25.7°	0.03	4.2	0.7765	1.125	0.051	1.2072	42.225	2.461	2.0956	0.3654	17.44
2	Augiades sylvanus	15.5	0.66	0.714	0.0425	0.046	90°	0.2837	18.303	1.733	1.682	0.154	3.12	49.36	4.844	3.617	1.227	33.92
3	Biston betularia	23.0	0.72	0.714	0.0312	0.031	40°	0.07143	3.1056	1.667	0.936	0.1435	4.463	32.15	5.557	4.393	0.964	21.944
4	Crambus hortuellus	9.64	0.171	0.156	0.018	0.016	3.5°	0	0.0	1.0384	1.033	0.027	1.51	17.88	2.9295	2.58	0.3495	13.55
5	Deilephila elpenor	31.0	0.052	1.2	0.034	0.039	40°	0.055	1.7742	1.473	1.2667	0.277	6.0	46.25	8.4	6.2	2.2	35.49
6	Drepana binaria	17.0	0.443	0.39	0.026	0.023	30°	0.043	2.53	2.258	1.0615	0.0471	2.39	19.707	3.77	3.21	0.56	17.445
7	Euproctis chrysorrhoea	17.5	0.42	0.415	0.024	0.024	26°	0.0702	4.0114	1.72	1.05	0.140	3.325	42.1	4.895	4.02	0.875	21.766
8	Evetria buoliana	8.42	0.195	0.156	0.023	0.0185	3.6°	0	0.0	0.8688	0.993	0.04	1.9172	20.86	2.83	2.345	0.485	20.682
9	Hepialus lupulinus	12.0	0.12	0.15	0.0097	0.0127	2°	-0.06	-5.0	0.28	0.898	0.127	3.035	42.845	4.042	3.535	0.507	14.34
10	Lophopteryx capucina	18.0	0.52	0.455	0.029	0.025	35°	0.0714	3.967	2.0	0.936	0.106	3.838	27.62	5.101	4.2253	0.8757	20.725
11	Micropteryx calthella	3.75	0.026	0.016	0.0069	0.0043	10°	0	0.0	0.40625	0.67	0.0365	0.61	5.98	1.33	1.22	0.11	9.0164
12	Mnemonica subpurpurella	5.17	0.0325	0.026	0.0063	0.005	25°	0.0286	5.532	0.325	0.756	0.0447	0.8345	5.356	1.69	1.44	0.25	17.36
13	Operophtera brumata	13.0	0.335	0.364	0.026	0.028	40° 90°	0.123	9.461	1.963	1.22	0.1092	0.5886	68.755	2.88	2.34	0.54	23.077
14	Orthosia gothica	16.5	0.643	0.552	0.039	0.0335	30°	0.071	4.303	1.73	1.098	0.132	3.617	36.49	5.0532	4.1844	0.8688	20.763
15	Pieris brassicae	32.4	0.91	0.63	0.028	0.019	100°	0.6338	19.562	2.56	1.8376	0.18776	2.75	68.276	5.5046	4.061	1.4436	35.55
16	Plodia interpunctella	6.25	0.078	0.0844	0.0125	0.0135	45°	0.0395	6.3152	0.833	1.0871	0.04	1.21	33.057	2.184	1.921	0.263	13.691
17	Plusia gamma	19.0	0.714	0.75	0.0376	0.039	28°	0.0475	2.5	1.712	1.05	0.132	4.225	31.24	5.194	4.49	0.704	15.679
18	Poecilocampa populi	16.4	0.6315	0.52	0.0385	0.0317	40°	0.04	2.38	1.2	0.9623	0.18	4.24	42.45	5.12	4.08	1.04	25.49
19	Polygonia c-album	26.6	0.73	0.69	0.0275	0.026	-	-	-	-	-	-	-	-	-	-	-	-
20	Polyommatus icarus	14.8	0.533	0.353	0.036	0.024	95°	0.357	24.122	2.073	1.59	0.25	2.1786	114.75	3.5714	2.5133	1.0581	42.1
21	Saturnia pavonia	30.0	0.844	0.68	0.028	0.023	50°	0.167	5.567	1.613	1.0	0.18	5.5	32.73	7.167	5.84	1.327	22.72
22	Scoparia ambigualis	8.47	0.17	0.13	0.0197	0.0153	46°	0.02632	3.107	1.15	1.125	0.041	1.36	30.147	2.705	2.38	0.325	13.655
23	Sitotroga cerealella	4.72	0.08	0.052	0.017	0.011	10°	0	0.0	0.721	0.8	0.0255	0.697	3.6	1.2	1.043	0.157	15.053
24	Spilosoma lubricipeda	19.0	0.536	0.493	0.028	0.026	36°	0.0383	2.13	1.5	1.0065	0.119	4.352	27.344	5.7	4.6	1.1	23.913
25	Stenoptilia pterodactyla	11.57	0.17	0.195	0.0146	0.0168	55°	0.08421	7.278	1.63	1.758	0.1316	1.0421	126.283	3.18	2.737	0.443	16.1856
26	Stigmella basalella	2.5	0.039	0.0365	0.0156	0.0146	25°	0.00674	2.696	0.94	0.65	0.0253	0.465	5.441	0.72	0.622	0.098	1.575
27	Tineola bisselliella	4.2	0.66	0.052	0.016	0.0123	15°	0.01143	2.7214	0.7633	0.887	0.021	0.682	3.079	1.2262	1.076	0.1502	13.959
28	Tortrix viridana	8.62	0.12	0.143	0.014	0.0166	3.2°	0	0.0	0.75	0.96	0.05	1.655	30.2115	2.7586	2.483	0.2756	11.1
29	Zeuzera pyrina	21.5	0.7	0.615	0.033	0.029	7°	0	0.0	1.66	1.43	0.325	5.135	63.29	5.85	4.745	1.105	23.287
30	Zygaena filipendulae	13.8	0.325	0.325	0.024	0.024	23°	0.05	3.6232	0.9232	1.17	0.07	2.907	24.08	4.452	3.595	0.857	19.25
31	Agrotis exclamationis	-	0.65	-	-	-	-	-	-	1.576	1.122							
32	Agrotis ypsilon	-	0.663	-	-	-	-	-	-	1.514	1.24							
33	Colotois pennaria	-	0.513	-	-	-	-	-	-	1.64	1.088							
34	Eilema lurideola	-	0.325	-	-	-	-	-	-	1.576	1.172							
35	Meristis trigrammica	-	0.55	-	-	-	-	-	-	1.571	1.086							
36	Rusina umbratica	-	0.475	-	-	-	-	-	-	1.41	1.037							
37	Selenia tetralunaris	-	0.453	-	-	-	-	-	-	1.657	1.333							
38	Triphaena pronuba	-	0.813	-	-	-	-	-	-	1.385	1.24							

APPENDIX 3.

Distance from tree.	Moth frequency.	Running means.
inches 0	19	19
1	13	
2	4	
3	6	7.6
4	6	
5	8	5.6
6	4	
7	2	
8	4	3.8
9	5	
10	4	4.4
11	5	
12	4	
13	3	3.8
14	5	
15	2	3.2
16	4	
17	2	
18	1	2.2
19	2	
20	2	1.2
21	0	
22	1	
23	1	1.2
24	1	
25	3	1.4
26	1	
27	1	
28	1	1.2

Distance from tree.	Moth frequency.	Running means.
29	1	
30	2	1.0
31	0	
32	1	
33	0	0.4
34	0	
35	1	0.6
36	2	
37	0	
38	1	1.2
39	2	
40	1	0.8
41	0	
42	0	
43	0	0.2
44	0	
45	1	0.4
46	1	
47	0	
48	2	0.6
49	0	
50	0	0.6
51	0	
52	1	
53	0	0.6
54	1	
55	1	0.4
56	0	
57	0	
58	1	0.4

APPENDIX 3 (continued).

Distance from tree.	Moth frequency.	Running means.	Distance from tree.	Moth frequency.	Running means.
inches 59	1		84	0	
60	0	0.4	85	0	0.0
61	0		86	0	
62	0		87	0	
63	1	0.4	88	0	0.0
64	0		89	0	
65	1	0.6	90	0	0.0
66	1		91	0	
67	0		92	0	
68	0	0.2	93	1	0.2
69	0		94	0	
70	0	0.0	95	0	0.2
71	0		96	0	
72	0		97	0	
73	1	0.4	98	0	0.0
74	0		99	0	
75	1	0.4	100	0	0.2
76	0		101	0	
77	0		102	1	
78	0	0.2	103	0	0.2
79	0		104	0	
80	1	0.2	105	0	0.0
81	0		106	0	
82	0	0.0	107	0	
83	0		108	0	

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LIST of ABBREVIATIONS USED IN FIGURES

A = Anal vein
a = anterior
Act. = Acrotergite
Ad. = Apodeme
Aeps. = Anepisternum
an. = anal (adjective).
at. = atrophied
Ax. = Axillary sclerite
ax. = axillary (adjective)

B = Bridge
Ba. = Basalare
ba. = basalar
bd. = bending

C = Costa
c = costal
Cd. = Cord
Ct. = Cuticle
Cu. = Cubitus
cu. = cubital
Cx. = Coxa
cx. = coxal

d = dorsal

E = Emargination
Exoct. = Exocuticle
Endoct. = Endocuticle
Epm. = Epimeron
Eps. = Episternum
ex. = external

F = Fold
f = folding
Fs. = Furcasternum

H = Hinge
Ht. = Height

hu. = humeral

I = Insertion
In. = Incision
int. = internal
interseg. = intersegmental
Iv. = Invagination

Ju. = Jugum
ju. = jugal

Keps. = Katepisternum

l = lateral
Li. = Ligament
Lg. = Length
lg. = longitudinal
Lo. = Lobe.

M = Media
m = median
Mb. = Membrane
mb. = membranous.
Me. = Meron
Mu. = Muscle

N = Notum
n = notal

O = Origin
obl. = oblique

P = Pleuron
p = pleural
Pa. = Postalare
pa. = postalar
Ph. = Phragma
Pl. = Plate
Pn. = Postnotum
pn. = postnotal
po. = posterior
Pr. = Process
Psc. = Prescutum
psc. = prescutal

R = Radius
r = radial
Ri. = Ridge

S = Sternum
s = sternal
Sa. = Subalare
sa. = subalar
Sc. = Subcosta
Scl. = Scutellum
Sct. = Scutum
Sl. = Scale
sl. = scale (adjective)
Sp. = Spiracle
Spl. = Split

T = Tergum
t = tergal
Tg. = Tegula
tg. = tegular
Tn. = Trochanter

v = ventral
Va = Vannus
va = vannal

W = Wing
w = wing (adjective)
Wd. = Width.

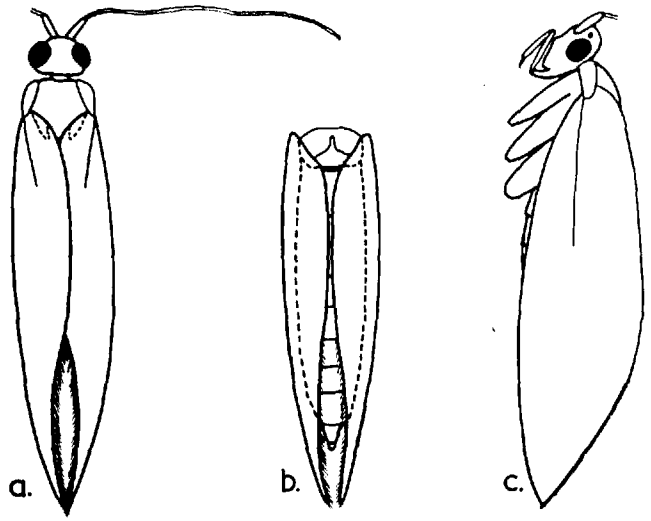
II = Mesothorax
III = Metathorax.

RESTING ATTITUDE

1

Micropteryx calthella

"Tectiform"

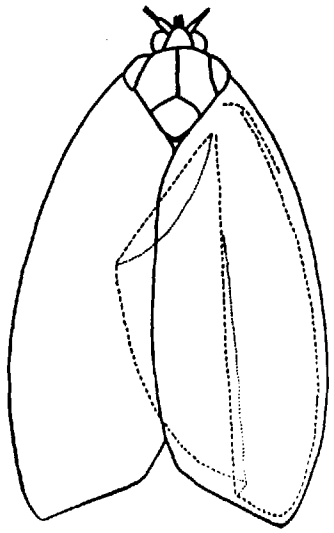


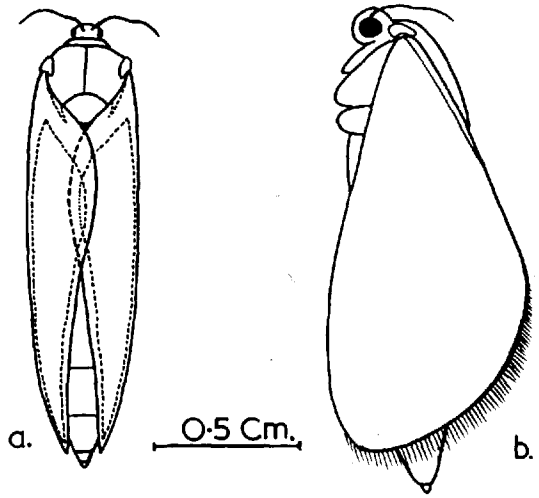
2 mm.

2

Hepialus lupulinus

"Lateral tectiform"





0·5 Cm.

3

TORTRIX VIRIDANA

"Flattened tectiform."

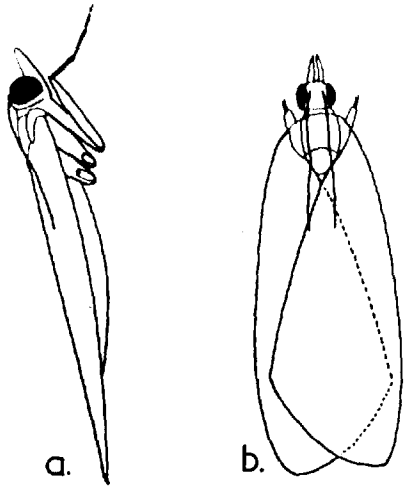
0·4 Cm.

4

Scoparia ambigualis

"Flat narrow"

5mm.

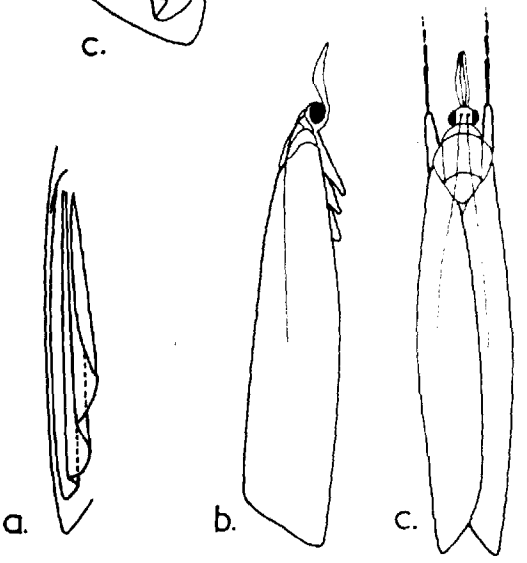


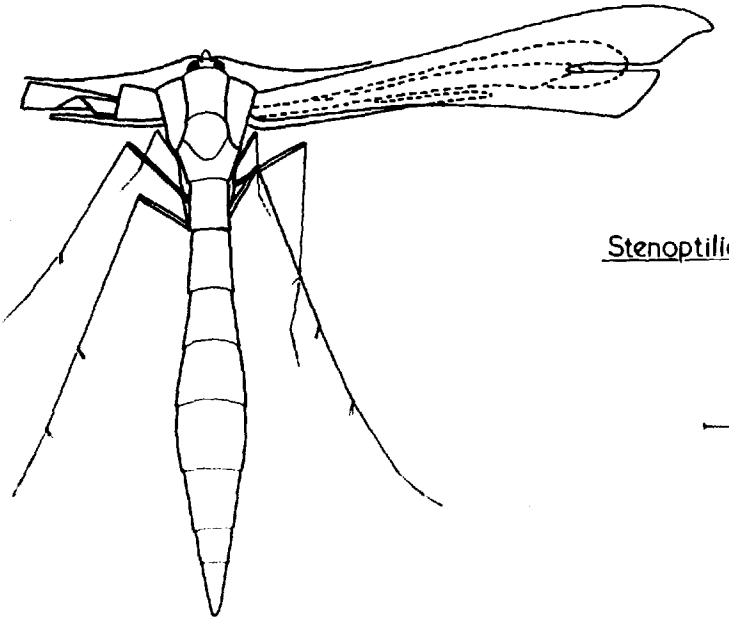
5

Crambus hortuellus

"Lateral linear"

5 mm.





6

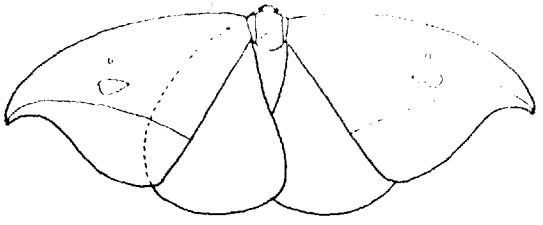
Stenoptilia pterodactyla

5 mm.

7

Drepana binaria.

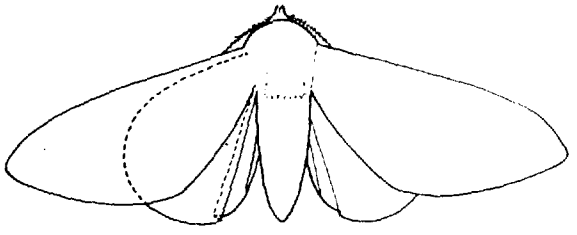
1cm.

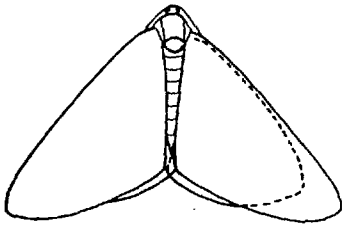


8

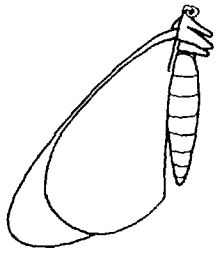
Biston betularia ⟶

1cm.





"Flat"



"Up"

9

Operophtera brumata.

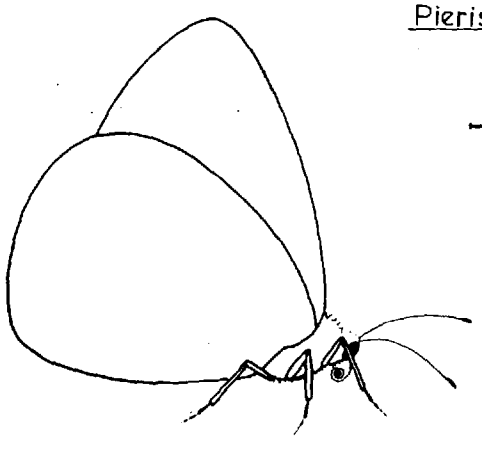
⟵

1cm.

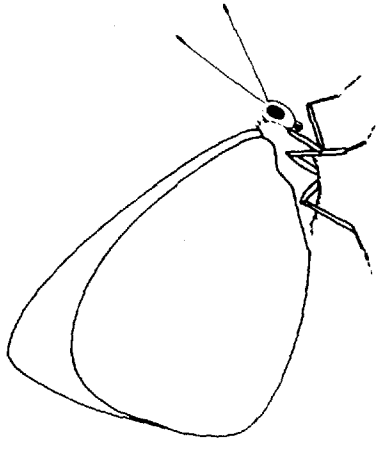
10

Pieris brassicae

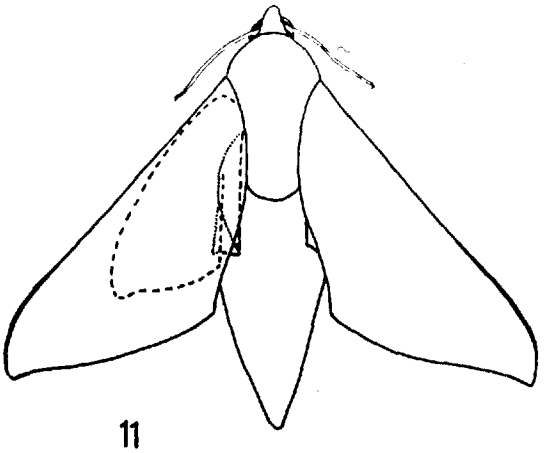
1cm.



a. Walking

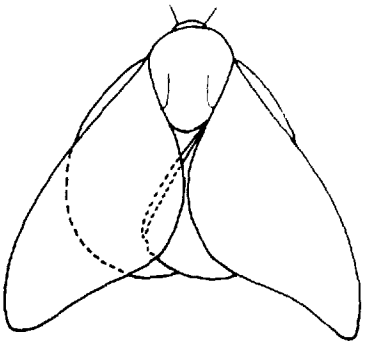


b. Resting



11
Deilephila elpenor

1 cm.

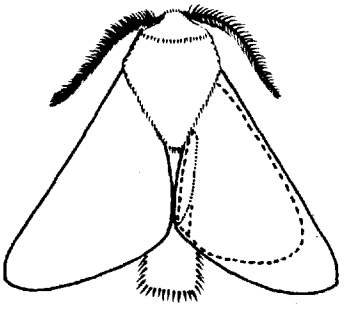


12
Saturnia pavonia.

1 cm.

13
Poecilocampa populi.

1 cm.

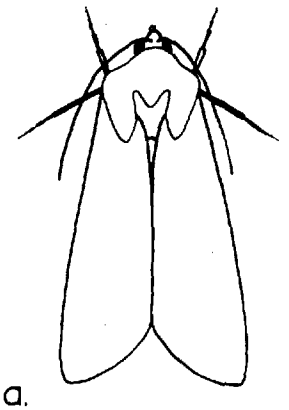


"Wide flat"

14
Plusia gamma

"Wide declivous"

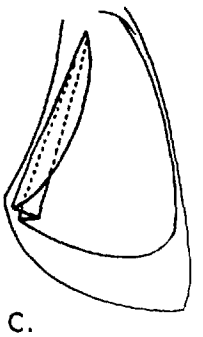
1 cm.



a.



b.

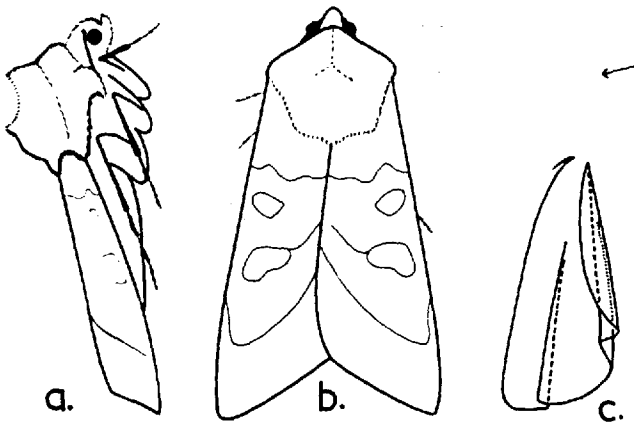


c.

15

Hydraecia micacea

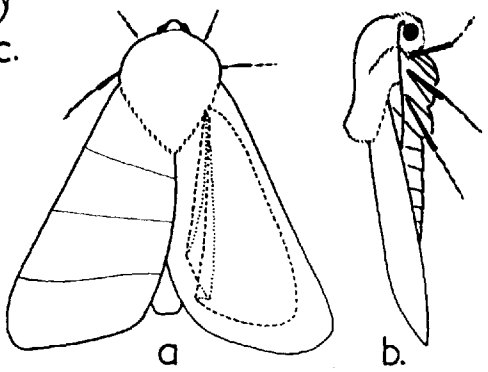
"Medium"



16

Meristis trigrammica.

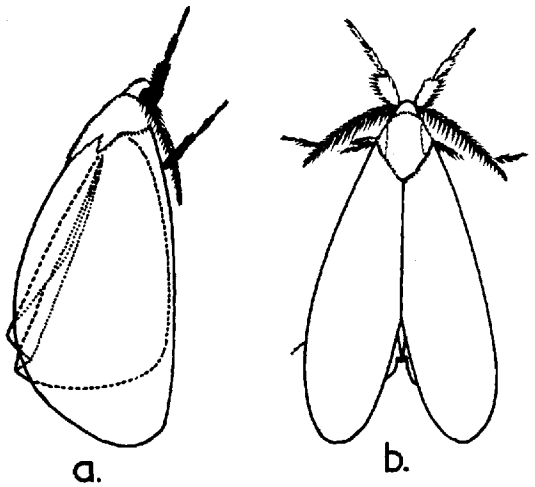
"Wide"



17

Euproctis chrysorrhoea.

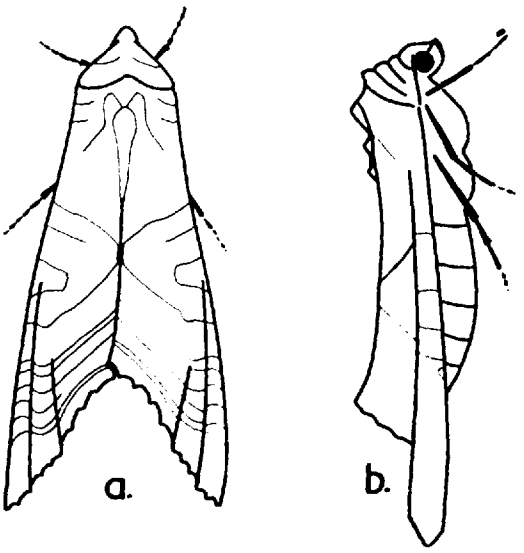
"Wide"



18

Phlogophora meticulosa

"Leaf Mimic"



1 Cm.

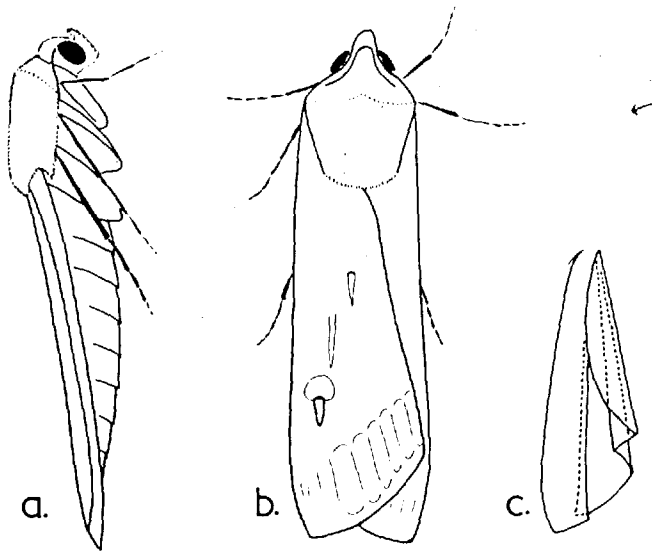
19

Agrotis ypsilon.

"Linear"

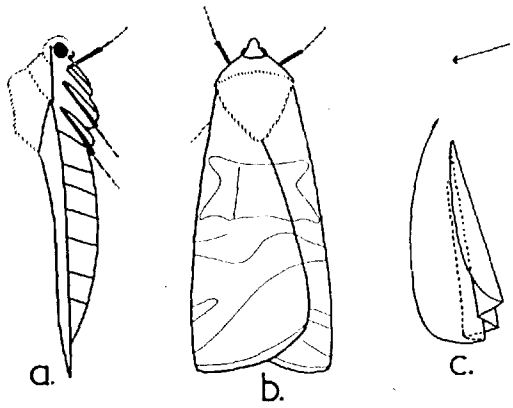
NOCTUOIDEA.

1 Cm.



Orthosia gothica 20

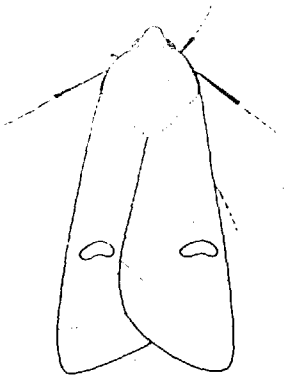
"Narrow"



21

Anchoscelis lunosa.

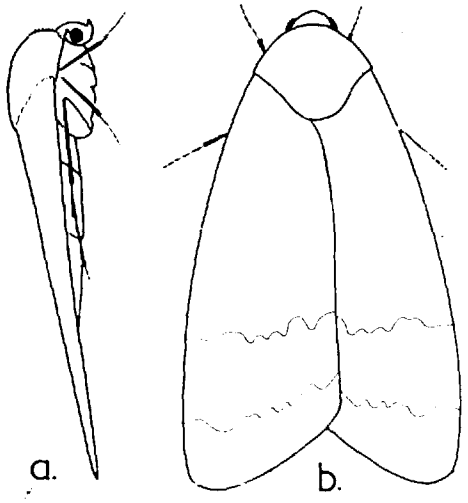
"Narrow"



22

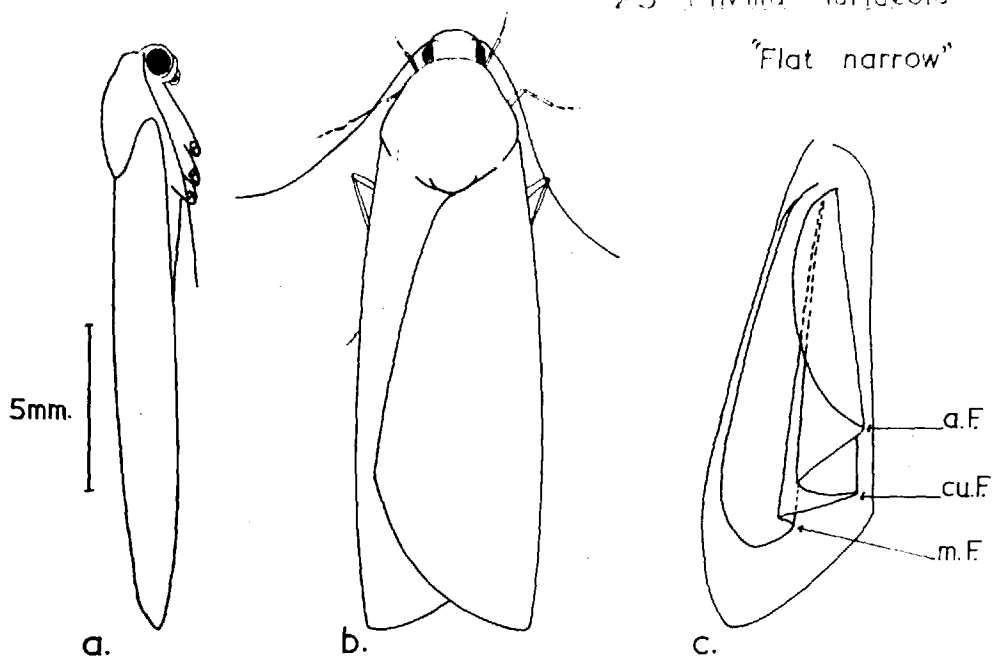
Amphipyra pyramidea.

"Flat"



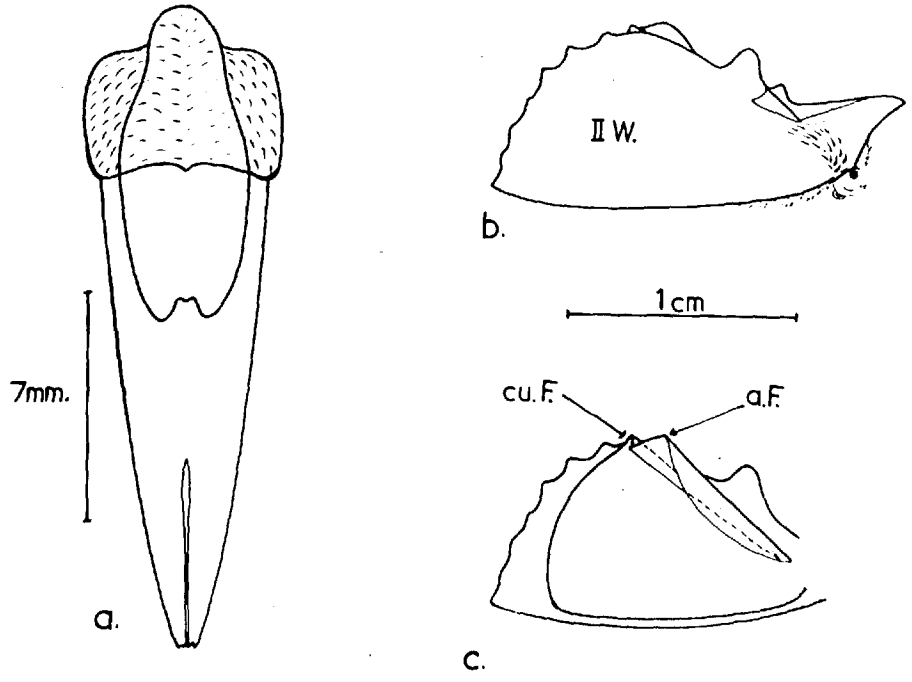
23 Tilema lurideola

"Flat narrow"



24

Lophopteryx capucina

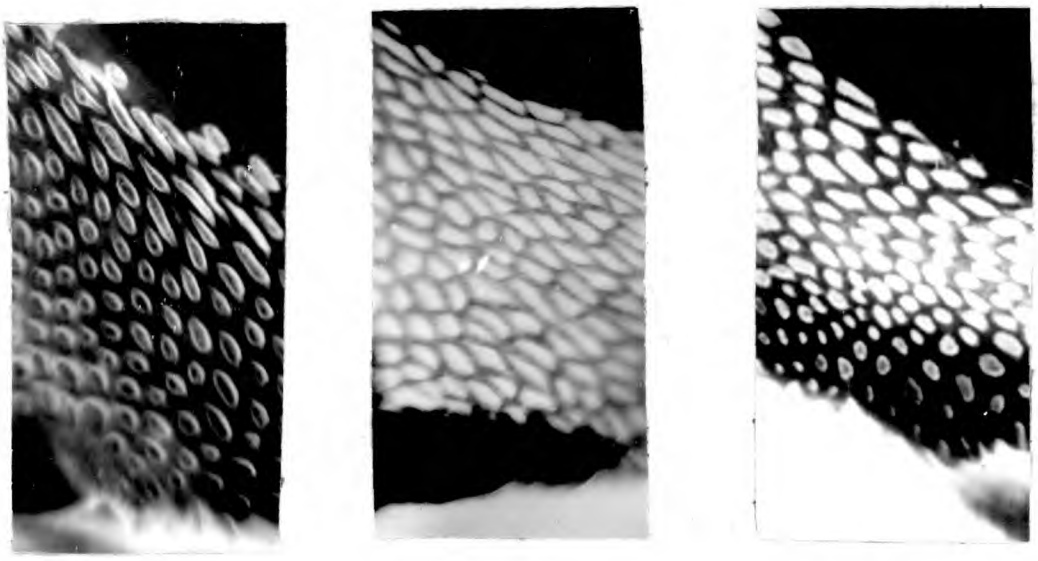




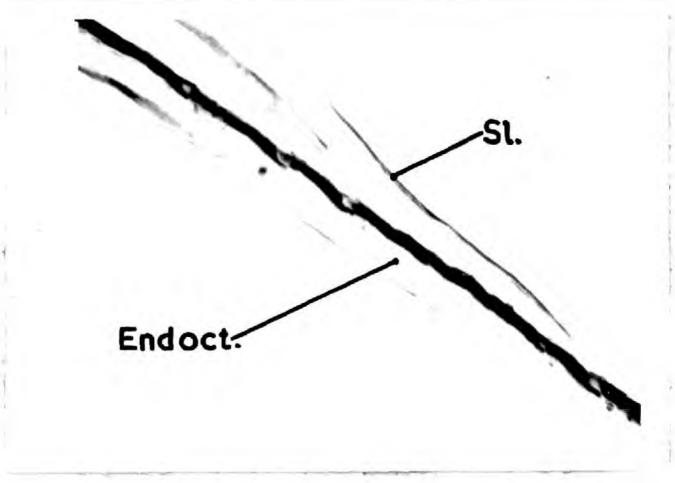
25. Photomicrograph of bending cuticle of Laothoe populi. Section stained in Mallory's triple stain X 380.



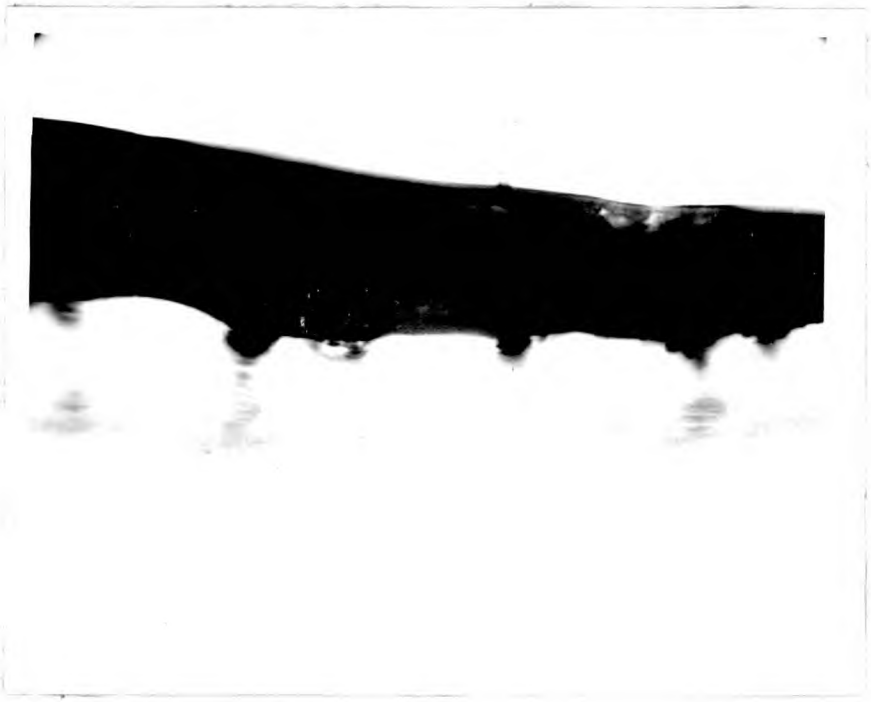
26. Section of L. populi bending cuticle showing exocuticular canals. X 1215.8



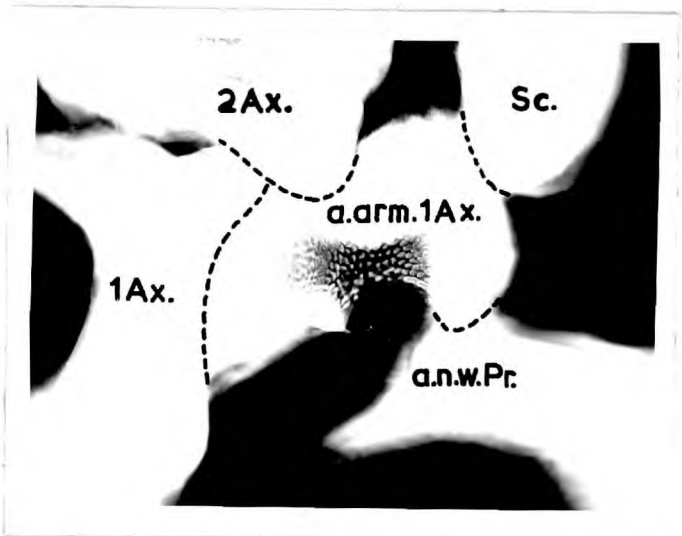
27. Spilosoma lutea S.lubricipeda Euproctis chrysorrhoea Bending cuticle in surface view - Mallory's triple stain. X 415.



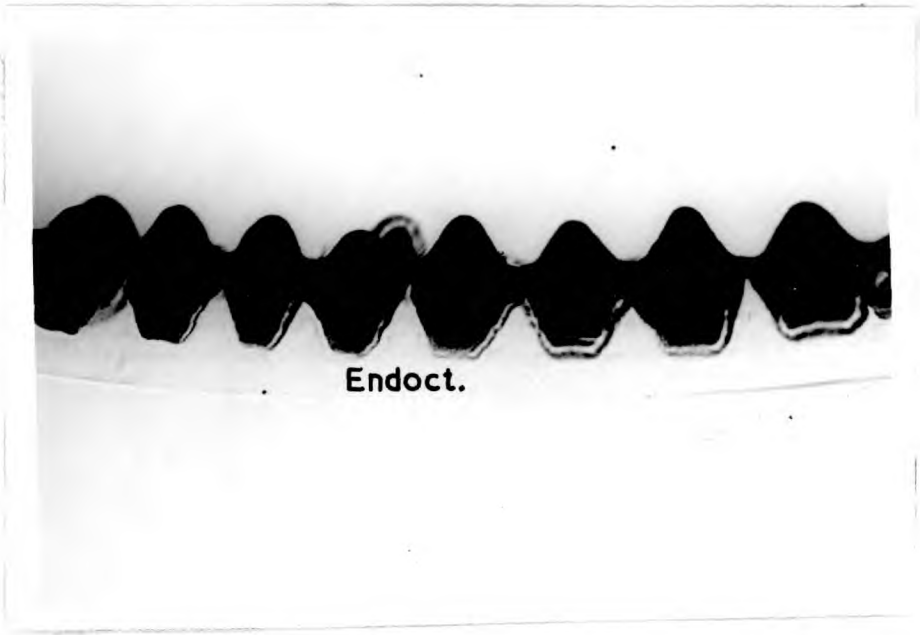
28. Section of the mesonotum of Spilosoma lubricipeda stained in M allory 's triple stain. X 260.



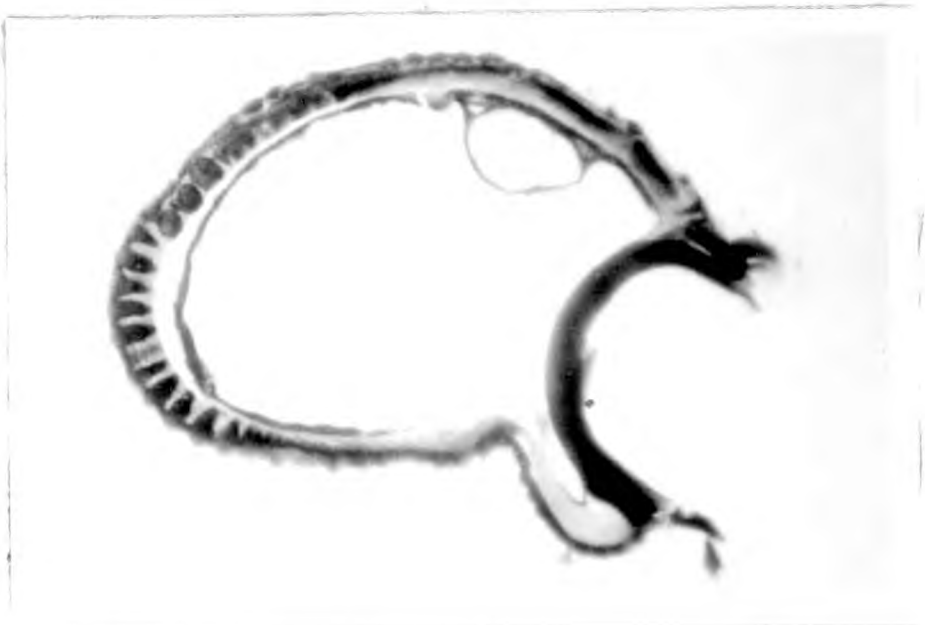
29. Bending cuticle of Laothoe populi treated in 2% KOH. Section stained in Mallory's triple stain. X 950.



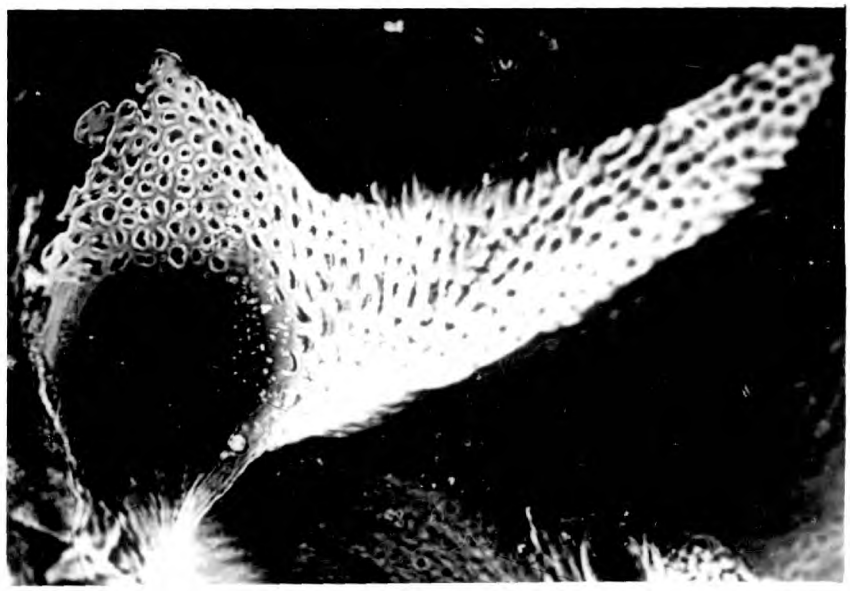
30. Negative photograph of bending cuticle in the anterior arm of the first axillary of the fore wing of Poecilocampa populi. X 130.



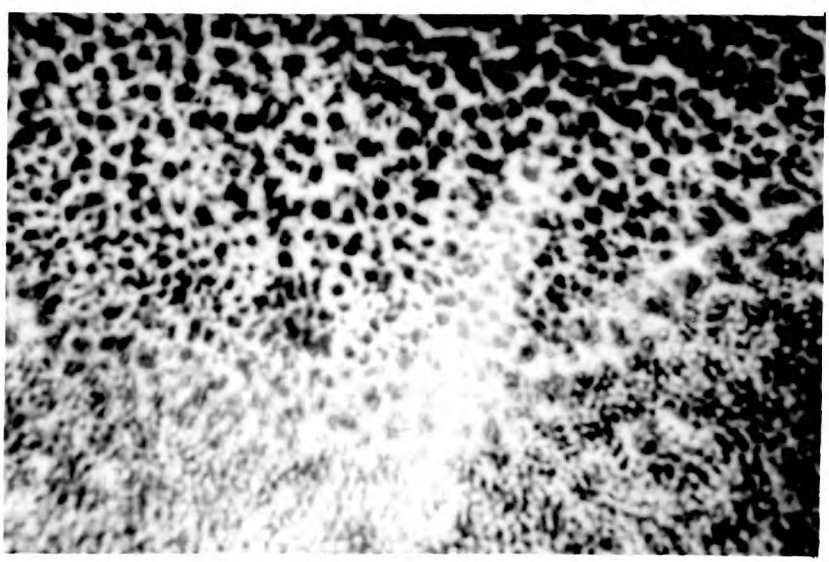
31. Section of the intersegmental membrane of Laothoe populi pupal abdomen. X 254.5 Unstained.



32. Section of galea of Aglais urticae stained in Mallory's triple stain. X 650.



33. Biston betularia - Notal incision of fore wing. X 230.

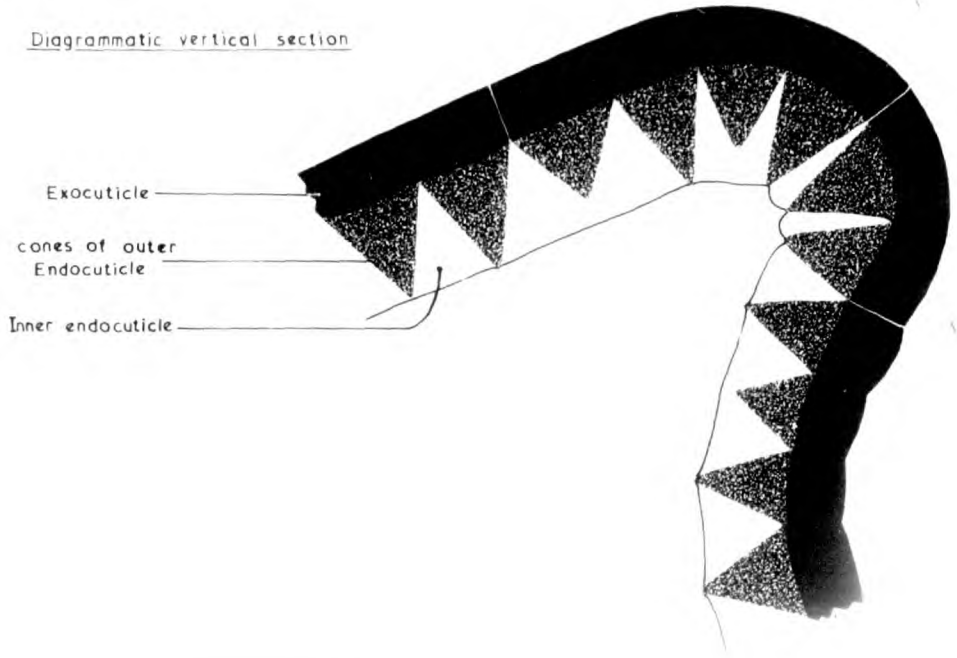


34. Zygaena filipendulae - Bending cuticle. X 1178.5. Surface view.

BENDING CUTICLE

35

Diagrammatic vertical section





36

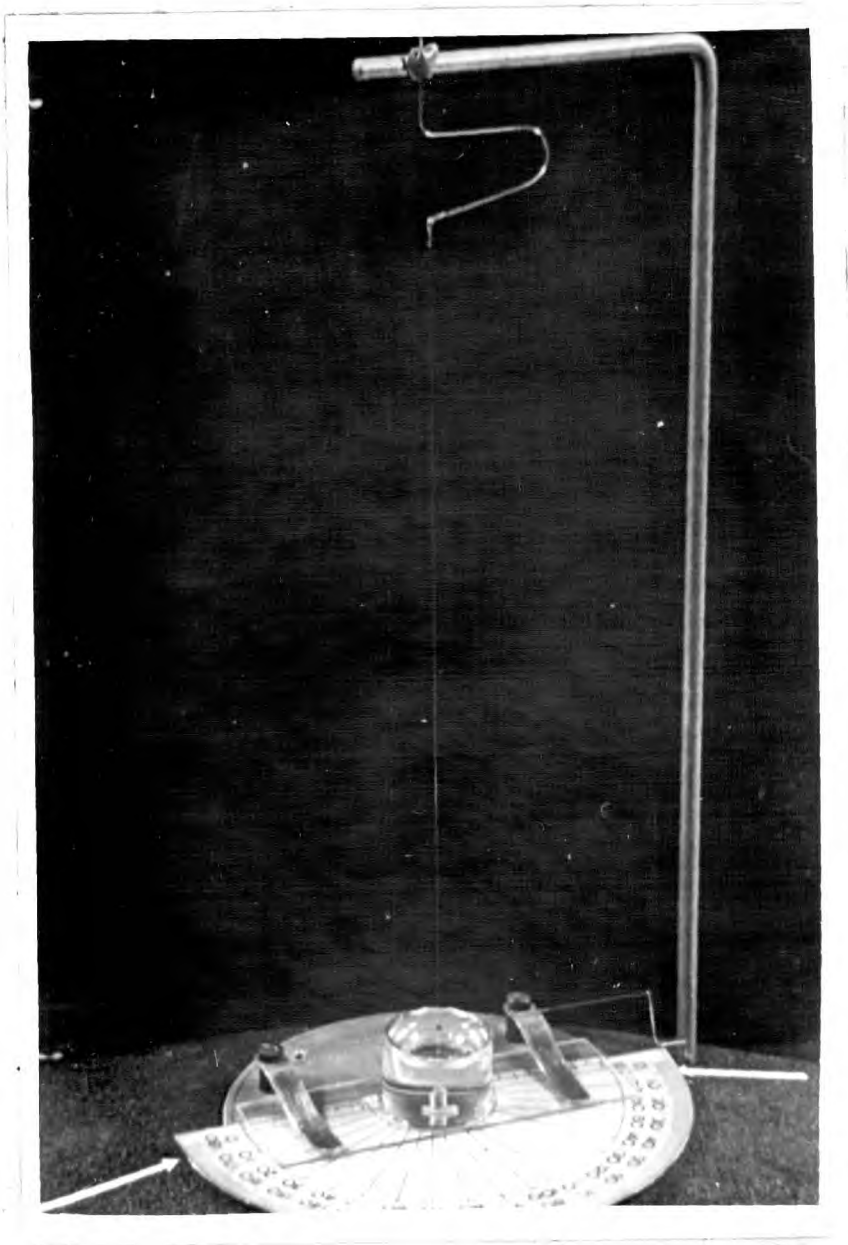
Laothoe populi

Photograph of bending cuticle in Ringer's solution taken with polarized light.

X 300.



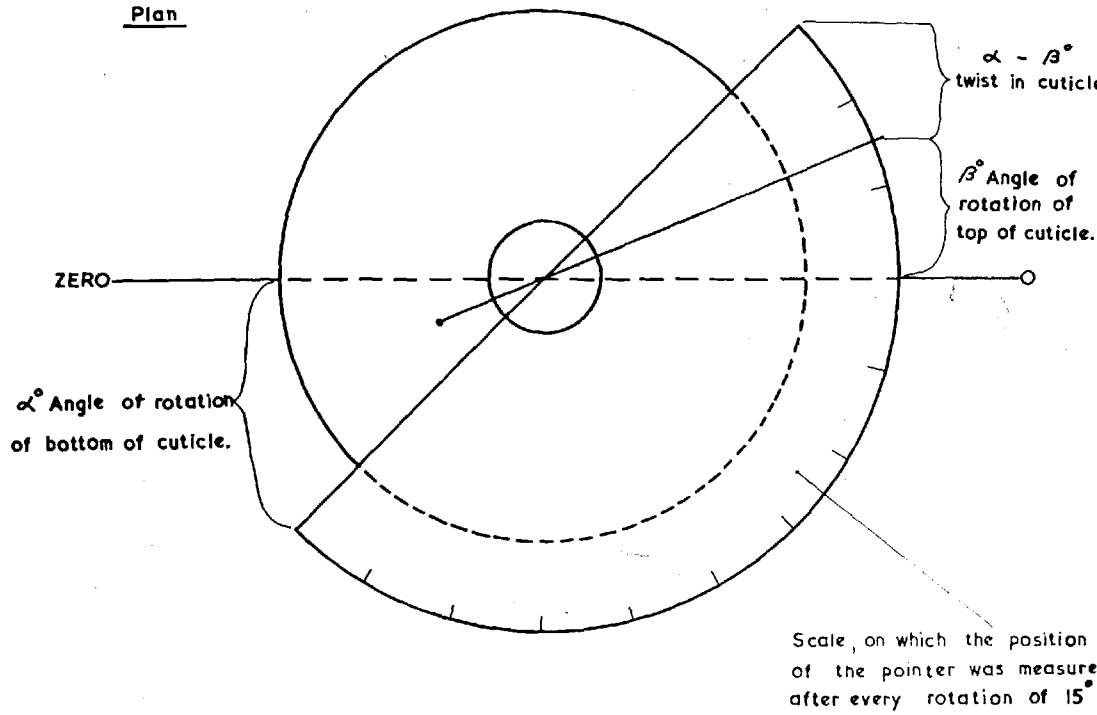
37. Bending cuticle twisted in the torsion apparatus.



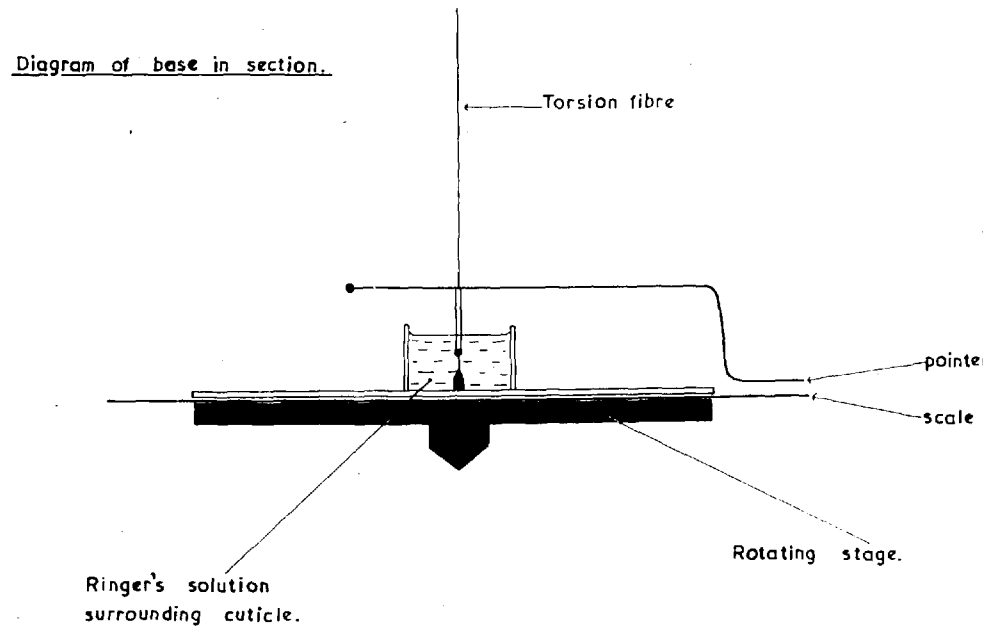
38. Torsion apparatus.

TORSION APPARATUS.

39

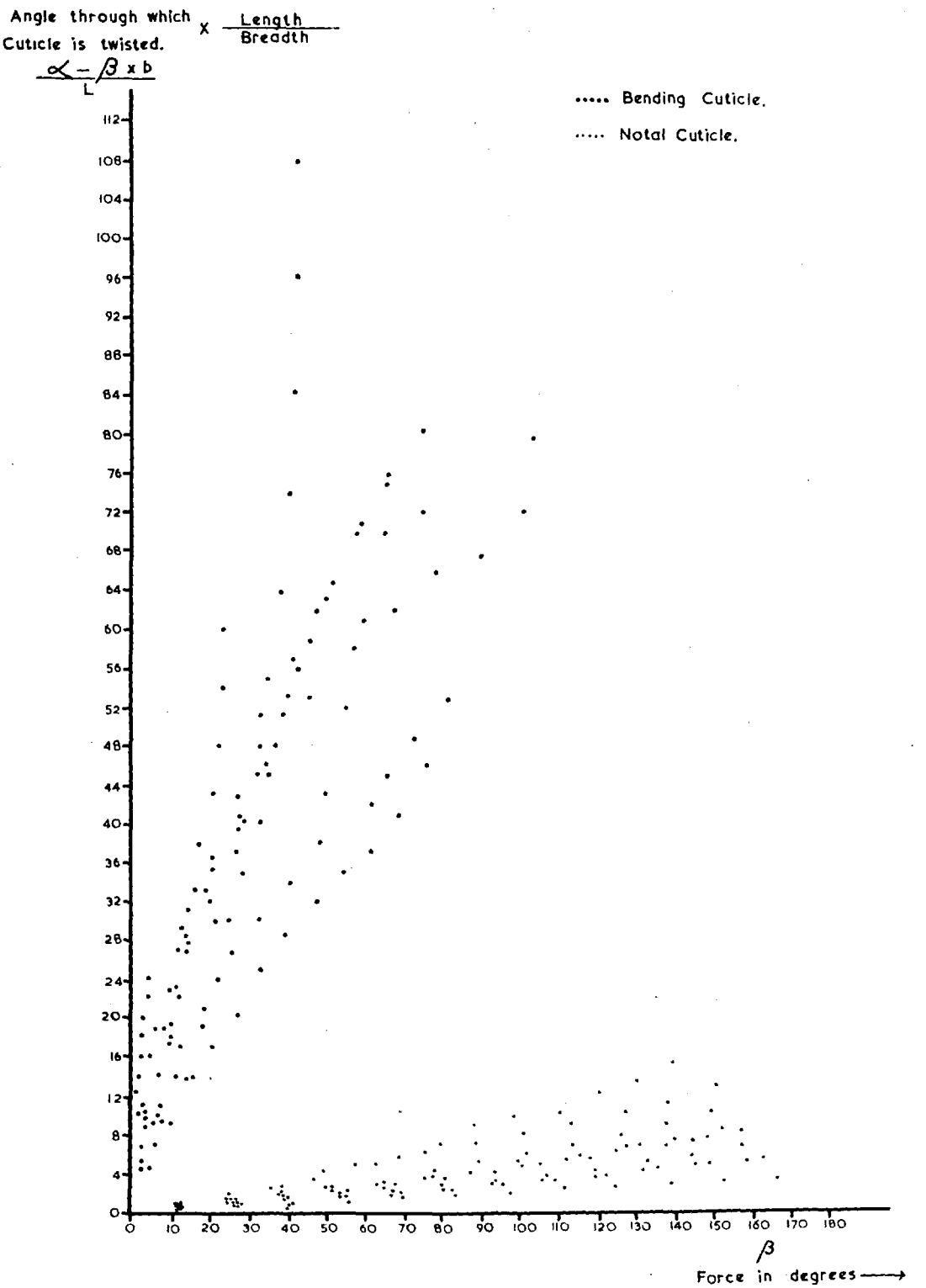


40



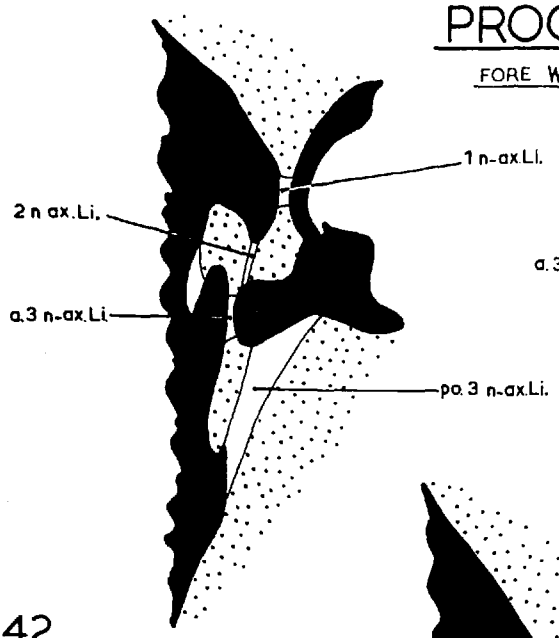
RESULTS of TORSION APPARATUS.

41



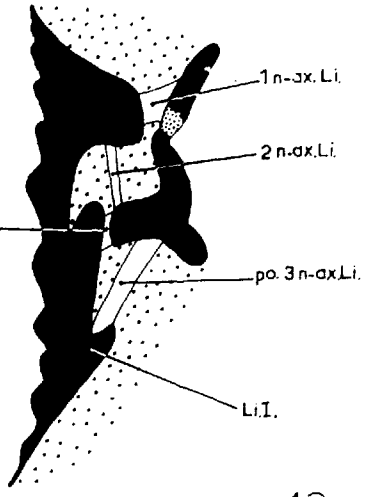
FIRST AXILLARY and MEDIAN NOTAL WING PROCESS

FORE WING



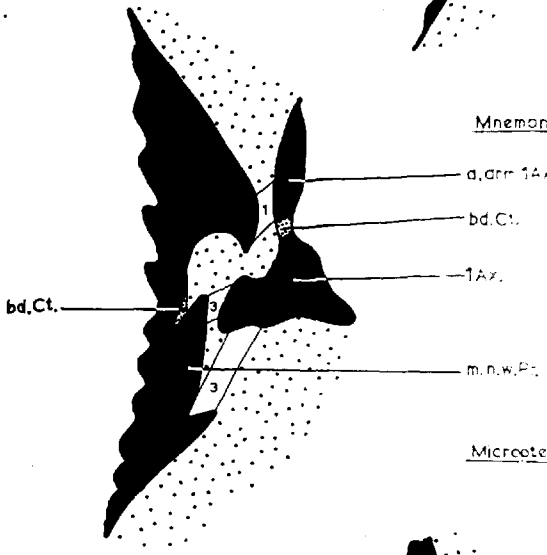
42

Limnephilus lunatus.



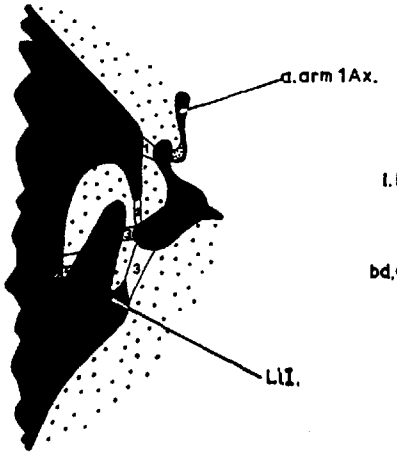
43

Mnemonica subpurpurella.



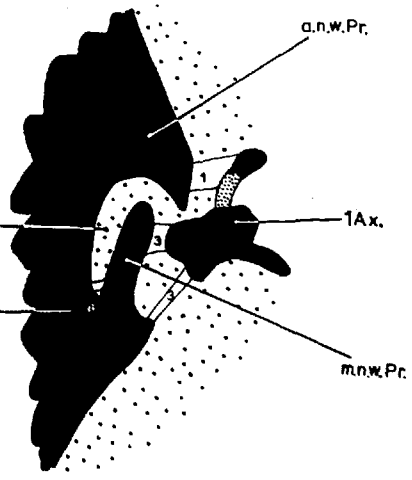
44

Micropteryx calthella.



45

Stigmella basalella

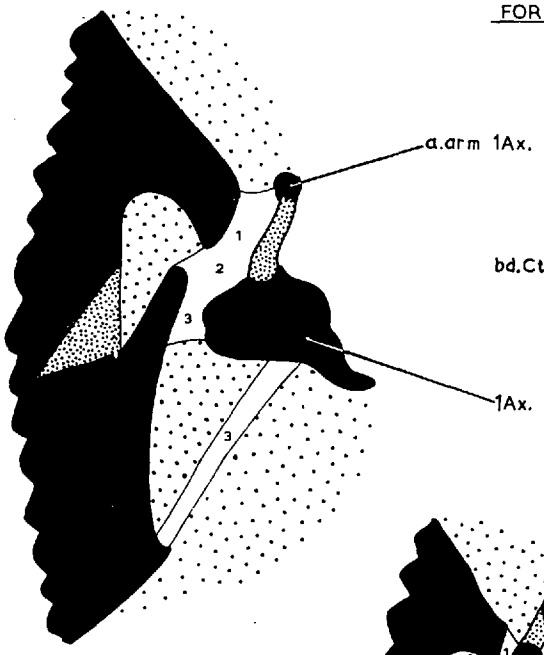


46

Adela reaumurella.

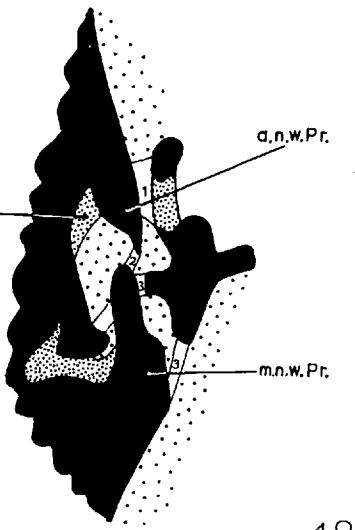
st. AXILLARY & MEDIAN NOTALWING PROCESS.

FORE WING



47

Hepialus lupulinus.



48

Zeuzera pyrina



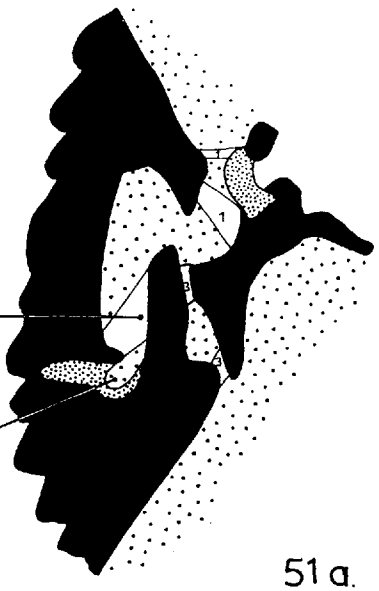
49

Tineola bisselliella



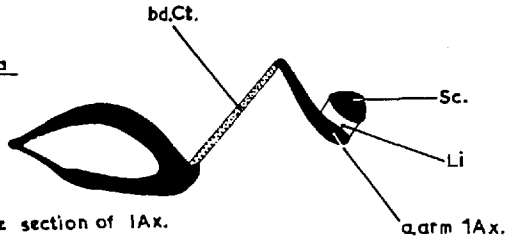
50

Evetria buoliana



51 a.

Plusia gamma

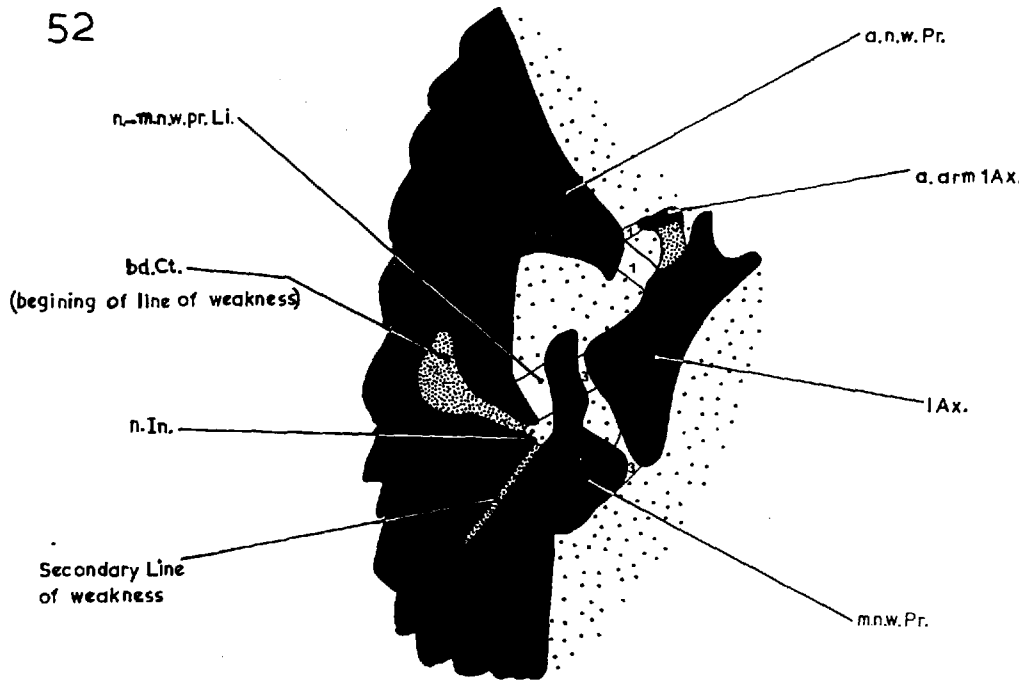


51 b.

Plusia — transverse section of 1Ax.

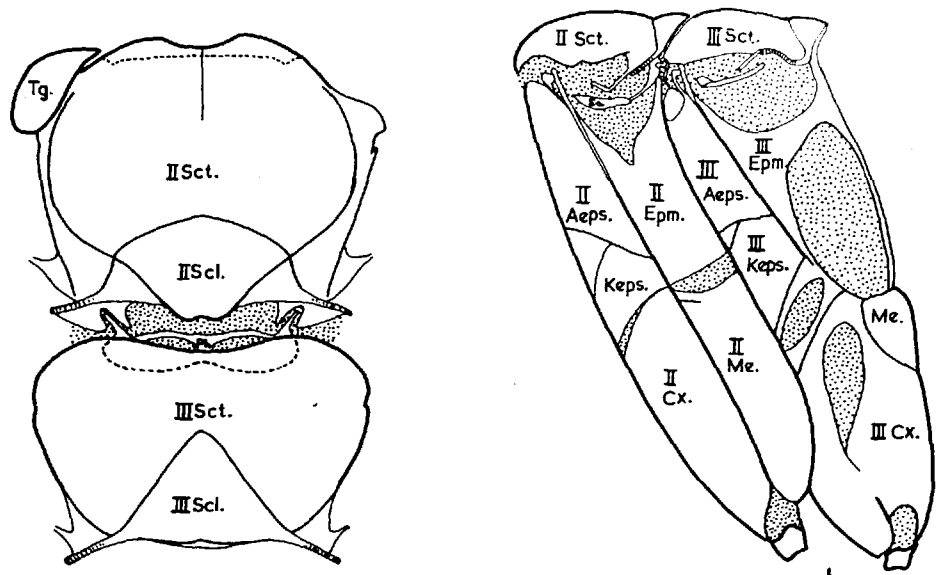
Pieris brassicae — Median Notal Wing Process & First Axillary. FORE WING

52



SHAPE OF THORAX.

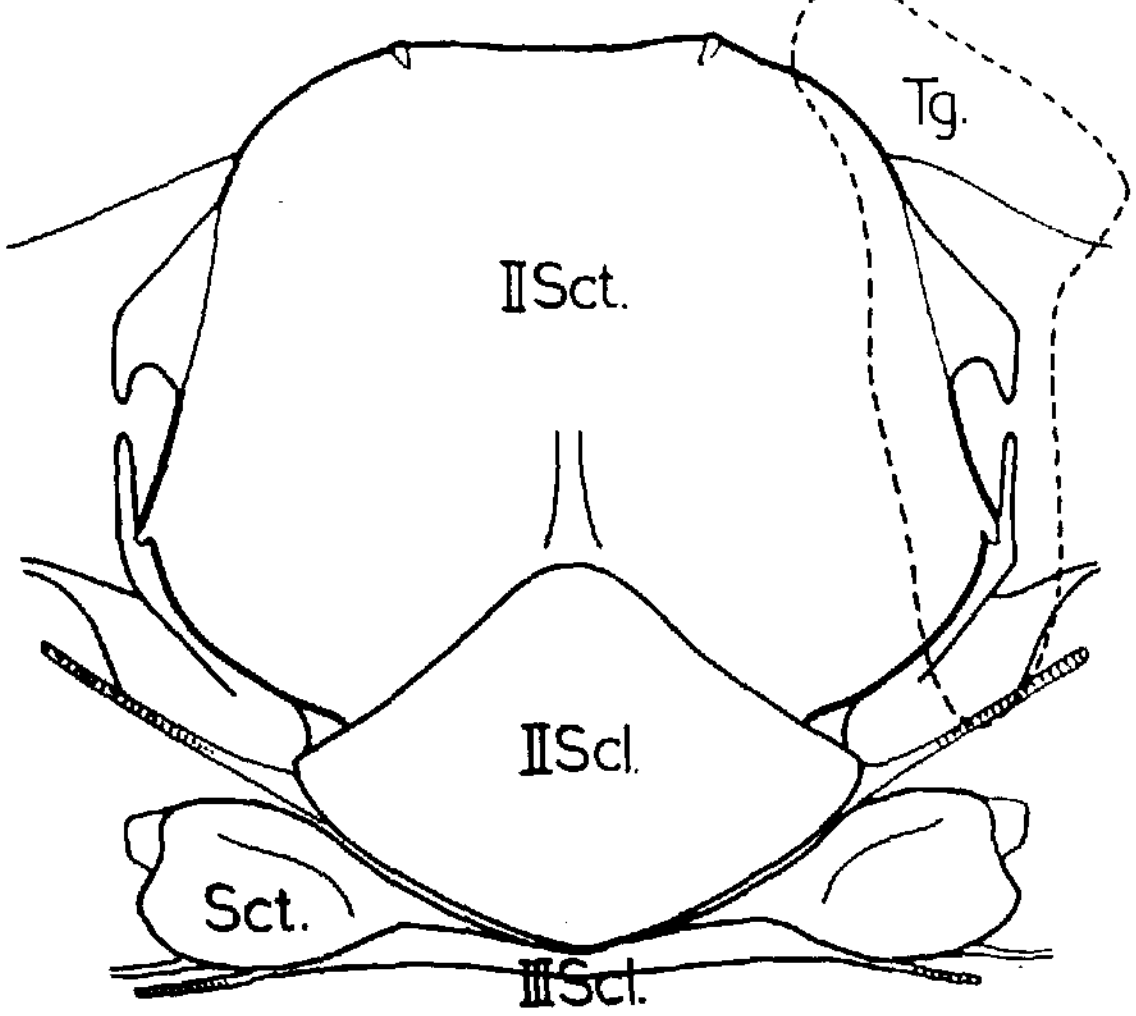
Dorsal. Meso. and Metathorax. Lateral.



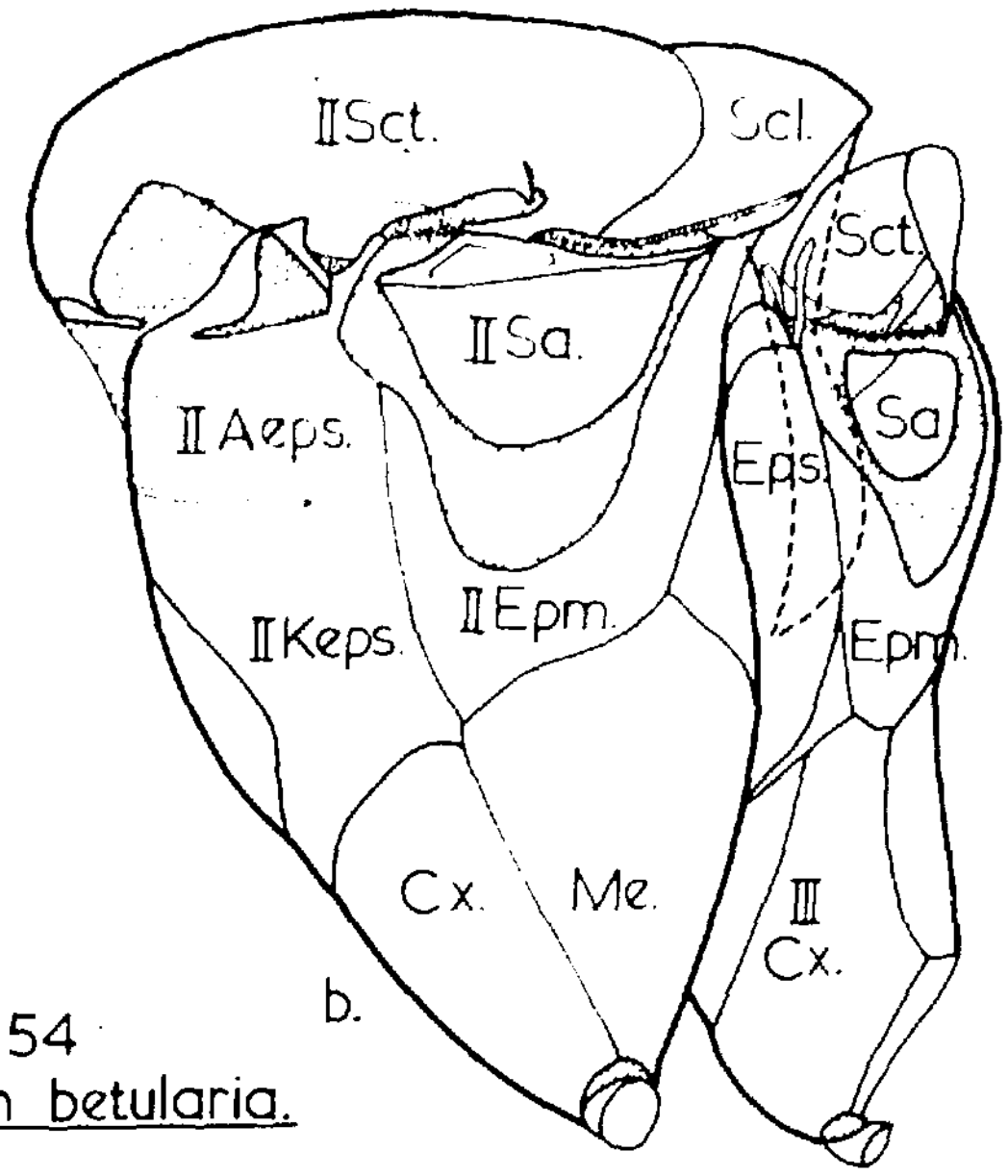
a. 53 b.

Micropteryx calthella.

0·313 mm.

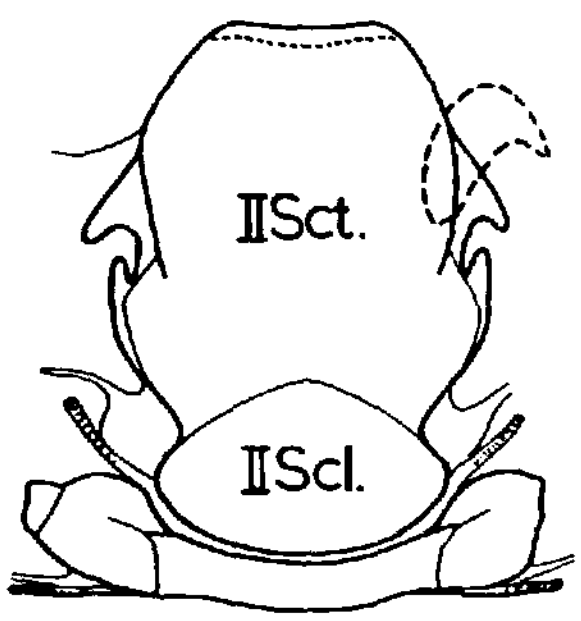


a.



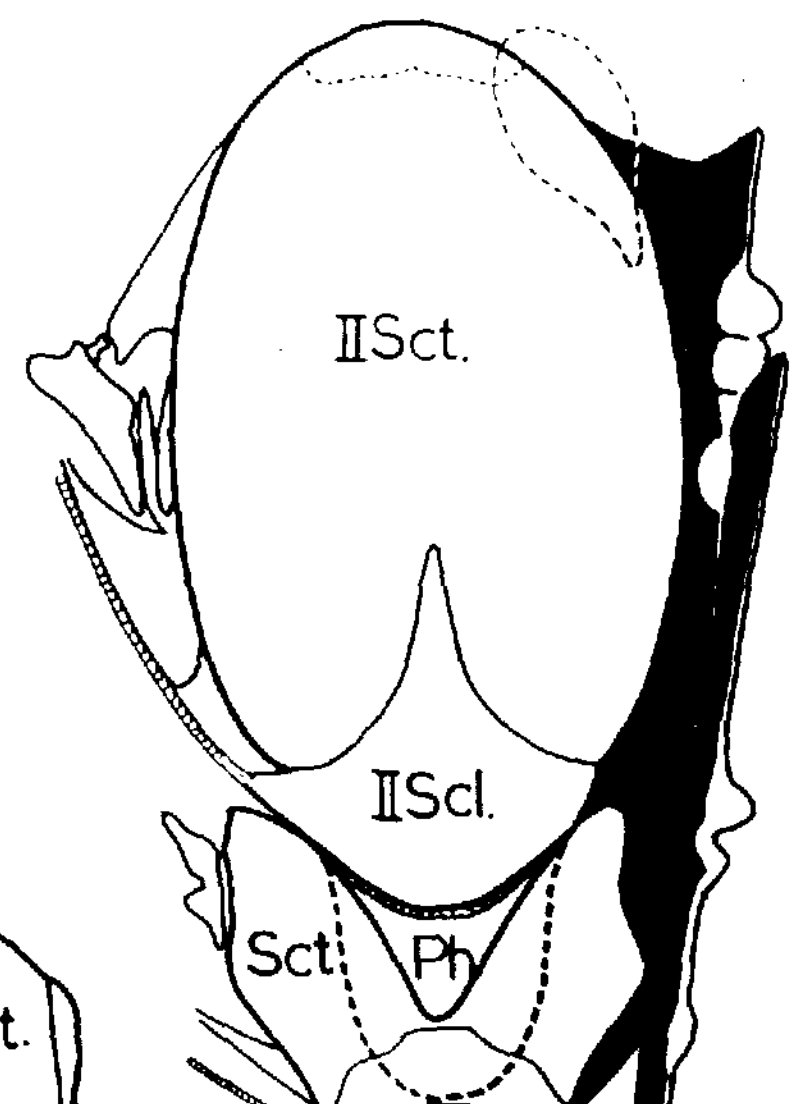
b.

54
Biston betularia.

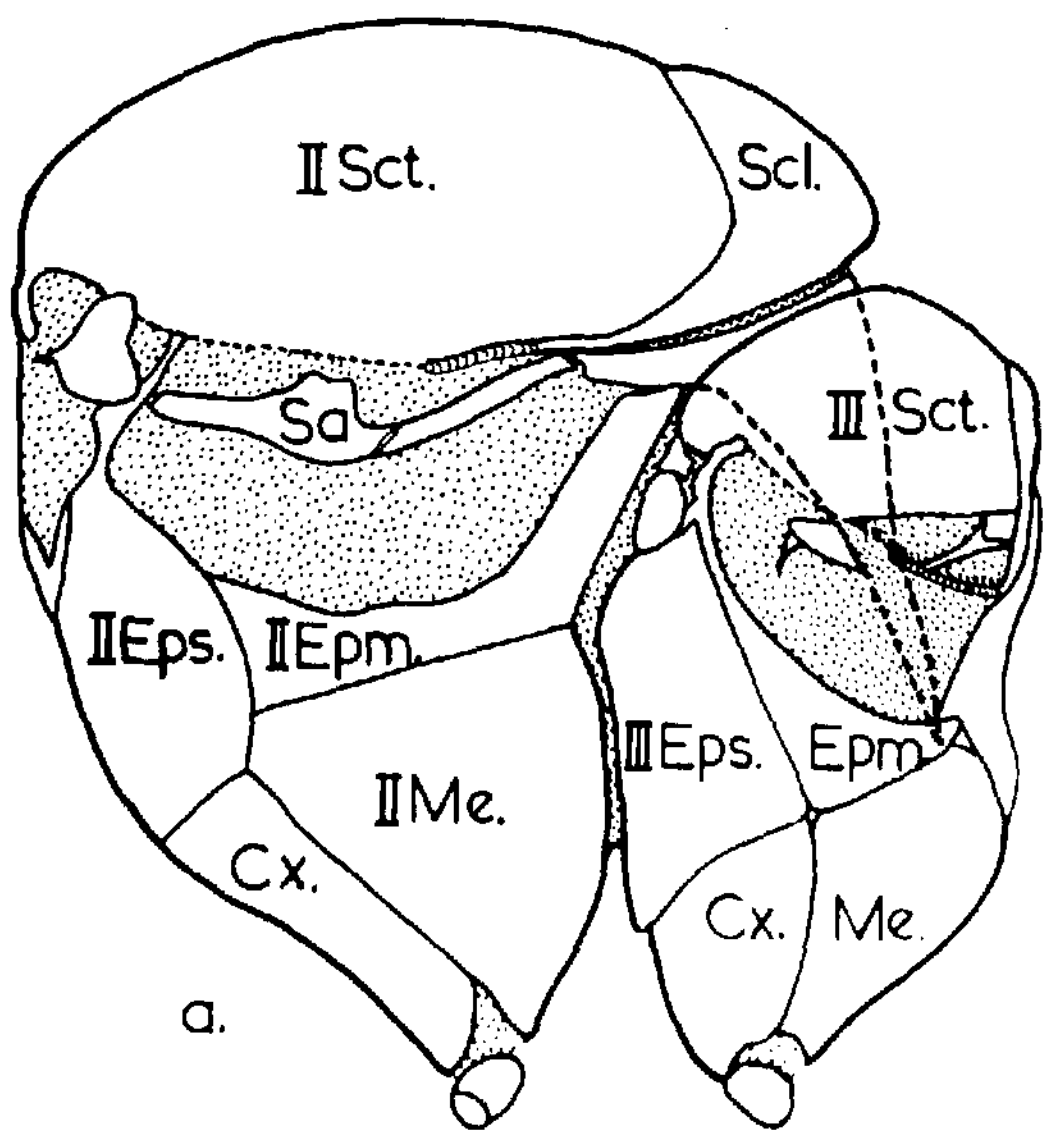


55
Operophtera brumata

0·935mm.



b.



1·36mm.

a.

56
Pieris brassicae.

SHAPE of NOTUM and FIRST AXILLARY.

MESOTHORAX.



57

○ Papilionoidea & Hesperioidea

○ Monotrysia

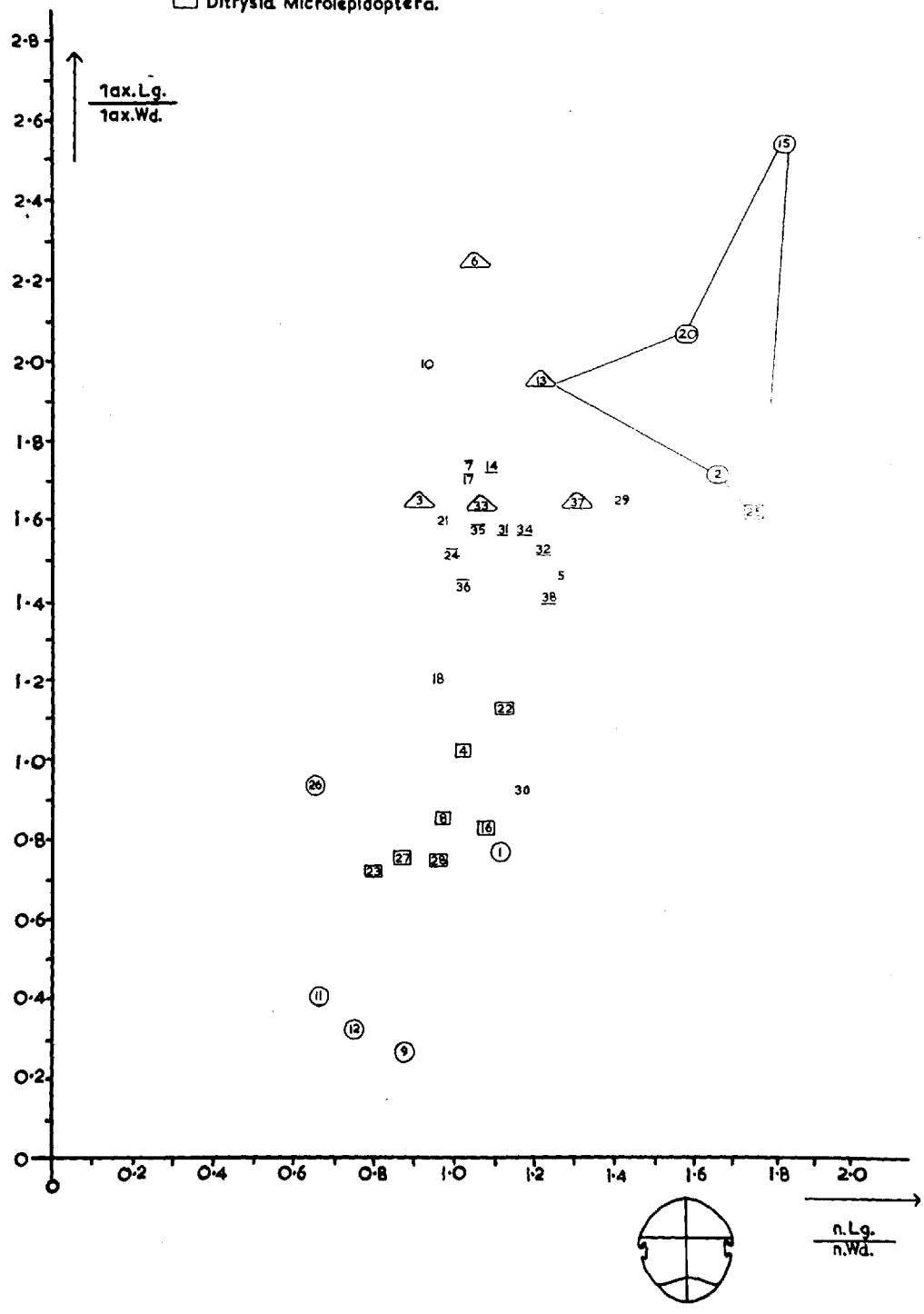
△ Geometroidea.

▭ Ditrysia Microlepidoptera.

x̄ Wide Noctuoidea

x̲ Narrow Noctuoidea

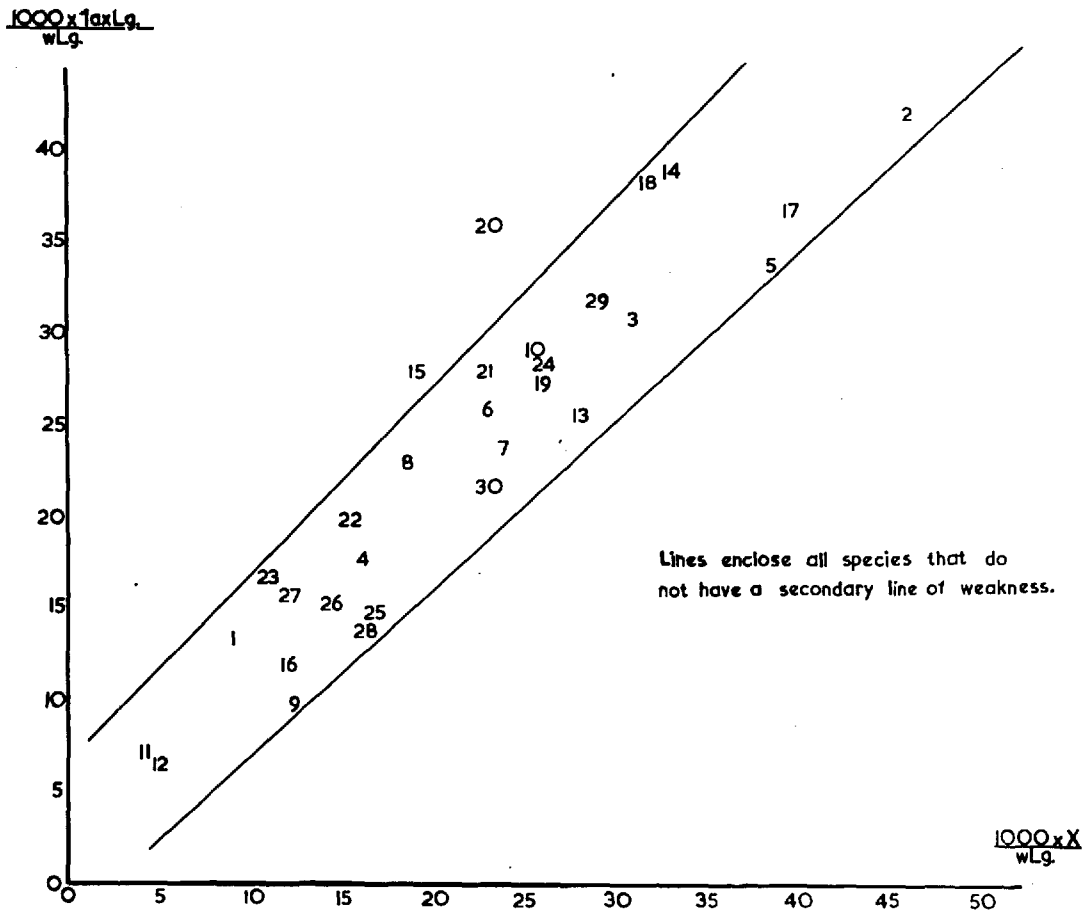
— Joins those that can sit with their Wings Up.



DEVELOPMENT of LATERAL EMARGINATION

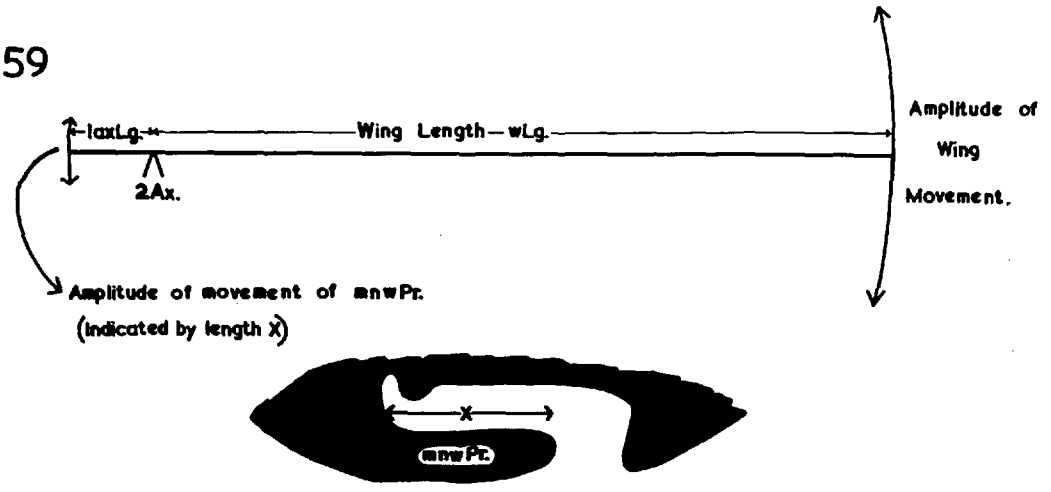
MESOTHORAX.

58



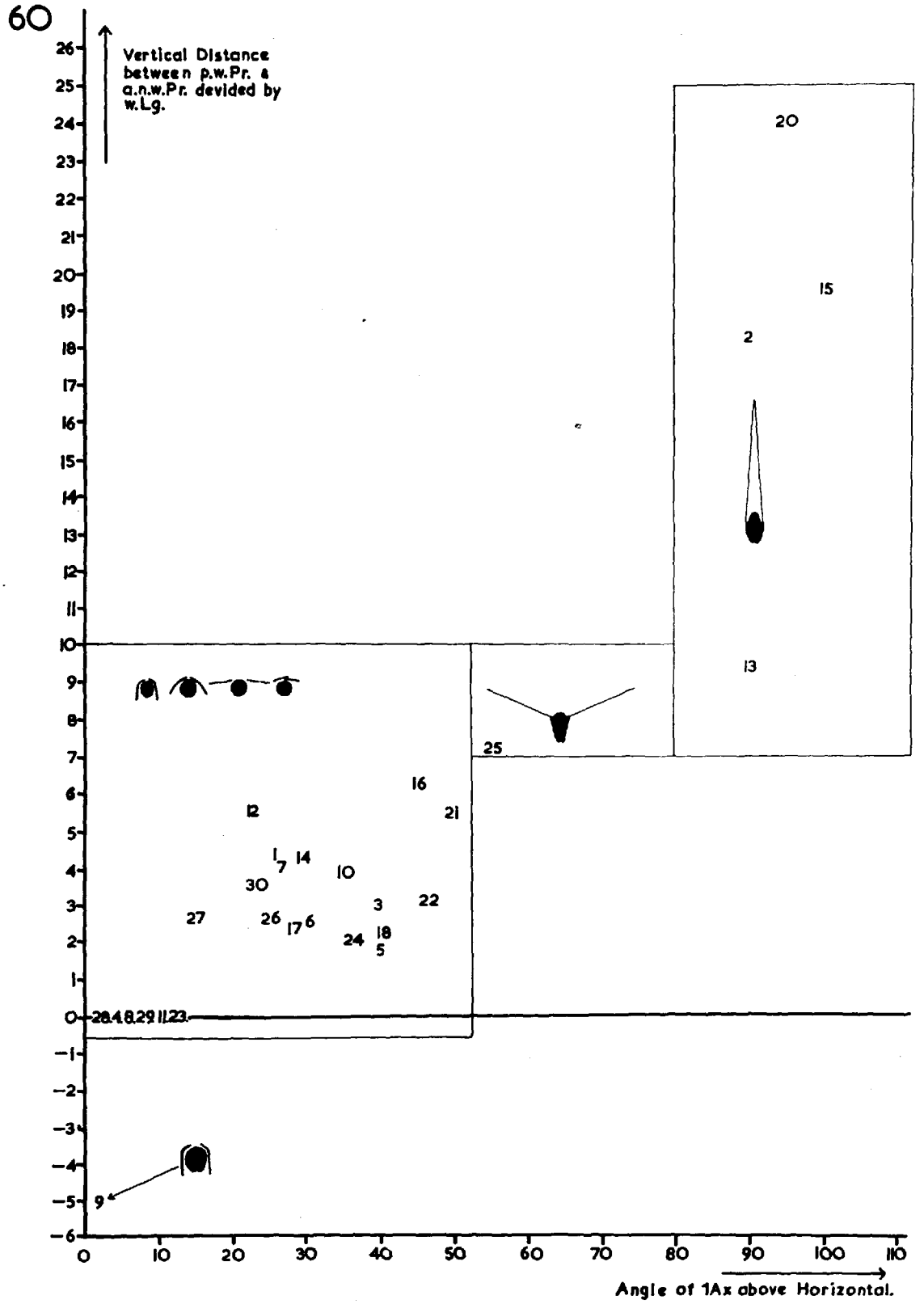
Diagrammatic Longitudinal Section of Wing.

59



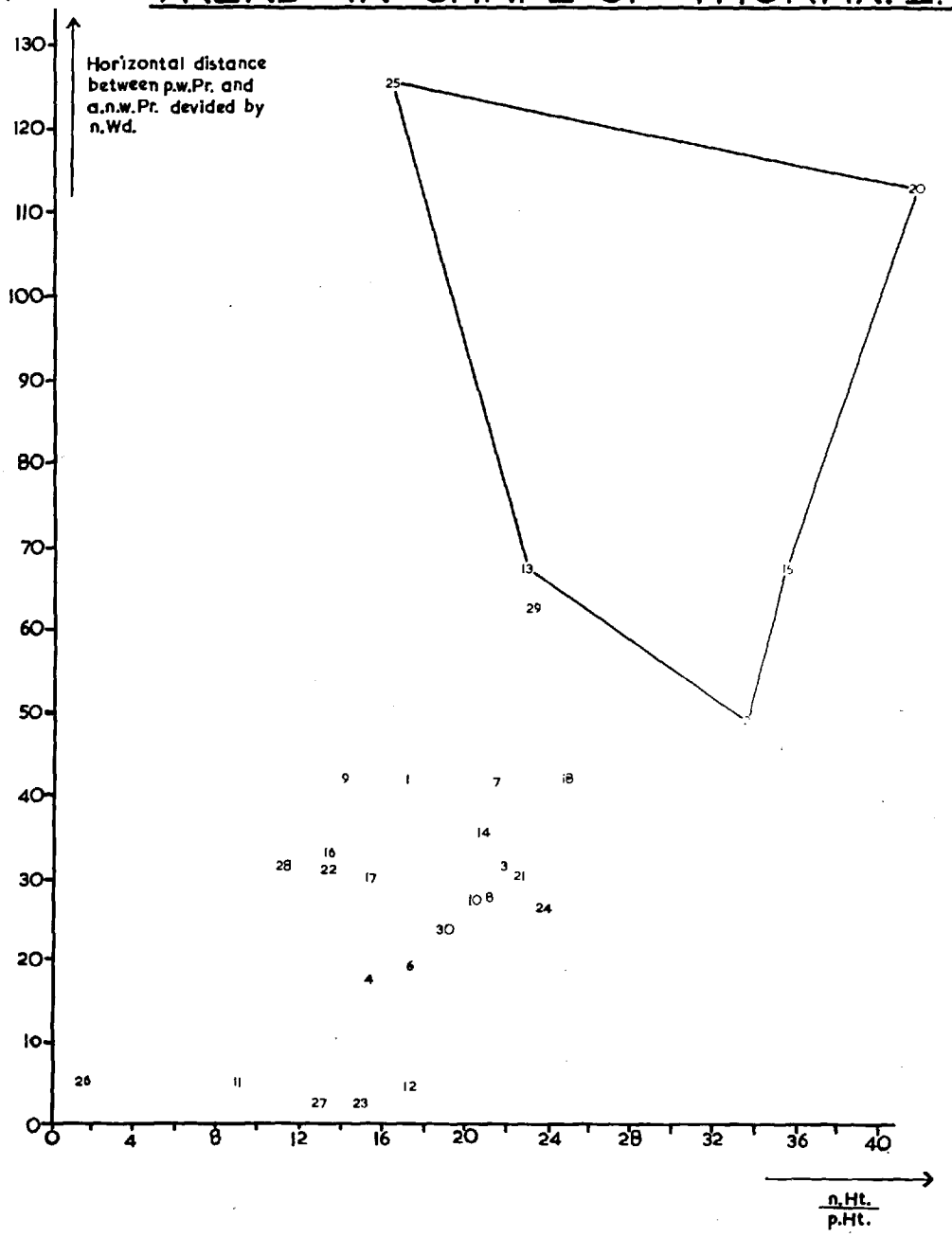
RELATIONSHIP BETWEEN SLOPE of 1AX AT REST, OVERLAP, and WING ATTITUDE.

FORE WING.

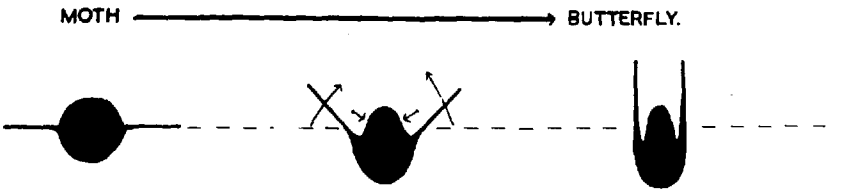


61

TREND IN SHAPE OF THORAX. II.



62

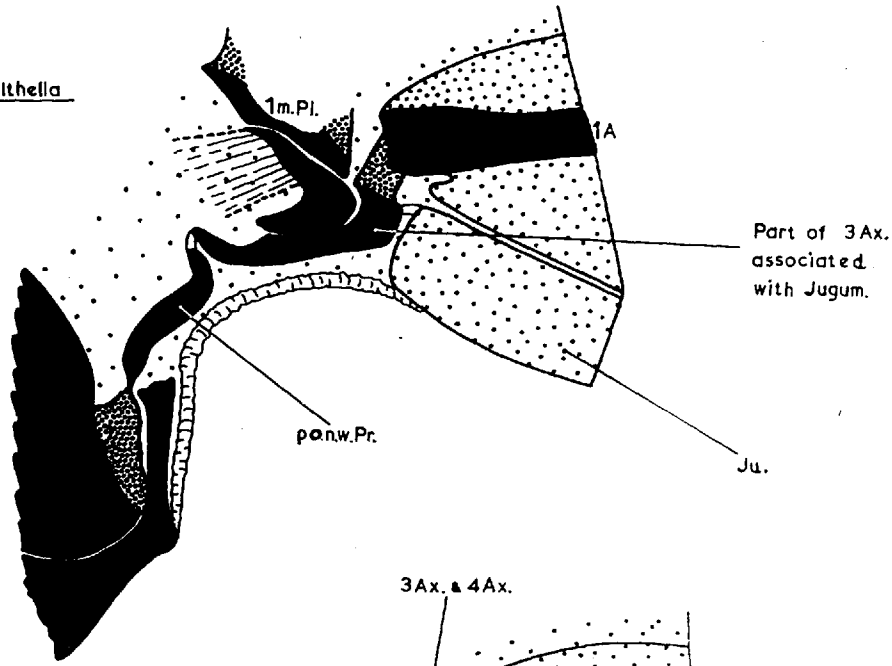


THIRD AXILLARY SCLERITE and JUGUM.

FORE WING

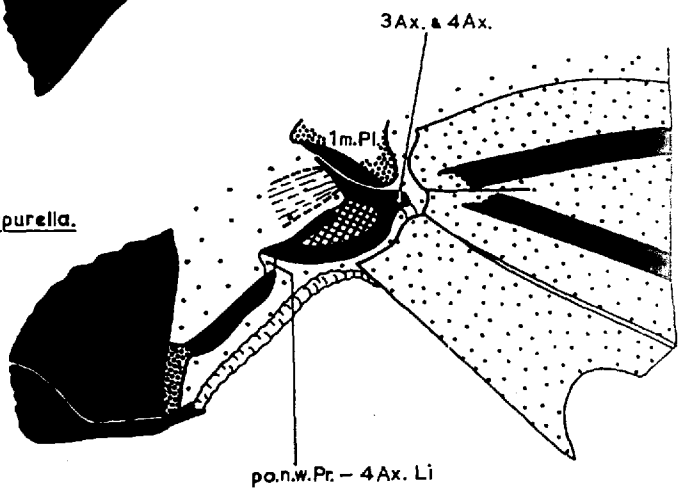
63

Micropteryx calthella



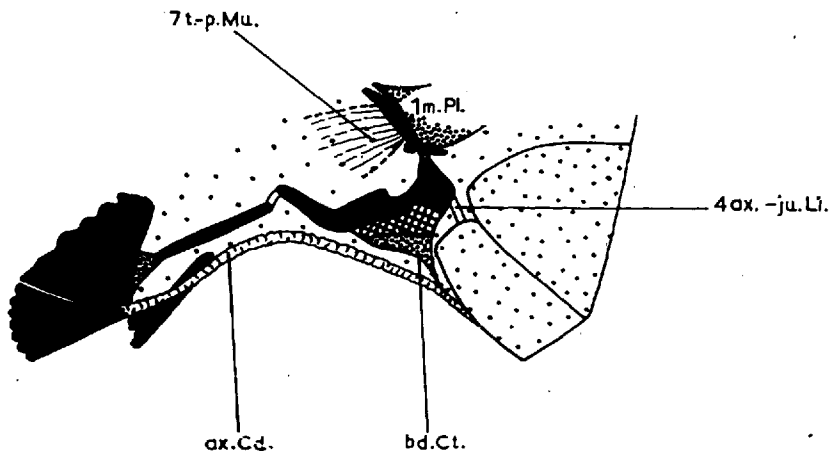
64

Mnemonica subpurpurella.



65

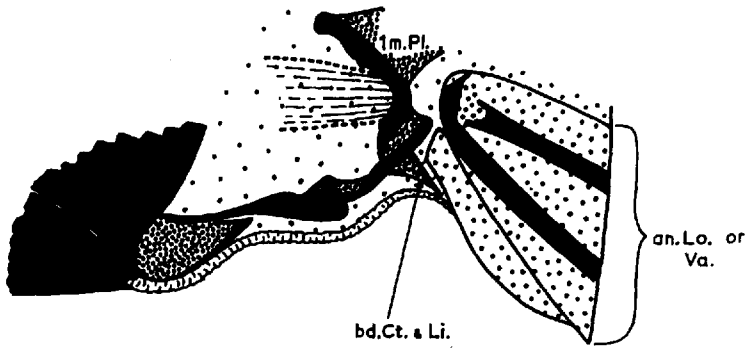
Stigmella basalella.



THIRD AXILLARY SCLERITE and JUGUM. FORE WING

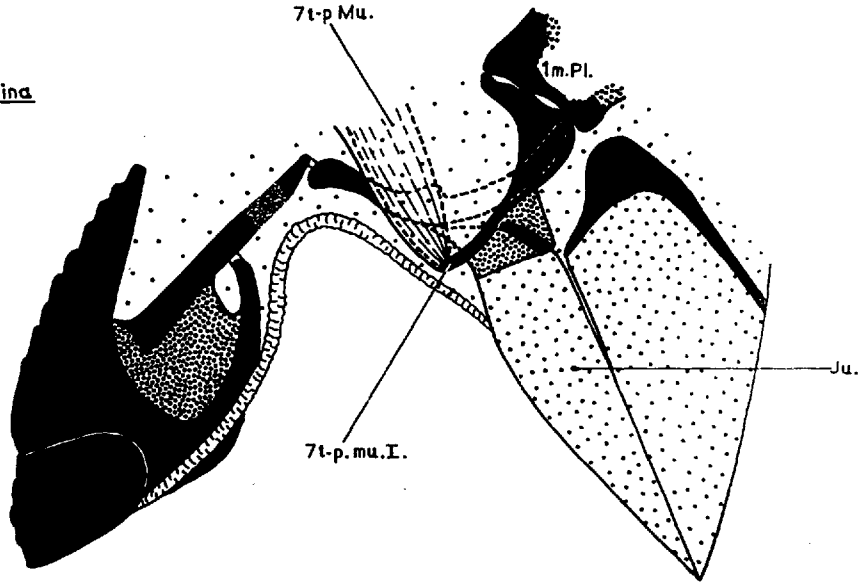
66

Adela reaumurella.



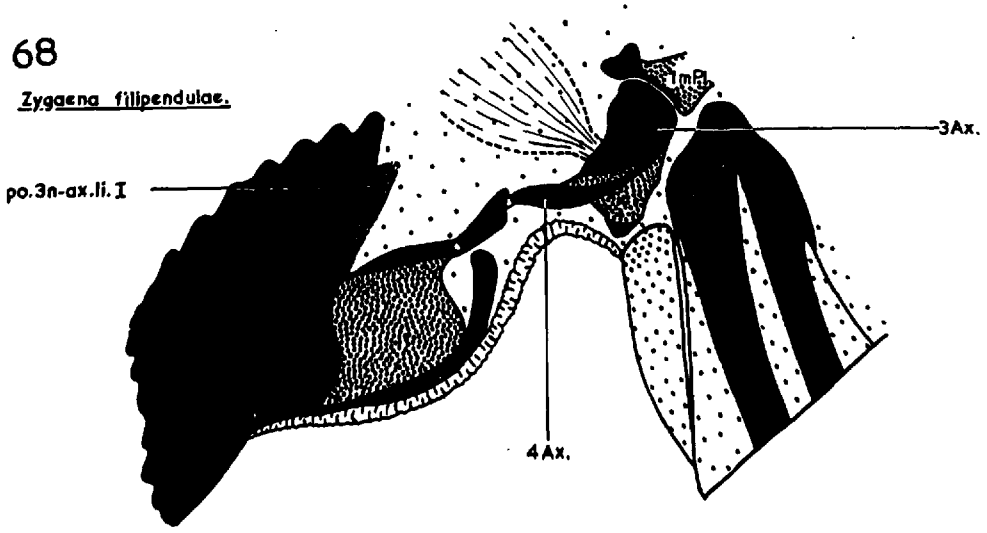
67

Zeuzera pyrina



68

Zygaena filipendulae.

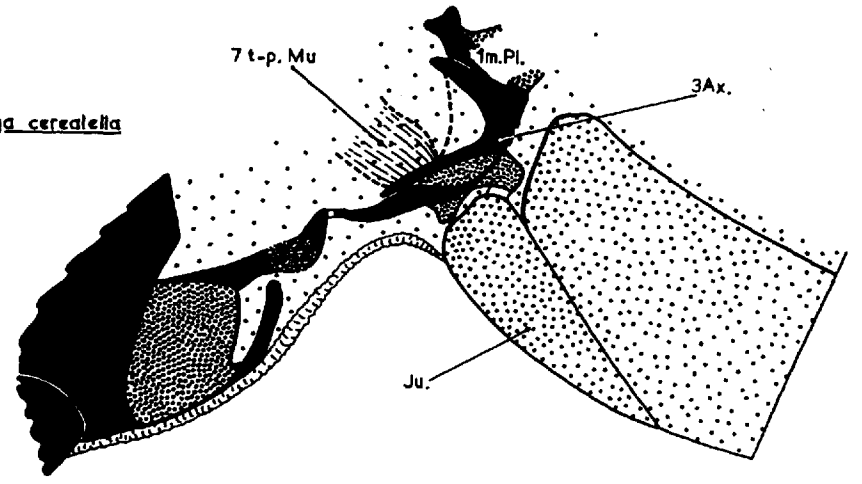


THIRD and FOURTH AXILLARY SCLERITES

FORE WING

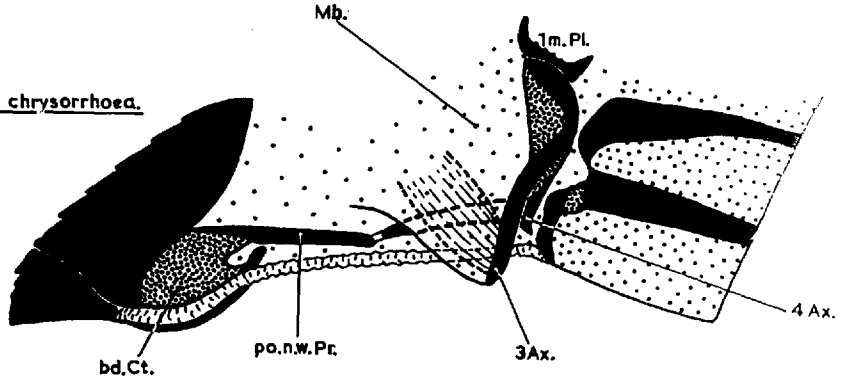
69

Sitotroga cerealella



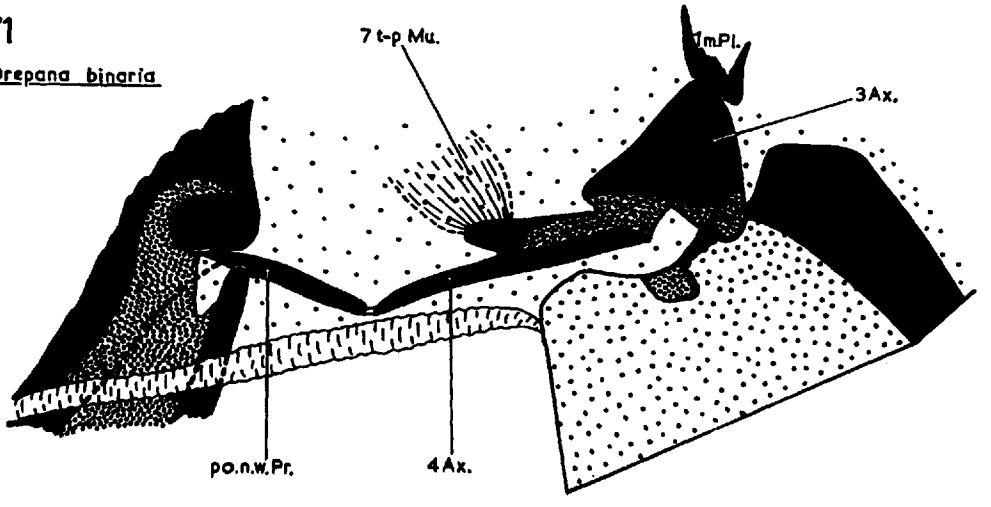
70

Euproctis chrysorrhoea.



71

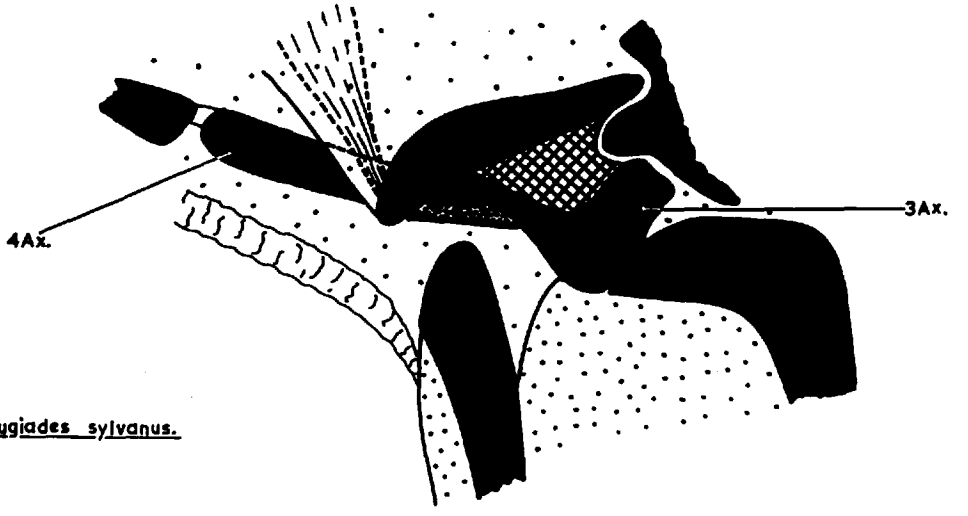
Drepana binaria



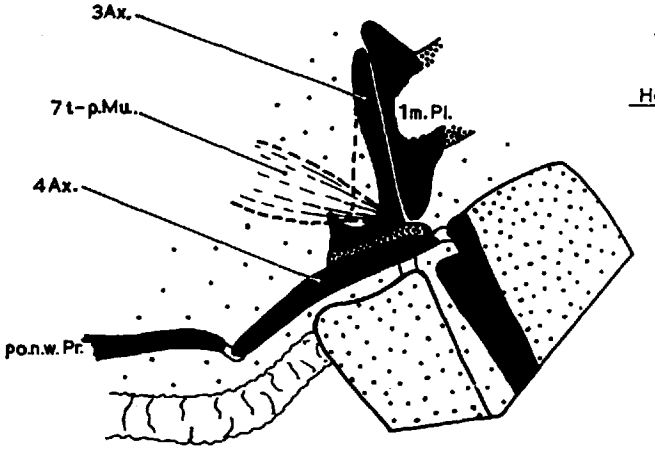
THIRD and FOURTH AXILLARY SCLERITES.

FORE WING.

72



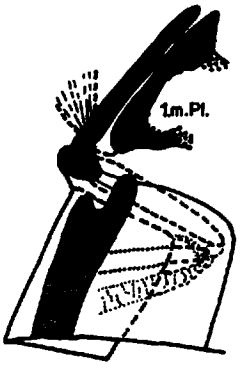
Augiades sylvanus.



73

Hepialus lupulinus

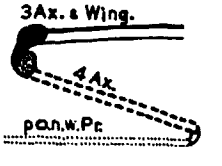
74a



H. lupulinus — folded.

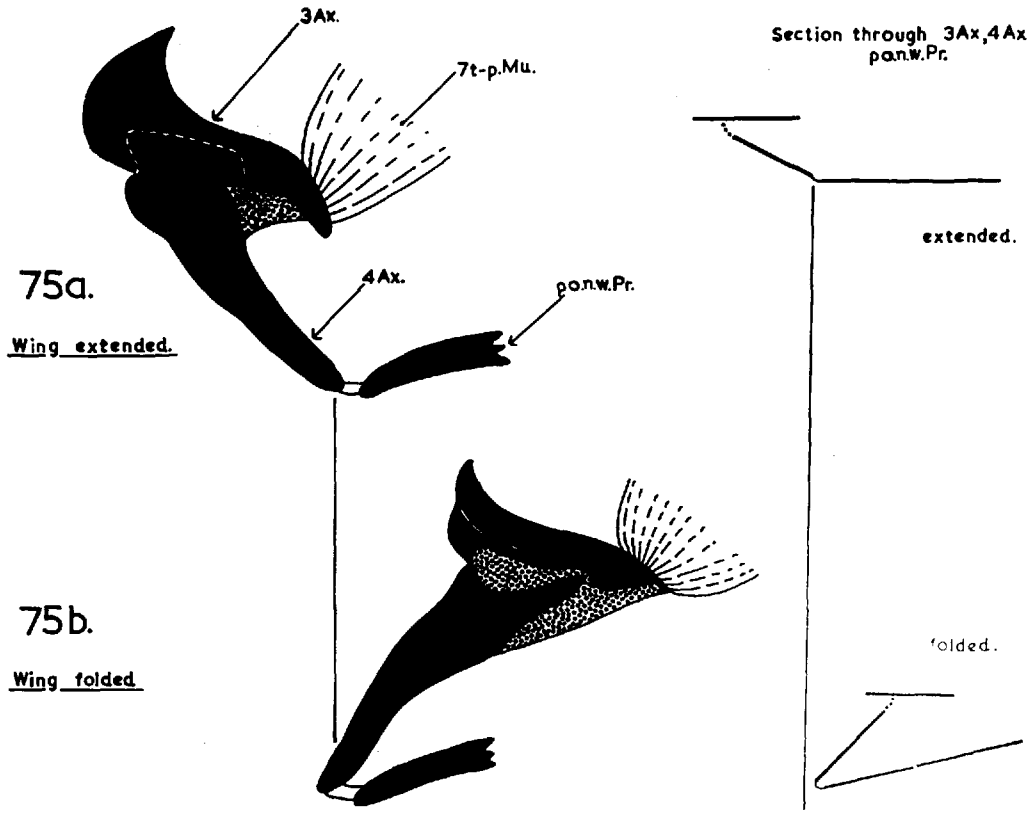
Section of Anal Fold of H. lupulinus

74b



POECILOCAMPA POPULI. THIRD & FOURTH AXILLARY SCLERITES. FORE WING.

Poecilocampa populi.

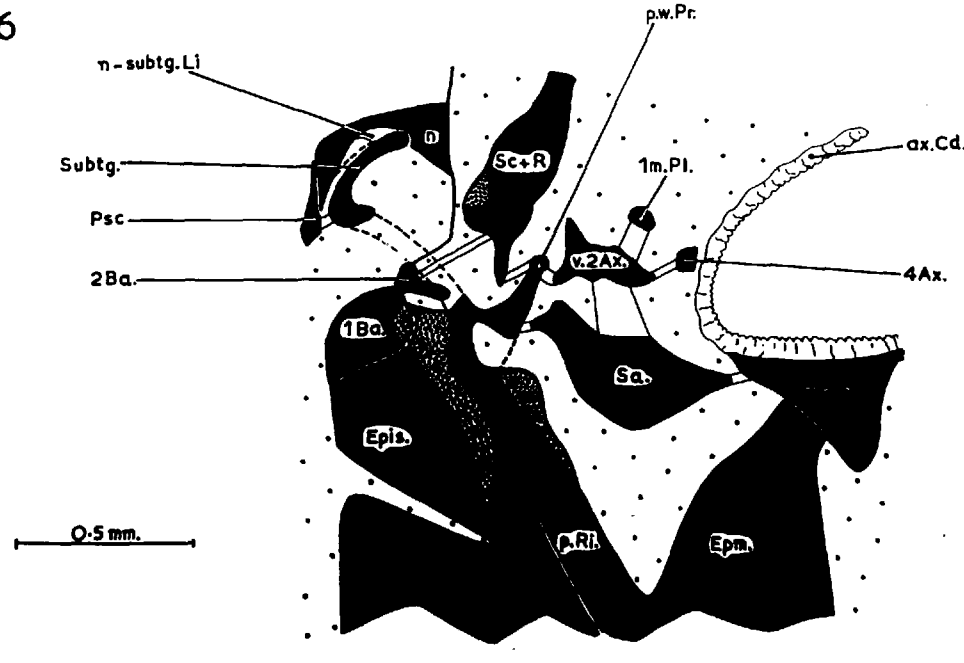


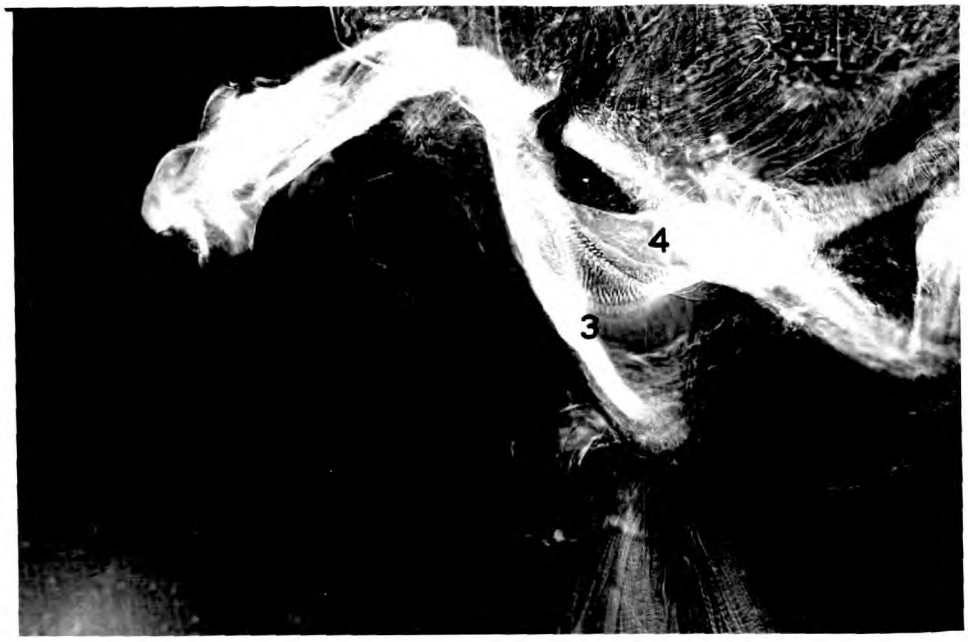
75a. Wing extended.

75b. Wing folded

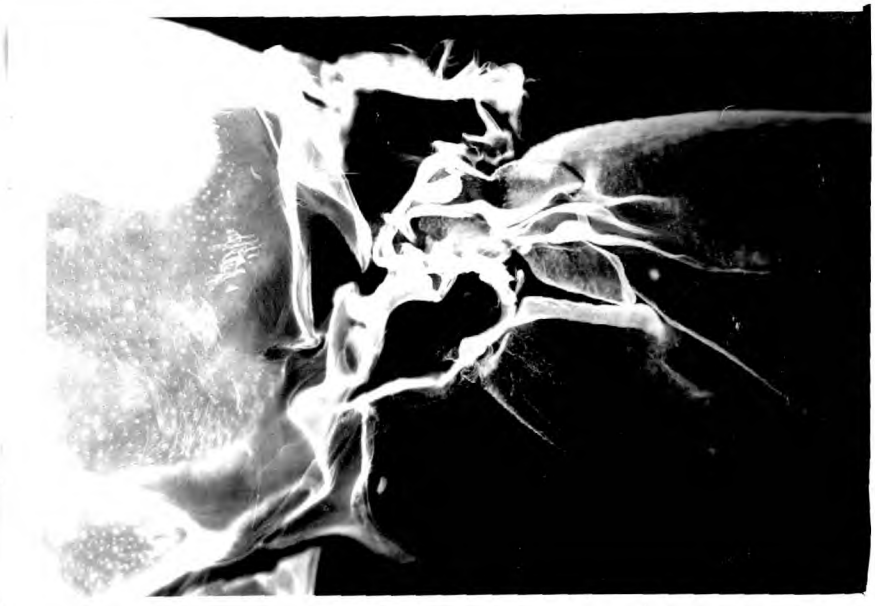
CRAMBUS HORTUELLUS. FORE WING BASE — VENTRAL VIEW & LATERAL PLEURON.

76





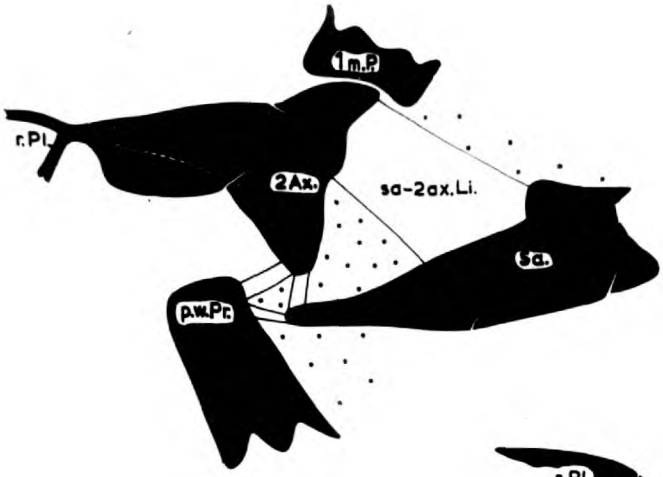
77. Third and fourth axillaries of Biston betularia fore wing. Negative photograph taken by polarized light. X 104.5



78. Colotois pennaria - Fore wing base, top lighting. X 78.

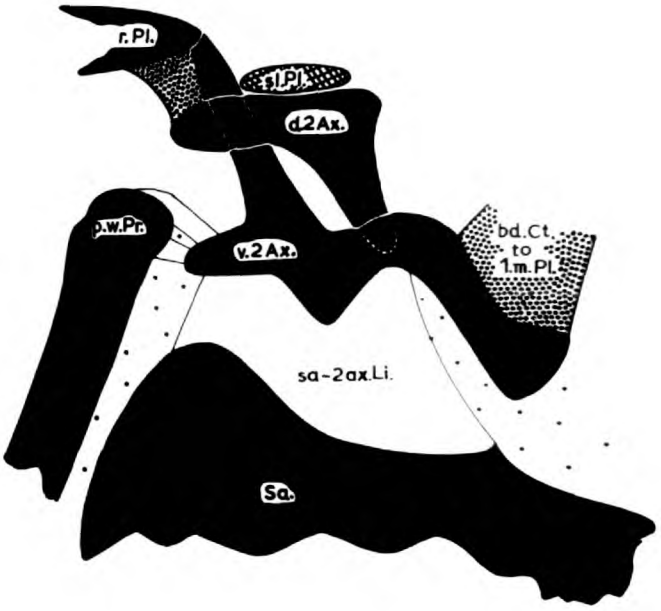
SECOND AXILLARY SCLERITE.

FORE WING.



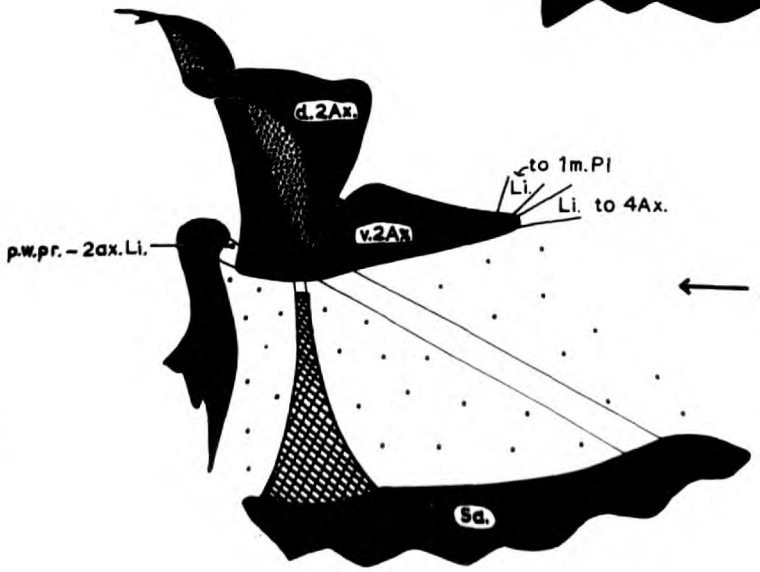
79

← Panorpa communis



80

Micropteryx calthella. →

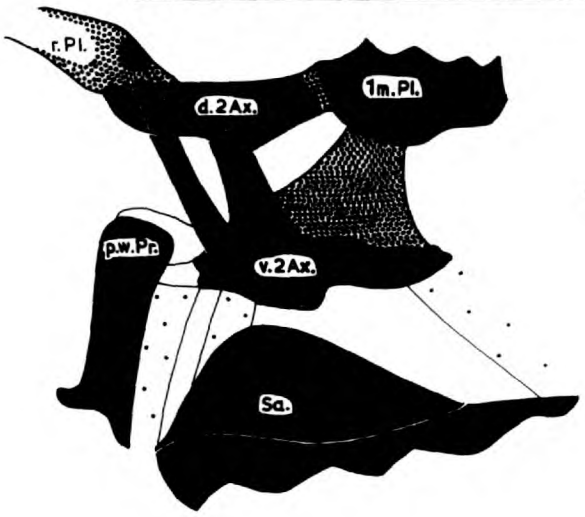


81

← Stigmella basalella.

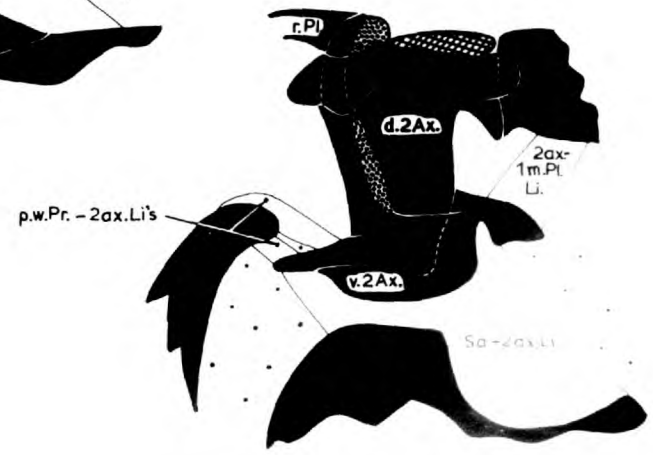
SECOND AXILLARY SCLERITE.

FORE WING.



82

← Hepialus lupulinus



83

Deilephila elpenor. →

84

Biston betularia.

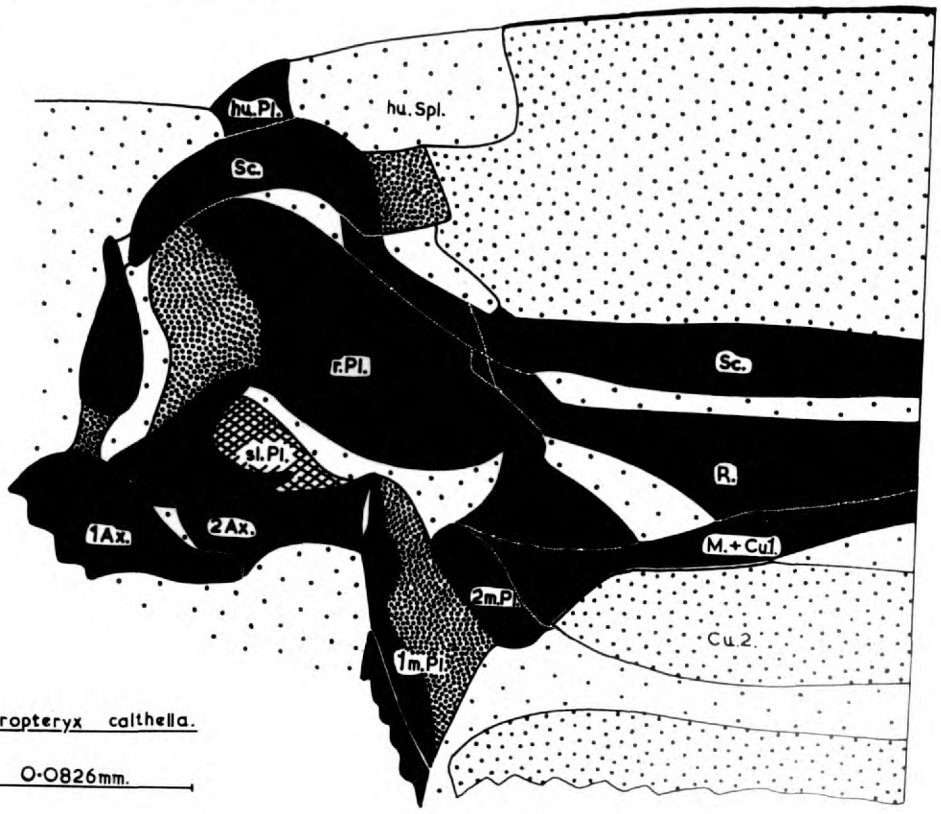
Photograph of Second Axillary, taken by polarized light.

Mag. X 100.



2nd. AXILLARY COMPLEX & MEDIAN PLATES.

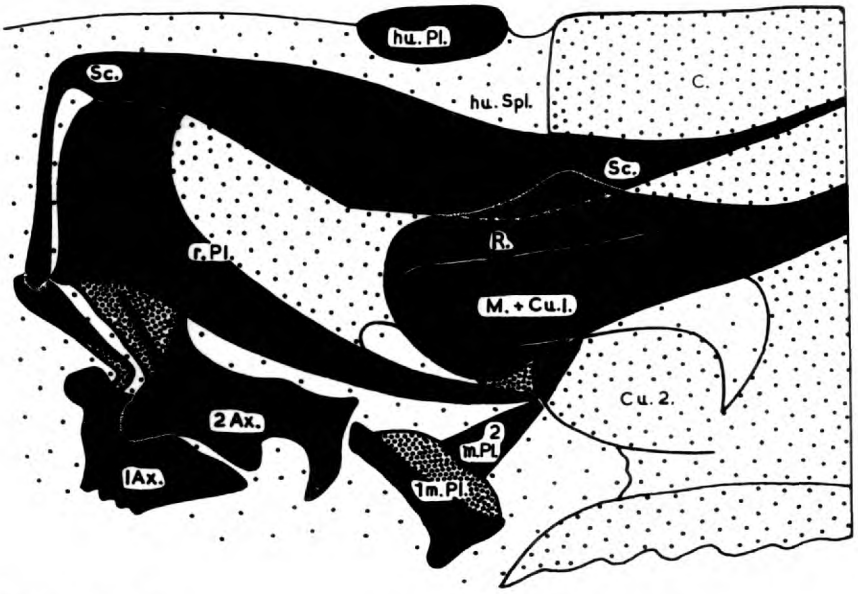
85 FORE WING.



Micropteryx calthella.

0·0826mm.

86



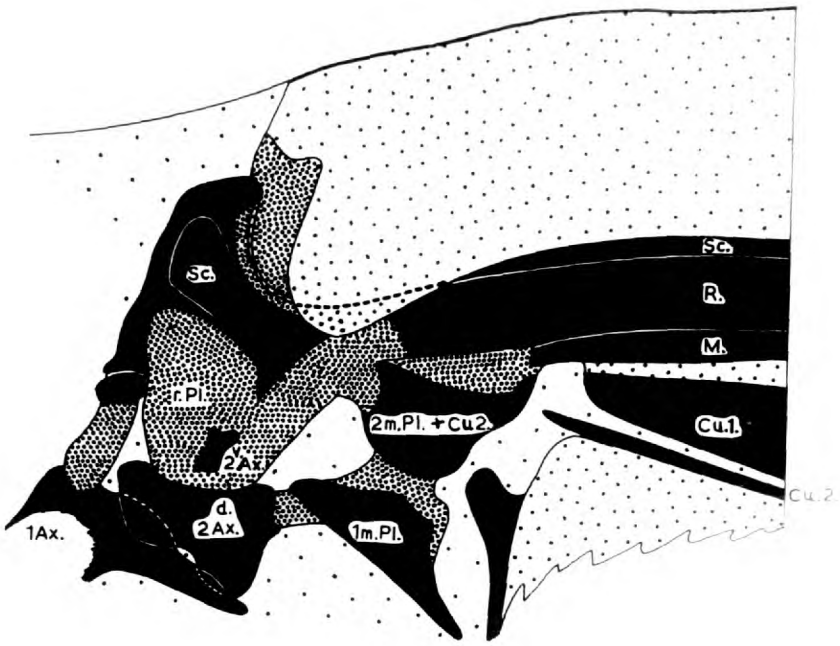
Stigmella basalella.

0·052mm.

2nd. AXILLARY COMPLEX & MEDIAN PLATES.

FORE WING

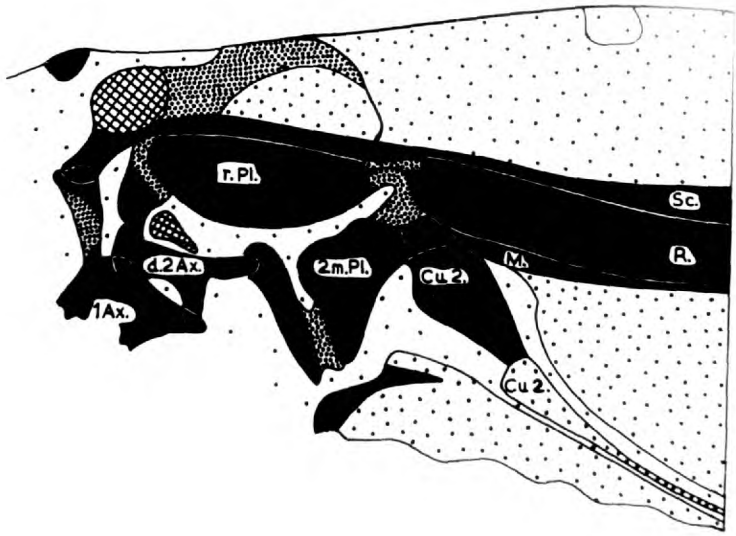
87



Hepialus lupulinus

0·5 mm

88



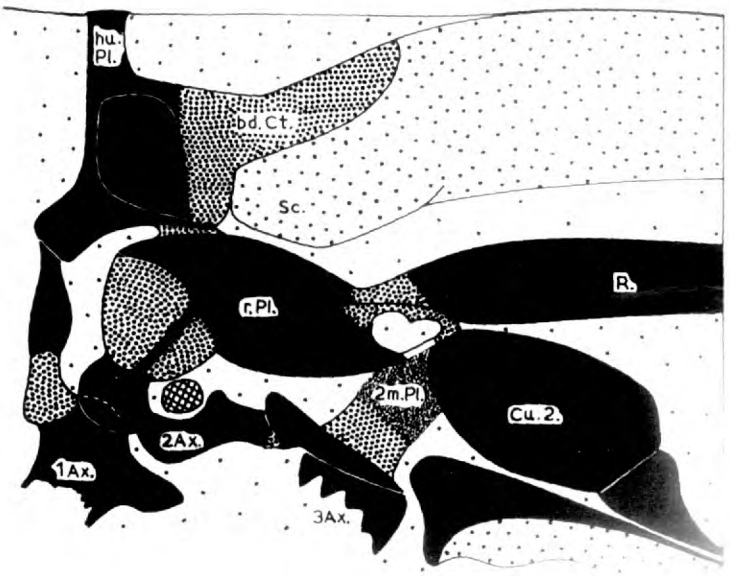
Adela reaumurella.

0·25 mm.

2nd. AXILLARY COMPLEX & MEDIAN PLATES.

FORE WING

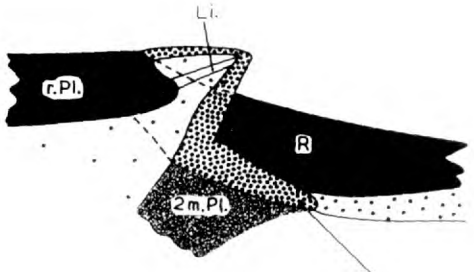
89



Zygaena filipendulae

0·5mm

90



Base of M. & Cu1. Detached. from veins further out in wing.

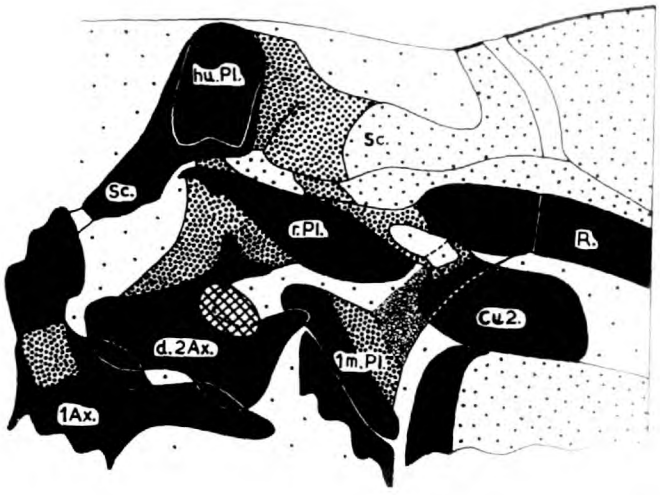
Zygaena filipendulae

Posterior Lateral Radius — at Junction with Second Median Plate.

2nd. AXILLARY COMPLEX & MEDIAN PLATES.

FORE WING.

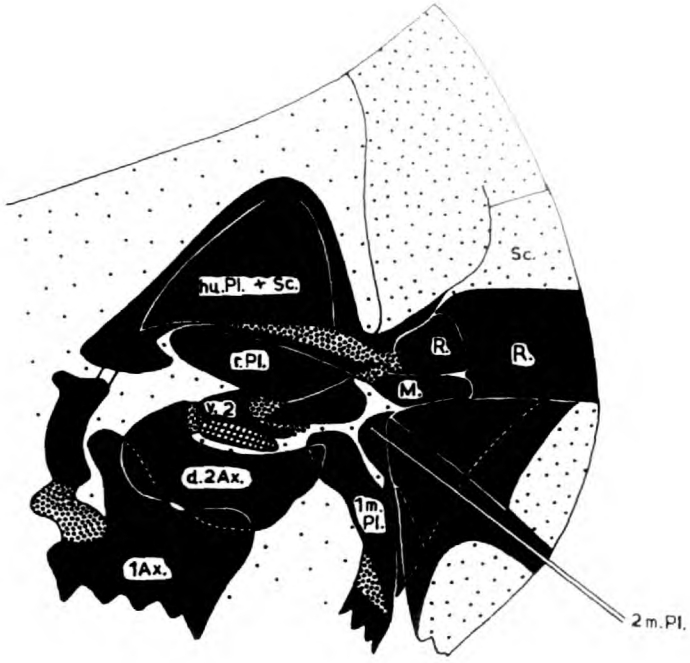
91



Plusia gamma.

0·5 mm.

92



Pieris brassicae

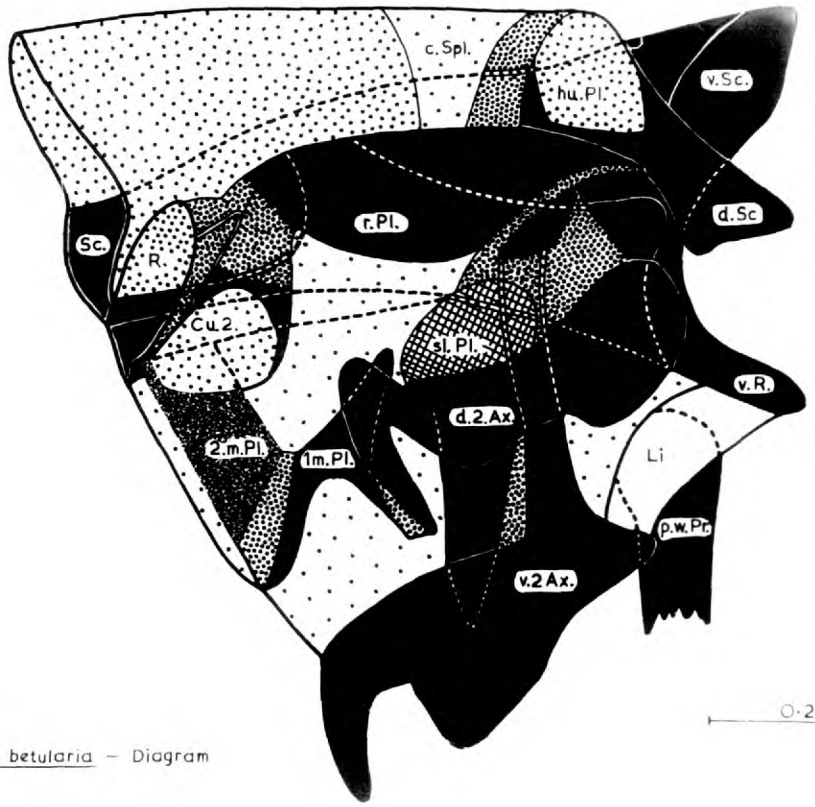
0·5 mm.

SECOND AXILLARY COMPLEX of FORE WING.



93

Biston betularia – Drawing



94

Biston betularia – Diagram



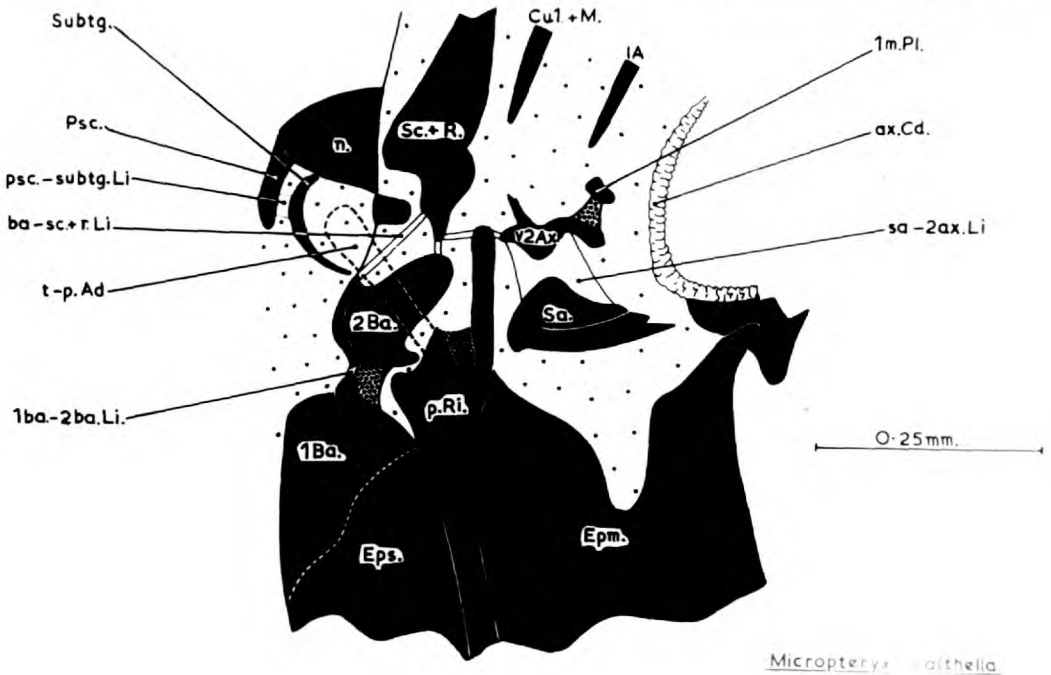
95. Operophtera brumata - Bending cuticle junction of radius and cubitus with the radial plate. Dorsal view, X 430.



96. Triphaena pronuba - Bending cuticle junction of radius and cubitus with the radial plate. Antero-dorsal view, X 104.

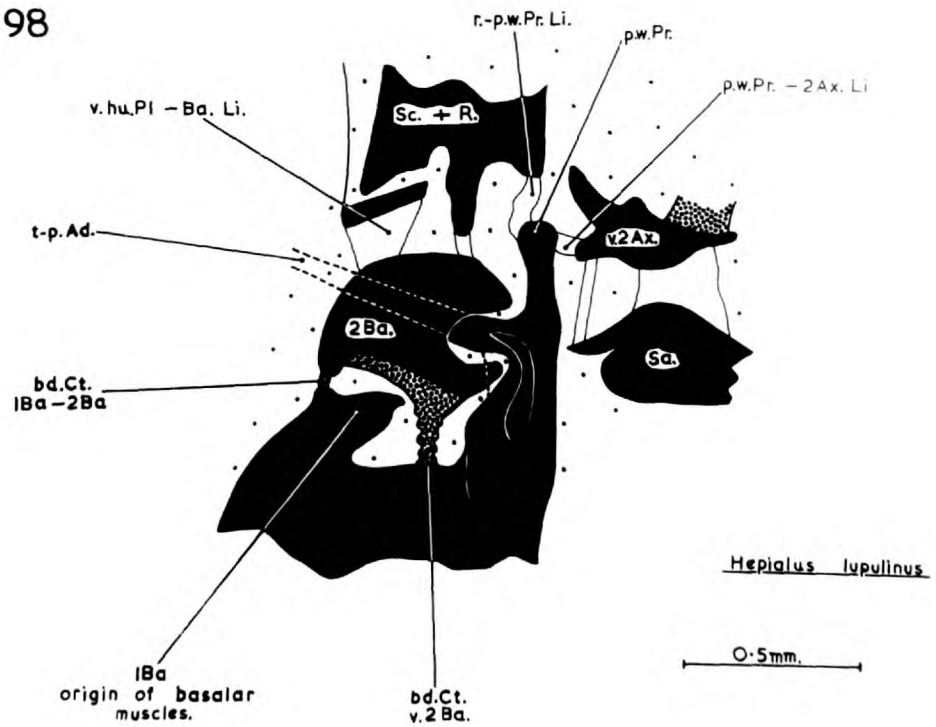
LATERAL PLEURON & VENTRAL FORE WING BASE.

97



Micropteryx calthella

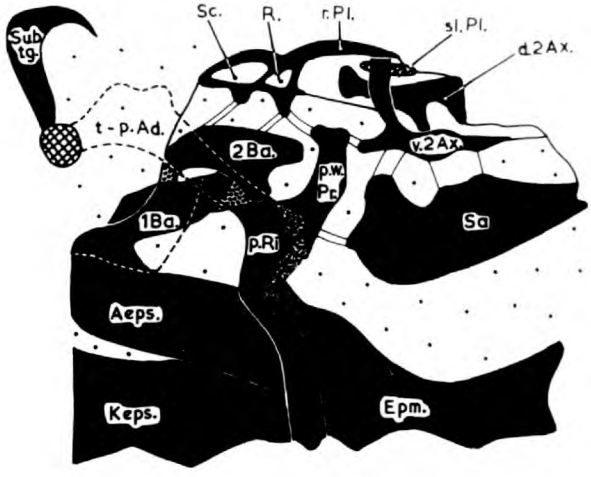
98



Hepialus lupulinus

VENTRAL FORE WING BASE.

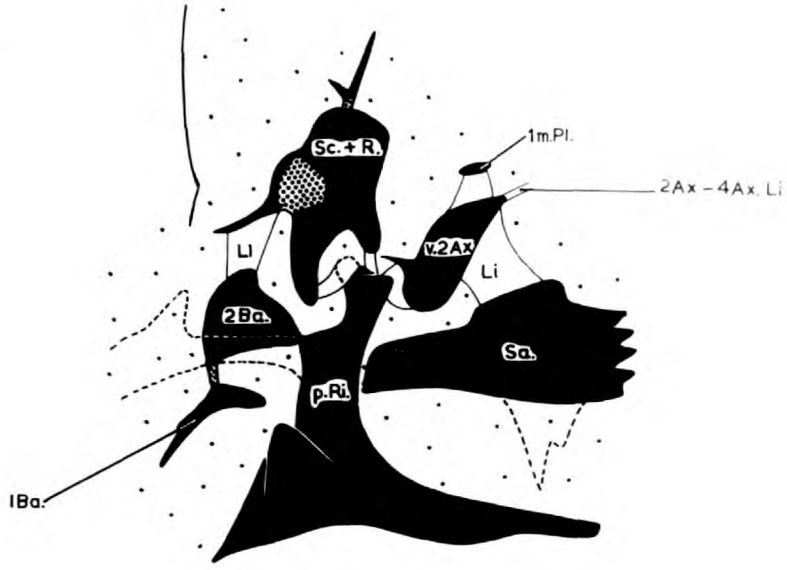
99



2 mm.

Zeuzera pyrina - drawn from the outside, with the wing cut off in the horizontal position.

100

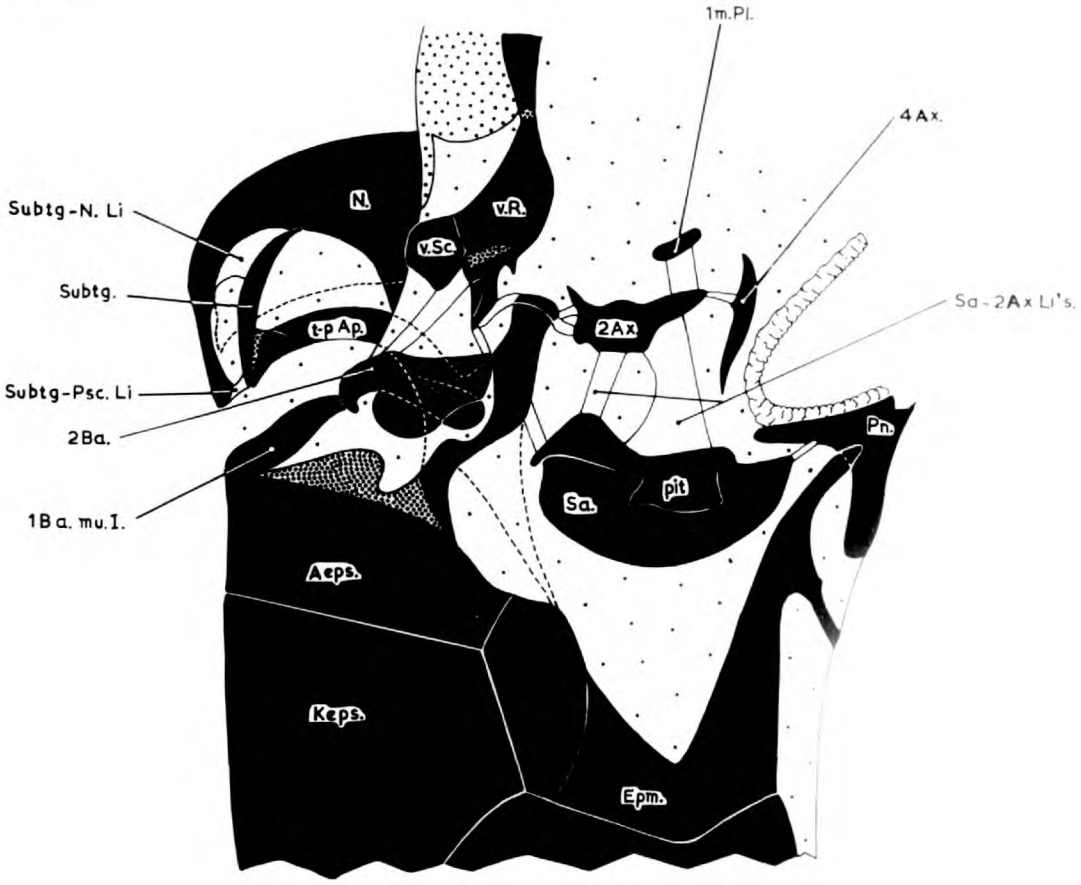


Pieris brassicae

1mm.

VENTRAL FORE WING BASE

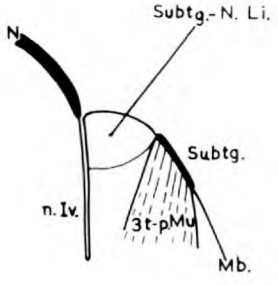
101



Triphaena pronuba.

0·7mm.

102



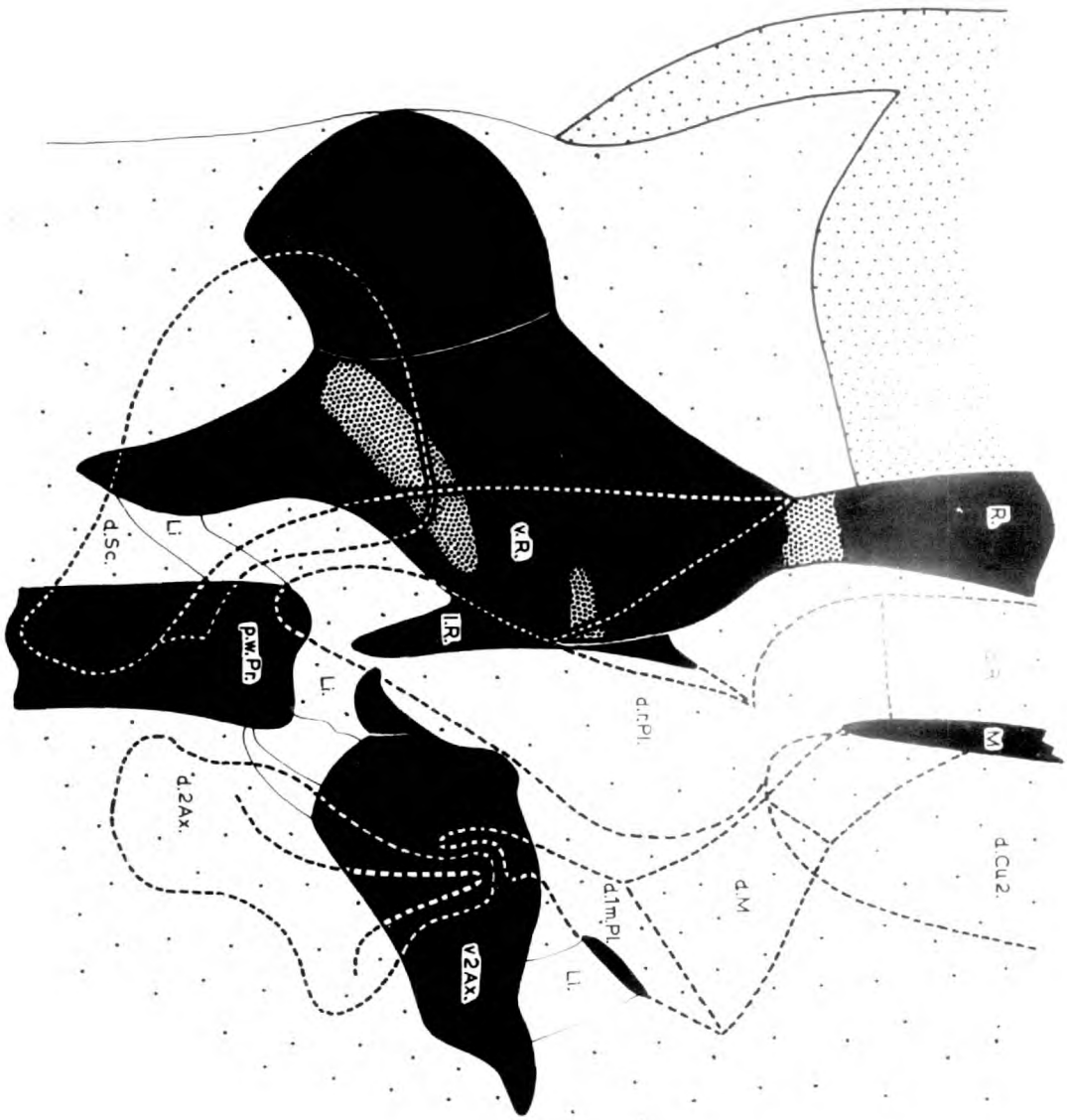
Diagrammatic vertical section of Subtg.-N. Li

VENTRAL RADIUS & SECOND AXILLARY

103

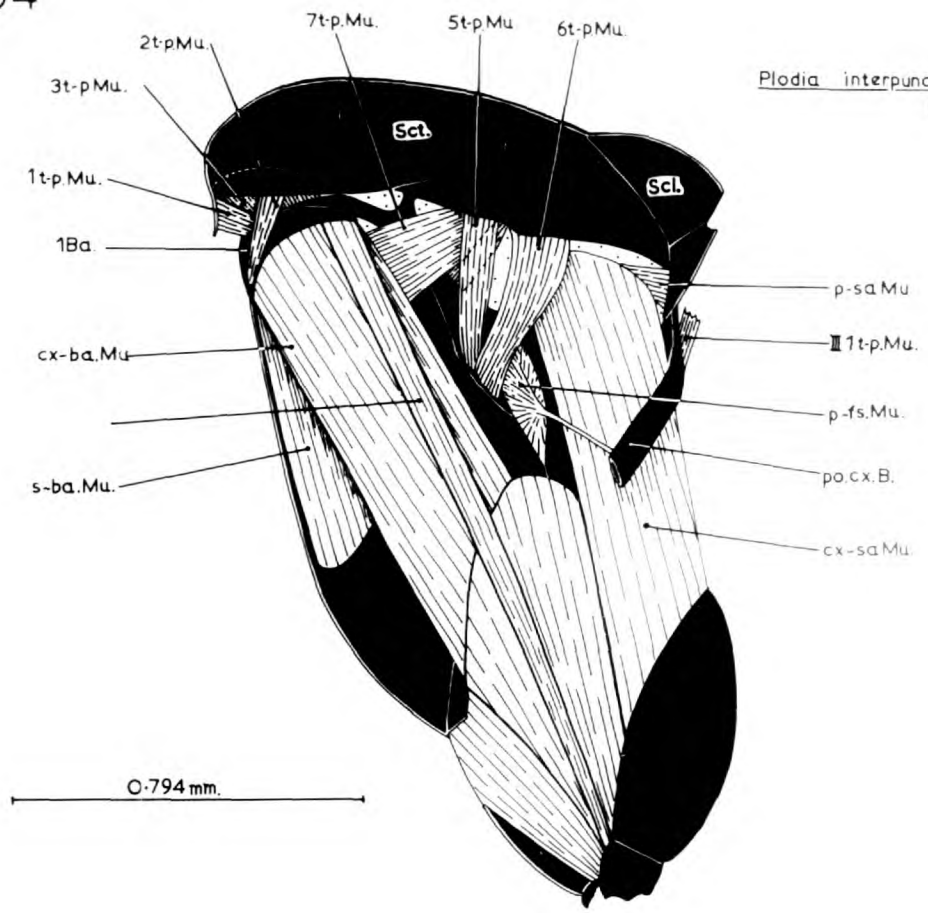
TRIPHAENA PRONUBA - FORE WING.

0·36mm.

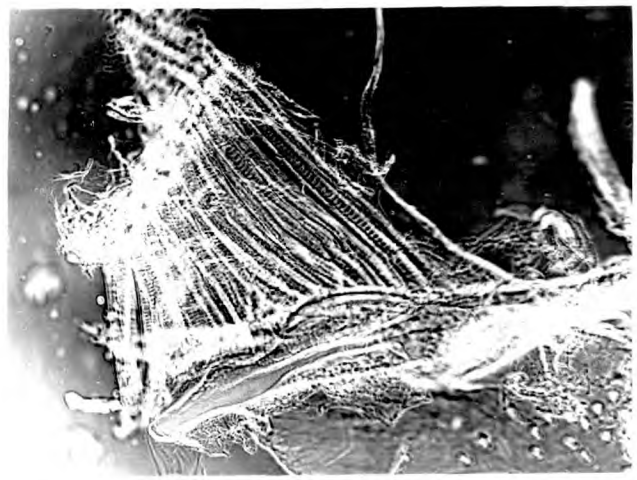


TERGOPLEURAL MUSCLES.

104



Plodia interpunctella.
Mesothorax.



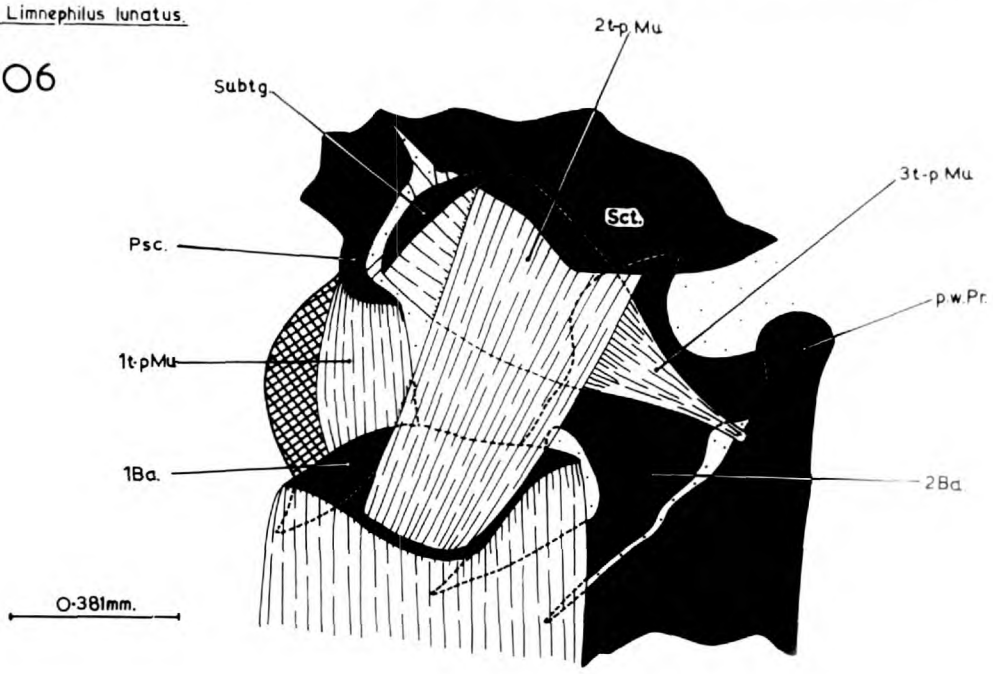
105

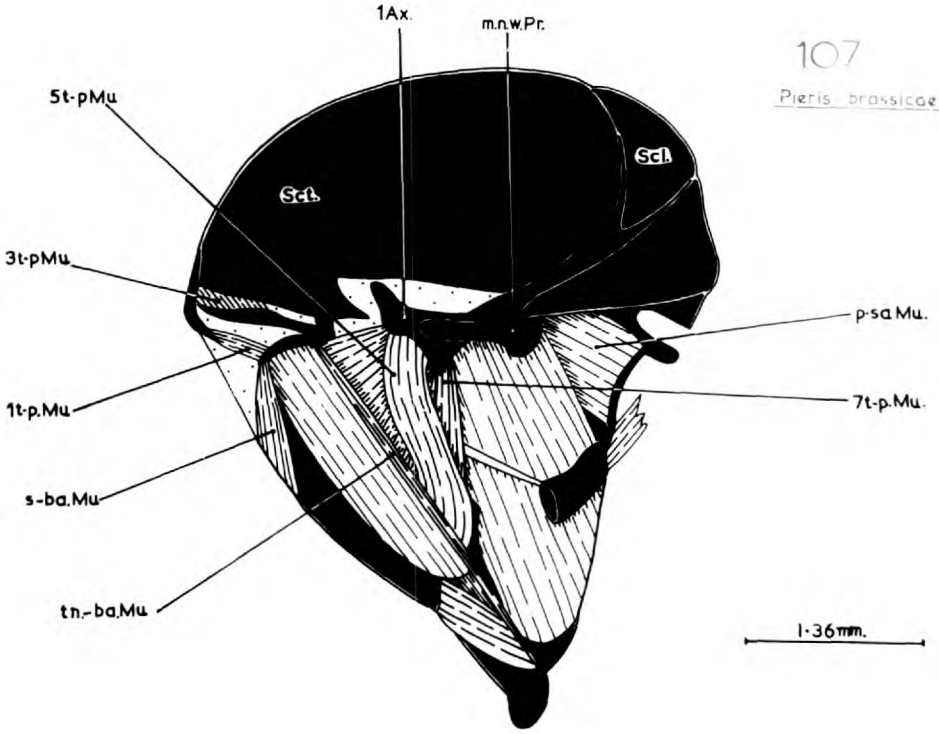
Plodia interpunctella. II 6t-p. Mu. on Median Notal Wing Process. X130.

TERGOPLEURAL MUSCLES - FORE WING.

Limnephilus lunatus.

106



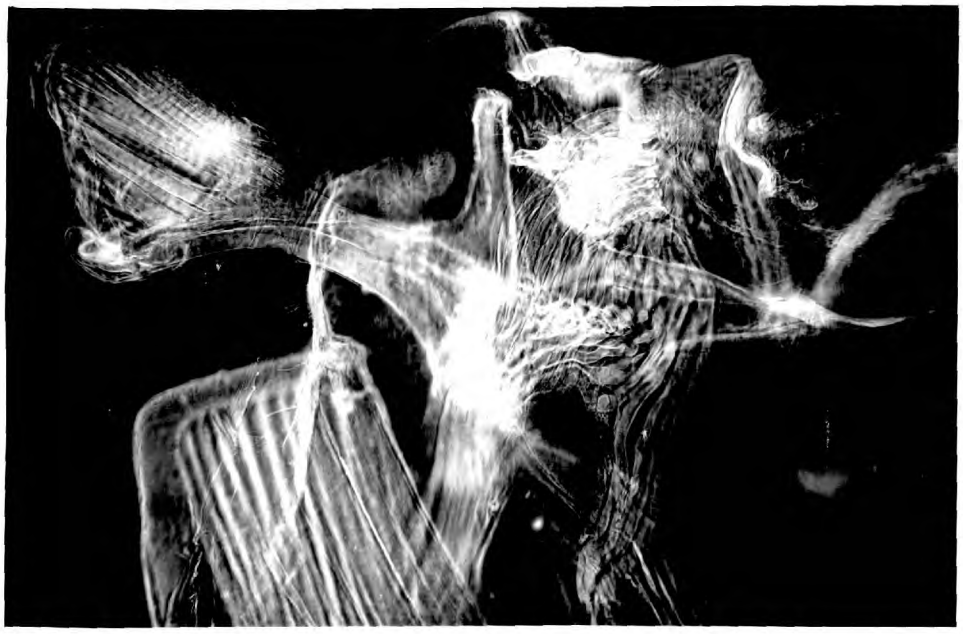


107

Pieris brassicae

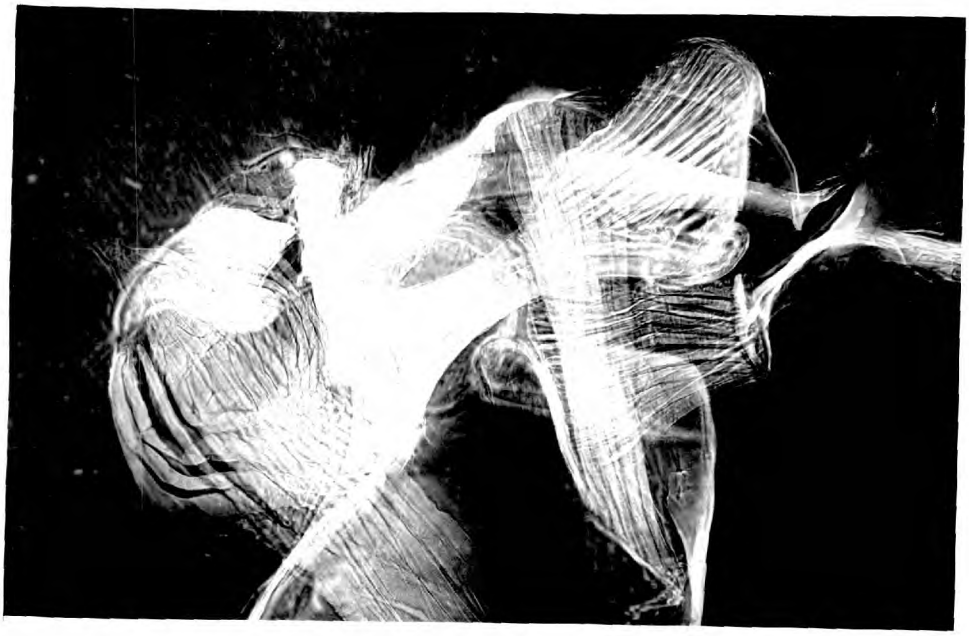


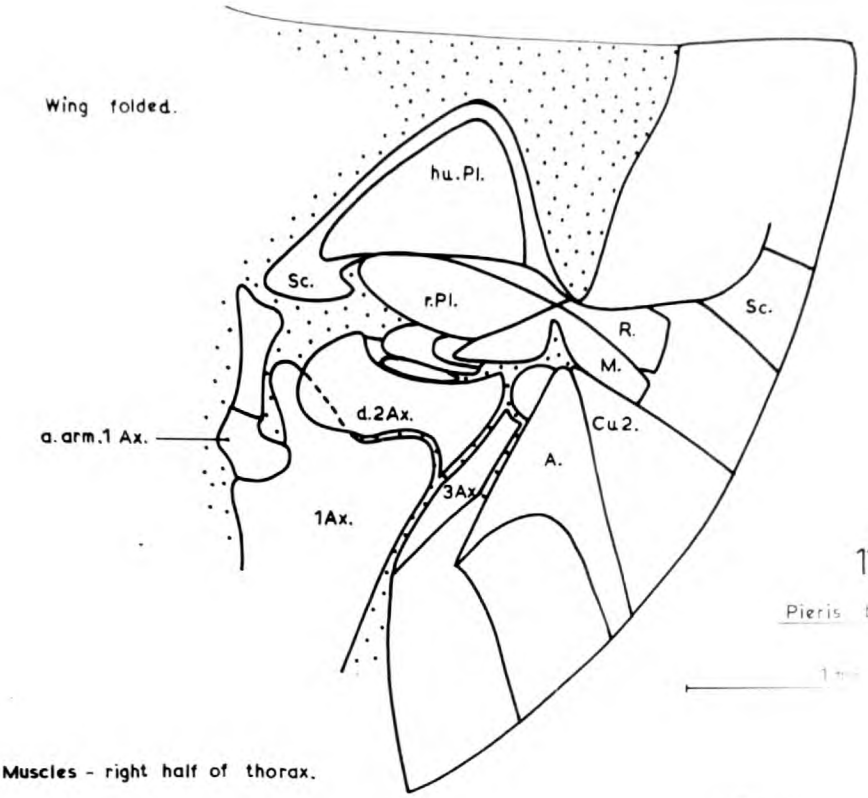
108. Anterior, mesothoracic, tergopleural muscles of Hepialus lupulinus. X 108.



109. Mesothoracic tergopleural muscles of Tortrix viridana

×120



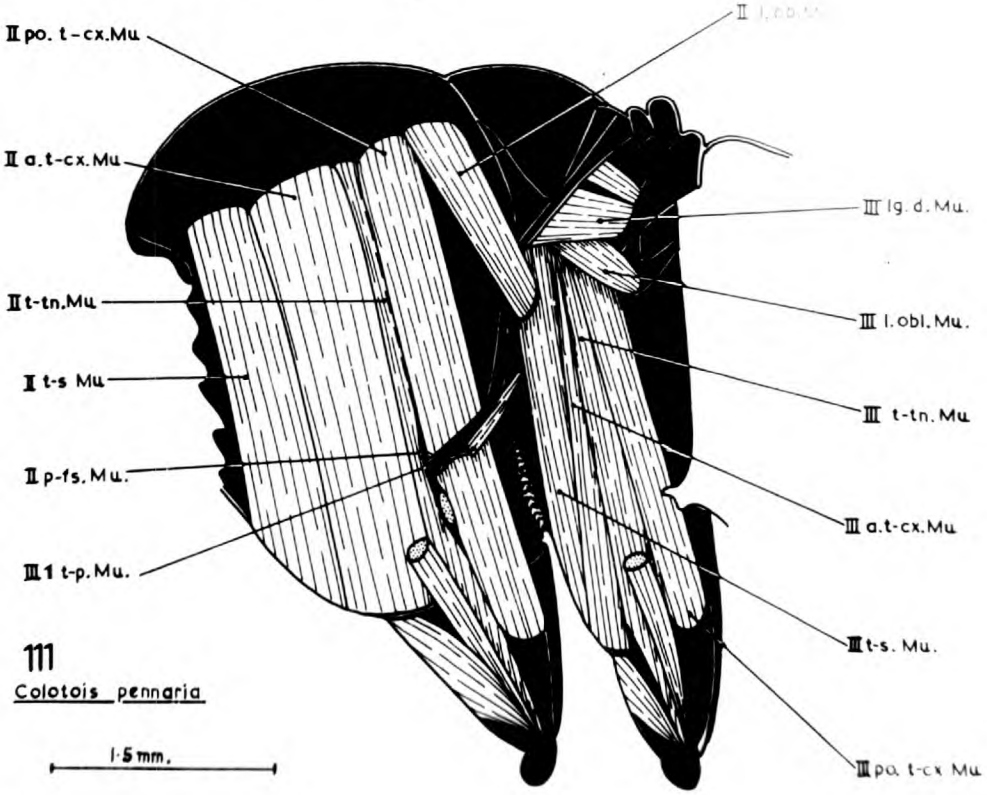


110

Pieris brassicae

1 mm

Muscles - right half of thorax.

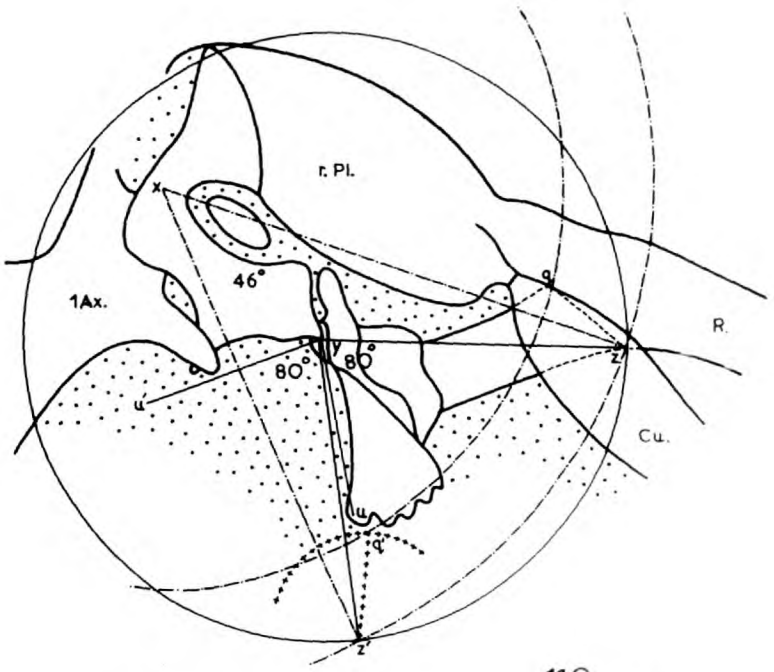


111

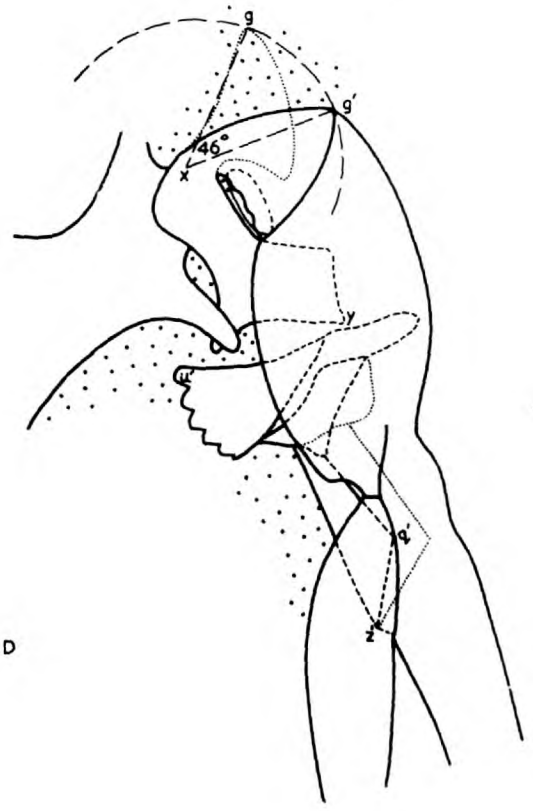
Colotois pennaria

1·5 mm.

TORTRIX VIRIDANA – FORE WING.



112 OPEN



0·187 mm.

113 FOLDED

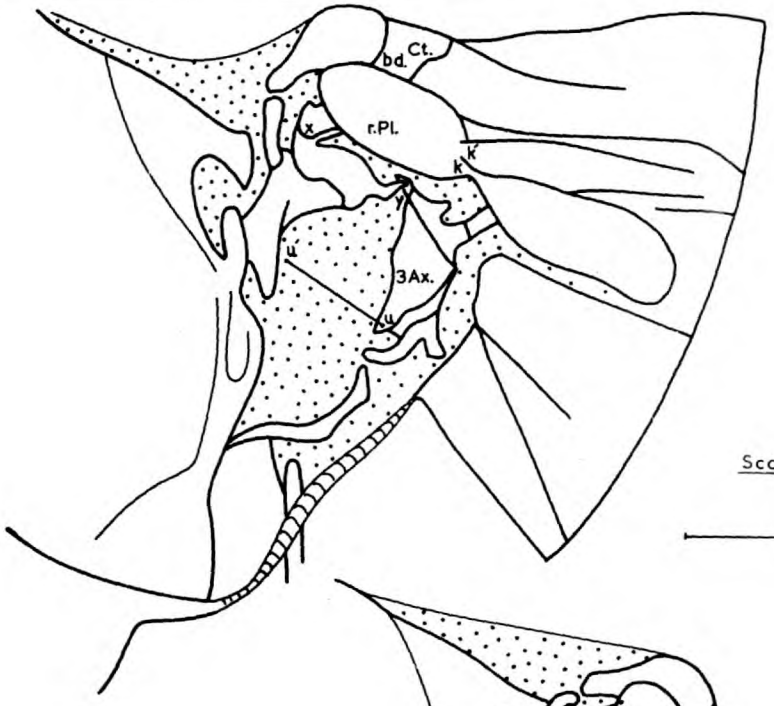
FORE WING FOLDING & MEDIAN PLATES



114 Tortrix viridana

Median Plates.

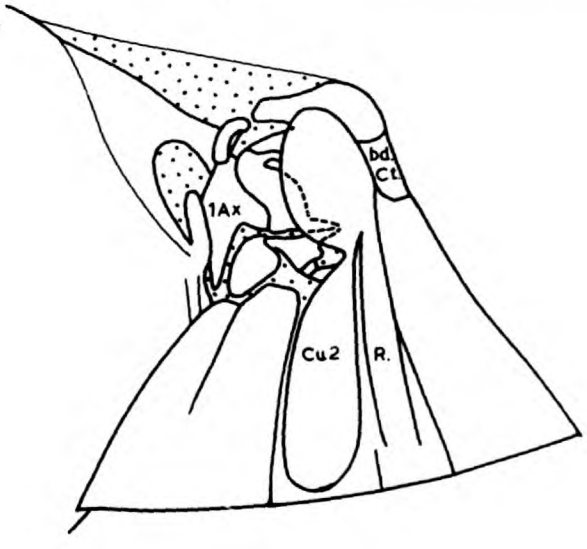
Mag. X 250·7



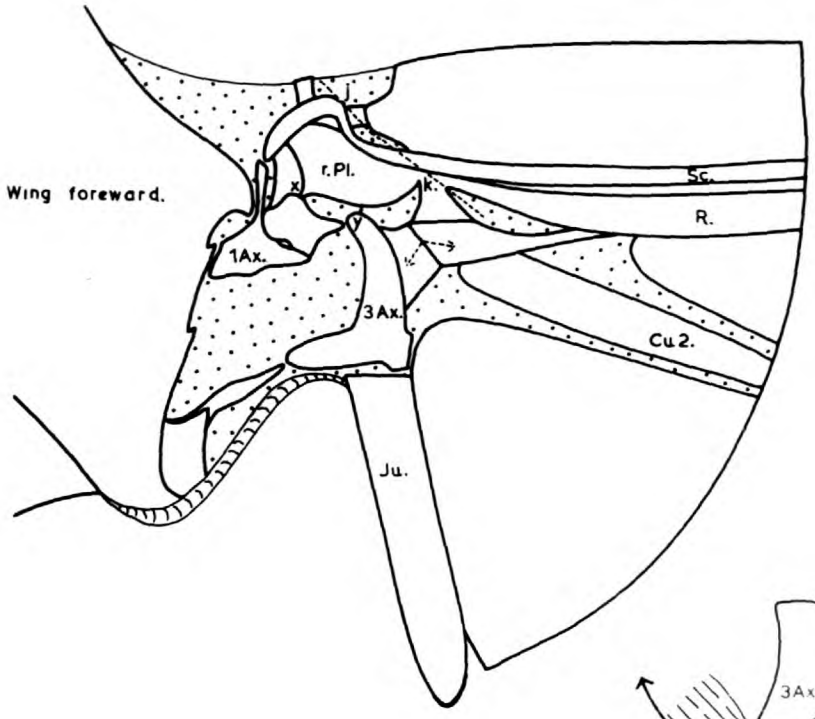
115

Scoparia ambigualis

0·47 mm.



FORE WING FOLDING



116

Micropteryx calthella.

0·125 mm.

118

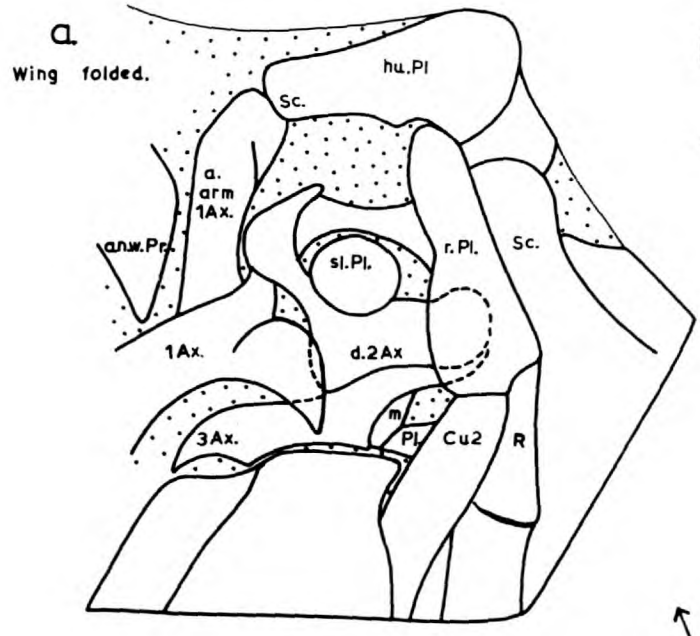
Tholera popularis

"wide"



a.

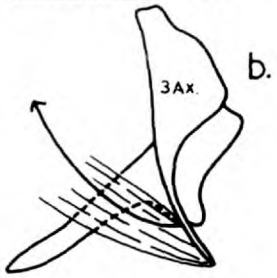
Wing folded.



0·54mm.

117

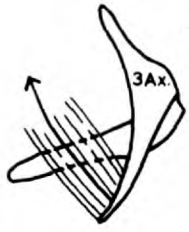
Agrotis ypsilon – "linear"



119

Phalera bucephala.

"lateral"





120



121

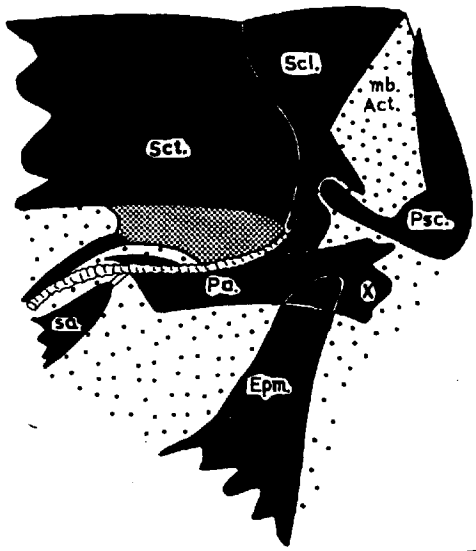
Triphaena pronuba - Before stimulation and during stimulation of the left mesothoracic basalar muscles.



122. Microelectrodes. X 114.

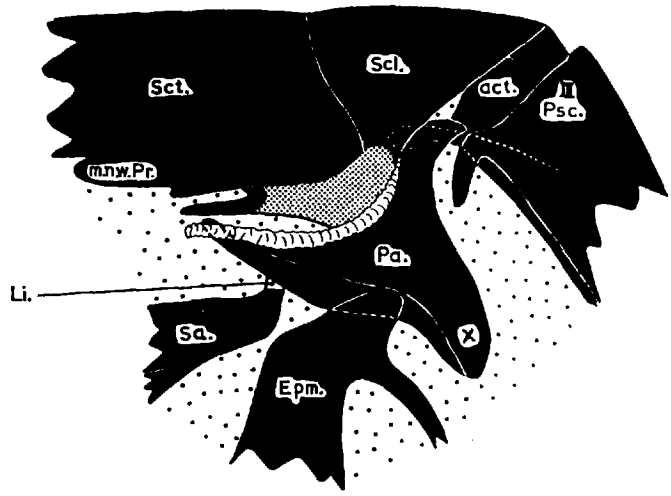
POSTALAR APODEME

(viewed from outside)



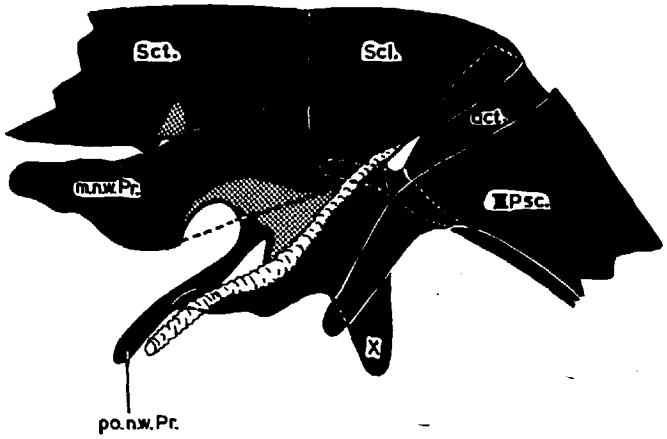
123

Micropteryx calthella.



124

Zygaena filipendulae



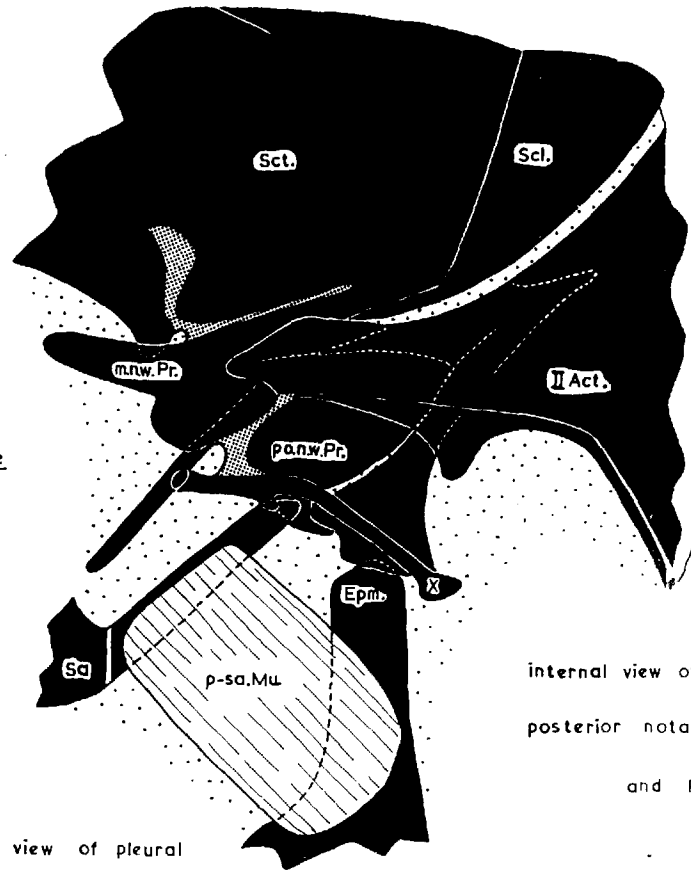
125

Triphaena pronuba

X = Postalar apodeme.

126

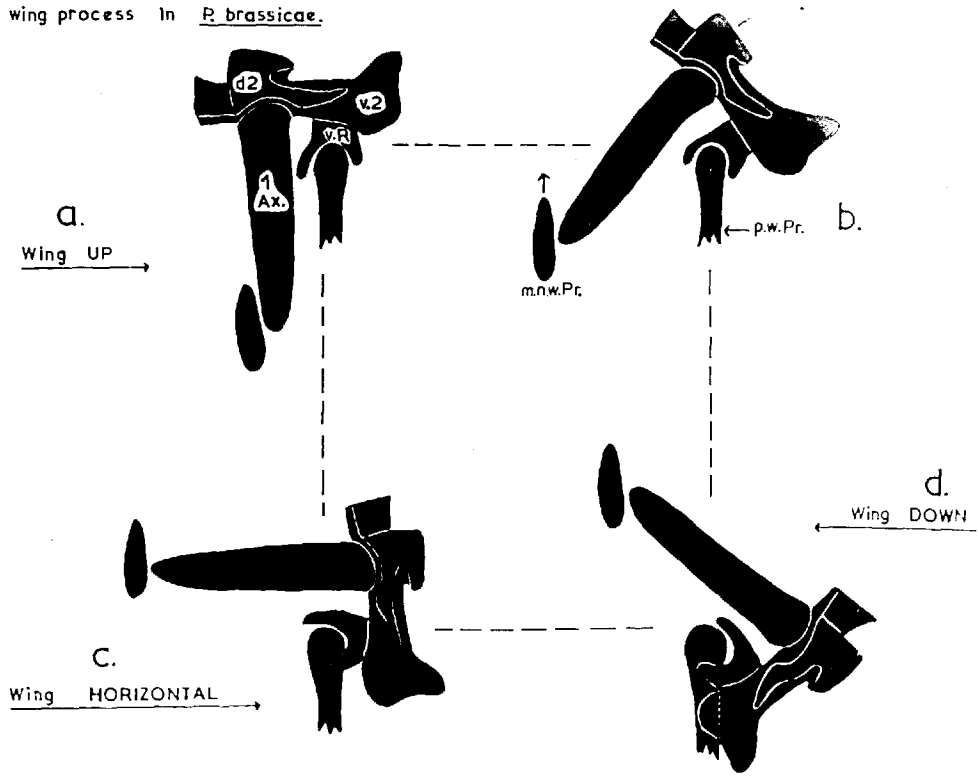
Pieris brassicae



internal view of median and posterior notal wing processes and Postalare.

127

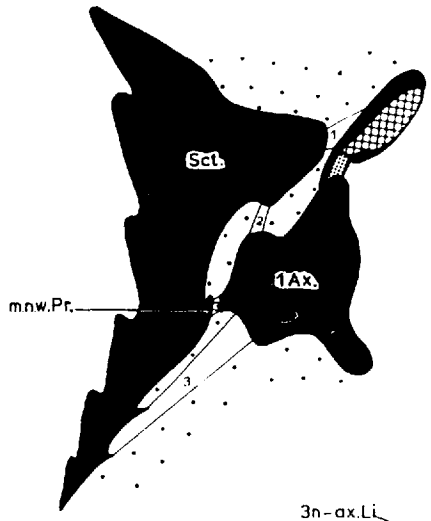
Postero-lateral view of pleural wing process in P. brassicae.



FIRST AXILLARY SCLERITE - HIND WING

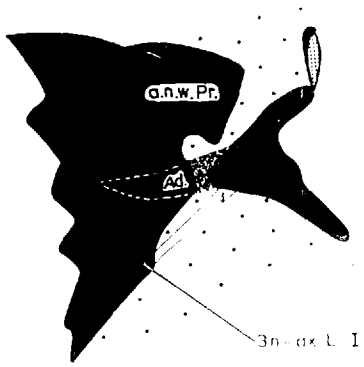
128

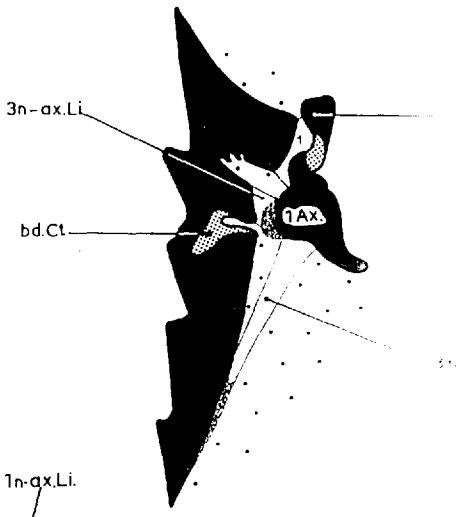
Micropteryx calthella



129

Stigmella basalella

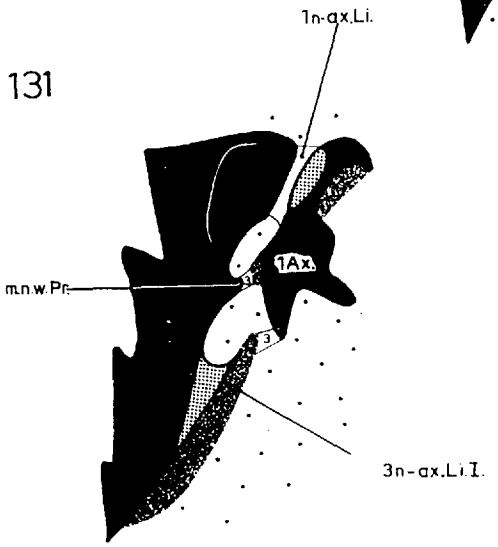




130

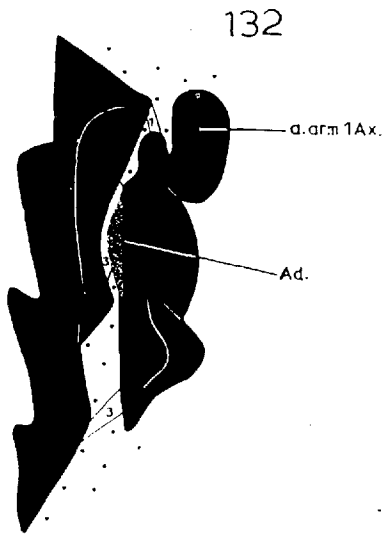
Hepialus lupulinus

131



Spilosoma lubricipeda

132



Pieris brassicae

HIND WING BASE

133

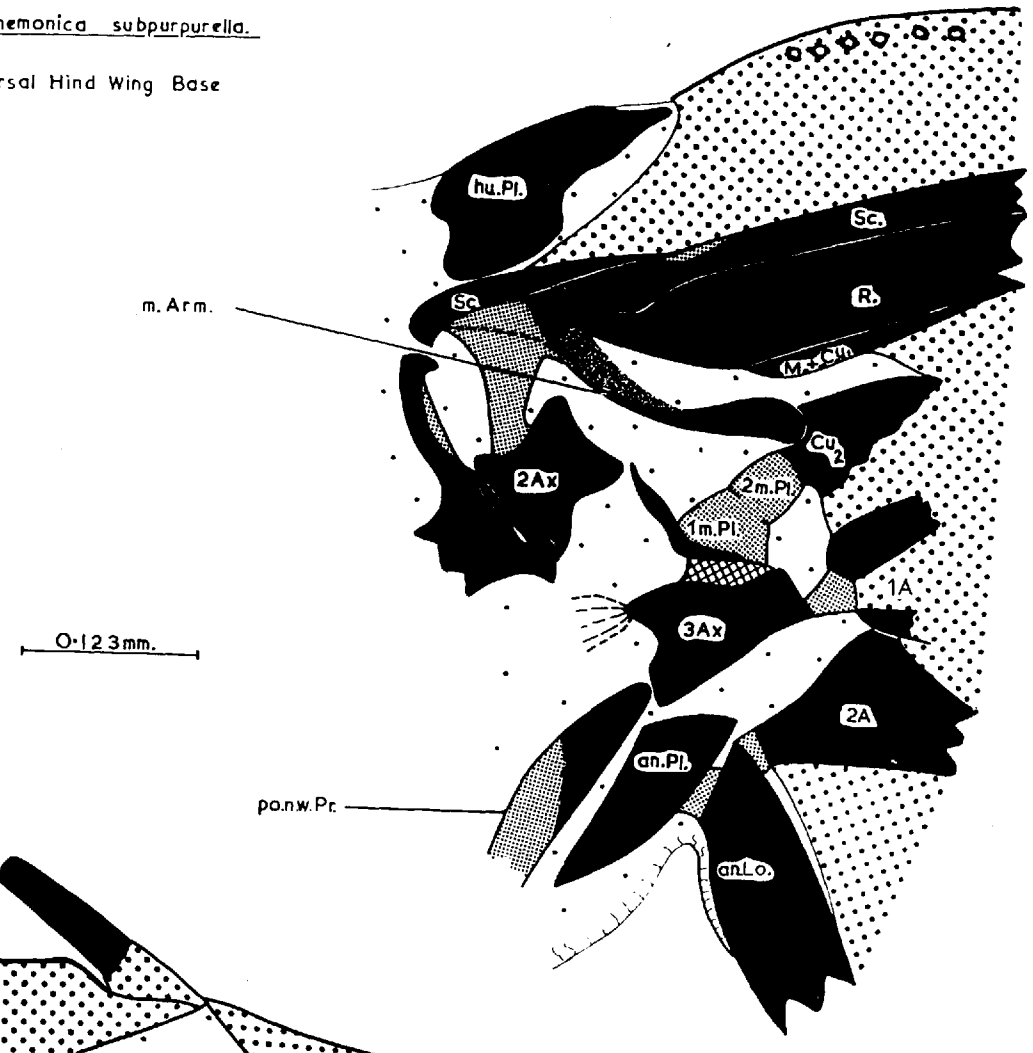
Micropteryx calthella



134

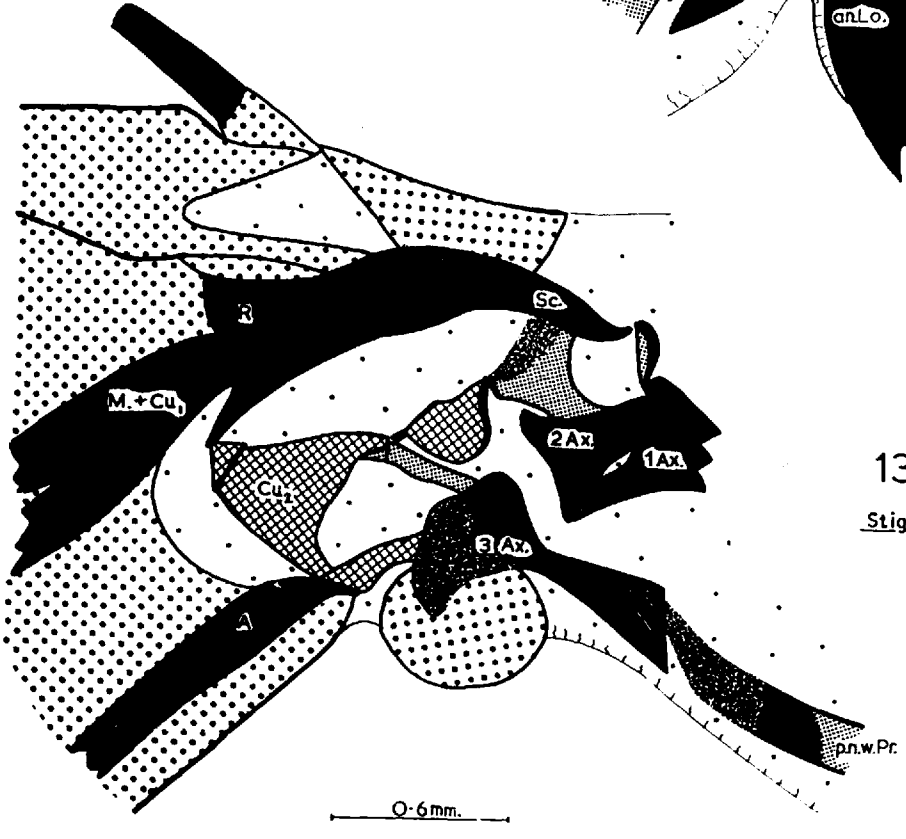
Mnemonica subpurpurella.

Dorsal Hind Wing Base



135

Stigmella basalella

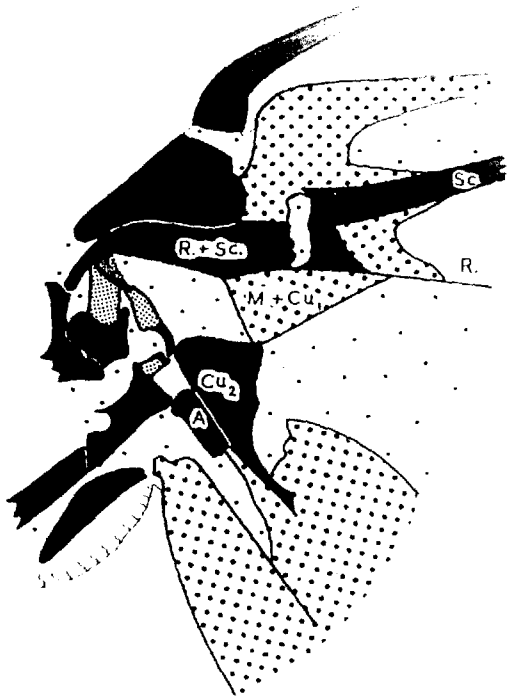


DORSAL HIND WING BASES



136 Hepialus lupulinus

0·56 mm.



137

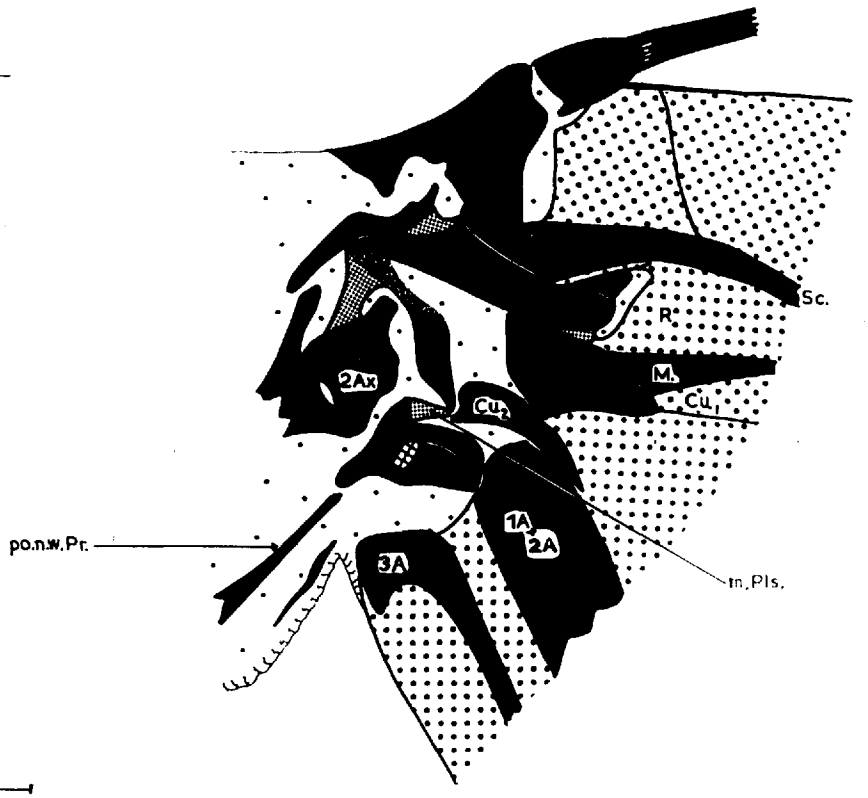
Adela reaumurella.

0·56mm

DORSAL HIND WING BASES

138

Tortrix viridana



0·28mm.



139

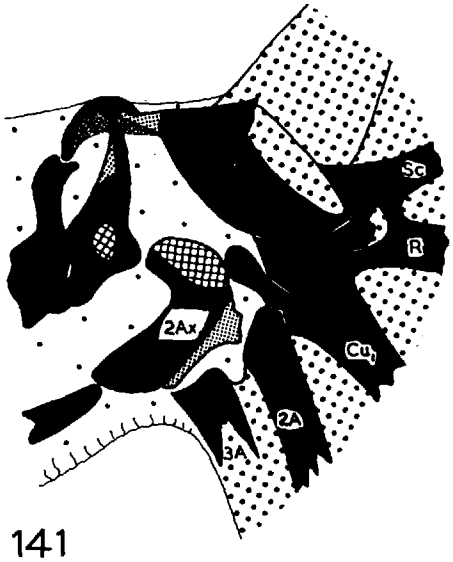
Drepana binaria

140

Spilosoma lubricipeda

0·56 mm.

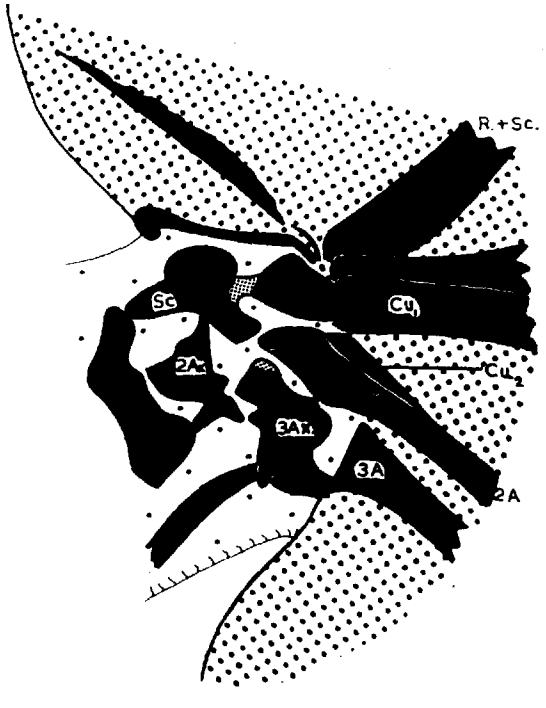




141

Operophtera brumata.

0·34 mm.



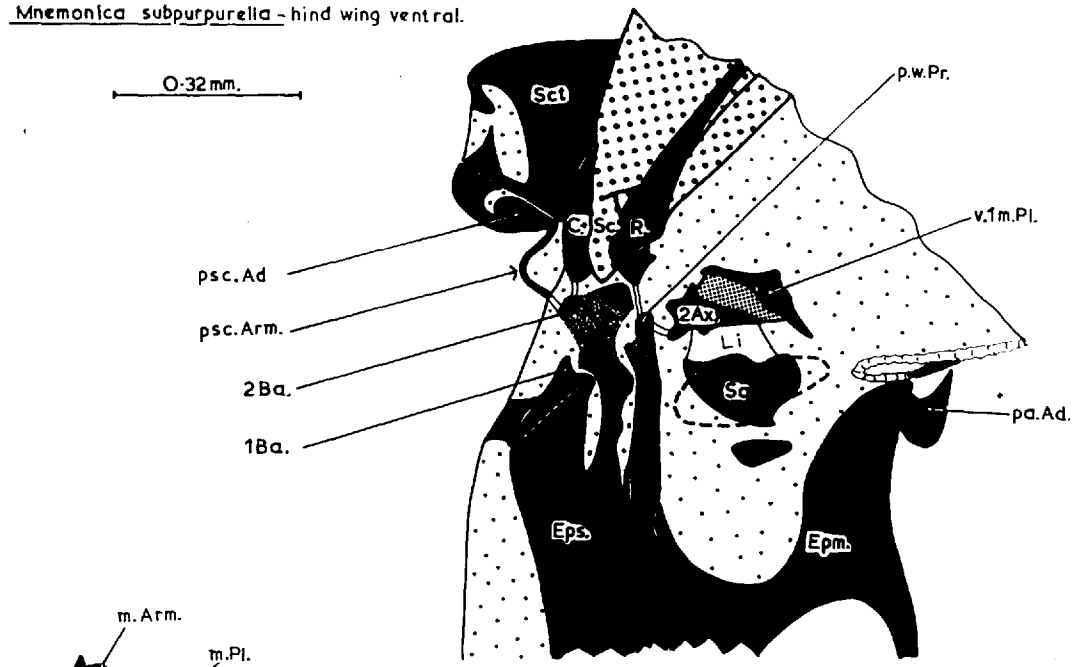
142

Polyommatus icarus.

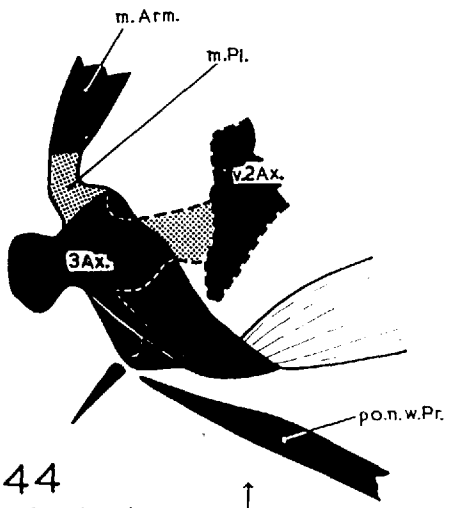
0·34 mm.

143

Mnemonica subpurpurella - hind wing ventral.

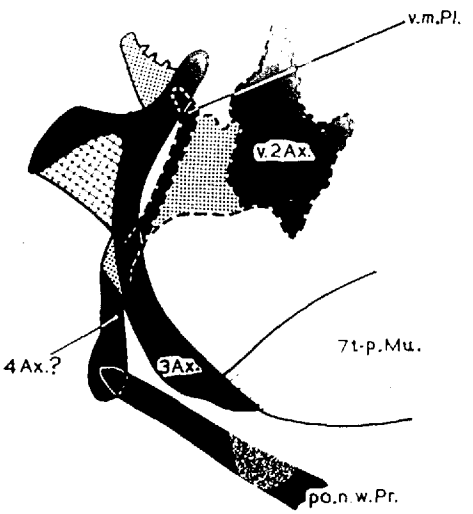


Postero-dorsal 3Ax. III

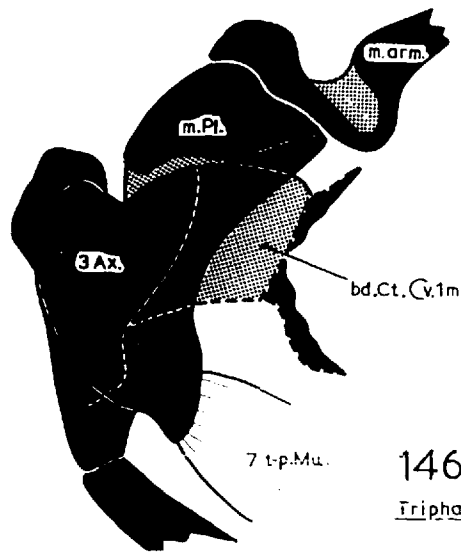


144

Crambus hortuellus ↑



145 Zeuzera pyrina ↑



146

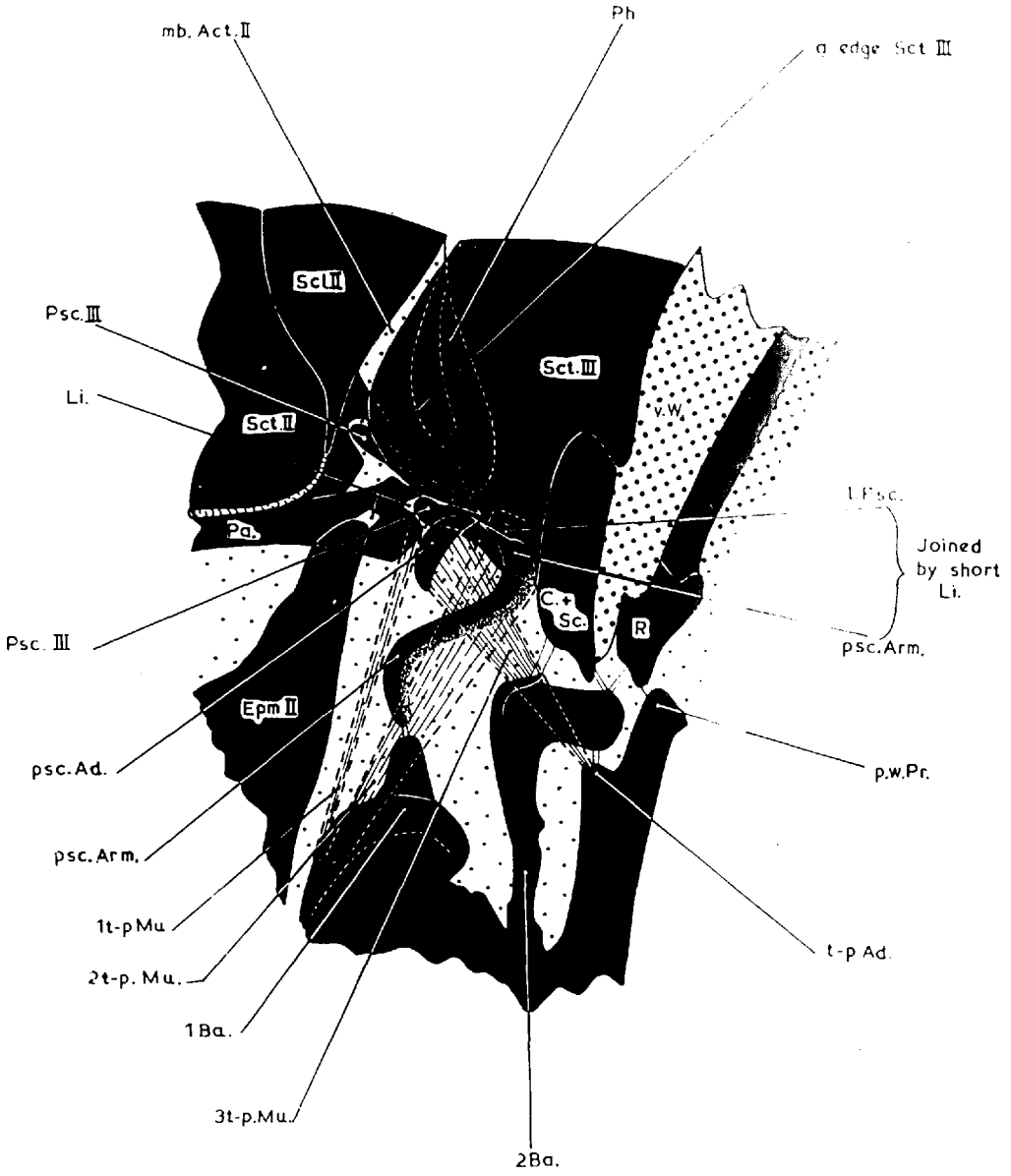
Triphaena pronuba

BASALAR REGION & TERGOPLEURAL MU'S.

147

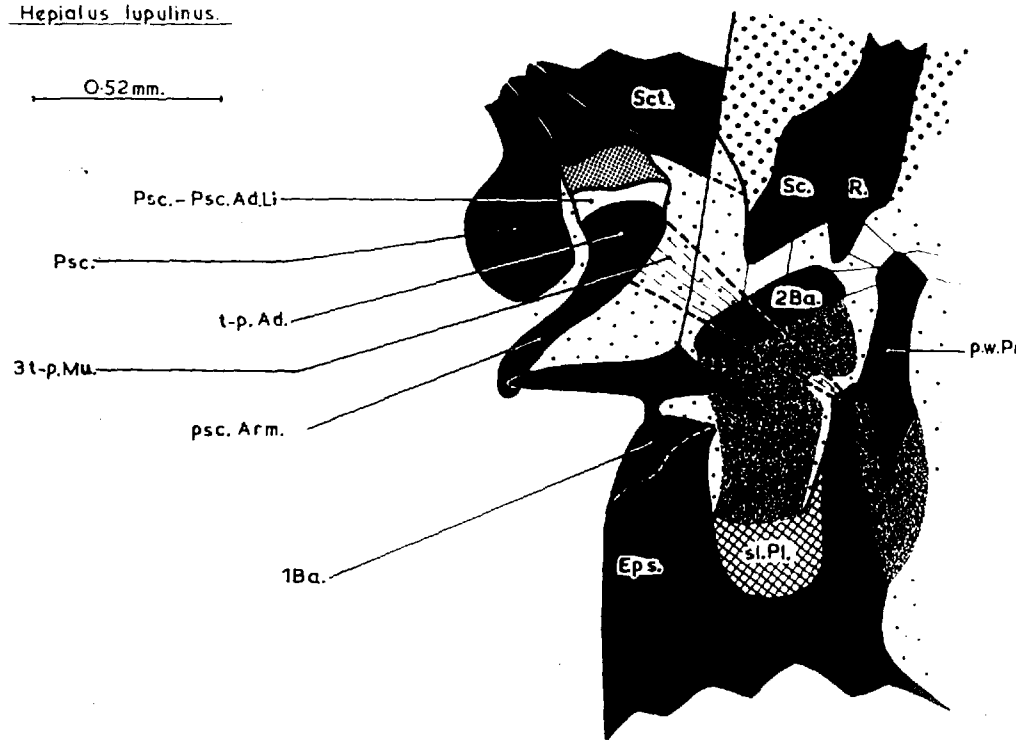
Micropteryx calthella.

0·08mm



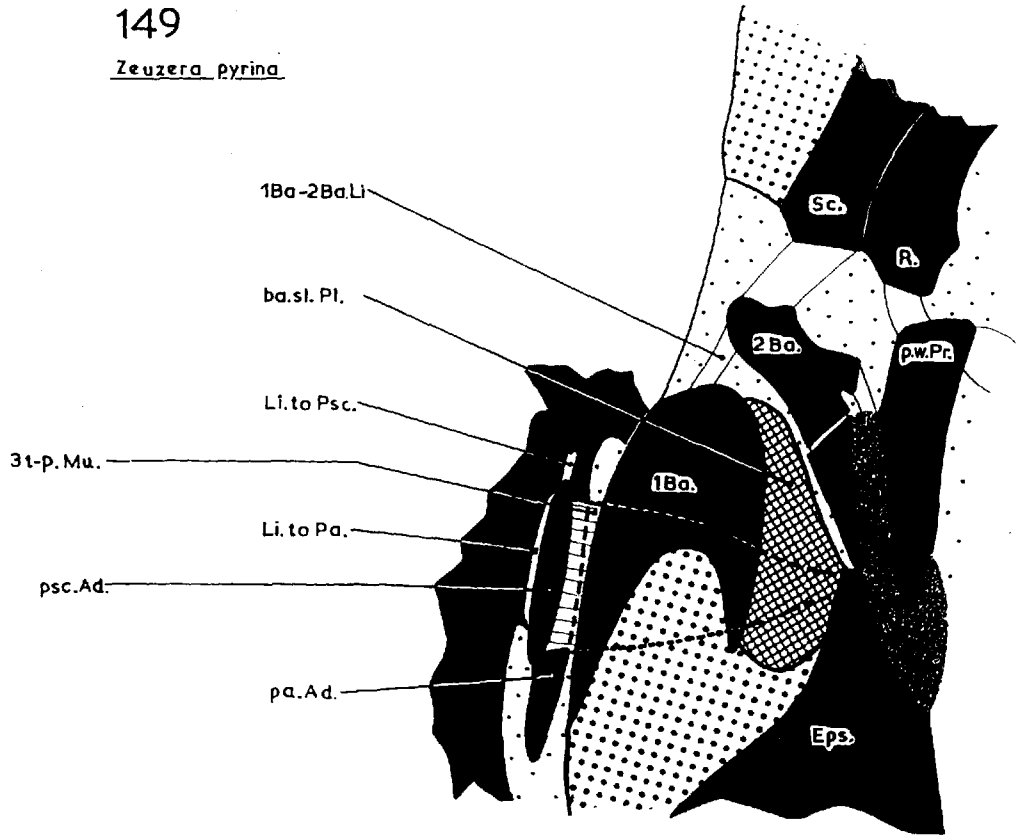
148

Hepialus lupulinus.

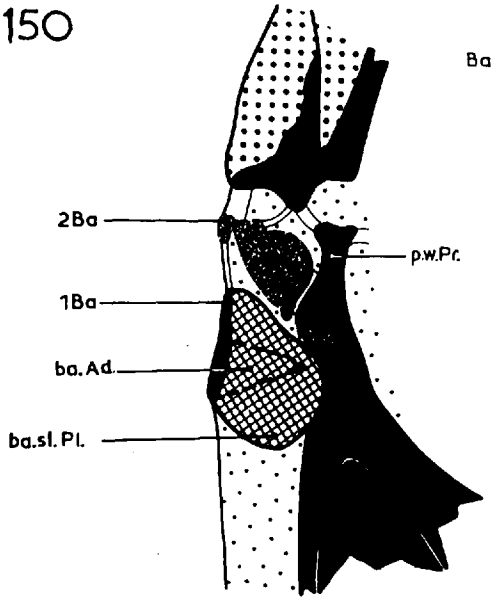


149

Zeuzera pyrina



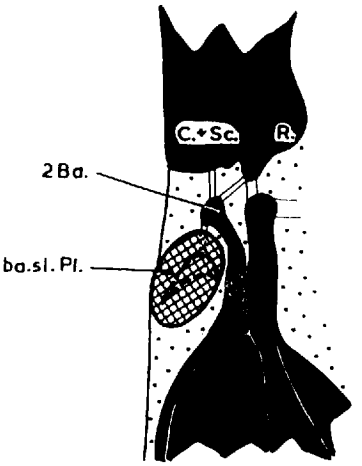
150



Operophtera brumata.

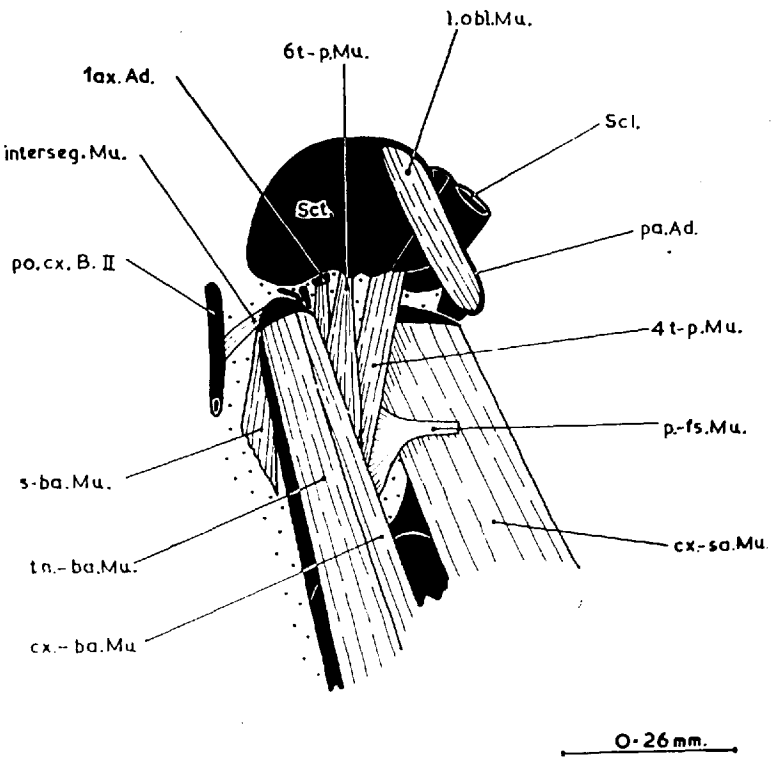
Basalar region of hind wing.

151

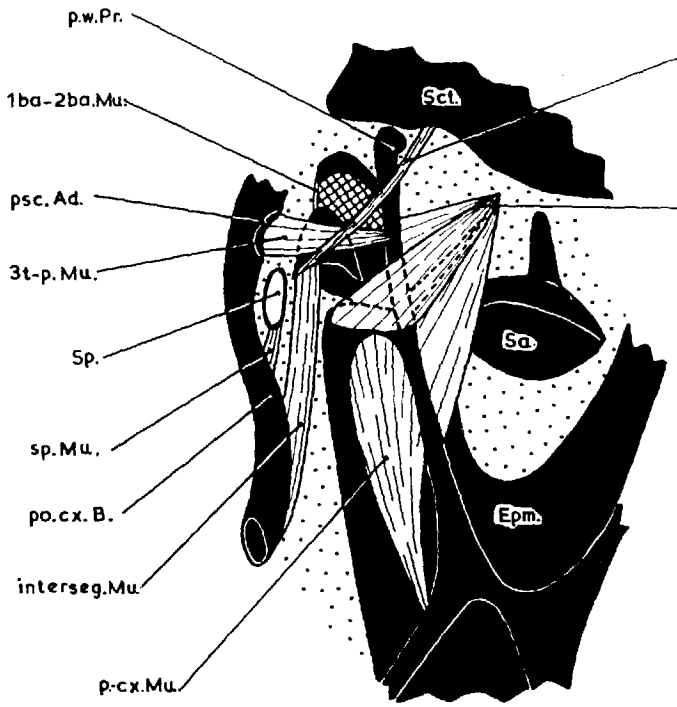


Plodia interpunctella

152 Sitotroga cerealella — 4,5 & 6 tergopleural muscles.



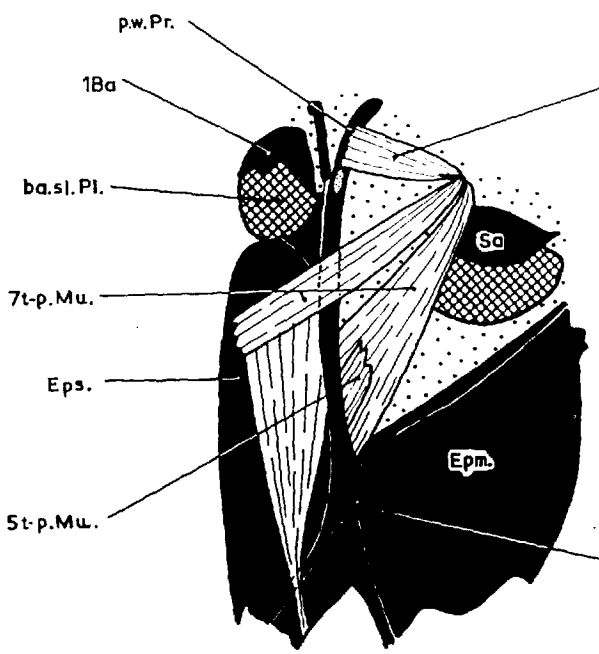
TERGOPLEURAL MUSCLES.



153

Saturnia pavonia

1mm.



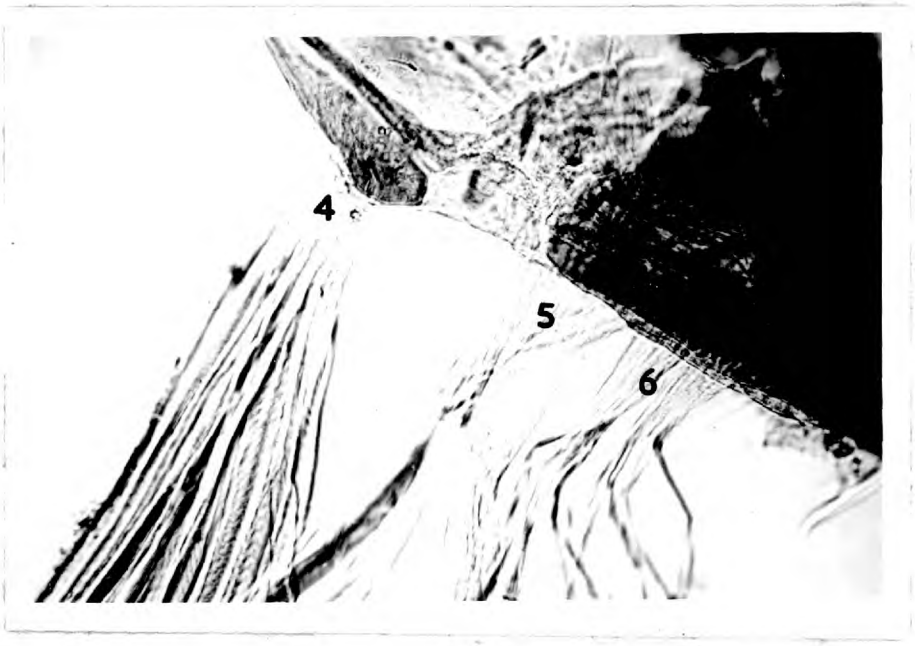
154

Colotois pennaria

0·74 mm.



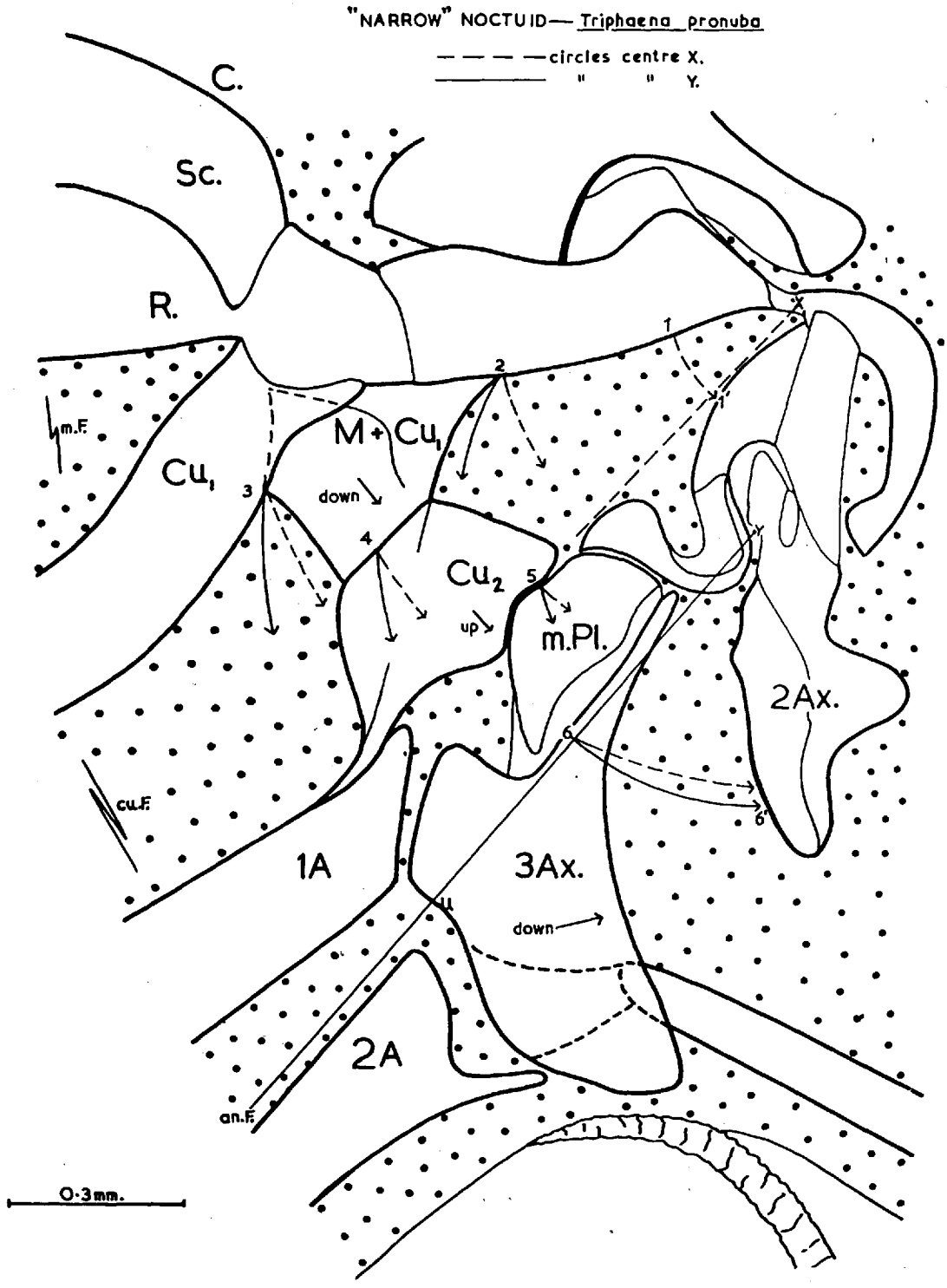
155. Evetria buoliana ♀ Junction of radius and second axillary of hind wing. X 200.



156. Poecilocampa populi - Fourth, fifth and sixth metathoracic tergopleural muscles. X 246.

HIND WING FOLDING.

157

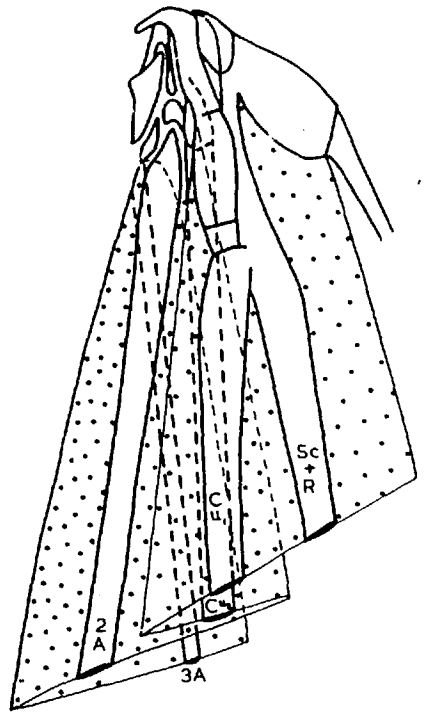


HIND WING FOLDING

158

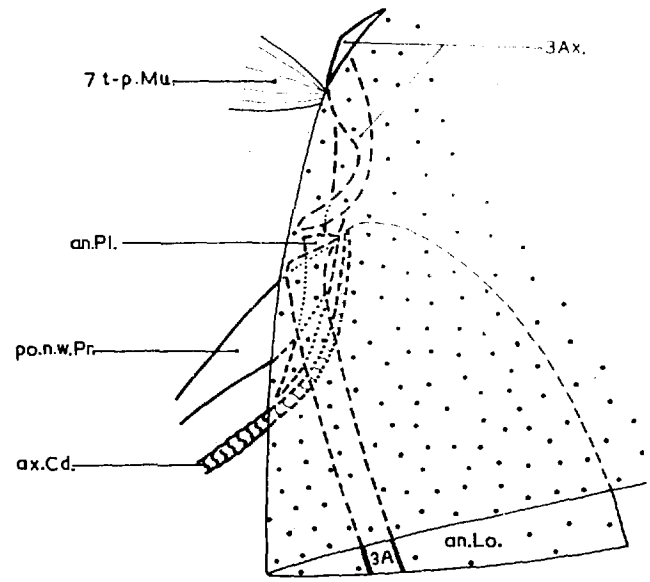
Plodia interpunctella

folded hind wing

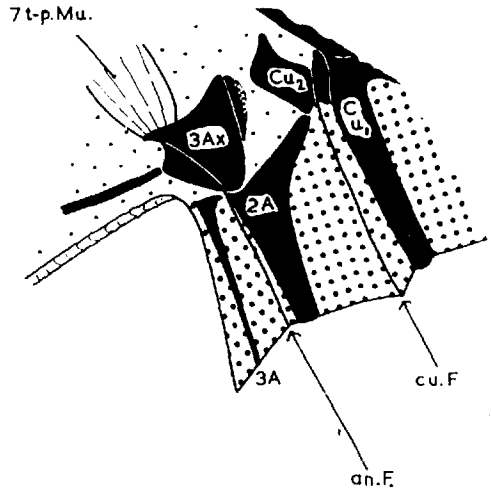


159

Anal fold of P. interpunctella.



an.Pl. lies above the po.n.w.Pr. and below the 3Ax.

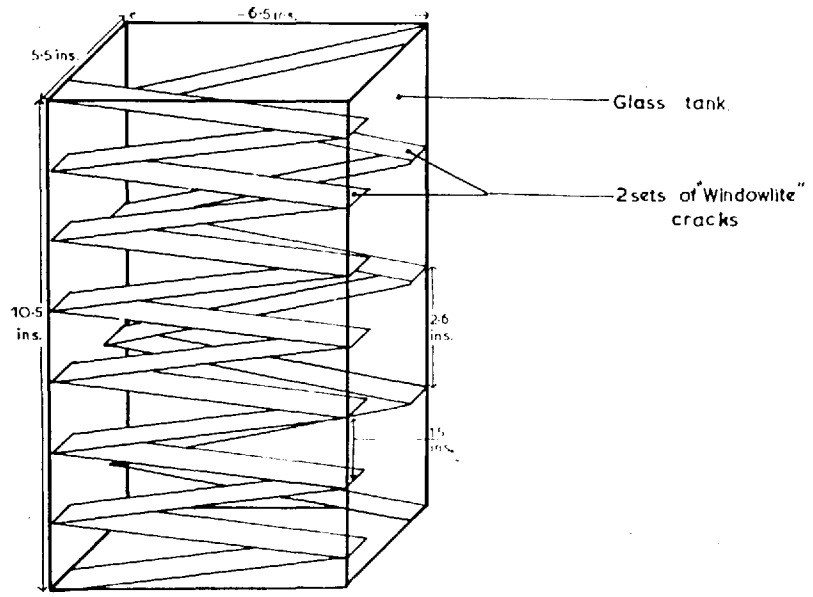


160

Biston betularia – posterior hind wing partly folded to show the positions of the folds.

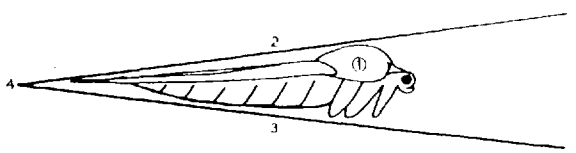
Crack choice chamber for Noctuolds

161

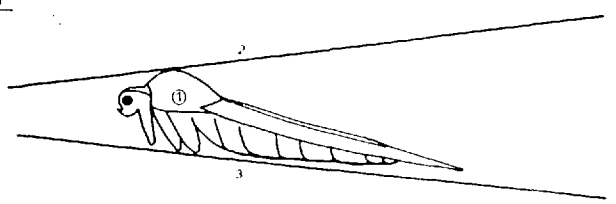


a. Score 4

162

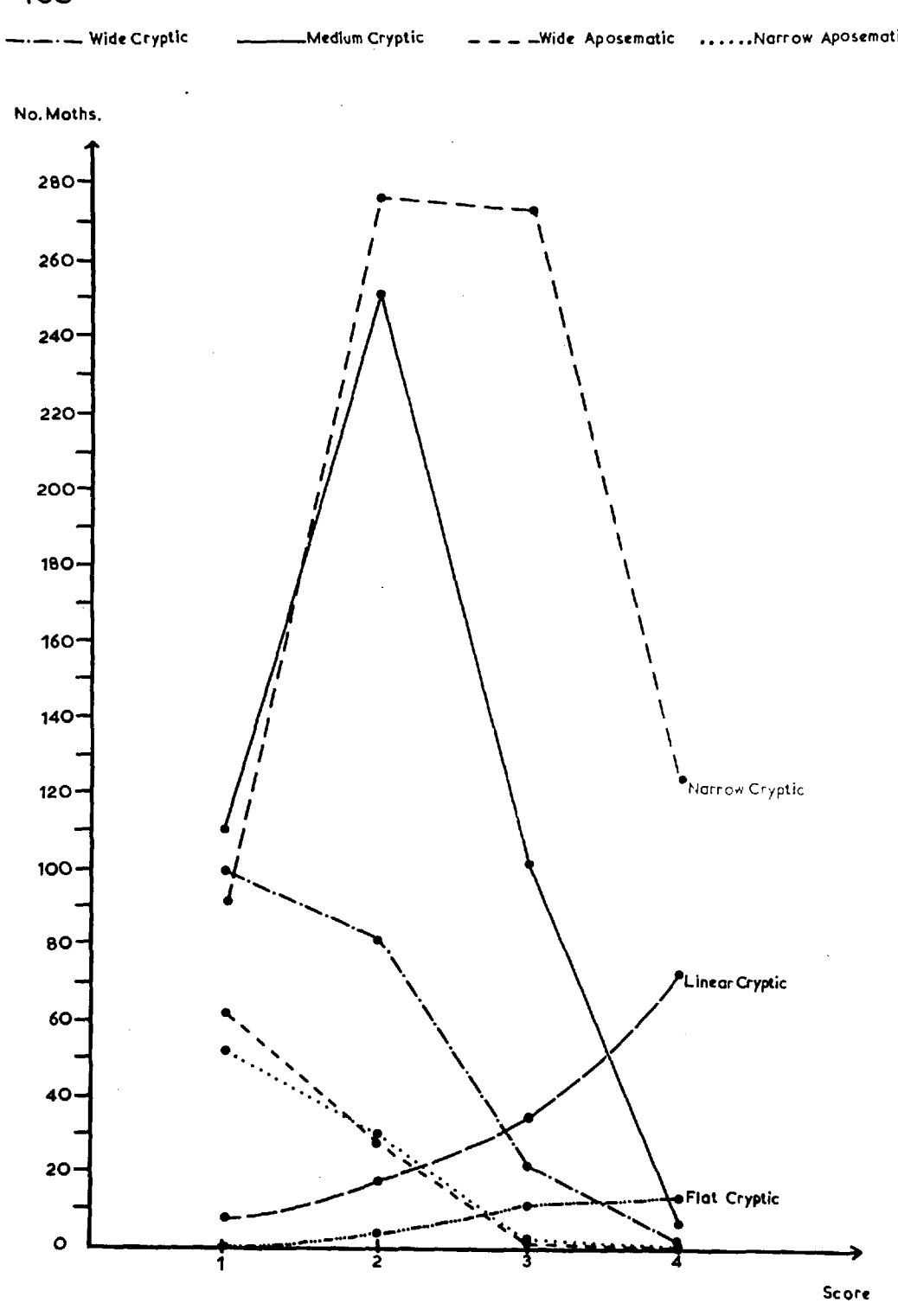


b. Score 3



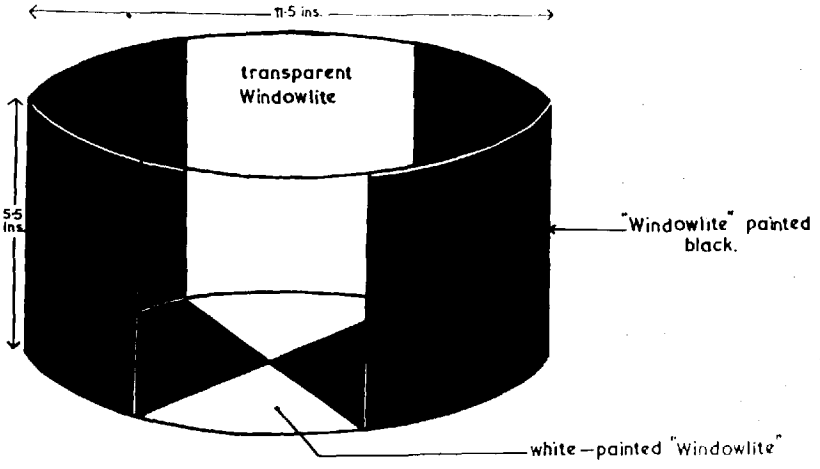
163

THIGMOTAXIS IN NOCTUOIDS

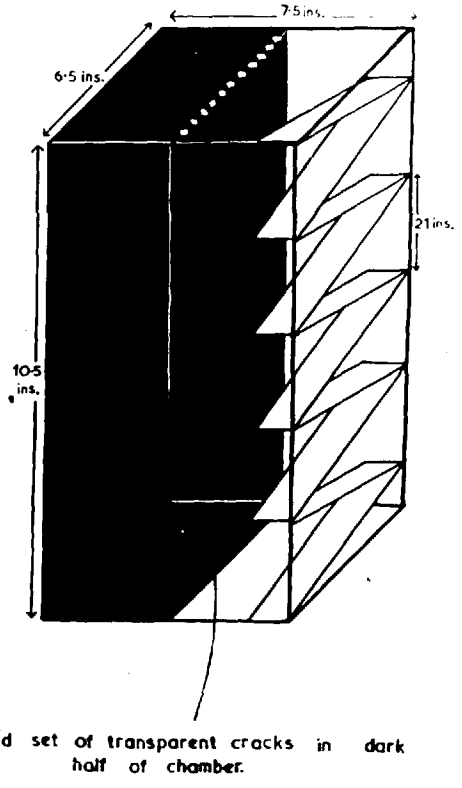


PHOTOTAXIS IN NOCTUOIDS

164



165



RECAPTURES of O. brumata

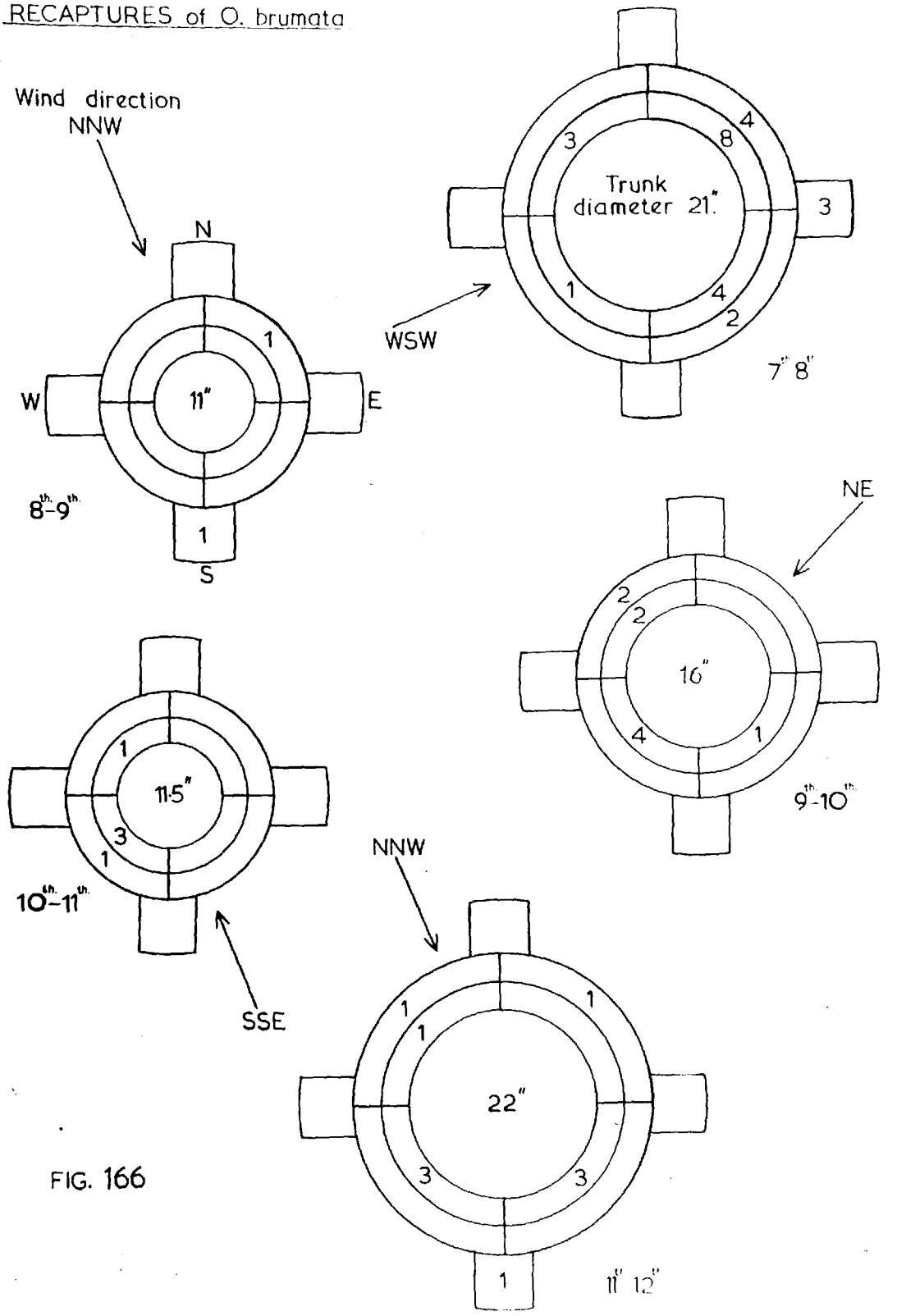
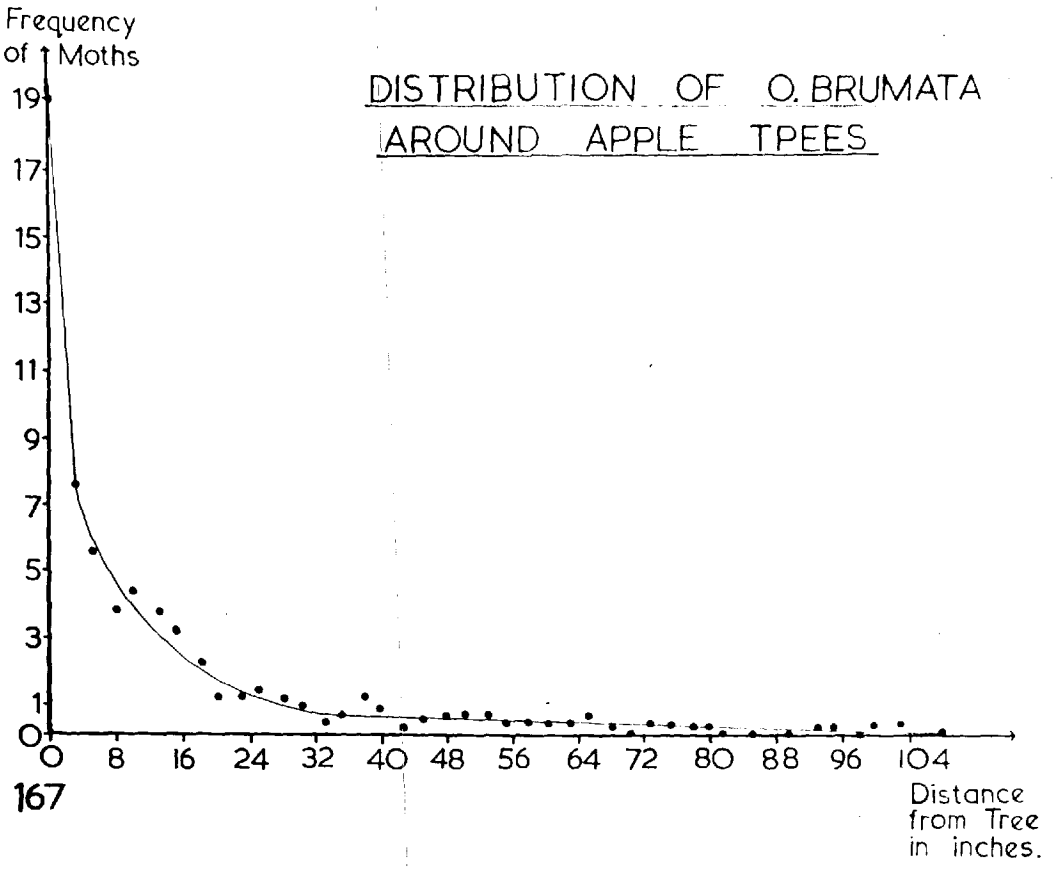
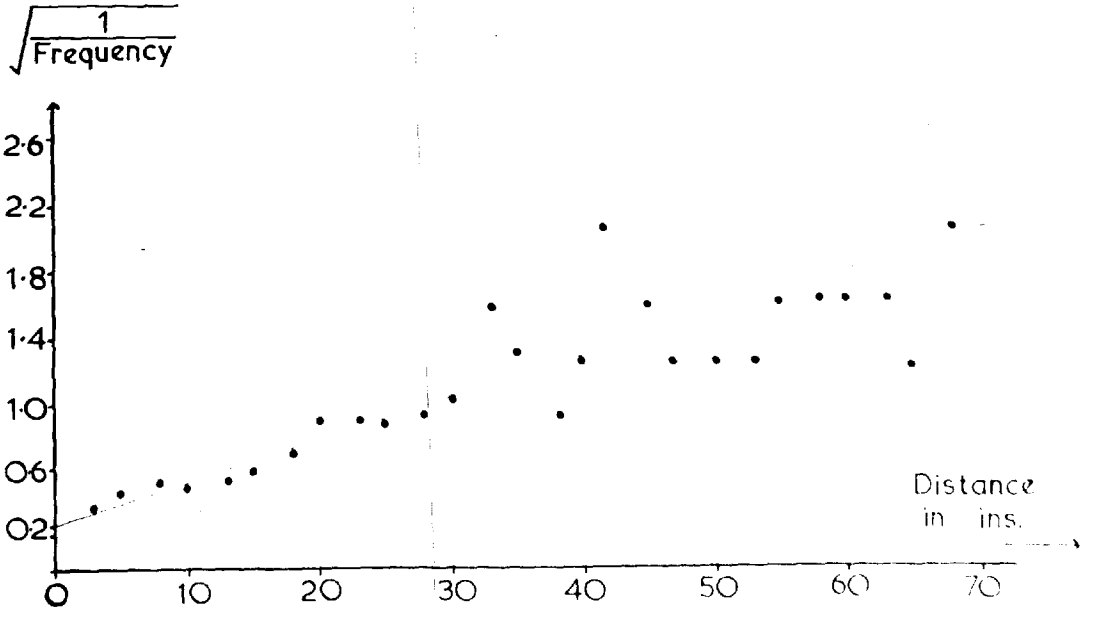


FIG. 166

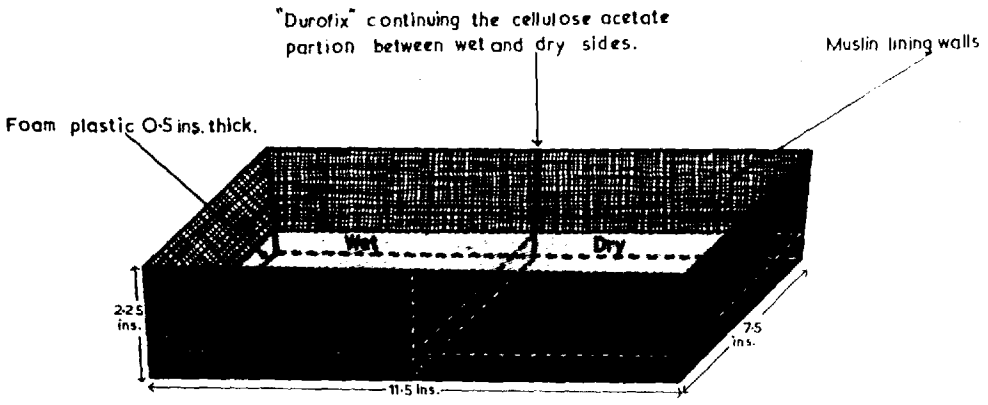

Frequency of Moths
DISTRIBUTION OF O. BRUMATA AROUND APPLE TPEES
19
17
15
13
11
9
7
5
3
1
0
0 8 16 24 32 40 48 56 64 72 80 88 96 104
Distance from Tree in inches.

167

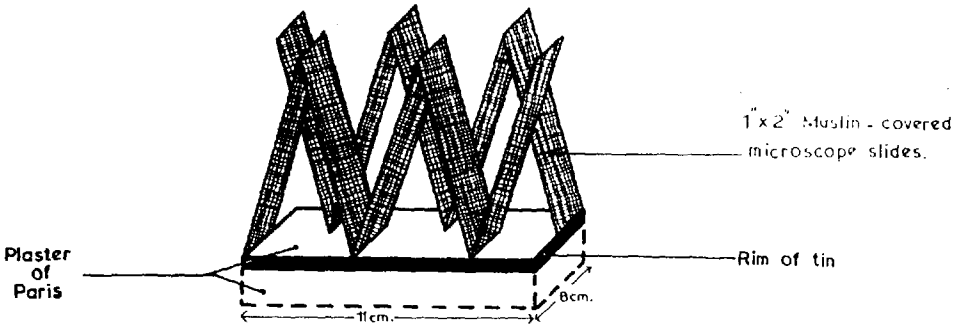
168


√(1/Frequency)
2·6
2·2
1·8
1·4
1·0
0·6
0·2
0
10 20 30 40 50 60 70
Distance in ins.

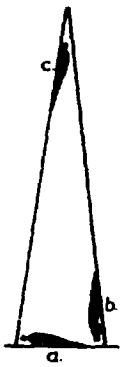
169



170



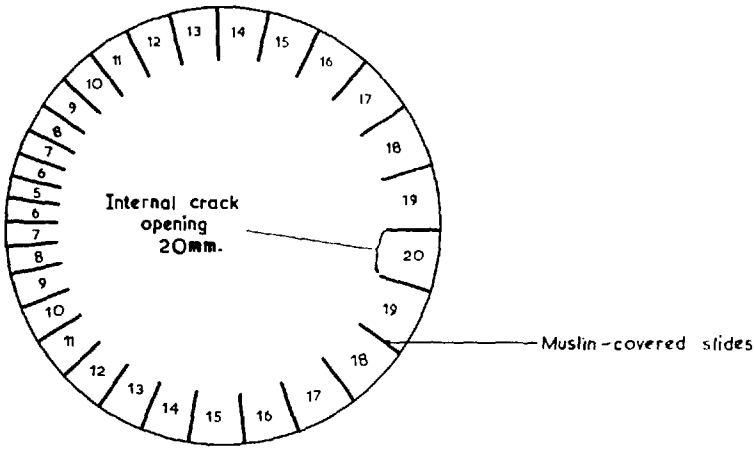
171



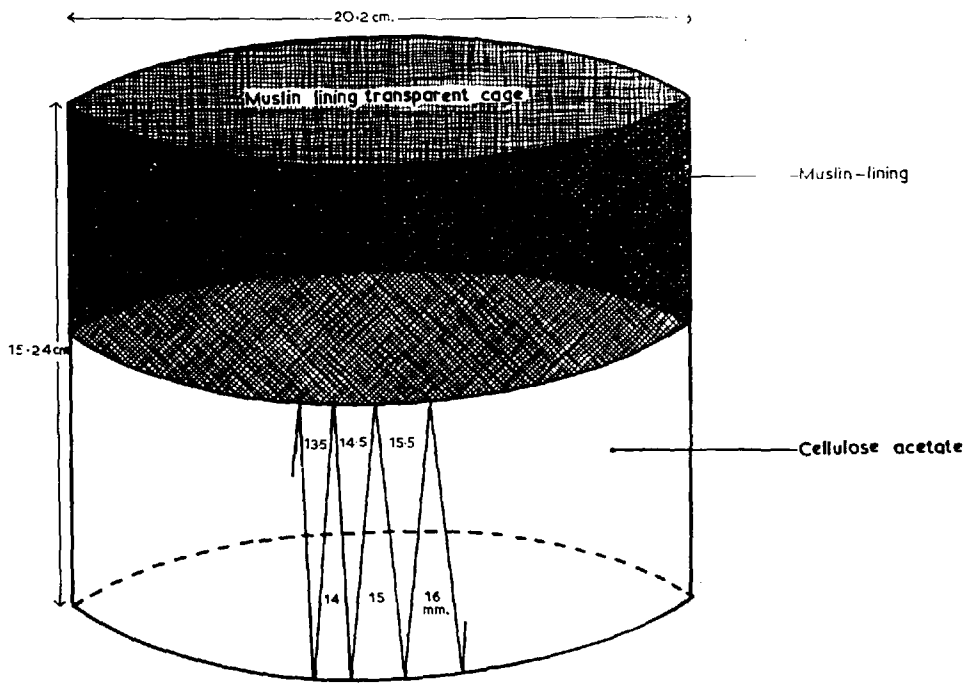
Positions of O. brumata in cracks.

Crack choice chamber for O. brumata

172 Plan

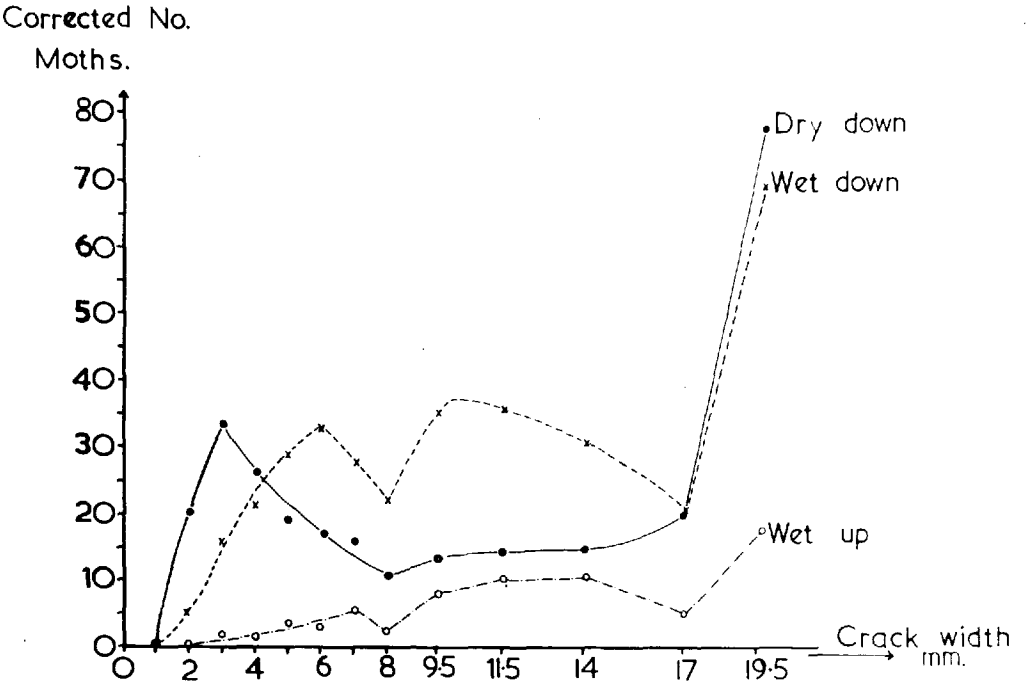


173
Side view



174

THIGMOTAXIS IN O.BRUMATA



175

