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CLASSIFICATION OF THE HELIOTHINAE

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CLASSIFICATION OF THE HELIOTHINAE

MARCUS MATTHEWS

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Contents

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Summaries

SUMMARY

The history of the classification of the sub-family Heliothinae (Lepidoptera: Noctuidae), and the nomenclatural problems that have been associated with *Heliothis*, are reviewed. Evidence for the monophyly of the Heliothinae is presented and discussed, followed by evidence for the monophyly of the Stiriinae. Certain Old World and South American species formerly included in the sub-family Noctuidae: Amphipyrinae are shown to be stiriines, the first time taxa outside North and Central America have been referred to this subfamily. The systematic relationship between the Heliothinae and the Stiriinae is discussed. The genera recognized in this study are listed. Two genera and one species are described as new, eight generic synonymies and 88 new combinations are proposed. Characters used in heliothine classification from the adults and the immature stages are reviewed and analysed. Host-plant information is presented, and its value for illuminating relationships within the subfamily assessed. Life-history strategy information is similarly treated. The various groupings within the Heliothinae supported by this study are presented, with a discussion of relationships. Seven hundred and twenty five scanning electron micrographs, light micrographs, and photographs, together with 46 line drawings, are presented to illustrate the features of heliothine morphology from all life-history stages, and certain aspects of heliothine biology, considered in the text.

RESUME

La présente étude donne une révision de l'histoire de la classification de la sous-famille Heliothinae (Lepidoptera: Noctuidae), ainsi que des problèmes de nomenclature qui ont été associés à *Heliothis*. Elle présente et discute les preuves de la monophylie des Heliothinae, et donne ensuite des preuves de la monophylie des Stiriinae. Certaines espèces du Vieux Monde et d'Amérique du Sud contenues autrefois dans la sous-famille Amphipyrinae sont montrées commme étant des stiriines; c'est la première fois que des taxa en dehors de l'Amérique du Nord et de l'Amérique Centrale ont été renvoyées à cette sous-famille. L'étude discute le rapport systématique entre les Heliothinae et les Stiriinae. Les genres reconnus dans cette étude sont catalogués. Deux genres et une espèce sont décrits comme nouveaux, huit synonymies génériques et 88 nouvelles combinaisons sont proposées. Les caractères utilisés dans la classification héliothine à partir des stades adultes et non mûrs sont revus et analysés. Des informations sont présentées sur les plantes-hôtes et leur valeur dans l'éclaircissement des rapports à l'intérieur de la sous-famille est évaluée. Les informations sur l'histoire de la vie sont traitées de manière semblable. Les groupements divers dans la sous-famille Heliothinae, qui sont ausi soutenus par la présente étude, sont présentés, accompagnés d'une discussion sur les rapports. Sept-cent vingt-cinq pantographes électroniques à balayage, pantographes lumineux et photographies, ainsi que 46 dessins linéaires, sont présentés pour illustrer les caractéristiques de la morphologie héliothine à partir de tous les stades de l'histoire de la vie, et certains aspects de la biologie héliothine sont considérés dans le texte.

RESUMEN

Se reseña la historia de la subfamilia Heliothinae (Lepidoptera : Noctuidae) y los problemas de nomenclatura que han estado relacionados con *Heliothis*. Se presentan y se discuten las pruebas de monofilia de las Heliothinae, y luego las pruebas de la monofilia de las Stiriinae. Se demuestra que ciertas especies del Viejo Mundo y de Suramérica anteriormente incluidas en la subfamilia Amphypirinae son stiriinas, la primera vez que los taxones fuera de Norteamérica y Centroamérica han sido referidos a esta subfamilia. Se discute la relación sistemática entre las Heliothinae y las Stiriinae. Se hace una relación de los géneros reconocidos en este estudio. Se describen como nuevos dos géneros y una especie, y se proponen ocho sinonimias genéricas y 88 combinaciones nuevas. Se reseñan y se analizan los caracteres usados en la clasificación heliotina desde las fases de adultas y de las inmaduras. Se presenta información sobre plantas huéspedes y se evalúa su importancia para ilustrar las relaciones dentro de la subfamilia. Se trata asimismo información sobre la estrategia de la historia vital. Se presentan varias agrupaciones dentro de las Heliothinae y demostradas por este estudio, con una discusión de las relaciones. Se presentan 725 micrografías de captación electrónica, micrografías luminosas y fotografías juntamente con 46 dibujos de líneas para ilustrar las características de la morfología heliotina de todas las fases de la historia vital, y ciertos aspectos de la biología heliotina presentados en el texto.

1. Introduction

This bulletin comprises, with a few changes, a thesis submitted in November 1987 for the degree of Doctor of Philosophy of the University of London.

The work is intended as an overview of the Heliothinae, not as a thorough revision of the subfamily. The evidence for the monophyly of the Heliothinae and the monophyly of its putative sister group, the Stiriinae, is examined. Evidence for the definition and relationships of sub-groups within the Heliothinae is also reviewed.

In the original thesis, no nomenclatural changes reflecting the study's findings were made. These changes are made here, with the erection of two new genera, and the proposal of eight generic synonymies and 88 new combinations.

The illustrations in this bulletin are the originals used in the thesis, with the exception of the colour plate of adults (Figs. 771-824).

The Heliothinae are well-defined, comprising about 400 species of small to medium-sized noctuid moths. They prefer the seasonally arid tropics and subtropics, inhabiting semi-desert, scrub, and savannah, where they feed mostly on low-growing herbaceous plants. The greatest numbers of species are found where these habitats are most widespread: in Australia, Africa, parts of Asia, and south western North America. This kind of habitat is apparently also preferred by the heliothines' closest relatives, the stiriines, although our understanding of the latter group is still very incomplete. Amongst the heliothines, it seems that only the *Heliothis virescens*-group occurs naturally in wetter parts of the tropics, with several species inhabiting the humid tropics of Central and South America. Pest species such as *Helicoverpa zea* and *H. armigera* have been recorded deep into forested areas, but these are doubtless only following Man and the cultivation of crops.

Most heliothines are nocturnal but some species are active diurnally. The larvae feed almost exclusively on the flowers, fruits, and seeds of their host-plants; when these are crops the larvae are therefore pests. Indeed, the status of *Heliothis virescens, Helicoverpa zea* and *H. armigera* amongst the world's most damaging pest Lepidoptera has brought the subfamily considerable notoriety. The history of heliothine classification, and the nomenclatural problems associated with *Heliothis,* are reviewed in Section 3 and Section 4 respectively; the latter has been included because of its importance to agricultural entomology.

Evidence for heliothine monophyly is presented in Section 5, and evidence for the monophyly of the Stiriinae and its wider distribution in South America and the Old World instead of just North America follows in Section 6. It would be fascinating to know the limits and internal relationships of the Stiriinae, which remain vague. However, the relationship between the heliothines and the stiriines is discussed in Section 7.

Section 8 lists genus-level groups recognized in the present study and the species examined in each of them. The evidence from adult structure for genus-level groupings in the Heliothinae is reviewed and discussed in Section 9. Little, if any, evidence for genus-level groups comes from the immature stages of the Heliothinae, despite the fact that the best autapomorphies for the subfamily are found in the larvae. However, characters from the immature stages have been proposed at the generic level in the past, and these are reviewed in Section 10. A survey of host-plant records, which aims for breadth of coverage of heliothine species without redundancy, rather than completeness, is given in Appendix 2 and discussed in Section 11. Next, the only previous hypothesis of relationships within the Heliothinae (Hardwick, 1970a) is considered in Section 13, before a discussion of the groupings and relationships supported by this study in Section 14.

2. Terminology

I follow Kitching (1987), and refer to abdominal segments A1-A8 in adults (A1-A10 in larvae), and to abdominal tergites and sternites as T1-T8 and St1-St8 respectively. The 'trifine hair-pencil' at the base of the abdomen in some males is the structure described and discussed by Birch (1972a, 1972b). Terminology for wing venation follows Nielsen (1985), and that for the genitalia follows Klots (1970), although I do use the term 'clasper' in the sense of Forbes (1939).

I believe Hogue (1963) is incorrect in referring to 'the distal half of the sacculus' in his Stiriini, and that this part of the valve is homologous with the clasper and ampulla of *Septis cariosa* as described and illustrated by Forbes (1954), and thus the clasper and harpe of Klots (1970).

In preparations of the male genitalia of *Apamea lithoxylea* (a species very close to *S. cariosa*) the harpe is attached to, or contiguous with, the clasper. Within the valve, the clasper has a substantial muscle attachment which stains quite deeply in chlorazol black. This is the attachment of muscle No. 5, the 'flexor of the clasper' in Forbes (1939). This attachment can be located, even when the clasper is extremely small, for example in species of *Helicoverpa* (Fig. 751) or *Pyrrhia* (Fig. 752), by tearing the valve to allow the stain to bathe its inner surface. When this is done in *Basliodes chrysopis*, a stiriine, the muscle attachment of the flexor of the clasper is found to attach to the base of what Hogue (1963) termed the 'distal half of the sacculus', as illustrated in Fig. 753, indicating that it is, in fact, the clasper.

Terminology of the hypopharyngeal complex in the larvae follows Godfrey (1972). I follow Hinton's (1946) system of setal nomenclature in the larvae.

3. A review of the classification of the Heliothinae

The first recognition of a group centred around the genus *Heliothis* was by Boisduval (1828). In his tribe Heliothidi he included *Anarta* (now a genus of the Noctuidae: Hadeninae) and *Acontia* (now a genus of the Noctuidae: Acontiinae). In 1840, his tribe Heliothides consisted of *Anarta, Anthoecia, Heliothis* and *Haemerosia*; *Acontia* he removed to the next tribe, which he called the Acontides.

The following year Guenée (1841) recognized a similar unit, the Heliothidi, to which he accorded tribal status. He also placed *Acontia* in a separate tribe. In 1852 he included fourteen genera in his family Heliothidae, and he defined it as containing small to medium-sized moths with non-pectinate antennae, short palps and a robust and often hairy thorax. The legs almost always spined or bearing claws, the upper surface of the wings almost always marked with black. He remarked that frequently they flew in full daylight and that the larvae often fed in flowers and seeds.

Between Guenée's publications, Duponchel (1844) divided the noctuids into 24 tribes corresponding largely to those of Guenée (1841). One, the Heliothides, comprised *Heliothis, Anthoecia, Anarta* and *Heliodes.*

In the 20 years following Guenée, the pioneering work of Grote and others upon a previously almost unknown fauna laid the foundations for attempts to classify the North American noctuids. Indeed, Grote (1883a) remarked that in 25 years the number of named North American noctuids had risen from less than a dozen to almost seventeen hundred.

Grote and Smith published various lists, each intended as a classification of the noctuids (Grote 1874, 1875, 1882a, 1890; Smith 1891, 1893). Both authors dealt specifically with the Heliothinae in two consecutive papers in the same publication (Smith 1882a, 1882b; Grote 1883a). Grote evidently felt he had been scooped by Smith, whose paper was the first full treatment of the group, and disagreed with him over certain generic usages while accusing him of plagiarism.

Smith (1882a) admitted that the group was difficult to define and recognized by the sum of its parts rather than any good uniquely derived characters. He also realised that the group was structurally very homogeneous, remarking that the genera, if numerous, would be based upon trivial differences. Indeed, he sank several of Grote's small genera into *Schinia,* where they remain today following Hardwick's extensive examination of the genitalia.

Both Smith and Grote altered the ordering of their heliothine genera in successive lists and added new genera as the fauna continued to be described. The number of genera in Grote's lists increased from 17 in 1874 to 29 in 1890. It is important to note that Smith and Grote each recognized not only the heliothines as a group (including only a few extraneous elements) but also the close relationship of the heliothines to the stiriines. Neither author segregated the genera with spined tibiae from those without spined tibiae.

Smith never formally subdivided the noctuid but he did list the genera in what he considered a natural arrangement. Grote, however, divided the family into numerous small units: the tribes of 1882 and corresponding subfamilies of 1890. With the acceptance of Hampson's system, many of the natural groups that were recognized at that time have been obscured. That the heliothines of Smith and of Grote have suffered in this respect has been pointed out by Hardwick (1970a).

Hampson divided the two major lineages of the Heliothinae, and placed them well apart in his classification of 1903. This was a direct result of his division of the trifid noctuids on the basis of the characters: eyes hairy/not hairy, eyes lashed/unlashed, and tibiae spined/unspined. Despite this, he did at the same time note the 'close affinities' of *Heliothis* and its allies with the *Eutricopis*-group.

In his *Catalogue*, Hampson grouped those heliothine genera with spined tibiae (the '*Heliothis*-stem') at the beginning of the Agrotinae (= Noctuinae); he also recognized the affinity of *Adisura* (which has no fore-tibial spines) with the group. In contrast, he scattered both the heliothine genera with unarmed tibiae (the '*Pyrrhia*-stem') and the stiriine genera throughout the latter part of his heterogeneous Acronyctinae (Hampson, 1910). Interestingly, in his moths of British India (1894) he placed *Pyrrhia* just before *Heliothis*, recognizing the intimate relationship he was to sever nine years later.

Warren's classification of the Palaearctic fauna in Seitz (1911) although different from Hampson's was certainly no improvement. He placed the heliothines with elliptoid or reduced eyes in the Heliothidinae and those with globular eyes in the Melicleptriinae (exactly the reverse of Smith who had used *Melicleptria* in a generic sense for those with elliptoid eyes). *Pyrrhia* he placed well apart amongst unrelated genera in the Amphipyrinae. The Heliothidinae, so he thought,

> ' ... may plausibly be regarded as scattered remnants of archaic types, the conditions of whose existence synchronised with the more rigorous climate and scantier light of an earlier cosmic period.'

Draudt revised the New World fauna in Seitz (1927). Although he placed the elements of the '*Pyrrhia*-stem' apart from the rest in the Amphipyrinae because of their unspined tibiae, he did recognize their relationship to one another, and *Rhodoecia*, *Pyrrhia*, and *Erythroecia* were adjacent in his arrangement. In his Heliothinae, Draudt included three stiriine genera (*Grotella*, *Neogrotella*, and *Hemigrotella*), the noctuine genus *Copablepharon* (which is superficially similar to the Old World *Aedophron* and the New World *Schinia snowi*), *Metopoplacis*, and *Manruta*.

A structural character in the larvae was recognized as a possible synapomorphy for the group for the first time in 1931. Cockayne (1931) in England described the spiny skin of heliothine larvae and considered that it united *Pyrrhia* with *Heliothis* and its allies.

McDunnough (1938) continued to separate those heliothine genera with spined tibiae from those without spined tibiae. The former he placed in his Heliothiinae (again including *Manruta*, *Grotella*, *Neogrotella*, and *Hemigrotella*) and the latter in the Amphipyrinae.

Gardner worked on the structure of noctuid larvae in India and proposed groupings based on his findings. Apparently unaware of Cockayne's suggestion, he also grouped *Pyrrhia* with *Heliothis* and *Adisura* in his group A IV (Gardner 1946).

In his work on the larvae of North American Noctuidae, Crumb (1956) placed *Rhodoecia aurantiago* and *Pyhia umbra* (both without spined mid- and hind-tibiae in the adults) with the other species of Heliothinae, remarking that the former were 'entirely normal heliothids'.

The last treatment before that of Hardwick and a return to the Heliothinae of Smith and of Grote, was Forbes (1954). Although the study of genitalia was by then well established, and despite the similarity of the male valves of *Pyrrhia* and

Heliothis, he split the group into the Heliothidini of the Agrotinae and the Pyrrhiini of the Acronyctinae, in which he also placed the stiriines.

The most detailed study of the subfamily has been that of Hardwick in North America, published in a series of papers including three monographs (1958, 1965, & 1970a) and 17 separate life-histories. During the last 30 years he has demonstrated (especially in 1970a) that, despite Smith's (1882b) belief that genitalic characters were uninformative, Grote and Smith each had an overall concept of the group (uniting both forms with and those without spined mid- and hind-tibiae) which was very similar to that derived from a careful study of their genitalia, larvae, and biology. Furthermore, the same consideration of structural and biological characteristics underlies his suggestion of the close relationship between heliothines and stiriines. In his taxonomic work, Hardwick has stressed the importance of the genitalia, especially the male vesica, in defining the genera within the Heliothinae.

Hardwick's work on the life-histories of North American species has been considerable (Hardwick, 1958, 1965, 1966a, 1966b, 1967, 1969, 1970c, 1970d, 1970e, 1971a, 1971b, 1971c, 1971d, 1971e, 1971f, 1972a, 1972b, 1972c, 1972d, 1983a, 1983b). These publications deal in detail with female fecundity, sites of oviposition, feeding habits of the larvae throughout their various instars, sites of pupation, etc., in addition to descriptions of the structure of the immature stages.

However, apart from his study of the cosmopolitan genus *Helicoverpa,* Hardwick's investigations have been confined, more or less, to the North American fauna.

The history of the Heliothinae can be summed up as follows. The group was recognized as an entity by the earlier workers until split by Hampson into forms with spined mid- and hind- tibiae (which he placed in his Agrotinae) and those without such spines (which he placed in his Acronyctinae). This division was perpetuated by those working subsequently on the adults, who by and large simply stuck to Hampson's system—its artificiality was frequently pointed out by others working on the larvae. Most recently, the subfamily has been reunited by Hardwick following his work on adult and larval structure, and the insects' natural history.

4. A review of nomenclatural problems associated with *Heliothis*

For many years the generic name *Heliothis* was surrounded by nomenclatural problems, the last of which were not solved until 1985 (ICZN 1985). Nye (1982) discussed the whole matter in detail.

In 1806, Hübner distributed his *Tentamen*, which consisted of a single quarto sheet printed on both sides. Of the 107 generic names appearing in the *Tentamen*, 94 (including *Heliothis*) were new. After much controversy, the International Commission on Zoological Nomenclature ruled in Opinion 97 (ICZN 1926) that the *Tentamen*

> '... was obviously prepared essentially as a manifolded manuscript, or as a proof sheet ... and not for general distribution as a record in Zoology.'

In Opinion 278 (ICZN 1954), the *Tentamen* was placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature as Work No. 14.

However, the rediscovery of another pamphlet by Hübner (1808), entitled *Erste Zuträge zur Sammlung exotischer Schmetterlinge*, ensured that the problems continued. Nye (1982) said:

> '... Hübner stated that lepidopterists in foreign countries ... had sent him specimens of a large number of a new species, which he proposed to figure and describe in a work entitled *Zuträge zur Sammlung exotischer Schmetterlinge*. He then listed 75 combinations of generic plus specific names, and above each placed two numbers that ran consecutively from 1 to 150. Figure numbers 81 and 82 were named *Heliothis jucunda*, a North American species in a different subfamily from the American *dipsacea*.'
>
> 'During the period 1808-1818, Hübner published the plates of the first volume of his *Zuträge zur Sammlung exotischer Schmettlinge* (sic) ... The plate containing Figures 81-82 was published by 1813, and these illustrations, together with the name *Heliothis jucunda* proposed in the 1808 *Erste Zuträge*, would have made *Heliothis* Hübner, 1813, nomenclaturally available for a generic concept entirely different from that in the *Tentamen* ... when in 1818 he published the text and descriptions to the illustrations, he usually retained the same specific name that he had used in his *Erste Zuträge*, but he proposed many new generic names. Figures 81-82 were then named *Melipotis jucunda*.'

The International Commission on Zoological Nomenclature ruled (ICZN 1966) that the names in the *Erste Zuträge* were not available for nomenclatural purposes, and it was placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature as Work No. 72. At the same time (Opinion 789), the name *Heliothis* Hübner (1808) was placed on the Official Index of Rejected and Invalid Generic Names in Zoology as Name No. 1857. This removed the nomenclatural obstacles to the use of *Heliothis* Ochsenheimer, 1816.

However, there were two further problems. Five years earlier, Todd (1978) had asserted that although the name had generally been treated as feminine, *Heliothis* was masculine, and changed all the endings of specific names to agree. The difficulty this raised was that certain names in common use by hundreds if not thousands of agricultural entomologists were changed in a way many thought highly unnecessary. In Opinion 1312 (ICZN 1985) it was ruled that the name *Heliothis* is feminine, thus the changes proposed by Todd (1978) may be ignored.

Finally, there have been some differences in the spelling of the subfamily name derived from *Heliothis;* most recently Hardwick (1958 *et seq.*) has referred to the 'Heliothidinae'. Steyskal (1971) considered the stem used in forming the subfamily name to be Helioth-, and the subfamily name to be, therefore, Heliothinae.

The *Commission* (ICZN 1985) placed the family-group name HELIOTHINAE, with type genus *Heliothis* Ochsenheimer (1816), on the Official List of Family-group Names in Zoology with the Name Number 568 (Opinion 1312).

5. The monophyly of the Heliothinae

The best autapomorphies discovered for the clade 'Heliothinae' are the spiny skin of the larvae, and the transverse position of the lateral setae on the prothorax of the larvae in later instars.

5.1 THE SPINY SKIN OF THE LARVAE

The skin of all heliothine larvae bears minute spines (spinules) strongly dilated at the base. In the most spiny species this feature is visible to the naked eye, for example in *Heliothis peltigera* (Fig. 743). In first and second instar larvae of *Schinia* species, the spinules are of 'essentially equal size' (Hardwick, 1958); in the third and subsequent instars, the spinules are relatively larger and usually more variable in size (Hardwick, 1958). Variation in skin type of larval Heliothinae is illustrated in Figs. 721-737 by a comparative series of SEMs of the area around seta L3 of the mesothorax in final instar larvae. Stout, almost conical spinules occur in *Heliothis tergemina*, *H. virescens*, and *Schinia citrinella*. Intermediate forms occur in, for example, *Pyrrhia exprimens*, whereas the spinules in *Eutricopis nexilis*, *Baptarma felicita*, and *Heliothis viriplaca* are slender and needle-like. Dense spinulation is exhibited by *Heliothis virescens*, intermediate conditions by *H. tergemina* and *Schinia indiana*, whilst in *Schinia triolata* (which I have not examined) the distribution of spinules over the body is extremely reduced: they are present only on the suranal shield (Hardwick, 1958).

This character was first proposed more or less explicitly as an autapomorphy of the subfamily by Cockayne (1931), making his short paper historically important for the systematics of the Heliothinae. The feature was noted again by Gardner (1946), while Crumb (1956) mentioned the character only in his key to the subfamilies of Noctuidae. The first sentence of couplet 5 reads: 'Spinules present on hind coxae except in *Schinia obscurata*.' He also noted, albeit indirectly, that the spinules may be very restricted in distribution.

Spiny skin occurs in other noctuid larvae: in some Herminiinae (Beck, 1960; Rawlins, 1984), some Cuculliinae (Beck, 1960), and some Plusiinae (Beck, 1960; Ichinose, 1962). To demonstrate that the spiny skin of the Heliothinae is autapomorphic in the strictest sense, it must be shown that a certain condition of spiny skin is peculiar to the Heliothinae. Should this prove to be the case, the autapomorphy of the Heliothinae would be the particular condition of spiny skin itself, not the more general condition 'spiny skin'. For the time being, however, the spiny skin present in at least some degree in all heliothine larvae is adduced as strong evidence of monophyly.

5.2 THE POSITION OF L1 AND L2 OF THE PROTHORAX IN THE LARVAE

Generally, setae L1 and L2 of the prothorax in noctuid larvae (following the terminology of Hinton, 1946) are set in a vertical plane, with L1 above L2. In heliothine larvae, however, L1 and L2 of the prothorax lie more or less in a horizontal plane, with L2 set caudad (towards the head) of L1. However this appears to be the case only in later instars.

Hardwick (1958) discovered that in the first instar of *Heliothis phloxiphaga* L1 and L2 of the prothorax lie in a vertical plane. In successive instars the relative position of these setae changes, so that in the final instar they come to lie in a horizontal plane.

Although L2 *may* lie directly caudad of L1 in some species, for example *Helicoverpa fletcheri*, the relative position of these setae varies slightly, even within individuals, as do the relative positions of the other setae in both the Heliothinae and other noctuids. In many species this amounts to an approximation of the horizontal condition present in others. For example, in *Schinia sueta californica* and *Schinia pulchripennis* (Hardwick, 1958), and *Baptarma felicita, Eutricopis nexilis,* and *Heliocheilus albipunctella*, a line through the bases of L1 and L2 lies between 15 to 45 degrees *below* a line passing through the base of L1 along the body's longitudinal axis. In other words, the condition they exhibit is between that of the most extreme heliothines in this respect, and other noctuids.

5.3 DISCUSSION

Together, spiny skin and the transverse condition of L1 and L2 provide a unique character combination defining the Heliothinae.

It is very difficult to point to any structural characters of the adults as being autapomorphic for the Heliothinae. Hardwick felt that if a combination of characters or character complexes is considered, then a uniquely heliothine condition exists in the male genitalia. This he described as the association of a simple, strap-like valve which may or may not bear a harpe, with a vesica either without cornuti, or with only isolated or small clusters of cornuti (Hardwick, 1970a). I find it impossible, however, to define discrete conditions in the valves of, for example, *Aedophron* spp. (Figs. 155, 157, & 159), *Baptarma felicita* (Fig. 161), *Eutricopis nexilis* (Fig. 175), and *Microhelia angelica* (Fig. 185), and those of stiriines which have a simple, flat valve with no corona or harpe, such as *Panemeria tenebrata* (Fig. 424), and *Xanthothrix* spp. Nevertheless, although 'strap-like' may at first be considered somewhat vague, this idea, together with the photographs of valves provided here, conveys the condition found in the *Schinia*-group and the *Heliothis*-group, and a few *Pyrrhia*-group species (for example *Pyrrhia umbra* Fig. 199, or *Erythroecia suavis* Fig. 169) in a way that would only otherwise be possible by a lengthy and complex description.

There are two further characters that distinguish the Heliothinae from the Stiriinae very well. However, neither state of either character is unique solely to the Heliothinae or the Stiriinae, so they cannot be regarded as strict autapomorphies of either subfamily.

First, the anterior edge of sternum 8 in male heliothines bears two 'arms' which are often very long (Figs. 432-470). In only one or two cases are these arms absent, for example *Erythrophaia suavis*, and I attribute this to reduction because *Erythrophaia eudoxia* does possess them. These arms are never present in stiriines; they have a form of sternum 8 in the male which is very similar to that in *Cucullia* and *Oncocnemis* (Figs. 471-482). Second, whereas the heliothines all have 'trifid' hind-wing venation (Hardwick, 1970a) with at most a faint remnant of M2 in the hind-wing (Figs. 612-631), the stiriines are all at least minimally 'quadrifid' (Figs. 632-642).

The habit of larval heliothines of feeding almost exclusively on the flowers, fruits, and seeds of their host plants was cited by Hardwick (1970a) as evidence that those heliothines placed in the Noctuinae because of their spined mid- and hind-tibiae were not actually related to the true noctuines or cutworms, but to the rest of the heliothines with unspined mid- and hind-tibiae. This habit cannot, however, be cited as evidence of monophyly of the subfamily. To begin with, it is a habit shared, so far as is known, with all larval Stiriinae. Furthermore, feeding on flowers, fruits, and seeds of the host plant also occurs in some cuculliines, for example species of *Cucullia*, and some hadenines, for example *Hadena bicruris*.

No plusiine appears to feed exclusively on flowers, fruits, or seeds: when they do feed on these parts of the host plant, it seems it is out of a lack of preference for any other part alone (I. J. Kitching, pers. comm.). No noctuine larvae are known to feed exclusively on flowers, fruits, and seeds.

6. The distribution and monophyly of the Stiriinae

6.1 THE DISTRIBUTION OF THE STIRIINAE

Hogue (1963) apparently made no attempt to determine whether or not close relatives of his Stiriini, or perhaps even elements of the group itself, occurred outside North America. Hardwick's (1970a) assessment of this has already been discussed. Evidence is presented below for an even 'more comprehensive Stiriinae' than that suggested by Hardwick (1970a), which still comprised only North American genera, with elements from South America, Africa, and the Palaearctic now included. My suspicion is that Hogue's Stiriini may best be considered a single genus, with what may turn out to be a similar distribution to those of *Schinia* and *Oncocnemis.* Approximately ten species each of *Schinia* and *Oncocnemis* occur in the Palaearctic with over ten times this number in each genus in the New World, mainly in the dry south western part of North America.

6.2 THE MONOPHYLY OF THE STIRIINAE

A highly characteristic scale-like spinneret in larval stiriines provides the best evidence for monophyly of the group (Figs. 717-720). Comparatively few stiriine larvae are known but all those studied exhibit this form of spinneret.

Crumb (1956) included the seven species of Stiriinae available to him in his Amphipyrinae, group 5. These he distinguished from the other genera in group 5 by the absence of SV3 (his setigerous tubercle VIIc) on A1, and 'The normally projecting portion of the spinneret present but reduced to a thin scalelike structure appressed to the labium.' Hogue (1963) did not mention this most important character; nor did Hardwick (1970a), who was doubtless quite correct in asserting that the group around *Stiria* is considerably larger than that considered by Hogue, even in North America. *Oslaria viridifera* (Grote) (Figs. 149, 420, & 421) and *Prothrinax luteomedia* (Smith) (Figs. 153, 428, & 429), not included by Hogue (1963) in his Stiriini, but included by Hardwick (1970a) in the Stiriinae, are figured here.

Dissection of the following Old World species left little doubt that they are indeed stiriines. *Aegle koekeritziana* (Hübner), Figs. 139, 400, & 401; *Aegle subflava* (Erschov), Figs. 140, 402, & 403; *Aegle vespertalis* (Hübner), Figs. 141, 404, & 405; *Dipinacia schiniodes* Dognin, Figs. 144, 410, & 411; *Ectolopha marginata* Hampson, Figs. 145, 412, & 413; *Ectolopha viridescens* Hampson, Figs. 146, 414, & 415; *Megalodes eximia* (Freyer), Figs. 147, 416, & 417; *Metaegle pallida* (Staudinger), Figs. 142, 406, & 407; *Mycteroplus puniceago* (Boisduval), Figs. 148, 418, & 419; *Ochrocalama xanthiata* (Hampson), Figs. 422 & 423; *Panemeria tenebrata* (Scopoli), Figs. 150, 424, & 425; *Paralophata ansorgei* B-Baker, Figs. 151, 426, & 427; *Procrateria pterota* Hampson, Fig. 152; *Synthymia fixa* (Fabricius), Figs. 154, 430, & 431.

Furthermore, the life-histories, where known, reaffirmed this in that the larvae feed on the flowers, fruits, and seeds of their host plants. This information is presented in Table 1 below, in which plant family name abbreviations are the same as those used in Appendix 2.

The most important consideration here is whether or not the larvae of these Old World species possess a scale-like spinneret. The only species for which this information is available, *Panemeria tenebrata*, does possess such a spinneret (Figs. 717, 718 & 741).

Larvae of the following stiriines have been available for examination; numbers in brackets indicate the number of specimens in each case; all material was preserved in alcohol. *Basilodes catharops* (1); *Basilodes pepita* (1); *Cirrophanus triangulifer* (1); *Panemeria tenebrata* (5); *Plagiomimicus expallidus* (1); *Plagiomimicus pityochromus* (1); *Stiria rugifrons* (1); *Xanthothrix numoegini* (2); *Xanthothrix ranunculi* (4).

A full description of the spinneret in stiriines must await a more comprehensive collection of the larvae so that its variation within the group can be assessed. The presence of minute spines on the hypopharynx all the way to the base of the labial palpi is also extremely similar in *Xanthothrix* and *Panemeria*, and may occur throughout the stiriines. For comparison, the spinneret of *Heliocheilus albipunctella* is illustrated (Figs. 715 & 716). This form of spinneret occurs throughout the Heliothinae and also in the Cuculliinae, Plusiinae, Bryophilinae, and *Amphipyra*, as pointed out by Beck (in press).

Table 1

Host plants of Stiriinae

Aegle koekeritziana	RANU	*Delphinium*	1
Aegle vespertalis	SCRO	*Antirrhinum*	2
Basilodes chrysopis	COMP	*Verbesina enceliodes*	3
Basilodes pepita	COMP	*Verbesina alternifolia*	4
Cirrhophanus triangulifer	COMP	*Bidens* spp.	5
Cirrhophanus triangulifer	COMP	*Bidens trichosperma*	6
Crambodes talidiformis	VERB	*Verbena*	7
Ectolopha viridescens	MALV	*Hibiscus cannabinus*	8
Megalodes eximia	MALV	*Malvus*	9
Panemeria tenebrata	CARY	*Cerastium* spp.	10
Panemeria tenebrata	CARY	*Stellaria*	11
Plagiomimicus expallidus	COMP	*Iva zanthifolia*	12
Plagiomimicus pityochromus	COMP	*Ambrosia trifida*	13
Stibadium spumosum	COMP	*Helianthus annuus*	14
Stibadium spumosum	COMP	*Helianthus*	15
Stiria rugifrons	COMP	*Helianthus microcephalus*	16
Synthymia fixa	LEGU	*Psoralea bituminosa*	17
Xanthothrix numoegini	COMP	*Chaenactis glabriscula*	18
Xanthothrix ranunculi	COMP	*Coreopsis douglasii*	19

1. Hampson, 1910
2. Valletta, 1973
3. Crumb, 1956
4. Crumb, 1956
5. Crumb, 1956
6. Crumb, 1956
7. Crumb, 1956
8. BMNH label data
9. Hampson, 1910
10. Goater, 1983
11. Goater, 1983
12. Crumb, 1956
13. Crumb, 1956
14. Crumb, 1956
15. Crumb, 1956
16. Metzler, 1985 (pers. comm.)
17. Hampson, 1910
18. Comstock & Henne MS
19. Comstock & Henne, 1940

7. The Heliothine-Stiriine relationship

7.1 REVIEW

The name 'Stiriinae' was first used formally by Grote in 1882 (1882a) and his subfamily comprised *Stibadium, Stiria, Fala,* and *Plagiomimicus* (thereby omitting his own stiriine genus *Basilodes*). In another paper in the same year (1882b) he stated that *Bessula, Antaplaga, Pippona, Epinyctis, Plagiomimicus, Polenta, Stiria,* and *Stibadium* 'seem to fall in between *Heliothis* and *Plusia*'. *Epinyctis* is cuculliine, however, given that *Bessula* and *Pippona* are heliothine (both synonyms of *Schinia*) Grote clearly considered there to be a close relationship between the Heliothinae and the Stiriinae.

Smith (1882a, 1882b) included several stiriine genera in his Synopsis of North American Heliothinae, and in his catalogue of 1893 the heliothine genera are directly preceded and immediately followed by the stiriines.

Although Hampson destroyed all semblance of a compact group, he did place small numbers of stiriine genera together at certain points in his sequence in volume 9 of his Catalogue (Hampson, 1910) thereby indicating affinity. What is important here is that for the first time Old and New World stiriine genera were placed together: *Ectolopha* and *Centrogone* between *Chrysoecia, Neumoegenia,* and some other unrelated genera at one point, and *Paragele, Metagele, Aegle,* and *Antaplaga* at another.

McDunnough grouped the stiriine genera with unspined tibiae closely towards the end of his Amphipyrinae, all preceding the heliothines *Microhelia, Heliothodes, Eutricopis,* and *Baptarma,* except *Xanthothrix,* which followed them.

The North and Central American stiriine genera (excluding those without a foretibial 'claw' formed from either a single, stout seta or several apically fused setae, or with a soft, unmodified, pad-like ovipositor) were treated by Hogue (1963) as a monophyletic group at the tribal level. He did not point to the biological similarity of the two groups: that stiriines and heliothines both inhabit, on the whole, seasonally dry regions, with larvae feeding on the flowers and fruits of their host-plants.

Hardwick (1970a) considered the possibility of a very close relationship between the two groups in some detail, and drew attention to the close association of heliothine genera with unspined mid- and hind-tibiae, and stiriines. Further, he pointed out the inadequacy of merely treating those genera of Hogue's tribe as the unit around *Stiria.* He listed the following genera as belonging to 'a more comprehensive Stiriinae': *Azenia, Oslaria, Stiriodes, Lythrodes, Tristyla, Xanthothrix, Crimona, Podagra, Pseudacontia, Walterella,* and *Prothrinax.* He noted the similarity of *Annaphila* to that of some stiriines but felt that the valves in *Annaphila* were sufficiently different for the genus to be excluded from the subfamily. He placed three genera with spined mid- and hind-tibiae, *Grotella, Neogrotella,* and *Hemigrotella,* in the Stiriinae and thought them close to *Stiriodes.* Franclemont & Todd (1983) again placed them as a tribe of the Heliothinae, presumably due to their mid- and hind-tibial spines.

Hardwick continued his analysis of the heliothine-stiriine relationship by pointing out the shortened and thickened nature of the fore-femur and fore-tibia in some heliothine and some stiriine genera, and that in both groups the fore-tibia may bear single or multiple spines, either with a smooth surface or with a ridged surface indicating partial fusion of several setae. This fore-tibial spining and the development of the frons into a corneous frontal process, which assumes a surprising diversity of shapes between species, are thought to be fossorial structures to enable the imago to dig its way out of the pupal cell to the surface of the soil in arid habitats where the ground is likely to be hard. This is a very reasonable suggestion, although it leaves open the question of how other noctuids in the same habitats pupating in the same manner make their escape when they lack both a frontal process and fore-tibial claws. Neither a corneous frontal process nor fore-tibial claws or spines, both of which occur sporadically in the noctuid faunas of xeric habitats, are apomorphic for either the Heliothinae or Stiriinae.

Hardwick drew upon the 'relative simplicity' of the male genitalia, with the strap-like shape of the valve and lack of differentiation of the sacculus and cucullus from the rest of the valve, as possibly being evidence of relationship. However, he noted immediately afterwards that simplicity in this respect is a doubtful synapomorphy.

7.2 DISCUSSION

Except in *Grotella dis*, which has an appendix bursae, there is great similarity in the female genitalia of the Stiriinae and less derived Heliothinae, for example *Baptarma felicita*, *Erythroecia* spp., *Heliothodes* spp., *Melaporphyria immortua*, and *Pyrrhia treitschkei*, in which the appendix bursae is very broad and shallow. In these, the ribbed sclerotization occurs in a less localized way on the posterior part of the bursa copulatrix and over the shallow appendix bursae; its extent cephalad along the ductus bursae is variable.

This contrasts with the position in the more derived Heliothinae, where this sclerotization occurs in a characteristic localized band around the base of the appendix bursae, and again to a variable extent caudad along the ductus bursae. Presumably, this sclerotization serves to toughen the part of the female that directly accepts the vesica of the male, for when the latter bears cornuti these would otherwise puncture the wall of the bursa copulatrix. Hardwick (1965) noted that the male may puncture the female in this way in *Helicoverpa*, so the cornuti on a turgid vesica clearly present such a danger during copulation requiring a corresponding toughening in the female.

In both the stiriines and those heliothines with a shallow appendix bursae, the male vesica occupies the posterior part of the bursa copulatrix during copulation but is not closely accommodated on all sides, as it is in a more developed appendix bursae. That the vesica fits snugly into the appendix bursae during copulation in species of *Schinia* or *Helicoverpa*, for example, can be seen from the correspondence of the number of coils in each.

The ostium bursae in both groups shows similar variations of form and when sclerotized is usually 'scrolled' dorsally at both sides. There is no development of the posterior margin of sternum 7. The lamellae ante-vaginalis in either group may be well developed and sclerotized, for example *Plagiomimicus argyroplius* (Hogue 1963; fig. 14k) and *Heliothis maritima*; sclerotized but reduced to a thin strip, for example most of Hogue's Stiriini and *Heliothis radiata*; or membranous, for example *Pyrrhia treitschkei* and *Panemeria tenebrata*. Although none of Hogue's Stiriini possesses a signum on the bursa copulatrix, the Old World *Megalodes eximia* does, and signa may be present or absent in the Heliothinae.

The male vesica in stiriines is saccate, whereas in the heliothines both saccate and elongate forms occur. Clearly, the conformation of the vesica is intimately related to the form of the bursa copulatrix into which it must fit. It was noted earlier that the presence of an appendix bursae in female heliothines is apparently the derived condition. If this is so, the elongate condition of the vesica in the male of these species must also be derived.

The vesica in stiriines generally bears two 'fields' of cornuti. In those heliothines with saccate vesicas bearing cornuti, the number of cornuti is considerably less than in stiriines, usually about six or less, although it can vary considerably even within a species. For example, some individuals of *Eutricopis nexilis* possess four cornuti, some three, some have none at all. Again, *Melaporphyria immortua* was not noted by Hardwick (1970a) as having cornuti. Very few males were available for dissection and those he examined evidently had none, but the single male of this species that I have dissected has two cornuti on a basal diverticulum (Fig. 184). In some stiriines the number of cornuti is reduced, for example in *Prothrinax luteomedia* (Fig. 429) and *Antaplaga composita*, or highly localized as in *Chamaeclea pernana*. It is therefore impossible in this respect to distinguish absolutely between the vesicas of certain Stiriinae and those of plesiomorphic Heliothinae.

Furthermore, in most heliothines a group of denticles occurs, situated towards the tip of the aedeagus or at the base of the vesica. This may be described as a scobinate bar or denticulate patch, depending upon how widespread the denticles are. Similar structures occur in many other noctuids. *Agrotis ipsilon*, for example, has a scobinate bar at the base of the vesica very similar to that in many *Heliothis* species. Such structures also occur in stiriines. A scobinate bar in the membrane of the base of the vesica is present in *Ectolopha viridescens* (Fig. 415) and *Megalodes eximia* (Fig. 417), and a denticulate patch, which is very like that on the tip of the aedeagus in *Aedophron* spp. (Figs. 156, 158, & 160), occurs in *Aegle koekeritziana* (Fig. 401), *A. vespertalis* (Fig. 405), and *Metaegle pallida* (Fig. 407).

It is also impossible to distinguish absolutely between the valves of both the Stiriinae and the Heliothinae. Generally, the valves of heliothines are less diverse in form than those of stiriines. Although a harpe occurs in some heliothines, they never have both a harpe and an additional process from the clasper as do some stiriines, for example *Plagiomimicus argyropolius* (Hogue 1963; fig. 26g). However, the simple valves of *Chamaeclea pernana, Panemeria tenebrata* (Fig. 424), *Aegle* spp (Figs. 400, 402 & 404), and *Metaegle* (Fig. 406), for example, cannot be differentiated satisfactorily from those of certain plesiomorphic heliothines, such as *Eutricopis nexilis* (Fig. 175), *Erythrophaia* spp. (Fig. 173), *Pyrrhia treitschkei* (Fig. 197), *Melaporphyria immortua* (Fig. 183), and *Derrima stellata* (Fig. 163).

As previously noted, Hardwick (1970a) indicated that *Annaphila* might be stiriine but did not include the genus in the Stiriinae on account of the form of the male valves.

Rindge and Smith (1952) described the life-histories of *Annaphila arvalis, A. depicta, A. diva,* and *A. evansi.* These differ somewhat from the life histories of heliothines and stiriines. *A. arvalis* feeds on the buds and blossoms of *Montia perfoliata* (Portulacaceae) and occasionally on the leaves in the last two instars. *A. diva,* on the same host plant, feeds on the flowers and buds in the first two instars and in later instars on the leaves as well. *A. depicta* feeds on the leaves of *Nemophila menziesii* (Hydrophyllaceae) 'in all instars, and the flowers, although sometimes eaten, appear not to be essential'. Only *A. evansi* feeds on the flowers of its host plants *Gilia lutea* and *G. brevicula* (Portulacaceae), never on the leaves. In these species the pupa is formed above ground, either inside hollow twigs (*A. arvalis* and *A. depicta*) or in a cocoon of dirt and silk attached to a twig (*A. diva* and *A. evansi*).

8. Taxa recognized in this study

The following list comprises the heliothine genera recognized in this study and the species in each which have been examined: it is not a checklist. The 14 generic names in the *Pyrrhia*-group are retained rather than synonymized with *Pyrrhia* for the reasons given in Section 14.1.1. At least one male and one female were examined for all the species listed unless otherwise stated. The three new taxa are described in Appendix 1.

1. THE *PYRRHIA*-GROUP
  - *Aedophron* Lederer, 1857
    - Type species: *Heliothis rhodites* Eversmann, 1851
      - *phlebophora* Lederer, 1858
      - *rhodites* Eversmann, 1851
      - *venosa* Christoph, 1887
  - *Baptarma* Smith, 1904
    - Type species: *Baptarma felicita* Smith, 1904
      - *felicita* Smith, 1904
  - *Derrima* Walker, [1858] 1857
    - Type species: *Derrima stellata* Walker, [1858] 1857
      - *stellata* Walker, 1857
  - *Erythroecia* Hampson, 1910
    - Type species: *Heliothis suavis* Edwards, 1884
      - *hebardi* Skinner, 1917 (Male only)
      - *rhodophora* Hampson, 1910 (Male only)
      - *suavis* Edwards, 1884
  - *Erythrophaia* Staudinger, 1891
    - Type species: *Erythrophaia eudoxia* Staudinger, 1891
      - *eudoxia* Staudinger, 1891
      - *suavis* Staudinger, 1888
  - *Eutricopis* Morrison, 1875
    - Type species: *Eutricopis nexilis* Morrison, 1875
      - *nexilis* Morrison, 1875
  - *Heliothodes* Hampson, 1910
    - Type species: *Heliothis diminutivus* Grote, 1873
      - *diminutivus* Grote, 1873
      - *fasciata* Edwards, 1875 (Male only)
      - *joaquin* McDunnough, 1946 (Male only)
  - *Melaporphyria* Grote, 1874
    - Type species: *Melaporphyria immortua* Grote, 1874
      - *immortua* Grote, 1874
  - *Microhelia* Hampson, 1910
    - Type species: *Heliodes angelica* Smith, 1900
      - *angelica* Smith, 1900
  - *Periphanes* Hübner, [1821] 1816
    - Type species: *Phalaena delphinii* Linnaeus, 1785
    - *delphinii* Linnaeus, 1758

Psectrotarsia Dognin, 1907
  Type species: *Psectrotarsia flava* Dognin, 1907
    flava Dognin, 1907

Pyrocleptria Hampson, 1903
  Type species: *Heliothis cora* Eversmann, 1837
    cora Eversmann, 1837

Pyrrhia Hübner, [1821] 1816
  Type species: *Noctua rutilago* [Denis & Schiffermüller], 1775, by subsequent designation by Grote, 1874. *Noctua rutilago* is a junior subjective synonym of *Phalaena umbra* Hufnagel, 1766
    bifasciata Staudinger, 1888
    exprimens Walker, 1857
    purpurina Esper, 1798
    treitschkei Frivaldszky, 1835
    umbra Hufnagel, 1766
    victorina Sodoffsky, 1849

Rhodoecia Hampson, 1910
  Type species: *Xanthia aurantiago* Guenée, 1852
    aurantiago Guenée, 1852

2. *PROTADISURA* **gen. nov.**
  Type species: *Chloridea posttriphaena* Rothschild, 1924
    posttriphaena Rothschild, 1924 **comb. nov.**

3. *ADISURA* Moore, 1881

Astonycha Turner, 1920 **syn. nov.**
  Type species: *Astonycha litarga* Turner, 1920
    aerugo Felder, 1874
    affinis Rothschild, 1921
    atkinsoni Moore, 1881
    bella Gaede, 1915
    callima Bethune-Baker, 1911
    cana Hampson, 1903 **comb. nov.** (Female only)
    dulcis Moore, 1881
    litarga Turner, 1920 **comb. nov.**
    malagassica Rothschild, 1924
    marginalis Walker, 1857
    parva **sp. nov.**
    purgata Warren, 1926
    stigmatica Warren, 1926
    straminea Hampson, 1902

4. *SCHINIA* Hübner, 1818

Protoschinia Hardwick, 1970a **syn. nov.**
  Type species: *Noctua scutosa* [Denis & Schiffermüller], 1775
Tricraterifronta Berio, 1941 **syn. nov.**
  Type species: *Tricraterifronta xanthiata* Berio, 1941
Uollega Berio, 1945 **syn. nov.**
  Type species: *Uollega ungemachi* Berio, 1945
    accessa Smith, 1906
    acutilinea Grote, 1878
    albafascia Smith, 1883
    alensa Smith, 1906 (Female only)
    arcigera Guenée, 1852
    argentifascia Barnes & McD, 1912 (Female only)
    aurantiaca Edwards, 1881 (Female only)
    avemensis Dyar, 1904
    balba Grote, 1881 (Female only)
    bicuspida Smith, 1891 (Female only)

bifascia Hübner, 1818	(Female only)
bimatris Harvey, 1875	
bina Guenée, 1852	
biundulata Smith, 1891	
brunnea Barnes & McDunnough, 1913	
carolinensis Barnes & McD, 1911	
chilensis Hampson, 1903	
chrysella Grote, 1874	
ciliata Smith, 1900	(Female only)
citrinellus Grote & Robinson, 1870	
concinna Smith, 1891	(Female only)
crenilinea Smith, 1891	(Female only)
cumatilis Grote, 1865	
cupes Grote, 1875	
diffusa Smith, 1891	(Female only)
dobla Smith, 1906	
ennatae Laporte, 1984 **comb. nov.**	(Male only)
errans Smith, 1883	
felicitata Smith, 1894	
florida Guenée, 1852	
gaurae J. E. Smith, 1797	
gloriosa Strecker, 1876	(Male only)
honesta Grote, 1881	(Male only)
hulstia Tepper, 1883	(Female only)
illustra Smith, 1906	(Female only)
indiana Kwiat, 1908	
intrabilis Smith, 1893	
jaegeri Sperry, 1940	
jaguarina Guenée, 1852	
ligeae Smith, 1893	(Male only)
lucens Morrison, 1875	
luxa Grote, 1881	
lynx Guenée, 1852	(Male only)
magdalenae Laporte, 1976 **comb. nov.**	(Female only)
masoni Smith, 1896	
meadi Grote, 1873	
mexicana Hampson, 1903	
miniana Grote, 1881	(Female only)
mitis Grote, 1873	
mortua Grote, 1864	
niveicosta Smith, 1906	
nundina Drury, 1770	
obliqua Smith, 1889	(Female only)
obscurata Strecker, 1898	
oleagina Morrison, 1875	(Female only)
pallicincta Smith, 1906	
parmeliana Edwards, 1882	(Male only)
perminuta Edwards, 1881	(Female only)
persimilis Grote, 1873	
pulchra Köhler, 1953	
pulchripennis Grote, 1874	
purpurascens Tauscher, 1809	
rivulosa Guenée, 1852	
rosea Smith, 1891	
roseitincta Harvey, 1875	(Male only)
roseoflammata Pinhey, 1956 **comb. nov.**	
rufipenna Hardwick, 1983	
sanguinea Geyer, 1832	(Male only)
sara Smith, 1907	(Female only)
saturata Grote, 1874	(Male only)
scarletina Smith, 1900	

scutosa [Denis & Schiffermüller], 1775 **comb. nov.**
separata Grote, 1879
septentrionalis Walker, 1858
simplex Smith, 1891 (Male only)
siren Strecker, 1876 (Female only)
sordida Smith, 1883
spinosae Guenée, 1852
sueta Grote, 1873
tenuescens Grote, 1883
tertia Grote, 1874
thoreaui Grote & Robinson, 1870 (Male only)
tobia Smith, 1906 (Female only)
trifascia Hübner, 1818
triolata Smith, 1906
tuberculum Hübner, 1827
ultima Strecker, 1876 (Male only)
ungemachi Berio, 1941 **comb. nov.**
unimacula Smith, 1891
vacciniae Edwards, 1875
velaris Grote, 1879 (Female only)
velutina Barnes & McDunnough, 1912 (Female only)
verna Hardwick, 1983
villosa Grote, 1864
volupia Fitch, 1857 (Female only)
walsinghami Edwards, 1881
xanthiata Berio, 1941 **comb. nov.**
sp. No.1 (Chile)

5. *HELIOLONCHE* Grote, 1873
Type species: *Heliolonche modicella* Grote, 1873
carolus McDunnough, 1936
modicella Grote, 1873
pictipennis Grote, 1875

6. *HELIOTHIS* Ochsenheimer, 1816
Type species: *Phalaena dipsacea* Linnaeus, 1767. *Phalaena dipsacea* is a juniour subjective synonym of *Phalaena viriplaca* Hufnagel, 1766
Hebdomochondra Staudinger, 1879 **syn. nov.**
Type species: *Hebdomochondra syrticola* Staudinger, 1879
Masalia Moore, 1881 **syn. nov.**
Type species: *Masalia radiata* Moore, 1881
Neocleptria Hampson, 1903 **syn. nov.**
Type species: *Heliothis punctifera* Walker, 1857
Rhodocleptria Hampson, 1903 **syn. nov.**
Type species: *Heliothis incarnata* Freyer [1838] 1839
adamsoni Pinhey, 1956 **comb. nov.**
albicilia Hampson, 1903 **comb. nov.**
albipuncta Hampson, 1910 **comb. nov.**
artaxoides Moore, 1881 **comb. nov.**
aureola Walker, 1856 **comb. nov.**
beatrix Moore, 1881 **comb. nov.**
bimaculata Moore, 1881 **comb. nov.** (Female only)
bivittata Walker, 1856 **comb. nov.**
borealis Hampson, 1903 (Male only)
cheesemanae Seymour, 1972 **comb. nov.**
conifera Hampson, 1913
crofti Pinhey, 1956 **comb. nov.**
cruentata Moore, 1881 **comb. nov.**
daphoena Hampson, 1910 **comb. nov.**
decorata Moore, 1881 **comb. nov.**
disticta Hampson, 1902 **comb. nov.**

distincta Schaus, 1898	(Male only)
dora Swinhoe, 1891 **comb. nov.**	
epimethea Viette, 1958 **comb. nov.**	
feildi Erschov, 1874 **comb. nov.**	(Male only)
fissifascia Hampson, 1903 **comb. nov.**	
flaviceps Hampson, 1903 **comb. nov.**	
flavigera Hampson, 1907	
flavirufa Hampson, 1910 **comb. nov.**	
flavistrigata Hampson, 1903 **comb. nov.**	(Female only)
flavocarnea Hampson, 1903 **comb. nov.**	(Female only)
galatheae Wallengren, 1856 **comb. nov.**	
hololeuca Hampson, 1903 **comb. nov.**	
incarnata Freyer, 1839	
irrorata Moore, 1881 **comb. nov.**	
latinigra Hampson, 1907 **comb. nov.**	
leucosticta Hampson, 1902 **comb. nov.**	
maritima Graslin, 1855	
metachrisea Hampson, 1903	
metaphaea Hampson, 1903 **comb. nov.**	(Female only)
mittoni Pinhey, 1956 **comb. nov.**	
modesta Moore, 1881 **comb. nov.**	
molochitina Berg, 1882	
nubigera Herrich-Schäffer, 1851	
sp. No. 2 (near *nubigera*)	
nubila Hampson, 1903 **comb. nov.**	
ononis [Denis & Schiffermüller], 1775	
oregonica Edwards, 1875	
peltigera [Denis & Schiffermüller], 1775	
perstriata Hampson, 1903 **comb. nov.**	
philbyi Brandt, 1941 **comb. nov.**	
phloxiphaga Grote & Robinson, 1867	
sp. No. 3 (near *phloxiphaga*)	
prorupta Grote, 1873	
punctifera Walker, 1857	
quilengesi Seymour, 1972 **comb. nov.**	
radiata Moore, 1881 **comb. nov.**	
roseivena Walker, 1854 **comb. nov.**	
sanguinolenta Moore, 1881 **comb. nov.**	
scutiligera Guenée, 1852	
semifusca Seymour, 1972 **comb. nov.**	(Female only)
senegalensis Guenée, 1852 **comb. nov.**	(Female only)
showaki Pinhey, 1956 **comb. nov.**	
sinuata Moore, 1881 **comb. nov.**	
sturmhoefeli Draudt, 1927	(Male only)
subflexa Guenée, 1852	
sublimis Berio, 1962 **comb. nov.**	(Male only)
syrticola Staudinger, 1879	
tergemina Felder, 1874	
terracottoides Rothschild, 1921 **comb. nov.**	
tosta Moore, 1881 **comb. nov.**	
transvaalica Distant, 1902 **comb. nov.**	
turtur Berio, 1939 **comb. nov.**	(Male only)
umbrifasciata Hampson, 1913 **comb. nov.**	
uncta Swinhoe, 1885 **comb. nov.**	(Male only)
unifasciata Bethune-Baker, 1911 **comb. nov.**	(Female only)
uniformis Warren, 1926 **comb. nov.**	(Female only)
virescens Fabricius, 1777	
sp. No. 4 (near *virescens*)	(Male only)
sp. No. 5 (near *virescens*)	(Male only)
sp. No. 6 (near *virescens*)	(Male only)
viriplaca Hufnagel, 1766	

xanthiata Walker, 1865

7. *HELIOCHEILUS* Grote, 1865
Type species: *Heliocheilus paradoxus* Grote, 1865
aberrans Butler, 1886 **comb. nov.** (Female only)
albipunctella de Joannis, 1925
aleurota Lower, 1901 **comb. nov.**
canusina Swinhoe, 1901 **comb. nov.**
cistella Swinhoe, 1901 **comb. nov.** (Female only)
cladotus Swinhoe, 1901
confertissima Walker, 1865
confundens Warren, 1926 **comb. nov.** (Male only)
cramboides Guenée, 1852 **comb. nov.**
cystiphora Wallengren, 1860 **comb. nov.**
discalis Hampson, 1903
eodora Meyrick, 1902 **comb. nov.**
fervens Butler, 1881 **comb. nov.**
flavitincta Lower, 1908 **comb. nov.**
ionola Swinhoe, 1901 **comb. nov.**
julia Grote, 1883 **comb. nov.** (Female only)
melibaphes Hampson, 1903 **comb. nov.**
moribunda Guenée, 1852 **comb. nov.**
multiradiata Hampson, 1902
neurias Meyrick, 1902 **comb. nov.** (Male only)
puncticulata Warren, 1926 **comb. nov.** (Male only)
roseus Matthews, 1987
sericea Warren, 1926 **comb. nov.** (Male only)
sulphurea Warren, 1926 **comb. nov.** (Male only)
toralis Grote, 1881 **comb. nov.**
translucens Felder, 1874 (Male only)
turbata Walker, 1858 **comb. nov.**
stigmatia Hampson, 1903
sp. No. 7 (Argentina)

8. *AUSTRALOVERPA* **gen. nov.**
Type species: *Thalpophila rubrescens* Walker, 1858
rubrescens Walker, 1858 **comb. nov.**
tertia Roepke, 1941 **comb. nov.**

9. *HELICOVERPA* Hardwick, 1965
Type species: *Noctua armigera* Hübner 1808
armigera Hübner, 1827
assulta Guenée, 1852
atacamae Hardwick, 1965
confusa Hardwick, 1965
fletcheri Hardwick, 1965
geletopoeon Dyar, 1921
hawaiiensis Strand, 1916
helenae Hardwick, 1965
minuta Hardwick, 1965
pallida Hardwick, 1965
punctigera Wallengren, 1860
toddi Hardwick, 1965
zea Boddie, 1850

10. *ENGUSANACANTHA* Berio, 1941
Type species: *Engusanacantha bilineata* Berio, 1941
bilineata Berio, 1941

9. Character analysis

9.1 INTRODUCTION

The following have in the past been considered of significance at the generic level in the Heliothinae: the development of the frons; the development of the fronto-clypeal lip or shelf, a reduced ('elliptoid') condition of the compound eye, the condition of the body vestiture, the presence or absence of setae on the mid- and hind-tibiae, the presence or absence of setae on the fore-tibiae and their degree of development if present, the venation, the macular pattern, the degree of sclerotization of the ovipositor in the female, and in both sexes, the form of the genitalia.

9.2 ANALYSIS OF NON-GENITALIC CHARACTERS

9.2.1 The development of the frons

In most heliothines the frons is smooth, rounded, and bulging; it is ventrally excised, making the ventral lip pronounced. This condition occurs in the three major groups, for example *Pyrrhia exprimens* (Fig. 5), *Schinia jaguarina* (Fig. 2), and *Helicoverpa armigera* (Fig. 18). However, modifications of the frons also occur in these groups and are not of generic significance. The least extreme kind of modification is the flattening of the frons seen in, for example, *Protadisura posttriphaena* (Fig. 1) and *Australothis rubrescens* (Fig. 25).

Modification resulting in a slight protuberance, sometimes in the form of a ridge, or by roughening of the frons (neither of which greatly alters the bulging, rounded form) occurs in the following species illustrated here: *Adisura atkinsoni* (Fig. 16), *Adisura parva* (Fig. 17), *Heliothis terracottoides* (Fig. 19), and *Canthylidia moribunda* (Fig. 20).

There is a tendency in the species of *Heliothis* formerly assigned to *Masalia* and *Timora*, and in *Heliocheilus*, for the frons to bear a vertical ridge or central 'point', as in *Heliothis terracottoides* and *Heliocheilus moribunda*; however, this is a condition which grades into the smooth, bulging form, and cannot be described as a discrete state.

In *Heliothis incarnata* (male, Fig. 22 & female, Fig. 23) the frons is comparatively long and the ventral excision begins very high on the frons. A somewhat similar condition occurs in *Heliothis punctifera* (Fig. 24), where the frons appears to overhang the ventral lip, and this overhanging part is transversely sclerotized and rough.

It is merely a question of degree before any of the variation described above becomes sufficiently pronounced to be called a 'frontal protuberance' or 'transverse crenellation' ('ridging'); it is therefore not possible to discern discrete states in these modifications.

Almost all the gross frontal modifications in the Heliothinae, whether into a protuberance or transverse ridging, occur in the *Pyrrhia*-group. This is not surprising in view of the widespread gross modification of the frons into frontal protuberances in the stiriines (at least in Hogue's (1963) Stiriini) because the *Pyrrhia*-group appears most similar to the stiriines in other respects as well. Examples of such gross modification are seen in *Basilodes chrysopis* (Fig. 4) and the many excellent illustrations of different protruberances in Hogue (1963).

In *Eutricopis nexilis* (Fig. 12), although the head is compressed anteroposteriorly, as it also is in *Heliothodes diminutivus* (Fig. 13), the frons is rounded and bulging; in the latter species it is developed into a protuberance. In *Heliolonche modicella* (Fig. 3) the frons does not bulge, but this is apparently because the base of the much enlarged ventral lip occurs high on the frons.

9.2.1.1 The development of a frontal tubercle

Hardwick (1970a) thought the development of a frontal tubercle to be of generic significance in the Heliothinae. However, when the world fauna is considered, species with and species without frontal tubercles do occur in the same genus: *Schinia xanthiata* has a very pronounced frontal tubercle (Berio, 1941; figs. a & b) and so do *Schinia ungemachi* and *Schinia roseoflammata*. These three species are here included for the first time in *Schinia*, the other species of which do not have modified frons (e.g. *S. jaguarina*, Fig. 2). Furthermore, I do not find it possible to distinguish absolutely between a frontal tubercle and a transversely ridged frons (see Section 9.2.1.2. below). Frontal tubercles are illustrated by Hardwick (1970a) in *Baptarma felicita* (fig. 4), *Heliothodes diminutivus* (fig. 3), and *Microhelia angelica* (fig. 2).

9.2.1.2 The transverse ridging of the frons

Hardwick (1970a) was clearly not convinced of the value of this feature in providing characters at the generic level. Nor am I.

Two of the four species in the *Erythroecia suavis* species-group exhibit transverse ridging of the frons: *Erythroecia suavis* itself and *E. rhodophora*. In *E. hebardi*, which I have been able to examine through the kindness of Dr Eric Metzler (University of Maryland, USA), the frons is roughened: it could be interpreted as displaying the condition seen in *E. suavis* and *E. rhodophora* to a reduced degree. If this is the case, then the frons in *Periphanes delphinii* (Fig. 9) and *Pyrrhia victorina* (Fig. 6), both of which exhibit transverse crenellation, would be intermediate between [*Erythroecia suavis* + *E. rhodophora*] and *E. hebardi*. The condition in *E. hebardi* is perhaps closest to that in *Aedophron venosa* and *A. phlebophora*, and possibly also *Pyrrhia treitschkei* (Fig. 7). Furthermore, although the frons of the fourth *Erythroecia*-group species (*Psectrotarsia flava* from coastal Peru) is modified, in this species it forms a frontal tubercle with no trace of transverse ridging.

I have found it impossible to describe the modifications of the frons in heliothines in a way that permits breakdown into a few discrete states that can sensibly be placed in a transformation series. One can either say that the frons is modified or not modified, or describe each different modification separately. Neither is of any help in grouping species unless the species can be confidently said to display exactly the same sort of modification, and this is still no help in deciding how such a pair or cluster of species is related to any others. There seems to be no way in which the development of the frons can be used at the generic level in the Heliothinae.

9.2.2 The development of the clypeal lip

An unusual development of the clypeal lip occurs in *Heliolonche modicella*, (Fig. 3). Hardwick (1970a) did not consider this of generic importance and placed *Heliosea*, which does not possess the pronounced clypeal lip, in synonymy with *Heliolonche*.

9.2.3 The reduced or 'elliptoid' condition of the compound eye

Reduction of the compound eye to a smaller elliptoid shape has, in the past, been used as a character of generic significance in the subfamily. Warren (1911), whose classification has been discussed above, characterized his Heliothidinae in this way. Reduced, elliptoid eyes occur in *Baptarma felicita* (Hardwick, 1970;

fig. 4), *Eutricopis nexilis* (Fig. 12), *Heliolonche modicella* (Fig. 3), *Heliothodes diminutivus* (Fig. 13), several species of *Schinia*, and several species of *Heliothis*. The condition is correlated with a diurnal habit. After a detailed study, Hardwick (1958) did not even consider the elliptoid-eyed species within *Schinia* to be a monophyletic group.

9.2.4 The condition of the body vestiture

In the Heliothinae there is continuous variation of the body vestiture from the dense covering of spatulate scales in, for example, *Pyrrhia umbra* and *Helicoverpa* spp., to the sparse, hair-like scales of, for example, *Eutricopis nexilis*. The sparse, hair-like condition appears to be correlated with a diurnal habit and thus also with reduced eyes.

9.2.5 The presence or absence of setae on the mid- and hind-tibiae

The historical significance of these setae or spines has been discussed earlier. The splitting of the Heliothinae between the Agrotinae and the Amphipyrinae under Hampson's system provides an excellent example of how a well established 'character' can continue to obscure relationships for decades for no better reason than that it is well established.

Hardwick (1970a) considered it valuable at the generic level because if many small genera are accepted in the *Pyrrhia*-group, then the character works at the generic level in the restricted fauna he treated. However, when the world fauna is studied, this is not so. *Periphanes delphinii* has a few small setae on its mid- and hind-tibiae (Figs. 517 & 518) and species of *Erythrophaia* possess well developed setae on these tibiae, for example *E. eudoxia*, Figs. 502 & 503. The genitalia of these species are clearly so very similar in form to those in the rest of the *Pyrrhia*-group that to regard these spines as apomorphies (uniquely derived characters) at the generic level is not sensible.

This is further supported by the fact that in the *Heliothis*-group, classically split off from the *Pyrrhia*-group *because* of spines on the mid- and hind-tibiae, we find a continuous grade from quite heavy spining in, for example *Heliothis oregonica* (Figs. 570 & 571), to very light spining in the species hitherto assigned to *Masalia* and *Timora*. Indeed, the female specimen of *Heliothis radiata* I dissected has just two spines on each mid-tibia (Fig. 585) and none at all on either of the hind-tibiae (Fig. 586).

This raises the question of whether or not two discrete states of this 'character' actually exist in the Heliothinae at all. I do not believe they do. Is a condition such as that described above for a specimen of *Heliothis radiata* to be regarded as closer to one of heavier spining on all mid- and hind-tibiae, or one of no spines at all? In fact, spining of the mid- and hind-tibiae grades continuously from an absence of spines on all tibiae, through intermediate forms beginning with one spine on one of the mid- or hind-tibiae, to forms with a few spines on all mid- and hind-tibiae, to forms with heavier spining on all mid- and hind-tibiae, such as in *Heliothis oregonica*. Because such a grade cannot be divided into discrete states it cannot be used to characterise or group taxa within the Heliothinae. Berio (1959; p. 288) produced a table for tibial spining in the Ophiderinae and Catocalinae. By presenting the data in the following order: fore-tibia (male), fore-tibia (female); hind-tibia (male), hind-tibia (female); mid-tibia (male), mid-tibia (female), he formed a graded series from spining on all tibiae to no spining at all.

9.2.6 The presence or absence of setae on the fore-tibiae

Two separate problems exist with respect to assigning the fore-tibial setae to discrete states: one is that they continuously grade in size from small 'spinules' to more massive 'claws', the other is that there may be from one to many on each fore-tibia. Thus they pose a similar problem of character analysis to that of the mid- and hind-tibial setae.

The only reason that two different characters, namely fore-tibial spining *versus* mid- and hind-tibial spining, have been recognized in the past is that mid- and hind-tibial spining was one of Hampson's primary criteria for subdividing the Noctuidae. There is no reason to prefer Hampson's two 'characters' to either of the following: fore- and mid-tibial spining *versus* hind-tibial spining, or treating the spining on each of the three pairs of legs separately.

The best foil to the argument that mid- and hind-tibial spining exists in the discrete states 'present' and 'absent' is provided by specimens with spines present on the mid-tibiae but absent on the hind-tibiae, or *vice versa*, an example of which I gave earlier. The same rebuttal is not possible here because insects have only two fore-tibiae not four. However, this is no good reason to regard fore-tibial spining *per se* as in any sense different from mid- and hind-tibial spining.

Table 2

The possible combinations of tibial spining

Fore-tibia	Mid-tibia	Hind-tibia	Heliothine example
x	x	x	*Eutricopis nexilis*
x	x	spined	(no example known)
x	spined	x	(no example known)
x	spined	spined	*Adisura* spp.
spined	x	x	*Derrima stellata*
spined	x	spined	*Heliothis radiata*
spined	spined	x	(no example known)
spined	spined	spined	*Heliothis* spp.

If we consider just one character, 'tibial spining' in the Heliothinae, there are eight possible combinations of spine distribution on the tibiae and thus eight possible characters which could be treated separately. To date, examples of five of the eight possible combinations are known to occur (see Table 2 above). I do not believe it is possible to place these in a transformation series with any significance whatsoever for the illumination of generic relationships in the subfamily.

9.2.7 The venation

The modification of the forewing in the group around *Heliocheilus paradoxa* was described by Matthews (1987). Hardwick (1970a) considered that this characterized a section of *Heliothis* and said that *Heliocheilus* might be recognized in a subgeneric sense. In Matthews (1987), *Heliocheilus* is accorded generic status and the species of *Canthylidia, Raghuva,* and those in *Heliothis* with a modified forewing in the male, were grouped under it.

Although *Canthylidia* and *Raghuva* are certainly objective synonyms of *Heliocheilus,* by treating *Heliocheilus* as a full genus (Matthews, 1987) I created a formal problem because at the end of the present study I am unable to provide convincing synapomorphies to assign the other species of *Heliothis* (including those formerly placed in *Masalia* and *Timora*) to monophyletic groups, with the exception of the five species of the *virescens*-group (Poole and Mitter, in press). This means that to recognize *Heliocheilus* as a genus leaves *Heliothis* as a paraphyletic group. This problem will be resolved if apomorphies are found for other species groups within *Heliothis,* in addition to the *virescens*-group, which account for all these other species. Nevertheless, the forewing modification in the males of *Heliocheilus* species certainly seems to be a good apomorphy. Although not a genitalic structure it is clearly intimately associated with the sexual behaviour of the species that possess it (Matthews, 1987) (see Fig. 746) and thus might be regarded as being under similar selection pressures to the genitalia, rather than those pressures acting on structural features not directly associated with reproduction.

9.2.8 The macular pattern

The macular (spotting) pattern in the Heliothinae does not provide characters of significance at the generic level. Hardwick (1970a) stated this for the species of *Schinia*, which display a great range of macular patterns. He also recognized that the characteristic pattern of longitudinal streaks on the forewings of some species formerly assigned to *Masalia* and *Timora*, and in some species of *Heliocheilus*, does not characterize a group because it grades into other forms of maculation.

9.2.9 The degree of ovipositor sclerotization

According to Hardwick (1970a), the modification of the ovipositor into a hard, knife-like structure through sclerotization is a character of generic significance, a sclerotized condition being present in all species of *Schinia* and absent in all species of *Heliothis*. Although true for the North American fauna, this is not true for the Heliothinae as a whole. Within the genus *Schinia*, *S. chilensis*, *S. mexicana*, and an undescribed species from Chile have soft, pad-like ovipositors. Furthermore, sclerotized ovipositors do occur in some species of *Heliothis* hitherto assigned to *Masalia* and *Timora*, and in *Heliocheilus* (Matthews, 1987). In these *Heliothis* species the sclerotized ovipositor may be either laterally flattened, as in *Heliothis sanguinolenta* (Fig. 116), or dorsoventrally flattened, as in *Heliothis radiata* (Fig. 109). The same situation occurs in the *Pyrrhia*-group, where some species possess strongly sclerotized ovipositors, for example *Aedophron* spp. (Figs. 27, 28, & 29), and others soft, pad-like ovipositors, for example the four species in the *Pyrrhia umbra* species-group studied here (Figs. 42, 43, 44, & 46). Intermediate stages also occur, for example *Pyrrhia victorina* (Fig. 47).

The form of the ovipositor is intimately associated with the site of oviposition in each species. It is sclerotized in those species that force the tip of the abdomen into a confined space to lay their eggs. This aspect of heliothine biology is beautifully illustrated for many North American species in the life-histories published by Hardwick. I have observed this in the African species *Heliocheilus albipunctella*, where the female inserts her ovipositor beneath the surface of a developing millet head (Fig. 747) to deposit her eggs between the involucral bristles surrounding each grain and the grain itself (Fig. 745). Thus the degree of sclerotization of the ovipositor is determined by the preferred site of oviposition of the species concerned. The natural history of this is discussed in another section.

9.3 ANALYSIS OF GENITALIC CHARACTERS

9.3.1 The female genitalia

The great similarity of the male and female genitalia of stiriines and basal heliothines was noted in the section on the heliothine-stiriine relationship.

If the stiriines are the sister group of the heliothines then, by outgroup comparison, the forms of female genitalia in the *Heliothis*-group and the *Schinia*-group must be derived from heliothine ancestors with a very shallow appendix bursae, such as *Erythroecia suavis* (Fig. 33) and *Melaporphyria immortua* (Fig. 39). Of course, the vesica of the male in all these species is saccate. *Erythrophaia suavis* (Fig. 35), *E. eudoxia* (Fig. 34), and *Derrima stellata* (Fig. 31), which all have a saccate vesica in the male, do possess an appendix bursae in the female. It is, however, unlike that in the *Schinia*-group, *Heliothis*, or *Helicoverpa*; rather than being partially or wholly membranous, it is moderately sclerotized.

The four species in the *Pyrrhia umbra* species-group are unusual in that they appear on first inspection to have a well developed appendix bursae, with similar overall form and relationship to the remainder of the bursa copulatrix as in *Heliothis viriplaca* (Fig. 95). In fact, this is not the case at all. The ductus seminalis in the *Pyrrhia umbra* species-group is in the same place as in

Rhodoecia aurantiago, Erythroecia suavis, Baptarma felicita and so on, but in these species there has either been an invagination of the anterior part of the fundus bursae or a development of the fundus bursae behind the ductus seminalis. Whilst this additional sac resembles an appendix bursae, the position of the ductus seminalis indicates that it is not homologous with the appendix bursae in *Heliothis* and *Schinia*. There is no difficulty, therefore, in including the four species around *Pyrrhia umbra* studied here with other basal heliothines possessing a broad and shallow appendix bursae.

In the rest of the Heliothinae, the female possesses a well developed appendix bursae. Essentially, this consists in *Heliothis* of a simple sac which varies from almost spherical, for example *Heliothis adamsoni* (Fig. 113), to long and narrow, for example *Heliothis ononis* (Fig. 89); in *Helicoverpa* of a very long, tough sac which is alternately dilated and constricted and may be slightly coiled, especially distally, for example *H. armigera* (Fig. 137); and in *Schinia* of a comparatively narrow sac twisted into a regular spiral, for example *S. jaegeri* (Fig. 71). In these derived heliothines, it is in *Heliothis* that the correspondence of the shape of the appendix bursae to that of the vesica is least well developed. Although the vesica in *Helicoverpa* is regularly coiled, and so to an intermediate degree is the appendix bursae, this correspondence between the male and female genitalia is most pronounced in the *Schinia* group, where the coils of the appendix bursae precisely match those of the vesica.

In *Heliothis*, the ductus seminalis is attached 'anteriorly' to the appendix bursae in those forms with a long appendix, for example *Heliothis viriplaca* (Fig. 95) and *H. maritima* (Fig. 85). However, in the *Heliothis* species formerly assigned to *Masalia* and *Timora*, and in *Heliocheilus*, there is a strong tendency for the appendix bursae to be apparently oriented 'posteriorly'. This is most marked in *Heliocheilus* species, for example *H. cystiphora* (Fig. 125), *H. roseus* (Matthews, 1987; fig. 68), and *H. cladotus* (Fig. 123). Unfortunately, no discrete character states can be said to exist because this 'posterior' orientation grades through intermediates, such as *Heliothis showaki* (Fig. 117) and *Heliothis philbyi* (Fig. 108) with a 'lateral' orientation, into the 'anterior' orientation described above.

Does the alternately dilated and constricted appendix bursae in *Helicoverpa* represent either the character state from which that in the *Schinia*-group was derived, or one derived from that in the *Schinia*-group? I do not believe such a relationship exists for the following reason. In *Heliothis*, the sclerotization that begins on the ductus bursae extends cephalad and forms a 'collar' around the base of the appendix bursae. This sclerotization is not smooth but ridged, and, although very short, the ridges in the part forming the 'collar' are aligned with the long axis of the appendix bursae. In contrast, in the *Schinia*-group this sclerotization (which may be either smooth or ridged) follows the inside of the spiral of the appendix bursae almost to its tip, in a narrow and very well defined strip. In *Helicoverpa*, the sclerotization occurs along the ductus bursae and around the base of the appendix bursae, as it does in *Heliothis*. However, instead of being distinctly restricted to a narrow collar, the ridges in *Helicoverpa* do extend onto the appendix bursae, although there they are much less pronounced and thus less distinct from the membrane of the appendix bursae (which is in any case much toughened in this genus). It is as though the short ridges aligned with the long axis of the appendix bursae in *Heliothis* were extended up the appendix bursae in a less strongly expressed way in *Helicoverpa*.

A single species appears at first sight to present an intermediate condition between that of the *Heliothis*-group and that of the *Schinia*-group. In *Protadisura posttriphaena* (Fig. 49), the comparatively broad appendix bursae is curved into the basal part of a spiral. However, in this respect it forms no more of a spiral than the appendix bursae in, for example, *Heliothis xanthiata* (Fig. 96), *Heliothis radiata* (Fig. 109), *H. decorata* (Fig. 104), or *Heliothis daphoena* (Fig. 114). What is important is that in *Protadisura posttriphaena* the sclerotization on the ductus bursae follows the inside of the curve of the appendix bursae to the ductus seminalis at its tip. In this it resembles the other species of the *Schinia*-group, and is quite different from any *Heliothis*-group species with a curved appendix bursae.

The simplest way of interpreting the female genitalia in the Heliothinae, if it is accepted that the long and narrow appendix bursae of the *Schinia*-group and *Helicoverpa* do not represent consecutive character states in a transformation series, is as follows. The first heliothines possessed broad, shallow appendices bursarum that were not differentiated into distinct sacs as in *Baptarma felicita*, *Microhelia angelica*, and *Melaporphyria immortua* which are not appreciably different from those of stiriines. Some development of the part of the bursa copulatrix around the ductus seminalis then gave rise to forms such as the two *Erythrophaia* species and *Derrima stellata*, where, in as much as the appendix bursae is developed, it is covered with the sclerotization that in stiriines and other basal heliothines covers the area around the ductus seminalis.

For the reasons given above I do not regard the appendix bursae of *Heliothis* and *Helicoverpa* as homologous with that of the *Schinia*-group. It is therefore more plausible to suppose that, on the one hand, the appendix bursae in the *Schinia*-group was derived from the basal heliothine form as a spiral development of the area around the ductus seminalis, and, on the other hand, that the appendix bursae in the *Heliothis*-group was derived as a wholly membranous development *between* the ductus seminalis and the sclerotized area surrounding its origin on the bursa copulatrix.

9.3.2 The aedeagus and vesica

In the male, the aedeagus and eversible vesica are associated with deposition of the spermatophore within the bursa copulatrix so that the frenulum (Callahan, 1958) is deposited opposite the ductus seminalis, for it is from this end that the spermatozoa leave the spermatophore. The uncus and valves are associated with gripping the female just before and during copulation. Because of this independence of function, the aedeagus and vesica, and the valves and tegumen, are presumably subject to different selection pressures. This may explain, at least in part, how a certain constancy may be maintained in the form of the vesica while the form of the valves is more variable. Put another way, it may be that provided a correspondence between the vesica and bursa copulatrix is maintained for the successful transfer of spermatophores, the form of the valves is free, within certain limits, to change without affecting this process.

By outgroup comparison, the saccate vesica in the Heliothinae is the state that gave rise to more elongate forms because no stiriine with an elongate vesica is known. In any case, as I noted earlier in the section on the heliothine-stiriine relationship, I find it impossible to distinguish absolutely between the aedeagus and vesica, and the valves, of certain stiriines and those of some basal heliothines.

The features of the aedeagus and vesica for which I have tried to find discrete character states are the following. First, the scobinate bar or denticulate patch; when present this may be located on the distal end of the aedeagus, on the distal end of the aedeagus and the basal part of the vesica, or more or less entirely in the membrane of the basal part of the vesica. Second, the diverticula of the vesica, which may or may not bear cornuti. Third, the cornuti on the vesica of some forms. Fourth, the overall shape of the vesica.

The shape of the aedeagus itself simply seems to reflect the nature of the vesica contained within it. It is relatively long and slender when the vesica is long and elongate, and shorter and stouter when the vesica is short.

9.3.2.1 The scobinate bar or denticulate patch

This structure presumably serves to anchor the aedeagus and vesica more firmly in the bursa copulatrix during copulation. However, it is completely absent in the *Schinia*-group and is lost in certain *Heliothis*-group and *Pyrrhia*-group species also. When present it displays a considerable variety of form in the Heliothinae, both in its position on the aedeagus and vesica, and in the nature of the component denticles. This variety of form within the subfamily is illustrated by Figs. 643-674. I had hoped that this structure would provide characters enabling better resolution of the *Pyrrhia*-group but cannot with any confidence place the different forms exhibited into discrete states within a transformation series.

The denticles in the *Pyrrhia*-group tend to be spread over a greater area than in the *Heliothis*-group and are thus better described as a 'denticulate patch'. In the *Pyrrhia*-group, they may occupy a position wholly on the aedeagus, such as in *Heliothodes diminutivus* (Figs. 651 & 652) or *Aedophron* spp., for example *A. rhodites* (Figs. 643 & 644). They may be partly on the aedeagus and partly on the vesica, such as in *Pyrrhia umbra* (Figs. 655 & 656), *P. treitschkei* (Figs. 653 & 654), and *P. victorina* (Figs. 657 & 658) in which the tube formed by the aedeagus appears, at least in scanning electron micrographs, to be extended by the stiffening of the vesica on account of the denticles. Finally, they may be almost wholly in the membrane of the vesica, as in *Erythroecia suavis* (Figs. 171, 647, & 648). A scobinate patch may be entirely lacking in the *Pyrrhia*-group, as in *Periphanes delphinii* (Figs. 188, 189, & 190) and *Melaporphyria immortua* (Fig. 184).

In the *Heliothis*-group, the denticles are typically expressed in a long, narrow bar at the very base of the vesica, for example *Heliothis flavigera* (Figs. 659 & 660) and *Heliocheilus cystiphora* (Figs. 669 & 670). They may be almost lost, as in *Heliothis decorata* (Figs. 665 & 666), or compressed into a much shorter group of denticles, as in *Australothis rubrescens* (Figs. 671 & 672) or *Heliothis radiata* (Figs. 667 & 668). In certain *Heliothis* species formerly assigned to *Masalia* and *Timora*, the denticles are developed into long, finger-like structures; this is well illustrated by Figs. 667 & 668 (*Heliothis radiata*).

The denticles are absent in *Heliothis maritima*, and a sclerotized strip or plaque occurs in the vesical membrane at its base. However, this is not in the same place as the scobinate bar but is in a ventral position (Figs. 661 & 662).

In some *Heliothis* species, especially those formerly assigned to *Masalia* and *Timora*, a structure associated with the scobinate bar occurs. A 'scale-like cornutus' (Seymour, 1972) is developed in the membrane on the part of the vesica which opposes the scobinate bar during copulation in such a way that the sclerotized 'collar' around the base of the appendix bursae must be gripped between them. This structure was used by Seymour (1972) to characterize the genus *Masalia*, and the species he included tend also to have stout forelegs (the tibiae of which bear two heavy claws) and a longitudinally streaked pattern on the forewings. Unfortunately, he did not examine a sufficient number of other *Heliothis* species to see that this 'scale-like cornutus' also occurred outside his genus *Masalia*. Of the species I have examined, *Heliothis peltigera* (Fig. 294) has a 'scale-like cornutus', and the structure is partially developed in *H. xanthiata* (Fig. 304) and *H. flavigera* (Fig. 278).

It is these species that provide a clue to the derivation of this feature. Minute sclerotized granules occur on the vesicas of many noctuids, giving those parts on which they occur a speckled appearance. In the *Heliothis*-group, the surface of the vesica is more or less differentiated into three types, although some overlap does occur. Part of it appears smooth, another part appears speckled, and the rest to be lightly sclerotized and ridged, with the ridges at right-angles to the long axis of the vesica. In forms exhibiting an intermediate condition between a well developed 'scale-like cornutus' and none at all, one or more of the ridges become sclerotized and protrude somewhat from the surface of the vesica. Not only are there intermediates, but the 'scale-like cornutus' occurs both in those species formerly assigned to *Masalia* and *Timora*, and in the group around *Heliothis viriplaca*, namely in *H. nubigera*.

In *Helicoverpa*, the scobinate bar is expressed mainly on the very edge of the aedeagus, and the denticles are rather finer and more delicate than in *Heliothis*. However, at the posterior end of the bar (i.e. towards the tip of the aedeagus) they move onto the vesical membrane (see Figs. 673 & 674). *Australothis rubrescens* and *A. tertia* both possess quite small, oval patches of denticles. In both species the patch is well away from the edge of the aedeagus; in this they resemble *Heliothis*, not *Helicoverpa*.

9.3.2.2 The diverticula of the vesica

In no heliothine is the vesica just a simple sac: they all possess diverticula to a greater or lesser degree, which must contribute towards anchoring the vesica in the bursa copulatrix during copulation. These diverticula are most prominent in the *Pyrrhia*-group and one or two species of *Adisura*; they almost always bear cornuti in the *Pyrrhia*-group and in *Adisura*. Cornuti are present in *Protadisura*.

The diverticula may be little more than 'bumps' on the surface of the everted vesica, as for example in *Baptarma felicita* (Fig. 162) and *Eutricopis nexilis* (Fig. 176). They are relatively larger in species such as *Derrima stellata* (Fig. 164) and *Erythrophaia* spp. (Figs. 172 & 174), and reach their greatest development in, for example *Pyrrhia umbra* (Fig. 200), *Erythroecia* spp. (Figs. 168 & 170), and *Adisura bella* (Fig. 215).

When well everted and hardened, so that they maintain the shape they must assume when turgid within the bursa copulatrix during copulation, the saccate vesicas in many of the *Pyrrhia*-group present complex three-dimensional shapes. Once again, I hoped at first that careful preparation of these structures would enable improved resolution of relationships within the *Pyrrhia*-group. Diagramatic representations of the vesicas of sixteen *Pyrrhia*-group species and *Adisura bella*, drawn from my slides, are given in Figs. 754-770. In several species, certain arrangements of diverticula and cornuti appeared to be homologous, for example the basal sausage-shaped diverticulum (which I have shaded) in *Derrima stellata* (Fig. 757), *Pyrrhia tretischkei* (Fig. 759), *Baptarma felicita* (Fig. 762), and possibly *Erythroecia suavis* (Fig. 764). However, I found it quite impossible to devise a system that could account for all the diverticula as homologous for more than three or four species at a time. Furthermore, the surprising variety of diverticula in the four specimens of *Periphanes delphinii* that I have dissected, three of which are illustrated in Figs. 188, 189, & 190, makes it clear that a thorough assessment of intraspecific variation of the vesica of *Pyrrhia*-group species is necessary before a serious attempt can be made to homologize these diverticula, if indeed they really are all homologous which I suspect in many cases they are not.

The coiled distal part of the vesica in *Schinia* species is produced from a basal pouch. The basal pouch is generally simple although there is always at least a single bulge on the side opposite the base of the distal part of the vesica. Sometimes this may be divided into more than one sac, for example in *Schinia snowi* (Hardwick, 1970a; fig. 84).

In the *Heliothis*-group, the diverticula are comparatively small and located at the very base of the vesica. In species with a longer vesica there is generally a single basal pouch opposite the base of the long part of the vesica; this is well illustrated in, for example, *Heliothis prorupta* (Fig. 298), *H. borealis* (Fig. 274), and *H. peltigera* (Fig. 294). Almost all the species of *Heliocheilus* have five small, but well defined diverticula on the base of the vesica, and this is clearly visible in the undescribed Argentinian species illustrated in Fig. 355. However, such a condition also occurs in some species formerly assigned to *Masalia* and *Timora*, for example *Heliothis roseivena* (Fig. 337). Furthermore, not all *Heliocheilus* species possess as many as five small diverticula: *Heliocheilus paradoxus*, for example, has only two larger diverticula (Fig. 381, & Hardwick, 1970a; fig. 46). Thus, although there is a strong tendency in the '*Masalia-Timora*' section of *Heliothis*, and in *Heliocheilus*, for the vesica to possess five small diverticula, this condition grades into one of fewer, larger diverticula, and cannot be divided into discrete states.

It may simply be that the number and size of the diverticula in *Heliothis* are correlated in a broad way with the overall length of the vesica, because single, large diverticula occur in the species with the longest vesicas, and multiple, smaller diverticula occur in those with the shortest vesicas.

The base of the complex vesica of *Helicoverpa* bears from two to several diverticula. Although small in relation to the whole vesica, which is very long and slender, they may nevertheless be quite prominent and finger-like, as is clearly visible in *Helicoverpa fletcheri* (Fig. 397). In addition, they may bear smaller, subsidiary diverticula themselves, for example *Helicoverpa hawaiiensis* (Hardwick, 1965; fig. 34). The two species of *Australothis*, the genus intermediate between *Heliothis* and *Helicoverpa* in other characters, possess two well developed basal diverticula. These appear to be slightly less broad, and are thus more finger-like, in *Australothis rubrescens* (Fig. 391) than in *A. tertia* (Fig. 393).

9.3.2.3 The vesical cornuti.

Cornuti are present on the vesicas of all *Pyrrhia*-group species, within the *Schinia*-group in *Adisura* and *Protadisura*, and in the *Heliothis*-group in *Helicoverpa* and *Australothis.*

In the Heliothinae, the cornuti on the saccate vesicas of the *Pyrrhia*-group display the greatest variety of size and form. They may be stout and tooth-like, for example the rearward-pointing cornutus in the four species of the *Pyrrhia umbra* species-group studied here (Figs. 192, 194, 196, & 200), or they may have well-developed disc-like bases as in *Pyrrhia treitschkei* (Fig. 198), or they may be bent at the base as in the two *Erythrophaia* species (Figs. 172 & 174). More usually they are simply straight and needle-like.

The cornuti present a very similar problem of homology to that of the vesical diverticula in the *Pyrrhia*-group which is scarcely surprising because the diverticula generally bear the cornuti. It is easy enough to identify the short, tooth-like cornutus, and the long, needle-like cornutus in each of the four species of the *Pyrrhia umbra* species-group considered here. But it is another matter to fit these into a system of homologous cornuti for all the species in the *Pyrrhia*-group; I have tried, but found it impossible. The contention that such a system may not exist is supported by the fact that the cornuti are often quite variable within species. As I noted earlier, none of the specimens of *Melaporphyria immortua* that Hardwick (1970a) examined has any cornuti, but the single specimen I have examined has two (Fig. 184); *Eutricopis nexilis* may have from one (Fig. 176) to four cornuti (Hardwick, 1970a), while in *Periphanes delphinii* (Figs. 188, 189, & 190) cornuti show considerable variation.

In the *Schinia*-group, cornuti are absent in all species of *Schinia* and *Heliolonche*, but present in all *Adisura* species examined except a single Kenyan specimen (Fig. 225). In this individual, the distal part of the vesica is scarcely coiled (as it is in all other *Adisura* species), and it may be an aberrant individual. I have dissected malformed genitalia of male *Heliothis maritima* and female *Heliocheilus albipunctella* during this study, thus such an occurrence is not so infrequent as to be out of the question. Malformation of the male and female genitalia in a heliothine is documented by Hardwick (1970b), who pointed out that *Heliothis stombleri* Okumura & Bauer was described on the basis of aberrant genitalia in *Helicoverpa zea*. It will not be possible to say with any certainty, however, whether or not this truly represents an *Adisura* species without cornuti until the species-level taxonomy of *Adisura* is better understood.

In *Adisura*, the cornuti, of which there are almost always only two, are borne side by side on a basal diverticulum. Occasionally there are three cornuti, and sometimes only one. The diverticulum that bears them may be short, as in *A. dulcis* (Fig. 219) and *A. parva* (Fig. 233); moderately long, for example in *A. callima* (Fig. 217); or very long, as in *A. bella* (Fig. 215) where it bears a surprising resemblance to the tentacle-like diverticulum of *Pyrrhia umbra* (Fig. 200), *P. bifasciata* (Fig. 192), *P. exprimens* (Fig. 194), and *P. purpurina* (Fig. 196).

In the specimen of *Protadisura posttriphaena* I dissected for this study (Fig. 208), there is a single cornutus on one part of a two-pouched basal diverticulum.

Another male dissected in the BMNH clearly possesses two cornuti (BM Noct 4044), and perhaps more usually in this species each of these pouches bears a cornutus making a total of two (as is typical in *Adisura*). However, it is impossible to see the relation of the two cornuti to the basal pouches in this second specimen (BM Noct 4044) because the vesica is not properly everted.

If the single specimen of an *Adisura* species without cornuti (Fig. 225) described above is indeed aberrant, then the presence or absence of cornuti provides a good discontinuous character separating the species of the *Schinia*-group into [*Schinia* + *Heliolonche*] and [*Protadisura* + *Adisura*].

All species of *Helicoverpa* bear cornuti on the vesica. Hardwick (1965) identified a transformation from a primitive state (most closely allied to that exhibited by *Australothis*) to a derived state for this character as follows.

> 'Moreover, the spines on the outer side of the coils of the vesica, which in the primitive species are of similar size and arranged in a continuous or broken series, are in the higher groups of dissimilar size and arranged in graded clusters, with the largest spine in the middle of each cluster. In addition to other changes in the structure of the vesica, a great reduction has occurred in the size of the spine borne on the basal plate; in primitive species it is large and prominent, in more recently evolved species it is small, inconspicuous or even absent.'

The derived condition that he describes is illustrated by *Helicoverpa armigera* (Fig. 395).

An intermediate stage between the larger, sparser cornuti of *Helicoverpa* species and the naked vesica of *Heliothis* occurs in the long and narrow strip of minute, dense, spinule-like cornuti of *Australothis rubrescens* and *A. tertia* (Figs. 391 & 393). These two species are again intermediate between other *Heliothis* species and *Helicoverpa* with respect to the 'basal spine'. This spine is absent in *A. tertia* and all *Heliothis* species, but present, albeit in reduced form, in *A. rubrescens.*

9.3.2.4 The overall shape of the vesica

The forms of vesica found in the Heliothinae have been described earlier. The problem here is whether or not the discrete states described above can be placed in a convincing transformation series.

Without a thorough understanding of how spermatophores are formed during copulation in such a way that the frenulum lies opposite the ductus seminalis, we might be wrong to assume that simply because there is no close correspondence evident to the human eye there is not, in fact, a very restricted set of shapes which the vesicas of the *Pyrrhia*-group can assume for successful deposition of spermatophores. It is highly likely that an important factor in this will be the influence of a spermatophore already deposited within the bursa copulatrix. Not only must a male copulating with a non-virgin female be able to inflate his vesica within the bursa copulatrix which already contains a spermatophore, he must also ensure that the first spermatophore is displaced so that the frenulum of the spermatophore he deposits lies opposite the ductus seminalis, a position already occupied by the frenulum of the first spermatophore.

Certain species can be grouped together within the *Pyrrhia*-group on the basis of the overall shape of the vesica. This is true of the four species in the *Pyrrhia umbra* species-group studied here, and the four species in the *Erythroecia suavis* species-group. Broadly speaking, the larger species, such as *Pyrrhia* spp. and *Erythrophaia* spp., have more structurally complex vesicas than the smaller species, such as *Eutricopis nexilis, Heliothodes* spp., and *Microhelia angelica.* However, this is probably a reflection of size itself rather than of phylogeny. I am unable to account for the diversity of forms in the *Pyrrhia*-group other than by calling them all 'saccate', or by describing them all separately. The latter would be both lengthy and provide no help in the resolution of relationships within the group.

The most important question to be answered in this section is as follows. Is the regular coiling of the vesica in the *Schinia*-group homologous with the regular coiling of the vesica in *Helicoverpa*? I have already explained why I do not regard the coiled appendix bursae in the *Schinia*-group as morphologically homologous with that in *Helicoverpa*. If this is correct, it would be impossible for the coiling of the vesica in *Helicoverpa* to be homologous with that in the *Schinia*-group if the coiling of the appendix bursae in these groups is non-homologous.

Further support for this contention is provided by the cornuti on the vesicas of, on one hand, *Adisura* species, and on the other *Helicoverpa* and *Australothis*. In *Adisura*, the cornuti always occur on a basal diverticulum of the vesica whereas in *Helicoverpa* they do not: they occur along the entire length of the vesica. In itself, this would be strong evidence to support the notion that the state 'cornuti present on the vesica' is non-homologous in *Adisura* and *Helicoverpa*. However, additional evidence for this view is provided by the two species of *Australothis*. Given the form of the vesica in these two species, the intermediate state between an absence of cornuti in *Heliothis* and their arrangement on the vesica in *Helicoverpa* is not one in which, say, the basal half of the vesica bears cornuti and the distal half does not. If it was, then the hypothesis that the coiled vesica bearing cornuti along its length in *Helicoverpa* was derived from a coiled vesica bearing cornuti only at its base would be stronger. However, this is not the case. Whether or not the state of the vesica in *Heliothis* was derived from that in *Helicoverpa* or *vice versa* is not important; it seems clear that the cornuti on the vesica in the *Heliothis*-group either all appeared or disappeared along its entire length at once. They do not, therefore, appear to be homologous with the basal cornuti in *Adisura*.

This leads to the following question. Is it possible to derive the vesica in *Adisura*, or that in *Helicoverpa*, from the saccate vesica bearing cornuti of the *Pyrrhia*-group? It was noted earlier that the cornuti on the vesicas of the *Pyrrhia*-group tend to be borne on the diverticula. It was also noted that there is a similarity of form and position in the basal diverticulum which is sausage-shaped in *Derrima stellata*, *Pyrrhia treitschkei*, *Baptarma felicita*, *Erythroecia suavis*, *Melaporphyria immortua*, and *Pyrocleptria cora*. In these species, this basal diverticulum tends to bear two cornuti, although I cannot say with confidence that this is an homologous structure in all of them; to do so would require all the other cornuti to be accounted for in a system of homology and this I am unable to do. Nevertheless, should a saccate vesica bearing cornuti on diverticula become elongate distally, with the diverticula and cornuti bearing the same relation to the aedeagus as they did before, then an elongate vesica bearing cornuti on basal diverticula would result. In this way, it would be possible to derive the vesica of *Adisura* from that of the *Pyrrhia*-group. An apparently intermediate species exists. *Protadisura posttriphaena* could be interpreted as possessing the basal diverticulum of *Adisura* (with the two cornuti) without having developed the regular distal coiling of the other *Adisura* species, and it provides evidence supporting this hypothesis of derivation.

9.3.3 The valves

Broadly speaking, the valves of heliothines with saccate vesicas, that is the *Pyrrhia*-group, display a much greater variety of form between species than do the valves in the *Heliothis*-group and the *Schinia*-group. In fact, because of their overall homogeneity of form, the valves contribute very little towards resolution of relationships in the subfamily. Their variability is restricted to differing degrees of stoutness of the valve and clasper, the presence or absence of a harpe, and the presence or absence of a corona. They are at their simplest in the flat, unelaborated valves of *Aedophron* spp. (Figs. 155, 157, & 159), *Baptarma felicita*

(Fig. 161), *Eutricopis nexilis* (Fig. 175), *Erythrophaia* spp. (e.g. Fig. 173), *Microhelia angelica* (Fig. 185), *Pyrrhia treitschkei* (Fig. 197), and *Pyrocleptria cora* (Fig. 205) which have neither a harpe nor a corona. These are very like certain stiriines, for example *Aegle vespertalis* (Fig. 404), *Chalcopasta koebelei*, *Chamaeclea pernana*, *Ochrocalama xanthiata* (Fig. 422), *Panemeria tenebrata* (Fig. 424), and *Xanthothrix* spp.

There are forms in the *Pyrrhia*-group in which the valves strongly resemble those in the *Heliothis*-group and the *Schinia*-group, particularly in that they are 'recurved' distally in a very characteristic heliothine fashion. This is especially so in the four species in the *Pyrrhia umbra* species-group studied here (Figs. 191, 193, 195, & 199), *Periphanes delphinii* (Fig. 187), and even the very small *Heliothodes diminutivus* (Fig. 177).

In the *Pyrrhia*-group, the following possess a harpe: *Pyrrhia umbra* (Fig. 199), *P. bifasciata* (Fig. 191), *P. exprimens* (Fig. 193), and *P. purpurina* (Fig. 195), the four species in the *Erythroecia suavis*-species group studied here (Figs. 165, 167, & 169); *E. hebardi* (not illustrated), and *Melaporphyria immortua* (Fig. 183).

Whereas the valves of most stiriines possess a harpe, the only large species-group of heliothines to do so is *Schinia*. Almost all species of *Schinia* itself possess a harpe; an exception to this, however, is the group of species containing *Schinia snowi* (Hardwick, 1970a; fig. 84), *S. rosea* (Fig. 259), *S. ennatae* (Fig. 271), *S. magdalanae*, *S. roseoflammata* (Fig. 267), and *S. xanthiata* (Fig. 269). There is no harpe in *Heliolonche*. In *Adisura*, several species have a slight bump on the part of the valve that bears a harpe when a harpe is present but in no case is it ever produced as a finger-like process. *Protadisura posttriphaena* (Fig. 207), however, does possess a harpe.

Some *Adisura* species possess remarkable valves, which are ventrally very strongly emarginate, for example *A. stigmatica* (Fig. 228). This modification of the valve gives the rather angular sacculus the appearance of protruding beyond the margin of the valve. However, this cannot be used as an apomorphy of *Adisura* because it grades from its most pronounced development in species such as *A. stigmatica* through intermediates such as *A. litarga* (Fig. 234) and *A. marginalis* (Fig. 222) to a more typical heliothine condition, such as in *A. parva* (Fig. 232). Further evidence for the grouping of *Protadisura posttriphaena* with the species of *Adisura* is provided by the valve shape which is like that in moderately emarginate forms and possesses the characteristic protruding, angular sacculus. This latter feature also occurs to a greater or lesser degree in many species of *Schinia*.

The harpe is evidently a labile structure, being frequently gained or lost, so it is perhaps not surprising that 'presence of a harpe' cannot be used as a firm synapomorphy between any two groups in the Heliothinae; it is at best an 'underlying synapomorphy' or homoiology. Nevertheless, features which are felt to be homoiologies can be put forward as supporting evidence for groupings defined by other characters. In this regard, the presence of a harpe in certain *Pyrrhia*-group species and in *Schinia* and *Protadisura posttriphaena* supports the hypothesis that the *Schinia*-group was derived directly from forms with saccate vesicas like the *Pyrrhia*-group.

Neither the degree of development of the corona nor the stoutness of the valve and clasper can be used at the generic level in the Heliothinae.

10. THE IMMATURE STAGES

10.1 OVA

Hardwick (1958) studied and described in detail the eggs of the North American species of elliptoid-eyed *Schinia*. He was, however, not able to distinguish absolutely between the eggs of the different species, nor did he identify any generic characters from the eggs of the Heliothinae.

There is considerable variety in the form of heliothine eggs. Rather than being of phylogenetic significance, this variation appears to have clear ecological correlates in that the form of the eggs depends upon their size and site of oviposition. It is, in other words, a corollary of the life-history strategy, as pointed out by Hardwick (1958). Those species which oviposit inside the heads of their foodplants generally have eggs which are elongate and comparatively large, whereas those which oviposit on the outside generally have eggs which are short and broad.

The eggs of seven species of Heliothinae are illustrated here in a comparative series of SEMs. The micropylar area of each species is figured at approximately the same magnification; the micrographs of whole eggs are at a range of magnifications, depending upon their size. The *Pyrrhia*-group is represented by *Eutricopis nexilis* (Figs. 675 & 676); the *Schinia*-group by *Schinia niveicosta* (Figs. 681 & 682), *S. jaegeri* (Figs. 679 & 680), and *Adisura bella* (Figs. 677 & 678); the *Heliothis*-group by *Heliothis decorata* (Figs. 683 & 684), *Heliocheilus confertissima* (Figs. 685 & 686), and *Helicoverpa armigera* (Figs. 687 & 688).

Schinia jaegeri clearly illustrates the elongate, elliptical shape described by Hardwick (1958). We know from his work on the life-history of this rare species that it has a very low fecundity: no wild-caught female that he confined laid more than 19 eggs (Hardwick, 1972c). Two species with ovoid eggs are illustrated here: *Eutricopis nexilis* and *Schinia niveicosta*; *E. nexilis* has a very low fecundity, but *S. niveicosta* is in fact moderately fecund (see Table 4). The other species illustrated have more or less spherical eggs. Except in *Heliothis decorata*, where the secondary and tertiary cells surrounding the micropyle are better developed, only the primary cells in this region are clearly visible. In *Heliothis decorata* and *Heliocheilus confertissima*, the reticulation on the surface of the egg is more or less absent, leaving prominent ridges radiating away from the micropylar area that give the egg a 'flanged' appearence.

When the eggs of heliothines are elongate, the reticulations of the surface are confined to the micropylar end: they are not spread out over the surface, most of which thus appears smooth. It is also in the elongate eggs of heliothines that aeropyles are apparent; when they occur, they are situated at the angles of the cells around the micropyle as in *Schinia niveicosta*, or along the ridges as in *Eutricopis nexilis*. They appear to be absent in those species with smaller, more spherical eggs.

That the shape of the egg is not of great significance for the development of the larva within is illustrated by Hardwick's (1958) observation that in *Schinia separata* the egg is deposited 'between the bases of the innermost sepals' of a bud of *Artemisia tridentata*, where it may be squeezed and severly distorted. In Hardwick (1971f), he states that the same is true for *Schinia walsinghami*, which feeds on *Chrysothamnus nauseosus*.

It may well be that the elongate shape facilitates deposition in flower heads as Hardwick suggested, however, it probably also facilitates passage of the egg through the oviduct. By becoming elongate, the egg may increase in volume without increasing in diameter, thus the oviduct need undergo no gross changes in order to permit eggs to pass through it in those species where an increase in egg volume accompanies specialization of feeding preferences.

10.2 LARVAE

The best apomorphies of the Heliothinae are structural characters of the larvae. However, only one structural character from this life-history stage has been found which may characterize a species-group, although certain other characters have been suggested, and these are also discussed below.

Hardwick (1958) considered in detail the larvae of elliptoid-eyed species of *Schinia* available to him, and said that at the specific level they were 'much more readily separable on the basis of colour, maculation, and food plant than of morphological features.' He further noted that he was unable to distinguish larvae of species of *Schinia* from those of species of *Heliothis*.

Crumb (1926) provisionally suggested that the third segment of the labial palp being equal in length to, or only slightly longer than the second segment, was apomorphic for *Heliothis*. He considered four species: *Heliothis phloxiphaga*, *H. virescens*, *Helicoverpa zea*, and *Heliocheilus cystiphora*. However, Hardwick (1958) stated that this was also true for *Schinia villosa*, and, in addition, that in some species of *Schinia* the third segment of the labial palp is up to twice as long as the second.

Baker, Parrott, & Jenkins (1986) compared the sensory receptors on the larval maxillae and labia of *Helicoverpa zea* and *Heliothis virescens*. In view of the overlap between genera in other characters from the mouthparts discussed above, it is not sensible to propose the use of these differences as characters at the generic level, and in any case, no real comparison is possible without data for at least a third species from either *Helicoverpa* or *Heliothis*.

The third segment of the maxillary palp of *Schinia mitis* is illustrated by SEMs in Grimes & Neunzig (1986a; figs. 61-63). In another paper these authors illustrate the maxillary lobe of *Helicoverpa zea* by SEMs (Grimes & Neunzig, 1986b; Figs. 49-52).

In the first couplet of his key to the family, Crumb (1956) divided the Noctuidae into *larvae liberae* if the 'venter is free posteriorly' and *larvae confluentae* if the venter is 'confluent with the subanal area'. This character was later clarified by Godfrey and Stehr (1985) in a short paper illustrated with light micrographs and SEMs. The larvae of the Heliothinae (and Stiriinae) are *larvae liberae*, as is illustrated for *Pyrrhia exprimens* (Fig. 713) and *Helicoverpa fletcheri* (Fig. 714).

Crumb (1956) distinguished two sections of the subfamily in his key to heliothine larvae 'on fairly good grounds'. The two characters he employed for this separation were as follows.

1. Height of prothoracic spiracle, at most, but slightly less than height of spiracle on abdominal segment 8 (23:25), their heights usually equal. Crochets on prolegs uniordinal except in *Schinia gloriosa*.............................. 2

   Height of prothoracic spiracle decidedly less than height of spiracle on 8 (20:25). Crochets biordinal except in *Dasypoudaea* [*Schinia*] *lucens*.......... 14

The 'section' characterized by the first couplet comprises only certain *Schinia* species. That characterized by the second couplet comprises the other *Schinia* species Crumb treated, *Rhodoecia aurantiago*, *Pyrrhia umbra*, *Heliothis virescens*, *H. phloxiphaga*, and *Helicoverpa zea*. I am not at all convinced of the value of either of these characters. In the first place, while it is comparatively easy to identify the strongly uniordinal condition of the crochets in stiriine larvae, or the biordinal condition in, for example *Heliothis phloxiphaga*, I found that it was not always easy to make such a decision. It may well be that there is no clear distinction between the two states of this character in the Heliothinae, and Hardwick (1958) did not mention it. He also ignored the 'spiracle height' character given by Crumb (1956), presumably because he concluded, as I have, that it offers nothing upon which to base groups within the subfamily. The ratios within species seem to vary considerably, even with very small samples, so that I do not have confidence in Crumb's difference between 23:25 and 20:25. Again, although most of the *Heliothis*-group species I studied do have ratios of less than 20:25, the few *Heliocheilus* species I studied do not, and in *H. albipunctella* the ratio is almost unity.

I studied the chaetotaxy of the larvae listed at the end of this section but could find nothing of generic significance. Hardwick (1958) mentioned no such character, and merely remarked that there was nothing of significance at the specific level in the chaetotaxy of the North American species of elliptoid-eyed *Schinia*.

Hardwick discovered certain specific characters in the hypopharyngeal complex of elliptoid-eyed *Schinia* species. These differences were in the degree to which the distal- and proximomedial-regions are covered in spinules, and the form of the proximolateral spines. Beck (1960) and Godfrey (1972) in their systematic works on larvae considered the hypopharyngeal complex as good sources of taxonomic charcters. I prepared a comparative series of SEMs of the hypopharyngeal complexes of heliothine larvae, dissecting them out from the rest of the mouthparts as described by Godfrey (1972). However, despite variation of the same features as described by Hardwick (1958), I am unable to discern any characters that can be used at the generic level. This series is presented in Figs. 689-699 with representatives of the *Pyrrhia*-group (*Eutricopis nexilis, Pyrrhia umbra, P. purpurina, P. victorina*, and *Periphanes delphinii*), the *Schinia*-group (*Schinia florida*), and the *Heliothis*-group (*Heliothis virescens, H. tergemina, H. incarnata*, and *Heliocheilus albipunctella*).

Peterson (1962) considered four heliothines, *Heliothis ononis, H. virescens, H. subflexa*, and *Helicoverpa zea* in his treatment of lepidopteran larvae. He stated that the chalazae bearing D1 and D2 on A1, A2, and A8 of *Heliothis virescens* and *H. subflexa* bear 'microspines' like those on the rest of the skin, whereas those of *H. ononis* and *Helicoverpa zea* do not, and he illustrated this condition in *H. virescens* (fig. L36E), *H. subflexa* (fig. L36I), and *Helicoverpa zea* (fig. L36O). The spining of these chalazae is also prominent on blown material in the BMNH of another *virescens*-group species, *H. tergemina*. This may provide a larval apomorphy for the *virescens*-group of *Heliothis*, although it would be desirable to investigate more *Heliothis* species outside the *virescens*-group. The difference between the spined and unspined conditions of setal chalazae in heliothines is illustrated for those on A9 by Fig. 739 (*Heliothis viriplaca*), Fig. 738 (*Pyrrhia exprimens*), and Fig. 740 (*Helicoverpa fletcheri*).

Crumb (1926) noted in his key that *Heliothis virescens* has a large basal process on the oral face of the mandible, and that *Heliothis phloxiphaga* and *Helicoverpa zea* do not. Peterson (1962) also noted and illustrated this for *Heliothis virescens* (fig. L36F), and also for *H. subflexa*, in which the process is somewhat reduced (fig. L36J). Although such processes or 'teeth' are common on the mandibles of noctuids, the possibility that within the Heliothinae it might have proved apomorphic for the *virescens*-group of *Heliothis* was worth investigating. I prepared a series of SEMs of heliothine mandibles from the material available to me, and these are illustrated in Figs. 700-712. Unfortunately, many of these mandibles are worn to a greater or lesser extent and it is therefore difficult to assess whether a development of that part of the mandible represents a very worn large process, or a slightly worn small process. What is at once clear, however, is that although it is well developed in *Heliothis tergemina*, a basal process on the oral surface is not apomorphic for the *virescens*-group of *Heliothis*, because it also occurs in *Pyrrhia umbra, P. purpurina, P. exprimens*, and possibly *Pyrrhia victorina* and *Heliothis viriplaca*.

Larvae of the following species were examined. Numbers in brackets indicate the number of specimens available for study. *Baptarma felicita* (6); *Eutricopis nexilis* (5); *Helicoverpa armigera* (15); *H. fletcheri* (5); *H. gelotopoeon* (4); *H. zea* (1); *Heliocheilus albipunctella* (25); *H. cystiphora* (2); *H. lupata* (3); *H. paradoxus* (5); *Heliolonche modicella* (3); *H. pictipennis* (2); *Heliothis maritima* (7); *H. molochitina* (25); *H. oregonica* (3); *H.phloxiphaga* (3); *H. prorupta* (1); *H. tergemina* (25); *H. virescens* (5); *H. viriplaca* (5); *H. incarnata* (5); *H. punctifera* (3); *Periphanes delphinii* (3); *Pyrrhia exprimens* (4); *P. purpurina* (2); *P. umbra* (3); *P. victorina* (2); *Rhodoecia aurantiago* (2); *Schinia citrinella* (5); *S. cupes* (4); *S. felicitata* (3); *S. florida* (3); *S. imperialis* (1); *S. indiana* (5); *S. intrabilis* (4); *S. jaegeri* (7); *S. ligiae* (3); *S. niveicosta* (4); *S. pallicincta* (4); *S. pulchripennis* (4); *S. purpurascens* (4); *S. scarletina* (4); *S. sueta* (3); *S. triolata* (3); *S. walsinghami* (4).

10.3 PUPAE

Mosher (1916) considered the following heliothines in her study of lepidopteran pupae: *Schinia gaurae, Heliothis virescens,* and *Pyrrhia umbra.*

Her work remains the only review of this life-history stage for the order. As far as I am aware, nowhere else have the Heliothinae and Hadeninae been grouped together within the Noctuidae. However, Mosher treated these heliothines under the heading 'Hadeninae' with the following: *Cirphis [Pseudaletia] unipuncta, Meliana [Faronta] albilinea, Laphygma [Spodoptera] frugiperda, Prodenia [Spodoptera] ornithogalli, Lycophotia margaritosa [Peridroma saucia], Hadena [Apamea] vulgaris, Polia [Lacinipolia] renigera, Eriopus [Callopistria] floridensis,* and *Monima [Apamea] alia.*

As with the larvae, Hardwick (1958) did not point to any characters from the pupae which could be used at the generic level. However, he found that the following could be used for species differentiation: colour; the relative lengths of caudal and thoracic appendages, especially the length of the mesothoracic legs relative to that of the proboscis, (and to a lesser extent the 'relative lengths of proboscis and metathoracic legs'); the pits on the surface of A5-A7; and 'the presence or absence of punctations on other abdominal segments and the relative density of these' .

Nakamura (1974) discovered chaetotactic characters from the pupae of the 21 species of Japanese Plusiinae he studied which he considered of possible use at the generic level, but Hardwick (1958) did not find any such characters in the chaetotaxy of heliothine pupae.

11. Host-plant information

The number of host-plant references from the agricultural literature on heliothines is enormous, but most of them are redundant because the same moth species are recorded many times from the same crop plants.

I compiled a list of 862 host-plant references in an attempt to cover the Heliothinae as broadly as possible. It is very incomplete, but my aim was simply to see whether or not any patterns of host-plant preference might emerge, providing characters to illuminate phylogenetic relationships within the subfamily. Although I was surprised at the number of heliothine species for which host-plant references exist, the lack of structure in these data is disappointing; they are mostly crops, herbaceous weeds, and garden plants. The information I collected (of which 328 entries are redundant) is summarized in Appendix 2, in which only the first record of a given species on a given host-plant is included.

Although there are certain species and groups of species that display a high degree of host-plant specificity (especially in the genus *Schinia*) or appear to feed only on one plant family, there is apparently no overall pattern in the host-plant data other than a preponderance of higher dicotyledons in the Tubiflorae. Both host-specific and general feeders occur in the *Pyrrhia*-group, the *Schinia*-group, and the *Heliothis*-group.

However, there seem to be two groups of heliothines with restricted host-plant preferences. First, although other *Heliothis*-group species (both in *Heliothis* and *Helicoverpa*) feed on Gramineae, no *Heliocheilus* species has been recorded from any other plant family, and the geographical spread of these records is comprehensive (Africa, Australia, and North America). Second, many, but by no means all, *Schinia* species feed on Compositae.

12. Life-history strategies

The host-plant information available for the Heliothinae is the result of the work of many entomologists around the world. We also have some data on the fecundity of certain species in each of the three major groups, this being almost entirely due to the painstaking efforts of Hardwick both in the field and laboratory. These data are summarized in Table 3.

Table 3

The fecundities of certain Heliothinae

Species	Mean	Maximum	No. of Females	Refs.
Eutricopis nexilis	7.8	10	5	1
Heliolonche carolus	14	26	4	2
H. pictipennis	28.5	41	4	3
Schinia jaegeri	-	19	several	4
S. pallicincta	40.3	74	5	5
S. walsinghami	67	69	2	6
S. intrabilis	83	132	3	7
S. separata	91	119	3	8
S. cupes	-	93	1	9
S. felicitata	116	161	5	10
S. niveicosta	157	183	5	11
S. citrinellus	-	176	1	12
Heliothis oregonica	172	202	3	13
Heliocheilus albipunctella	400	-	-	14
Pyrrhia exprimens	-	724	1	15
Helicoverpa assulta	688	1011	8	16
H. zea	1075	2240	18	17
H. hawaiiensis	1368	2392	4	18
H. armigera	1072	4394	24	19

1. Hardwick, 1970c
2. Hardwick, 1969
3. Hardwick, 1971
4. Hardwick, 1972c
5. Hardwick, 1972d
6. Hardwick, 1971f
7. Hardwick, 1972b
8. Hardwick, 1971e
9. Hardwick, 1971c
10. Hardwick, 1967
11. Hardwick, 1966a
12. Hardwick, 1972d
13. Hardwick, 1971b
14. Gahukar *et al.*, 1986
15. Hardwick, 1970d
16. Hardwick, 1965
17. Hardwick, 1965
18. Hardwick, 1965
19. Hardwick, 1965

In his monograph on the genus *Helicoverpa*, Hardwick (1965) outlined his ideas on the evolution of life-history strategies within the Heliothinae. Given the very great range of fecundities among heliothines, he pointed out that correlated with low fecundity and increased egg-size are: sclerotization of the ovipositor, associated with deposition of the eggs within the blossom of the food-plant; increased food-plant specificity; modification of the typical noctuid maculation of, for example, *Helicoverpa* species, to one that camouflages the adult on the flowers of the food-plant; and decreased adult vagility (mobility).

Faced with the correlation of traits described above, the following may be asked. Do the groupings supported by structural characters indicate a transformation through heliothine evolution from generalized feeding and high fecundity, to specialized feeding and low fecundity, or *vice versa*? Or do specialized feeding and low fecundity, and generalized feeding and high fecundity (and their associated traits), occur together in the major groups of the subfamily? If the latter is true, then the derivation of one life-history strategy from the other must have occurred several times.

The results of the present analysis suggest that the correlation of traits described by Hardwick (1965), which does hold when the North American fauna is considered, may be a simplification of the situation in the subfamily as a whole. First, the relationships of *Helicoverpa, Heliothis,* and the *Schinia*-group in Hardwick's (1970a) cladogram are not supported. This means that if more-or-less discrete states of a life-history strategy character really did occur in *Helicoverpa, Heliothis,* and the *Schinia*-group, they would still not form the transformation series outlined by Hardwick (1965). Second, despite the fact that in most instances the correlation of traits described above does hold across the range of life-history strategies, there are anomalies. *Heliocheilus albipunctella* is recorded as laying about 400 eggs (Gahukar *et al.*, 1986). This is not surprising, as it seems that *Heliothis* species do in general lay hundreds rather than tens or thousands of eggs (Hardwick, 1965), but *H. albipunctella* has a well-sclerotized ovipositor.

In fact, sclerotized ovipositors occur in several species of *Heliothis* formerly assigned to *Masalia* and *Timora,* and several *Heliocheilus* species, and it may prove that a sclerotized ovipositor is not necessarily associated with a particularly low fecundity in this group. Furthermore, when the world fauna is considered, there are *Schinia* species with soft, pad-like ovipositors (see below), and in *Adisura* there are both forms with soft, pad-like ovipositors, and others with well sclerotized, knife-like ovipositors.

Last, although the status of *Helicoverpa* as a group of high fecundity and broad feeding preferences remains at present unchanged (but see below), *Schinia* is apparently not exclusively a group of low fecundity and high host-plant specificity. We know that *Schinia chilensis,* which has a soft, pad-like ovipositor, is a pest of economic importance in Chile (Jana-Saenz & Angulo, 1985), where it attacks maize, beans, cotton, vetches, and other crops. Clearly, this species does not have low fecundity and a restricted host range, but a life-history strategy more like that of a *Heliothis* or *Helicoverpa* species. Two further species of *Schinia* discussed here (those undescribed from Chile and Mexico) have soft, pad-like ovipositors and the elements of typical noctuid maculation like *S. chilensis.*

Most interestingly, there is a distinct possibility that a *Helicoverpa* species exists with a life-history strategy of low fecundity and restricted host-plant preference. However, *Heliothis pauliana* Viette, 1959 from Amsterdam Island is known only from a single female which Hardwick was unable to examine until after his revision of *Helicoverpa* (Hardwick, 1965). In the following year he drew attention to the liklihood that *Heliothis pauliana* is a species of *Helicoverpa* (Hardwick, 1966b), contrasting the bright colouring and unusual maculation of *H. pauliana* with the typical facies of *Helicoverpa* species. Unfortunately, because Amsterdam Island (37°52'S 77°32'E) is in the southern Indian Ocean, about half-way between Australia and South Africa, further material will be difficult to obtain.

Thus it does not appear that a transformation from high fecundity and its correlated traits to low fecundity and its correlated traits has occurred in the evolution of the Heliothinae as Hardwick (1965) suggested. This is for the following reasons. First, the morphological evidence does not support the groupings which underlay his suggestion. Second, within the world fauna of a major heliothine group such as *Schinia* very different life-history strategies occur. In addition, the correlation of life-history and morphological traits described by Hardwick (1965), although true for the North American fauna, does not hold for the world fauna.

13. Hardwick's classification

As will be apparent, Hardwick's contribution to the systematics of the Heliothinae has been prodigious. However, apart from his work on *Helicoverpa*, a well defined natural group that he was the first to recognize (Hardwick, 1965), his studies have been focused on the North American fauna. The limitations imposed on the phylogenetic analysis of a cosmopolitan group by a regional perspective are similar to those imposed by the 'exemplar' method. Both suffer from a restricted view of the character variation that actually exists in the group. This is despite the fact that the heliothines are very well represented in North America; about 40% of the described species occur there, although this bias is attributable to the quite remarkable diversity of *Schinia* on that continent.

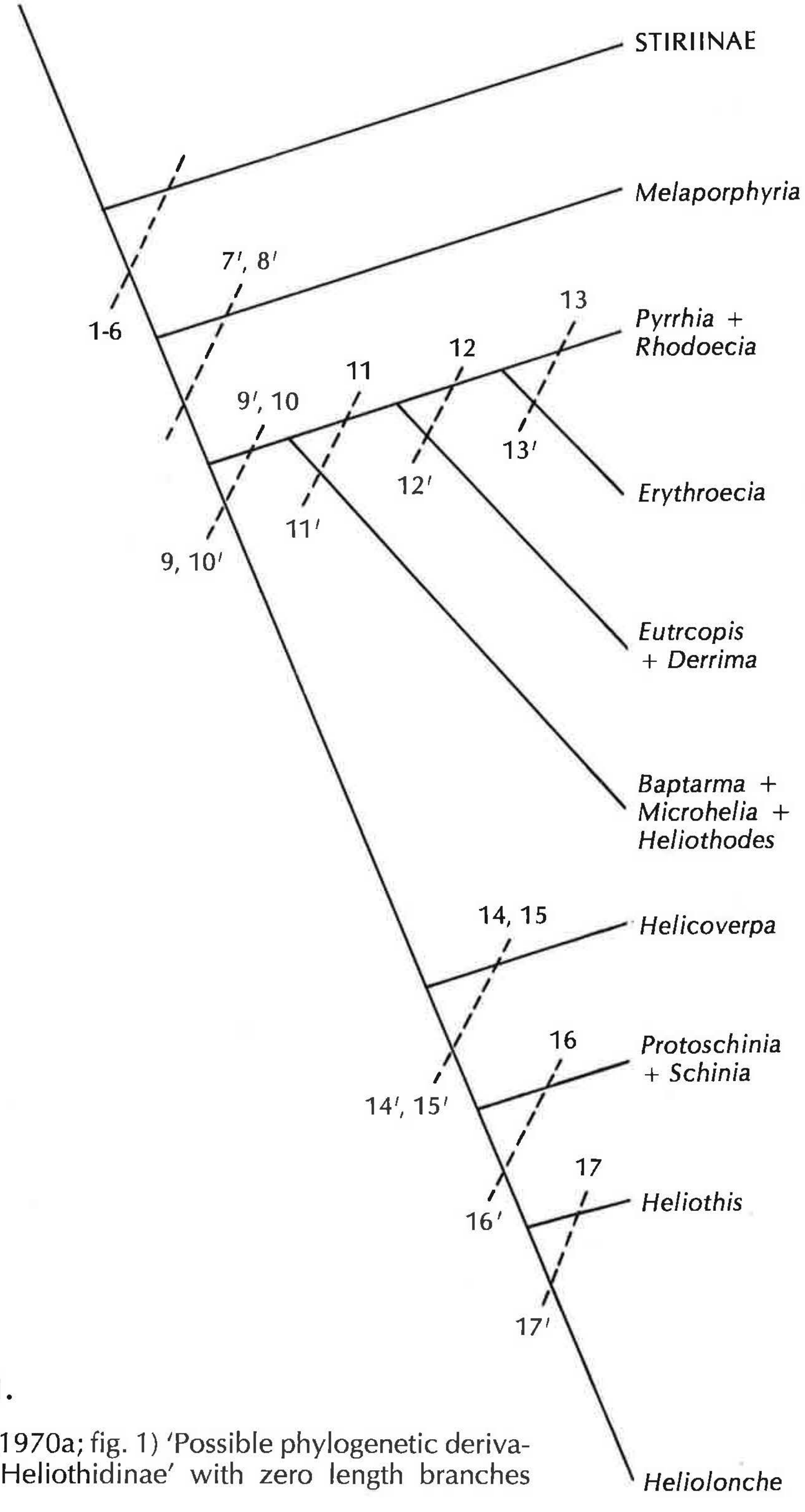
Hardwick (1970a; fig. 1) presented a 'possible phylogenetic derivation of the Heliothidinae'. This hypothesis of relationships was based on the fauna of North America, and was produced before the widespread use of Hennigian methods in systematics. Rather than discussing each of the seventeen characters defining the branches in Hardwick's diagram, which would in any case only repeat much of what has been said earlier in Section 9, I wish to consider his arrangement in a different way.

If the undefined branches in Hardwick's diagram are removed, then the result is as shown in Cladogram 1. If this is then further 'collapsed' (Cladogram 2), we see how he felt the *Pyrrhia*-group, *Schinia*-group, *Heliothis* and *Helicoverpa* were related. Perhaps this can be accounted for as follows.

Hardwick considered the Hampsonian character 'mid- and hind-tibiae spined/not spined' as useful at the generic level in the Heliothinae. No *Pyrrhia*-group species in North America except *Melaporphyria immortua* has spines on the mid- and hind- tibiae, and this is presumably why he excluded it from the *Pyrrhia*-group.

A tale of successive character loss then leads to Hardwick's arrangement of *Helicoverpa, Heliothis,* [*Schinia* + *Protoschinia*], and *Heliolonche*: the cornuti go first, then the scobinate bar, and then the vesical coil.

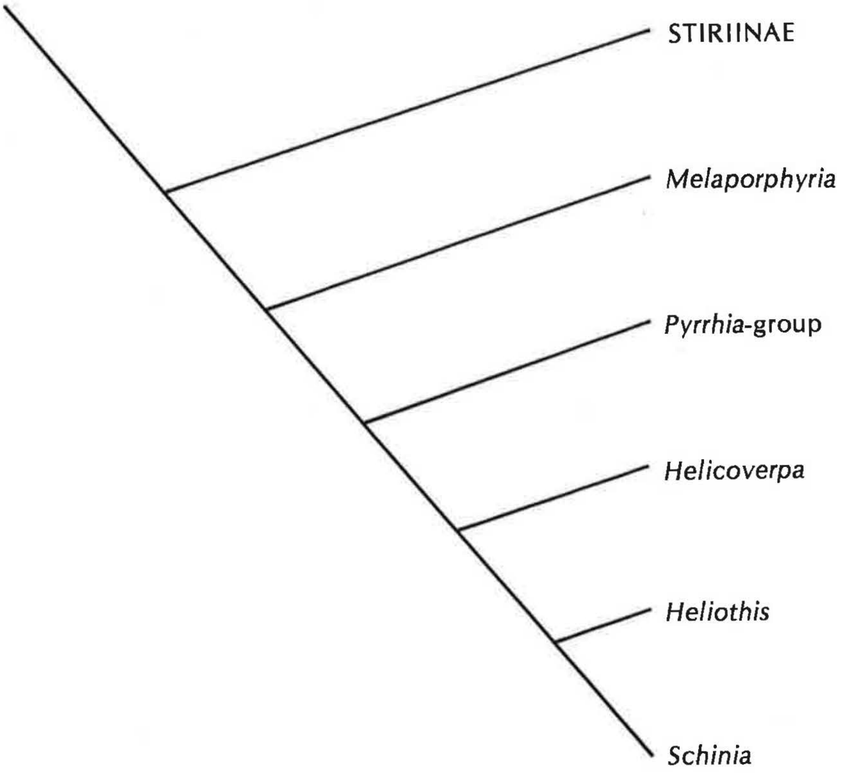
It must be remembered that Hardwick never pointed to the relationship which exists between the Old World *Adisura*, which does have cornuti on the vesica, and *Schinia*, which does not. Had he done so, he would presumably either have suggested a different arrangement, or would have had to postulate that the cornuti lost in [*Heliothis* + *Protoschinia* + *Schinia* + *Heliolonche*] were regained in *Adisura*. This might have influenced his interpretation of the 'presence of cornuti' in *Helicoverpa* as homologous with 'presence of cornuti' in the *Pyrrhia*-group, with which I do not agree. How this in turn might have caused him to change his arrangement of the clade is difficult to say, because his idea of increasing specialization of life-history strategies from *Helicoverpa*, through *Heliothis*, to *Schinia* may equally well have contributed to the arrangement in Cladogram 2 as have been derived from it.



Cladogram 1.

Hardwick's (1970a; fig. 1) 'Possible phylogenetic derivation of the Heliothidinae' with zero length branches collapsed.

1, valve of male genitalia elongate, simple (Heliothinae) / valve of male genitalia short, modified (Stiriinae).
2, vesica with small groups of cornuti (Heliothinae) / vesica with fields of cornuti (Stiriinae).
3, scobinated aedeagal plate (Heliothinae) / no scobinated aedeagal plate (Stiriinae).
4, frons non-tuberculate (Heliothinae) / frons tuberculate (Stiriinae).
5, venation ultimately trifid (Heliothinae) / venation minimally quadrifid (Stiriinae).
6, tibiae setose (Heliothinae) / tibiae non-setose (Stiriinae).
7, valve elongate / **7'**, valve shortened.
8, vesical cornuti retained / **8'**, vesical cornuti lost.
9, tibial setae retained / **9'**, tibial setae lost.
10, vesica uncoiled / **10'**, vesica coiled.
11, non-tuberculate frons / **11'**, tuberculate frons.
12, ovipositor valves soft, pad-like / **12'**, ovipositor valves sclerotized.
13, ampulla short / **13'**, ampulla very long.
14, vesical cornuti retained / **14'**, vesical cornuti lost.
15, scobinated plate retained at apex of aedeagus / **15'**, scobinated plate to base of vesica.
16, scobinated vesical plate retained / **16'**, scobinated vesical plate lost.
17, vesical coil retained / **17'**, vesical coil lost.



Cladogram 2.

The relationships of *Melaporphyria,* the *Pyrrhia*-group, *Helicoverpa, Heliothis,* and the *Schinia*-group in Hardwick's (1970a; fig. 1) diagram.

14. The groups within the Heliothinae and their relationships

14.1 THE GROUPS WITHIN THE HELIOTHINAE

For the purposes of discussion of species-group relationships in the subfamily, I recognize ten groups, nine genera and the *Pyrrhia*-group, as follows. The species in each which I examined during the study are listed in Section 8.

1. The *Pyrrhia*-group
2. *Protadisura*
3. *Adisura*
4. *Schinia*
5. *Heliolonche*
6. *Heliothis*
7. *Heliocheilus*
8. *Australothis*
9. *Helicoverpa*
10. *Engusanacantha*

14.1.1 The *Pyrrhia*-group

The *Pyrrhia*-group contains the forms in the Heliothinae with genitalia most similar to those of certain stiriines. By outgroup comparison they are the least derived heliothines. Within the Heliothinae, the *Pyrrhia*-group can be diagnosed by the saccate vesica which usually bears cornuti on diverticula. As has been discussed in Section 7, this saccate condition in some basal heliothines cannot be adequately distinguished from that in certain stiriines, so perhaps it is best regarded as derived at a more inclusive level (including at least some stiriines) than the clade Heliothinae. It cannot, therefore, be regarded as an autapomorphy of the *Pyrrhia*-group.

The *Pyrrhia*-group is almost certainly paraphyletic. Nevertheless, in view of the oversplitting of the subfamily in the past, the term '*Pyrrhia*-group' is a useful one. There are certain pairs and clusters of extremely similar species in the *Pyrrhia*-group corresponding to existing genera, or parts of them. These are: [*Aedophron rhodites* + *A. phlebophora* + *A. venosa*]; [*Erythroecia suavis* + *E. rhodophora* + *E. hebardi* + *Psectrotarsia flava*]; [*Heliothodes diminutivus* + *H. fasciata* + *H. joaquin*]; and [*Pyrrhia bifasciata* + *P. exprimens* + *P. purpurina* + *P. umbra*]. In addition, [*Melaporphyria immortua* + *Pyrocleptria cora*] are evidently very closely related, as are [*Erythrophaia* spp. + *Derrima stellata*].

As indicated in Section 9.3.3, there is greater variability of form in the genitalia of the *Pyrrhia*-group than in any other group of heliothines. When considered alongside the remarkable homogeneity of structure in the genitalia of tens or scores of species in *Heliothis*, *Helicoverpa*, and the *Schinia*-group, this greater stuctural diversity has probably contributed to the maintenance of so many small genera. Furthermore, most genera in the *Pyrrhia*-group, for example *Pyrrhia* itself, do not have spined mid- and hind-tibiae; but others, such as *Melaporphyria* and *Erythrophaia* do, and the influence of Hampson's tibial spining character has doubtless played a part in preventing a broader concept of *Pyrrhia* from being proposed. In fact, a very similar state of affairs already exists in *Heliothis*. On one hand there is heavy mid- and hind-tibial spining in *Heliothis* *oregonica*; on the other hand, in *H. radiata* there are only two very slender spinules on each hind-tibia, and none at all on the mid-tibiae (see Section 9.2.5).

Despite this greater structural diversity in the *Pyrrhia*-group, I can find no characters that can be regarded as synapomorphies either of any of these species clusters, or of any of them with any of the monobasic genera. Because of this lack of resolution there would seem to be little point in maintaining so many distinct genera. If the *Pyrrhia*-group is one day shown to be monophyletic by the recognition of a derived condition of their genitalia with respect to the Stiriinae (as may happen after a detailed investigation of the Stiriinae) the best course would be to synonymize these genera with *Pyrrhia* Hübner. However, this is clearly impossible at a time when available evidence suggests the *Pyrrhia*-group is paraphyletic because, if it is paraphyletic, then either *Pyrrhia* itself will sink into a more inclusive group, or relationships between some of the taxa within it will become resolved, in which case some of these generic names will be required to label them.

14.1.2 *Protadisura*

I consider *Protadisura posttriphaena* to be the sister taxon of the rest of the *Schinia*-group for the following reasons. First, the form of the female genitalia in relation to those of *Adisura* species and *Schinia* species, as discussed in Section 9.3.1. Second, the vesica possesses one or two cornuti on a basal diverticulum like those of *Adisura* spp., as discussed in Section 9.3.2.3. Third, the valves are very similar to those of *Adisura* spp., as discussed in Section 9.3.3. As argued in Section 9.3, this species displays a condition that is plausibly intermediate between those of basal heliothines and the *Schinia*-group; it is therefore useful to treat it separately.

14.1.3 *Adisura*

Adisura is diagnosed by the coiling of the female appendix bursae in conjunction with the possession of two cornuti (occasionally three or one) on a basal diverticulum. The monobasic Australian genus *Astonycha* is clearly a synonym of *Adisura*.

14.1.4 *Schinia*

Schinia is a large group, with over 120 species in North America. Twenty-six generic names were regarded as synonyms of *Schinia* by Hardwick (1970a), fifteen for the first time. *Tricraterifronta* Berio, 1941b and *Uollega* Berio, 1945 are also clearly synonyms of *Schinia*, and *Schinia xanthiata, S. ungemachi, S. roseoflammata, S. ennatae*, and *S. magdalanae* (all from Africa) form a closely related group. These five species are here recognized for the first time as belonging to *Schinia*, indeed, this is the first recognition of *Schinia* from Africa south of the Sahara.

Unfortunately, [*Schinia* + *Heliolonche*] is characterized only by a loss: the loss of the two cornuti seen on a basal diverticulum in *Adisura*. However, I have confidence in this for the following reasons. The form of the appendix bursae in the female genitalia of *Adisura* and *Schinia* is so distinctive that it provides an extremely firm synapomorphy between the two genera. I consider it to be independently derived from the basal heliothine form, and not homologous with the appendix in *Heliothis* and *Helicoverpa*, as discussed in Section 9.3.1. The saccate vesicas of the basal heliothines generally possess cornuti on their diverticula. If, as I suggested in Section 9.3.3.4, the form of the vesica in [*Protadisura* + *Adisura*] can be easily derived from the saccate vesica of many of the basal heliothines, then the plesiomorphic (primitive character state) condition is the possession of cornuti on a basal diverticulum as in *Protadisura* and *Adisura*. Therefore the autapomorphy (uniquely derived character occurring in only one taxon) characterizing [*Schinia* + *Heliolonche*] is 'loss of cornuti'.

Schinia is rendered paraphyletic by the removal of *Heliolonche* (see Section 14.1.5 below).

14.1.5 *Heliolonche*

Heliolonche, which contains five species (three of which I have examined), is restricted to North America. Hardwick, who has reared *H. carolus* (Hardwick, 1969) and *H. pictipennis* (Hardwick, 1971a), regarded the genus as derived from *Schinia* by loss of the coiled appendix bursae in the female with an accompanying reduction of the male vesica. This suggestion is supported by the fact that the males of the species I have examined all possess trifid noctuid scent brushes at the base of the abdomen. In the Heliothinae these structures only occur in the *Schinia*-group: namely in some *Adisura* species, in some *Schinia* species, and in *Heliolonche*.

14.1.6 *Heliothis*

Heliothis as treated here, that is without *Heliocheilus*, is paraphyletic. Although there is evidence for the monophyly of the included *virescens*-group (Poole & Mitter, in press), there is no reason to suppose that the other species in *Heliothis* together form a monophyletic group, nor is there evidence at present to define monophyletic groups within this remainder. I do, however, refer informally to the '*Masalia-Timora* section' of *Heliothis*, the species of which tend to have stout forelegs bearing two heavy 'claws' on the tibia, and a longitudinally streaked pattern on the forewings. It is impossible, however, to provide firm autapomorphies for this group and I use it only as a convenient term for the species assigned to *Masalia* and *Timora* following Seymour's (1972) revision of *Masalia*. The '*Masalia-Timora*' section of *Heliothis* may prove to be monophyletic.

The manuscript for Matthews (1987) was prepared early in this study, when it was apparent that *Raghuva* and *Canthylidia* were composed of species with modified forewings in the male; the other species with this modification were at that time placed in *Heliothis*. This character, described and figured in Matthews (1987), is uniquely derived in the subfamily and therefore a good autapomorphy of *Heliocheilus*. *Heliothis perstriata* possesses a similar but distinct modification of the forewing in the male (described and figured in Matthews, 1987; fig. 43). Apart from a strong superficial resemblance to other *Heliothis* species formerly assigned to *Masalia* and *Timora*, there is no evidence either that *H. perstriata* is derived from *Heliocheilus* or that it is the sister group of *Heliocheilus*.

As mentioned earlier in Section 10.2, evidence exists for the monophyly of the *virescens* group of *Heliothis* in the existence of spinules on the chalazae bearing D1 and D2 on A1, A2, and A8 of the larvae. In addition, the greenish or greenish-yellow colour of the forewings and their characteristic transverse maculation (Todd, 1978b) is a condition unique to the subfamily. This group has been recently revised (Poole & Mitter, in press).

Timora diarhoda Hampson was not removed from the Heliothinae by Seymour (1972) following his investigation of the '*Masalia-Timora*' section of *Heliothis*. This is because in preparing the genitalia of a male, he mounted the vesica of a heliothine with the valves of *Timora diarhoda* on the same slide (BM Noct 8050). My own preparation (BM Noct 13520, Figs. 346 & 347) shows that although *T. diarhoda* bears a superficial resemblance to, for example *Heliothis decorata*, it is not in fact a heliothine.

14.1.7 *Heliocheilus*

Heliocheilus is characterized by the presence of a modified forewing in the male as described in Matthews (1987). In addition, those species for which host-plant records exist have only been recorded from grasses. In 1985, I reared *H. confertissima* (Fig. 744, larva) on the grass *Setaria pallide-fusca* in Mali at Mourdiah. Although the larvae became fully grown and burrowed into sand, none pupated successfully. I have searched *S. pallide-fusca* in the field but have never found *H. confertissima* larva feeding on it, so this is not included as a host-plant record in Appendix 2.

Recognizing *Heliocheilus* as distinct from *Heliothis* renders *Heliothis* paraphyletic; this problem has been discussed in Section 9.2.7, and is dealt with further below.

14.1.8 *Australothis*

The two very closely related species from the Australian region which form this genus display a condition intermediate between that of *Heliothis* and that of *Helicoverpa*. With respect to the cornuti on the vesica, their condition is arguably truly intermediate between that in *Heliothis* and that in *Helicoverpa*; with respect to other features, they either display the condition in *Heliothis* or that in *Helicoverpa*.

The vesica and appendix bursae are both very long. The appendix bursae is longer in these species than in any species of *Heliothis*, and is of approximately the same length relative to other parts of the genitalia as the appendix bursae in *Helicoverpa*. However, the appendix bursae in *Helicoverpa* is of a tough, leathery consistency; in *Australothis*, it is membranous, as it is in all *Heliothis* species. Furthermore, as noted in Section 9.3.1, the sclerotization on the ductus bursae forms a well defined 'collar' around the base of the appendix bursae in *Australothis* in the same way as in *Heliothis*. This is clearly visible in Figs. 135 & 136. In *Helicoverpa* the sclerotization does form such a 'collar', but it is also present (although diffuse) on the surface of the appendix bursae.

It is in the male that the intermediate condition of *Australothis rubrescens* and *A. tertia* is perhaps most striking: the vesica in each of these species bears a dense strip of minute cornuti along its length. Whereas in *Heliothis* the vesica is naked, in *Helicoverpa* the cornuti present along the length of the vesica also form a strip; in different species they range from similar in size and more-or-less equally spaced (as in *H. punctigera*, Hardwick, 1965; fig. 8), to dissimilar in size and 'clustered', with the largest cornutus in each cluster in the middle (as in *H. armigera*, Fig. 395). Hardwick (1965) interpreted this latter state as the most derived within *Helicoverpa*, and the form and arrangement of cornuti in *A. rubrescens* and *A. tertia* supports this contention. The scobinate bar in the membrane at the base of the vesicas of *A. rubrescens* and *A. tertia* occurs in the same form as that in many species of *Heliothis*, in contrast to the long denticulate patch on the edge of the tip of the aedeagus in *Helicoverpa*. Finally, there is a single 'spine' (which may be quite short and broad) at the base of the vesica in some *Helicoverpa* species: this is absent in all species of *Heliothis*. This 'spine' is present in *A. rubrescens* but absent in *A. tertia*.

14.1.9 *Helicoverpa*

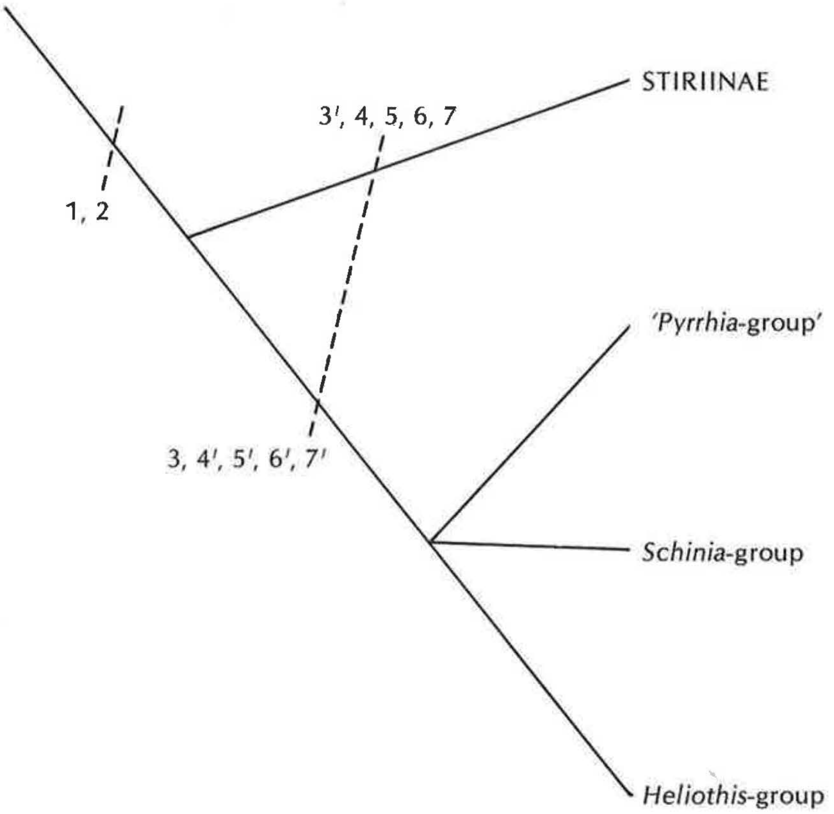
Helicoverpa is a well defined group with the following autapomorphies: a unique leathery texture of the appendix bursae, and regular coiling of the vesica (regarded as distinct from that in *Schinia* and *Adisura* for reasons given in Section 9.3.2.4). A specialized patch of flattened scales in deep sockets on the femur of the foreleg in the male (Fig. 605) (Hardwick, 1965; figs. 12, 17, 26, 29, 37, 42, 64 & 73) was also considered autapomorphic for *Helicoverpa*, until Poole (Poole & Mitter, in press) pointed out that it also occurs in the *virescens*-complex of *Heliothis*.

14.1.10 *Engusanacantha*

Engusanacantha was described to accommodate a single species, *E. bilineata*, from Kenya and Ethiopia. Although *E. bilineata* is clearly heliothine, its relationships with other species-groups in the subfamily are unclear at present. The female genitalia are indistinguishable from those of some species in *Heliothis*. The male valves are very stout, and most resemble forms such as *Periphanes delphinii* in the *Pyrrhia*-group. The vesica is little help here as it bears neither cornuti nor a scobinate bar. There is no denticulate patch on the vesica and/or the aedeagus.

14.2 THE RELATIONSHIPS OF THE GROUPS WITHIN THE HELIOTHINAE

The evidence presented supports the groups and their arrangement expressed in Cladogram 3. The greatest problem remaining is the paraphyly of the *Pyrrhia*-group. This status arises for the following reason: the best evidence for the monophyly of the Heliothinae, and that of the Stiriinae, comes from the larvae. In contrast, all the evidence to resolve relationships within the Heliothinae comes from the adults. Although the members of the *Pyrrhia*-group are certainly heliothines, as we know from their larvae, it is impossible to differentiate their genitalia adequately from those of many stiriines, as discussed in Section 7 and Section 9.3. Thus at present they remain 'basal heliothines' without any of the derived characters that enable definition of the *Schinia*-group and the *Heliothis*-group, and the resolution of relationships within them.



Cladogram 3.

The relationships of the Stiriinae and major groups of Heliothinae.

1, similarity of male and female genitalia (Section 7 & Section 9.3).
2, similarity of life-histories (Section 7).
3, larval spinneret unmodified; **3′**, larval spinneret reduced to a small scale-like structure (Section 6.2).
4, sternum 8 in the male without anterior arms; **4′**, sternum 8 in the male with anterior arms (Section 5.3).
5, hindwing quadrifid; **5′**, hindwing trifid or only minimally quadrifid (Section 5.3).
6, larval skin smooth; **6′**, larval skin spiny (Section 5.1).
7, setae L1 and L2 of the prothorax in the larvae vertical; **7′**, setae L1 and L2 of the prothorax in the larvae transverse (Section 5.2).

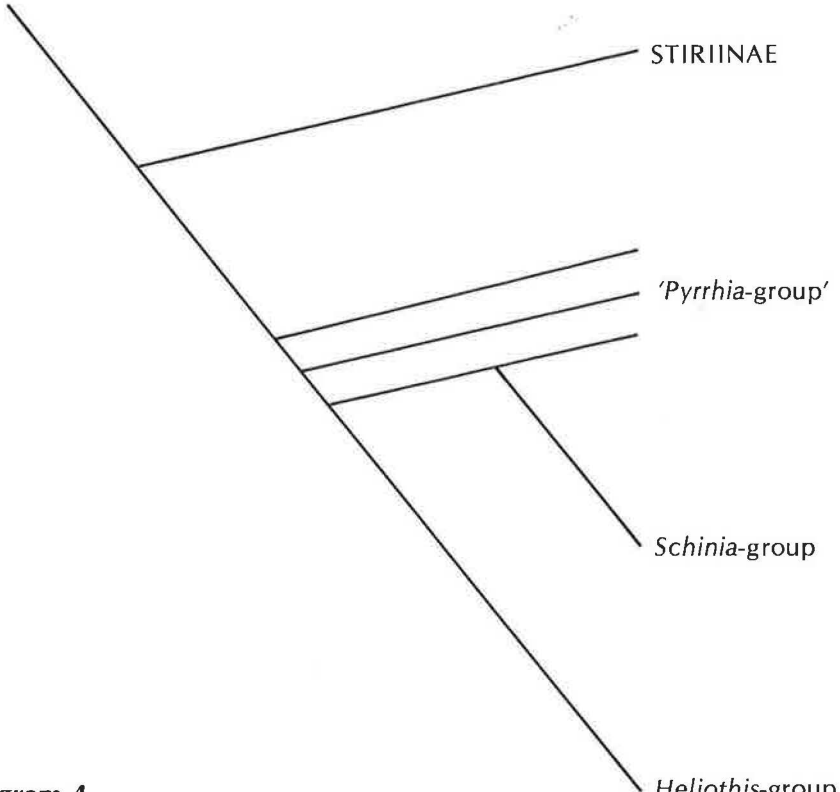
The possibility of deriving the vesica of the *Schinia*-group from that of certain forms in the *Pyrrhia*-group was discussed at the end of Section 9.3.3.4. In effect, this form would be a saccate vesica, retaining cornuti on a basal diverticulum, which had become distally very elongate and coiled.

I am unable to put forward any characters to support such a hypothesis at present. This is because I cannot provide characters to define either the *Pyrrhia*-group or the relationships of groups within it. It might be possible with a better understanding of the Stiriinae to distinguish a derived condition in the genitalia of the *Pyrrhia*-group. If the *Pyrrhia*-group can be shown to be monophyletic or the relationships of the taxa at present contained within it resolved, then (if the derivation of the *Schinia*-group vesica in the manner described above is accepted) the *Schinia*-group would become the sister group of a taxon at present contained within the *Pyrrhia*-group. The fact that in the Heliothinae a harpe on the male valve occurs only in some *Schinia*-group species and some *Pyrrhia*-group species (Section 9.3.3.) provides supporting evidence for such a derivation of the *Schinia*-group. It is, however, only an underlying synapomorphy or homoiology. Although I cannot provide uniquely derived characters to define the branches of such a cladogram, the relationships implied are expressed in, for example, Cladogram 4.

Evidence discussed in Section 9.3 supports the relationships within the *Schinia*-group expressed in Cladogram 5. The unique coiling of the female appendix bursae in *Adisura* and *Schinia* is a very strong synapomorphy of these groups.

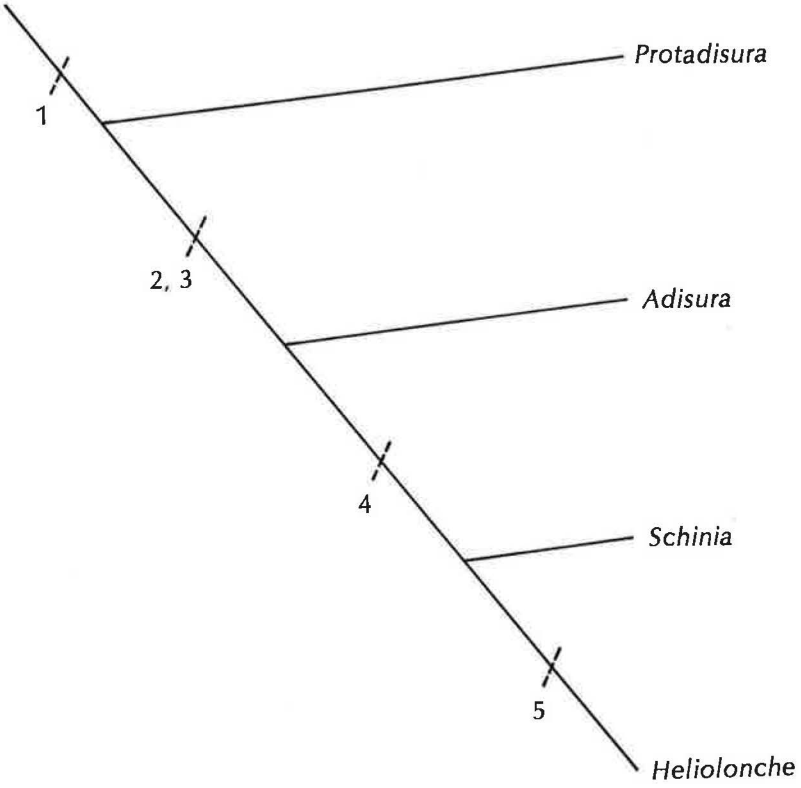
Because the trifid noctuid scent brush does not occur in all *Adisura* or *Schinia* species, it could be argued that it is homoiologous and therefore of no use in grouping these taxa. However, this structure is known to be very labile and may be present and absent in other groups of trifid noctuids that are extremely closely related to each other. Since these are the only heliothine groups that possess the structure, I present it as supporting evidence for the monophyly of [*Adisura* + *Schinia* + *Heliolonche*].

The evidence presented supports the relationships within the *Heliothis*-group expressed in Cladogram 6. The most serious remaining problem for our understanding of the relationships within this clade is the paraphyly of *Heliothis* as here constituted, discussed in Section 14.1.6.



Cladogram 4.

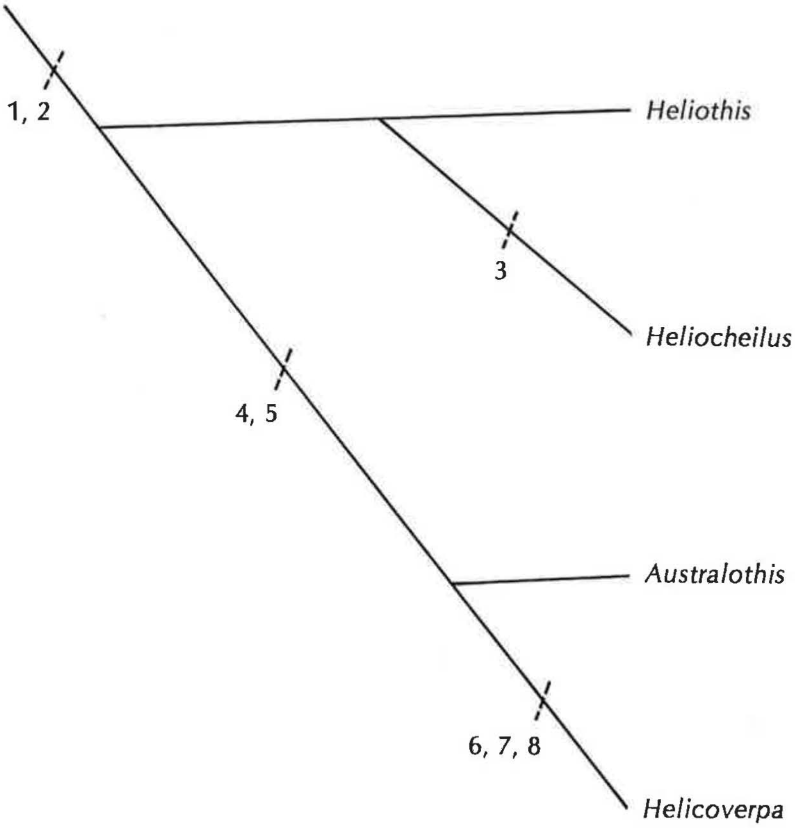
The relationships between the Stiriinae and major groups of Heliothinae if the *Pyrrhia*-group can be shown to be monophyletic, and if the derivation of the *Schinia*-group vesica discussed in Section 9.3.3.4 is accepted.



Cladogram 5.

The relationships within the *Schinia*-group.

1, *Schinia* group condition of the appendix bursae (sclerotization following the inside of the spiral described by the appendix bursae to the ductus seminalis, Section 9.3.1); and the condition of the vesica (Section 9.3.3.4).
2, more derived condition of 1 (above) (Section 9.3.1 and Section 9.3.3.4).
3, presence in some taxa of the trifid noctuid scent brush (Section 14.2).
4, loss of cornuti on the basal diverticulum of the vesica.
5, loss of coiling of the appendix bursae, and the vesica, (Section 9.3.1 and Section 9.3.3.4).



Cladogram 6.

The relationships within the *Heliothis*-group.

1, presence of a sclerotized collar around the base of the appendix bursae (Section 9.3.1).
2, elongate appendix bursae and vesica (Section 9.3.1 and Section 9.3.3.4).
3, the modification of the forewing in the male (Section 9.2.7).
4, appearance of cornuti in a long, continuous strip up the vesica (Section 9.3.2.3).
5, elongation of the appendix bursae, and the vesica (Section 9.3.1., and Section 9.3.3.4).
6, leathery consistency of the appendix bursae (Section 9.3.1).
7, reduction in number, and increase in size of the cornuti on the vesica (Section 9.3.2.3).
8, regular coiling of the vesica (Section 9.3.3.4).

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APPENDIX 1

Descriptions of new taxa

AUSTRALOTHIS GEN. NOV.

Type species: *Thalpophila rubrescens* Walker, 1858.

FIGURES. *Australothis rubrescens.* Adult male, Fig. 820; adult female, Fig. 819; head, Fig. 25; female genitalia, Fig. 135; male genitalia, Fig. 390 (valves) & Figs. 391, 671 & 672 (vesica). *A. tertia.* Adult female, Fig. 821; Female genitalia, Fig. 136; male genitalia, Fig. 392 (valves) & Fig. 393 (vesica); male A8, Fig. 468; fore-, mid-, & hind-legs, Figs. 602, 603 & 604.

DIAGNOSIS. The male genitalia provide the most diagnostic features. The valves display the simple, flattened, distally recurved form found in *Heliothis* and *Helicoverpa*, and typical of many heliothines. The vesica, however, is quite different from that in any other heliothine genus. It is long, describes two turns of a spiral, and bears a band of minute cornuti along its length. In no other heliothine genus is this band of minute cornuti present. The denticles of the scobinate patch at the base of the vesica are well separated from the aedeagus, and point away from it at right-angles to its long axis.

PROTADISURA GEN. NOV.

Type species: *Chloridea posttriphaena* Rothschild, 1924.

FIGURES. Adult female, Fig. 785; head, Fig. 1; female genitalia, Fig. 49; male genitalia, Fig. 207 (valves) & Fig. 208 (vesica).

DIAGNOSIS. Male. The valve is quite slender, recurved distally, and bears a small harpe. The base of the valve is emarginate as in *Adisura* species. The vesica is short, bearing two quite well developed basal sacs. In one of the two males examined (BM Noct 13394, Fig. 208), one of these sacs bears a single, moderately long cornutus; in the other, two cornuti are present (BM Noct 4044). There are no trifid noctuid scent brushes at the base of the abdomen.

Female. The appendix bursae bears ribbed sclerotization of typical heliothine form at its base; it is broad, and curves distally describing half a turn dorsal to the ductus and fundus bursae. The ribbed sclerotization, although less well-developed distally, extends up the inside of the curve of the appendix bursae to the ductus seminalis and over the distal end of the appendix bursae, around the base of the ductus seminalis.

The combination of a vesica bearing a moderately long cornutus on a basal sac (as in *Adisura*) in the male, and a female without an appendix bursae which is coiled (as in *Adisura* and *Schinia*) distinguishes *Protadisura* from other heliothine genera.

ADISURA PARVA SP. NOV.

FIGURES. Adult males, paratypes, Figs. 788 & 790; adult females, paratypes, Figs. 787 & 789; head, Fig. 17; female genitalia, Fig. 62; male genitalia, Fig.232 (valves) & 233 (vesica); male A8, Fig. 446; fore-, mid-, & hind-legs, Figs. 540, 541 & 542.

DIAGNOSIS. This is the smallest species of *Adisura*. Upperside with a characteristic reddish-ochre ground colour in the forewing. The main elements of typical trifid noctuid maculation are better defined than in other members of the genus, with the antemedian fascia and postmedian fascia quite well distingushed. The orbicular, claviform, and reniform stigmata are present. The hindwing is paler towards the base, with a quite faint discal spot. The underside is paler than the upperside, with a well defined postmedian fascia and reniform stigma. Male genitalia. The valves are slender, distally recurved in typical heliothine fashion, and slightly emarginate basally, athough this emargination is much weaker than in some other *Adisura* species. The corona is formed from a single row of spines. There is no harpe. The vesica describes three turns of a spiral which narrows slightly distally. In the single male examined, three quite long, slender cornuti are borne on a single basal diverticulum. There is no scobinate patch at the base of the vesica. Female genitalia. The appendix bursae describes a spiral of three turns dorsal to the ductus bursae, with the ribbed sclerotization on the surface of the ductus bursae ascending the inside of the spiral. The ovipositor is unsclerotized, soft, and pad-like.

OTHER OBSERVATIONS. The forelegs of this species bear a slender spine at the tip of the tibia. *Adisura parva* and *A. cana*, both of which are here included for the first time in *Adisura*, are thus the only two known species in the genus to possess spined fore-tibiae.

TYPE MATERIAL EXAMINED. Holotype female, MALI: Mourdiah 14.28N 7.28W (at light) 6.viii.1985 (Matthews) (BMNH). Paratypes, all same locality and collector as holotype (BMNH), 1 male, 1.viii.1985; 2 males, 1 female, 2.viii.1985; 1 male, 14 females, 3.viii.1985; 1 male, 10 females, 4.viii.1985; 1 male, 8 females, 5.viii.1985; 2 males, 7 females, 6.viii.1985; 5 males, 1 female, 7.viii.1985; 1 male, 5 females, 8.viii.1985; 2 females, 9.viii.1985; 2 females, 10.viii.1985; 1 female, 13.viii.1985; 1 male, 2 females, 14.viii.1985; 1 male, 16.viii.1985; 1 female, 19.viii.1985; 1 female, 20.viii.1985; 1 female, 21.viii.1985; (USNM) 1 male, 6.viii.1985; 1 female, 8.viii.1985; (ANIC) 1 male, 5.viii.1985; 1 female, 8.viii.1985.

ADDITIONAL MATERIAL EXAMINED. NIGER: 64 km E. Dogondontchi, 2 females, 27.viii.1973.

APPENDIX 2

1. HOST PLANT RECORDS FOR HELIOTHINAE

The first list below contains 534 entries, and is ordered as follows. First by heliothine generic name, second by heliothine specific name, third by plant family name, fourth by host plant generic name, and last by host plant specific name. The references for each record can be traced in the second list below, by finding the author and date corresponding to a number in the first list. Plant family names used are those in Willis (1973), and they are abbreviated as follows.

ACAN	Acanthaceae	JUGL	Juglandaceae
AIZO	Aizoaceae	LABI	Labiatae
ALLI	Alliaceae	LEGU	Leguminosae
ANAC	Anacardiaceae	LINA	Linaceae
APOC	Apocynaceae	MALV	Malvaceae
ASTE	Asteraceae	MUSA	Musaceae
BETU	Betulaceae	ONAG	Onagraceae
CANN	Cannabidaceae	PEDA	Pedaliaceae
CARY	Caryophyllaceae	POLE	Polemoniaceae
CHEN	Chenopodiaceae	POLY	Polygonaceae
CLEO	Cleomaceae	RANU	Ranunculaceae
COMP	Compositae	RESE	Resedaceae
CONV	Convolvulaceae	ROSA	Rosaceae
CRUC	Cruciferae	RUBI	Rubiaceae
CUCU	Cucurbitaceae	RUTA	Rutaceae
DIPS	Dipsacaceae	SALI	Salicaceae
ERIC	Ericaceae	SCRO	Scrophulariaceae
EUPH	Euphorbiaceae	SOLA	Solanaceae
FABA	Fabaceae	UMBE	Umbelliferae
GERA	Geraniaceae	VALE	Valerianaceae
GRAM	Gramineae	VERB	Verbenaceae
HYDR	Hydrophyllaceae	VITI	Vitidaceae
IRID	Iridaceae	ZYGO	Zygophyllaceae

(Compositae = Asteraceae, Cruciferae = Brassicaceae, Labiate = Lamiaceae, Leguminosae = Fabaceae.)

Heliothine species	**Plant family**	**Host plant**	**Reference**
Adisura atkinsoni	LEGU	*Lablab niger*	856
	MALV	*Hibiscus mutabilis*	001
Aedophron phlebophora	LABI	*Phlomis*	793
Australothis rubrescens	COMP	*Sigesbeckia orientalis*	401
Baptarma felicita	HYDR	*Phacelia*	824
Eutricopis nexilis	COMP	*Antennaria*	144
	COMP	*Grindelia*	373
Helicoverpa armigera	ACAN	*Justicia*	052
	AIZO	*Trianthema portulacastrum*	157
	ANAC	*Anacardium occidentale*	212
	APOC	*Apocynum cannabinum*	012
	CANN	*Cannabis*	182
	CARY	*Dianthus caryophyllus*	150
	CLEO	*Cleome*	042
	COMP	*Chrysanthemum coronarium*	187
	COMP	*Gerbera jamesonii*	159
	COMP	*Helianthus annuus*	160
	COMP	*Lactuca sativa*	161
	COMP	*Senecio*	007
	CRUC	*Brassica oleracea*	155
	CUCU	*Cucurbita pepo*	013
	GERA	*Pelargonium*	006
	GRAM	*Eleusine coracan*	047
	GRAM	*Panicum miliaceum*	163
	GRAM	*Pennisetum*	057
	GRAM	*Pennisetum cinereum*	038
	GRAM	*Sorghum*	164
	GRAM	*Zea mays*	004
	IRID	*Gladiolus*	010
	LABI	*Calamintha*	804
	LEGU	(unspecified)	019
	LEGU	*Cajanus cajan*	040
	LEGU	*Cicer*	041
	LEGU	*Crotalaria*	044
	LEGU	*Lablab niger*	035
	LEGU	*Lablab purpureus*	202
	LEGU	*Medicago denticulata*	168
	LEGU	*Medicago sativa*	008
	LEGU	*Phaseolus*	156
	LEGU	*Phaseolus vulgaris*	169
	LEGU	*Pisum sativum*	011
	LEGU	*Trifolium*	028
	LEGU	*Vigna unguiculata*	062
	LINA	*Linum*	018
	LINA	*Linum usitatissimum*	171
	MALV	*Abelmoschus esculentus*	197
	MALV	*Gossypium*	016
	MALV	*Gossypium hirsutum*	172
	MALV	*Hibiscus cannabinus*	050
	MALV	*Hibiscus esculentus*	173
	MALV	*Hibiscus mutabilis*	039
	MUSA	*Musa acuminata*	174
	MYRT	*Eucalyptus torelliana*	198
	RESE	*Reseda*	803
	ROSA	*Fragaria ananassa*	175
	ROSA	*Malus pumila*	024
	ROSA	*Prunus*	022

Heliothine species	Plant family	Host plant	Reference
	ROSA	*Prunus armeniaca*	031
	ROSA	*Prunus persica*	032
	ROSA	*Pyrus communis*	023
	ROSA	*Rosa*	802
	RUBI	*Coffea arabica*	027
	RUTA	*Citrus*	025
	RUTA	*Citrus sinensis*	176
	SCRO	*Antirrhinum*	209
	SOLA	*Hyoscyamus niger*	009
	SOLA	*Lycopersicon esculentum*	015
	SOLA	*Nicotiana*	181
	SOLA	*Nicotiana tabacum*	005
	VITI	*Vitis vinifera*	179
	ZYGO	*Tribulus terrestris*	826
Helicoverpa assulta	SOLA	*Lycopersicon esculentum*	216
	SOLA	*Nicotiana tabacum*	215
	SOLA	*Physalis minima*	217
	SOLA	*Physalis peruviana*	214
Helicoverpa atacamae	GRAM	*Zea mays*	067
Helicoverpa fletcheri	LEGU	*Zornia glochidiata*	829
	MALV	*Hibiscus*	830
	PEDA	*Sesamum elatum*	828
Helicoverpa gelotopoeon	ALLI	*Allium cepum*	076
	COMP	*Calendula*	071
	GRAM	*Zea mays*	071
	LEGU	*Medicago sativa*	068
	LEGU	*Trifolium*	074
	LINA	*Linum*	070
	ROSA	*Rosa*	075
	SOLA	*Lycopersicon esculentum*	073
	SOLA	*Nicotiana tabacum*	072
Helicoverpa punctigera	AIZO	*Trianthema portulacastrum*	844
	CARY	*Dianthus*	843
	COMP	*Calendula*	842
	COMP	*Carthamus tinctorius*	228
	COMP	*Xanthium pungens*	229
	CRUC	*Brassica oleracea*	225
	CUCU	*Citrullus vulgaris*	230
	IRID	*Gladiolus*	231
	LEGU	*Medicago sativa*	223
	LEGU	*Pisum sativum*	224
	LEGU	*Trifolium*	221
	LINA	*Linum usitatissimum*	222
	ROSA	*Fragaria* x *ananassa*	850
	ROSA	*Prunus armeniaca*	226
	SCRO	*?Antirrhinum*	227
	SCRO	*Antirrhinum majus*	851
	SOLA	*Lycopersicon esculentum*	220
	SOLA	*Nicotiana tabacum*	853
Helicoverpa zea	CHEN	*Spinacia oleracea*	101
	COMP	*Calendula*	102
	COMP	*Chrysanthemum coronarium*	110
	COMP	*Lactuca sativa*	083
	CRUC	*Brassica*	109
	CRUC	*Brassica oleracea*	089
	CUCU	*Cucumis sativa*	108
	GERA	*Erodium cicutarium*	812

Heliothine species	Plant family	Host plant	Reference
	GRAM	*Avena sativa*	093
	GRAM	*Oryza sativa*	099
	GRAM	*Pennisetum americanum*	106
	GRAM	*Saccharum officinarum*	123
	GRAM	*Secale cereale*	100
	GRAM	*Sorghum bicolor*	107
	GRAM	*Triticum aestivum*	103
	GRAM	*Zea mays*	113
	HYDR	*Phacelia*	823
	IRID	*Gladiolus*	141
	LEGU	*Arachis hypogea*	095
	LEGU	*Cicer arietinum*	088
	LEGU	*Medicago sativa*	080
	LEGU	*Phaseolus*	118
	LEGU	*Phaseolus lunatus*	259
	LEGU	*Phaseolus vulgaris*	140
	LEGU	*Trifolium*	254
	LEGU	*Vicia*	084
	LEGU	*Vigna unguiculata*	245
	LINA	*Linum*	087
	MALV	*Gossypium*	082
	MALV	*Hibiscus esculentus*	104
	MALV	*Hibiscus sabdariffa*	139
	MALV	*Sphaeralcea coulteri*	811
	ROSA	*Fragaria*	081
	ROSA	*Prunus*	097
	ROSA	*Pyrus communis*	096
	ROSA	*Rosa*	117
	RUTA	*Citrus*	132
	RUTA	*Citrus limon*	092
	RUTA	*Citrus sinensis*	094
	SOLA	*Capsicum*	085
	SOLA	*Capsicum annuum*	086
	SOLA	*Hibiscus*	133
	SOLA	*Lycopersicon esculentum*	078
	SOLA	*Nicotiana tabacum*	079
	SOLA	*Physalis*	116
	SOLA	*Solanum melongena*	105
	SOLA	*Solanum tuberosum*	098
	UMBE	*Apium graviolens*	090
	VITI	*Vitis vinifera*	091
Heliocheilus albipunctella	GRAM	*Pennisetum americanum*	841
Heliocheilus turbatus	GRAM	*Triodia fusca*	145
Heliocheilus paradoxus	GRAM	*Cynodon dactylon*	146
Heliocheilus zorophanes	GRAM	*Spinifex longifolius*	003
Heliolonche carolus	COMP	*Rafinesquia neomexicana*	266
Heliolonche pictipennis	COMP	*Malacothrix glabrata*	267
Heliolonche flavirufa	LABI	*Coleus*	268
	LABI	*Iboza*	269
Heliothis maritima	CARY	*Spergula arvensis*	276
	CARY	*Spergularia*	272
	CARY	*Spergularia marginata*	270
	CARY	*Spergularia media*	275
	CARY	*Spergularia rubra*	273
	CARY	*Spergularia salina*	274
	ERIC	*Erica cinerea*	836
	ERIC	*Erica tetralix*	271

Heliothine species	Plant family	Host plant	Reference
Heliothis nubigera	COMP	*Chrysanthemum coronarium*	278
	LEGU	*Cicer arietinum*	279
	SOLA	*Lycopersicon esculentum*	277
Heliothis ononis	CARY	*Silene nutans*	287
	CARY	*Vaccaria vulgaris*	290
	LABI	*Salvia pratensis*	284
	LEGU	*Astragalus goniatus*	291
	LEGU	*Melilotus alba*	292
	LEGU	*Ononis*	285
	LINA	*Linum*	283
	LINA	*Linum lewsii*	289
Heliothis oregonica	GERA	*Geranium*	297
	SCRO	*Castilleja*	296
Heliothis peltigera	CARY	*Arenaria*	807
	CARY	*Spergularia rubra*	302
	COMP	*Calendula officinalis*	305
	COMP	*Carthamus tinctorius*	318
	COMP	*Chrysanthemum coronarium*	313
	COMP	*Inula viscosa*	325
	COMP	*Matricaria inodora*	301
	COMP	*Senecio*	337
	COMP	*Senecio viscosus*	303
	COMP	*Senecio vulgaris*	352
	COMP	*Tanacetum*	806
	CONV	*Convolvulus*	346
	CONV	*Convolvulus soldanella*	300
	EUPH	*Ricinus communis*	317
	GERA	*Erodium*	308
	GRAM	*Zea mays*	321
	LABI	*Lavandula officinalis*	310
	LABI	*Mentha*	314
	LABI	*Salvia*	307
	LABI	*Salvia pratensis*	334
	LEGU	*Arachis hypogea*	315
	LEGU	*Cicer arietinum*	355
	LEGU	*Medicago sativa*	322
	LEGU	*Ononis*	805
	LEGU	*Ononis arvensis*	298
	LEGU	*Ononis spinosa*	347
	LEGU	*Trifolium*	309
	LEGU	*Ulex*	344
	LEGU	*Ulex europaeus*	306
	MALV	*Gossypium*	316
	MALV	*Hibiscus cannabinus*	827
	SCRO	*Linaria*	326
	SOLA	*Atropa belladonna*	323
	SOLA	*Datura*	345
	SOLA	*Datura stramonium*	304
	SOLA	*Hyoscyamus niger*	299
	SOLA	*Lycopersicon esculentum*	312
	SOLA	*Nicotiana tabacum*	311
Heliothis phloxiphaga	COMP	*Achillea millefolium*	367
	COMP	*Ambrosia elatior*	400
	COMP	*Aster*	372
	COMP	*Aster canescens*	361
	COMP	*Aster?novae-angliae*	398
	COMP	*Aster novae-angliae*	714

Heliothine species	**Plant family**	**Host plant**	**Reference**
	COMP	*Balsamorhiza*	368
	COMP	*Chaenactis douglasi*	362
	COMP	*Erigeron divergens*	377
	COMP	*Grindelia*	371
	COMP	*Grindelia camporum*	378
	COMP	*Grindelia robusta*	379
	COMP	*Grindelia squarrosa*	360
	COMP	*Hemizonia congesta*	381
	COMP	*Lactuca sativa*	382
	COMP	*Machaeranthera canescens*	383
	COMP	*Madia*	363
	COMP	*Parthenium argentatum*	384
	CONV	*Convolvulus*	399
	GERA	*Erodium cicutarium*	385
	GRAM	(unspecified)	359
	HYDR	*Phacelia*	825
	IRID	*Gladiolus*	369
	LEGU	*Lathyrus*	366
	LEGU	*Medicago sativa*	358
	POLE	*Gilia aggregata*	365
	POLE	*Phlox*	357
	RANU	*Aquilegia*	397
	RANU	*Delphinium*	364
	ROSA	*Fragaria*	370
	SCRO	*Antirrhinum*	391
	SOLA	*Schizanthus*	392
Heliothis scutiligera	COMP	*Helichrysum*	402
Heliothis punctifera	ASTE	(unspecified)	570
	CHEN	(unspecified)	569
	EUPH	(unspecified)	574
	FABA	(unspecified)	573
	GRAM	(unspecified)	568
	GRAM	*Triticum aestivum*	565
	GRAM	*Zea mays*	564
	LEGU	*Medicago sativa*	566
	MALV	(unspecified)	571
	MALV	*Gossypium*	567
	SOLA	(unspecified)	572
	ZYGO	(unspecified)	575
Heliothis subflexa	MELA	?*Rhexia*	405
	ROSA	*Rosa*	408
	SOLA	*Physalis*	404
	SOLA	*Physalis ixocarpa*	410
	SOLA	*Physalis pubescens*	409
	SOLA	*Solanum nigrum*	403
Heliothis virescens	COMP	*Ageratum*	433
	COMP	*Ageratum conyzoides*	483
	COMP	*Arctium*	418
	COMP	*Erigeron divergens*	819
	COMP	*Haplopappus divaricatus*	491
	COMP	*Heterotheca subaxillaris*	492
	COMP	*Pyrrhopappus carolinianus*	503
	CONV	*Ipomoea*	494
	GERA	*Erodium cicutarium*	817
	GERA	*Geranium*	430
	GERA	*Geranium maculatum*	489
	GRAM	*Avena sativa*	422

Heliothine species	Plant family	Host plant	Reference
	GRAM	*Zea mays*	411
	LEGU	*Arachis hypogea*	415
	LEGU	*Caesalpinia gilliesii*	820
	LEGU	*Cajanus cajan*	442
	LEGU	*Cicer arietinum*	816
	LEGU	*Desmodium canescens*	485
	LEGU	*Desmodium strictum*	486
	LEGU	*Desmodium tortosum*	487
	LEGU	*Lathyrus odoratus*	495
	LEGU	*Medicago sativa*	498
	LEGU	*Phaseolus*	420
	LEGU	*Pisum sativum*	464
	LEGU	*Vigna unguiculata*	441
	LINA	*Linum sulcatum*	497
	MALV	*Gossypium*	419
	MALV	*Gossypium herbaceum*	490
	MALV	*Hibiscus*	438
	MALV	*Hibiscus esculentus*	421
	MALV	*Sphaeralcea coulteri*	818
	MELA	*Rhexia*	412
	MELA	*?Rhexia*	451
	MELA	*Rhexia alifanus*	504
	MELA	*Rhexia virginica*	428
	PEDA	*Sesamum*	439
	PEDA	*Sesamum indicum*	416
	POLY	*Rumex crispus*	507
	ROSA	*Rosa*	437
	SCRO	*Linaria canadensis*	429
	SOLA	*Capsicum*	423
	SOLA	*Lycopersicon esculentum*	424
	SOLA	*Nicotiana tabacum*	414
	SOLA	*Physalis*	444
	SOLA	*Physalis angulata*	500
	SOLA	*Physalis turbinata*	501
	SOLA	*Physalis viscosa*	427
	SOLA	*Solanum*	452
	SOLA	*Solanum lycopersicum*	509
	SOLA	*Solanum melongena*	425
	SOLA	*Solanum nigrum*	510
	SOLA	*Solanum sieglinge*	413
	SOLA	*Solanum sisymbriifolium*	511
	SOLA	*Solanum tuberosum*	512
	VALE	*Valeriana*	417
Heliothis viriplaca	APOC	*Apocynum cannabinum*	530
	CARY	*Lychnis*	553
	CARY	*Silene*	539
	CARY	*Silene album*	561
	CARY	*Silene cucubalus*	516
	CARY	*Silene otites*	515
	CARY	*Silene vulgaris*	549
	CHEN	*Beta vulgaris*	531
	COMP	*Artemisia*	547
	COMP	*Artemisia campestris*	835
	COMP	*Centaurea*	524
	COMP	*Cichorium intybus*	518
	COMP	*Crepis*	541
	COMP	*Crepis capillaris*	520

Heliothine species	Plant family	Host plant	Reference
	COMP	*Hieracium*	523
	COMP	*Sonchus*	546
	DIPS	*Dipsacus*	545
	DIPS	*Scabiosa*	522
	GRAM	(unspecified)	533
	GRAM	*Secale cereale*	536
	LEGU	*Medicago sativa*	527
	LEGU	*Ononis*	808
	LEGU	*Ononis arvensis*	513
	LEGU	*Ononis otites*	560
	LEGU	*Ononis repens*	544
	LEGU	*Ononis spinosa*	557
	LEGU	*Phaseolus vulgaris*	526
	LEGU	*Trifolium*	540
	LEGU	*Trifolium pratense*	521
	LINA	*Linum*	534
	MALV	*Gossypium*	528
	OLEA	(unspecified)	535
	ONAG	*Oenothera*	525
	POLY	*Rumex*	542
	RANU	*Thalictrum*	548
	SCRO	*Linaria*	538
	SCRO	*Linaria vulgaris*	514
	SOLA	*Lycopersicon esculentum*	532
	SOLA	*Nicotiana tabacum*	529
	UMBE	*Daucus carota*	519
Periphanes delphinii	RANU	*Aconitum*	840
	RANU	*Aconitum lycoctonum*	578
	RANU	*Aconitum napellus*	577
	RANU	*Delphinium ajacis*	576
	RANU	*Delphinium ambiguum*	579
	RANU	*Delphinium consolida*	794
	RANU	*Delphinium regalis*	581
Pyrrhia exprimens	ANAC	*Rhus typhina*	604
	BETU	*Betula*	612
	CRUC	*Brassica oleracea*	600
	JUGL	*Juglans*	607
	LEGU	*Desmodium*	596
	MALV	*Althea*	613
	MYRI	*Myrica asplenifolia*	594
	POLY	*Polygonum*	595
	RANU	*Aconitum*	598
	RANU	*Delphinium*	597
	ROSA	*Prunus*	611
	ROSA	*Rosa*	599
	SALI	*Populus*	608
	SALI	*Salix*	609
Pyrrhia purpurina	COMP	*Centaurea scabiosa*	785
	DIPS	*Succisa pratensis*	786
Pyrrhia treitschkei	LABI	*Melissa*	779
Pyrrhia umbra	ROSA	(unspecified)	641
	BETU	*Alnus*	636
	CARY	*Honkenya peploides*	617
	CARY	*Honkenya peploides*	629
	COMP	*Sigesbeckia orientalis*	782
	CONV	*Convolvulus soldanella*	831
	CRUC	*Brassica nigra*	634

Heliothine species	Plant family	Host plant	Reference
	CRUC	*Brassica oleracea*	633
	ERIC	*Rhododendron arboreum*	637
	GERA	*Geranium*	602
	GERA	*Geranium pratense*	781
	LEGU	*Desmodium*	653
	LEGU	*Glycine max*	623
	LEGU	*Ononis*	627
	LEGU	*Ononis arvensis*	615
	LEGU	*Ononis repens*	645
	LEGU	*Ononis spinosa*	650
	LEGU	*Phaseolus vulgaris*	619
	POLY	*Polygonum*	640
	POLY	*Polygonum aviculare*	620
	POLY	*Polygonum nodosum*	621
	RANU	*Aconitum columbianum*	632
	RANU	*Aquilegia*	639
	RANU	*Delphinium*	638
	ROSA	*Prunus virginiana*	655
	ROSA	*Rosa*	626
	SALI	*Salix*	618
	SALI	*Salix viminalis*	833
	SCRO	*Antirrhinum majus*	625
	SCRO	*Linaria*	622
	SCRO	*Penstemon*	654
	SOLA	*Hyoscyamus niger*	616
	SOLA	*Nicotiana tabacum*	624
Pyrrhia victorina	LABI	*Salvia*	783
	RUTA	*Dictamnus*	784
Rhodoecia aurantiago	SCRO	*Afzelia macrophylla*	656
	SCRO	*Antirrhinum majus*	660
	SCRO	*Gerardia*	657
	SCRO	*Gerardia grandiflora*	661
	SCRO	*Gerardia pedicularia*	662
	SCRO	*Linaria*	659
Schinia arcigera	COMP	*Aster*	666
	COMP	*Aster laevis*	665
	COMP	*Aster?multiflorus*	671
	COMP	*Aster puniceus*	664
Schinia aurantiaca	POLE	*Gilia densifolia*	673
	POLE	*Gilia virgata*	672
Schinia brevis	COMP	*Aster laevis*	674
	COMP	*Aster novae-angliae*	713
Schinia cardui	COMP	*Picris hieracioides*	677
Schinia chilensis	GRAM	*Zea mays*	859
	LEGU	*Phaseolus*	860
	LEGU	*Vicia*	862
	MALV	*Gossypium*	861
Schinia citrinellus	EUPH	*Croton americanus*	678
	EUPH	*Croton californicus*	679
Schinia cupes	ONAG	*Oenothera clavaeformis*	680
Schinia dobla	COMP	*Ambrosia dumosa*	681
Schinia felicitata	ONAG	*Oenothera deltoides*	682
Schinia florida	ONAG	*Gaura*	689
	ONAG	*Gaura biennis*	684
	ONAG	*Oenothera*	683
	ONAG	*Oenothera biennis*	685
	ONAG	*Oenothera lamarkiana*	692

Heliothine species	**Plant family**	**Host plant**	**Reference**
Schinia fulleri	COMP	?*Actinospermum angustifolium*	697
Schinia gaurae	ONAG	*Gaura*	701
	ONAG	*Gaura biennis*	699
Schinia gloriosa	COMP	*Liatris*	704
	COMP	*Liatris cylindracea*	706
	COMP	*Liatris scariosa*	705
Schinia gracilenta	COMP	*Kuhnia eupatorioides*	707
Schinia imperialis	DIPS	*Cepalaria procera*	787
Schinia indiana	POLE	*Phlox divaricata*	717
	POLE	*Phlox pilosa*	715
Schinia intrabilis	COMP	*Pluchea sericea*	718
Schinia jaegeri	COMP	*Machaeranthera cognata*	720
	COMP	*Machaeranthera orcuttii*	719
Schinia ligae	COMP	*Machaeranthera tortifolius*	721
Schinia lucens	LEGU	*Amorpha canescens*	722
Schinia lynx	COMP	*Erigeron*	725
Schinia marginata	COMP	*Ambrosia*	729
	COMP	*Ambrosia artemisiaefolia*	726
	COMP	*Ambrosia elatior*	727
	COMP	*Ambrosia trifida*	728
Schinia mitis	COMP	?*Pyrrhopappus carolinianus*	731
Schinia mortua	COMP	*Grindelia squarrosa*	733
	COMP	*Haplopappus rubiginosa*	732
Schinia niveicosta	COMP	*Palafoxia linearis*	735
Schinia nubila	COMP	*Solidago*	736
Schinia nundina	COMP	*Aster*	738
	COMP	*Solidago*	737
	COMP	*Solidago canadensis*	663
Schinia obscurata	COMP	*Erigeron pennsylvanicum*	741
	COMP	*Erigeron philadelphicus*	742
Schinia oleagina	COMP	?*Kuhnia eupatorioides*	743
Schinia pallicincta	COMP	*Baileya pauciradiata*	744
Schinia pulchripennis	SCRO	*Orthocarpus purpurascens*	745
Schinia rivulosa	COMP	*Ambrosia artemisiaefolia*	746
Schinia rosea	ALLI	*Allium*	790
Schinia rufipenna	COMP	*Pityopsis graminifolia*	857
Schinia scarletina	COMP	*Stephanomeria exigua*	751
	COMP	*Stephanomeria pauciflora*	748
	COMP	*Stephanomeria runcinata*	752
	COMP	*Stephanomeria virgata*	747
Schinia scutosa	CHEN	*Chenopodium*	584
	COMP	*Artemisia*	585
	COMP	*Artemisia absinthium*	590
	COMP	*Artemisia campestris*	583
	COMP	*Artemisia scoparia*	588
	COMP	*Artemisia vulgaris*	589
Schinia separata	COMP	*Artemisia?cana*	754
	COMP	*Artemisia tridentata*	753
Schinia septentrionalis	COMP	*Aster laevis*	756
	COMP	*Aster novae-angliae*	758
	COMP	*Aster puniceus*	757
Schinia sueta	LEGU	*Lupinus nanus*	760
	LEGU	*Lupinus sericeus*	761
Schinia tertia	COMP	?*Liatris*	762
Schinia thoreaui	COMP	*Ambrosia trifida*	763
Schinia trifascia	COMP	*Eupatorium*	768
	COMP	*Eupatorium perfoliatum*	771

Heliothine species	Plant family	Host plant	Reference
	COMP	*Eupatorium purpureum*	712
	COMP	*Eupatorium sessilfolium*	766
	COMP	*Kuhnia eupatorioides*	767
Schinia triolata	COMP	*Chaenactis freemontii*	772
Schinia tuberculum	COMP	*Pityopsis graminifolia*	858
Schinia verna	COMP	*Antennaria neodioica*	773
Schinia villosa	COMP	*Aster*	775
	COMP	*Erigeron corymbosus*	777
	COMP	*Erigeron peregrinus*	776
	COMP	*Eucephalus ledophyllus*	774
Schinia walsinghami	COMP	*Chrysothamnus nauseosus*	778

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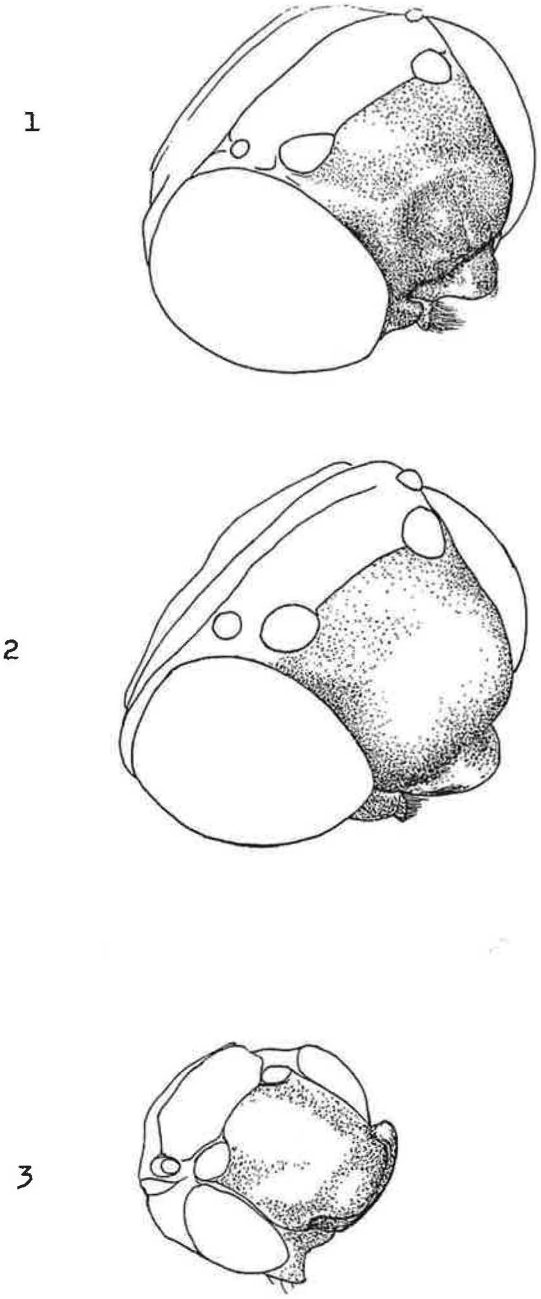
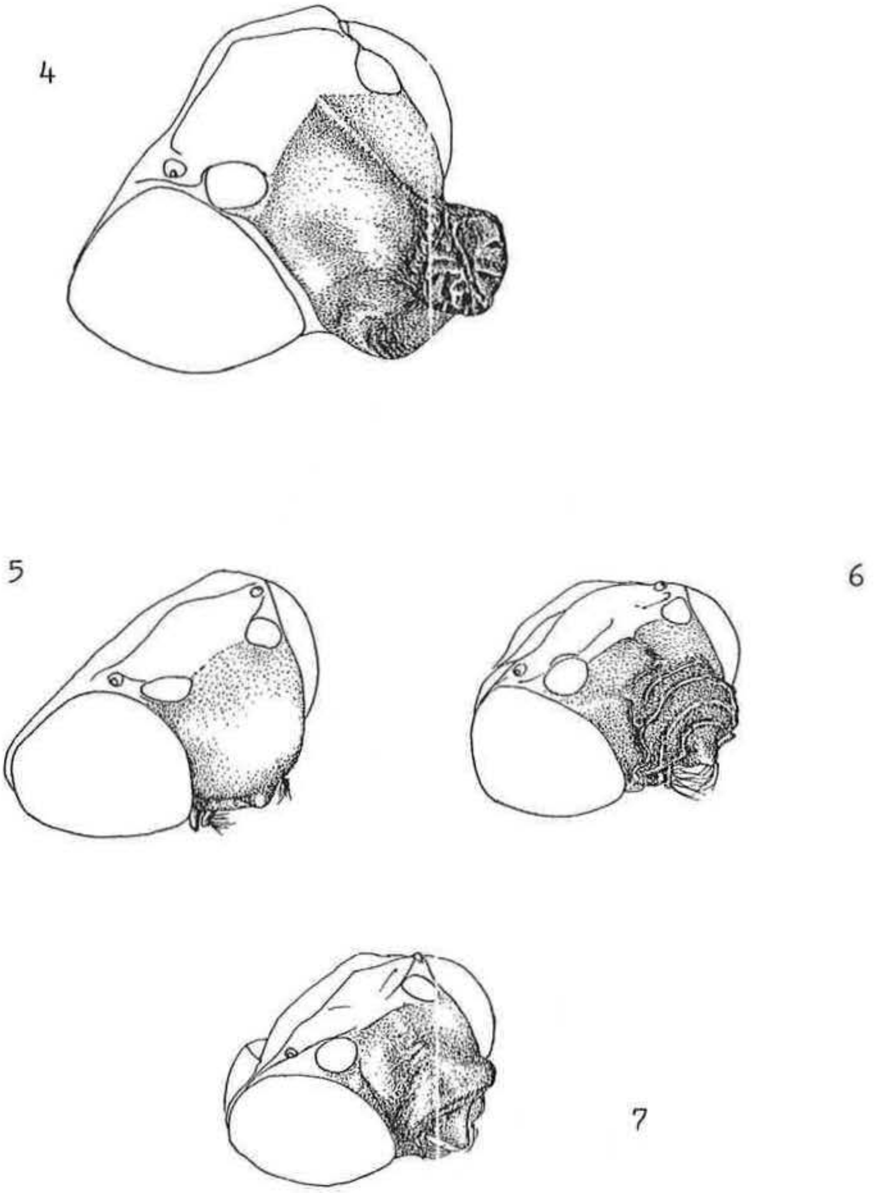
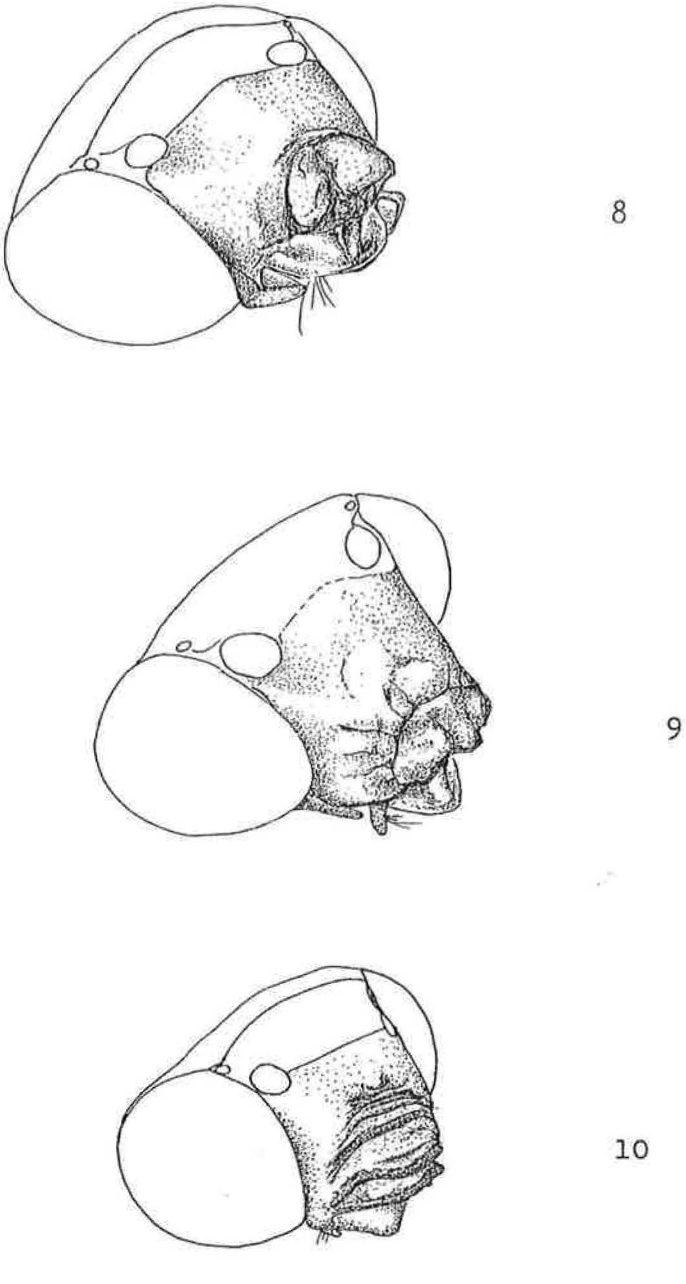


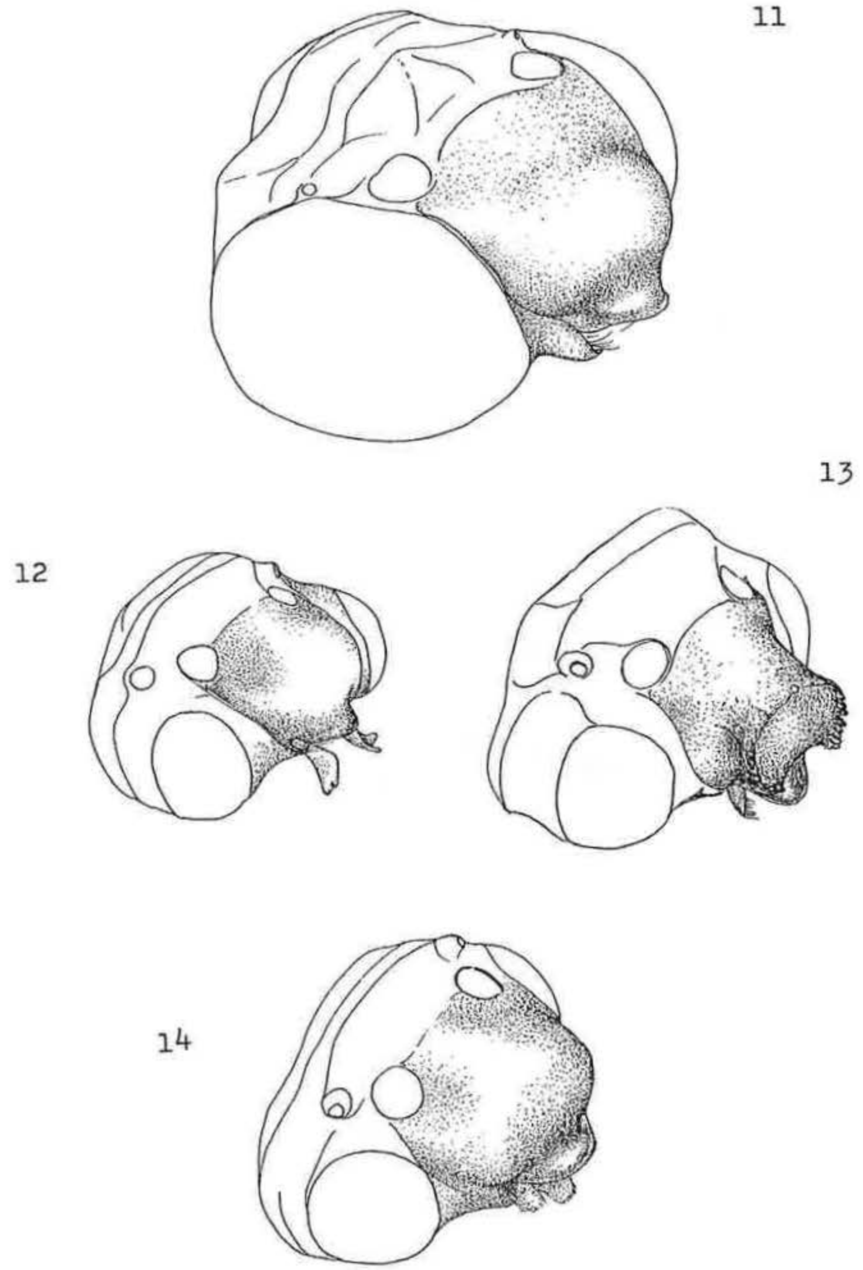
Figs. 1 - 3. Heads, Heliothinae. Fig. 1, *Protadisura posttriphaena*; Fig. 2, *Schinia jaguarina*; Fig. 3, *Helilonche modicella*.



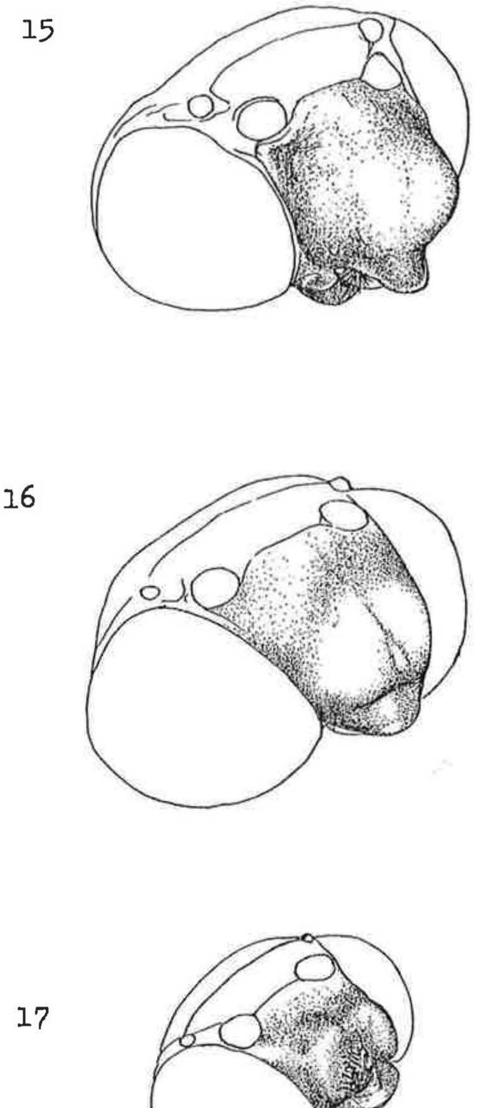
Figs. 4 - 7. Heads, Heliothinae & Stiriinae. Stiriinae. Fig. 4, *Basilodes chrysopis*. Heliothinae. Fig. 5, *Pyrrhia exprimens*; Fig. 6, *Pyrrhia victorina*; Fig. 7, *Pyrrhia treitschkei*.



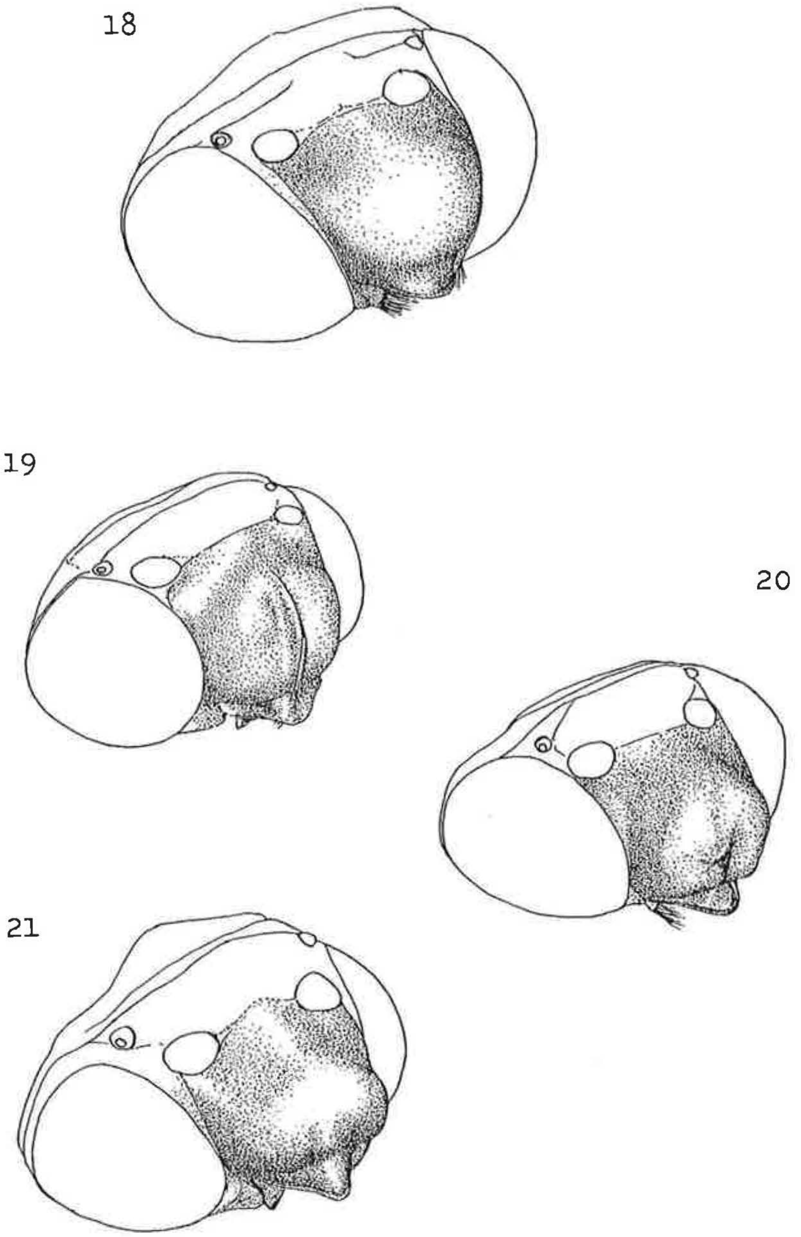
Figs. 8 - 10. Heads, Heliothinae. Fig. 8, *Aedophron rhodites*; Fig. 9, *Periphanes delphinii*; Fig. 10, *Erythroecia suavis*.



Figs. 11 - 14. Heads, Heliothinae. Fig. 11, *Erythrophaia eudoxia*; Fig. 12, *Eutricopis nexilis*; Fig. 13, *Heliothodes diminutivus*; Fig. 14, *Pyrocleptria cora*.



Figs. 15 - 17. Heads, Heliothinae. Fig. 15, *Schinia scutosa*; Fig. 16, *Adisura atkinsoni*; Fig. 17, *Adisura parva*.



Figs. 18 - 21. Heads, Heliothinae. Fig. 18, *Helicoverpa armigera*; Fig. 19, *Heliothis terracottoides*; Fig. 20, *Heliocheilus moribunda*; Fig. 21, *Heliothis viriplaca*.

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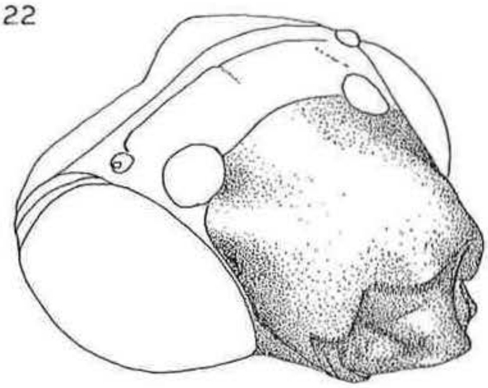

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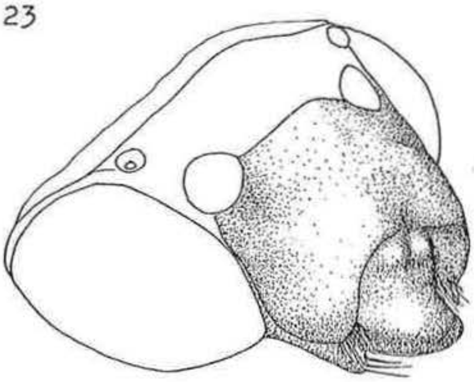
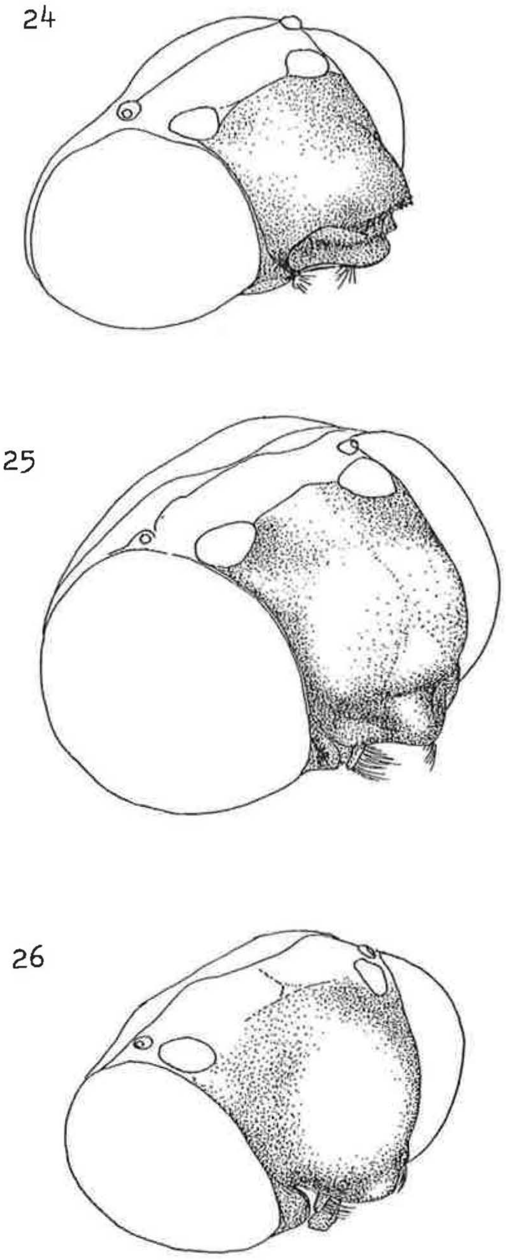
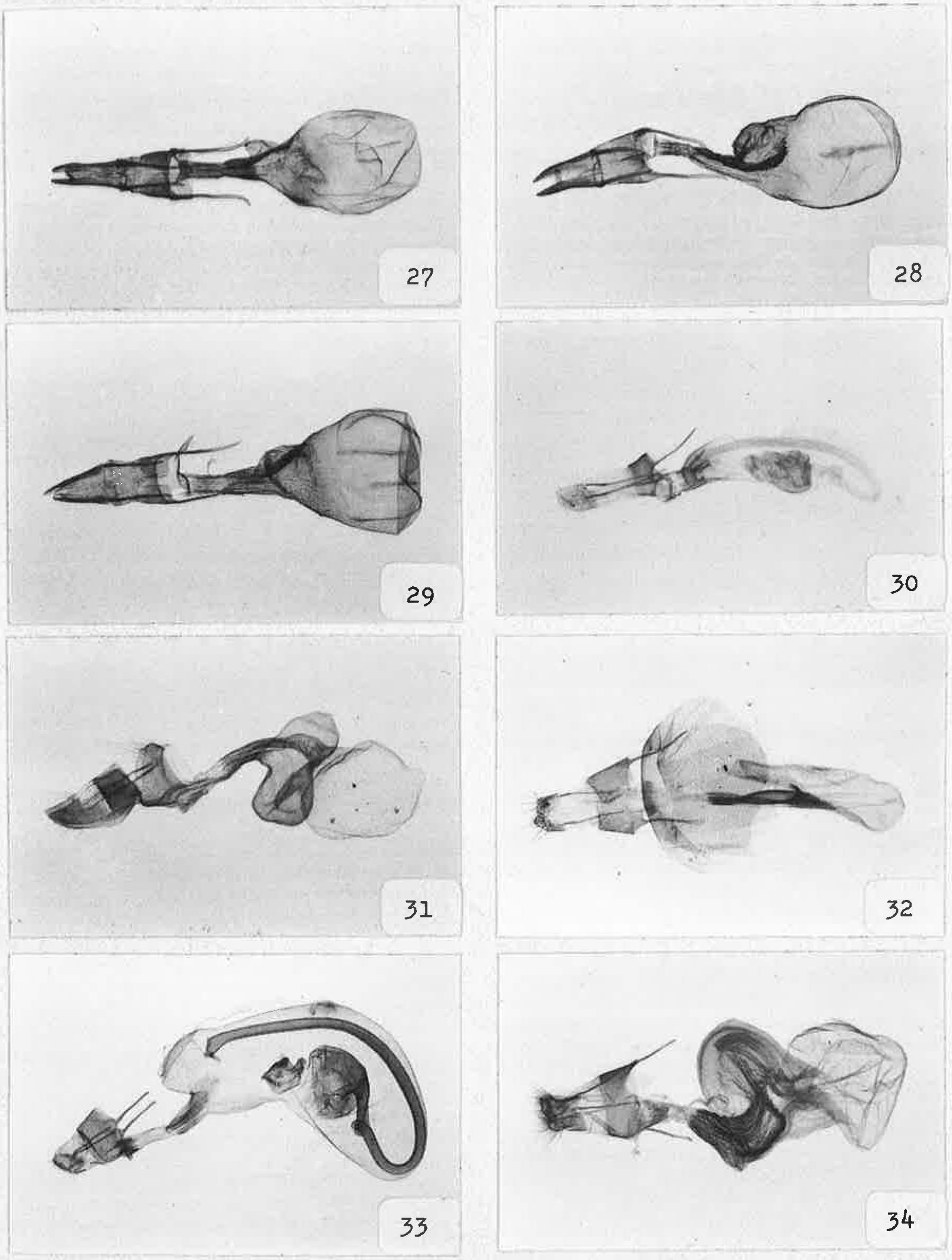


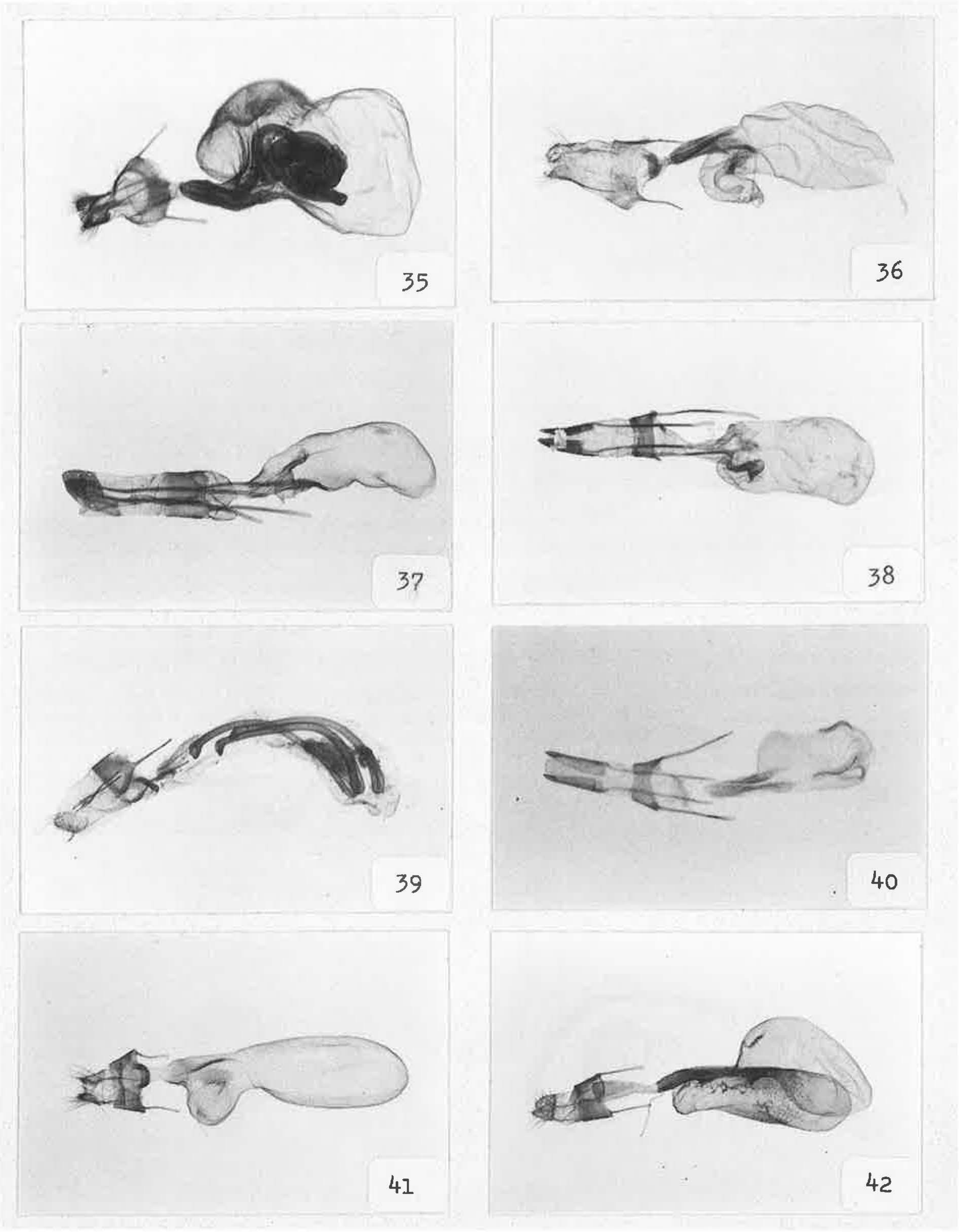
Figs. 22 & 23. *Heliothis incarnata*, heads. Fig. 22, male; Fig. 23, female.



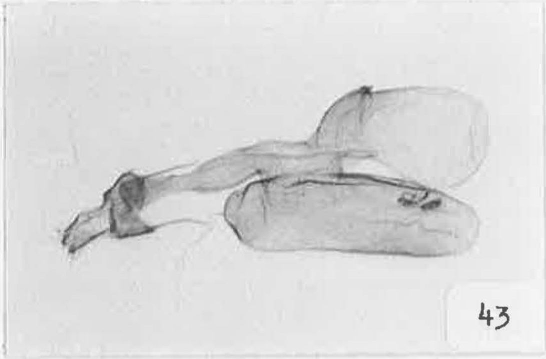
Figs. 24 - 26. Heads, Heliothinae. Fig. 24, *Heliothis punctifera*; Fig. 25, *Australothis rubrescens*; Fig. 26, *Heliothis syrticola*.



Figs. 27 - 34. Female genitalia, Heliothinae. Fig. 27, *Aedophron phlebophora* (BM Noct 13054); Fig. 28, *Aedophron rhodites* (BM Noct 13059); Fig. 29, *Aedophron venosa* (BM Noct 13069); Fig. 30, *Baptarma felicita* (AMNH); Fig. 31, *Derrima stellata* (BM Noct 13078); Fig. 32, *Psectrotarsia flava* (USNM 41174); Fig. 33, *Erythroecia suavis* (BM Noct 13090); Fig. 34, *Erythrophaia eudoxia* (BM Noct 13102).



Figs. 35 - 42. Female genitalia, Heliothinae. Fig. 35, *Erythrophaia suavis* (BM Noct 13113); Fig. 36, *Pyrocleptria cora* (BM Noct 13629); Fig. 37, *Eutricopis nexilis* (BM Noct 13123); Fig. 38, *Heliothodes diminutivus* (BM Noct 13562); Fig. 39, *Melaporphyria immortua* (CNC 4142); Fig. 40, *Microhelia angelica* (CNC 4391); Fig. 41, *Periphanes delphinii* (BM Noct 13574); Fig. 42, *Pyrrhia bifasciata* (BM Noct 13585).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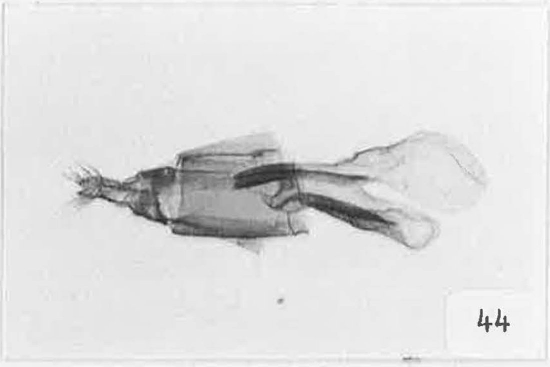
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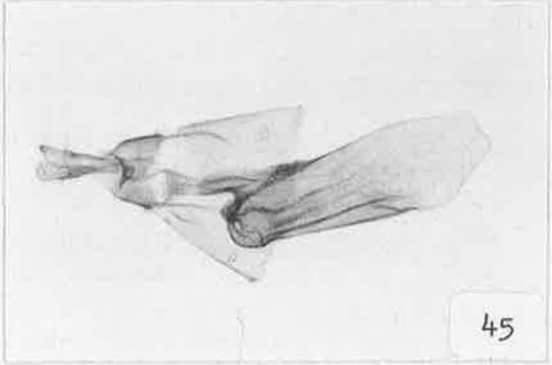
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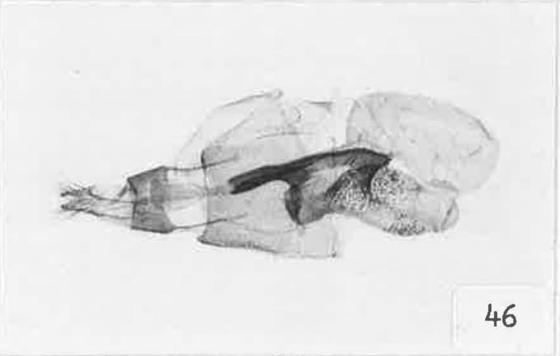
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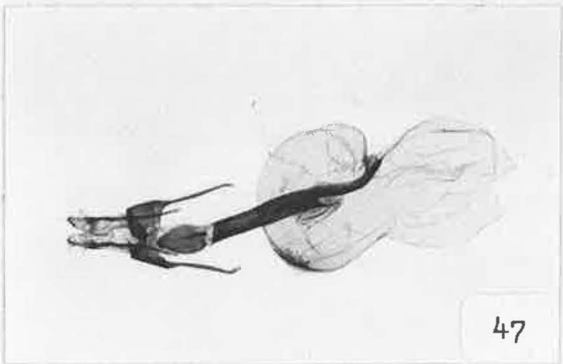
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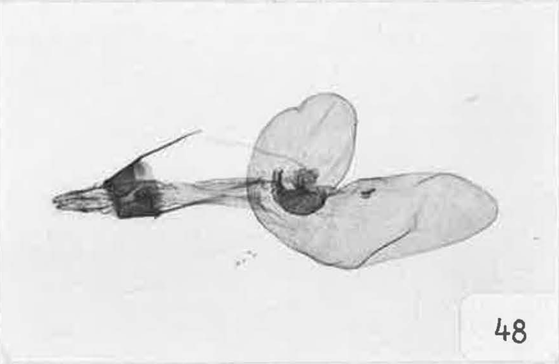
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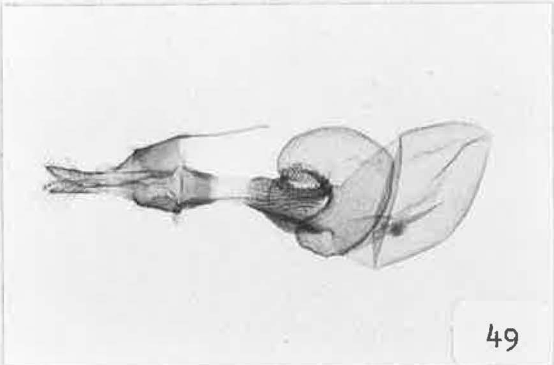
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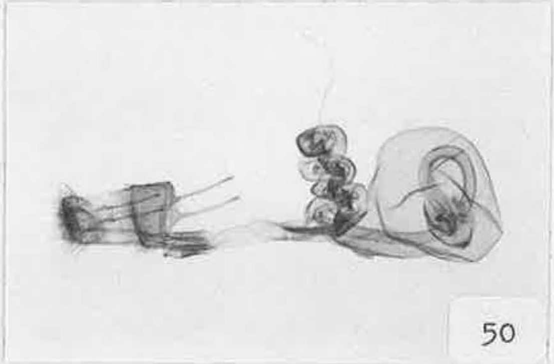
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Figs. 43 - 50. Female genitalia, Heliothinae. Fig. 43, *Pyrrhia exprimens* (BM Noct 13589); Fig. 44, *Pyrrhia purpurina* (BM Noct 13594); Fig. 45, *Pyrrhia treitschkei* (BM Noct 13599); Fig. 46, *Pyrrhia umbra* (BM Noct 13607); Fig. 47, *Pyrrhia victorina* (BM Noct 13618); Fig. 48, *Rhodoecia aurantiago* (BM Noct 13624); Fig. 49, *Protadisura posttriphaena* (BM Noct 13392); Fig. 50, *Adisura cana* (BM Noct 13031).

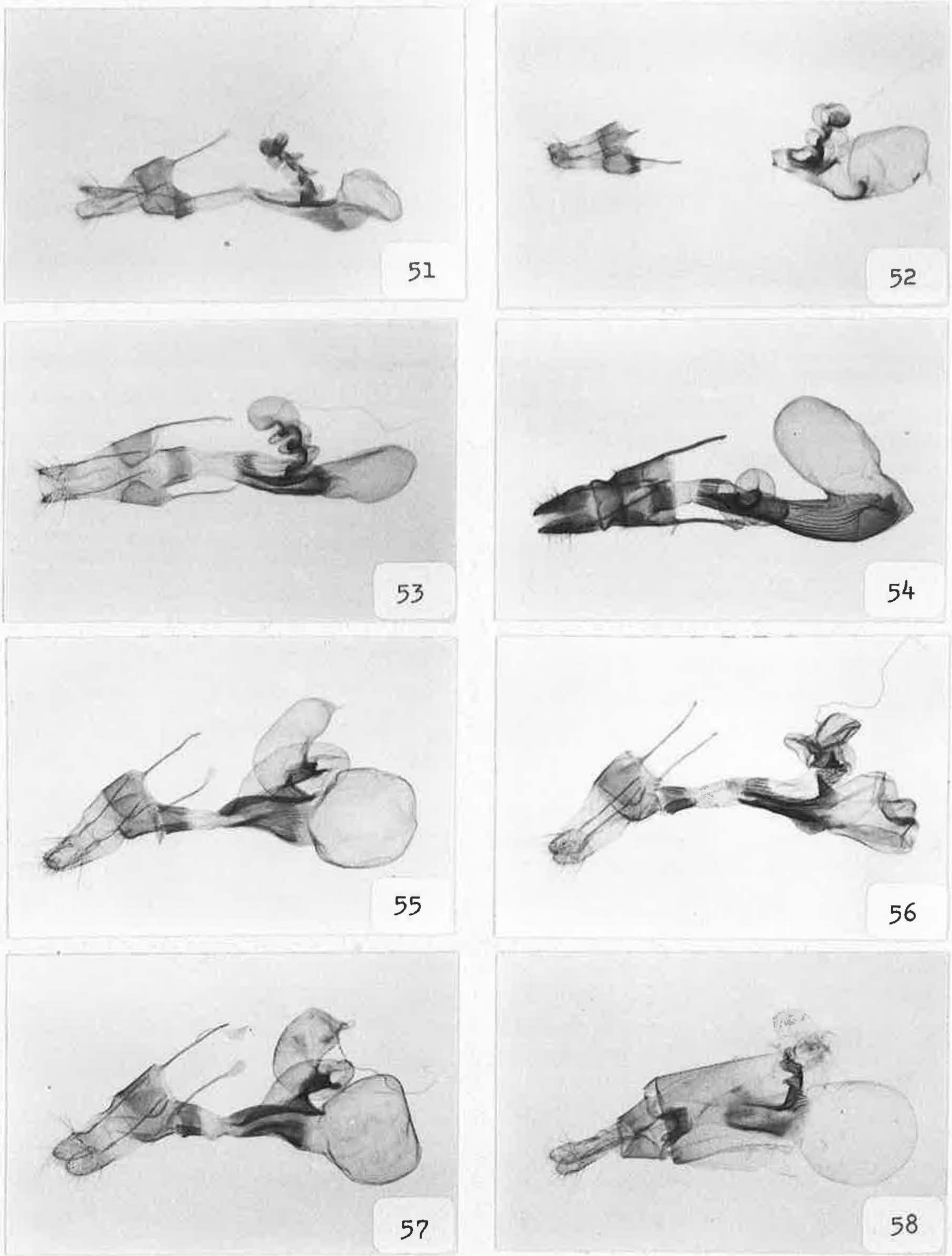
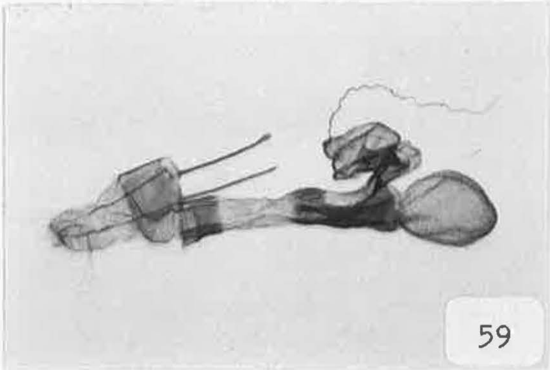


Fig. 51 - 58. Female genitalia, Heliothinae. Fig. 51, *Adisura aerugo* (BM Noct 13000); Fig. 52, *Adisura affinis* (BM Noct 13003); Fig. 53, *Adisura atkinsoni* (BM Noct 13022); Fig. 54, *Adisura bella* (BM Noct 13024); Fig. 55, *Adisura callima* (BM Noct 13028); Fig. 56, *Adisura dulcis* (BM Noct 13033); Fig. 57, *Adisura malagasica* (BM Noct 13036); Fig. 58, *Adisura marginalis* (BM Noct 13039).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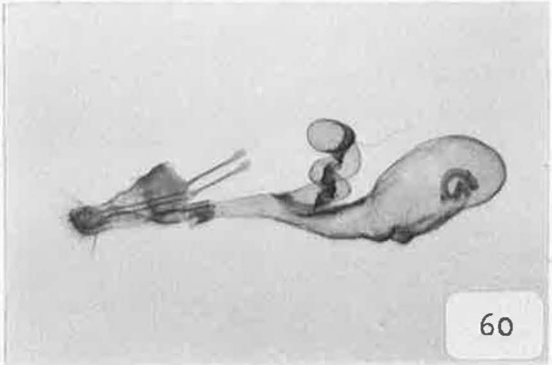
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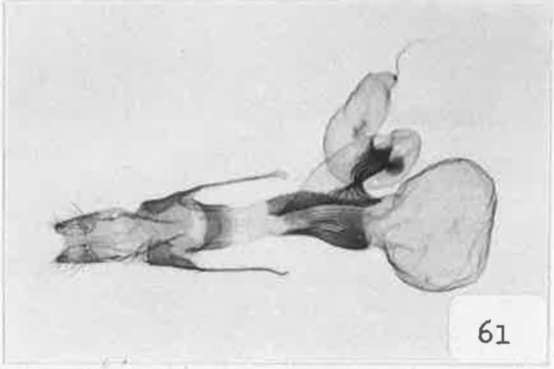
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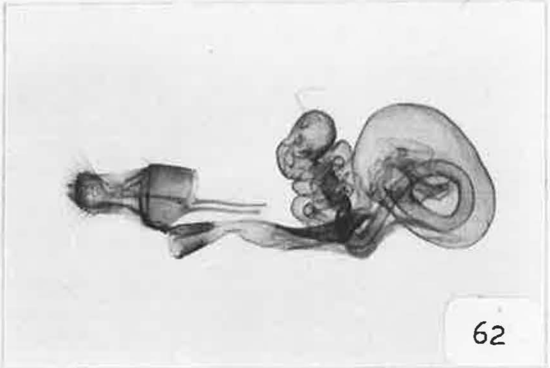
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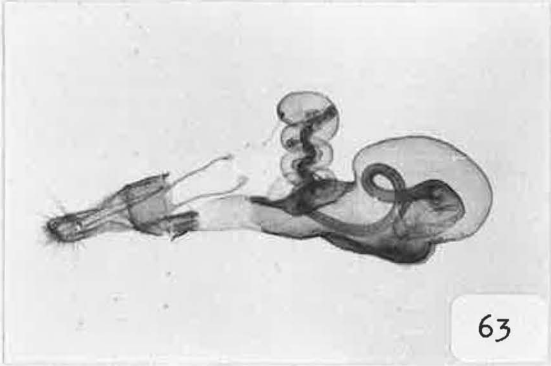
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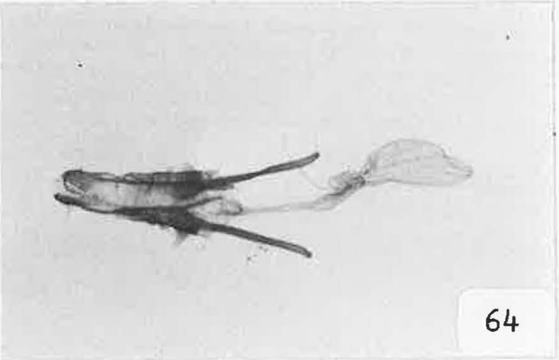
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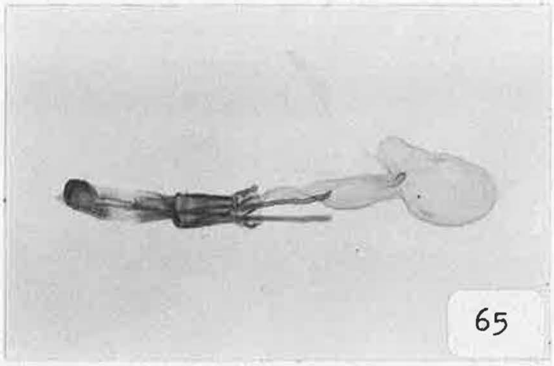
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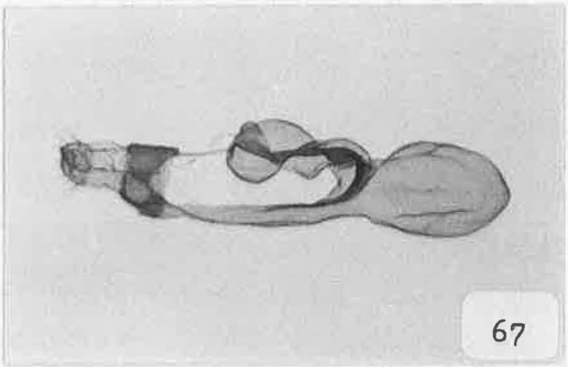
66

Figs. 59 - 66. Female genitalia, Heliothinae. Fig. 59, *Adisura purgata* (BM Noct 13041); Fig. 60, *Adisura stigmatica* (BM Noct 13044); Fig. 61, *Adisura straminea* (BM Noct 13047); Fig. 62, *Adisura parva* (BM Noct 13053); Fig. 63, *Adisura litarga* (ANIC); Fig. 64, *Heliolonche modicella* (BM Noct 13327); Fig. 65, *Heliolonche pictipennis* (BM Noct 13336); Fig. 66, *Schinia scutosa* (BM Noct 13682).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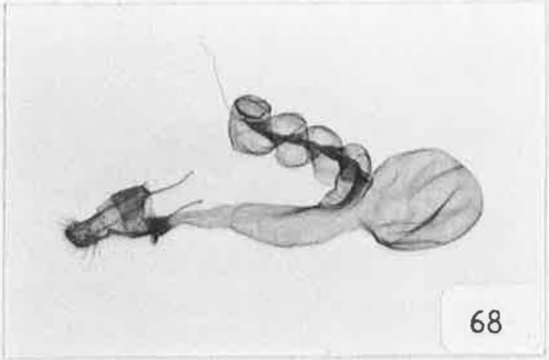
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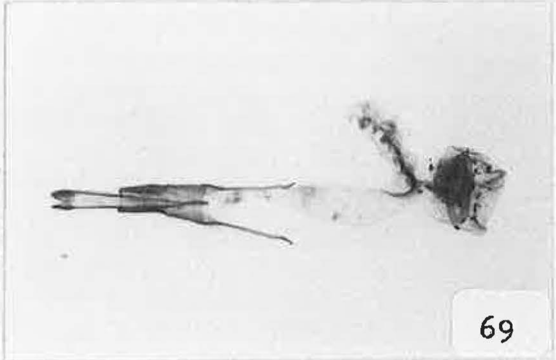
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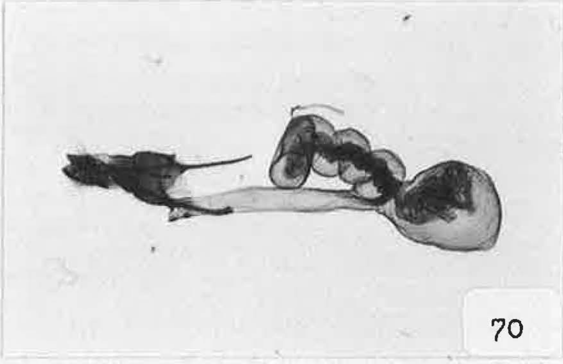
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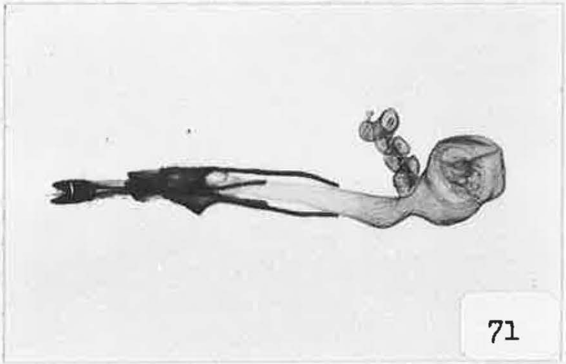
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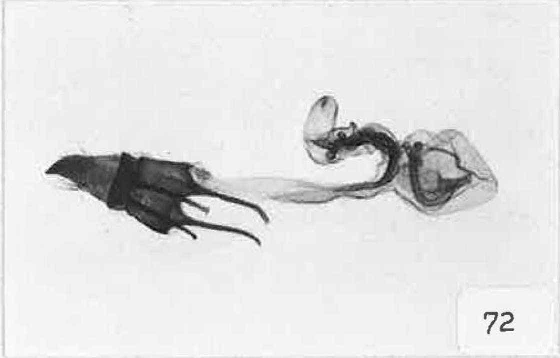
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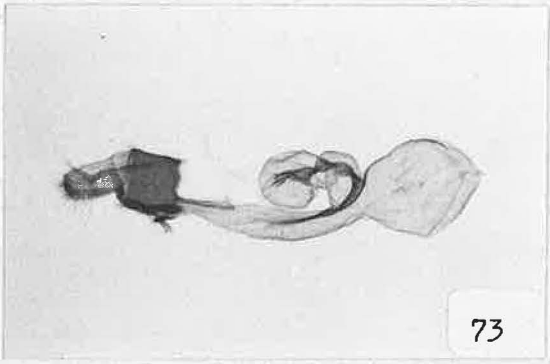
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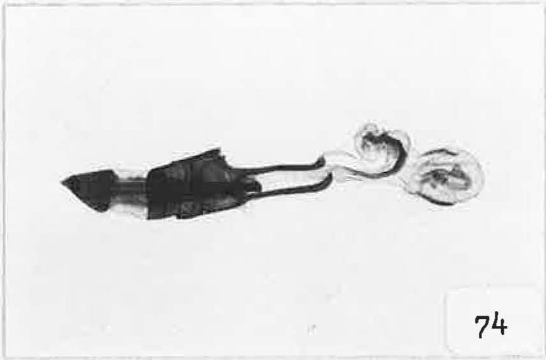
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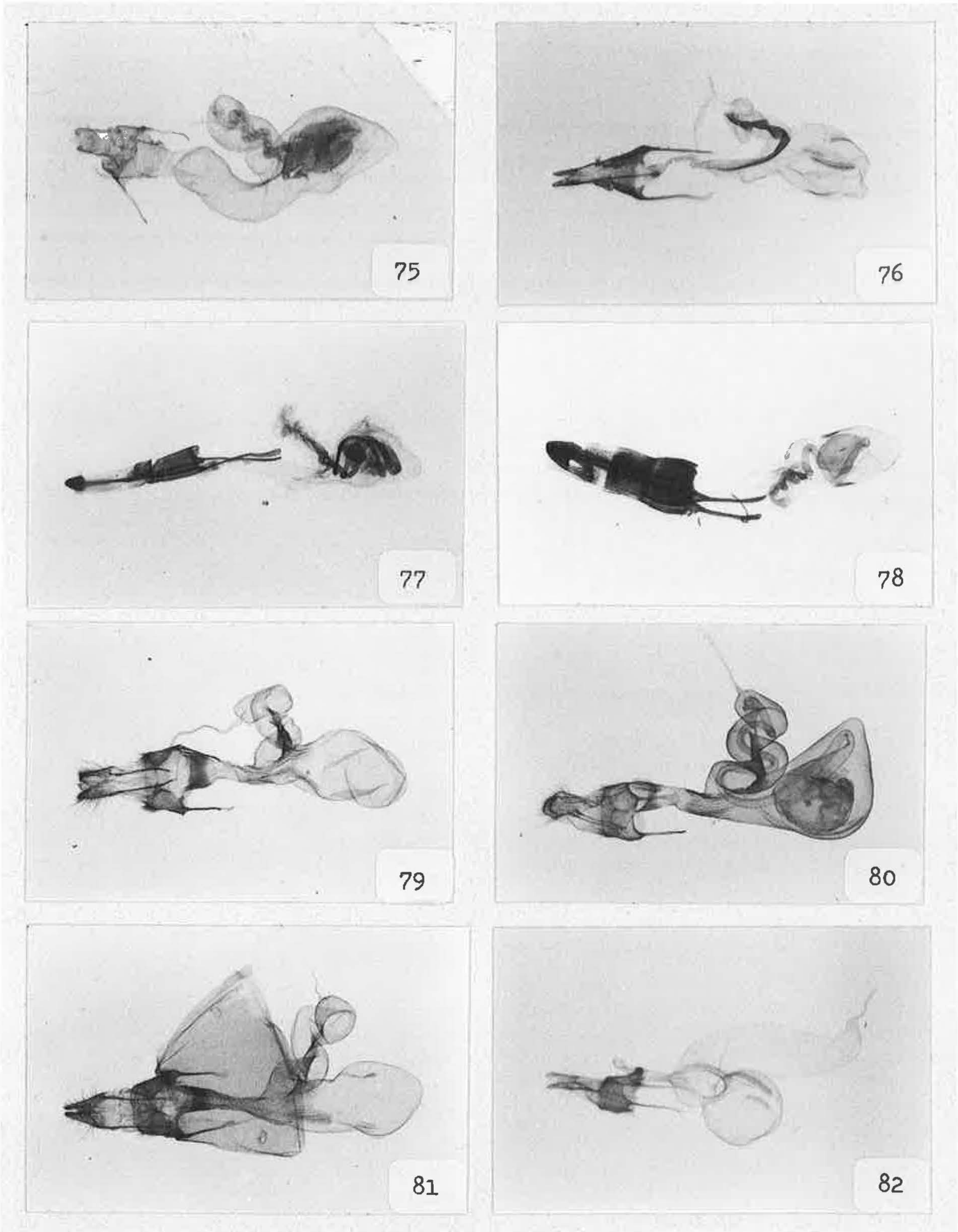
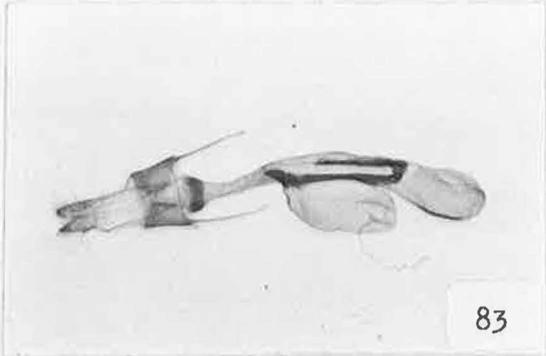
Figs. 67 - 74. Female genitalia, Heliothinae. Fig. 67, *Schinia chilensis* (AMNH); Fig. 68, *Schinia* sp. No. 1 (Chile) (AMNH); Fig. 69, *Schinia rufipenna* (CNC 7792); Fig. 70, *Schinia gaurae* (BM Noct 13638); Fig. 71, *Schinia jaegeri* (BM Noct 13641); Fig. 72, *Schinia jaguarina* (BM Noct 13643); Fig. 73, *Schinia pulchra* (AMNH); Fig. 74, *Schinia purpurascens* (BM Noct 13659).



Figs. 75 - 82. Female genitalia, Heliothinae. Fig. 75, *Schinia rosea* (CNC 2943); Fig. 76, *Schinia sexplagiata* (BM Noct 13670); Fig. 77, *Schinia tuberculum* (CNC 7785); Fig. 78, *Schinia verna* (CNC 7795); Fig. 79, *Schinia roseoflammata* (BM Noct 13678); Fig. 80, *Schinia xanthiata* (BM Noct 13675); Fig. 81, *Schinia ungemachi* (BM Noct 12887); Fig. 82, *Heliothis conifera* (BM Noct 13340).



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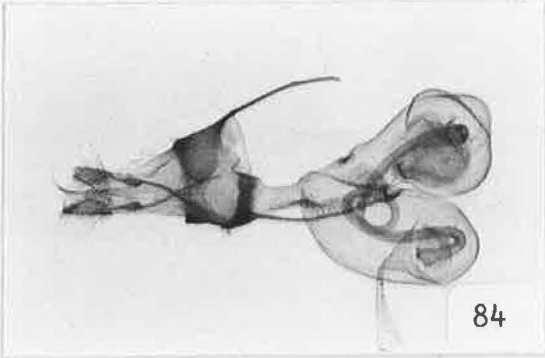

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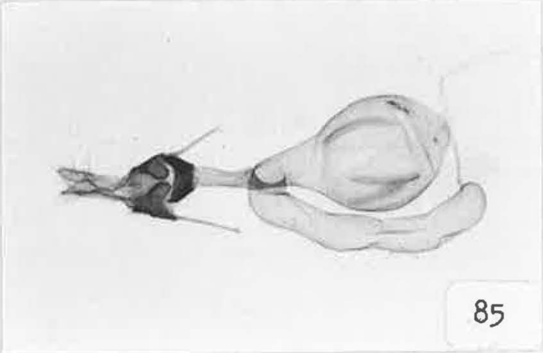

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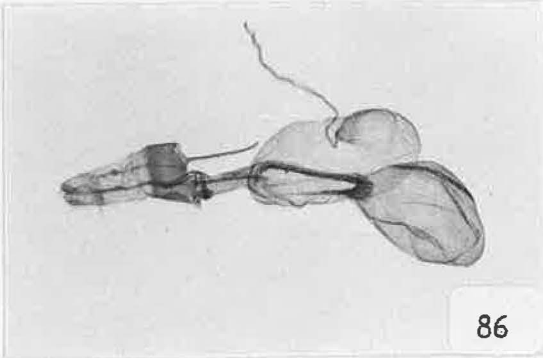

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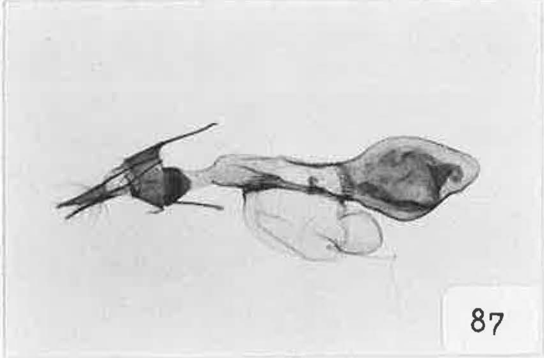

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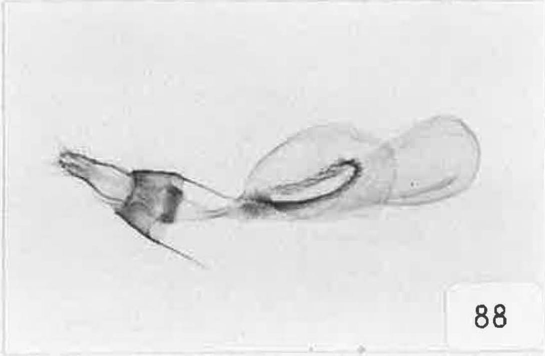

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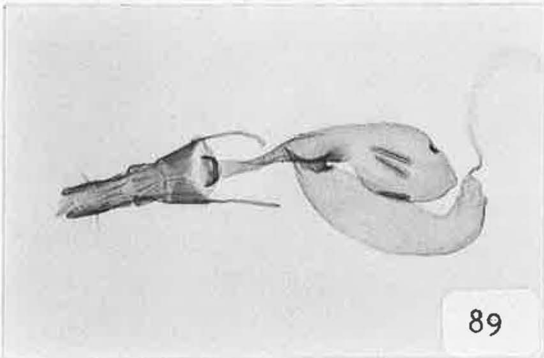

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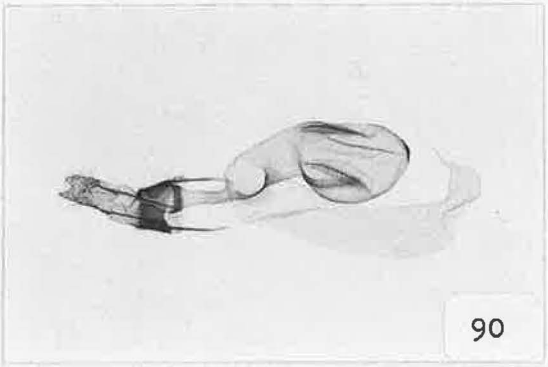

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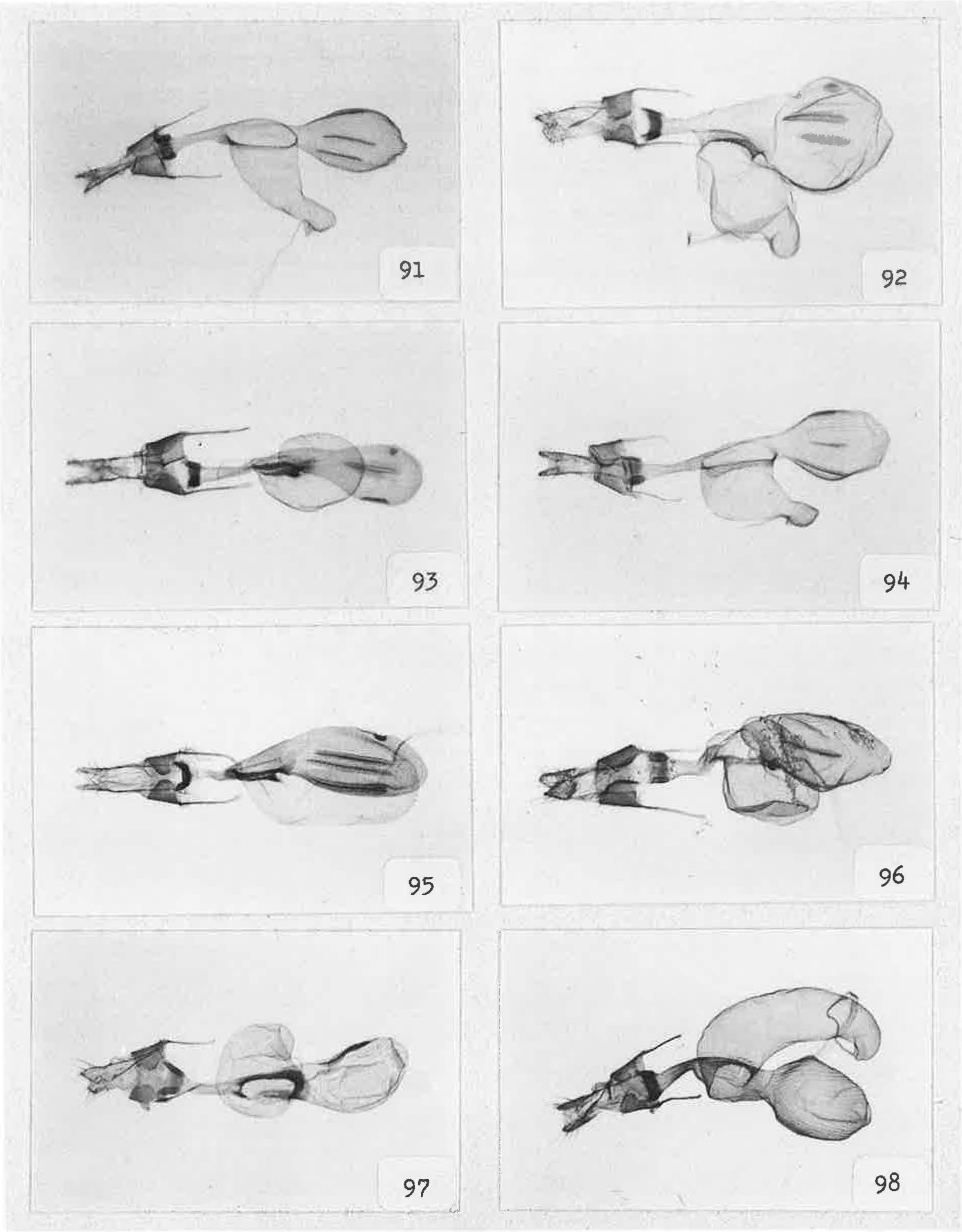
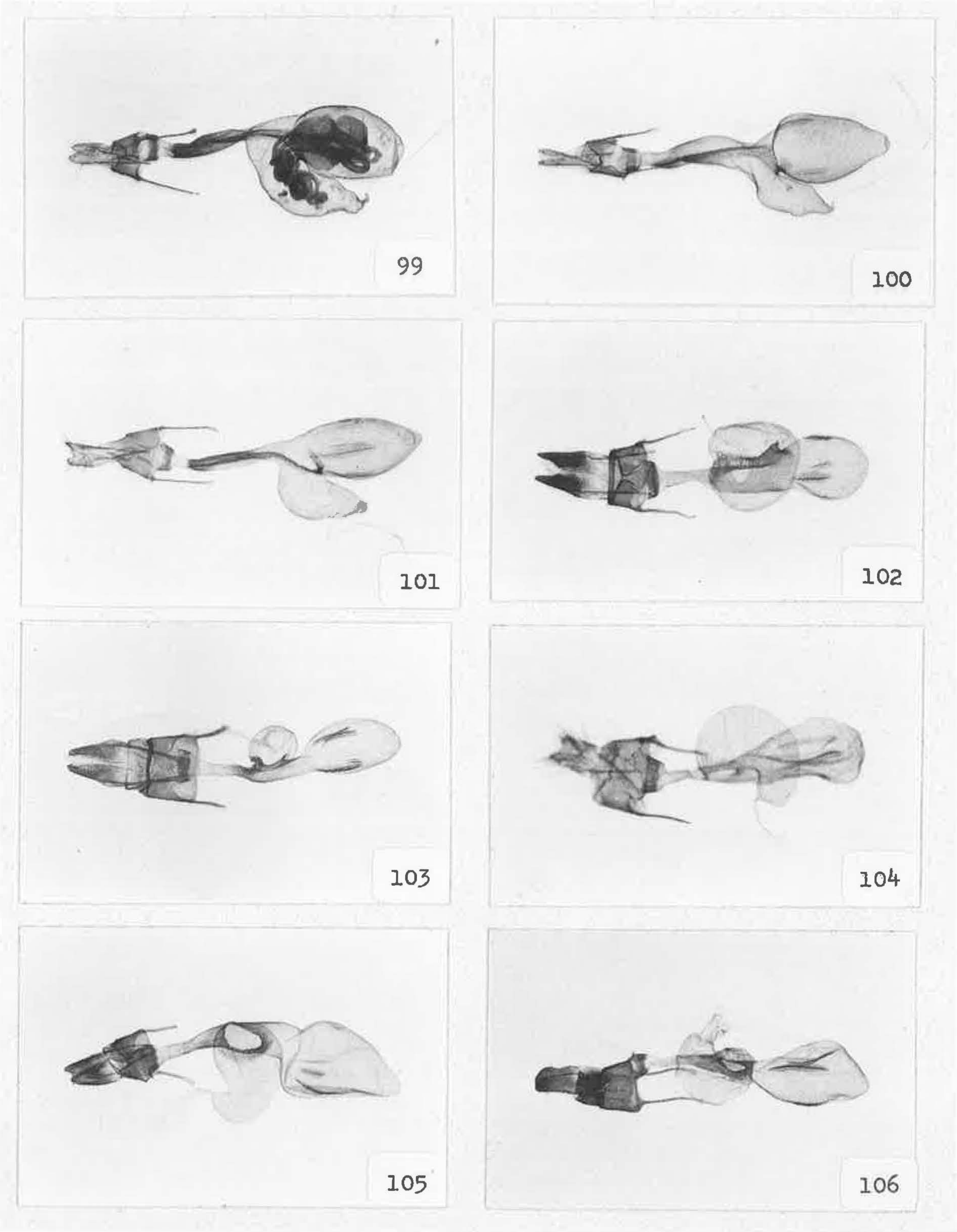
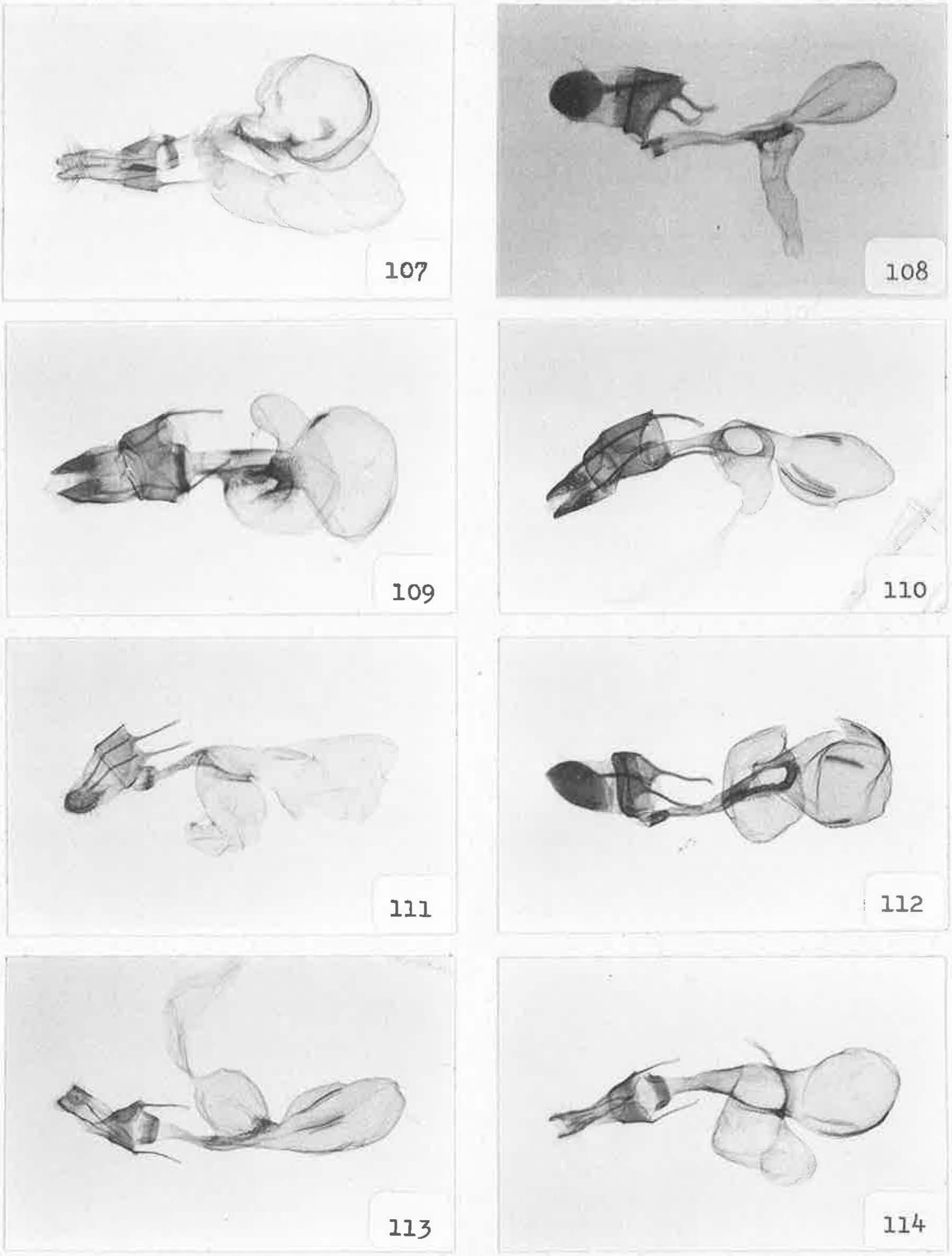
Figs. 83 - 90. Female genitalia, Heliothinae. Fig. 83, *Heliothis flavigera* (BM Noct 13346); Fig. 84, *Heliothis flavirufa* (BM Noct 13350); Fig. 85, *Heliothis maritima* (BM Noct 13353); Fig. 86, *Heliothis metachrisea* (BM Noct 13359); Fig. 87, *Heliothis nubigera* (BM Noct 13369); Fig. 88, *Heliothis* sp. No. 2 (near *nubigera*) (BM Noct 13373); Fig. 89, *Heliothis ononis* (BM Noct 13377); Fig. 90, *Heliothis oregonica* (BM Noct 13380).



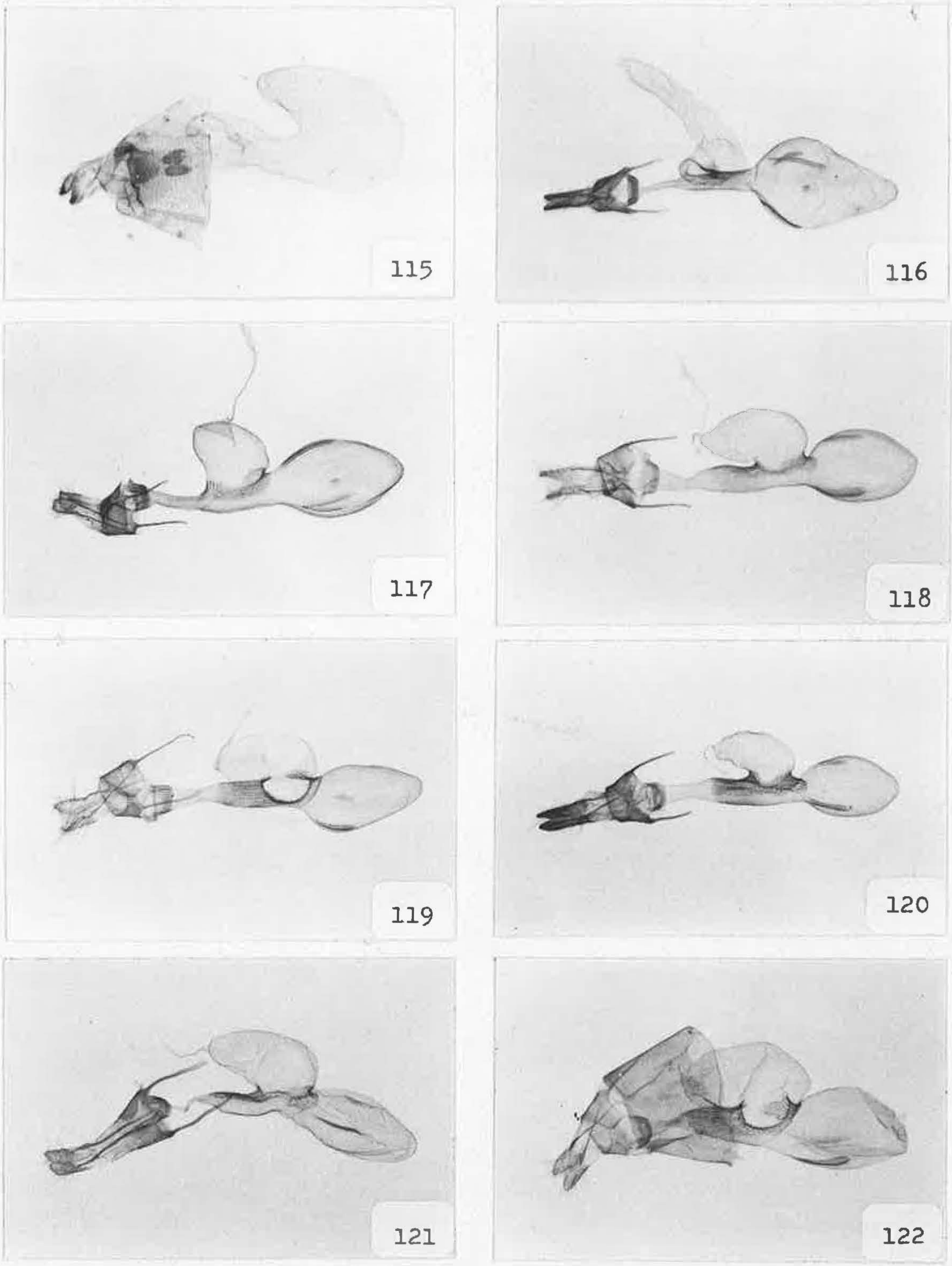
Figs. 91 - 98. Female genitalia, Heliothinae. Fig. 91, *Heliothis peltigera* (BM Noct 13383); Fig. 92, *Heliothis phloxiphaga* (BM Noct 13386); Fig. 93, *Heliothis prorupta* (BM Noct 13395); Fig. 94, *Heliothis scutiligera* (BM Noct 13403); Fig. 95, *Heliothis viriplaca* (BM Noct 13440); Fig. 96, *Heliothis xanthiata* (BM Noct 13451); Fig. 97, *Heliothis punctifera* (BM Noct 13530); Fig. 98, *Heliothis incarnata* (BM Noct 13546).



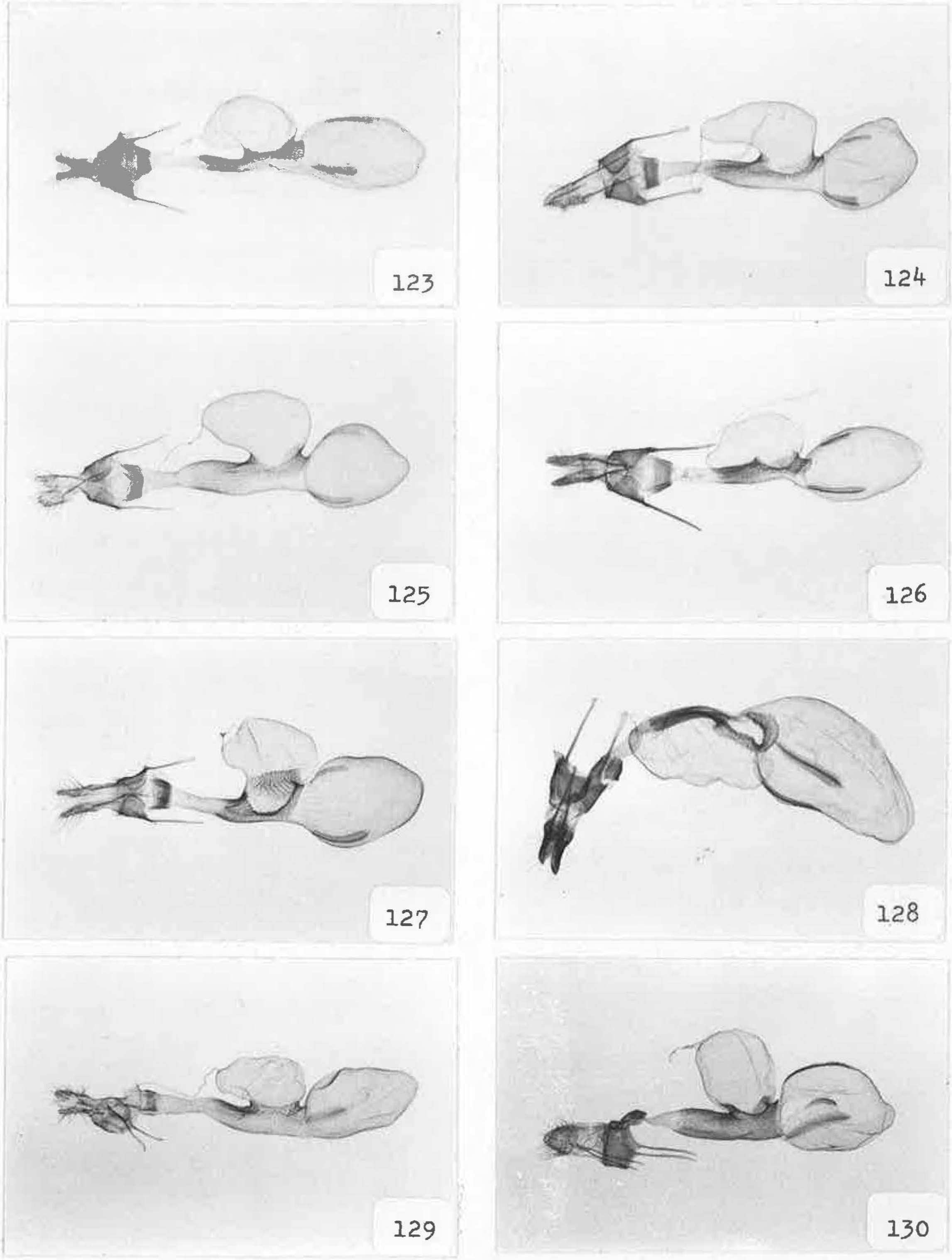
Figs. 99 - 106. Female genitalia, Heliothinae. Fig. 99, *Heliothis molochitina* (BM Noct 13362); Fig. 100, *Heliothis tergemina* (BM Noct 13412); Fig. 101, *Heliothis virescens* (BM Noct 13437); Fig. 102, *Heliothis bimaculata* (BM Noct 13455); Fig. 103, *Heliothis cruentata* (BM Noct 13456); Fig. 104, *Heliothis decorata* (BM Noct 13460); Fig. 105, *Heliothis galathae* (BM Noct 13466); Fig. 106, *Heliothis nubila* (BM Noct 13469).



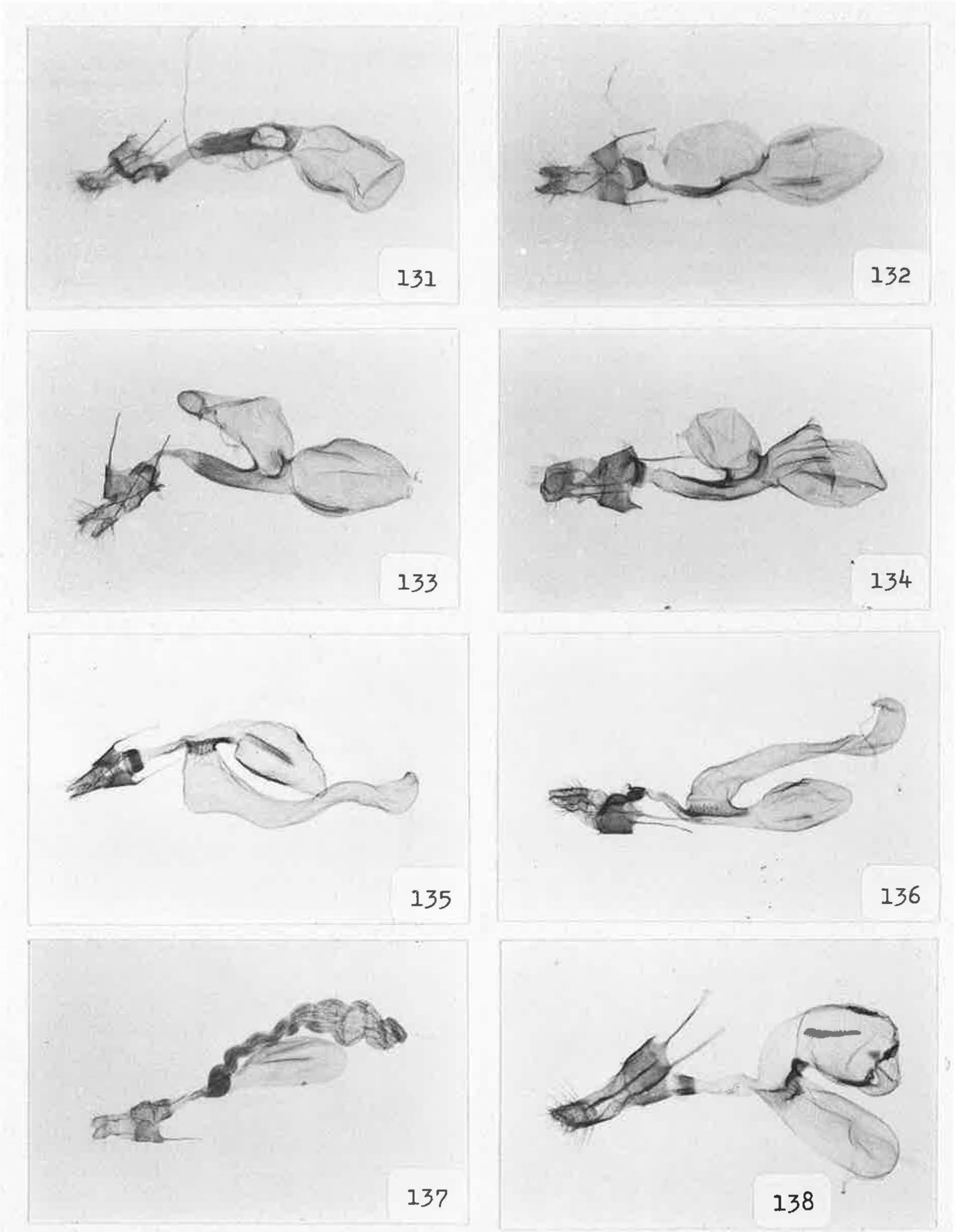
Figs. 107 - 114. Female genitalia, Heliothinae. Fig. 107, *Heliothis perstriata* (BM Noct 13475); Fig. 108, *Heliothis philbyi* (BM Noct 13482); Fig. 109, *Heliothis radiata* (BM Noct 13486); Fig. 110, *Heliothis roseivena* (BM Noct 13496); Fig. 111, *Heliothis syrticola* (BM Noct 13499); Fig. 112, *Heliothis terracottoides* (BM Noct 13507); Fig. 113, *Heliothis adamsoni* (BM Noct 13511); Fig. 114, *Heliothis daphoena* (BM Noct 13515).



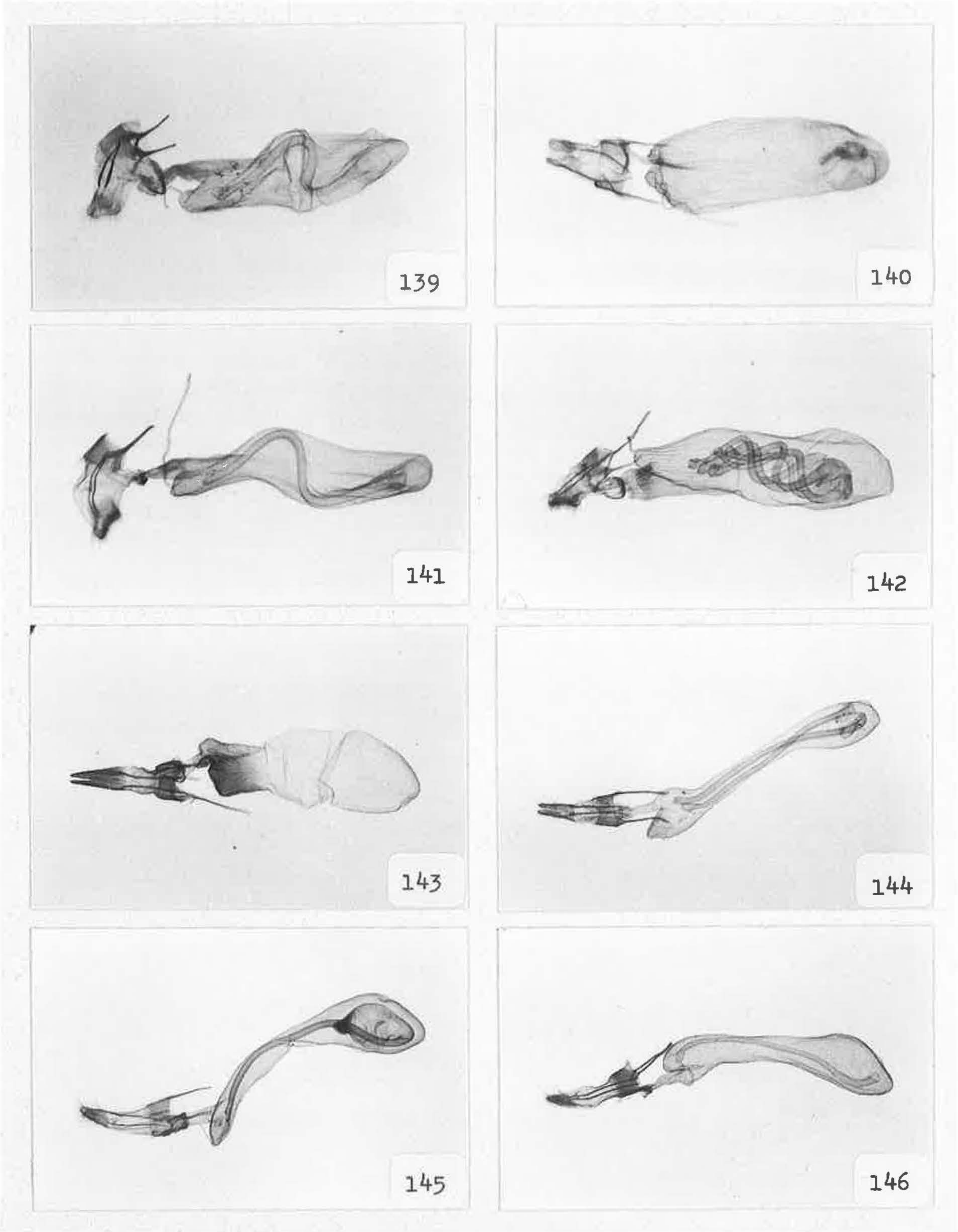
Figs. 115 - 122. Female genitalia, Heliothinae. Fig. 115, *Timora diarhoda* (BM Noct 13519); Fig. 116, *Heliothis sanguinolenta* (BM Noct 13521); Fig. 117, *Heliothis showaki* (BM Noct 13526); Fig. 118, *Heliocheilus aberrans* (BM Noct 13158); Fig. 119, *Heliocheilus aleurota* (BM Noct 13171); Fig. 120, *Heliocheilus* sp. No. 7 (Argentina) (BM Noct 13325); Fig. 121, *Heliocheilus canusina* (BM Noct 13174); Fig. 122, *Heliocheilus cistella* (BM Noct 13177).



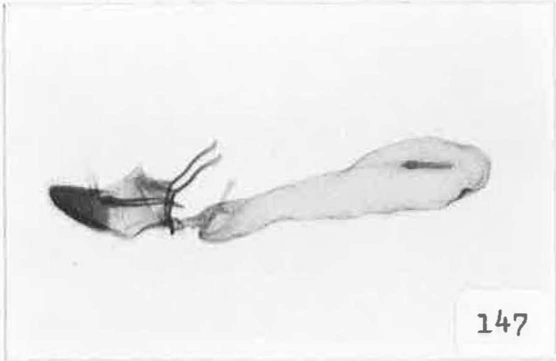
Figs. 123 - 130. Female genitalia, Heliothinae. Fig. 123, *Heliocheilus cladotus* (BM Noct 13179); Fig. 124, *Heliocheilus cramboides* (BM Noct 13217); Fig. 125, *Heliocheilus cystiphora* (BM Noct 13220); Fig. 126, *Heliocheilus eodora* (BM Noct 13234); Fig. 127, *Heliocheilus fervens* (BM Noct 13237); Fig. 128, *Heliocheilus flavitincta* (BM Noct 13240); Fig. 129, *Heliocheilus ionola* (BM Noct 13243); Fig. 130, *Heliocheilus julia* (BM Noct 13246).



Figs. 131 - 138. Female genitalia, Heliothinae. Fig. 131, *Heliocheilus melibaphes* (BM Noct 13247); Fig. 132, *Heliocheilus moribunda* (BM Noct 13255); Fig. 133, *Heliocheilus paradoxus* (BM Noct 13283); Fig. 134, *Heliocheilus toralis* (BM Noct 13315); Fig. 135, *Australothis rubrescens* (BM Noct 13398); Fig. 136, *Australothis tertia* (BM Noct 13420); Fig. 137, *Helicoverpa armigera* (BM Noct 13146); Fig. 138, *Engusanacantha bilineata* (BM Noct 13085).



Figs. 139 - 146. Female genitalia, Stiriinae. Fig. 139, *Aegle koekeritziana* (BM Noct 13831); Fig. 140, *Aegle subflava* (BM Noct 13834); Fig. 141, *Aegle vespertalis* (BM Noct 13836); Fig. 142, *Metaegle pallida* (BM Noct 13868); Fig. 143, *Basilodes chrysopis* (BM Noct 13839); Fig. 144, *Dipinacea schiniodes* (BM Noct 13854); Fig. 145, *Ectolopha marginata* (BM Noct 13858); Fig. 146, *Ectolopha viridescens* (BM Noct 13861).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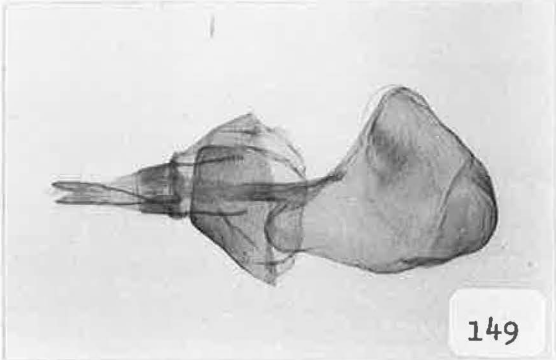
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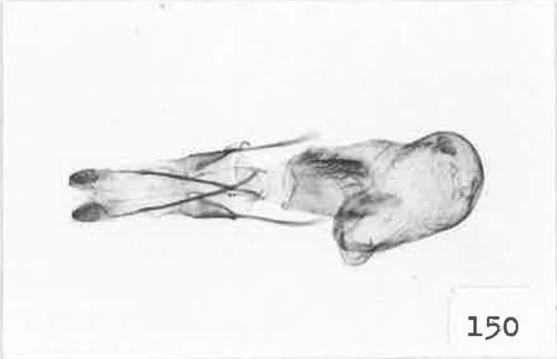
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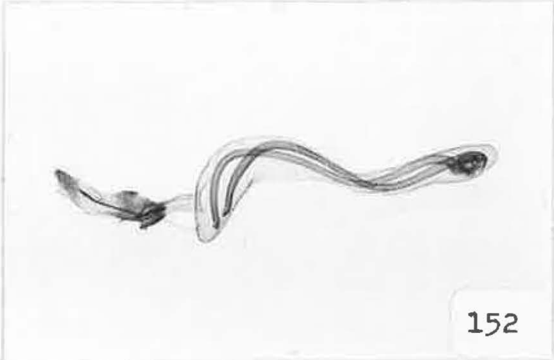
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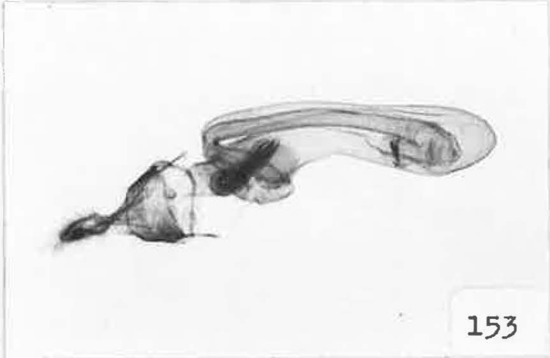
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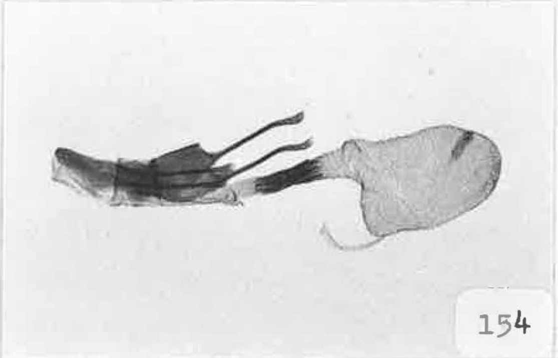
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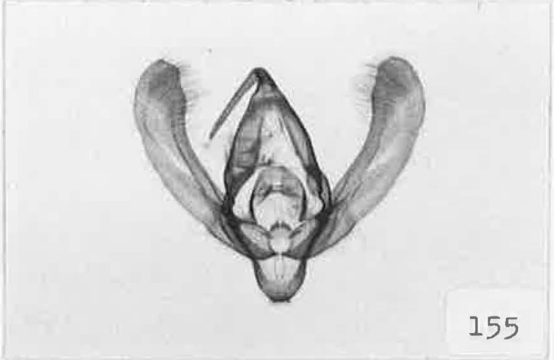
Figs. 147 - 154. Female genitalia, Stiriinae. Fig. 147, *Megalodes eximia* (BM Noct 13864); Fig. 148, *Mycteroplus puniceago* (BM Noct 13871); Fig. 149, *Oslaria viridifera* (BM Noct 13874); Fig. 150, *Panemeria tenebrata* (BM Noct 13881); Fig. 151, *Paralophata ansorgei* (BM Noct 13888); Fig. 152, *Procrateria pterota* (BM Noct 13892); Fig. 153, *Prothrinax luteomedia* (BM Noct 13894); Fig. 154, *Synthymia fixa* (BM Noct 13656).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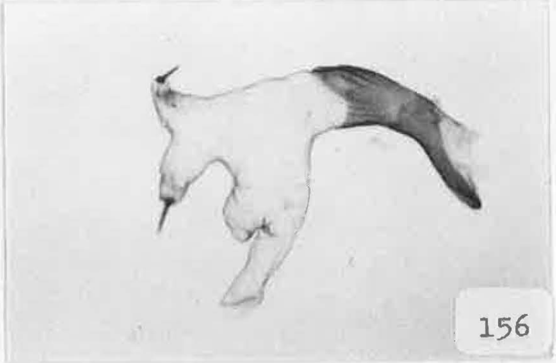
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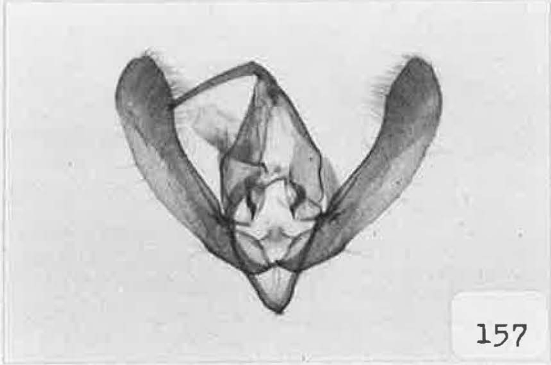
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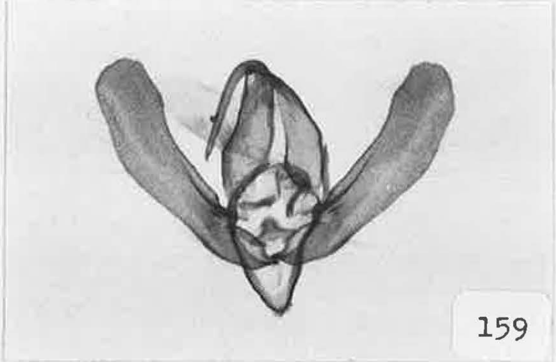
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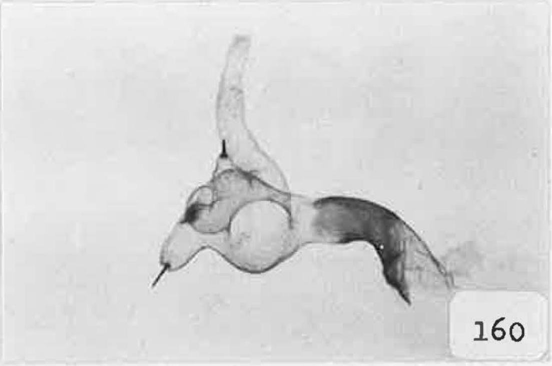
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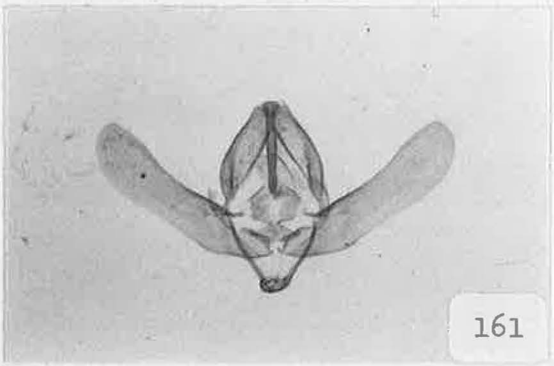
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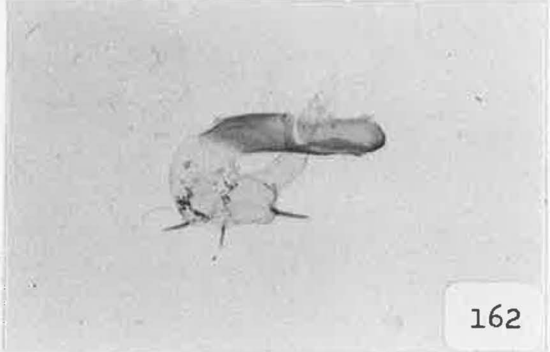
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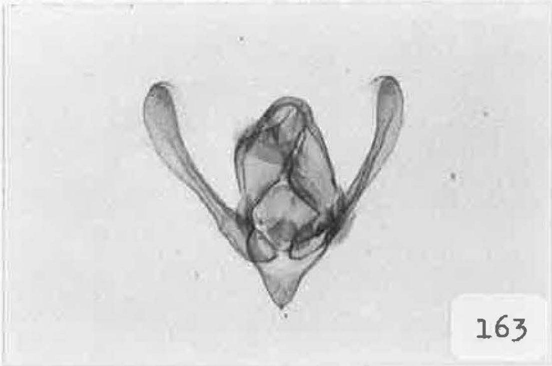
Figs. 155 - 162. Male genitalia, Heliothinae. *Aedophron phlebophora,* Fig. 155, valves, & Fig. 156, vesica (BM Noct 13058); *Aedophron rhodites,* Fig. 157, valves, & Fig. 158, vesica (BM Noct 13068); *Aedophron venosa,* Fig. 159, valves (BM Noct 13071) & Fig. 160, vesica (BM Noct 13073); *Baptarma felicita,* Fig. 161, valves, & Fig. 162, vesica (AMNH: 4407).



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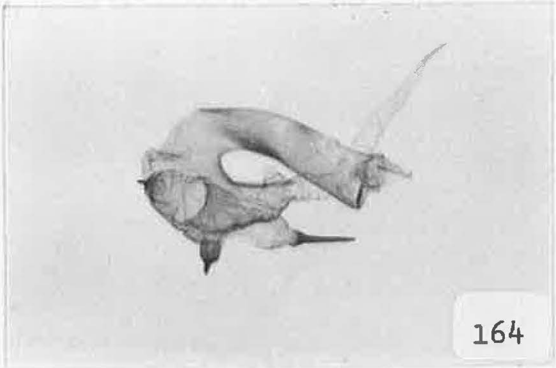

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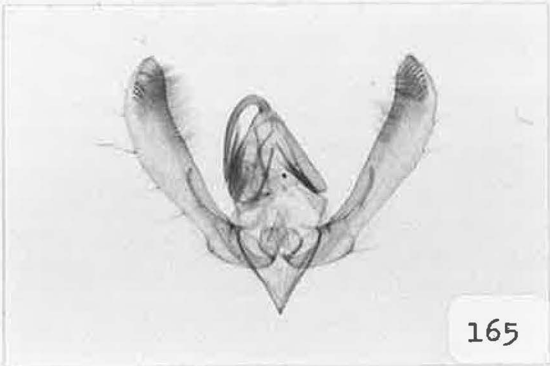

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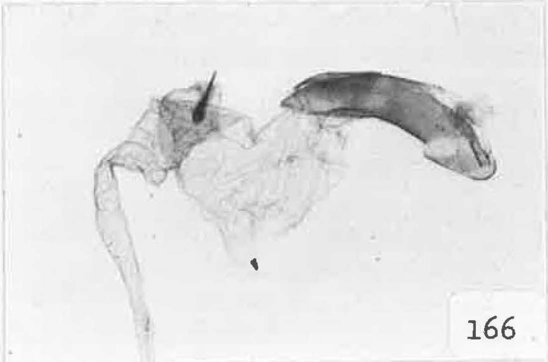

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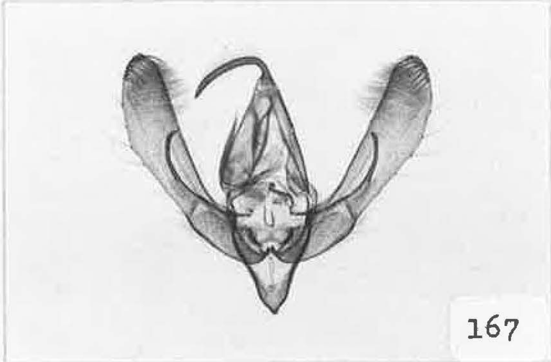

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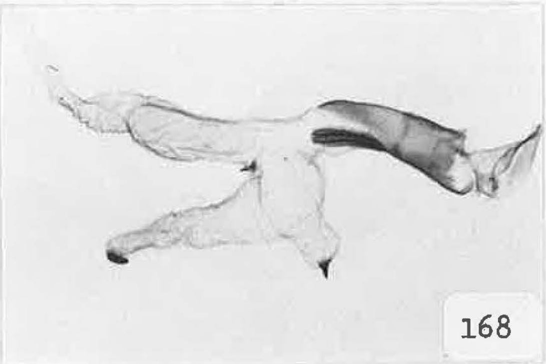

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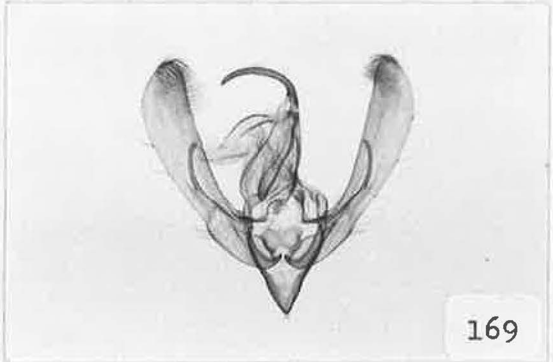

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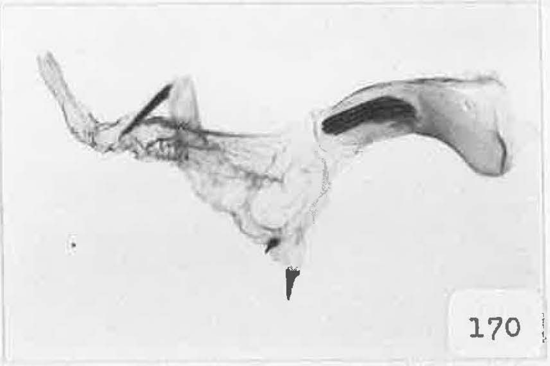

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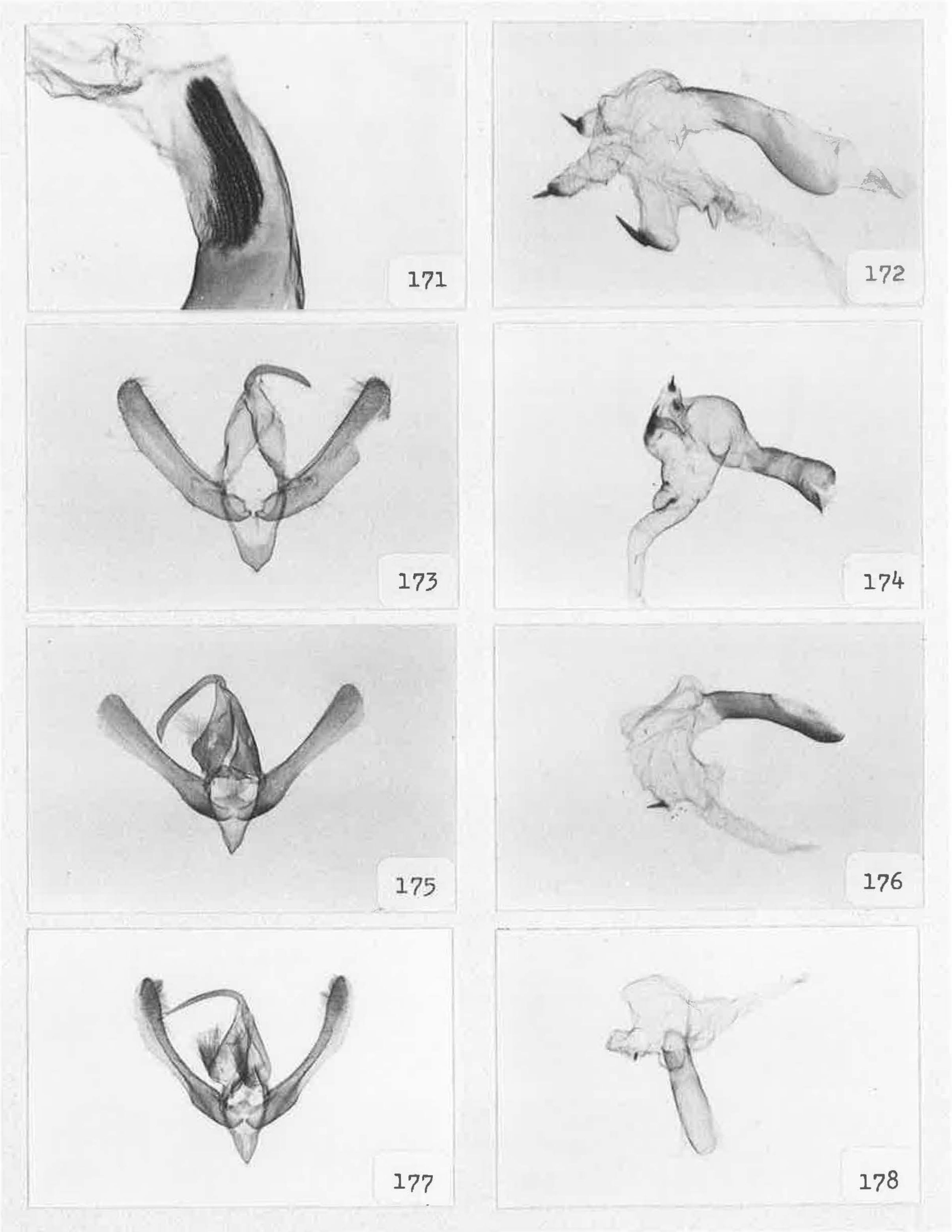
Figs. 163 - 170. Male genitalia, Heliothinae. *Derrima stellata*, Fig. 163, valves, & Fig. 164, vesica (BM Noct 13083); *Psectrotarsia flava*, Fig. 165, valves, & Fig. 166, vesica (USNM 41173); *Erythroecia rhodophora*, Fig. 167, valves, & Fig. 168, vesica (BM Noct 13089); *Erythroecia suavis*, Fig. 169, valves, & Fig. 170, vesica (BM Noct 13095).



Figs. 171 - 178. Male genitalia, Heliothinae. *Erythroecia suavis*, Fig. 171, denticulate patch (BM Noct 13095); *Erythrophaia eudoxia*, Fig. 172, vesica (BM Noct 13105); *Erythrophaia suavis*, Fig. 173, valves (BM Noct 13114) & Fig. 174, vesica (BM Noct 13118); *Eutricopis nexilis*, Fig. 175, valves (BM Noct 13129) & Fig. 176, vesica (BM Noct 13124); *Heliothodes diminutivus*, Fig. 177, valves, & Fig. 178, vesica (BM Noct 13567).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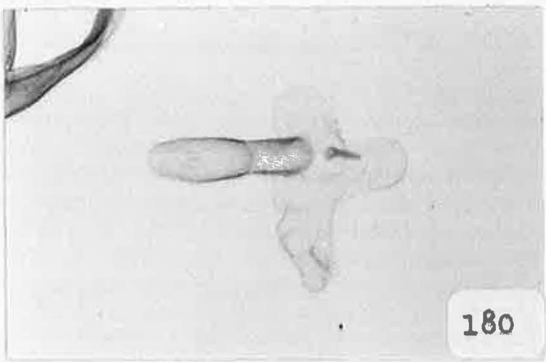
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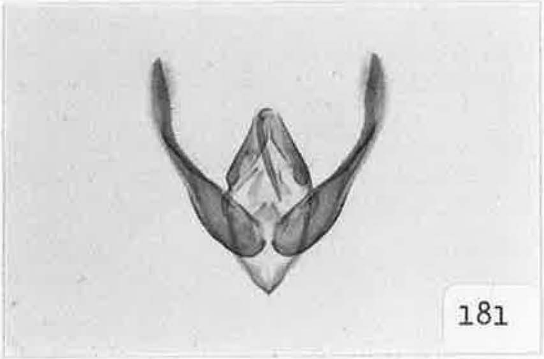
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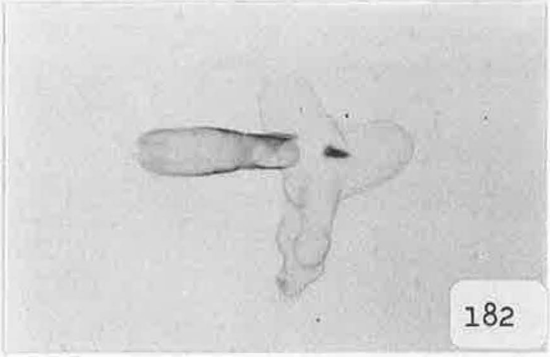
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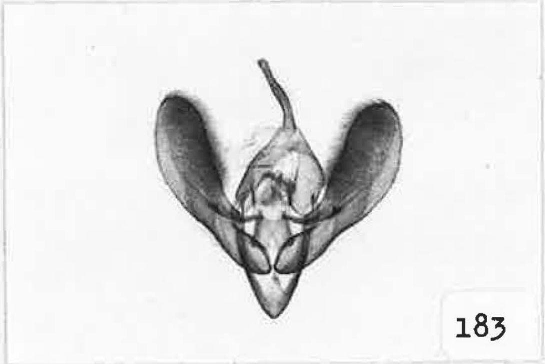
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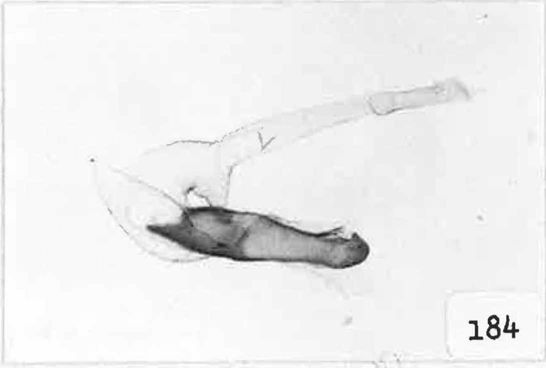
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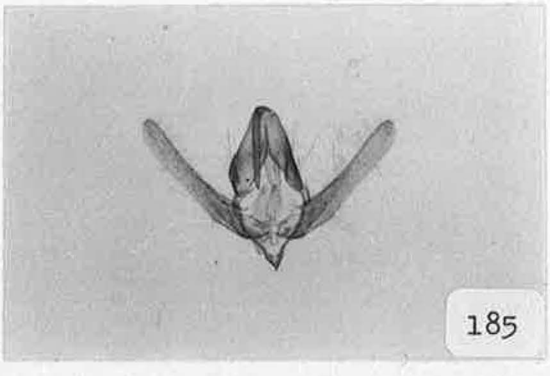
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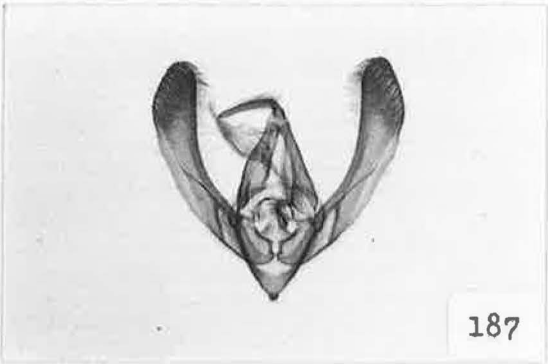
Figs. 179 - 186. Male genitalia, Heliothinae. *Heliothodes fasciata*, Fig. 179, valves, & Fig. 180, vesica (CNC: 4365); *Heliothodes joaquin*, Fig. 181, valves, & Fig. 182, vesica (CNC: 4366); *Melaporphyria immortua*, Fig. 183, valves, & Fig. 184, vesica (BM Noct 13569); *Microhelia angelica*, Fig. 185, valves, & Fig. 186, vesica (CNC: 4350).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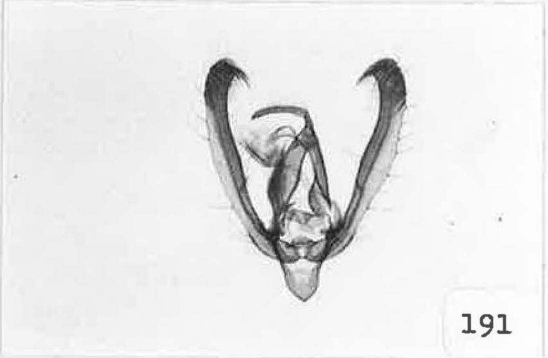
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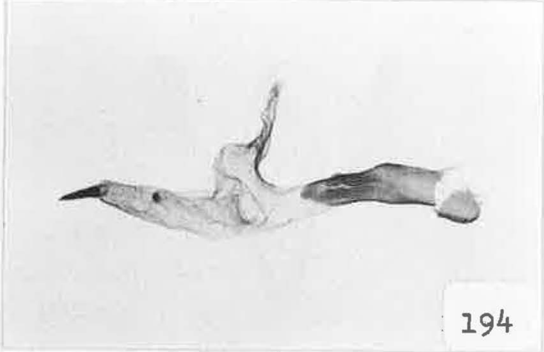
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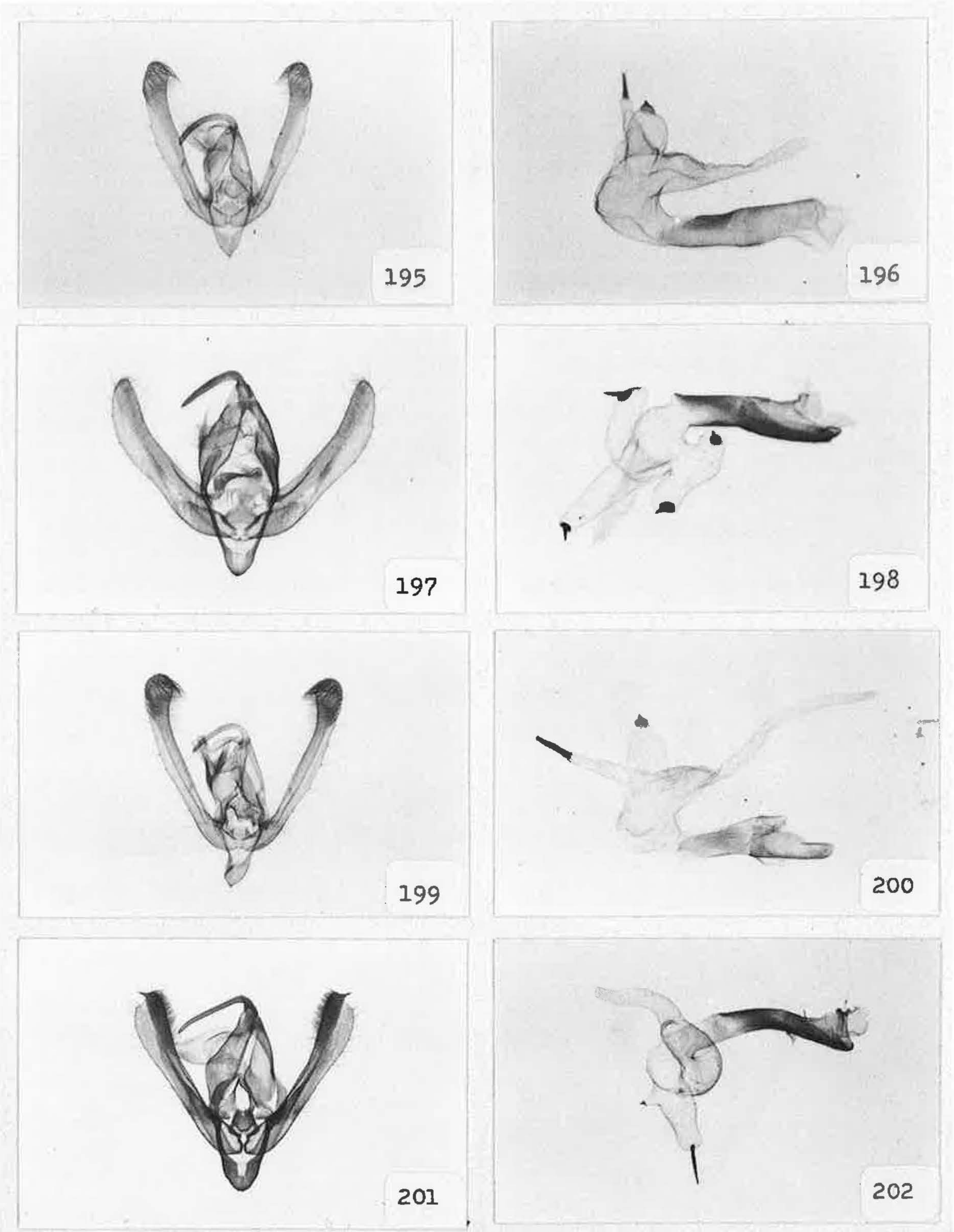
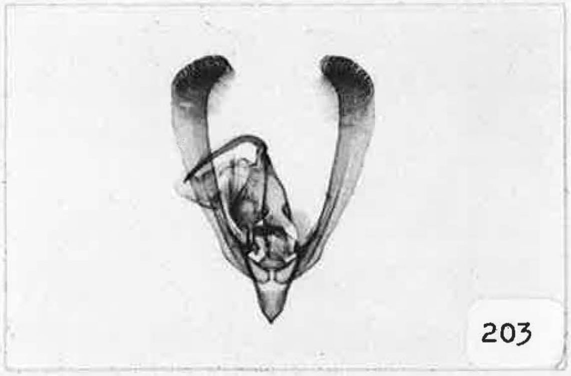
Figs. 187 - 194. Male genitalia, Heliothinae. *Periphanes delphinii*, Fig. 187, valves (BM Noct 13580), Fig. 188, vesica (BM Noct 13580), Fig. 189, vesica (BM Noct 13582), Fig. 190, vesica (BM Noct 13581); *Pyrrhia bifasciata*, Fig. 191, valves, & Fig. 192, vesica (BM Noct 13587); *Pyrrhia exprimens*, Fig. 193, valves, & Fig. 194, vesica, (BM Noct 13592).



Figs. 195 - 202. Male genitalia, Heliothinae. *Pyrrhia purpurina*, Fig. 195, valves, & Fig. 196, vesica (BM Noct 13598); *Pyrrhia treitschkei*, Fig. 197, valves, & Fig. 198, vesica (BM Noct 13603); *Pyrrhia umbra*, Fig. 199, valves (BM Noct 13616), & Fig. 200, vesica (BM Noct 13614); *Pyrrhia victorina*, Fig. 201, valves (BM Noct 13620), & Fig. 202, vesica (BM Noct 13622).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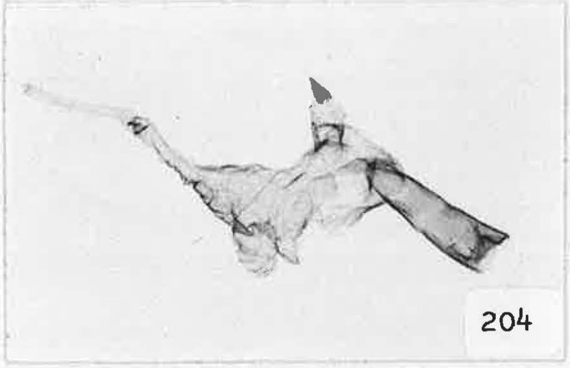
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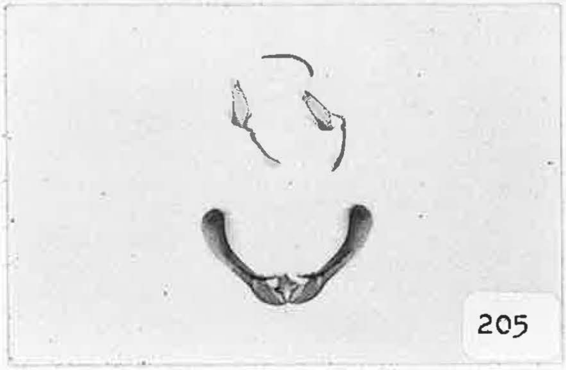
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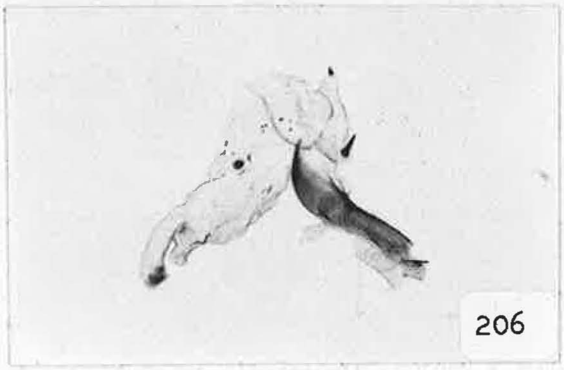
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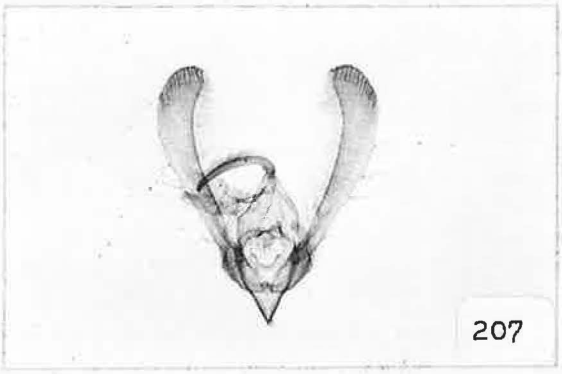
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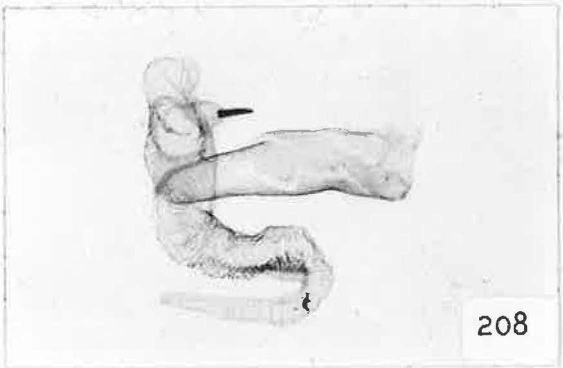
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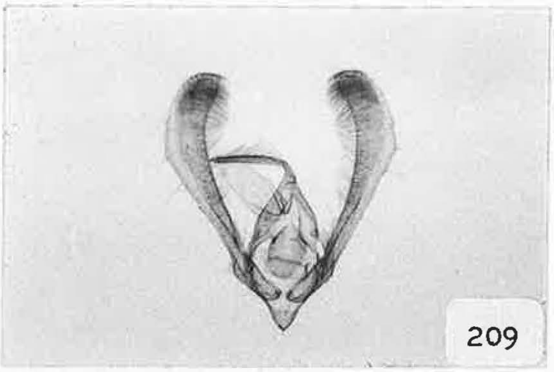
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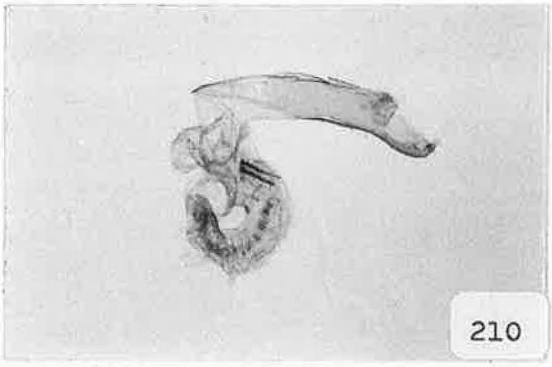
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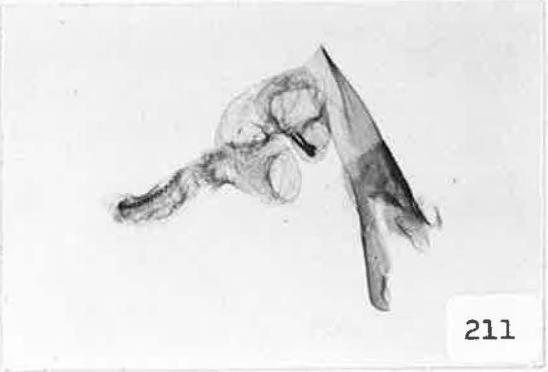
Figs. 203 - 210. Male genitalia, Heliothinae. *Rhodoecia aurantiago,* Fig. 203, valves, & Fig. 204, vesica (BM Noct 13692); *Pyrocleptria cora,* Fig. 205, valves, & Fig. 206, vesica (BM Noct 13633); *Protadisura posttriphaena,* Fig. 207, valves, & Fig. 208, vesica (BM Noct 13394); *Adisura aerugo,* Fig. 209, valves, & Fig. 210, vesica (BM Noct 13002).



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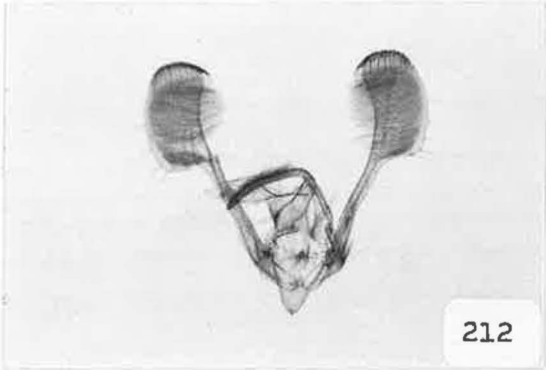

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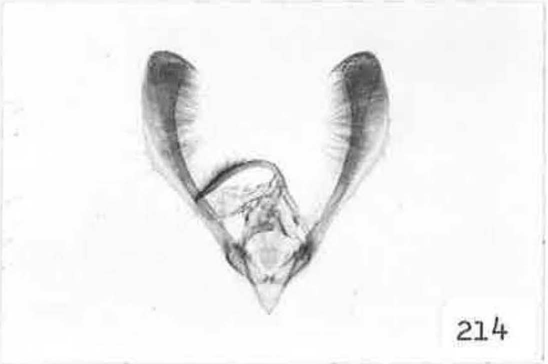

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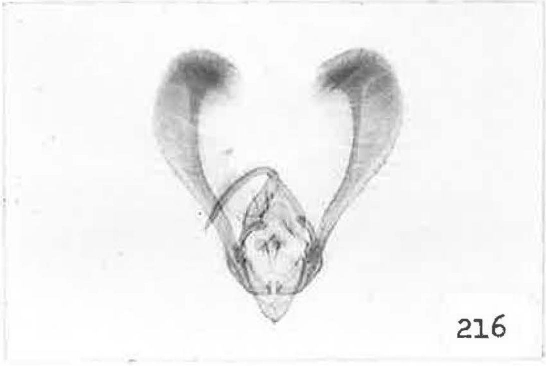

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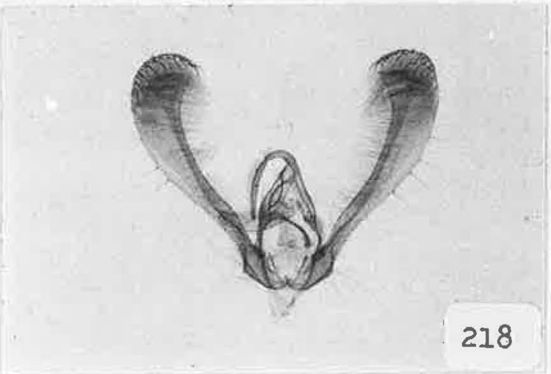
Figs. 211 - 217. Male genitalia, Heliothinae. *Adisura affinis,* Fig. 211, vesica (BM Noct 13008); *Adisura atkinsoni,* Fig. 212, valves, & Fig. 213, vesica (BM Noct 13023); *Adisura bella,* Fig. 214, valves, & Fig. 215, vesica (BM Noct 13025); *Adisura callima,* Fig. 216, valves, & Fig. 217, vesica (BM Noct 13030).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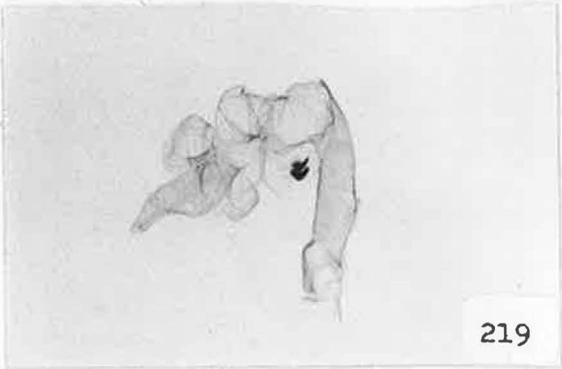
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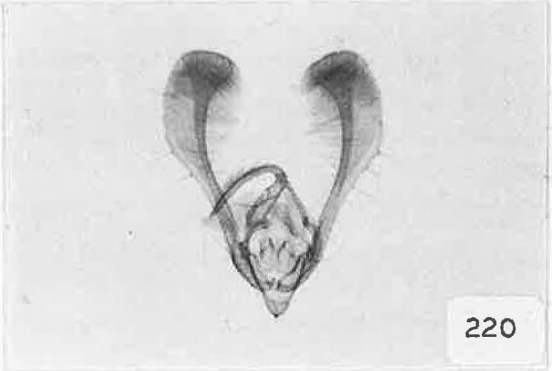
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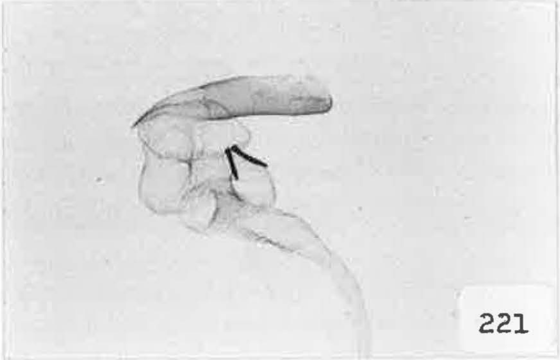
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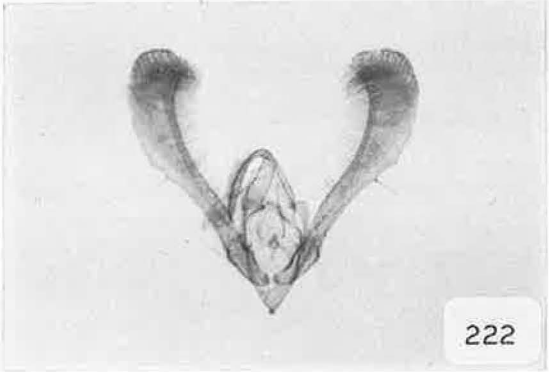
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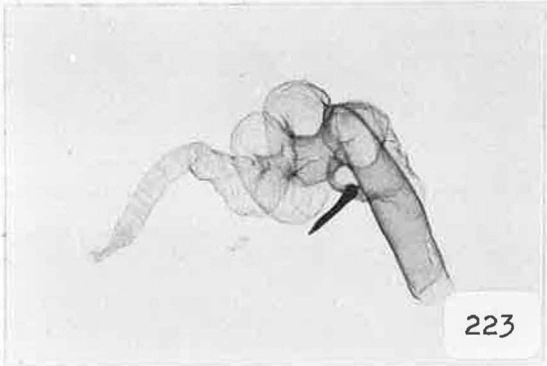
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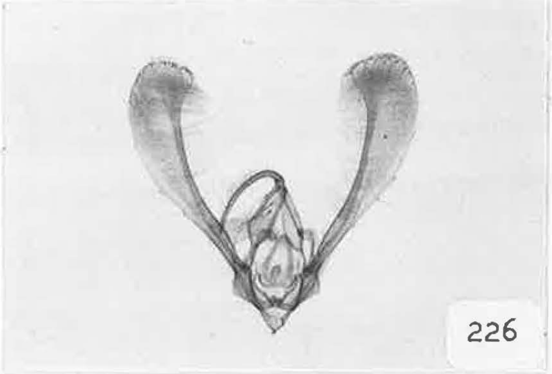
Figs. 218 - 225. Male genitalia, Heliothinae. *Adisura dulcis,* Fig. 218, valves, & Fig. 219, vesica (BM Noct 13034); *Adisura malagasica,* Fig. 220, valves, & Fig. 221, vesica (BM Noct 13037); *Adisura marginalis,* Fig. 222, valves, & Fig. 223, vesica (BM Noct 13040); *Adisura* sp., Fig. 224, valves, & Fig. 225, vesica (BM Noct 13027).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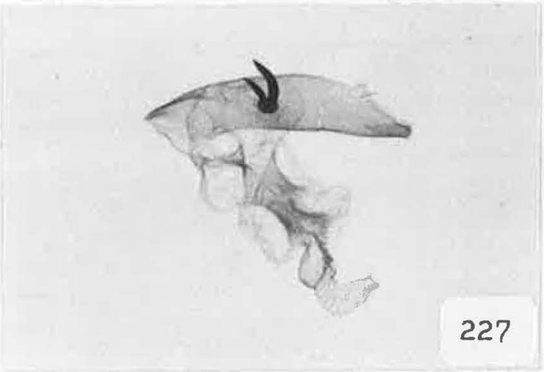
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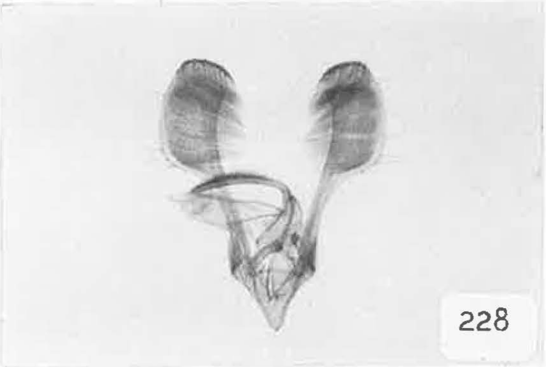
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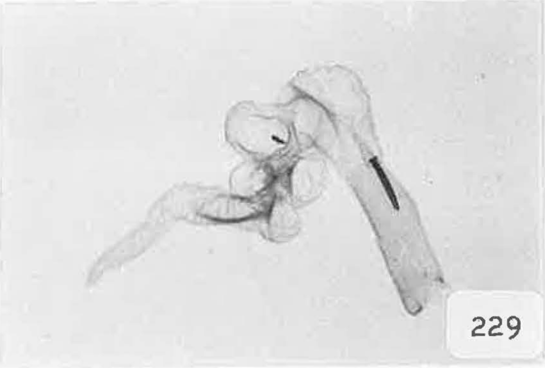
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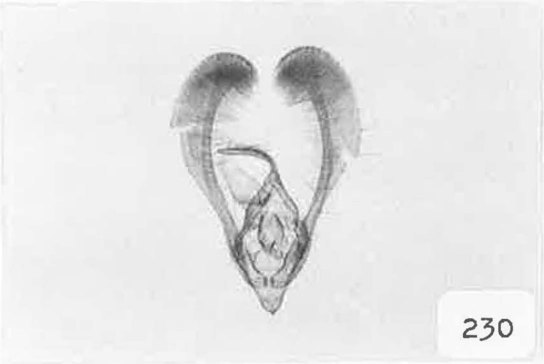
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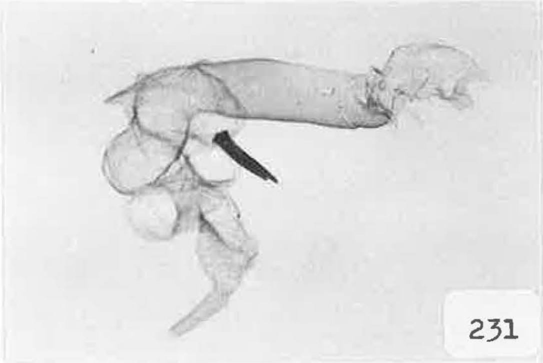
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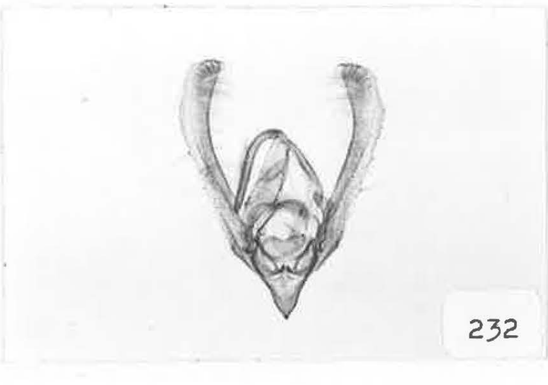
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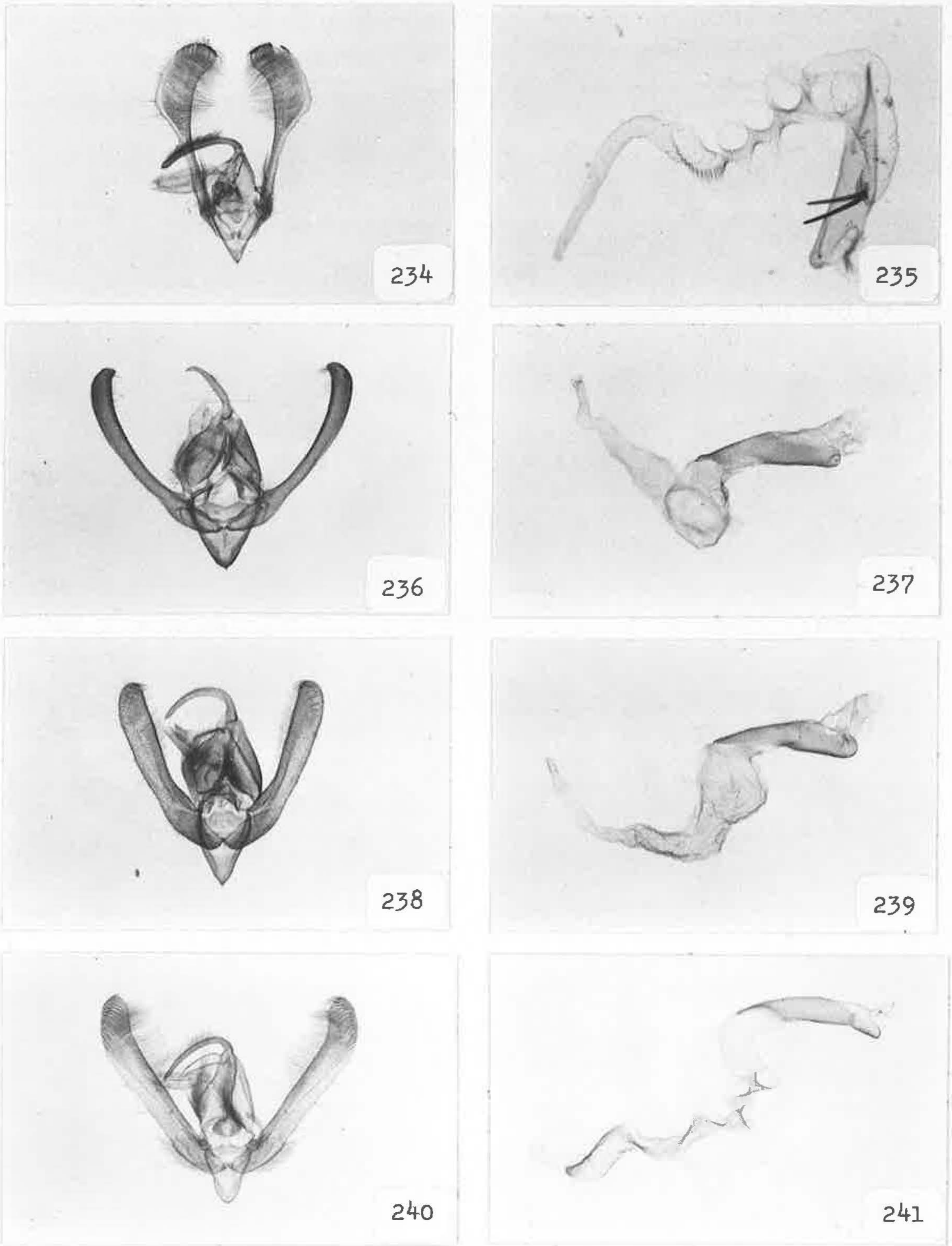
Figs. 226 - 233. Male genitalia, Heliothinae. *Adisura purgata*, Fig. 226, valves, & Fig. 227, vesica (BM Noct 13043); *Adisura stigmatica*, Fig. 228, valves, & Fig. 229, vesica (BM Noct 13045); *Adisura straminea*, Fig. 230, valves, & Fig. 231, vesica (BM Noct 13048); *Adisura parva*, Fig. 232, valves, & Fig. 233, vesica (BM Noct 13051).



Figs. 234 - 241. Male genitalia, Heliothinae. *Adisura litarga*, Fig. 234, valves, & Fig. 235, vesica (ANIC); *Heliolonche modicella*, Fig. 236, valves, & Fig. 237, vesica (BM Noct 13335); *Heliolonche pictipennis*, Fig. 238, valves, & Fig. 239, vesica (BM Noct 13337); *Schinia scutosa*, Fig. 240, valves, & Fig. 241, vesica (BM Noct 13690).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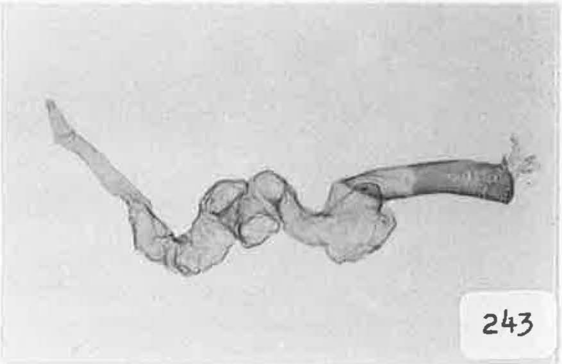
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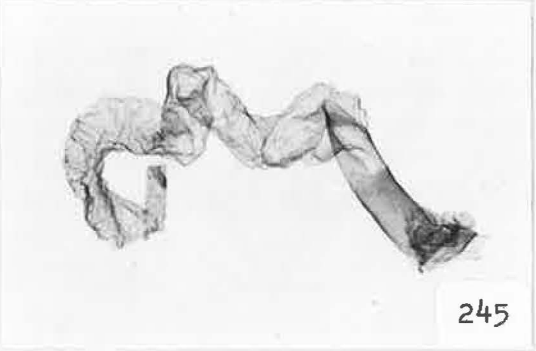
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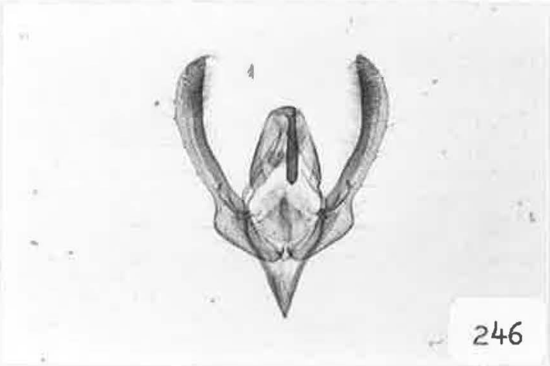
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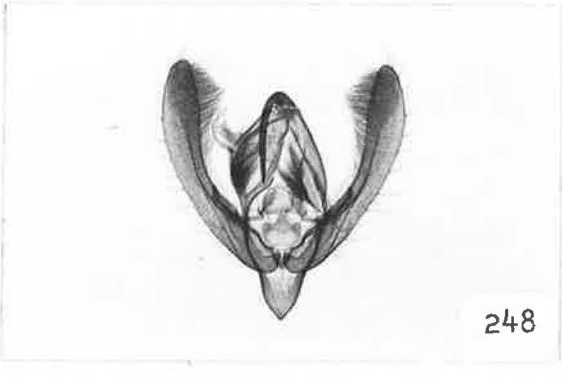
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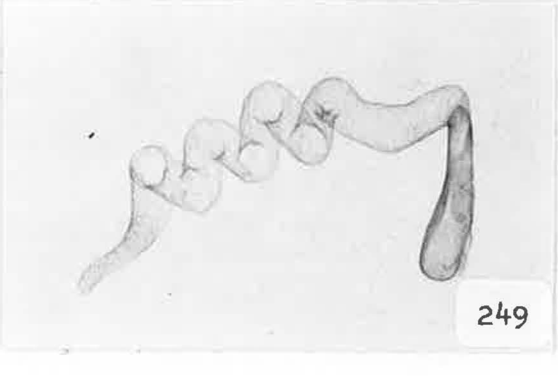
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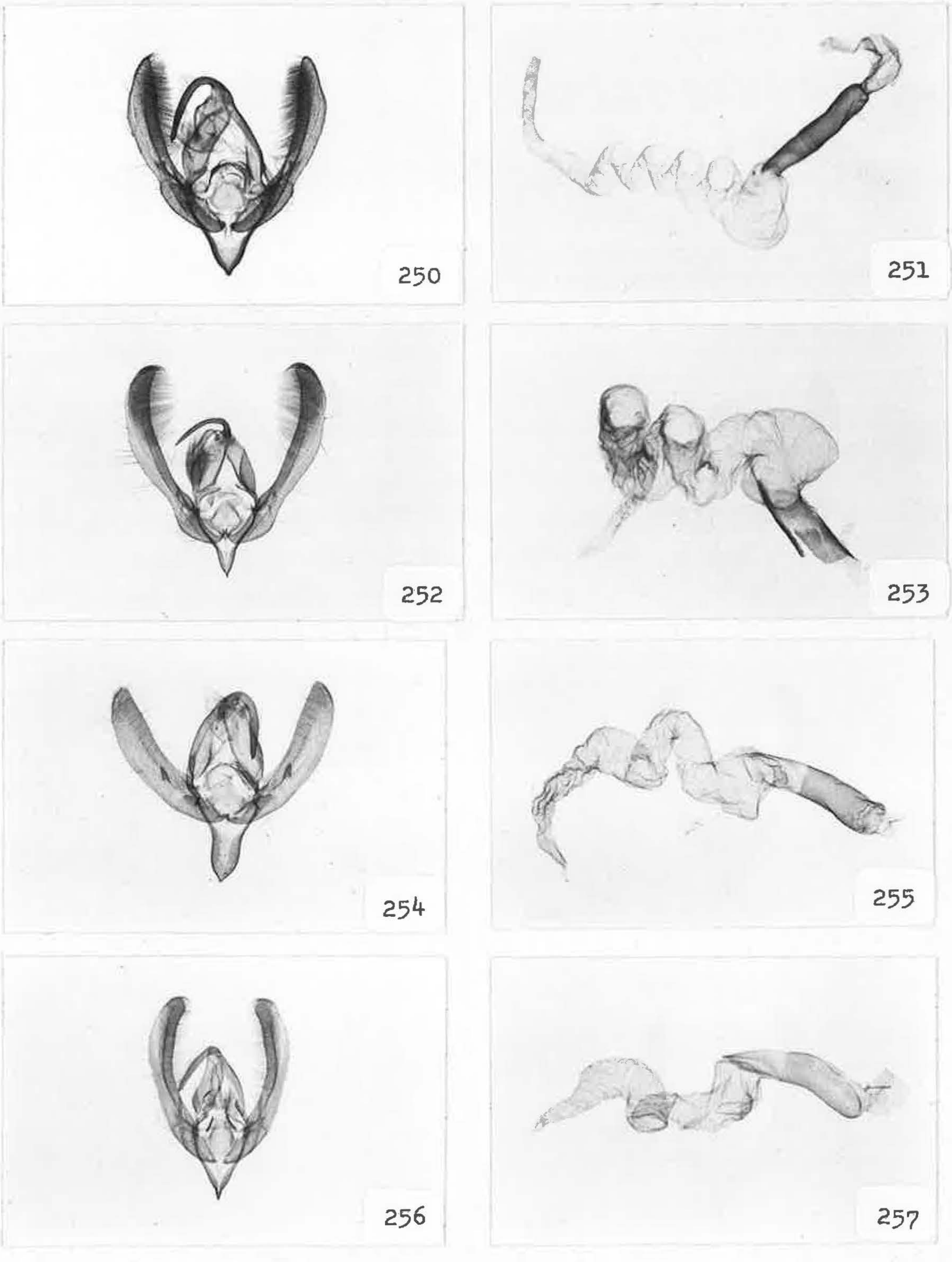
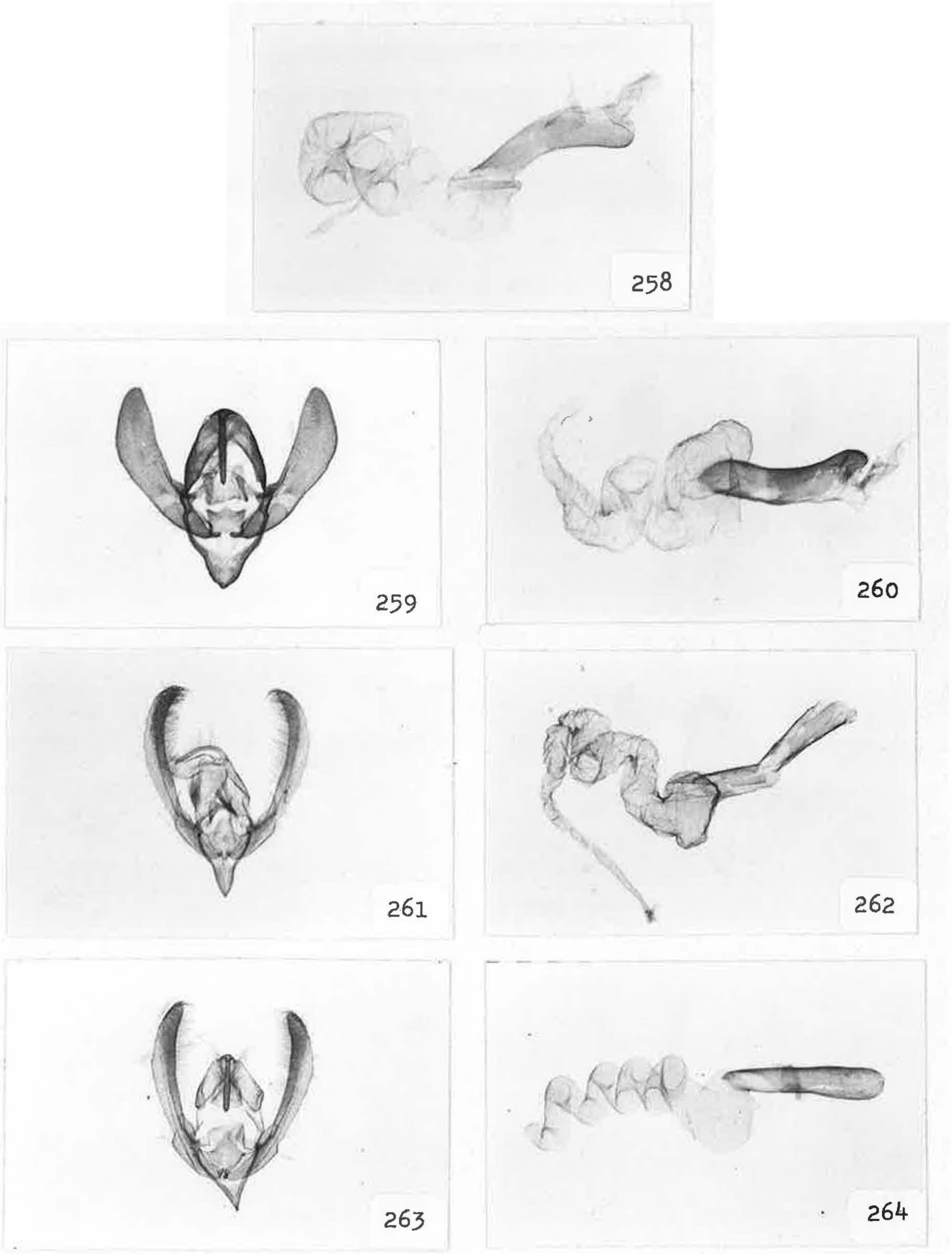
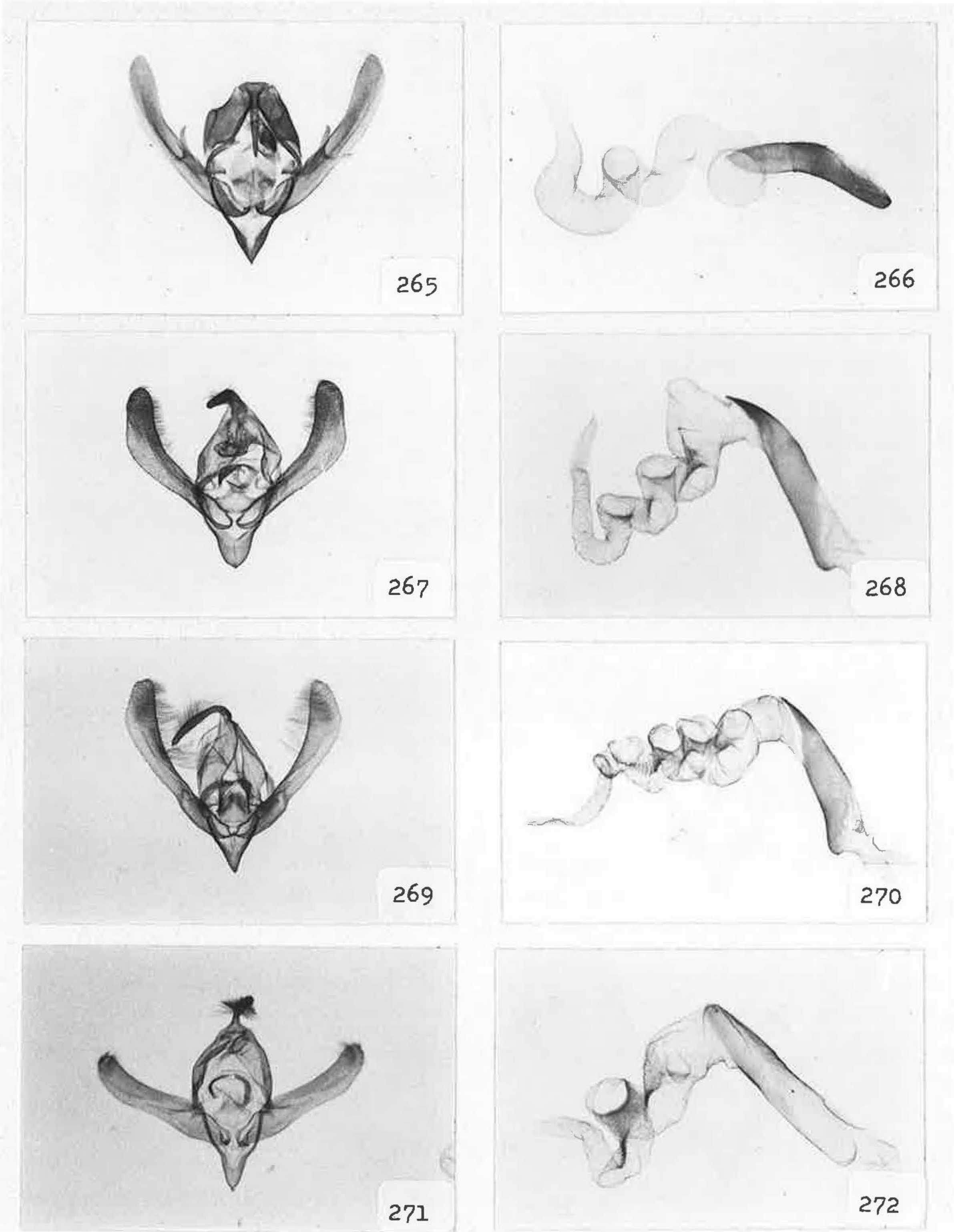
Figs. 242 - 249. Male genitalia, Heliothinae. *Schinia chilensis*, Fig. 242, valves, & Fig. 243, vesica (AMNH); *Schinia* sp. No. 1 (Chile), Fig. 244, valves, & Fig. 245, vesica (AMNH); *Schinia rufipenna*, Fig. 246, valves, & Fig. 247, vesica (CNC: 7786); *Schinia gaurae*, Fig. 248, valves (BM Noct 13640), & Fig. 249, vesica (BM Noct 13639).



Figs. 250 - 257. Male genitalia, Heliothinae. *Schinia jaegeri*, Fig. 250, valves, & Fig. 251, vesica (BM Noct 13642); *Schinia jaguarina*, Fig. 252, valves, & Fig. 253, vesica (BM Noct 13650); *Schinia mexicana*, Fig. 254, valves, & Fig. 255, vesica (AMNH); *Schinia pulchra*, Fig. 256, valves, & Fig. 257, vesica (AMNH).



Figs. 258 - 264. Male genitalia, Heliothinae. *Schinia purpurascens*, Fig. 258, vesica (BM Noct 13664); *Schinia rosea*, Fig. 259, valves, & Fig. 260, vesica (BM Noct 13668); *Schinia sexplagiata*, Fig. 261, valves, & Fig. 262, vesica (BM Noct 13672); *Schinia tuberculum*, Fig. 263, valves, & Fig. 264, vesica (CNC: 7780).



Figs. 265 - 272. Male genitalia, Heliothinae. *Schinia verna*, Fig. 265, valves, & Fig. 266, vesica (CNC: 7549); *Schinia roseoflammata*, Fig. 267, valves, & Fig. 268, vesica (BM Noct 13680); *Schinia xanthiata*, Fig. 269, valves, & Fig. 270, vesica (BM Noct 13677); *Schinia ennatae*, Fig. 271, valves, & Fig. 272, vesica (BM Noct 12073).

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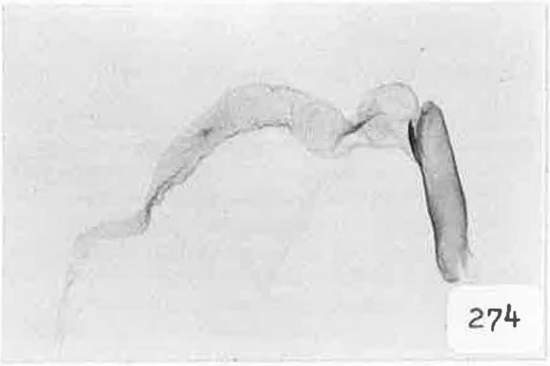

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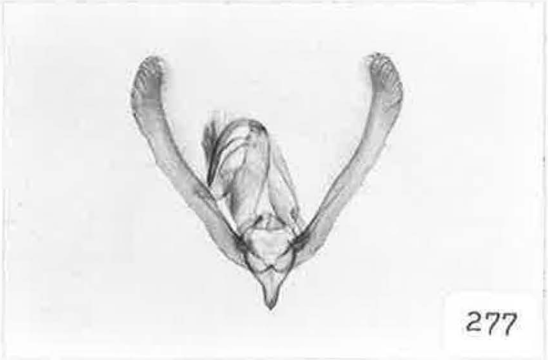

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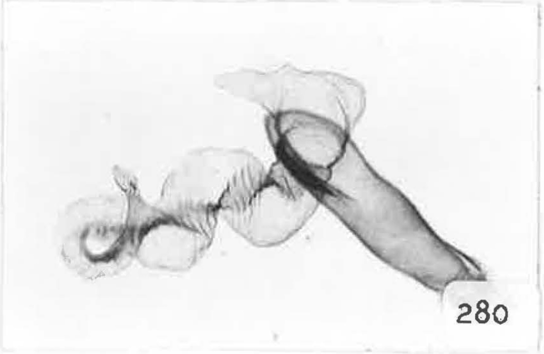

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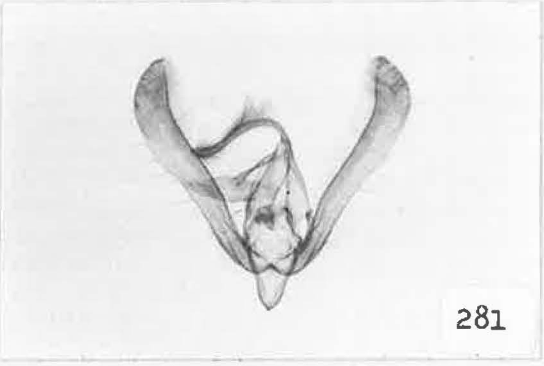
Figs. 273 - 280. Male genitalia, Heliothinae. *Heliothis borealis,* Fig. 273, valves, & Fig. 274, vesica (BM Noct 13338); *Heliothis conifera,* Fig. 275, valves, & Fig. 276, vesica (BM Noct 13341); *Heliothis flavigera,* Fig. 277, valves, & Fig. 278, vesica (BM Noct 13347); *Heliothis flavirufa,* Fig. 279, valves, & Fig. 280 (BM Noct 13351).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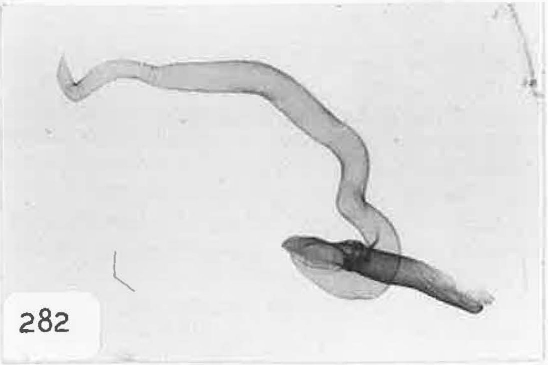
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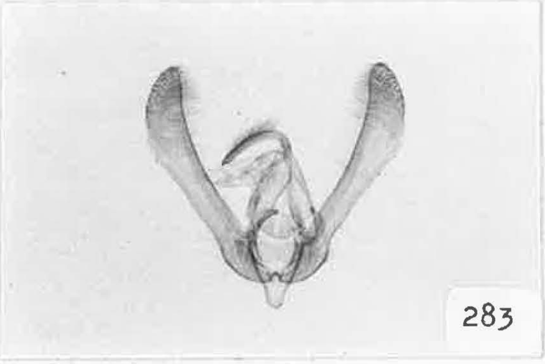
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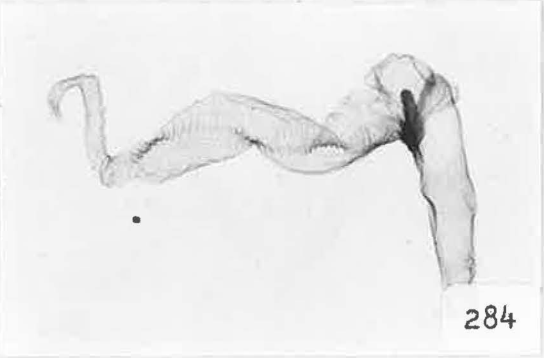
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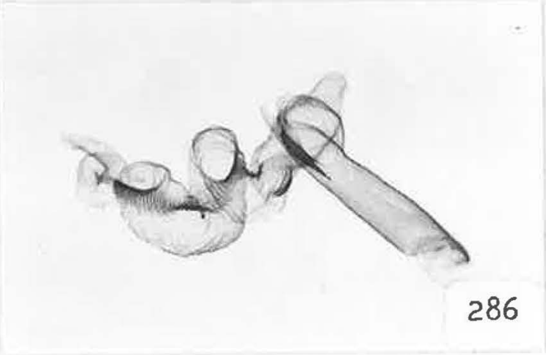
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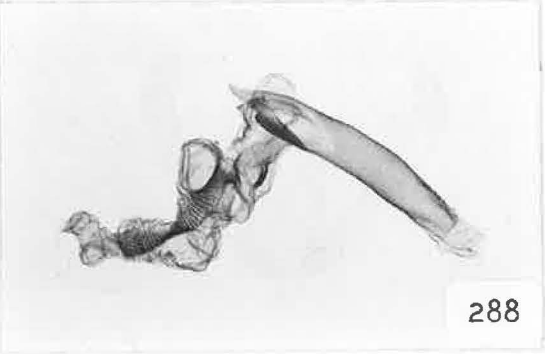
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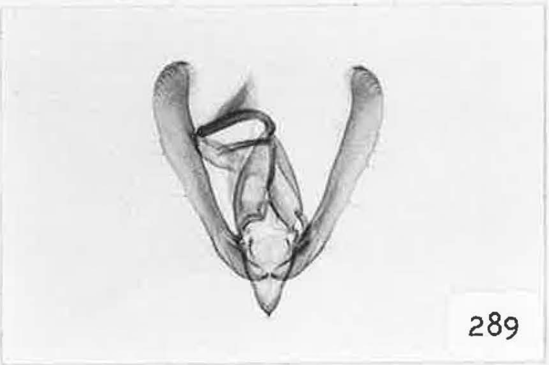
Figs. 281 - 288. Male genitalia, Heliothinae. *Heliothis maritima*, Fig. 281, valves (BM Noct 13356), & Fig. 282, vesica (CNC: 9142); *Heliothis metachrisea*, Fig. 283, valves, & Fig. 284, vesica (BM Noct 13360); *Heliothis nubigera*, Fig. 285, valves, & Fig. 286, vesica (BM Noct 13372); *Heliothis* sp. No. 2 (near *nubigera*), Fig. 287, valves, & Fig. 288, vesica (BM Noct 13375).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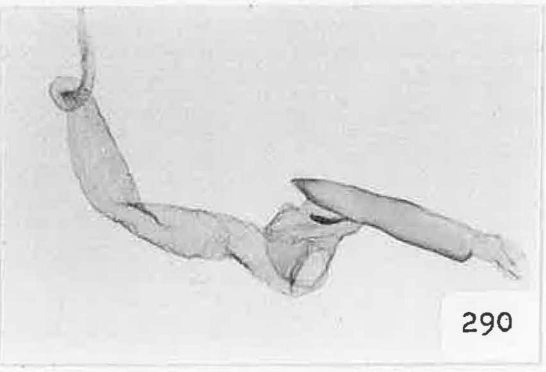
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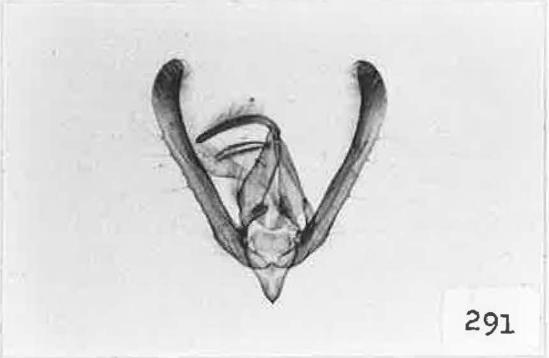
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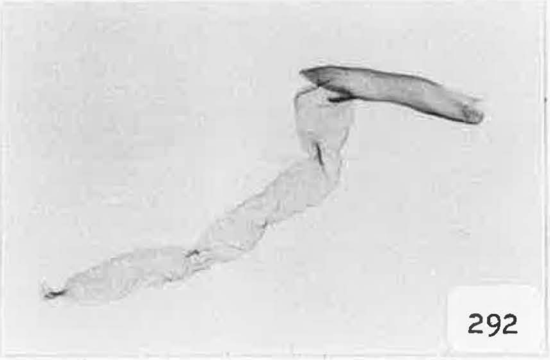
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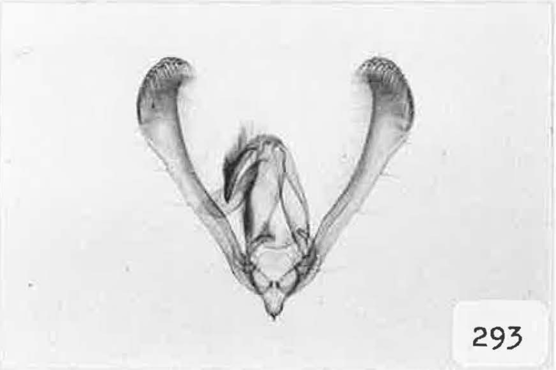
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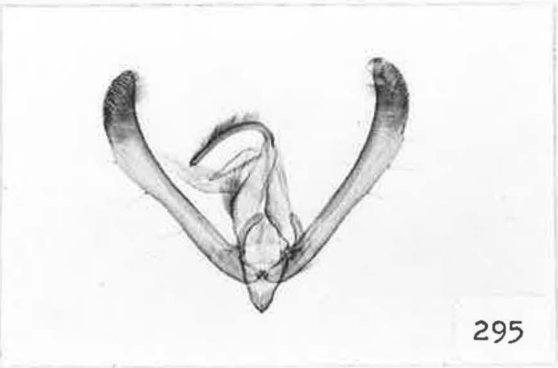
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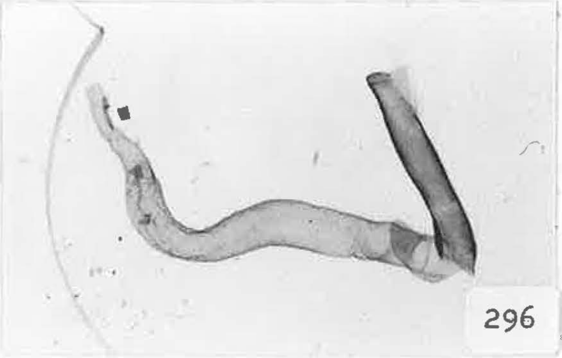
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Figs. 289 - 296. Male genitalia, Heliothinae. *Heliothis ononis,* Fig. 289, valves, & Fig. 290, vesica (BM Noct 13378); *Heliothis oregonica,* Fig. 291, valves, & Fig. 292, vesica (BM Noct 13382); *Heliothis peltigera,* Fig. 293, valves, & Fig. 294, vesica (BM Noct 13384); *Heliothis phloxiphaga,* Fig. 295, valves (BM Noct 13388), & Fig. 296, vesica (CNC: 9143).


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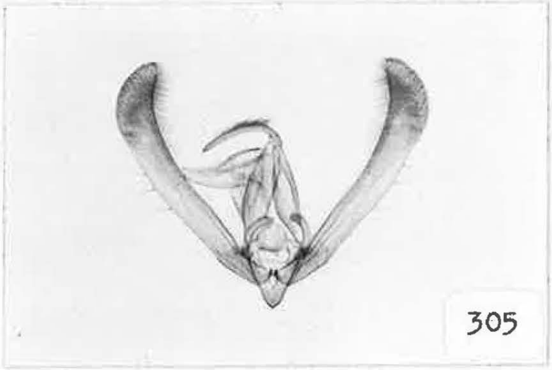
Figs. 297 - 304. Male genitalia, Heliothinae. *Heliothis prorupta*, Fig. 297, valves, & Fig. 298, vesica (BM Noct 13396); *Heliothis scutiligera*, Fig. 299, valves, & Fig. 300, vesica (BM Noct 13404); *Heliothis viriplaca*, Fig. 301, valves (BM Noct 13450), & Fig. 302, vesica (BM Noct 13444); *Heliothis xanthiata*, Fig. 303, valves, & Fig. 304, vesica (BM Noct 13454).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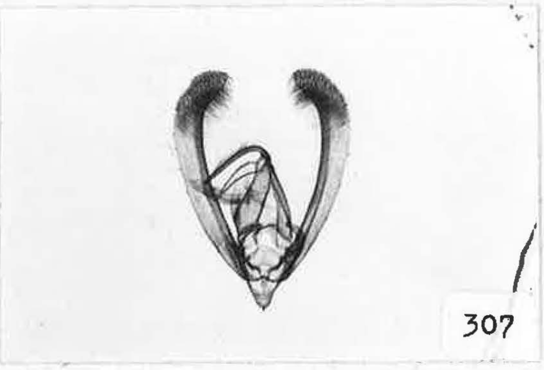
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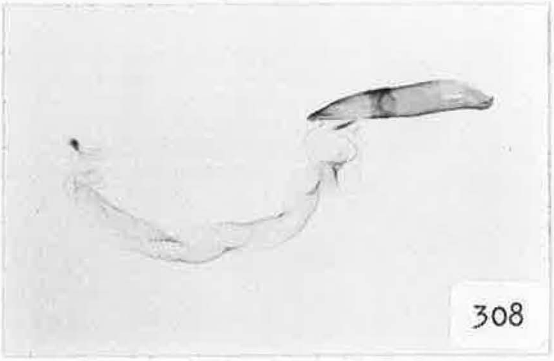
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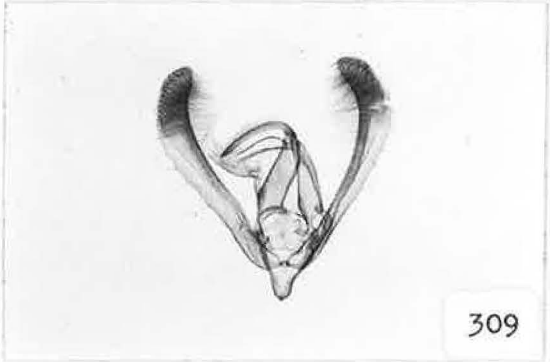
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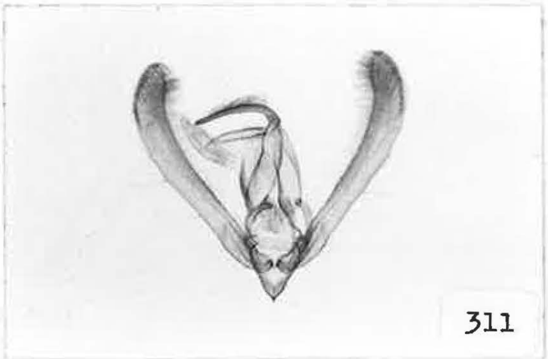
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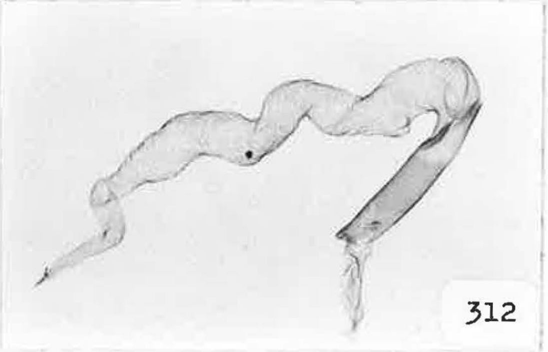
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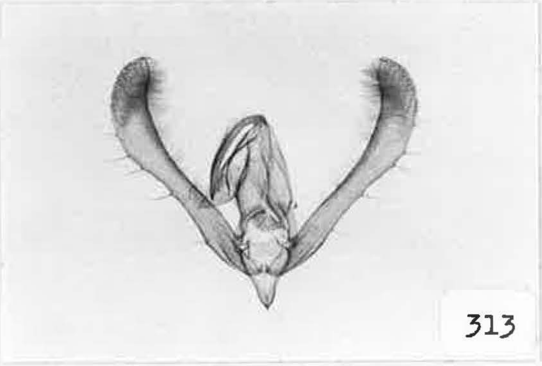
Figs. 305 - 312. Male genitalia, Heliothinae. *Heliothis punctifera*, Fig. 305, valves, & Fig. 306, vesica (BM Noct 13543); *Heliothis feildi*, Fig. 307, valves, & Fig. 308, vesica (BM Noct 13545); *Heliothis incarnata*, Fig. 309, valves, & Fig. 310, vesica (BM Noct 13552); *Heliothis distincta*, Fig. 311, valves, & Fig. 312, vesica (BM Noct 13345).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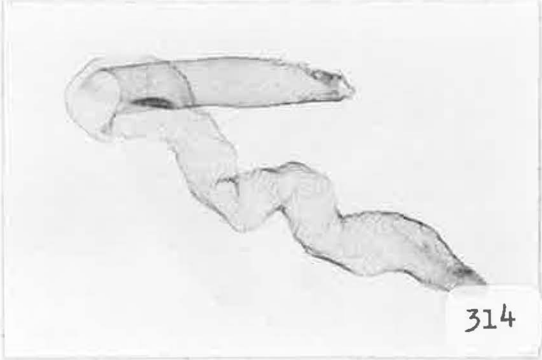
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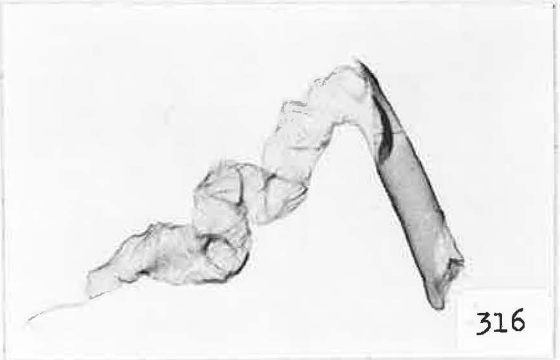
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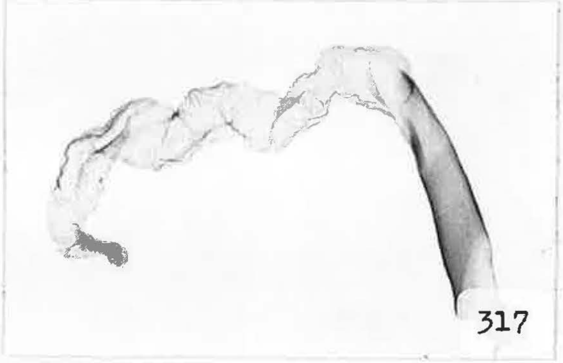
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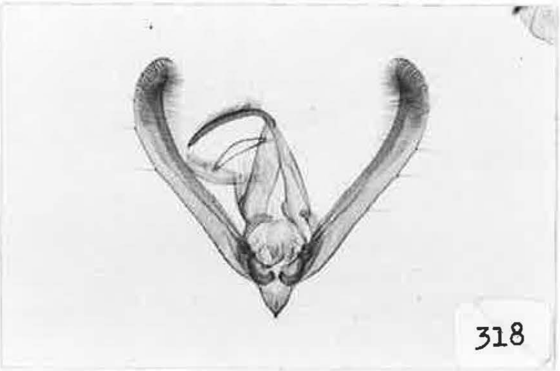
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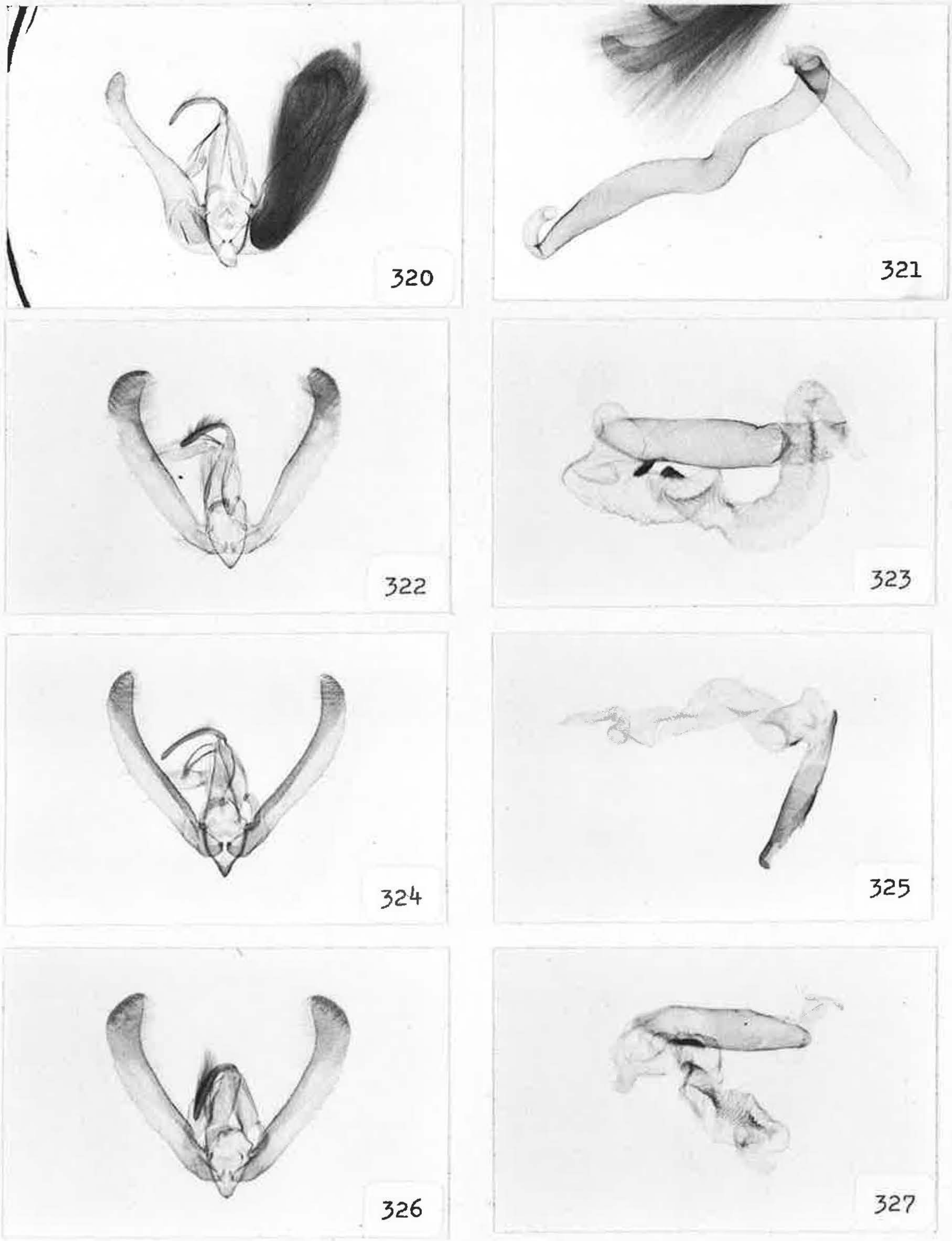
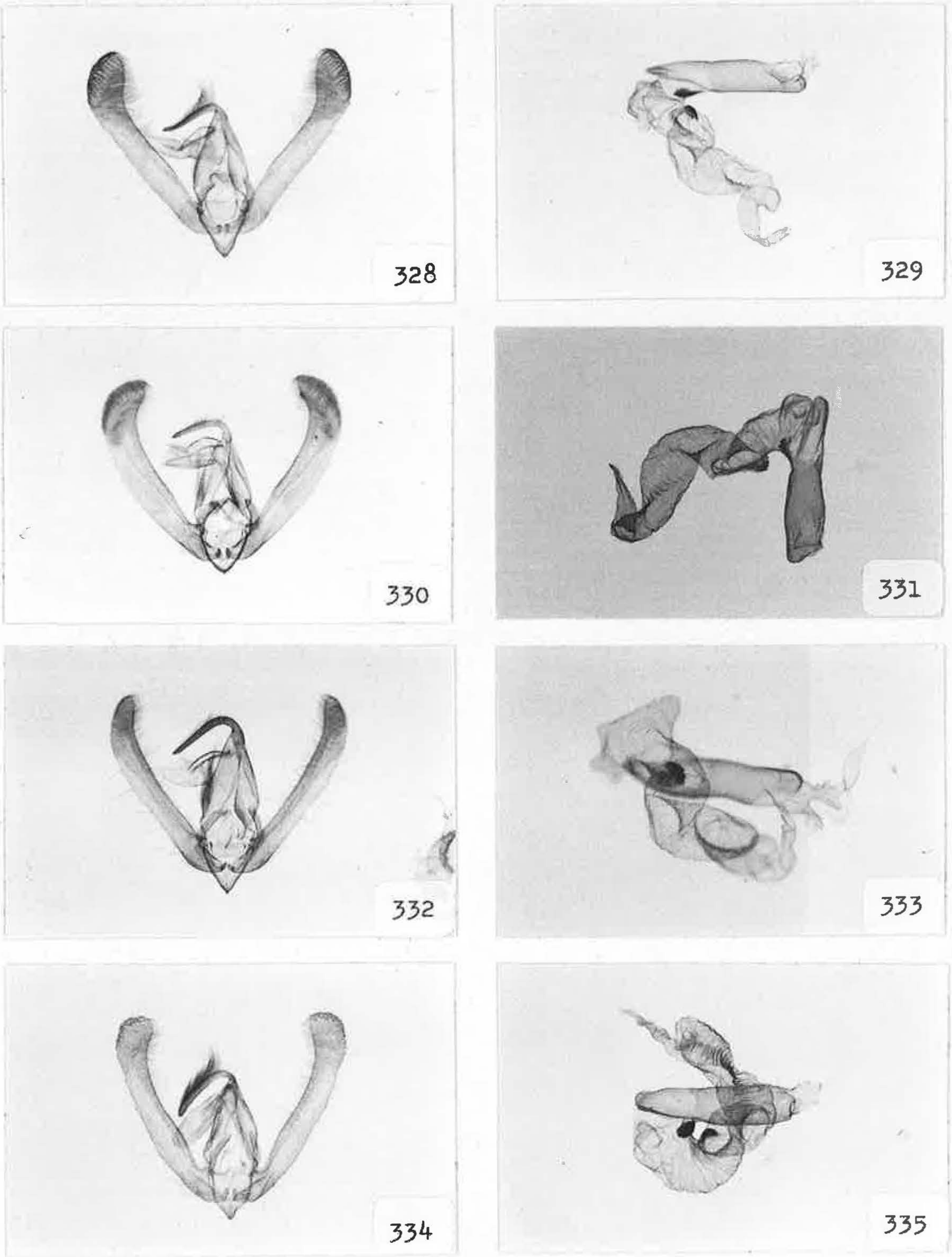
Figs. 313 - 319. Male genitalia, Heliothinae. *Heliothis molochitina*, Fig. 313, valves (BM Noct 13365), & Fig. 314, vesica (BM Noct 13366); *Heliothis sturmhoefeli*, Fig. 315, valves, & Fig. 316, vesica (BM Noct 13406); *Heliothis subflexa*, Fig. 317, vesica (BM Noct 13411); *Heliothis tergemina*, Fig. 318, valves, & Fig. 319, vesica (BM Noct 13416).



Figs. 320 - 327. Male genitalia, Heliothinae. *Heliothis virescens*, Fig. 320, valves (BM Noct 13439), & Fig. 321, vesica (CNC: 3538); *Heliothis cruentata*, Fig. 322, valves, & Fig. 323, vesica (BM Noct 13458); *Heliothis decorata*, Fig. 324, valves, & Fig. 325, vesica (BM Noct 13462); *Heliothis galathae*, Fig. 326, valves, & Fig. 327, vesica (BM Noct 13467).



Figs. 328 - 335. Male genitalia, Heliothinae. *Heliothis nubila*, Fig. 328, valves, & Fig. 329, vesica (BM Noct 13473); *Heliothis perstriata*, Fig. 330, valves, & Fig. 331, vesica (BM Noct 13477); *Heliothis philbyi*, Fig. 332, valves, & Fig. 333, vesica (BM Noct 13484); *Heliothis radiata*, Fig. 334, valves, & Fig. 335, vesica (BM Noct 13495).

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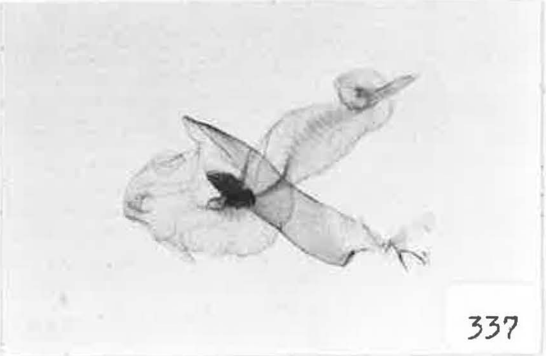

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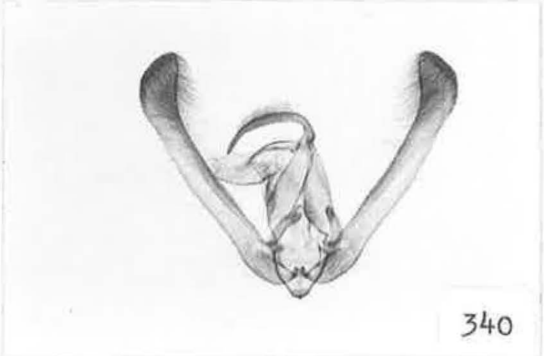

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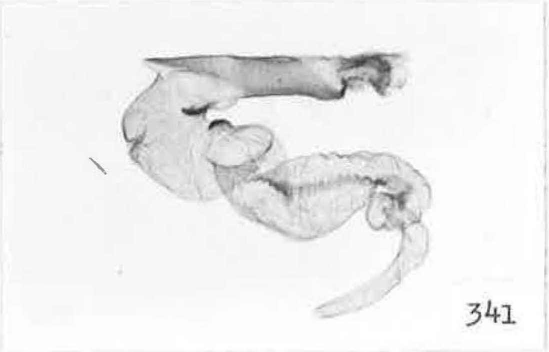

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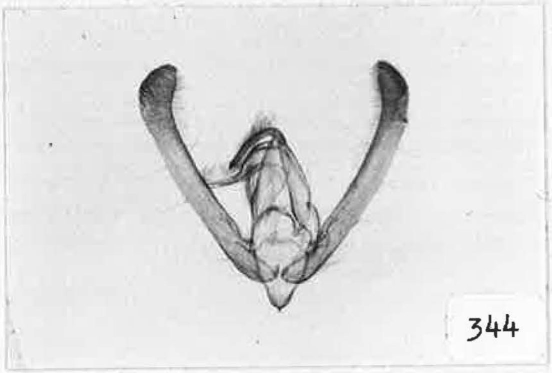
Figs. 336 - 343. Male genitalia, Heliothinae. *Heliothis roseivena,* Fig. 336, valves, & Fig. 337, vesica (BM Noct 13498); *Heliothis syrticola,* Fig. 338, valves, & Fig. 339, vesica (BM Noct 13503); *Heliothis terracottoides,* Fig. 340, valves, & Fig. 341, vesica (BM Noct 13509); *Heliothis adamsoni,* Fig. 342, valves, & Fig. 343, vesica (BM Noct 13555).



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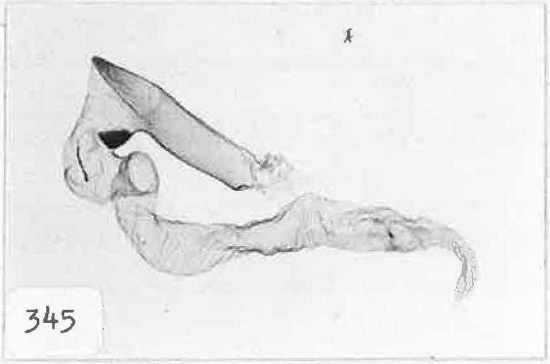

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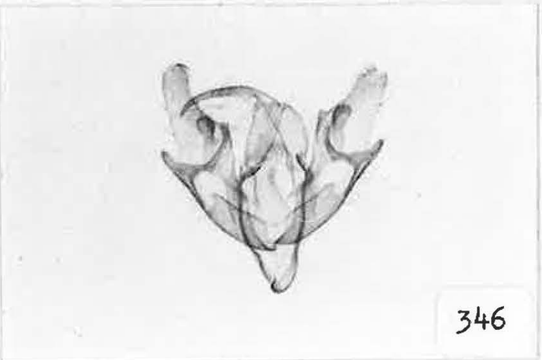

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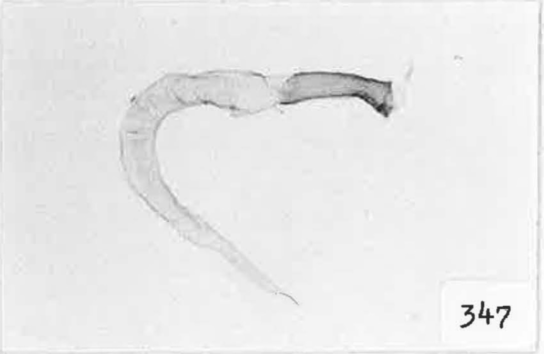

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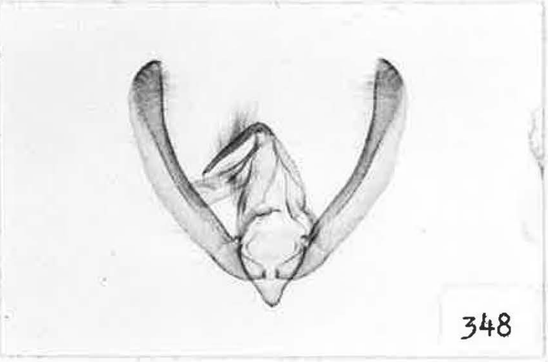

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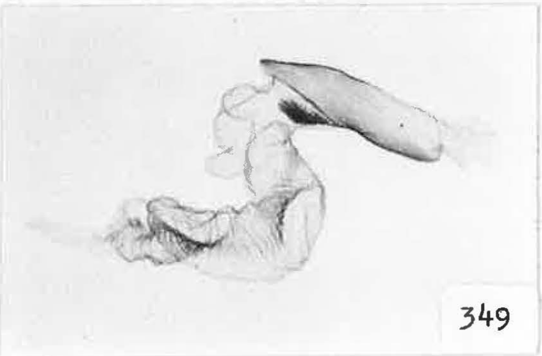

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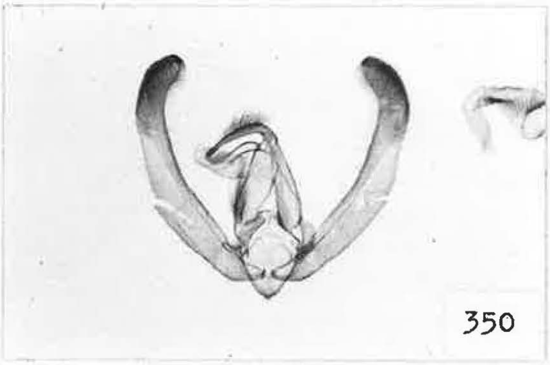

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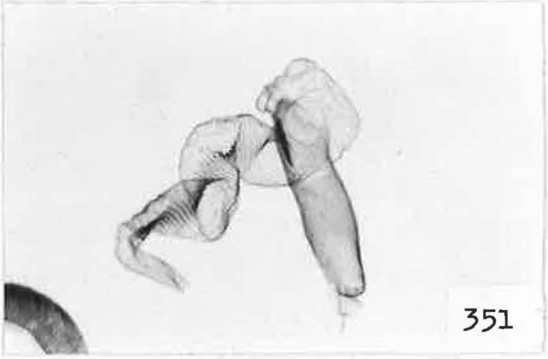

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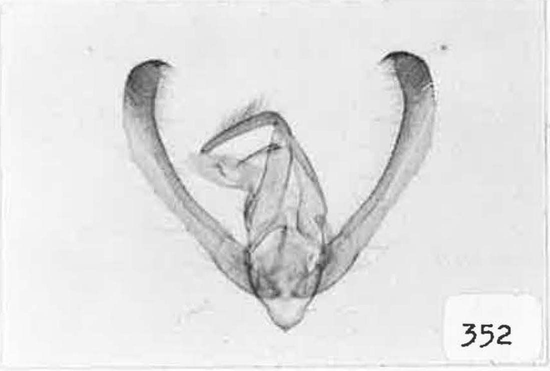
Figs. 344 - 351. Male genitalia, Heliothinae. *Heliothis daphoena*, Fig. 344, valves, & Fig. 345, vesica (BM Noct 13517); *Timora diarhoda*, Fig. 346, valves, & Fig. 347, vesica (BM Noct 13520); *Heliothis sanguinolenta*, Fig. 348, valves, & Fig. 349, vesica (BM Noct 13524); *Heliothis showaki*, Fig. 350, valves, & Fig. 351, vesica (BM Noct 13528).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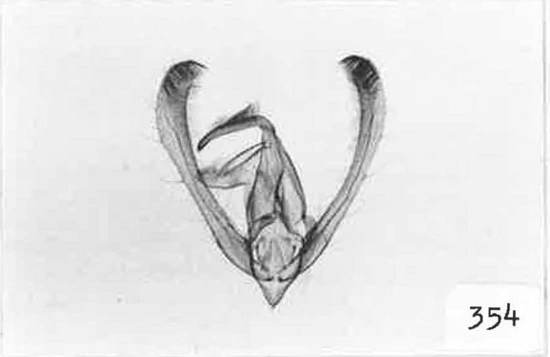
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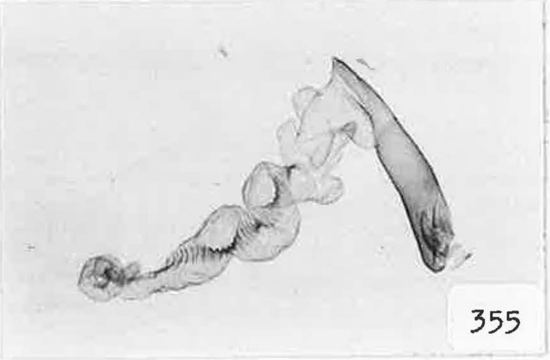
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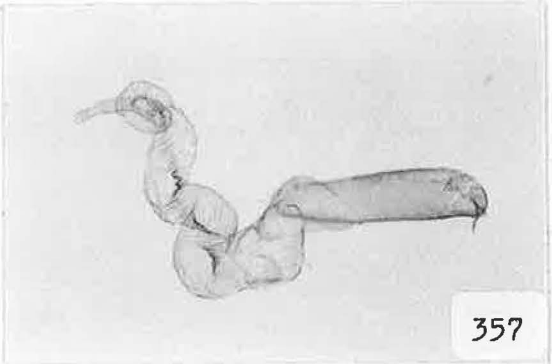
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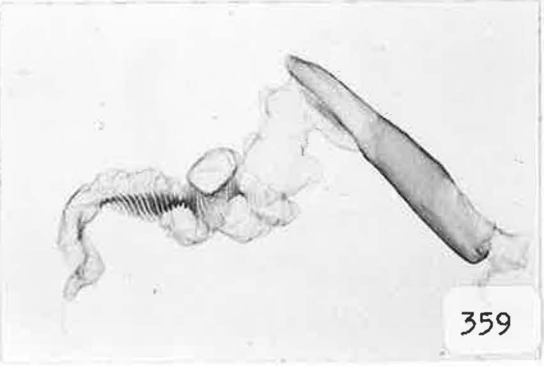
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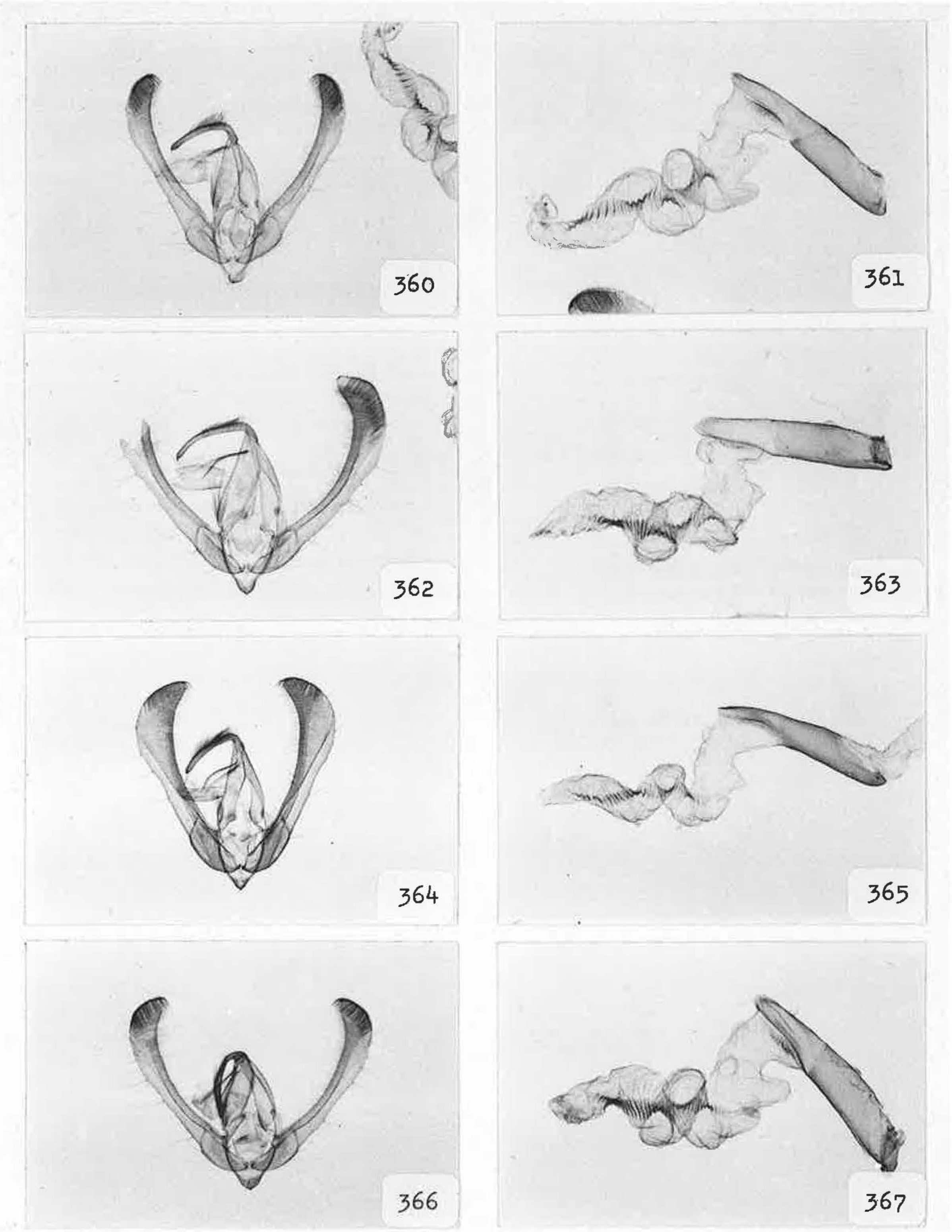
Figs. 352 - 359. Male genitalia, Heliothinae. *Heliocheilus aleurota*, Fig. 352, valves, & Fig. 353, vesica (BM Noct 13172); *Heliocheilus* sp. No. 7 (Argentina), Fig. 354, valves, & Fig. 355, vesica (BM Noct 13326); *Heliocheilus canusina*, Fig. 356, valves, & Fig. 357, vesica (BM Noct 13175); *Heliocheilus cladotus*, Fig. 358, valves, & Fig. 359, vesica (BM Noct 13180).



Figs. 360 - 367. Male genitalia, Heliothinae. *Heliocheilus confundens*, Fig. 360, valves, & Fig. 361, vesica (BM Noct 13215); *Heliocheilus cramboides*, Fig. 362, valves, & Fig. 363, vesica (BM Noct 13218); *Heliocheilus cystiphora*, Fig. 364, valves, & Fig. 365, vesica (BM Noct 13513); *Heliocheilus eodora*, Fig. 366, valves, & Fig. 367, vesica (BM Noct 13235).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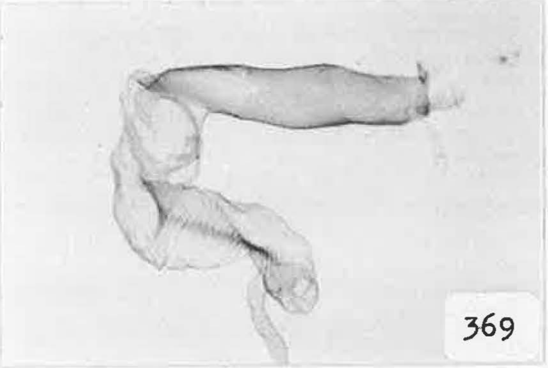
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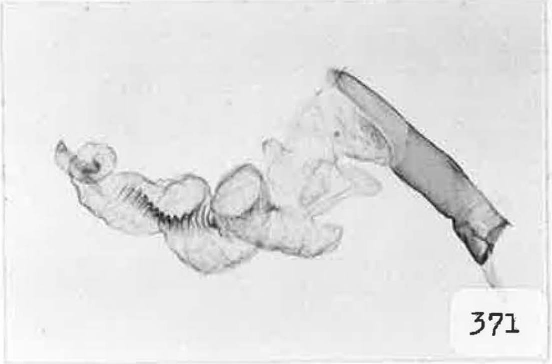
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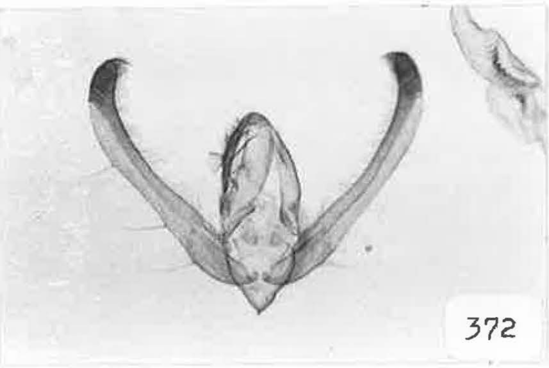
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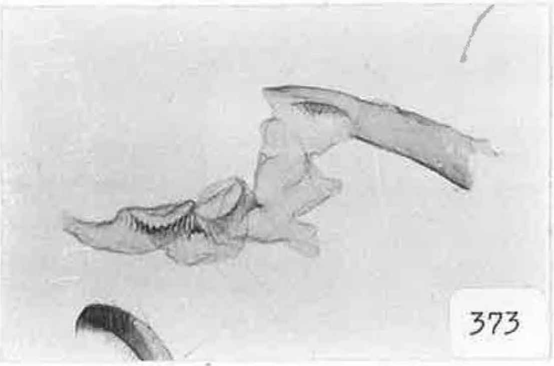
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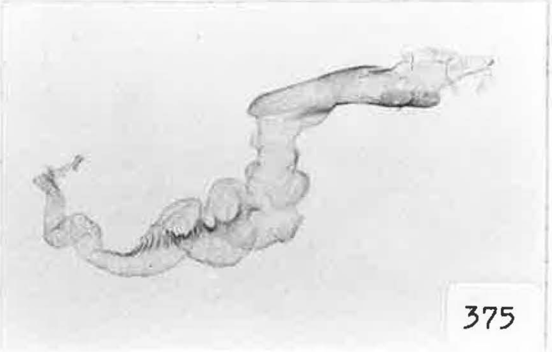
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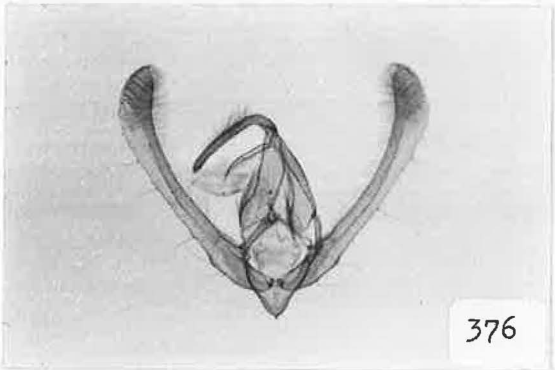
Figs. 368 - 375. Male genitalia, Heliothinae. *Heliocheilus fervens*, Fig. 368, valves, & Fig. 369, vesica (BM Noct 13238); *Heliocheilus flavitincta*, Fig. 370, valves, & Fig. 371, vesica (BM Noct 13241); *Heliocheilus ionola*, Fig. 372, valves, & Fig. 373, vesica (BM Noct 13244); *Heliocheilus melibaphes*, Fig. 374, valves, & Fig. 375, vesica (BM Noct 13248).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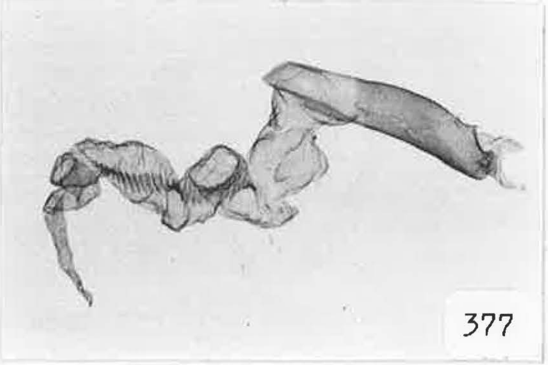
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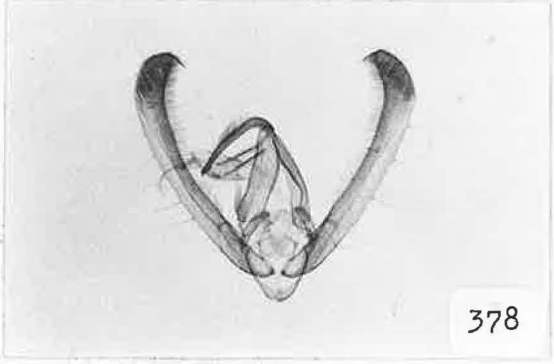
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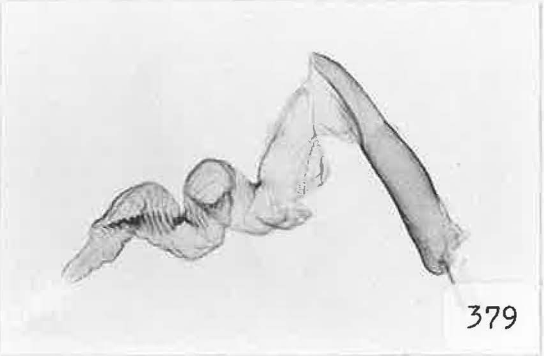
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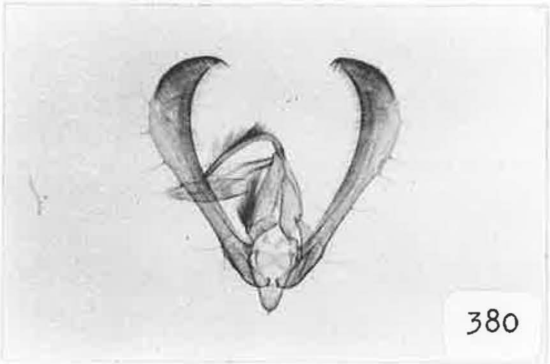
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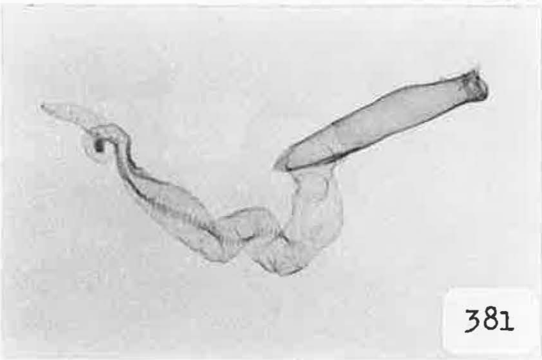
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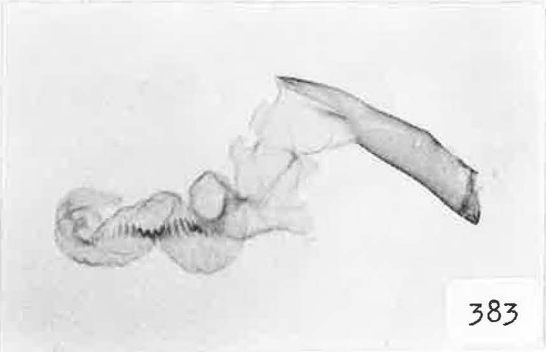
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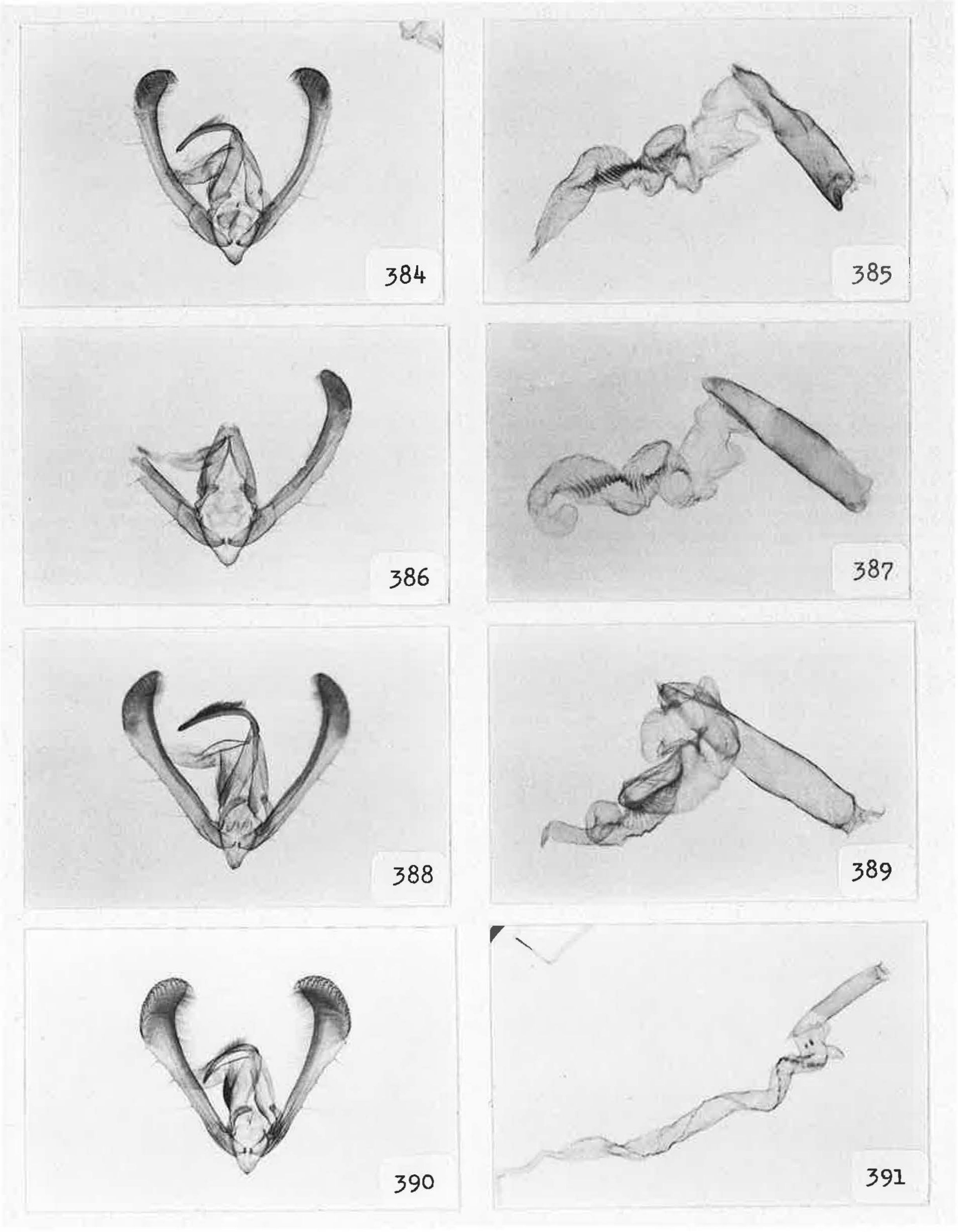
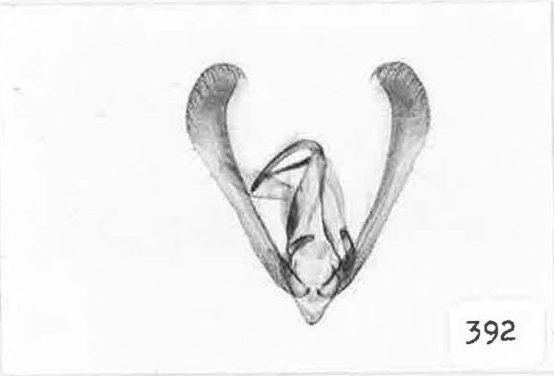
Figs. 376 - 383. Male genitalia, Heliothinae. *Heliocheilus moribunda*, Fig. 376, valves, & Fig. 377, vesica (BM Noct 13259); *Heliocheilus neurias*, Fig. 378, valves, & Fig. 379, vesica, (BM Noct 13281); *Heliocheilus paradoxus*, Fig. 380, valves, & Fig. 381, vesica (BM Noct 13284); *Heliocheilus puncticulata*, Fig. 382, valves, & Fig. 383, vesica (BM Noct 13286).



Figs. 384 - 391. Male genitalia, Heliothinae. *Heliocheilus sericea,* Fig. 384, valves, & Fig. 385, vesica (BM Noct 13298); *Heliocheilus sulphurea,* Fig. 386, valves, & Fig. 387 (BM Noct 13313); *Heliocheilus translucens,* Fig. 388, valves, & Fig. 389, vesica (BM Noct 13323); *Australothis rubrescens,* Fig. 390, valves, & Fig. 391, vesica (BM Noct 13400).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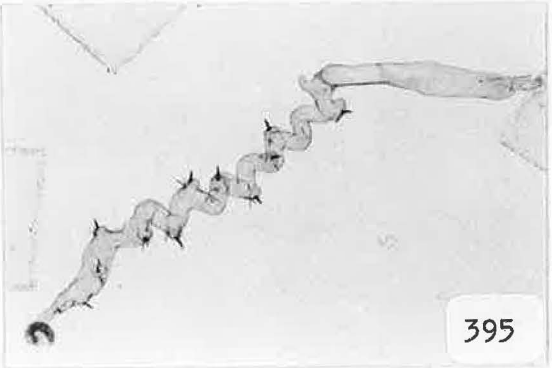
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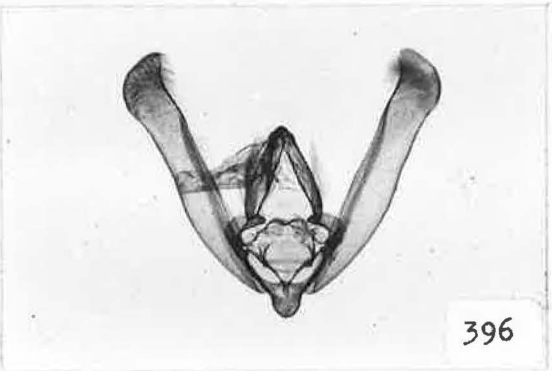
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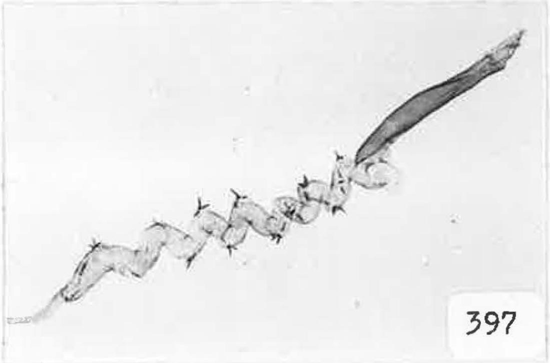
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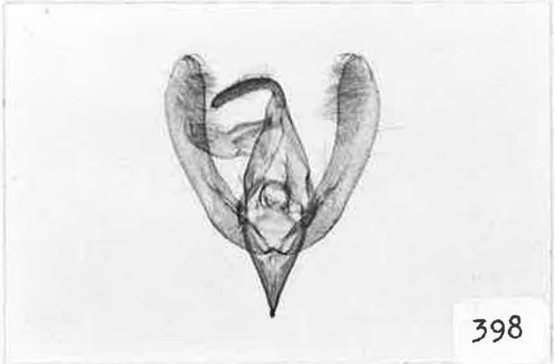
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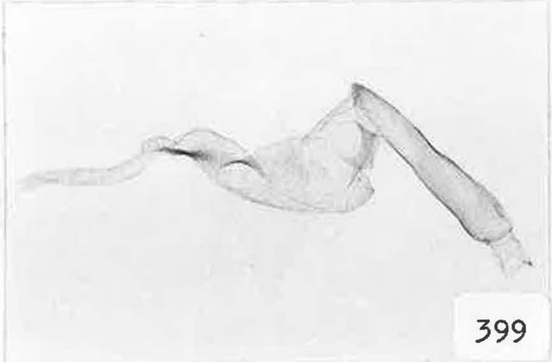
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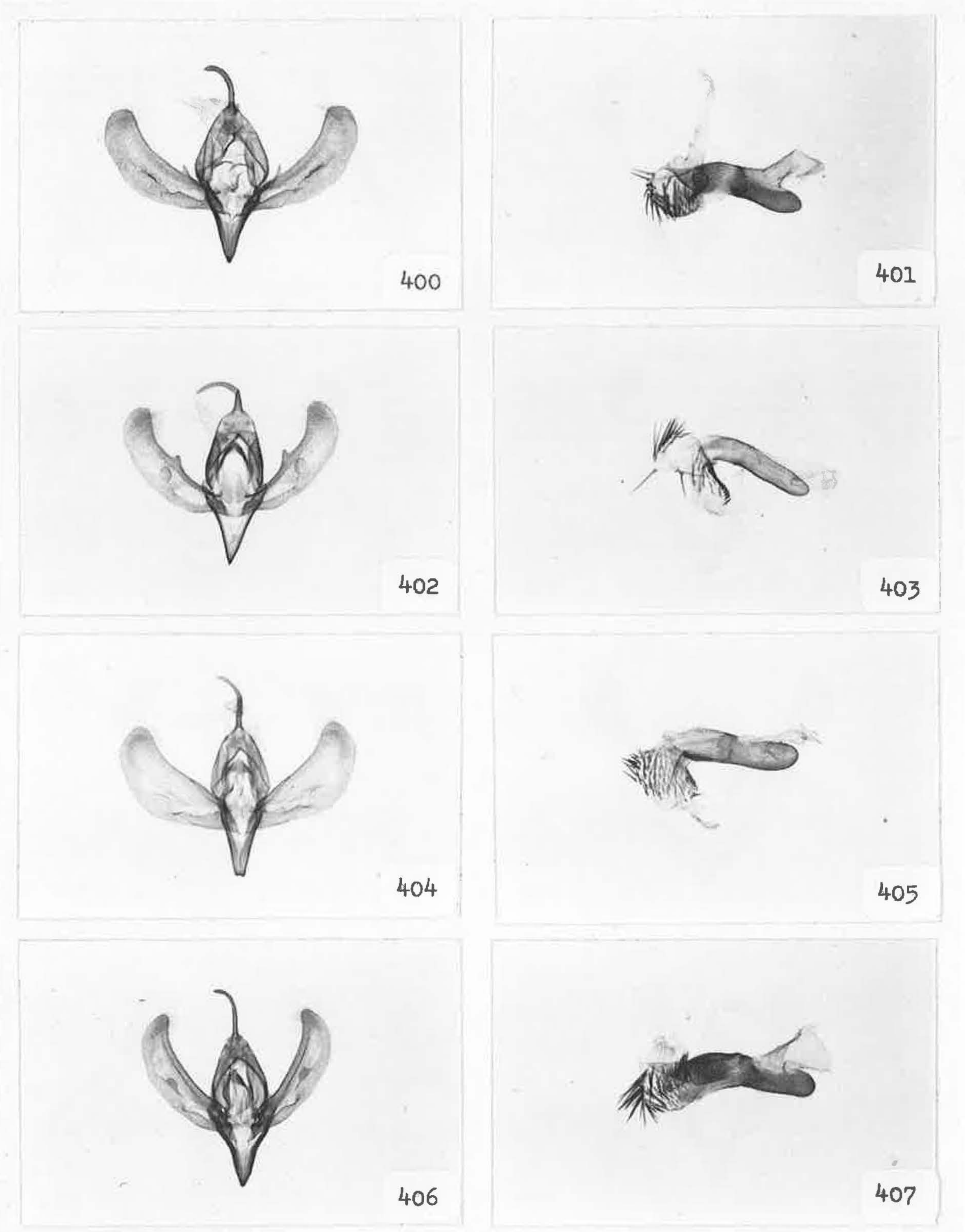
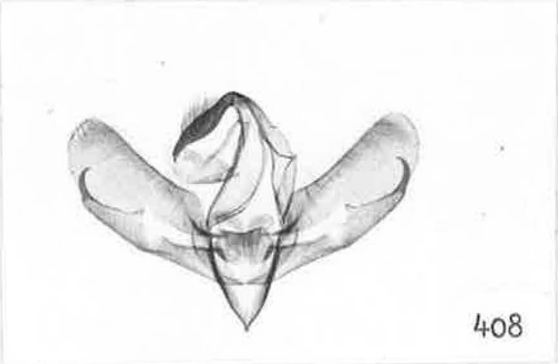
Figs. 392 - 399. Male genitalia, Heliothinae. *Australiothis tertia*, Fig. 392, valves, & Fig. 393, vesica (BM Noct 13424); *Helicoverpa armigera*, Fig. 394, valves (BM Noct 13150), & Fig. 395, vesica (BM Noct 13142); *Helicoverpa fletcheri*, Fig. 396, valves, & Fig. 397, vesica (BM Noct 13151); *Engusanacantha bilineata*, Fig. 398, valves, & Fig. 399, vesica (BM Noct 13087).



Figs. 400 - 407. Male genitalia, Stiriinae. *Aegle koekeritziana,* Fig. 400, valves, & Fig. 401, vesica (BM Noct 13832); *Aegle subflava,* Fig. 402, valves, & Fig. 403, vesica (BM Noct 13835); *Aegle vespertalis,* Fig. 404, valves, & Fig. 405, vesica (BM Noct 13837); *Metaegle pallida,* Fig. 406, valves, & Fig. 407, vesica (BM Noct 13870).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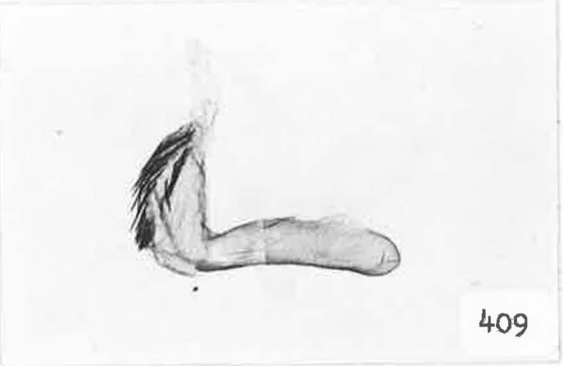
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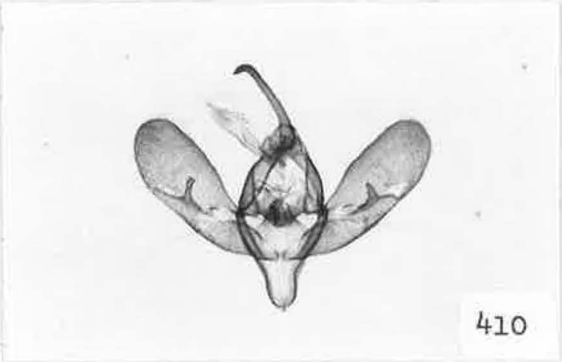
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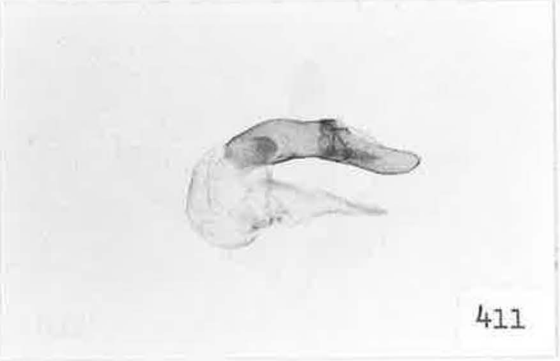
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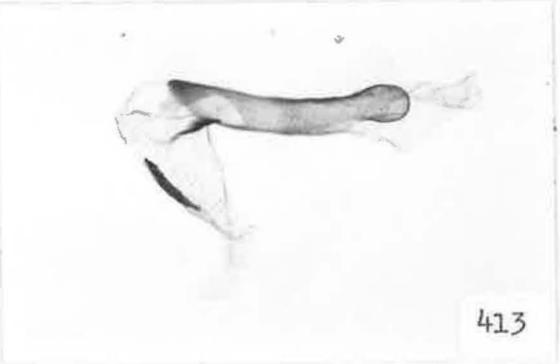
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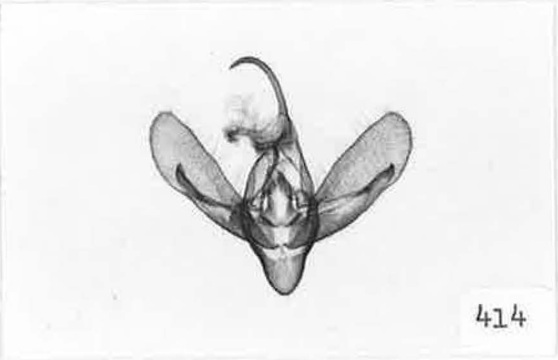
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Figs. 408 - 415. Male genitalia, Stiriinae. *Basilodes chrysopis,* Fig. 408, valves, & Fig. 409, vesica (BM Noct 13847); *Dipinacea schiniodes,* Fig. 410, valves, & Fig. 411, vesica (BM Noct 13856); *Ectolopha marginata,* Fig. 412, valves, & Fig. 413, vesica (BM Noct 13860); *Ectolopha viridescens,* Fig. 414, valves, & Fig. 415, vesica (BM Noct 13863).


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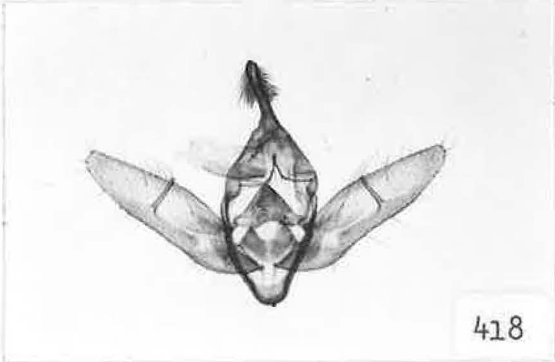
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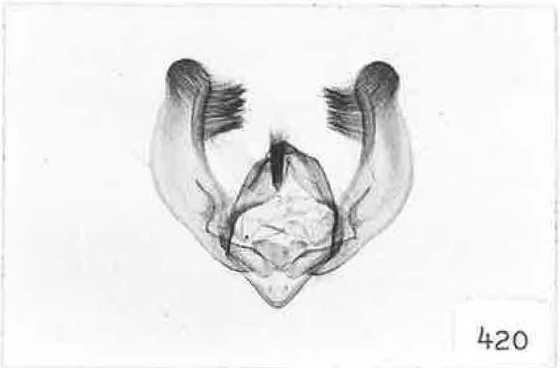
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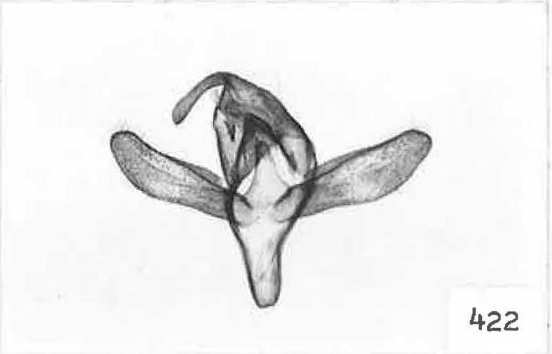
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Figs. 416 - 423. Male genitalia, Stiriinae. *Megalodes eximia,* Fig. 416, valves, & Fig. 417, vesica (BM Noct 13866); *Mycteroplus puniceago,* Fig. 418, valves, & Fig. 419, vesica (BM Noct 13872); *Oslaria viridifera,* Fig. 420, valves, & Fig. 421, vesica (BM Noct 13876); *Ochrocalama xanthiata,* Fig. 422, valves, & Fig. 423, vesica (BM Noct 13879).


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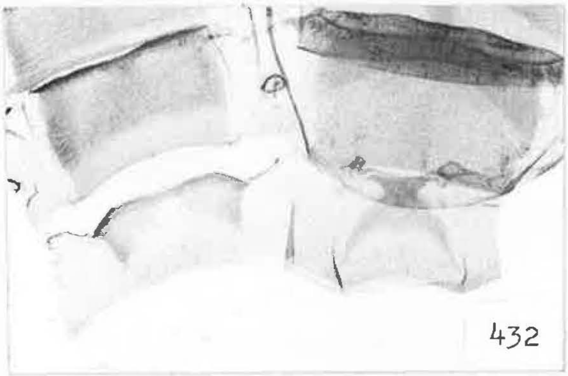
Figs. 424 - 431. Male genitalia, Stiriinae. *Panemeria tenebrata*, Fig. 424, valves, & Fig. 425, vesica (BM Noct 13882); *Paralophata ansorgei*, Fig. 426, valves, & Fig. 427, vesica (BM Noct 13890); *Prothrinax luteomedia*, Fig. 428, valves, & Fig. 429, vesica (BM Noct 13894); *Synthymia fixa*, Fig. 430, valves, & Fig. 431, vesica (BM Noct 13657).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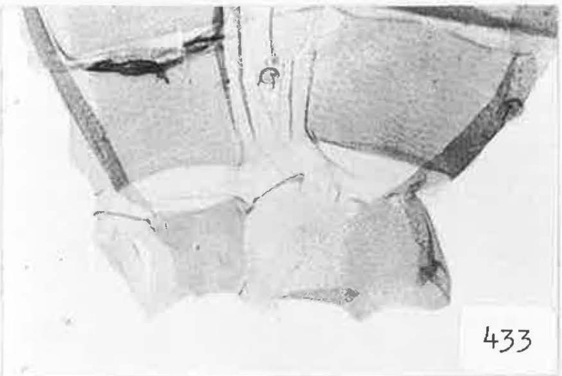
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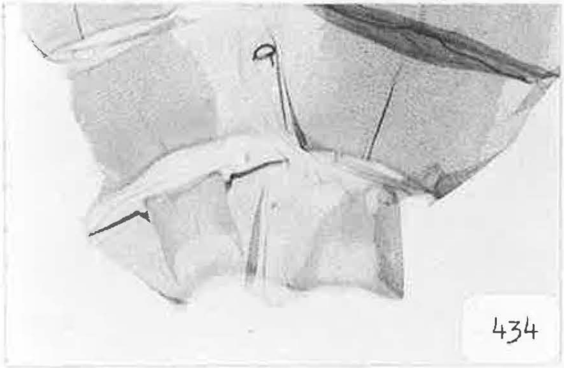
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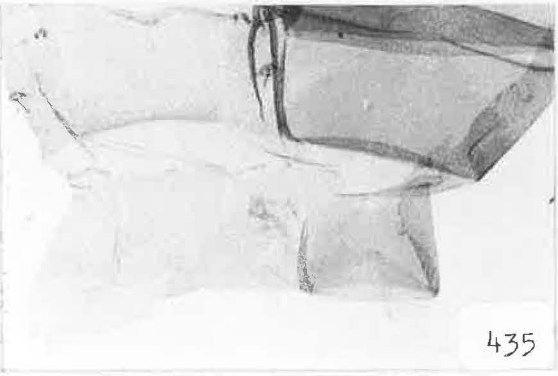
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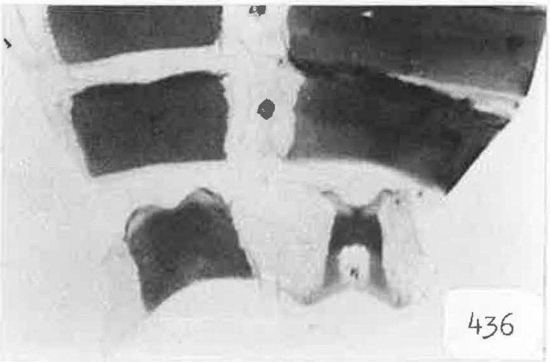
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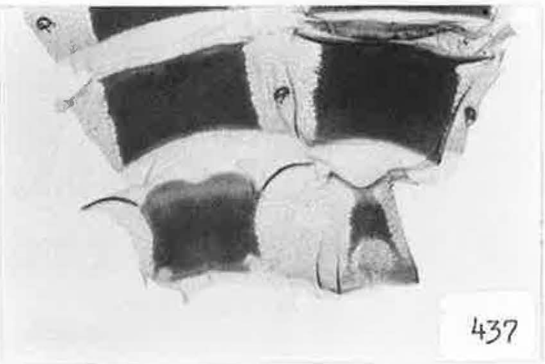
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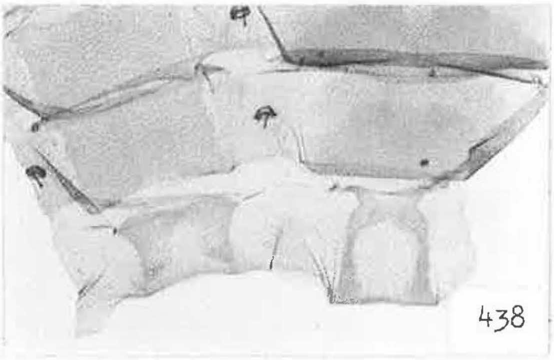
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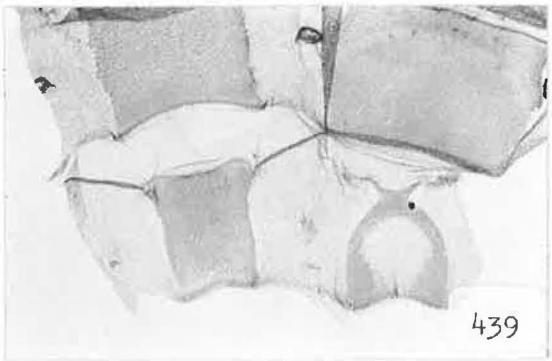
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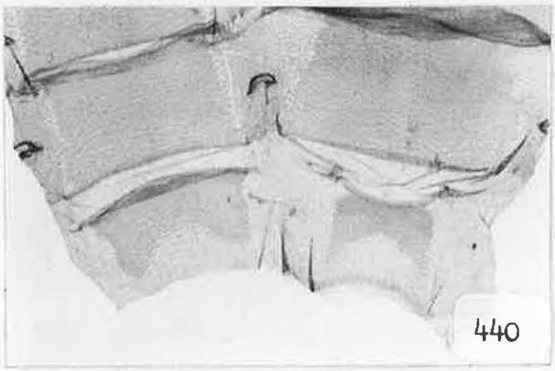
Figs. 432 - 439. Male A8, Heliothinae. Fig. 432, *Aedophron rhodites* (BM Noct 13068); Fig. 433, *Derrima stellata* (BM Noct 13084); Fig. 434, *Erythroecia suavis* (BM Noct 13095); Fig. 435, *Erythrophaia eudoxia* (BM Noct 13105); Fig. 436, *Eutricopis nexilis* (BM Noct 13124); Fig. 437, *Heliothodes diminutivus* (BM Noct 13628); Fig. 438, *Melaporphyria immortua* (BM Noct 13569); Fig. 439, *Periphanes delphinii* (BM Noct 13581).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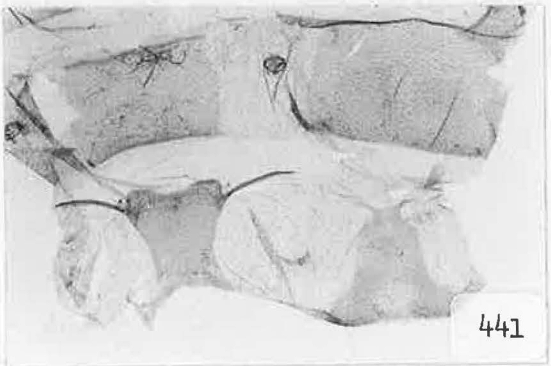
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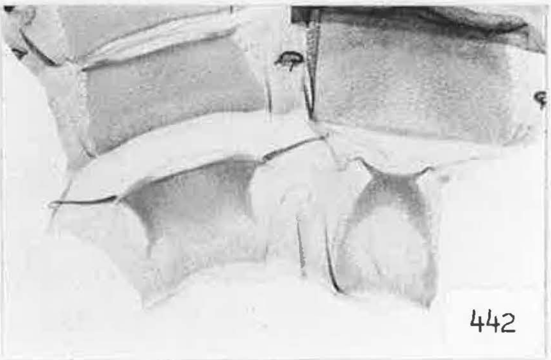
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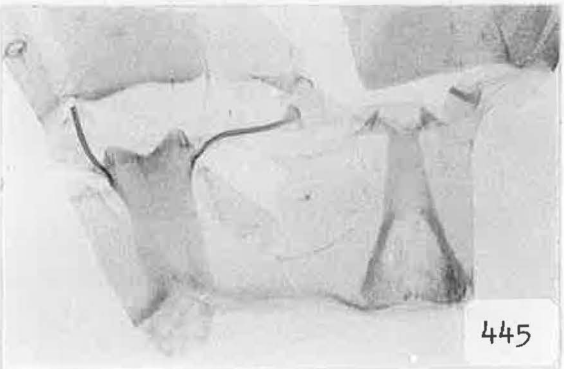
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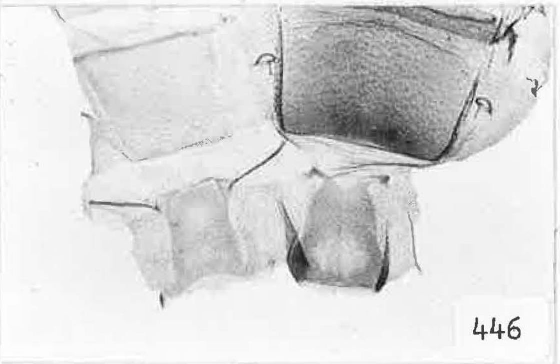
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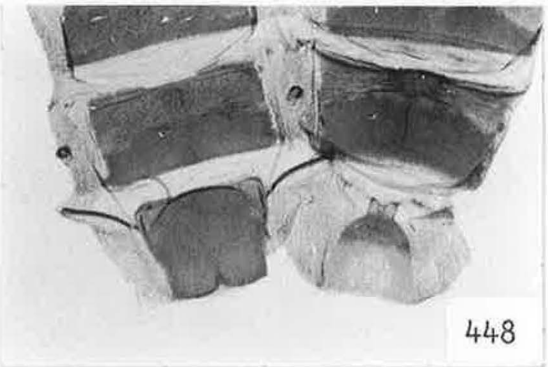
Figs. 440 - 447. Male A8, Heliothinae. Fig. 440, *Pyrrhia treitschkei* (BM Noct 13545); Fig. 441, *Pyrrhia umbra* (BM Noct 13617); Fig. 442, *Pyrrhia victorina* (BM Noct 13623); Fig. 443, *Rhodoecia aurantiago* (BM Noct 13692); Fig. 444, *Pyrocleptria cora* (BM Noct 13633); Fig. 445, *Adisura atkinsoni* (BM Noct 13016); Fig. 446, *Adisura parva* (BM Noct 13051); Fig. 447, *Adisura litarga* (ANIC).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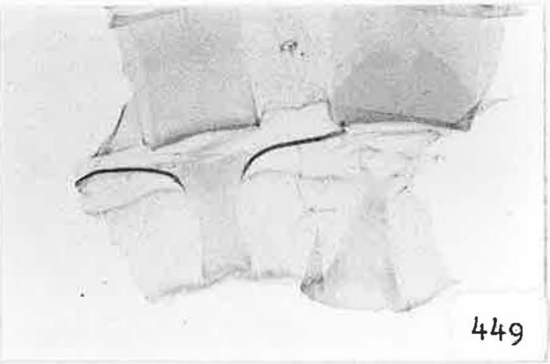
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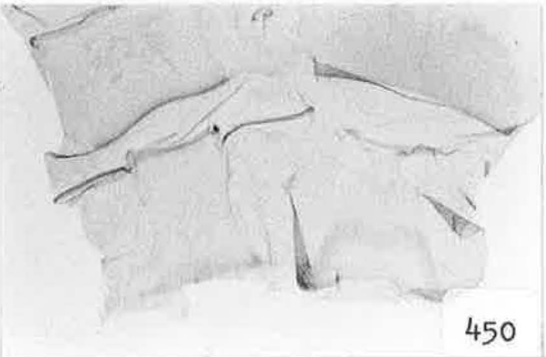
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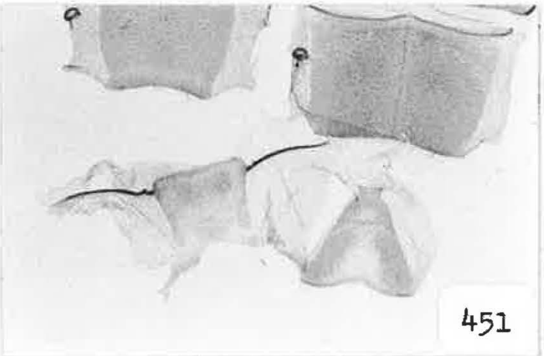
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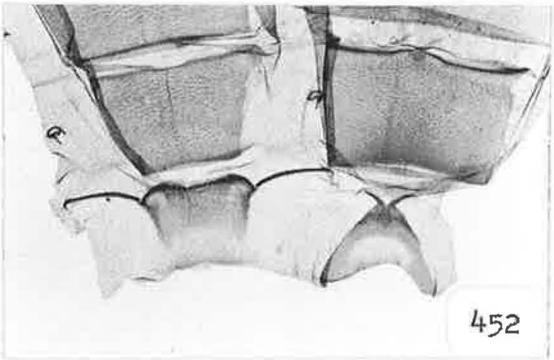
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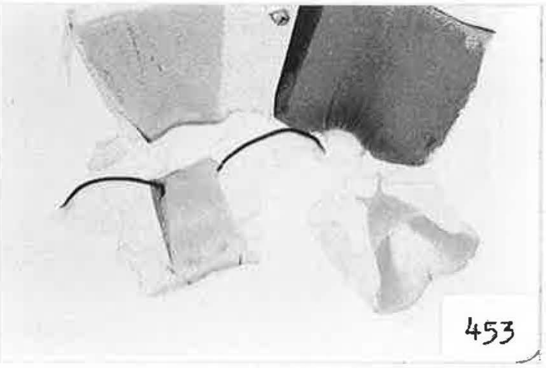
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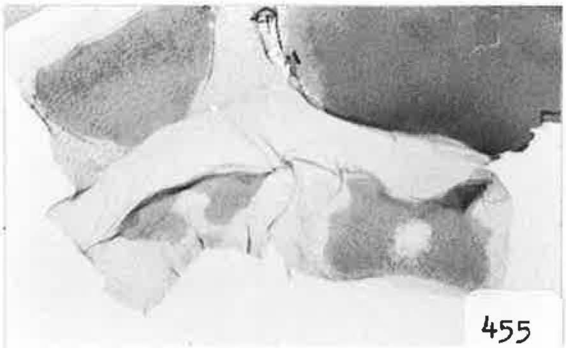
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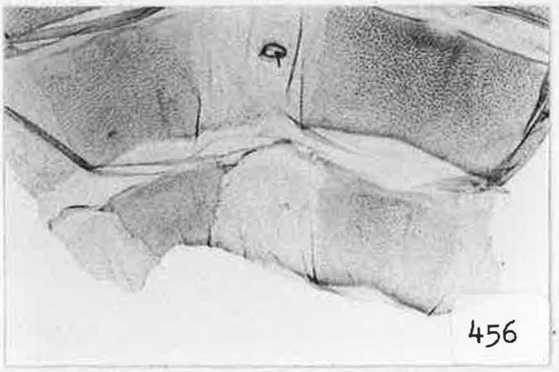
Figs. 448 - 455. Male A8, Heliothinae. Fig. 448, *Heliolonche modicella* (BM Noct 13335); Fig. 449, *Schinia scutosa* (BM Noct 13690); Fig. 450, *Schinia chilensis* (AMNH); Fig. 451, *Schinia gaurae* (BM Noct 13639); Fig. 452, *Schinia jaegeri* (BM Noct 13642); Fig. 453, *Schinia jaguarina* (BM Noct 13650); Fig. 454, *Schinia pulchra* (BM Noct AMNH); Fig. 455, *Schinia rosea* (BM Noct 13668).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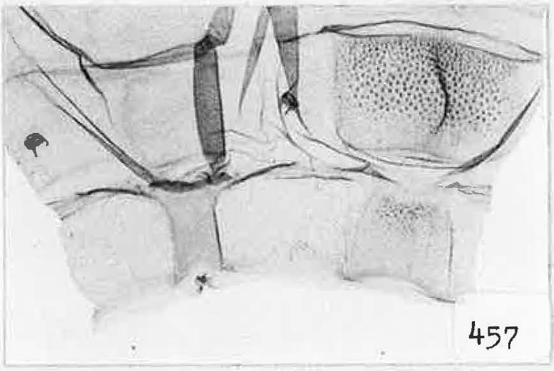
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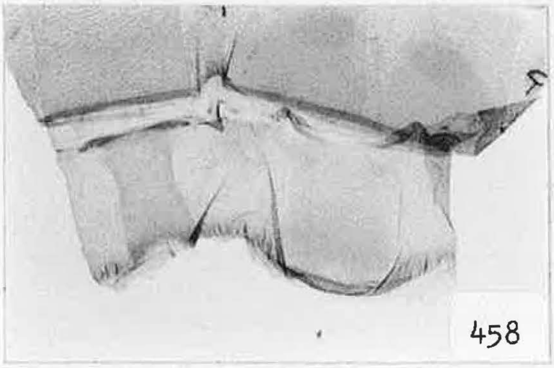
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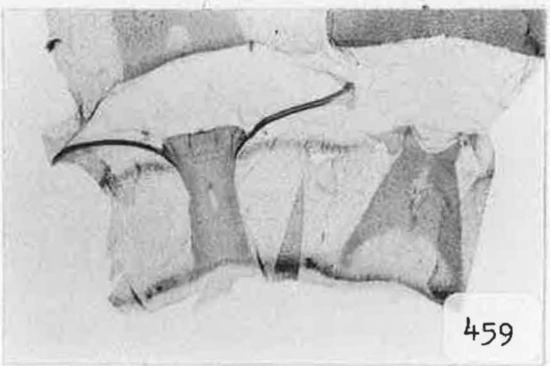
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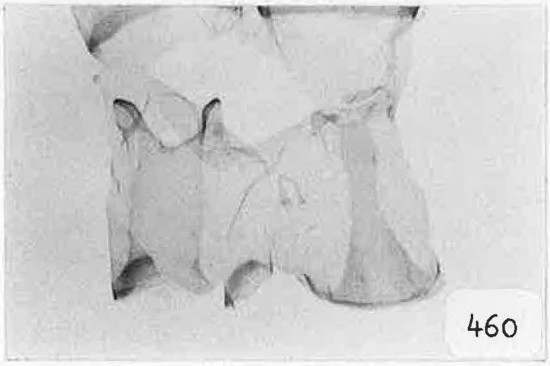
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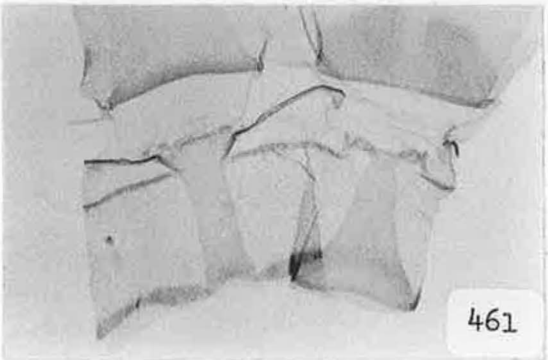
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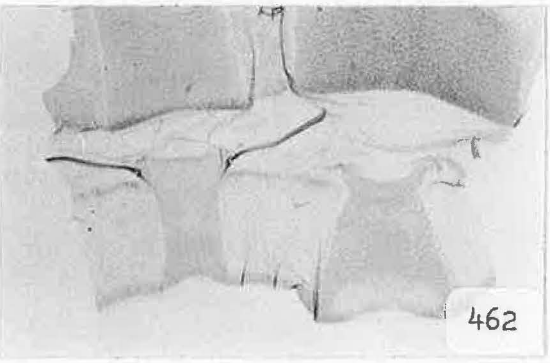
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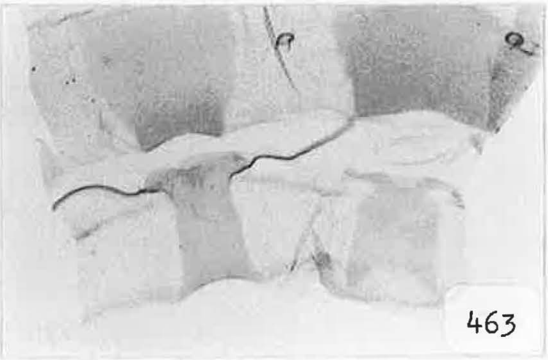
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Figs. 456 - 463. Male A8, Heliothinae. Fig. 456, *Schinia roseoflammata* (BM Noct 13680); Fig. 457, *Schinia xanthiata* (BM Noct 13677); Fig. 458, *Heliothis flavirufa* (BM Noct 13351); Fig. 459, *Heliothis viriplaca* (BM Noct 13450); Fig. 460, *Heliothis virescens* (BM Noct 13439); Fig. 461, *Heliothis punctifera* (BM Noct 13543); Fig. 462, *Heliothis incarnata* (BM Noct 13552); Fig. 463, *Heliothis radiata* (BM Noct 13494).


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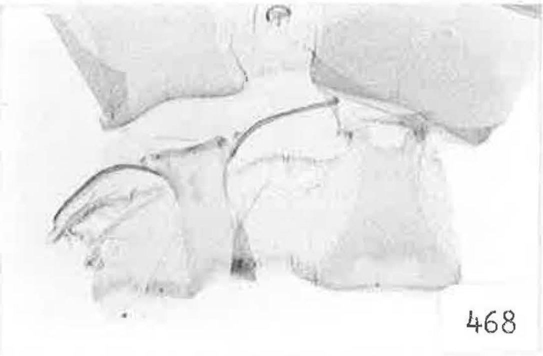
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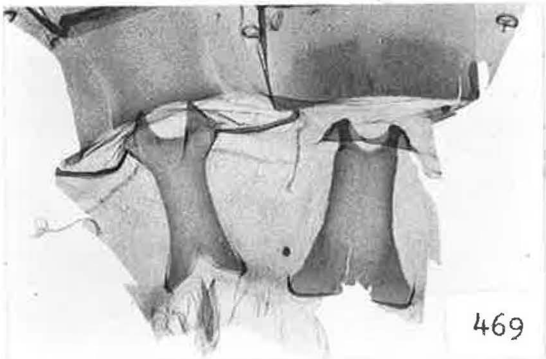
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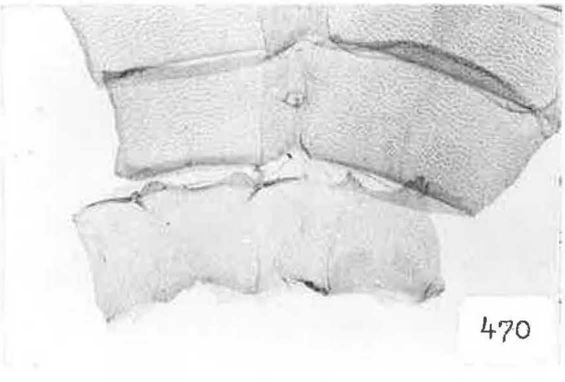
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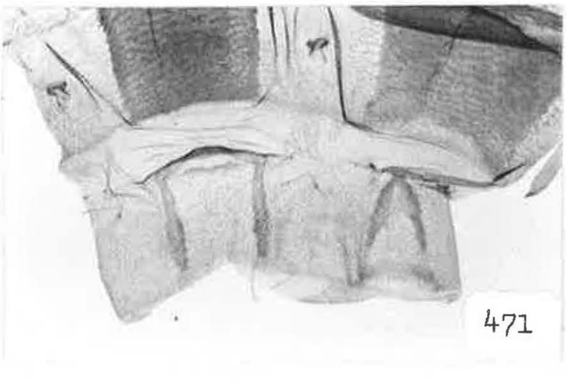
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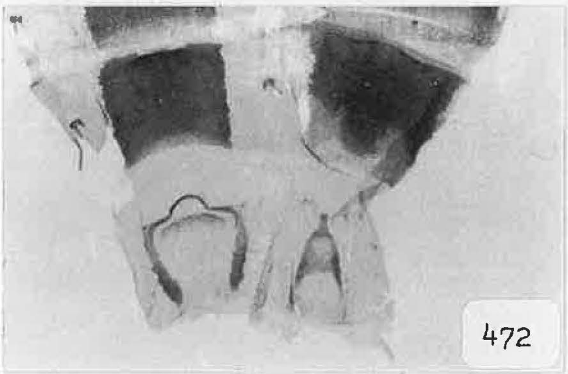
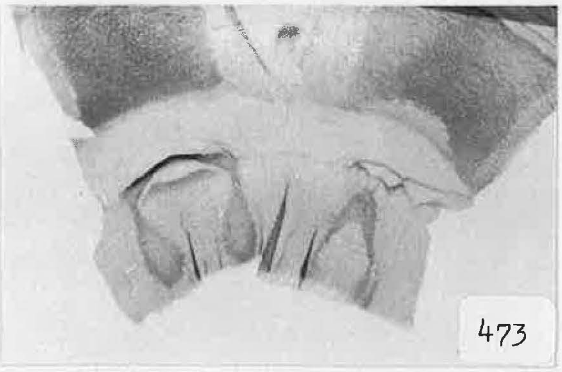
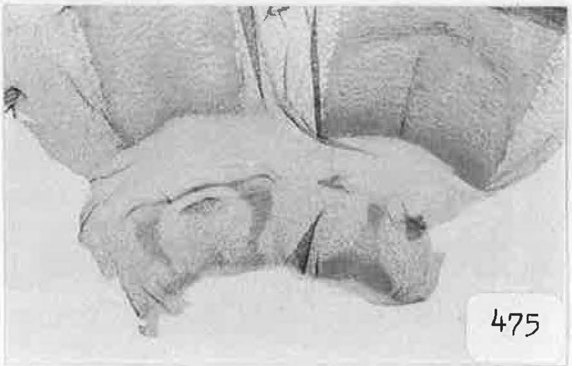
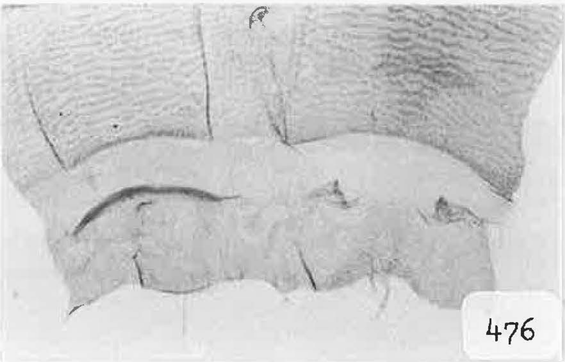
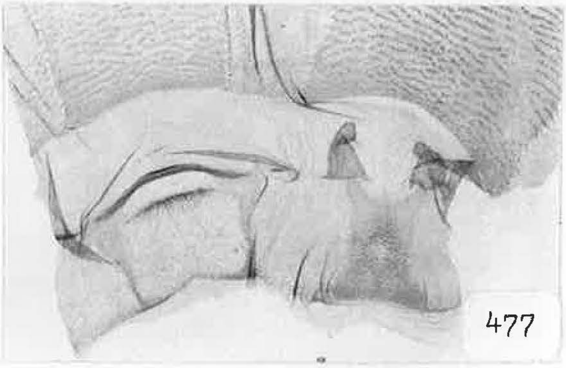
Figs. 464 - 471. Male A8, Heliothinae & Stiriinae. Heliothinae. Fig. 464, *Heliothis syrticola* (BM Noct 13503); Fig. 465, *Heliothis sanguinolenta* (BM Noct 13524); Fig. 466, *Heliocheilus moribunda* (BM Noct 13251); Fig. 467, *Heliocheilus paradoxa* (BM Noct 13284); Fig. 468, *Australothis tertia* (BM Noct 13424); Fig. 469, *Helicoverpa armigera* (BM Noct 13150); Fig. 470, *Engusanacantha bilineata* (BM Noct 13087). Stiriinae. Fig. 471, *Aegle koekeritziana* (BM Noct 13832).

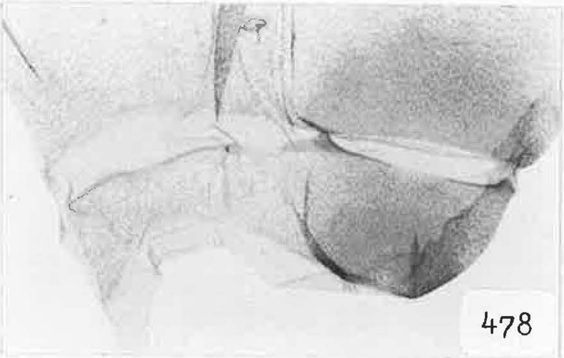


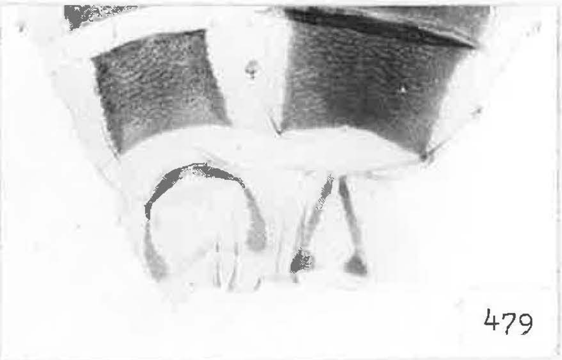




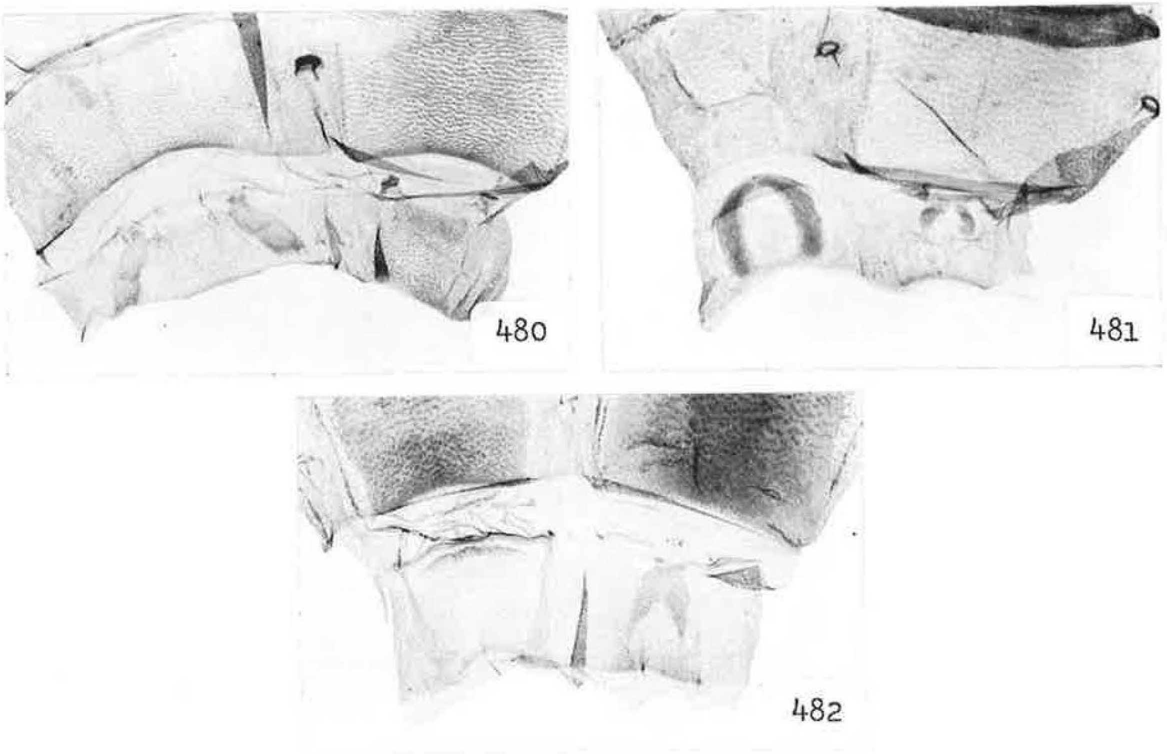




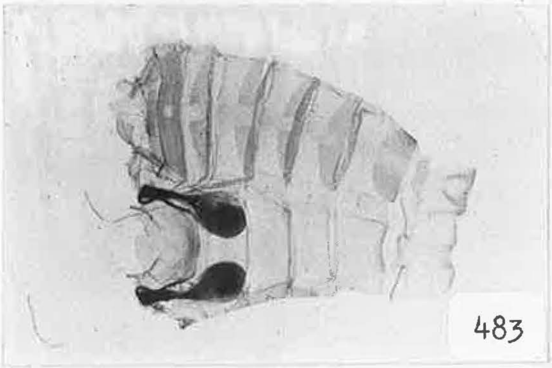




Figs. 472 - 479. Male A8, Stiriinae. Fig. 472, *Aegle subflava* (BM Noct 13835); Fig. 473, *Aegle vespertalis* (BM Noct 13837); Fig. 474, *Metaegle pallida* (BM Noct 13870); Fig. 475, *Dipinacea schiniodes* (BM Noct 13856); Fig. 476, *Ectolopha marginata* (BM Noct 13860); Fig. 477, *Ectolopha viridescens* (BM Noct 13863); Fig. 478, *Ochrocalama xanthiata* (BM Noct 13879); Fig. 479, *Panemeria tenebrata* (BM Noct 13887).



Figs. 480 - 482. Male A8, Stiriinae. Fig. 480, *Paralophata ansorgei* (BM Noct 13890); Fig. 481, *Prothrinax luteomedia* (BM Noct 13894); Fig. 482, *Synthymia fixa* (BM Noct 13657).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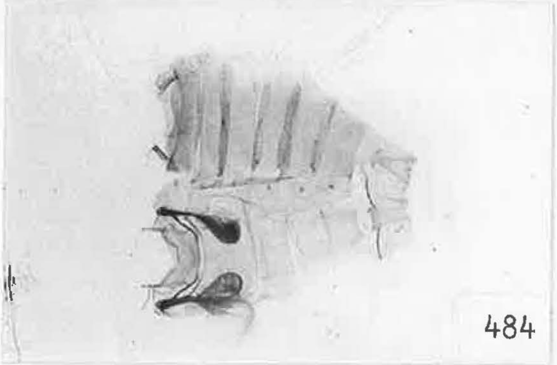
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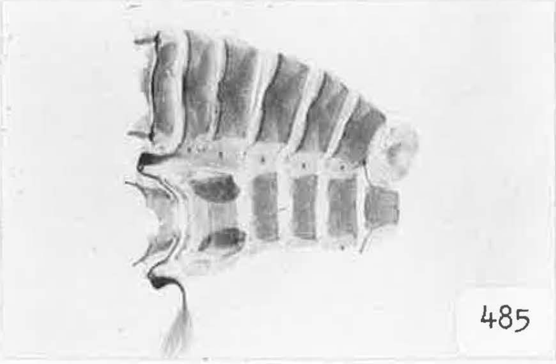
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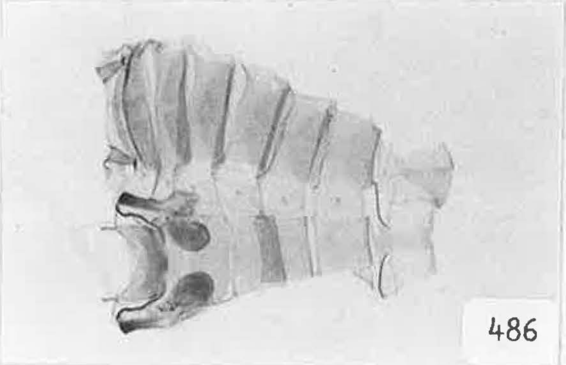
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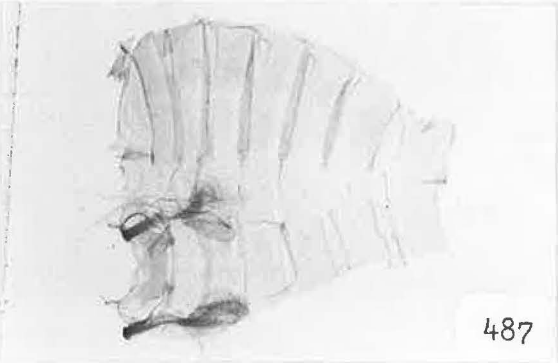
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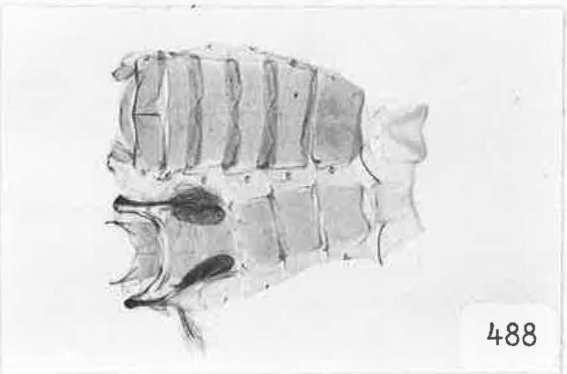
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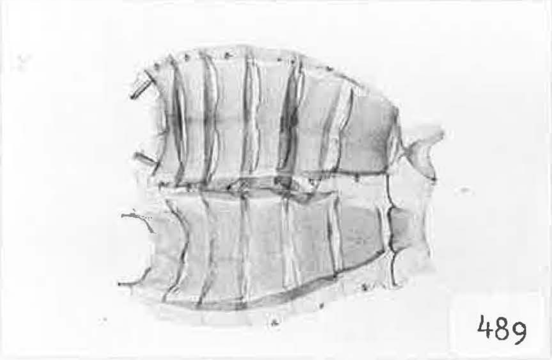
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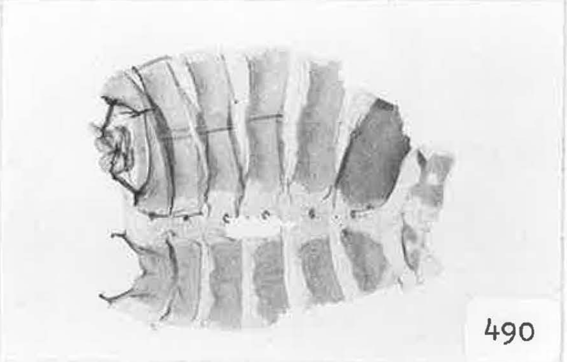
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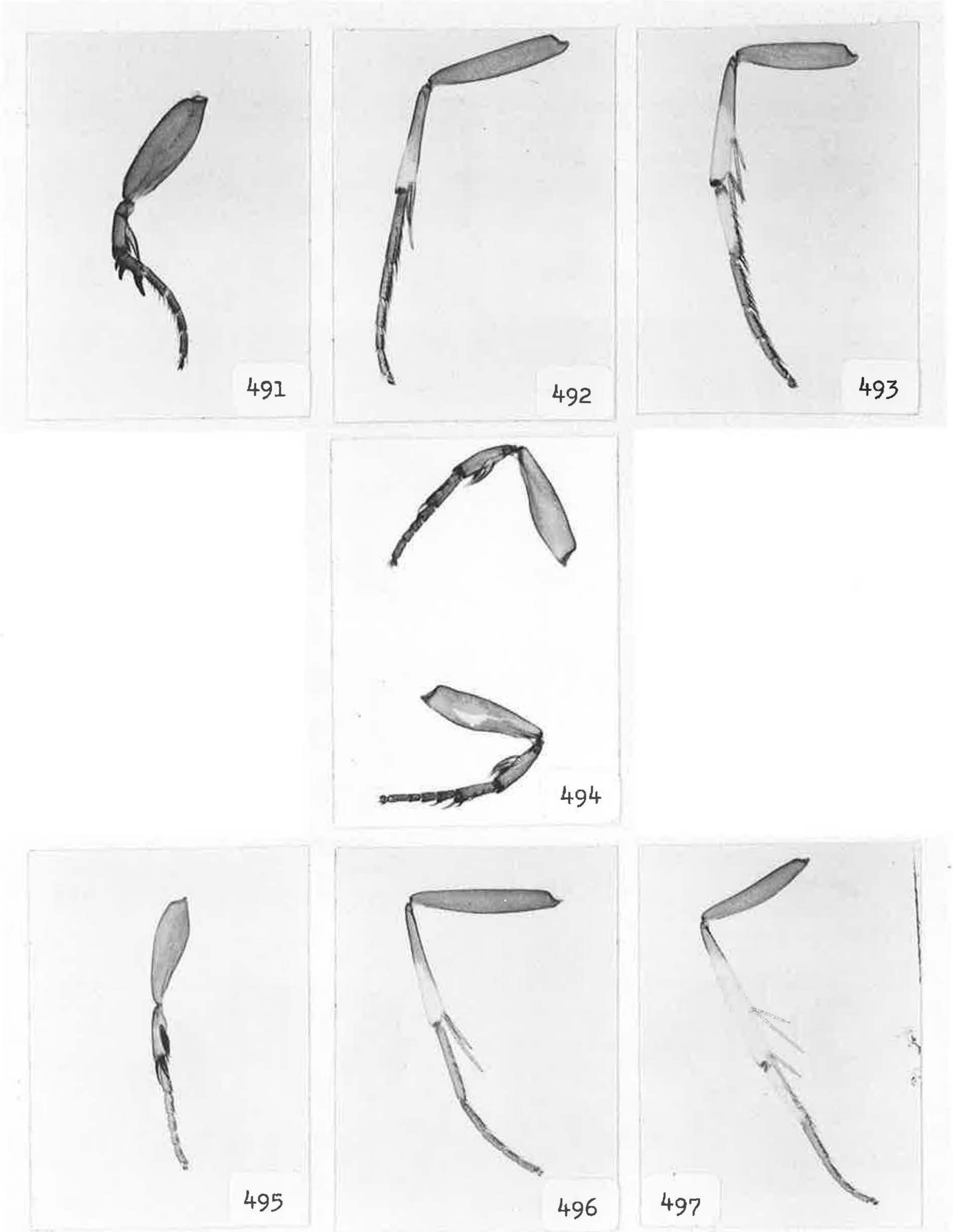
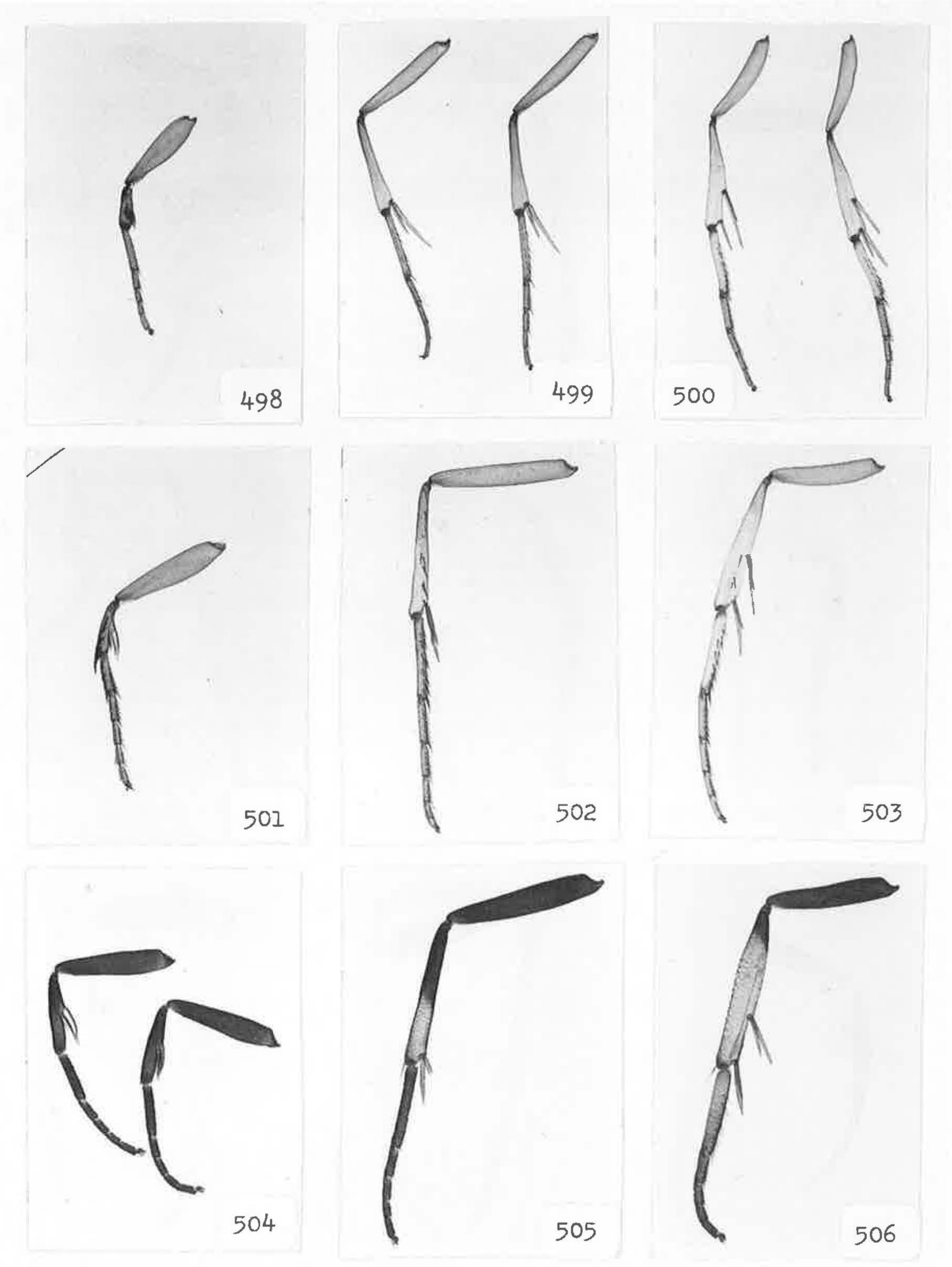
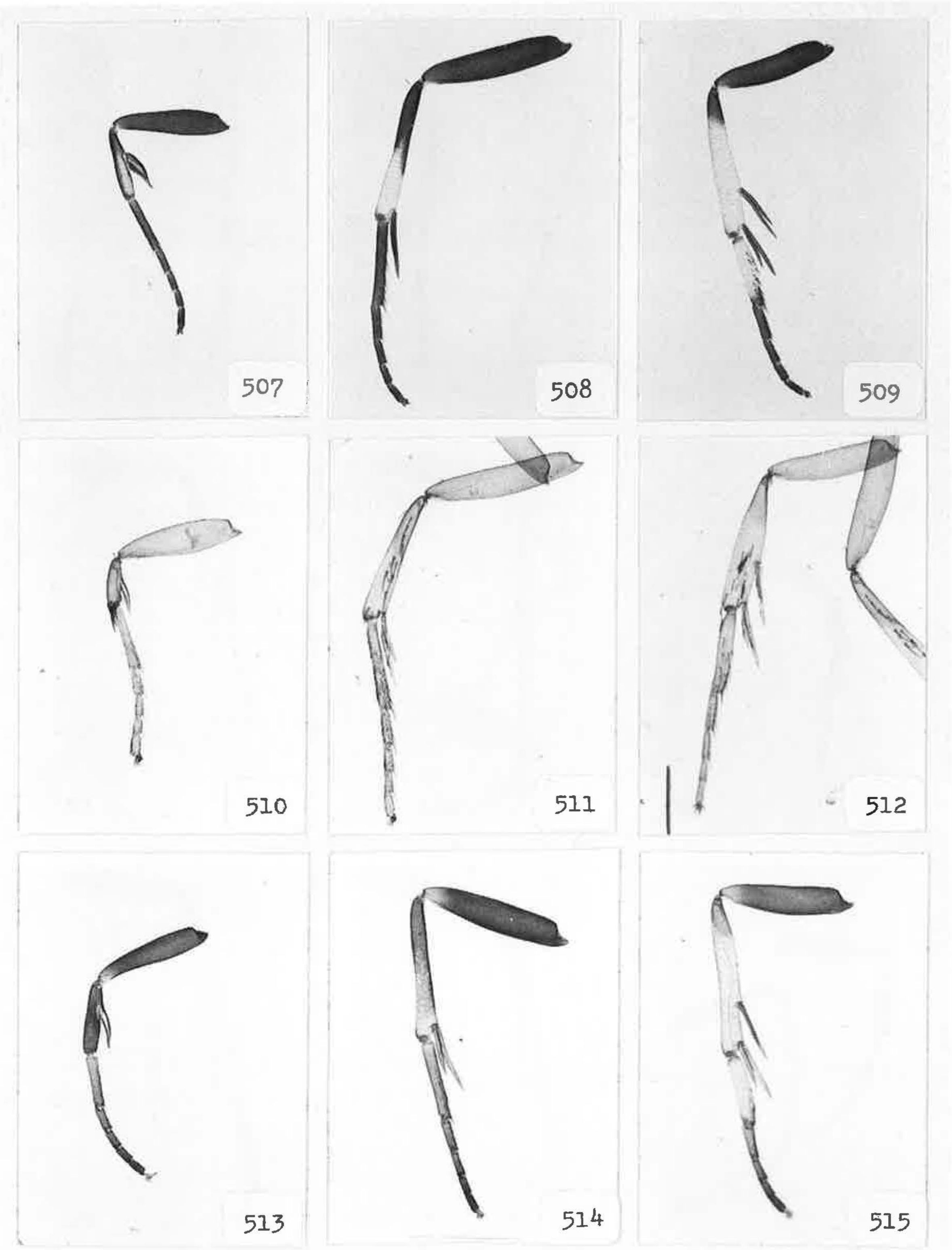
Figs. 483 - 490. Male abdomens, Heliothinae. Fig. 483, *Adisura bella* (BM Noct 13026); Fig. 484, *Adisura litarga* (ANIC); Fig. 485, *Heliolonche modicella* (BM Noct 13335); Fig. 486, *Protoschinia scutosa* (BM Noct 13690); Fig. 487, *Schinia chilensis* (AMNH); Fig. 488, *Schinia gaurae* (BM Noct 13640); Fig. 489, *Schinia jaegeri* (BM Noct 13642); Fig. 490, *Schinia rosea* (BM Noct 13668).



Figs. 491 - 497. Legs, Heliothinae. *Aedophron rhodites*, Fig. 491, fore-leg (BM Noct 13065), Fig. 492, mid-leg (BM Noct 13061), & Fig. 493, hind-leg (BM Noct 13065); *Baptarma felicita*, Fig. 494, fore-leg (CNC: 4407); *Derrima stellata*, Fig. 495, fore-leg, Fig. 496, mid-leg, & Fig. 497, hind-leg (BM Noct 13081).



Figs. 498 - 506. Legs, Heliothinae. *Erythroecia suavis*, Fig. 498, fore-leg, Fig. 499, mid-leg, & Fig. 500, hind-leg (BM Noct 13098); *Erythrophaia eudoxia*, Fig. 501, fore-leg, Fig. 502, mid-leg, & Fig. 503, hind-leg (BM Noct 13104); *Eutricopis nexilis*, Fig. 504, fore-leg, Fig. 505, mid-leg, & Fig. 506, hind-leg (BM Noct 13126).



Figs. 507 - 515. Legs, Heliothinae. *Heliothodes diminutivus*, Fig. 507, fore-leg, Fig. 508, mid-leg, & Fig. 509, hind-leg (BM Noct 13568); *Melaporphyria immortua*, Fig. 510, fore-leg, Fig. 511, mid-leg, & Fig. 512, hind-leg (CNC: 2916); *Microhelia angelica*, Fig. 513, fore-leg, Fig. 514, mid-leg, & Fig. 515, hind-leg (CNC: 4350).

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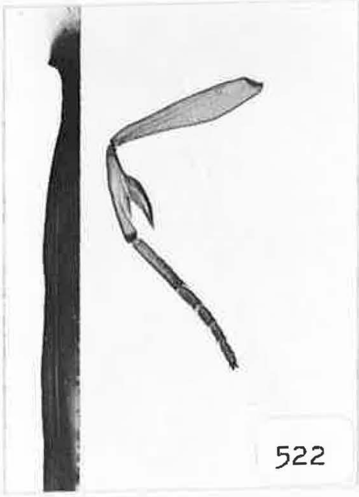

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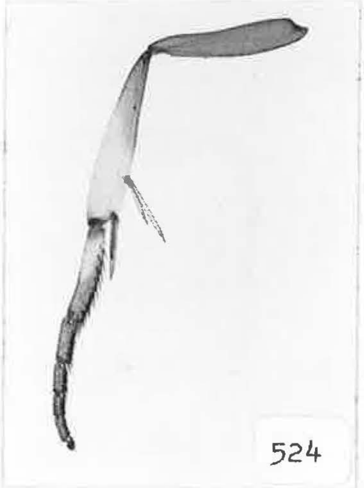

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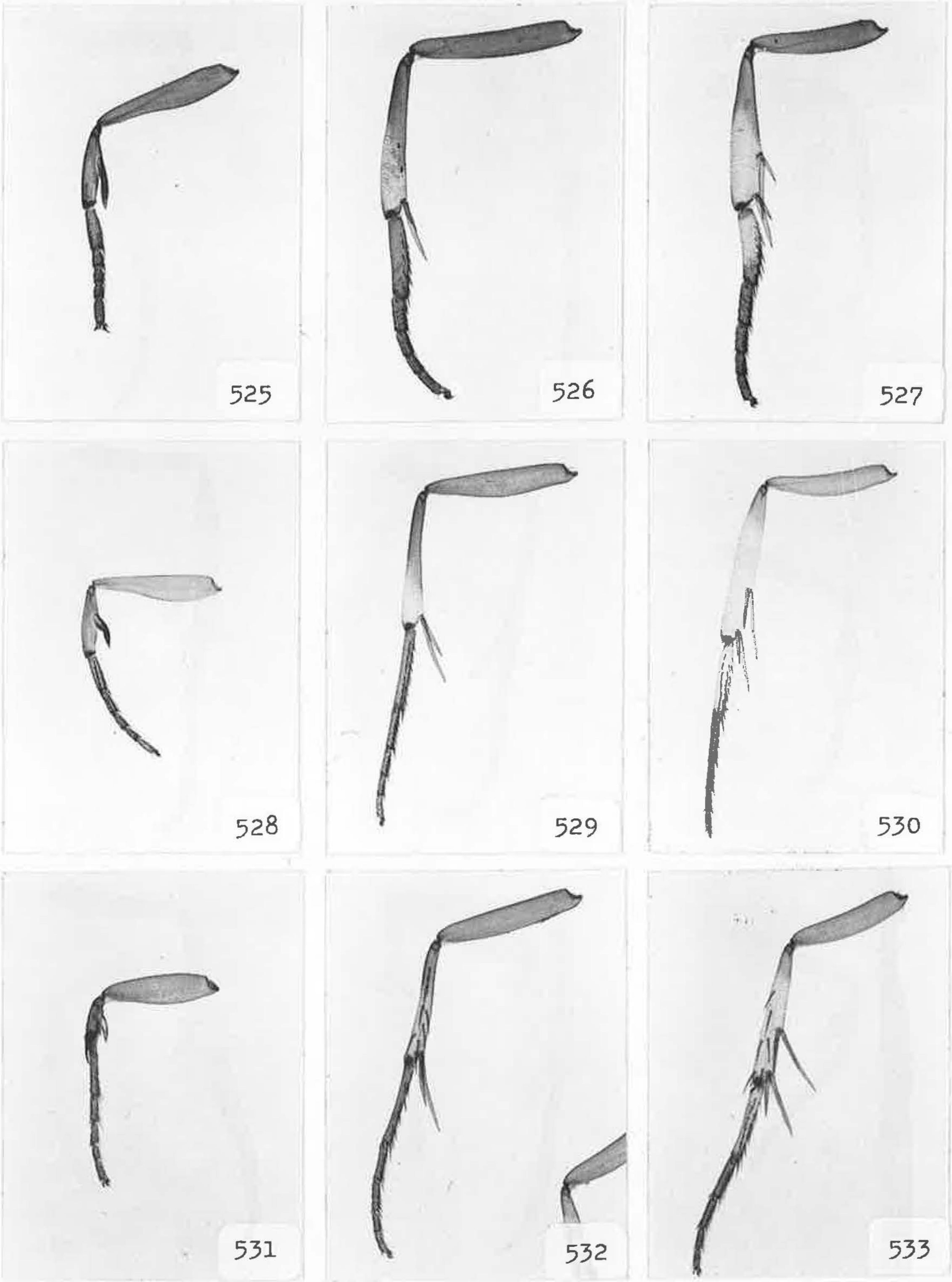
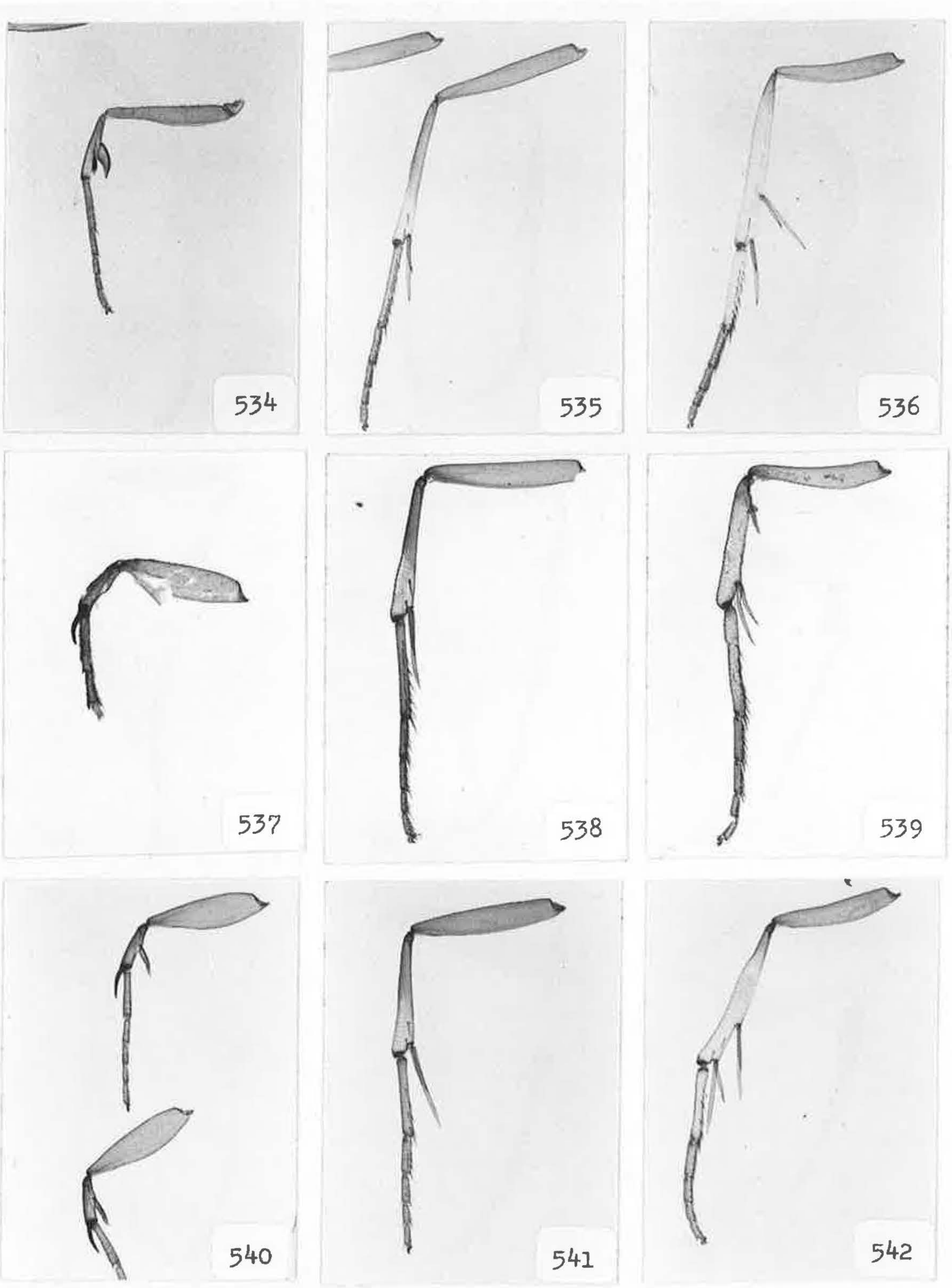
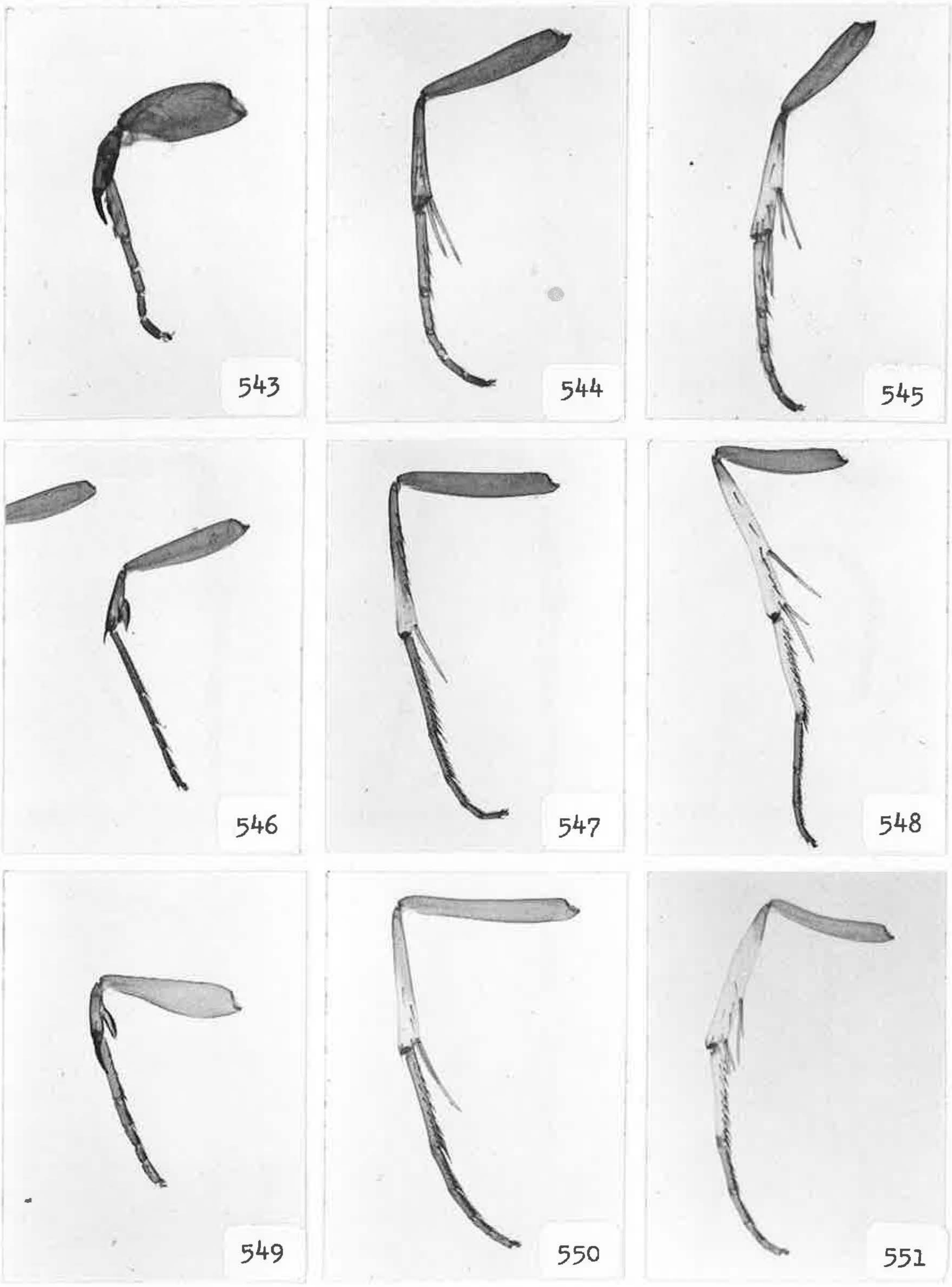
Figs. 516 - 524. Legs, Heliothinae. *Periphanes delphinii*, Fig. 516, fore-leg, Fig. 517, mid-leg, & Fig. 518, hind-leg (BM Noct 13572); *Pyrrhia exprimens*, Fig. 519, fore-leg, Fig. 520, mid-leg, & Fig. 521, hind-leg (BM Noct 13590); *Pyrrhia treitschkei*, Fig. 522, fore-leg, Fig. 523, mid-leg, & Fig. 524, hind-leg (BM Noct 13602).



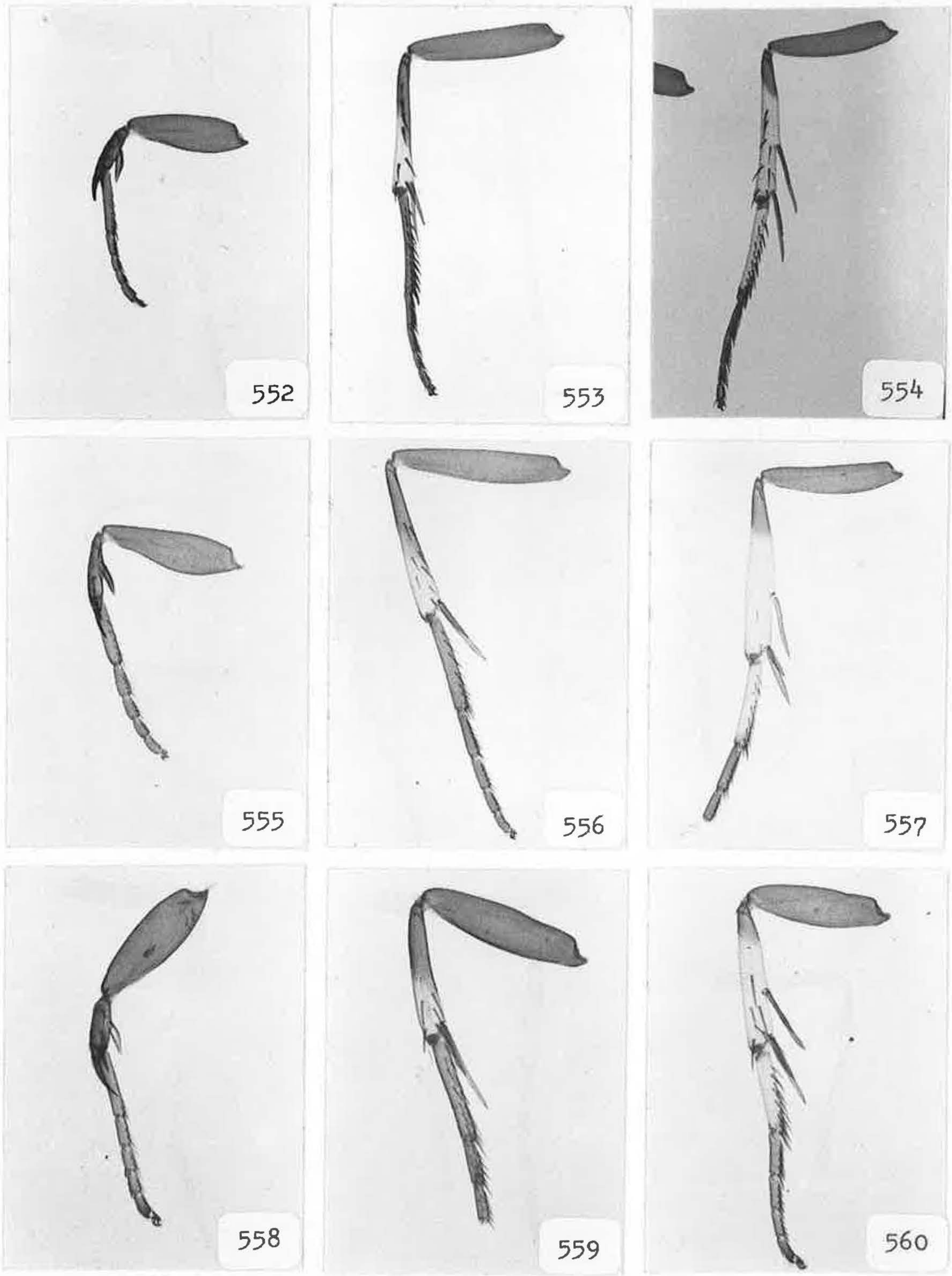
Figs. 525 - 533. Legs, Heliothinae. *Pyrrhia victorina,* Fig. 525, fore-leg, Fig. 526, mid-leg, & Fig. 527, hind-leg (BM Noct 13619); *Rhodoecia aurantiago,* Fig. 528, fore-leg, Fig. 529, mid-leg, & Fig. 530, hind-leg (BM Noct 13691); *Pyrocleptria cora,* Fig. 531, fore-leg, Fig. 532, mid-leg, & Fig. 533, hind-leg (BM Noct 13631).



Figs. 534 - 542. Legs, Heliothinae. *Adisura atkinsoni*, Fig. 534, fore-leg (BM Noct 13014), Fig. 535, mid-leg, & Fig. 536, hind-leg (BM Noct 13018); *Adisura cana*, Fig. 537, fore-leg, Fig. 538, mid-leg, & Fig. 539, hind-leg (BM Noct 13032); *Adisura parva*, Fig. 540, fore-leg, Fig. 541, mid-leg, & Fig. 542, hind-leg (BM Noct 13052).



Figs. 543 - 551. Legs, Heliothinae. *Heliolonche modicella*, Fig. 543, fore-leg, Fig. 544, mid-leg, & Fig. 545, hind-leg (BM Noct 13329); *Schinia scutosa*, Fig. 546, fore-leg, Fig. 547, mid-leg, & Fig. 548, hind-leg (BM Noct 13684); *Schinia chilensis*, Fig. 549, fore-leg, Fig. 550, mid-leg, & Fig. 551, hind-leg (AMNH).



Figs. 552 - 560. Legs, Heliothinae. *Schinia jaguarina*, Fig. 552, fore-leg, Fig. 553, mid-leg, & Fig. 554, hind-leg (BM Noct 13649); *Schinia pulchra*, Fig. 555, fore-leg, Fig. 556, mid-leg, & Fig. 557, hind-leg (AMNH); *Schinia purpurascens*, Fig. 558, fore-leg, Fig. 559, mid-leg, & Fig. 560, hind-leg (BM Noct 13667).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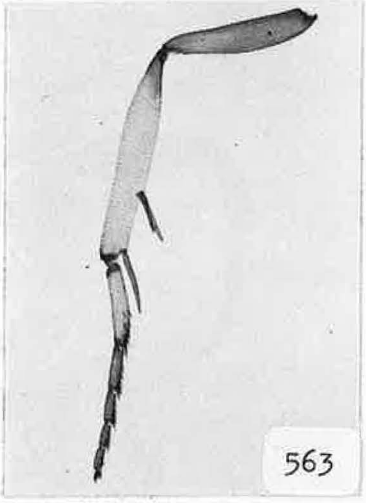
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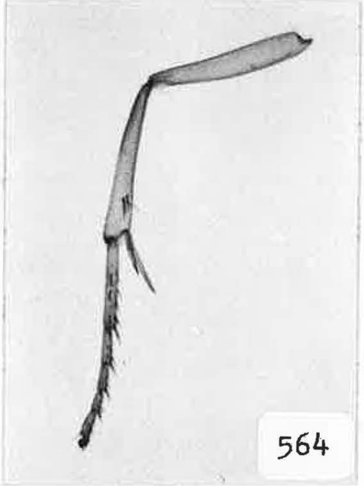
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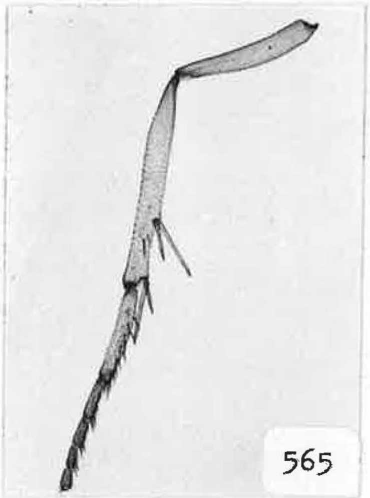
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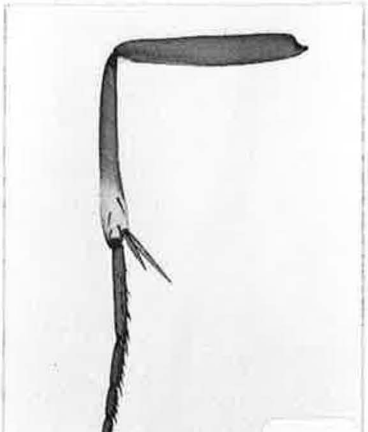
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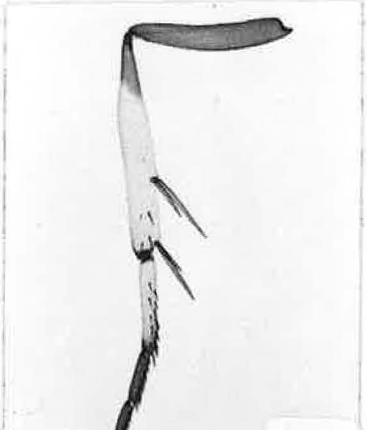
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Figs. 561 - 568. Legs, Heliothinae. *Schinia roseoflammata*, Fig. 561, fore-leg, Fig. 562, mid-leg, & Fig. 563, hind-leg (BM Noct 13679); *Schinia xanthiata*, Fig. 564, mid-leg, & Fig. 565, hind-leg (BM Noct 13676); *Heliothis flavirufa*, Fig. 566, fore-leg, Fig. 567, mid-leg, & Fig. 568, hind-leg (BM Noct 13352).


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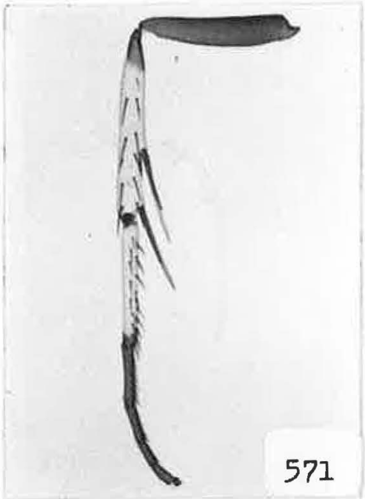
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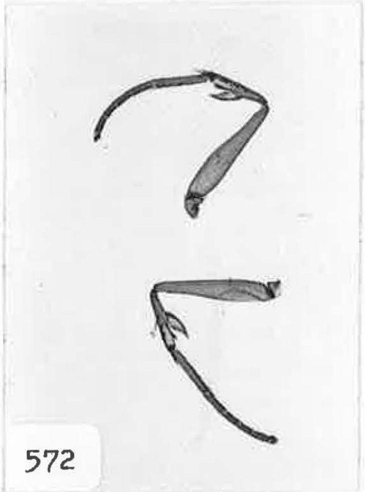
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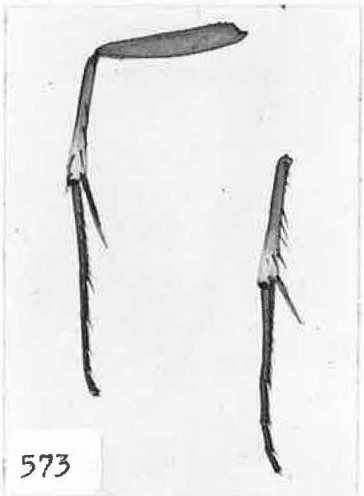
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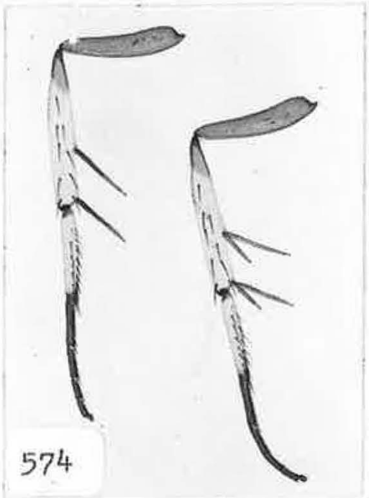
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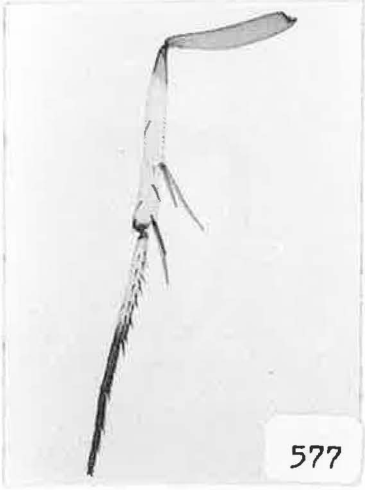
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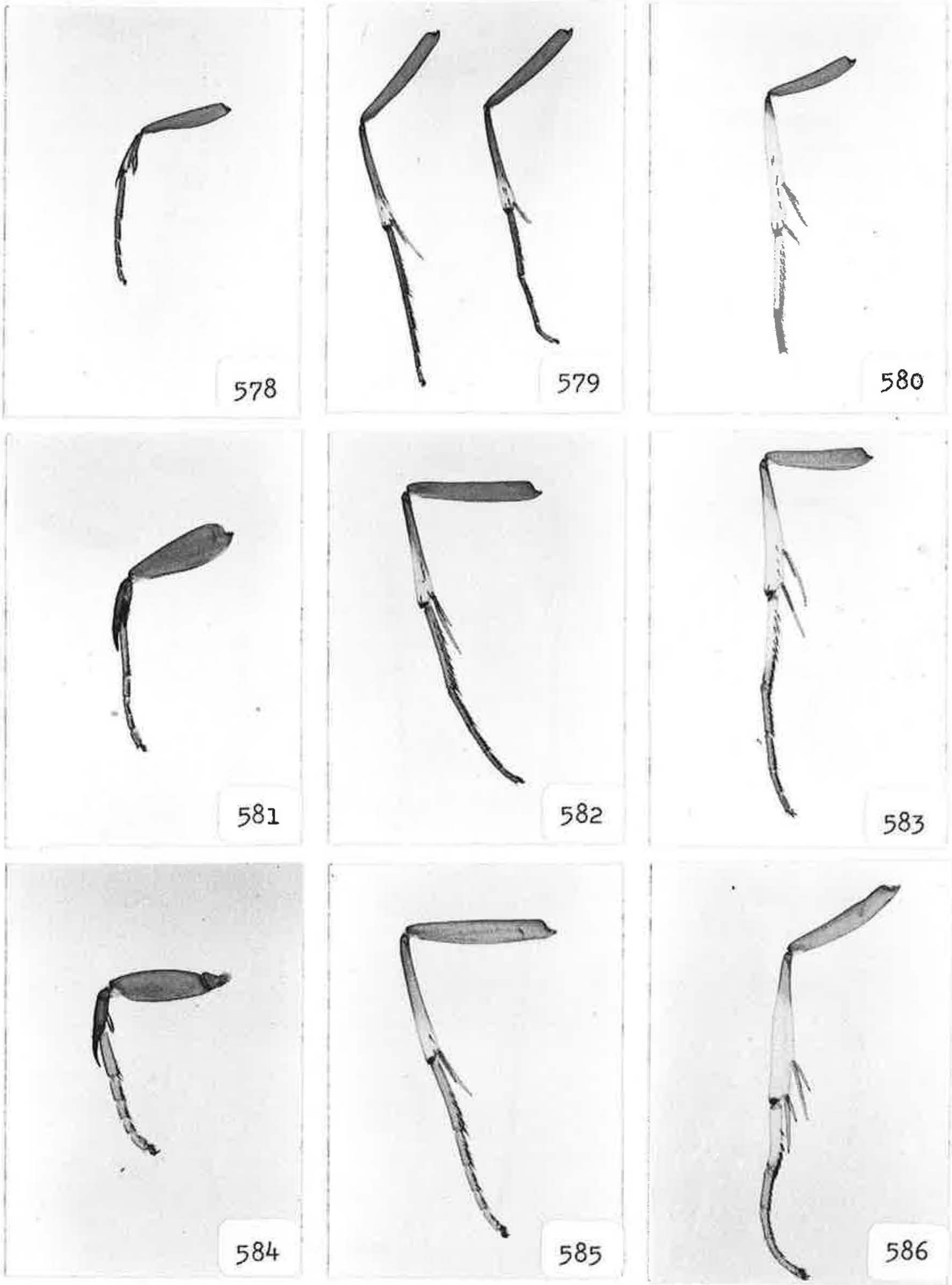
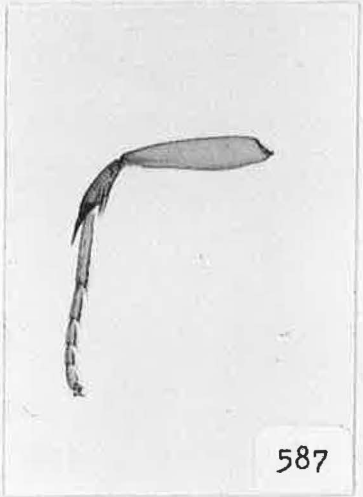
Figs. 569 - 577. Legs, Heliothinae. *Heliothis oregonica,* Fig. 569, fore-leg, Fig. 570, mid-leg, & Fig. 571, hind-leg (BM Noct 13381); *Heliothis viriplaca,* Fig. 572, fore-leg, Fig. 573, mid-leg, & Fig. 574, hind-leg (BM Noct 13446); *Heliothis virescens,* Fig. 575, fore-leg, Fig. 576, mid-leg, & Fig. 577, hind-leg (BM Noct 13438).



Figs. 578 - 586. Legs, Heliothinae. *Heliothis punctifera*, Fig. 578, fore-leg, Fig. 579, mid-leg, & Fig. 580, hind-leg (BM Noct 13541); *Heliothis incarnata*, Fig. 581, fore-leg, Fig. 582, mid-leg, & Fig. 583, hind-leg (BM Noct 13553); *Heliothis radiata*, Fig. 584, fore-leg, Fig. 585, mid-leg, & Fig. 586, hind-leg (BM Noct 13488).



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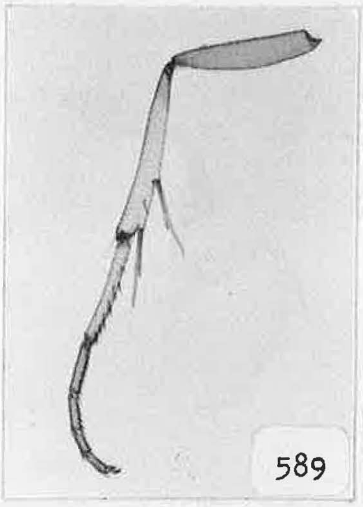

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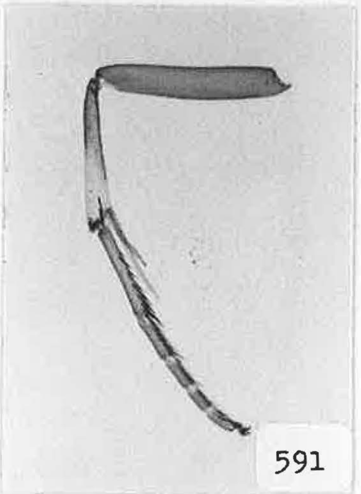

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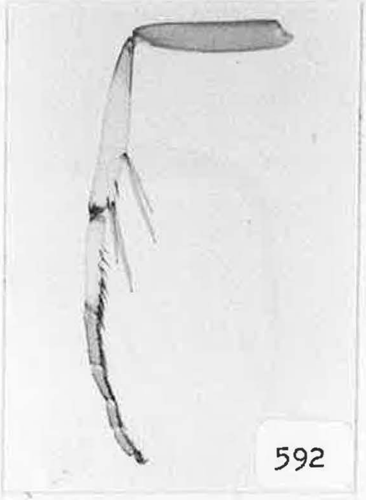

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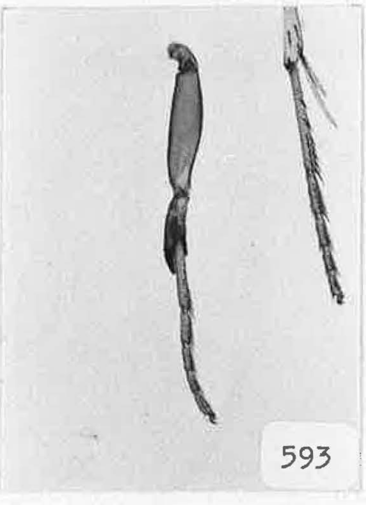

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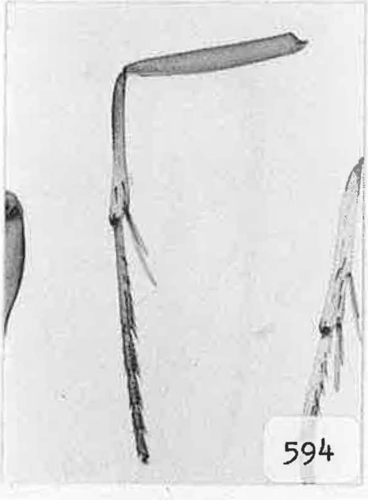

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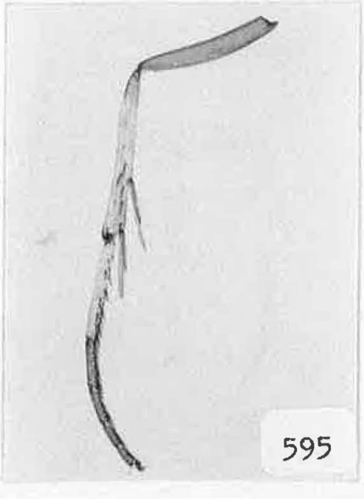

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Figs. 587 - 595. Legs, Heliothinae. *Heliothis syrticola*, Fig. 587, fore-leg, Fig. 588, mid-leg, & Fig. 589, hind-leg (BM Noct 13501); *Heliothis sanguinolenta*, Fig. 590, fore-leg, Fig. 591, mid-leg, & Fig. 592, hind-leg (BM Noct 13522); *Heliocheilus confertissima*, Fig. 593, fore-leg, Fig. 594, mid-leg, & Fig. 595, hind-leg (BM Noct 13191).


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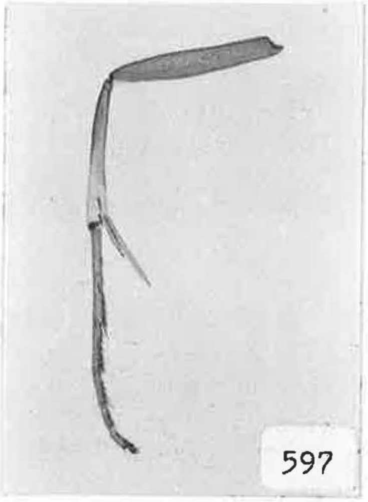
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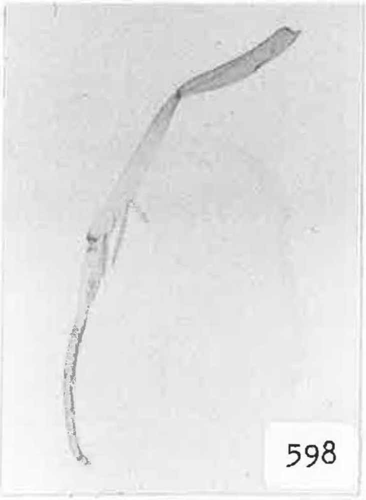
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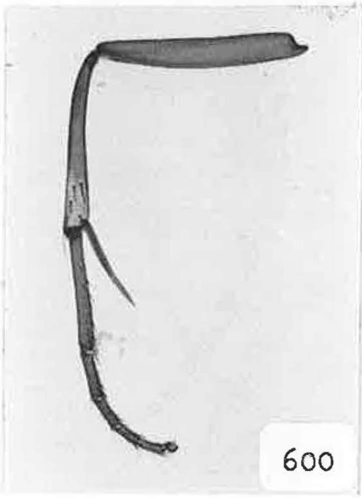
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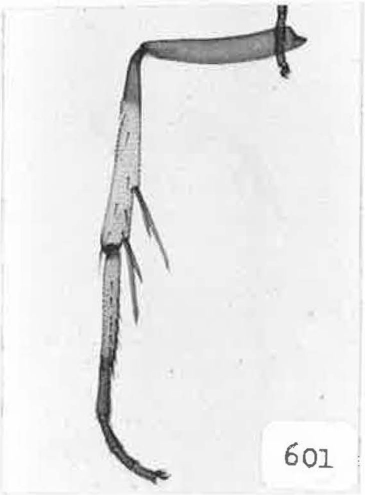
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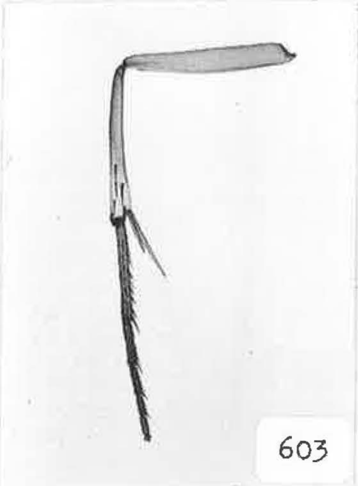
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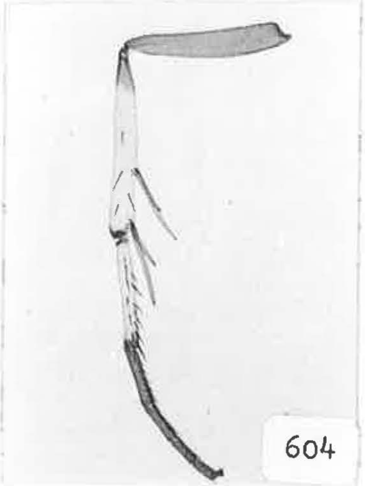
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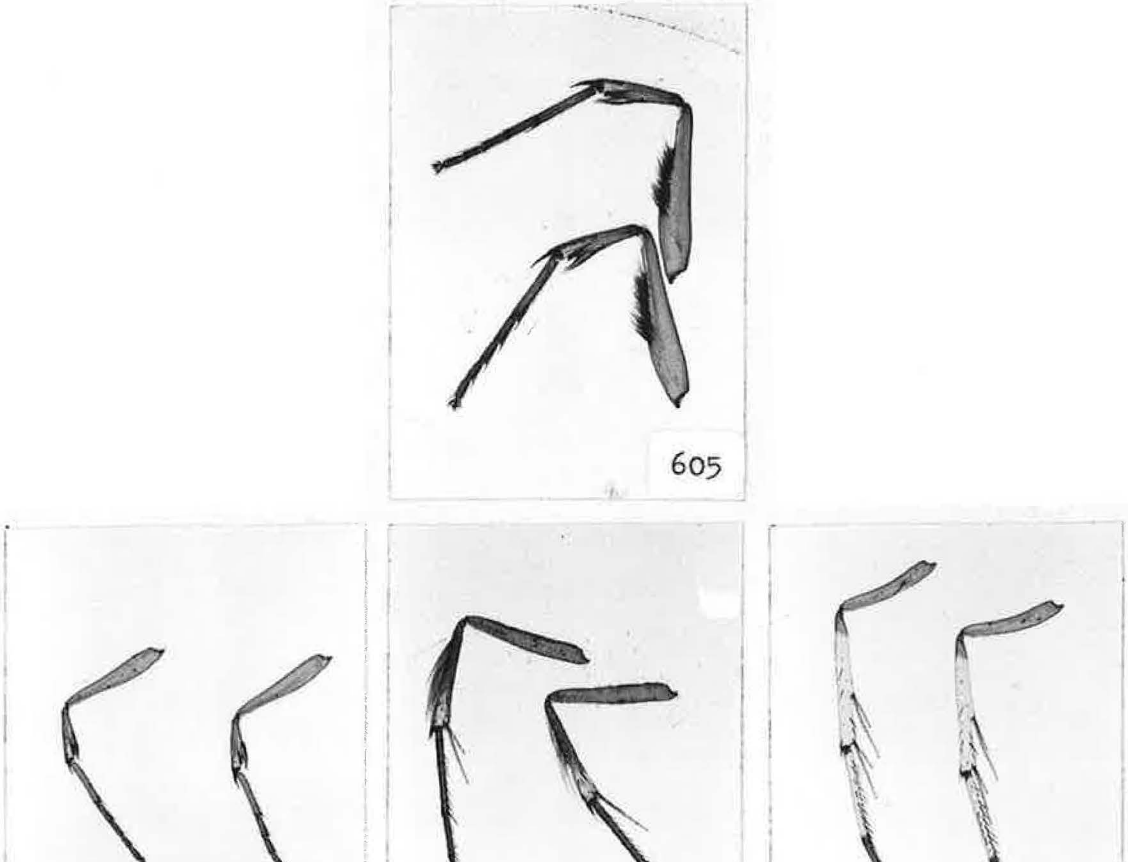
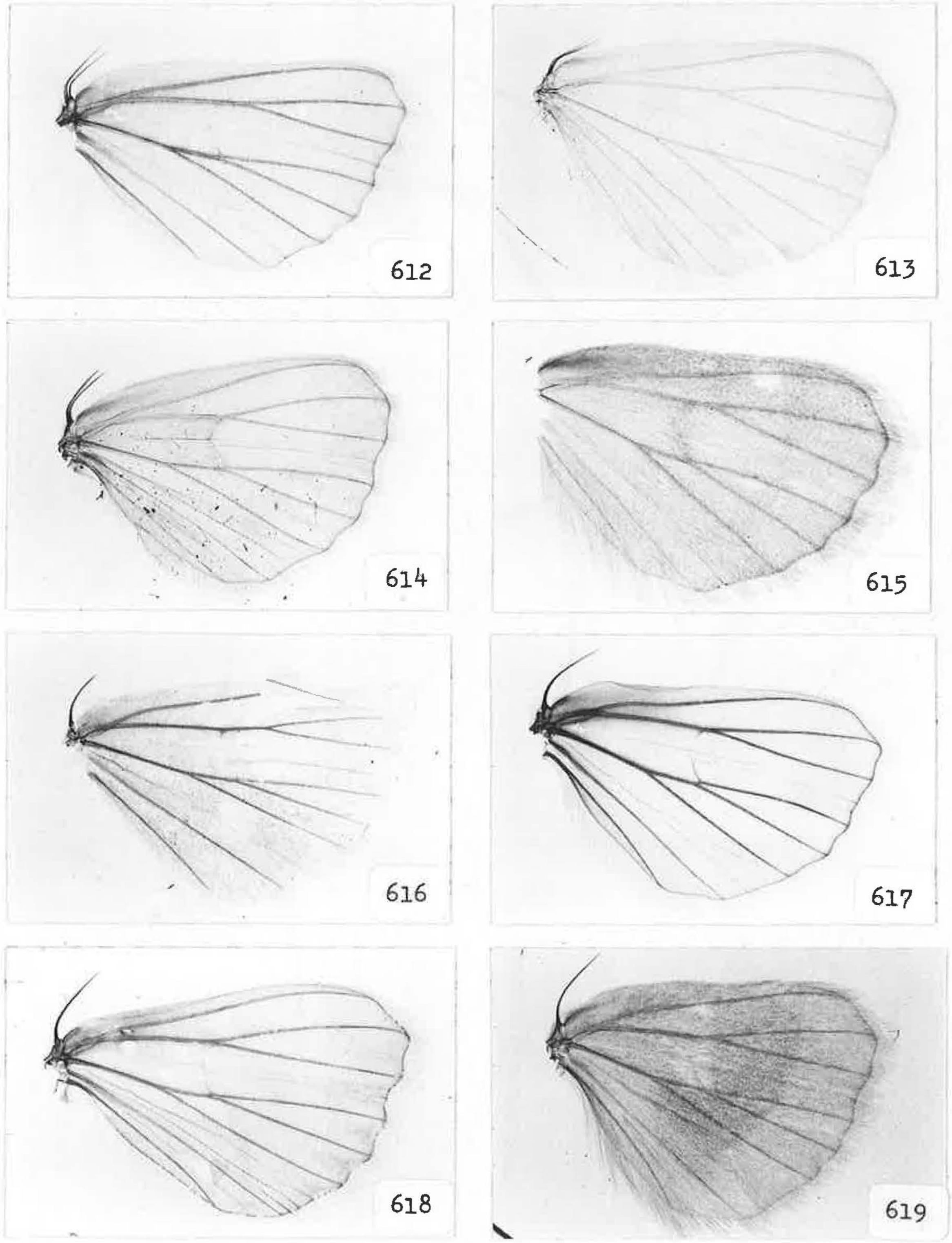
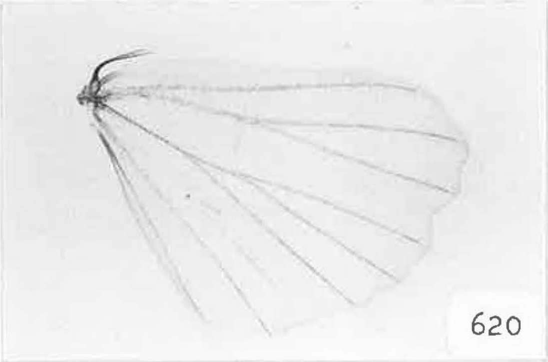
Figs. 596 - 604. Legs, Heliothinae. *Heliocheilus moribunda*, Fig. 596, fore-leg, Fig. 597, mid-leg, & Fig. 598, hind-leg (BM Noct 13253); *Heliocheilus roseus*, Fig. 599, fore-leg, Fig. 600, mid-leg, & Fig. 601, hind-leg (BM Noct 13295); *Australothis tertia*, Fig. 602, fore-leg, Fig. 603, mid-leg, & Fig. 604, hind-leg (BM Noct 13425).



Figs. 605 - 611. Legs, Heliothinae. *Helicoverpa armigera*, Fig. 605, male fore-leg showing patch of specialized scales on femur (BM Noct 13138), Fig. 606, female fore-leg, Fig. 607, female mid-leg, & Fig. 608, female hind-leg (BM Noct 13133); *Engusanacantha bilineata*, Fig. 609, fore-leg, Fig. 610, mid-leg, & Fig. 611, hind-leg (BM Noct 13088).



Figs. 612 - 619. Hind-wings, Heliothinae. Fig. 612, *Aedophron rhodites* (BM Noct 13060); Fig. 613, *Derrima stellata* (BM Noct 13075); Fig. 614, *Erythroecia suavis* (BM Noct 13091); Fig. 615, *Erythrophaia eudoxia* (BM Noct 13103); Fig. 616, *Eutricopis nexilis* (BM Noct 13125); Fig. 617, *Periphanes delphinii* (BM Noct 13577); Fig. 618, *Pyrrhia umbra* (BM Noct 13611); Fig. 619, *Pyrocleptria cora* (BM Noct 13637).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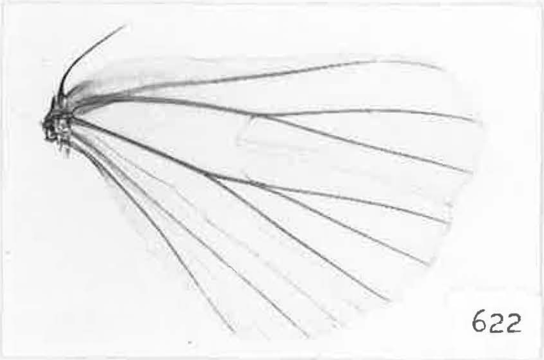
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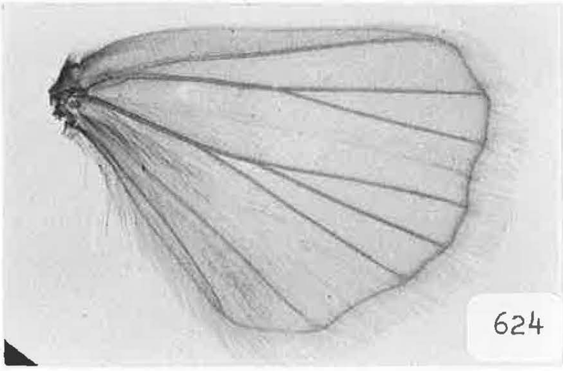
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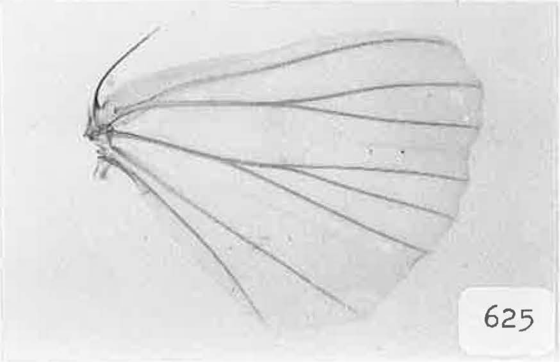
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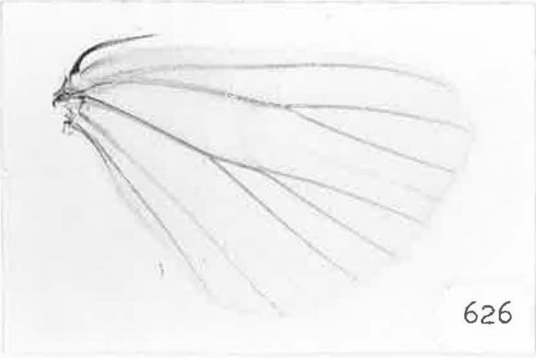
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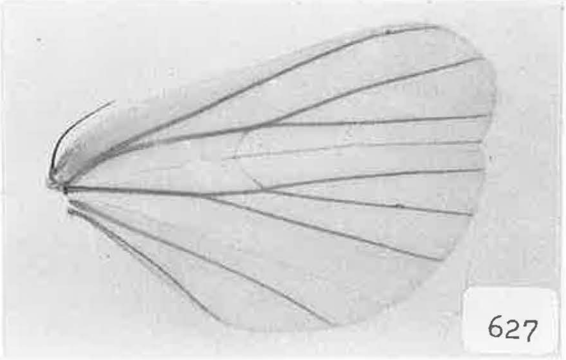
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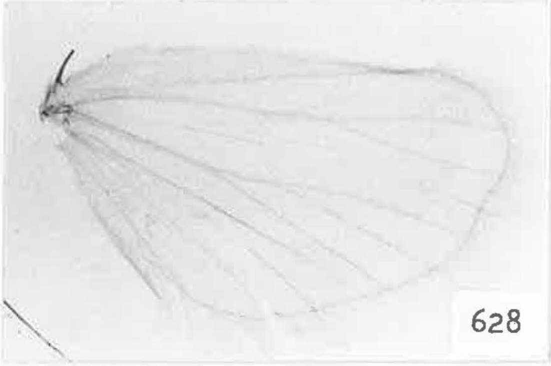
Figs. 620 - 627. Hind-wings, Heliothinae. Fig. 620, *Adisura atkinsoni* (BM Noct 13013); Fig. 621, *Heliolonche modicella* (BM Noct 13332); Fig. 622, *Schinia scutosa* (BM Noct 13688); Fig. 623, *Schinia jaguarina* (BM Noct 13644); Fig. 624, *Schinia purpurascens* (BM Noct 13660); Fig. 625, *Heliothis viriplaca* (BM Noct 13449); Fig. 626, *Heliothis incarnata* (BM Noct 13547); Fig. 627, *Heliothis radiata* (BM Noct 13491).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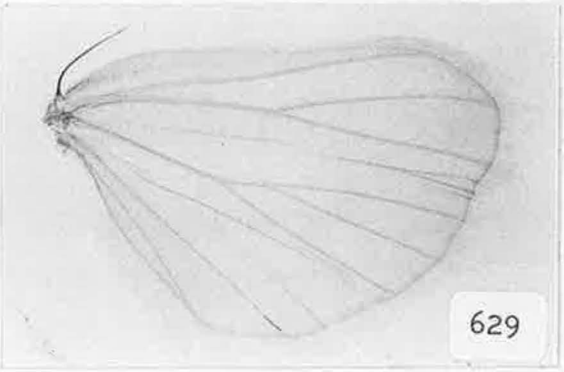
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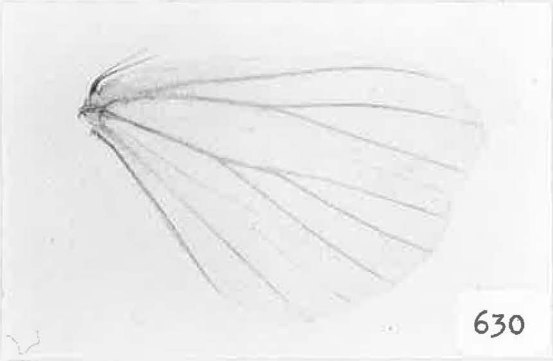
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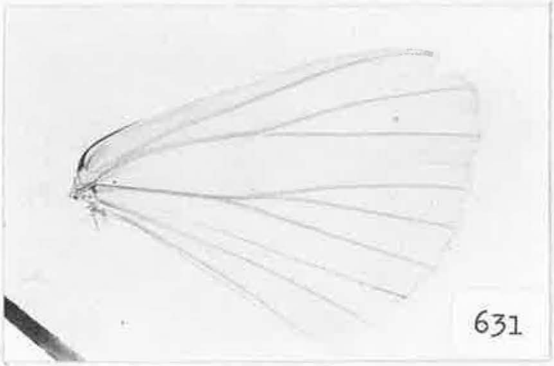
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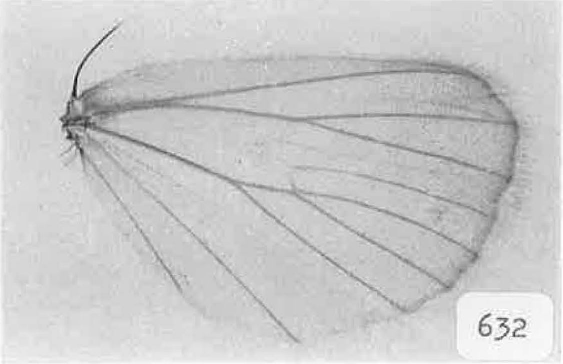
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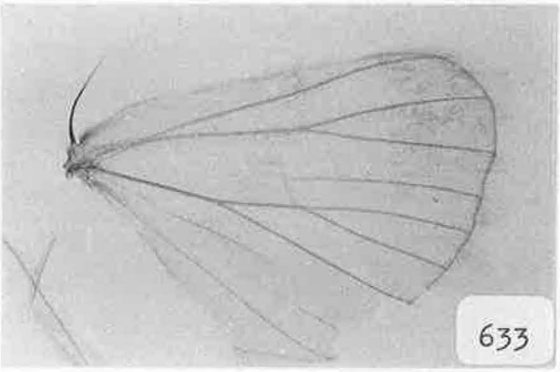
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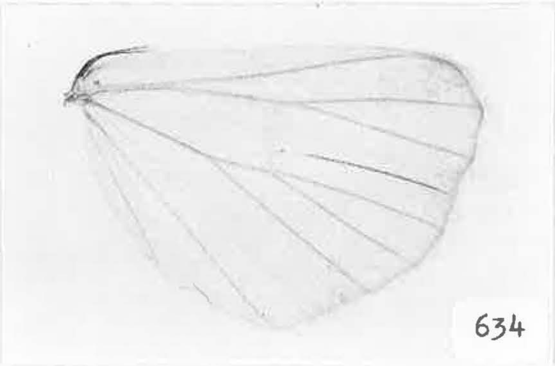
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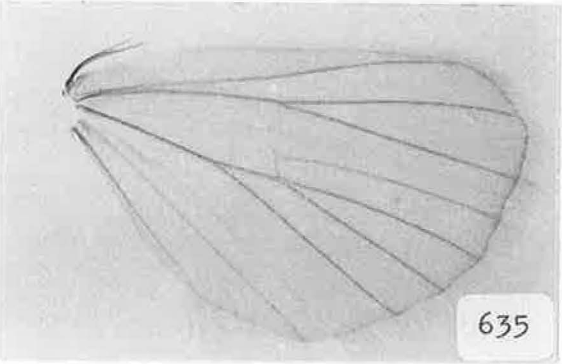
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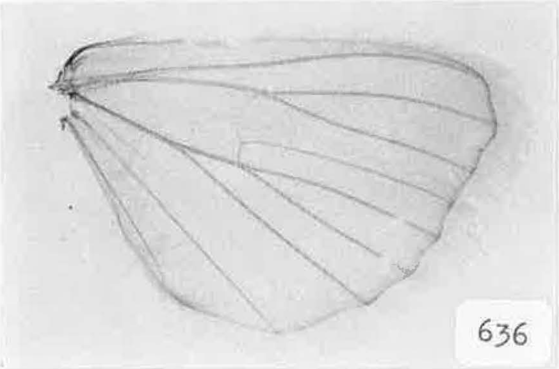
Figs. 628 - 635. Hind-wings, Heliothinae & Stiriinae. Heliothinae. Fig. 628, *Heliothis syrticola* (BM Noct 13504); Fig. 629, *Heliocheilus confertissima* (BM Noct 13193); Fig. 630, *Heliocheilus moribunda* (BM Noct 13256); Fig. 631, *Helicoverpa armigera* (BM Noct 13136). Stiriinae. Fig. 632, *Aegle koekeritziana* (BM Noct 13833); Fig. 633, *Aegle vespertalis* (BM Noct 13838); Fig. 634, *Metaegle pallida* (BM Noct 13868); Fig. 635, *Dipinacea schiniodes* (BM Noct 13855).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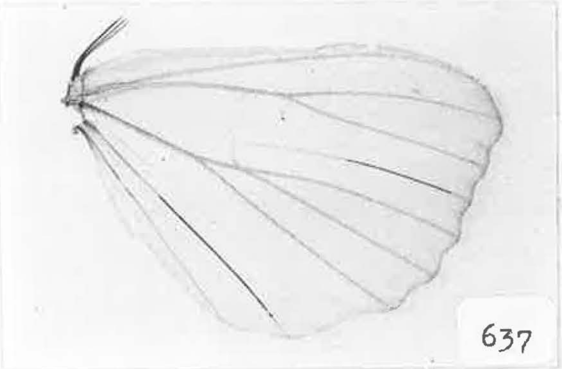
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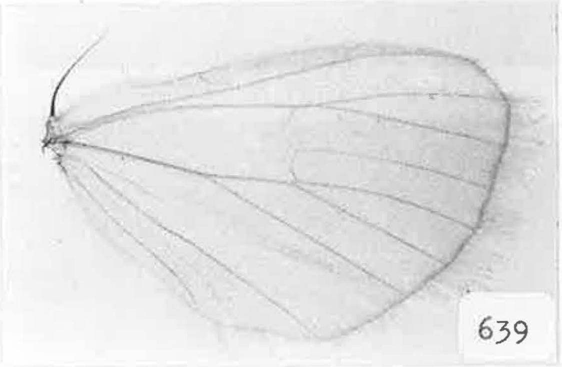
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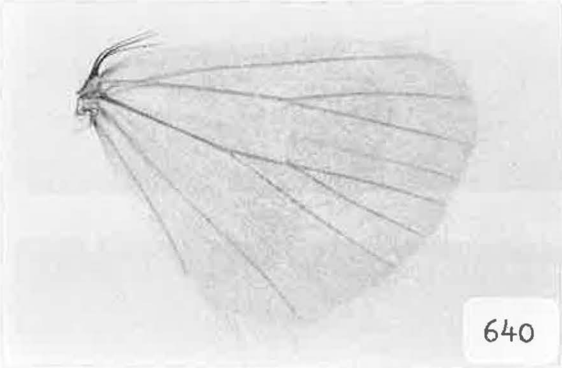
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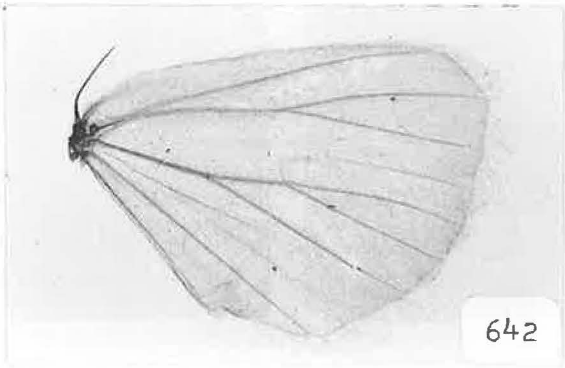
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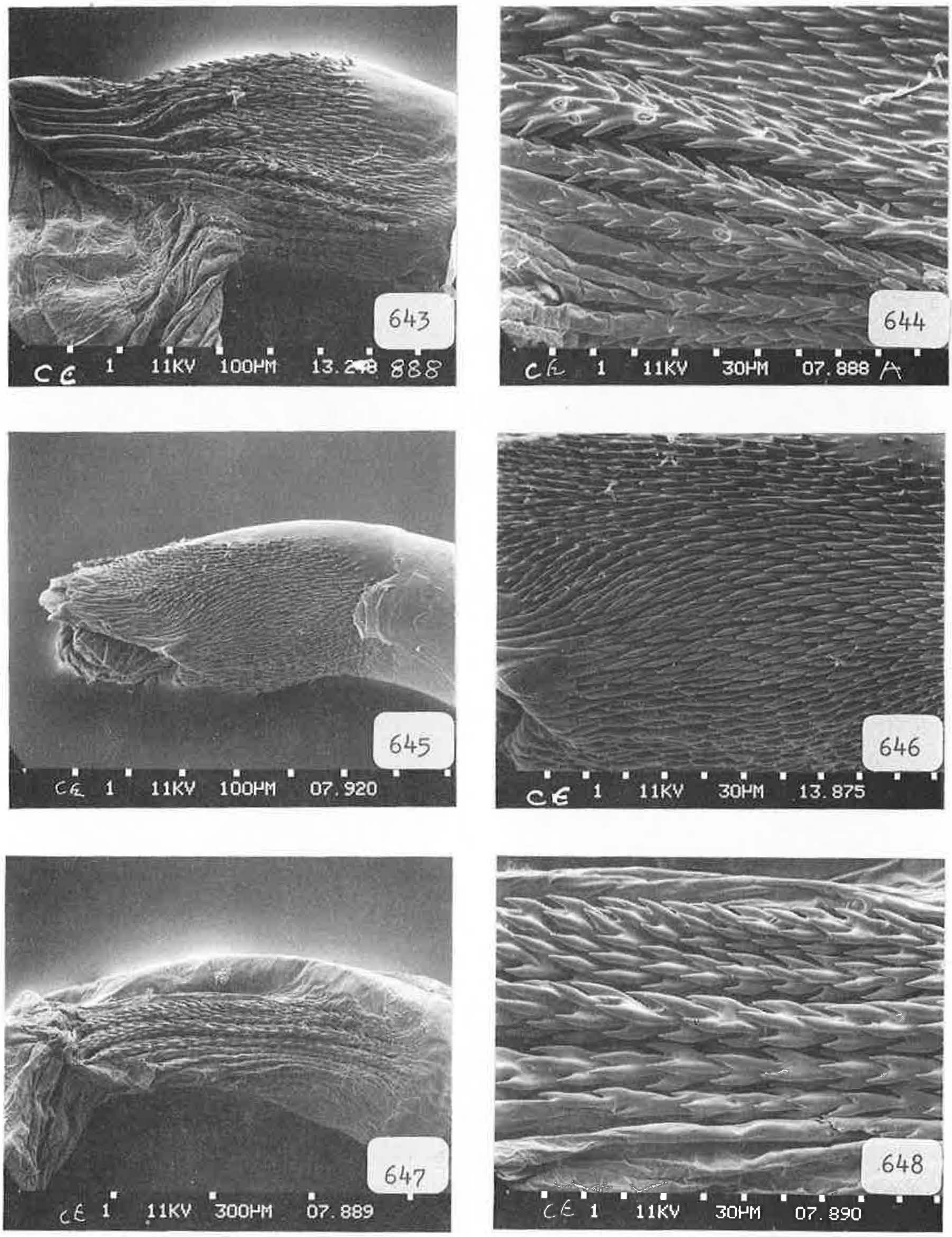
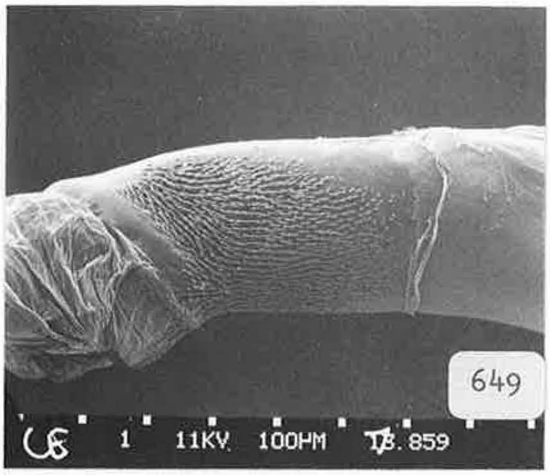
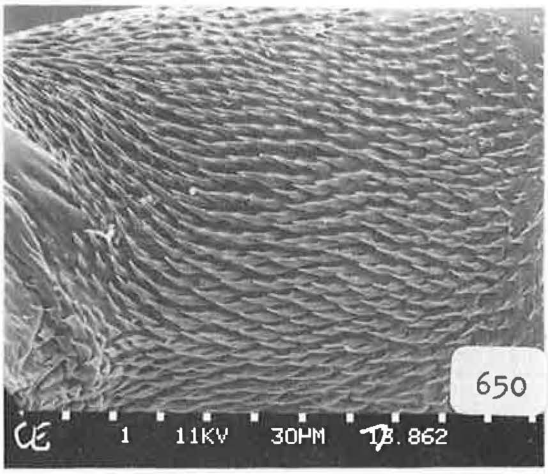
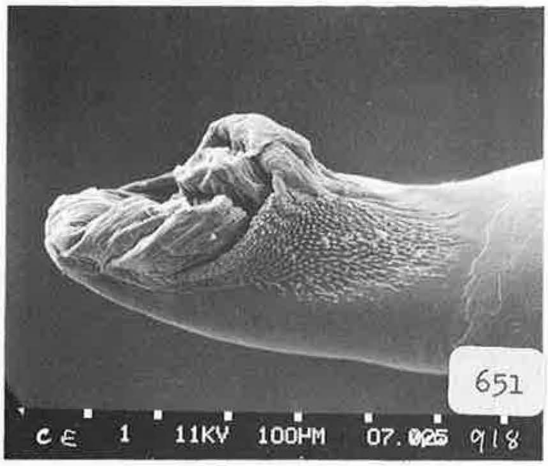
Figs. 636 - 642. Hind-wings, Stiriinae. Fig. 636, *Ectolopha marginata* (BM Noct 13859); Fig. 637, *Ectolopha viridescens* (BM Noct 13861); Fig. 638, *Megalodes eximia* (BM Noct 13864); Fig. 639, *Ochrocalama xanthiata* (BM Noct 13880); Fig. 640, *Panemeria tenebrata* (BM Noct 13884); Fig. 641, *Paralophata ansorgei* (BM Noct 13889); Fig. 642, *Synthymia fixa* (BM Noct 13658).

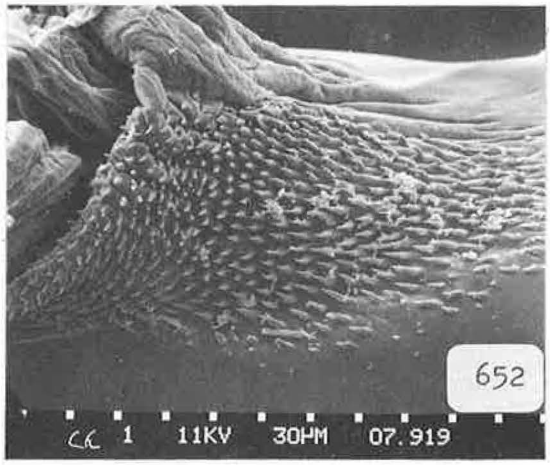


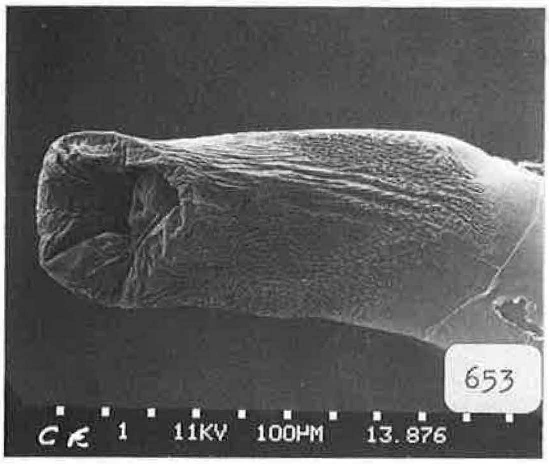
Figs. 643 - 648. Aedeagae, Heliothinae. Figs. 643 & 644, *Aedophron rhodites*; Figs. 645 & 646, *Derrima stellata*; Figs. 647 & 648, *Erythroecia suavis*.

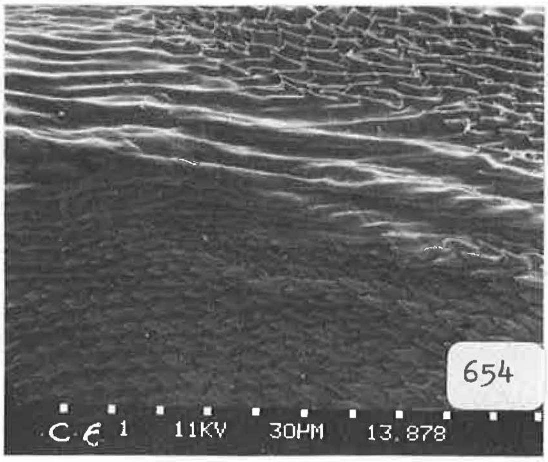




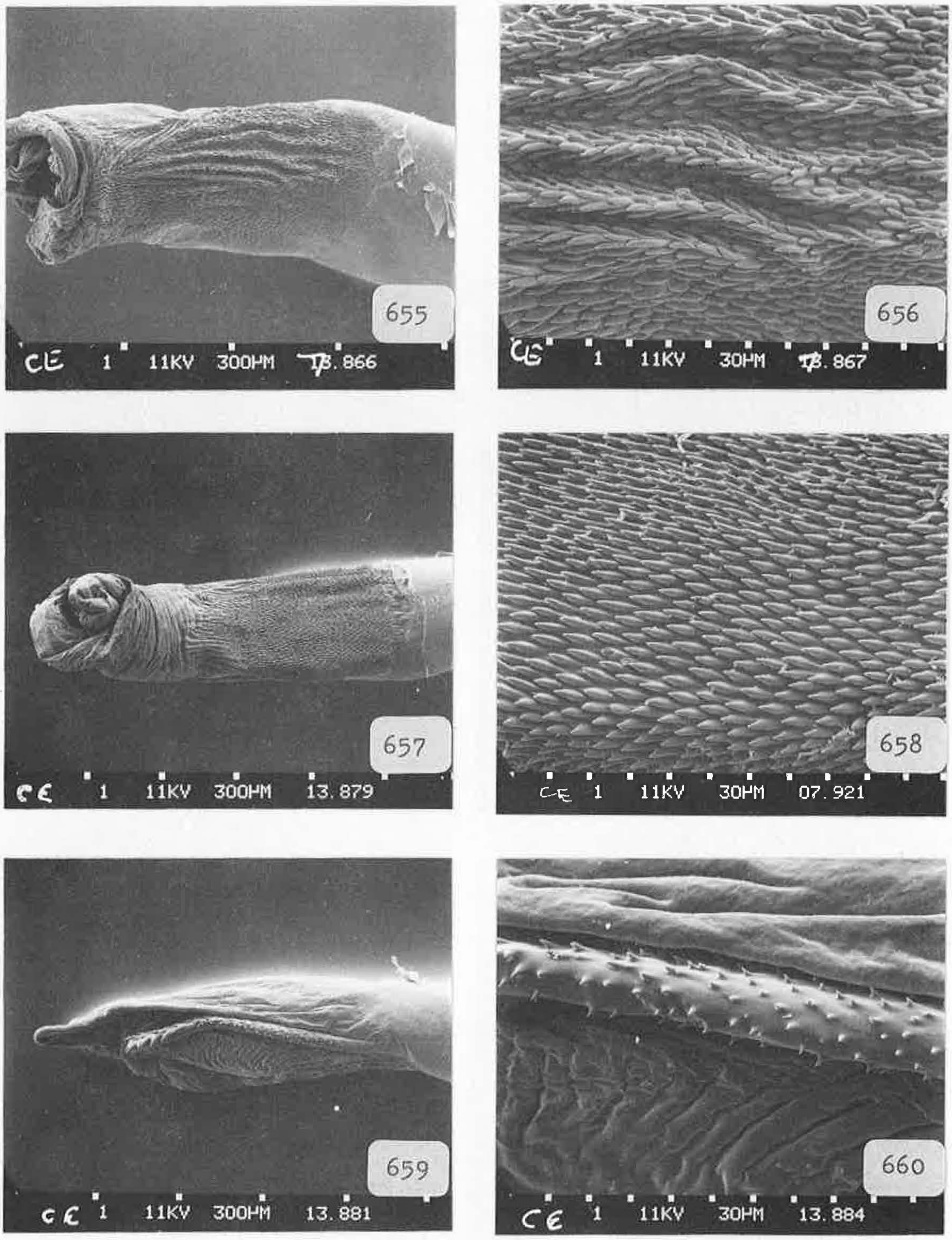




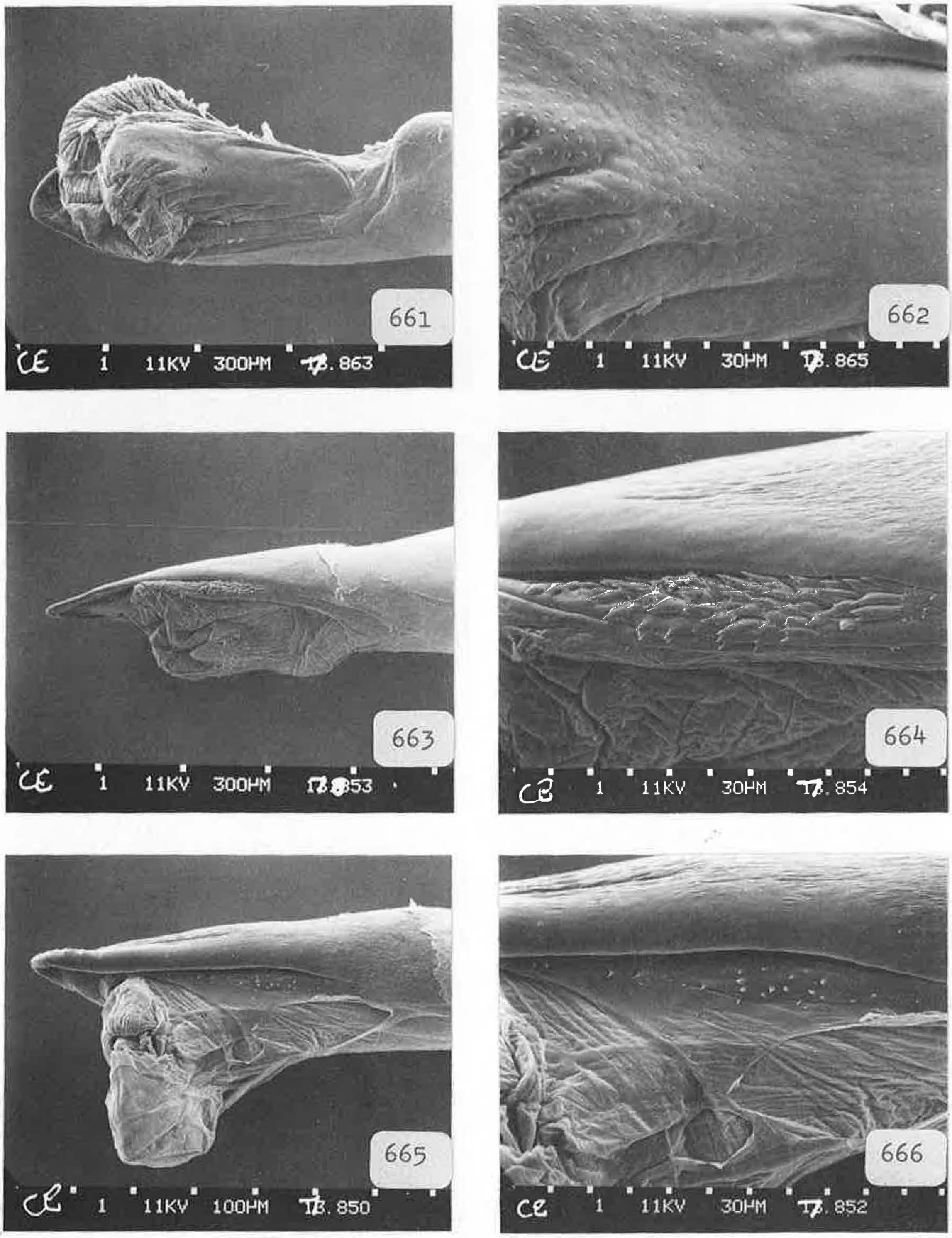




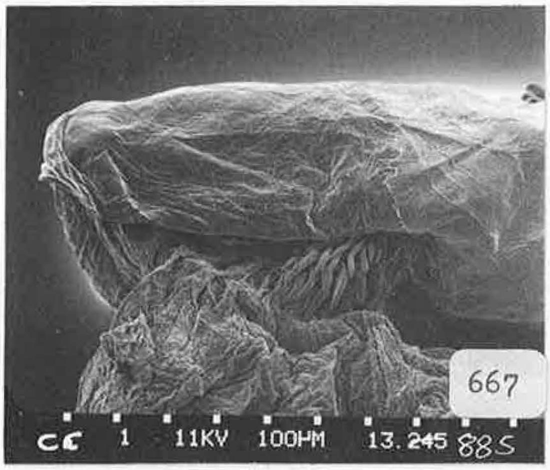
Figs. 649 - 654. Aedeagae, Heliothinae. Figs. 649 & 650, *Eutricopis nexilis*; Figs. 651 & 652, *Heliothodes diminutivus*; Figs. 653 & 654, *Pyrrhia treitschkei*.

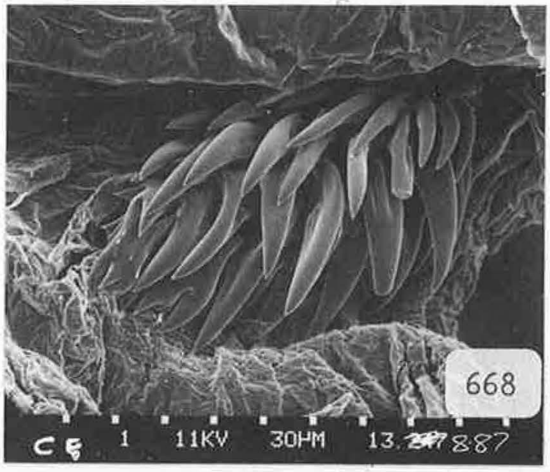


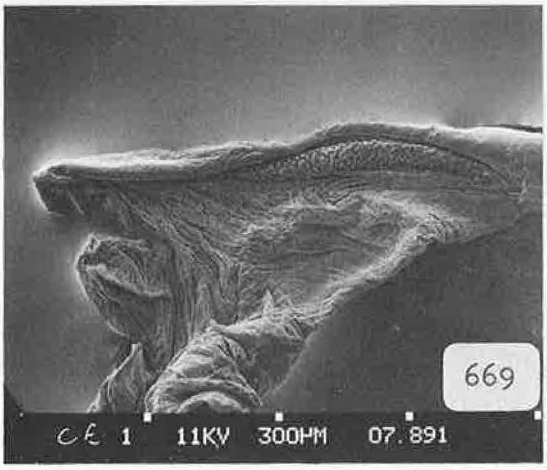
Figs. 655 - 660. Aedeagae, Heliothinae. Figs. 655 & 656, *Pyrrhia umbra*; Figs. 657 & 658, *Pyrrhia victorina*; Figs. 659 & 660, *Heliothis flavigera*.

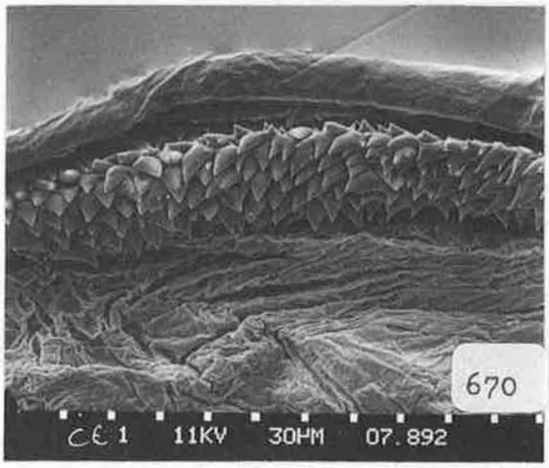


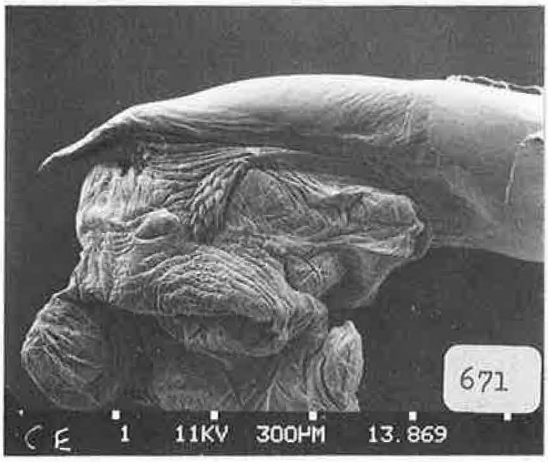
Figs. 661 - 666. Aedeagae, Heliothinae. Figs. 661 & 662, *Heliothis maritima*; Figs. 663 & 664, *Heliothis viriplaca*; Figs. 665 & 666, *Heliothis decorata*.

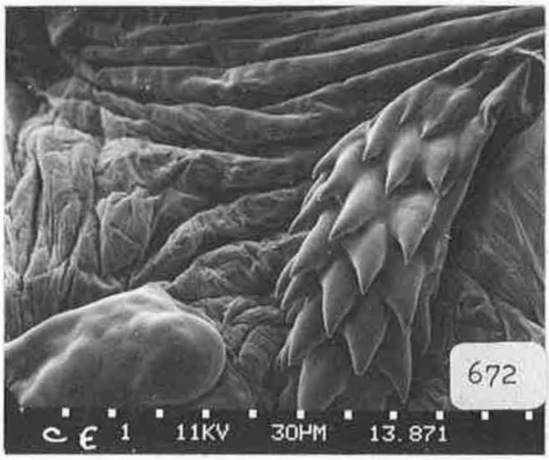




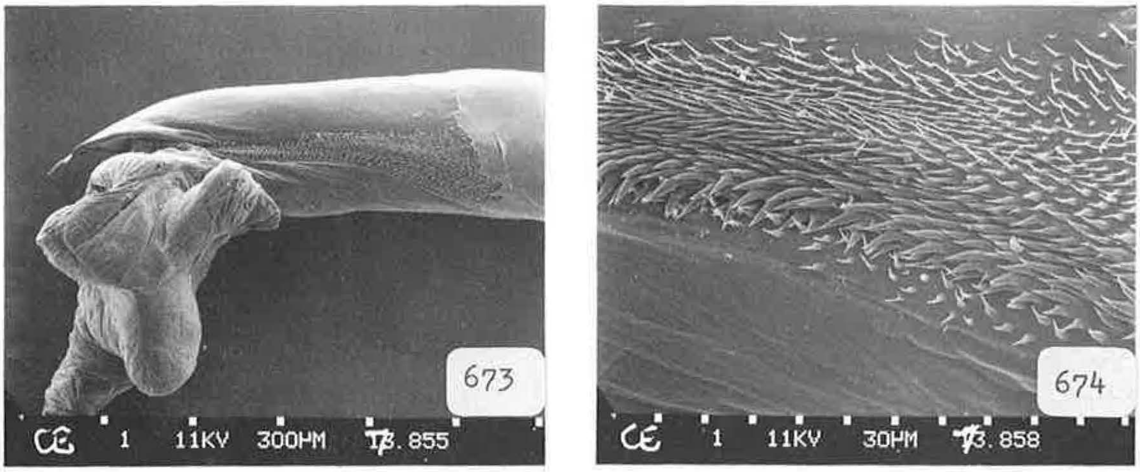








Figs. 667 - 672. Aedeagae, Heliothinae. Figs. 667 & 668, *Heliothis radiata*; Figs. 669 & 670, *Heliocheilus cystiphora*; Figs. 671 & 672, *Australothis rubrescens*.



Figs. 673 & 674, *Helicoverpa fletcheri*, aedeagus.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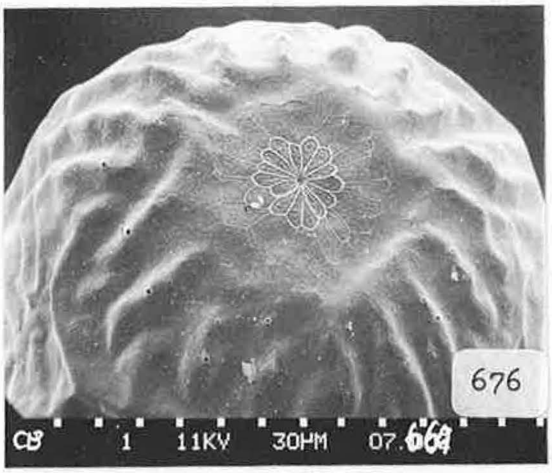
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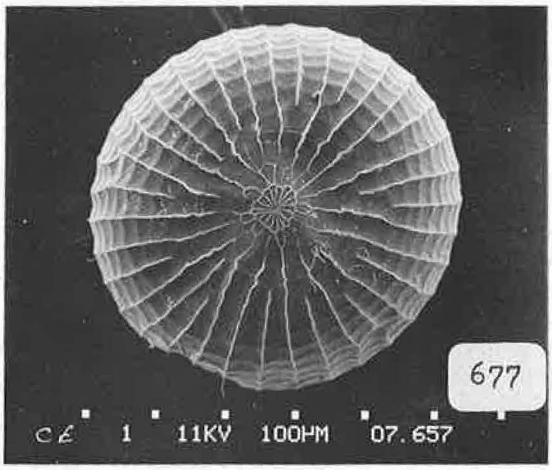
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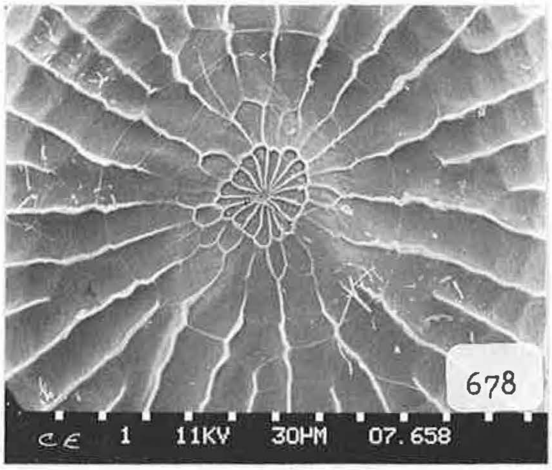
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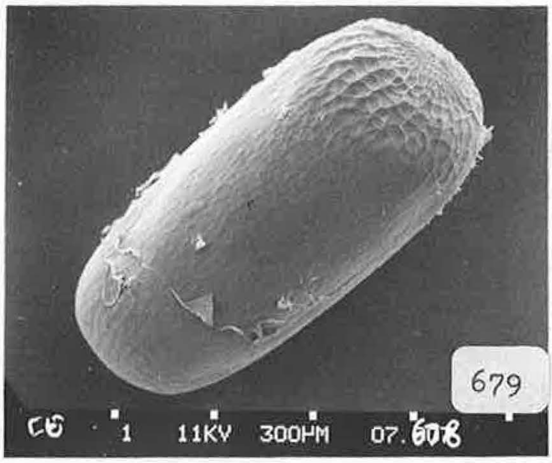
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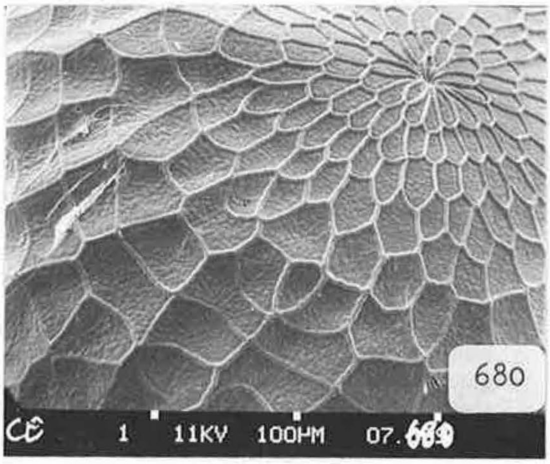
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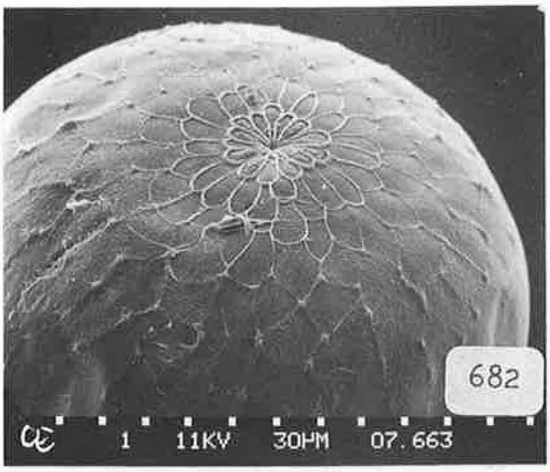
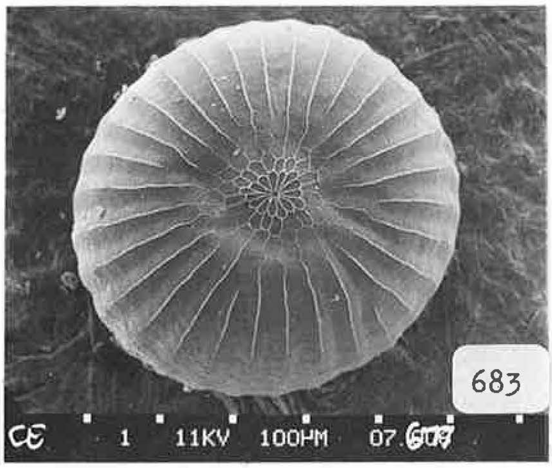
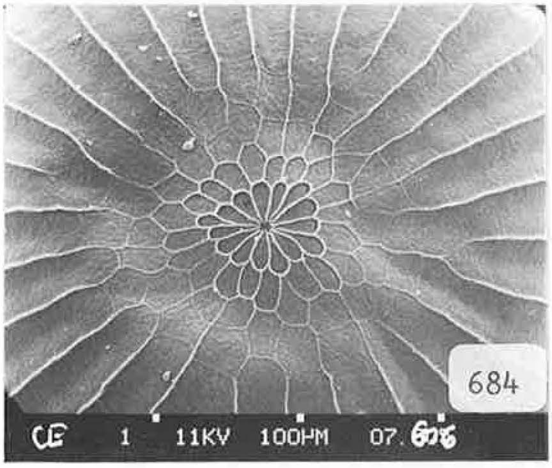
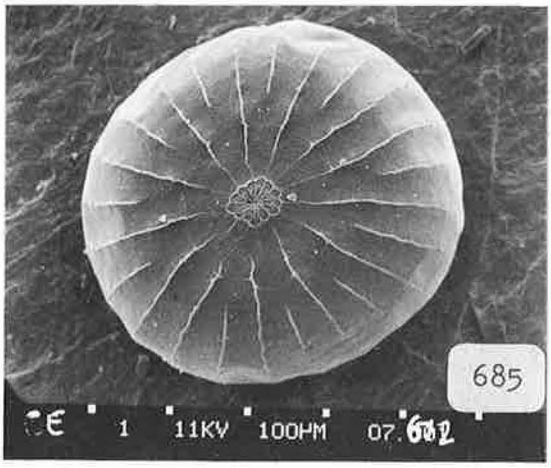
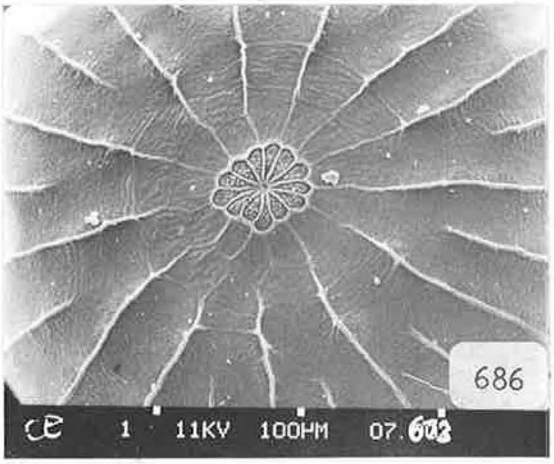
Figs. 675 - 680. Ova, Heliothinae. Figs. 675 & 676, *Eutricopis nexilis*; Figs. 677 & 678, *Adisura bella*; Figs. 679 & 680, *Schinia jaegeri*.



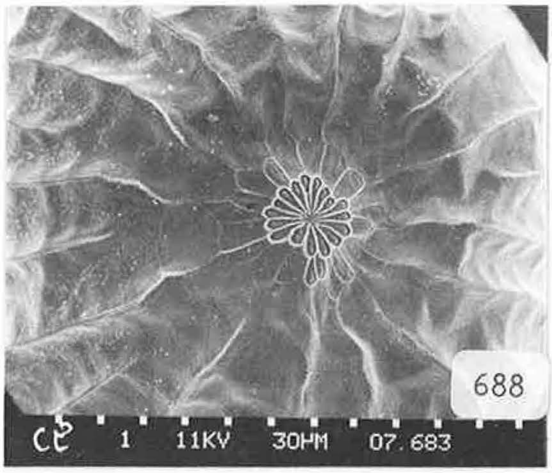


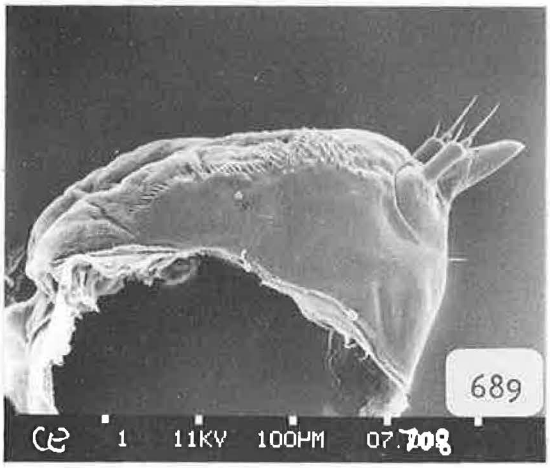


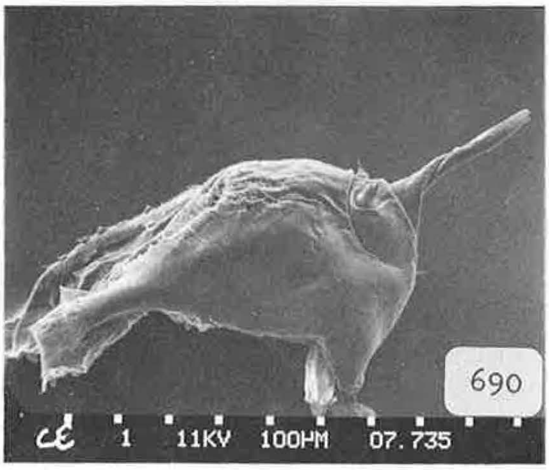


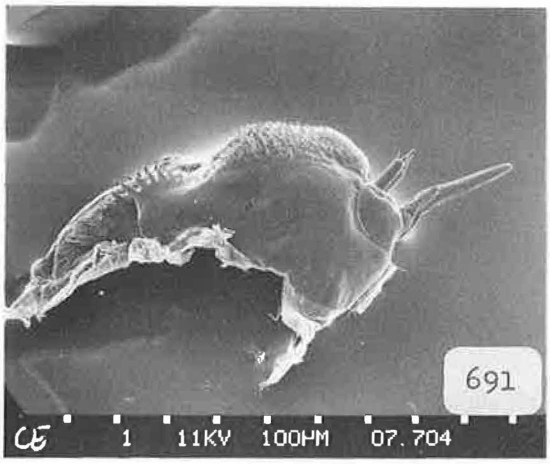


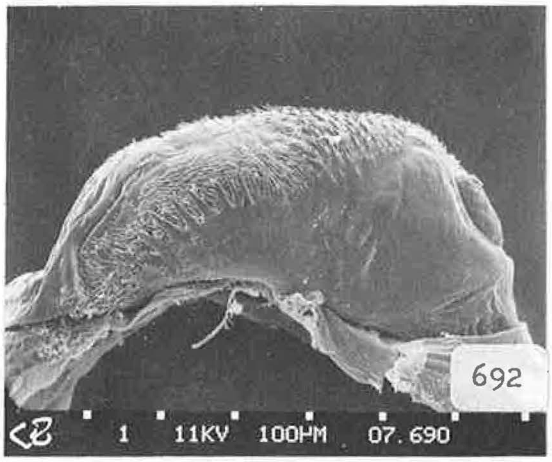
Figs. 681 - 686. Ova, Heliothinae. Figs. 681 & 682, *Schinia niveicosta*; Figs. 683 & 684, *Heliothis decorata*; Figs. 685 & 686, *Heliocheilus confertissima*.



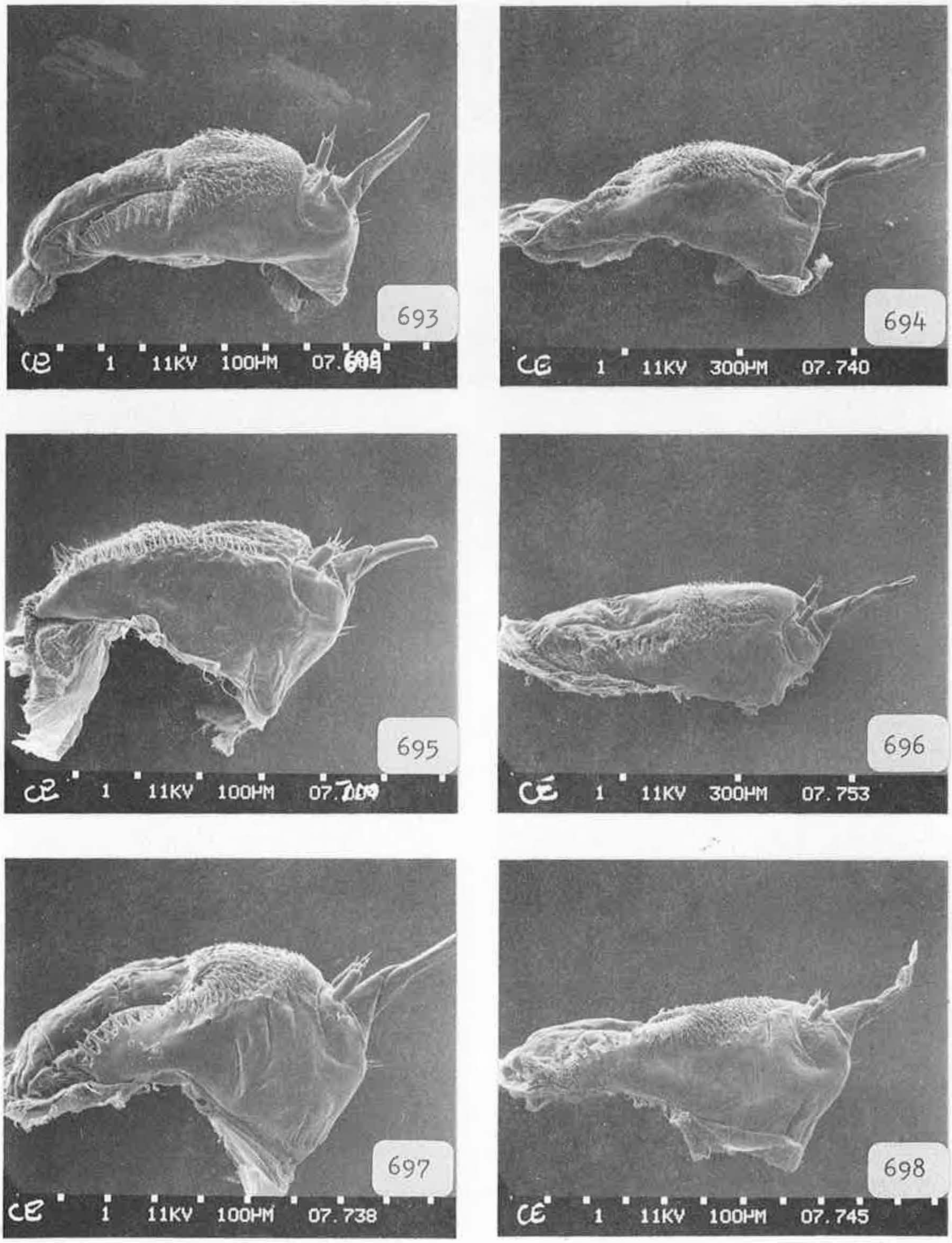




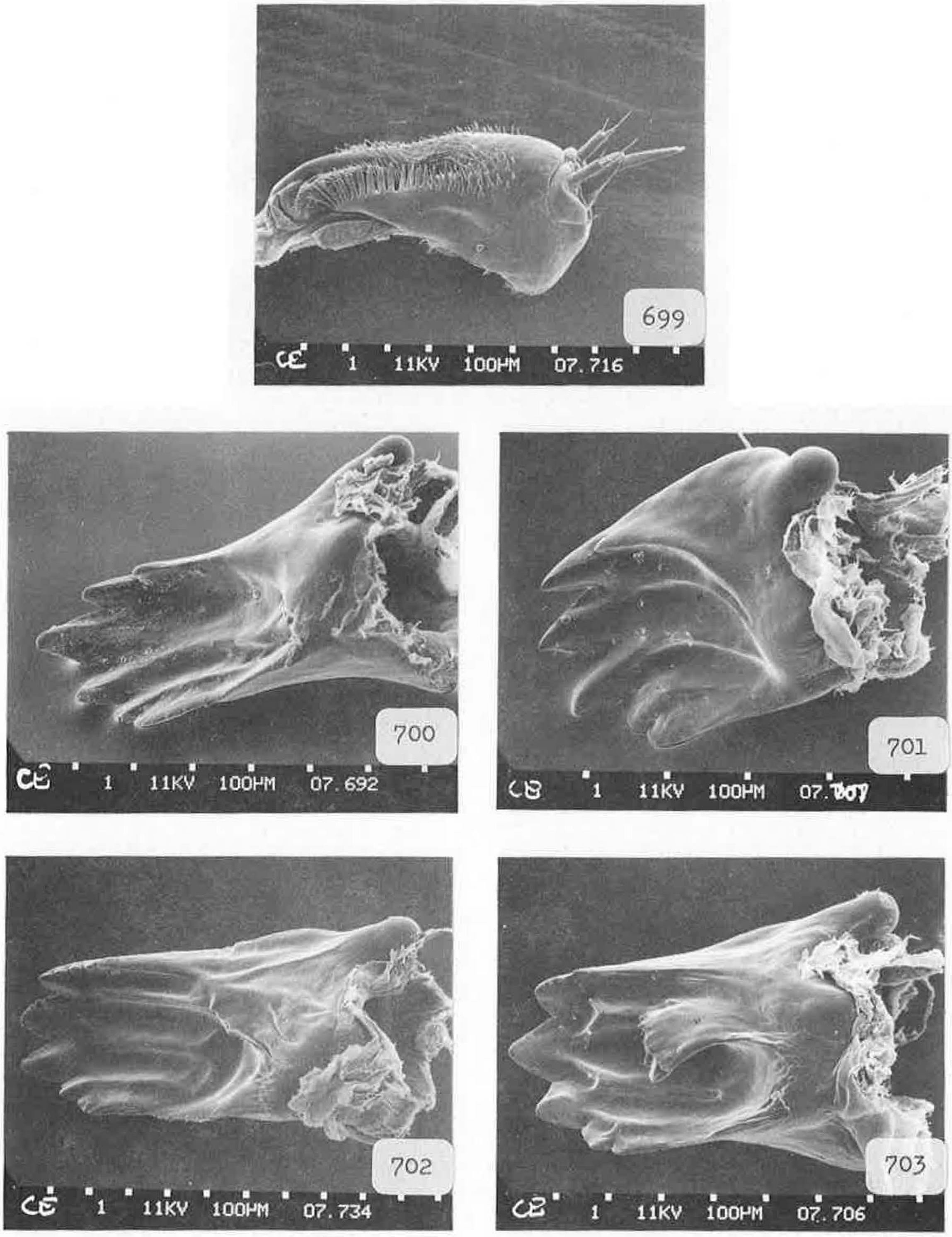




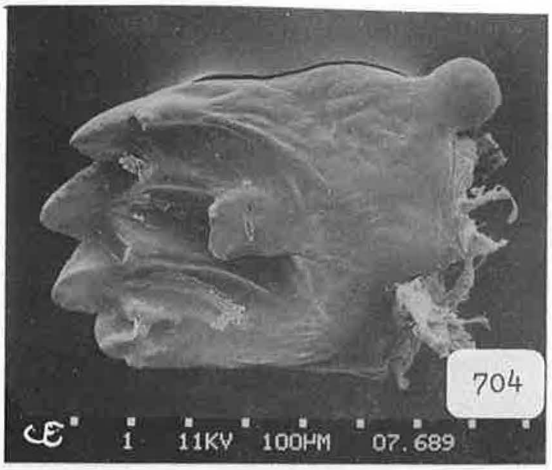
Figs. 687 - 692. Ova & hypopharynxes, Heliothinae. Figs. 687 & 688, *Helicoverpa armigera.* Hypopharynxes, Heliothinae. Fig. 689, *Eutricopis nexilis*; Fig. 690, *Periphanes delphinii*; Fig. 691, *Pyrrhia exprimens*; Fig. 692, *Pyrrhia purpurina.*

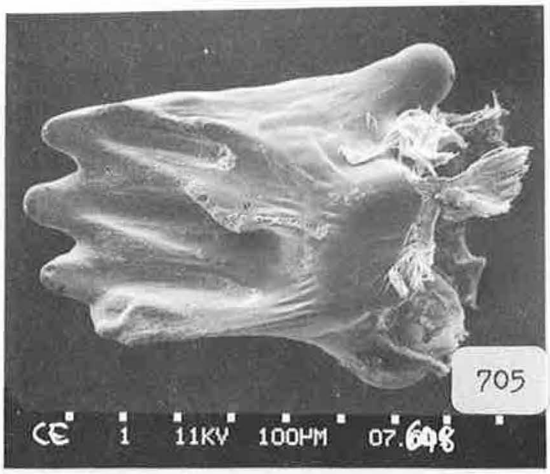


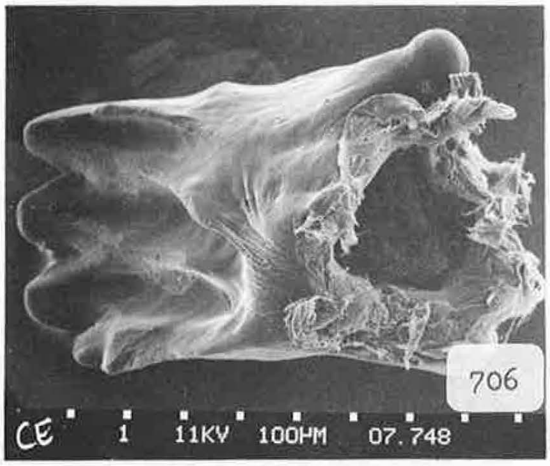
Figs. 693 - 698. Hypopharynxes, Heliothinae. Fig. 693, *Pyrrhia umbra*; Fig. 694, *Pyrrhia victorina*; Fig. 695, *Schinia florida*; Fig. 696, *Heliothis tergemina*; Fig. 697, *Heliothis virescens*; Fig. 698, *Heliothis incarnata*.

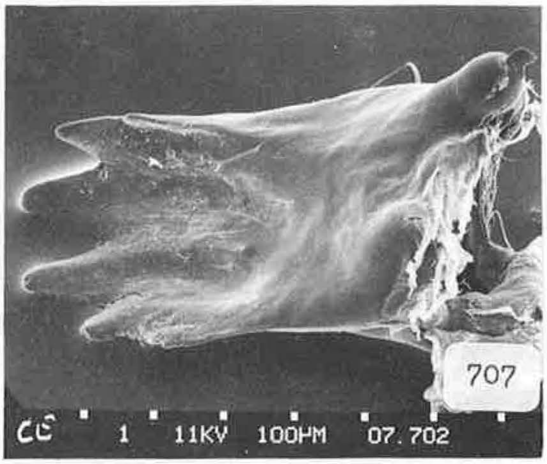


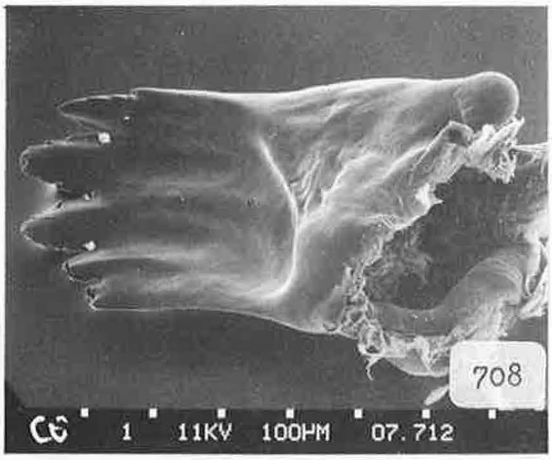
Figs. 699 - 703. Hypopharynx & mandibles, Heliothinae. Hypopharynx. Fig. 699, *Heliocheilus albipunctella.* Mandibles. Fig. 700, *Baptarma felicita*; Fig. 701, *Eutricopis nexilis*; Fig. 702, *Periphanes delphinii*; Fig. 703, *Pyrrhia exprimens.*

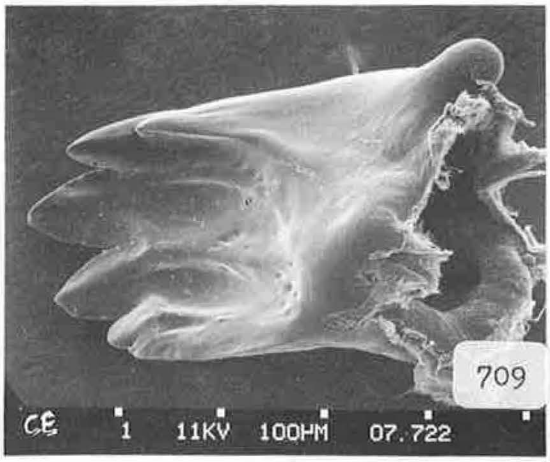




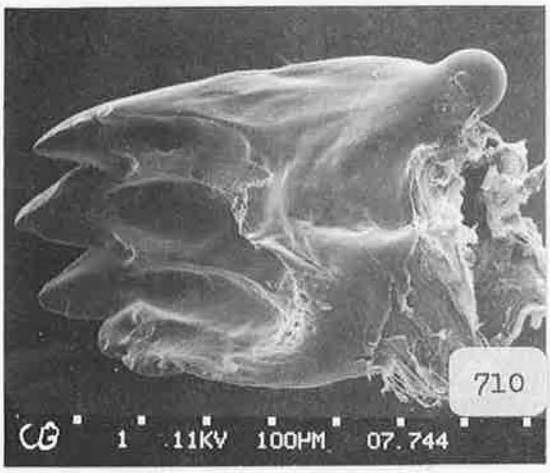


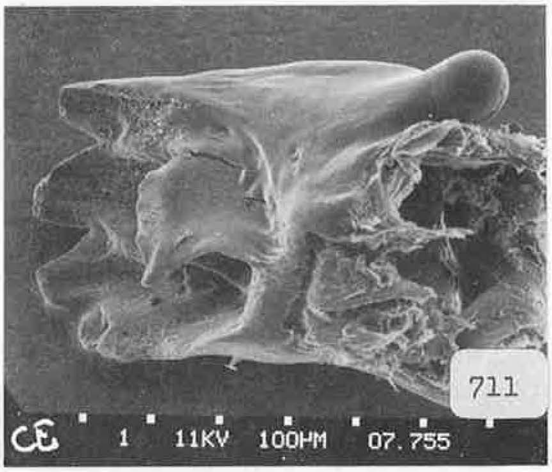


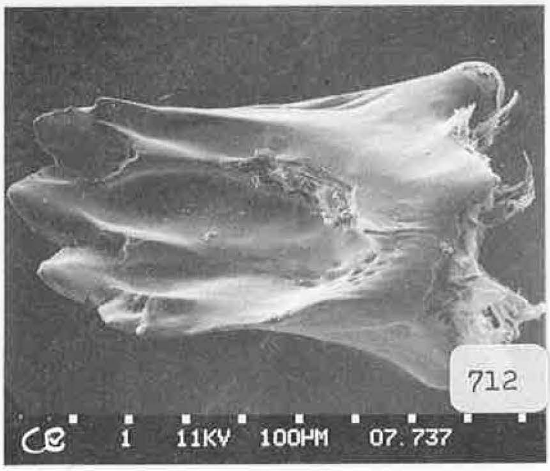


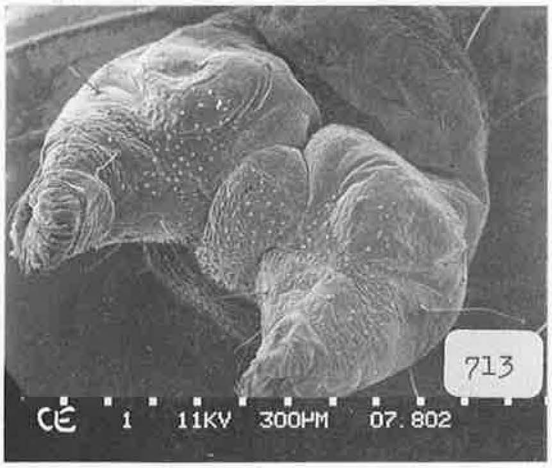


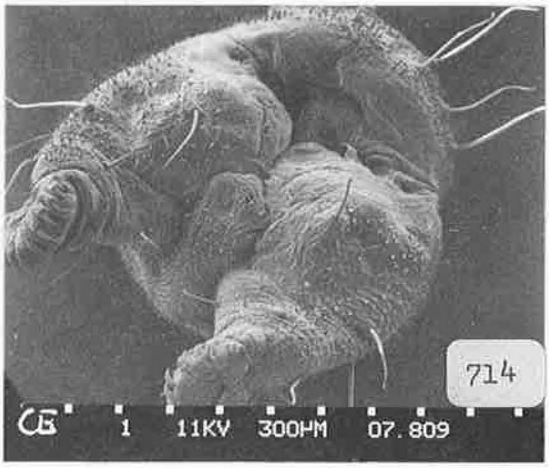
Figs. 704 - 709. Mandibles, Heliothinae. Fig. 704, *Pyrrhia purpurina*; Fig. 705, *Pyrrhia umbra*; Fig. 706, *Pyrrhia victorina*; Fig. 707, *Schinia citrinella*; Fig. 708, *Schinia florida*; Fig. 709, *Schinia villosa.*



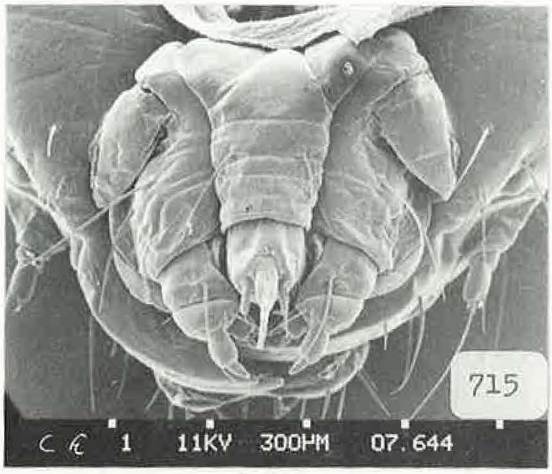








Figs. 710 - 714. Mandibles & larval A10s, Heliothinae. Mandibles. Fig. 710, *Heliothis viriplaca*; Fig. 711, *Heliothis tergemina*; Fig. 712, *Heliothis virescens*. Larval A10s. Fig. 713, *Pyrrhia exprimens*; Fig. 714, *Helicoverpa fletcheri*.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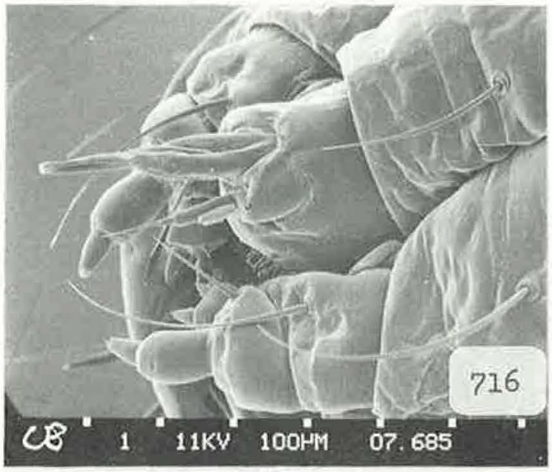
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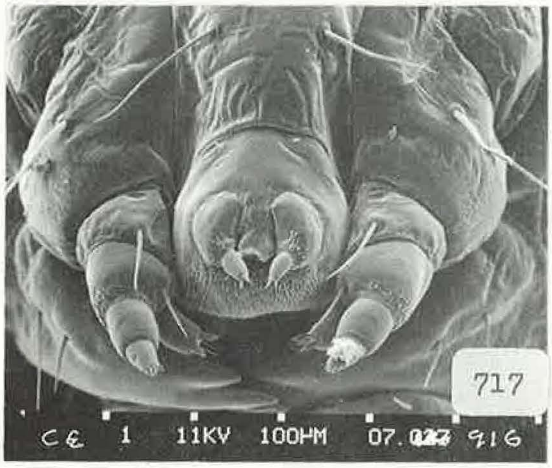
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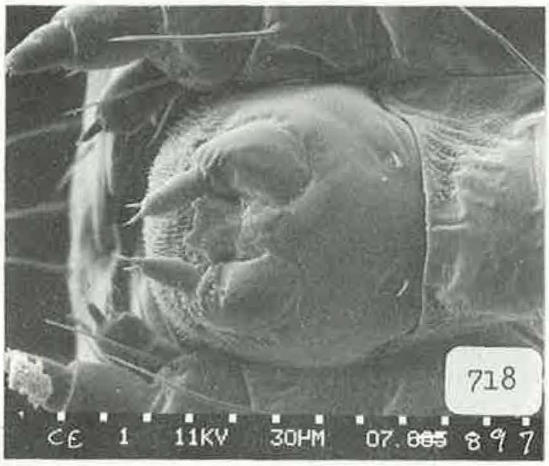
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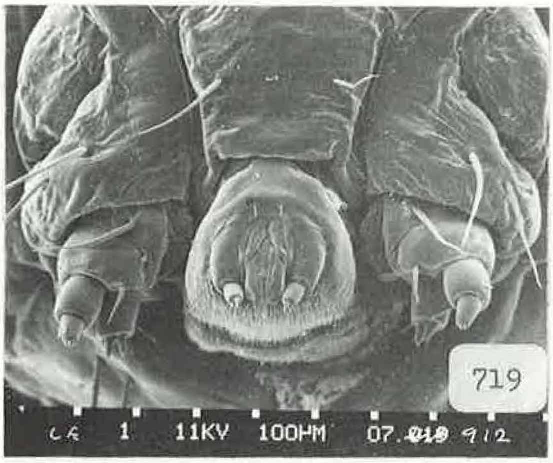
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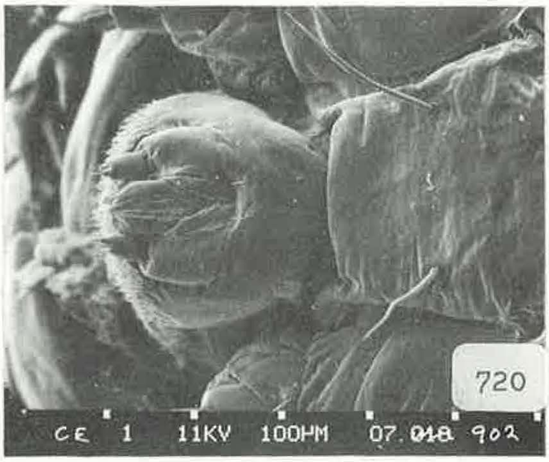
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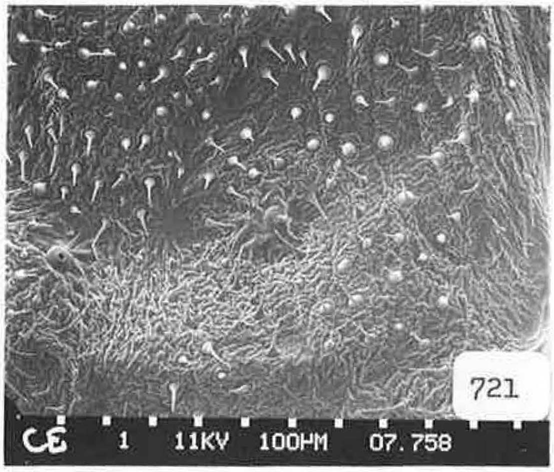
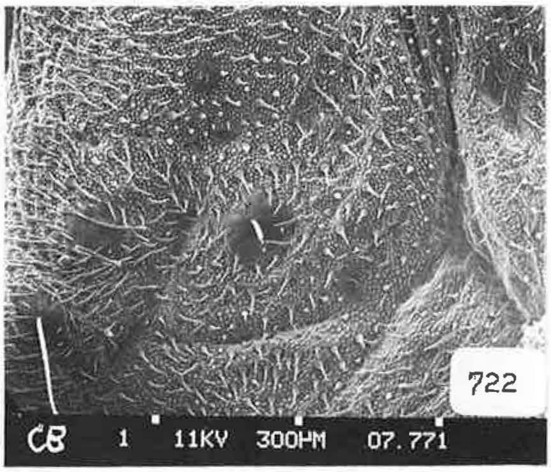
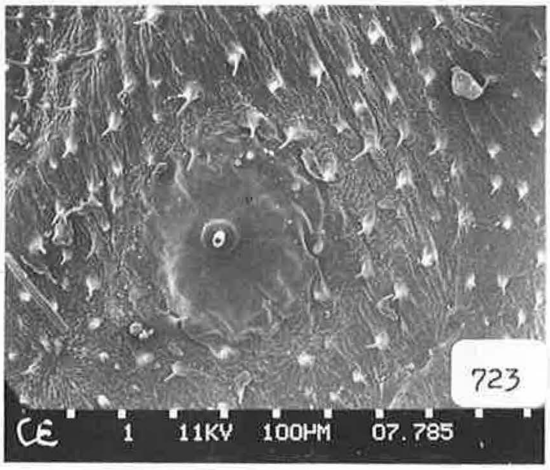
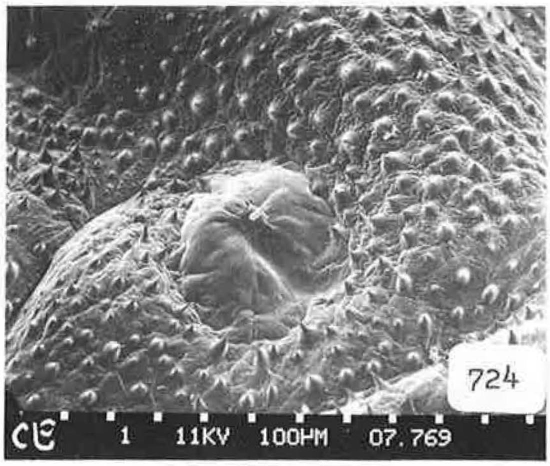
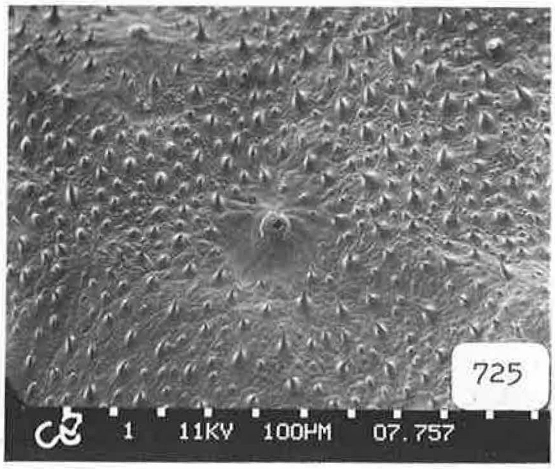
Figs. 715 - 720. Spinnerets, Heliothinae & Stiriinae. Figs. 715, & 716, *Heliocheilus albipunctella*; Figs. 717, & 718, *Panemeria tenebrata*; Figs. 719, & 720, *Xanthothrix ranunculi.*

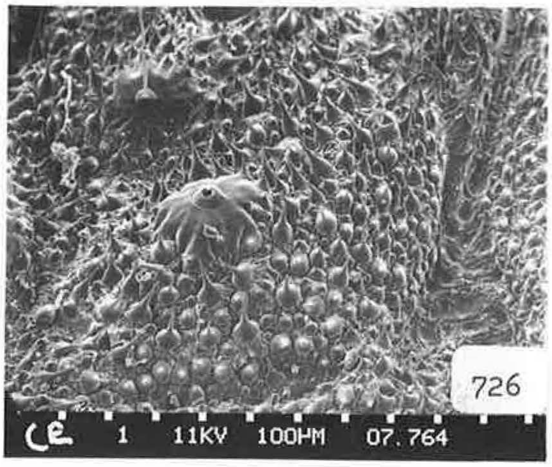




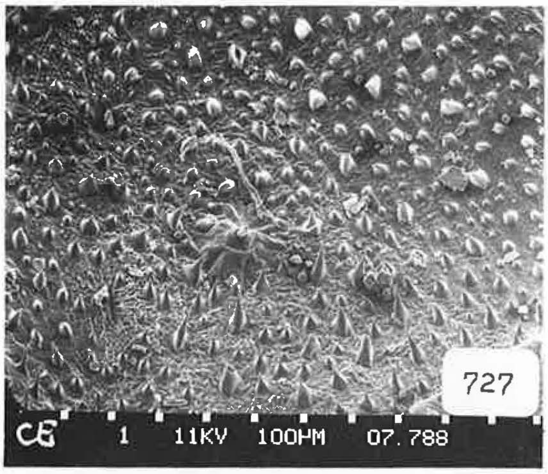


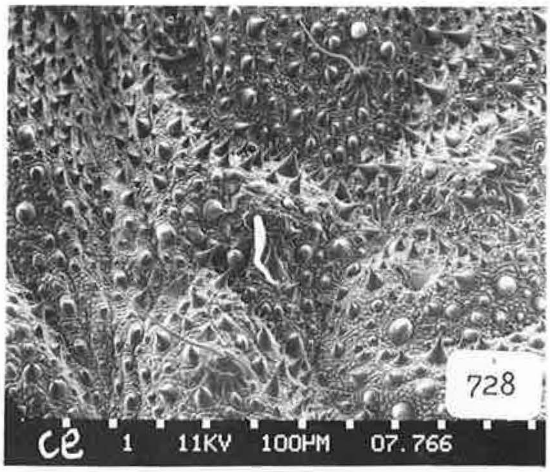


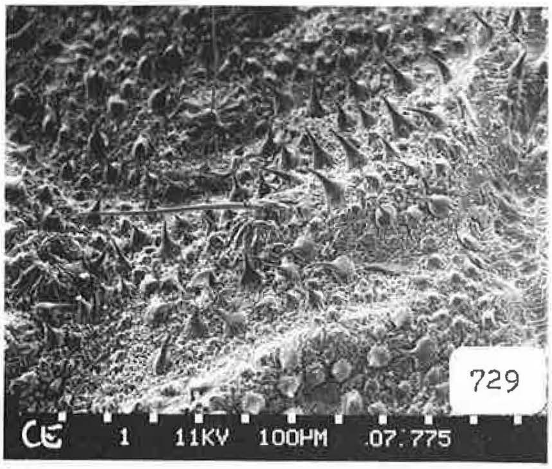


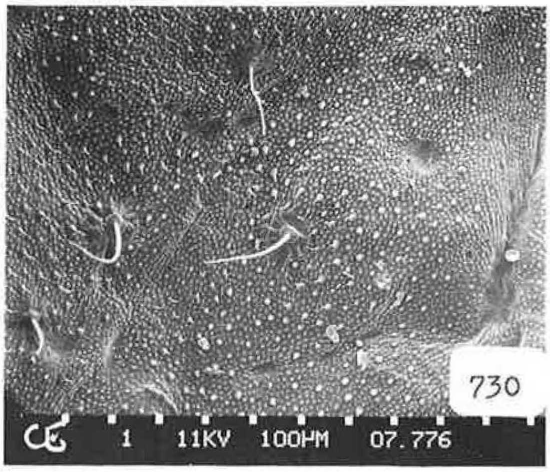


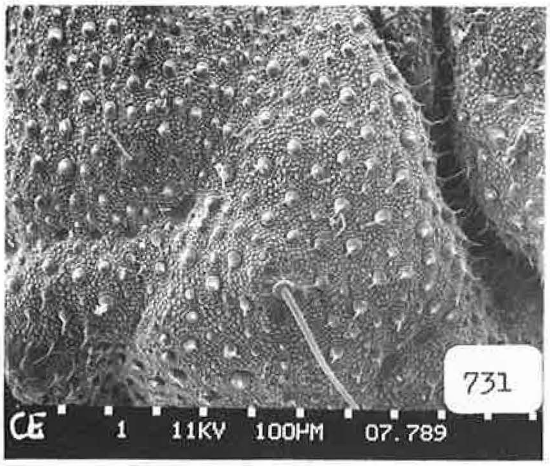
Figs. 721 - 726. Larval skin, Heliothinae. Fig. 721, *Baptarma felicita*; Fig. 722, *Eutricopis nexilis*; Fig. 723, *Periphanes delphinii*; Fig. 724, *Pyrrhia exprimens*; Fig. 725, *Pyrrhia purpurina*; Fig. 726, *Pyrrhia umbra*.

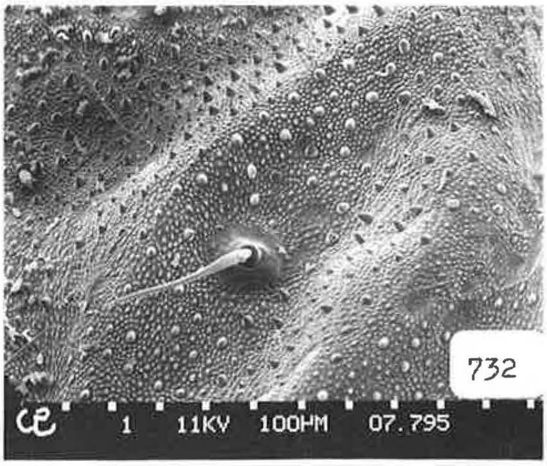




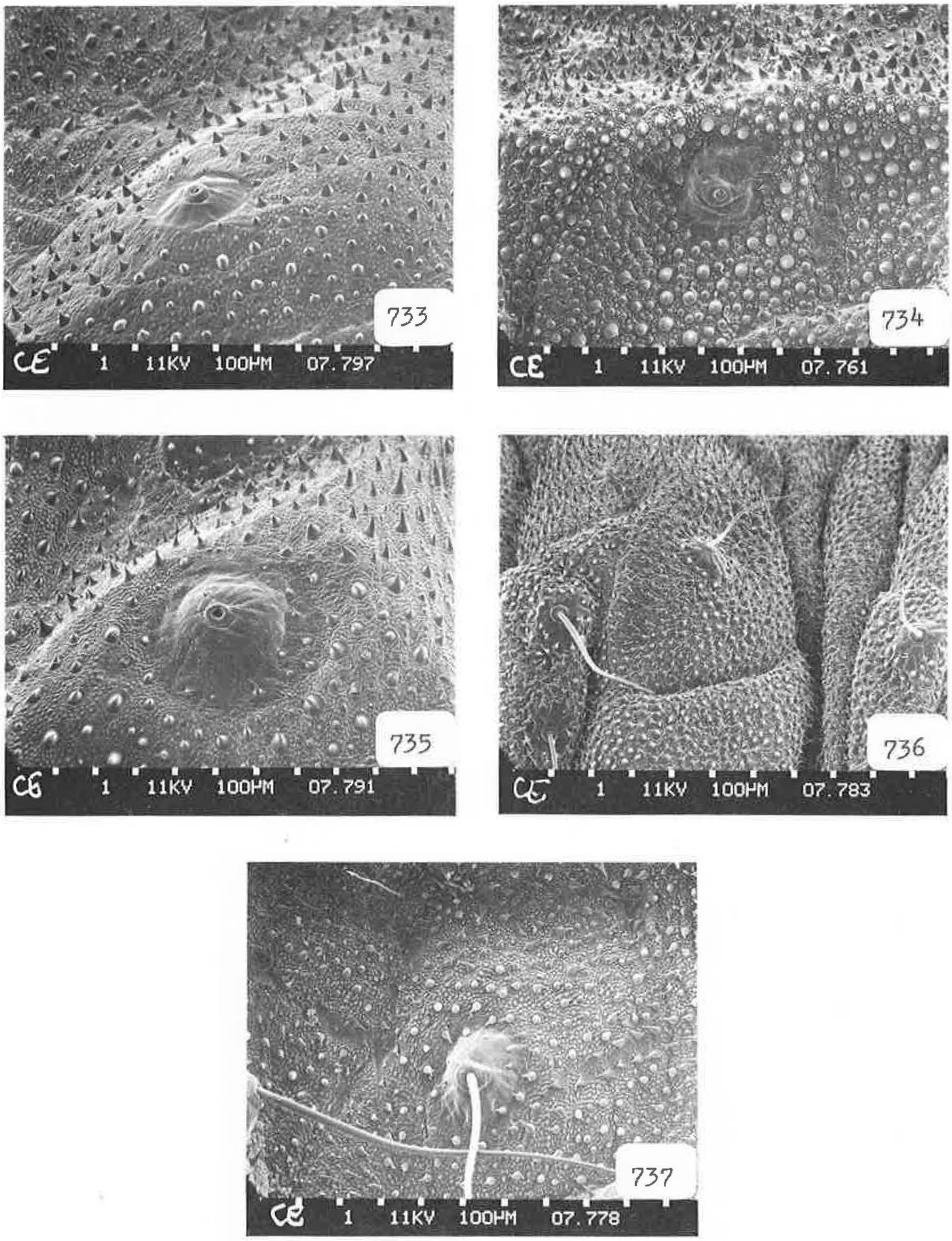




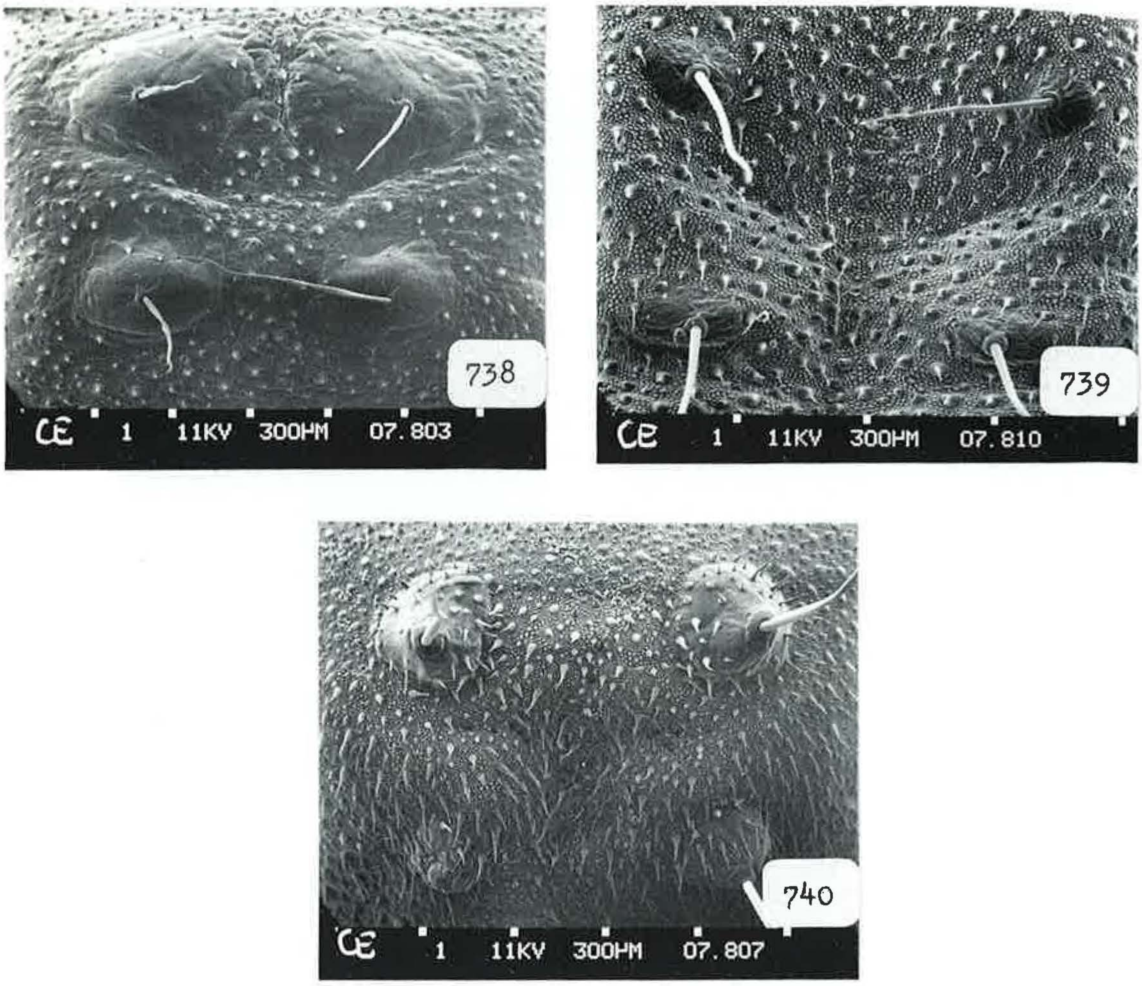




Figs. 727 - 732. Larval skin, Heliothinae. Fig. 727, *Pyrrhia victorina*; Fig. 728, *Schinia citrinella*; Fig. 729, *Schinia florida*; Fig. 730, *Schinia indiana*; Fig. 731, *Heliothis viriplaca*; Fig. 732, *Heliothis molochitina*.



Figs. 733 - 737. Larval skin, Heliothinae. Fig. 733, *Heliothis tergemina*; Fig. 734, *Heliothis virescens*; Fig. 735, *Heliothis incarnata*; Fig. 736, *Heliocheilus albipunctella*; Fig. 737, *Helicoverpa fletcheri*.



Figs. 738 - 740. Chalazae, Heliothinae. Fig. 738, *Pyrrhia exprimens*; Fig. 739, *Heliothis viriplaca*; Fig. 740, *Helicoverpa fletcheri*.

Figs. 741 & 742. Larvae. Fig. 741, *Panemeria tenebrata* feeding on *Cerastium fontanum* (larva collected near Dunsfold, West Sussex, UK, 18 June 1987); Fig. 742, *Baptarma felicita* feeding on *Phacelia* sp. (larva collected 15km S. Quartzite, Arizona, USA, 18 March 1986).

Figs. 743 & 744. Larvae. Fig. 743, *Heliothis peltigera* (MALI, Mourdiah, September 1985); Fig. 744, *Heliocheilus confertissima* feeding on *Setaria pallide-fusca* (MALI, Mourdiah, 24 August 1985).

Figs. 745 & 746. *Heliocheilus albipunctella* ova & adults. Fig. 745, ova laid in head of pearl millet (*Pennisetum americanum*) (MALI, Mourdiah, 30 August 1986); Fig. 746, cluster of six adults comprising two mating pairs, and two unpaired, buzzing males (MALI, Mourdiah, September 1985).

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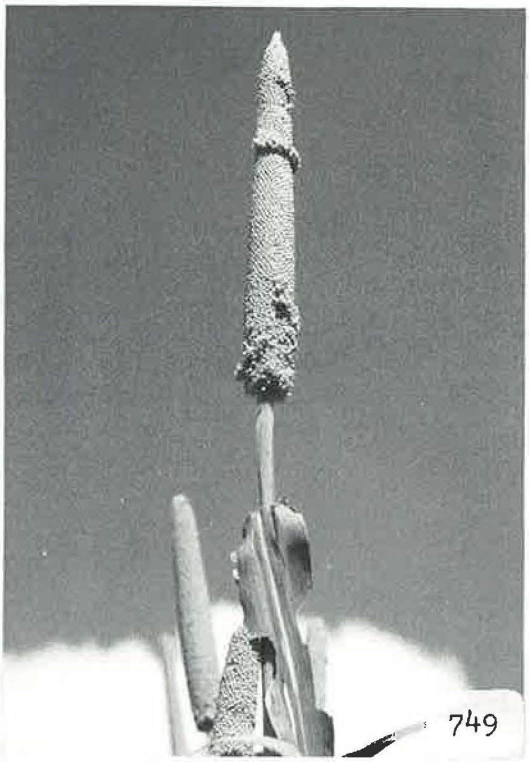

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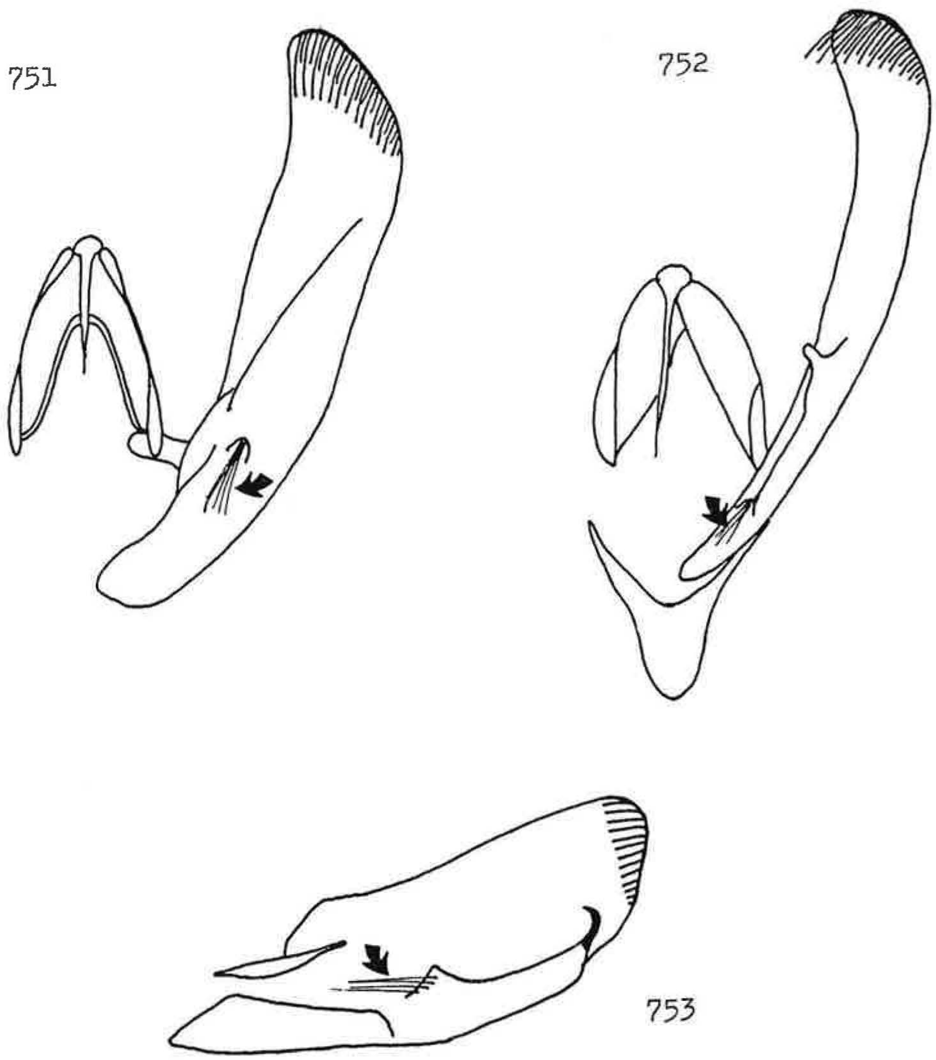
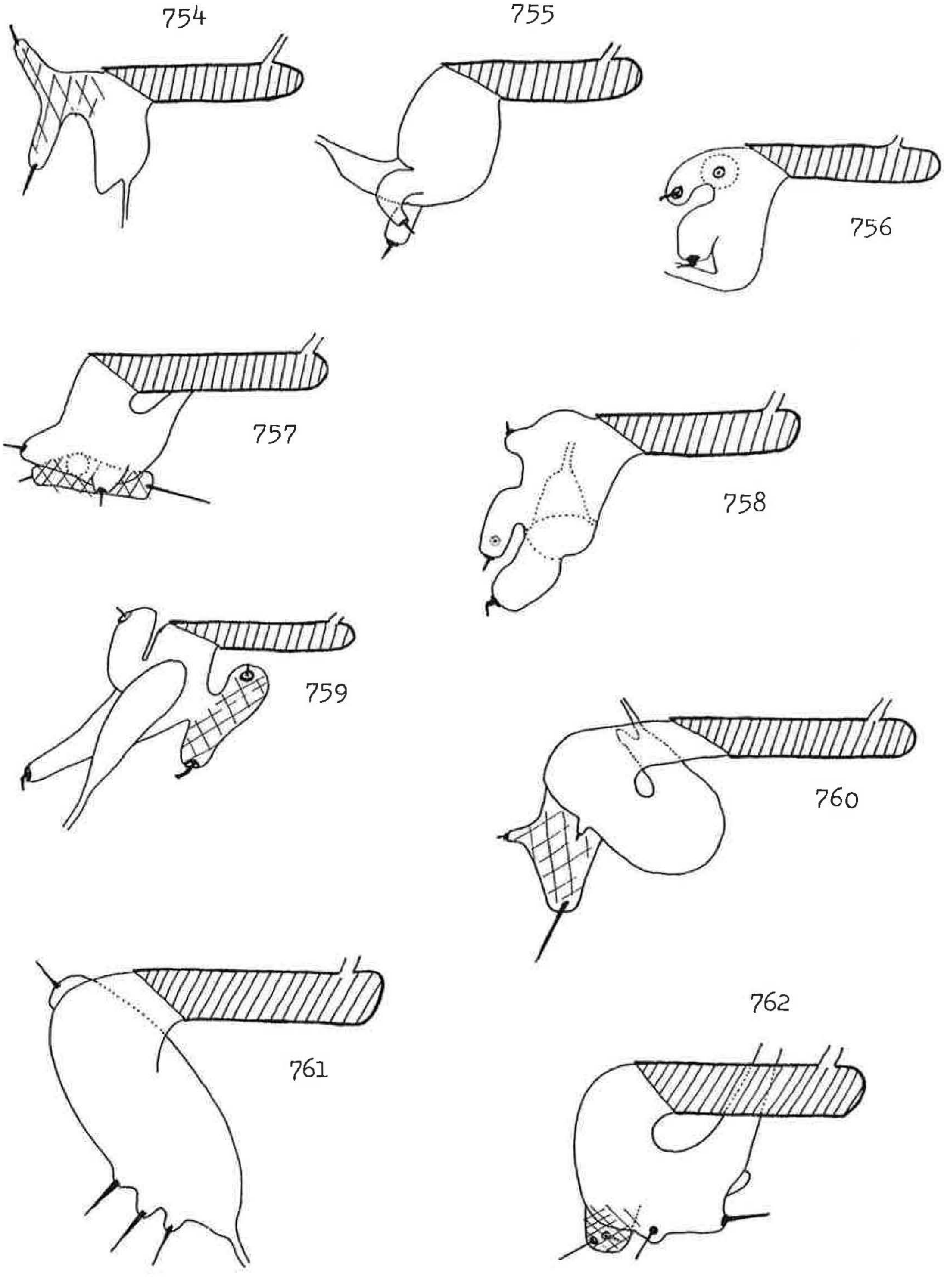
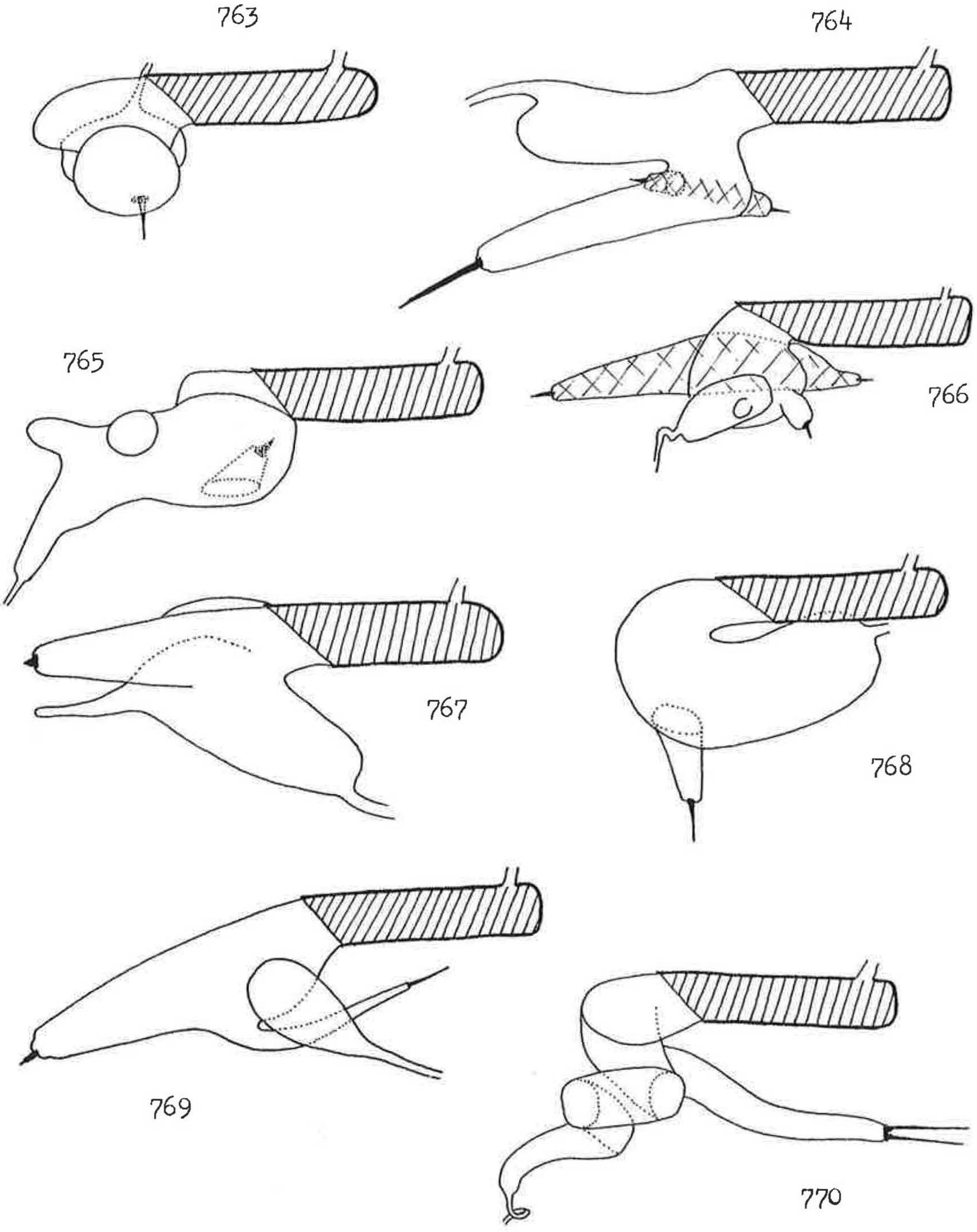
Figs. 747 - 750. Fig. 747, *H. albipunctella* female ovipositing into a millet head at night (with larva of *Amsacta moloneyi* Druce at bottom) (MALI, Mourdiah; September, 1985); Fig. 748, undamaged mature millet head (MALI, Mourdiah; October, 1985); Fig. 749, millet head showing 'tracks' characteristic of *H. albipunctella* damage (MALI, Mourdiah; September, 1985); Fig. 750, millet head destroyed by *H. albipunctella* (MALI, Kaloumba; September, 1986).



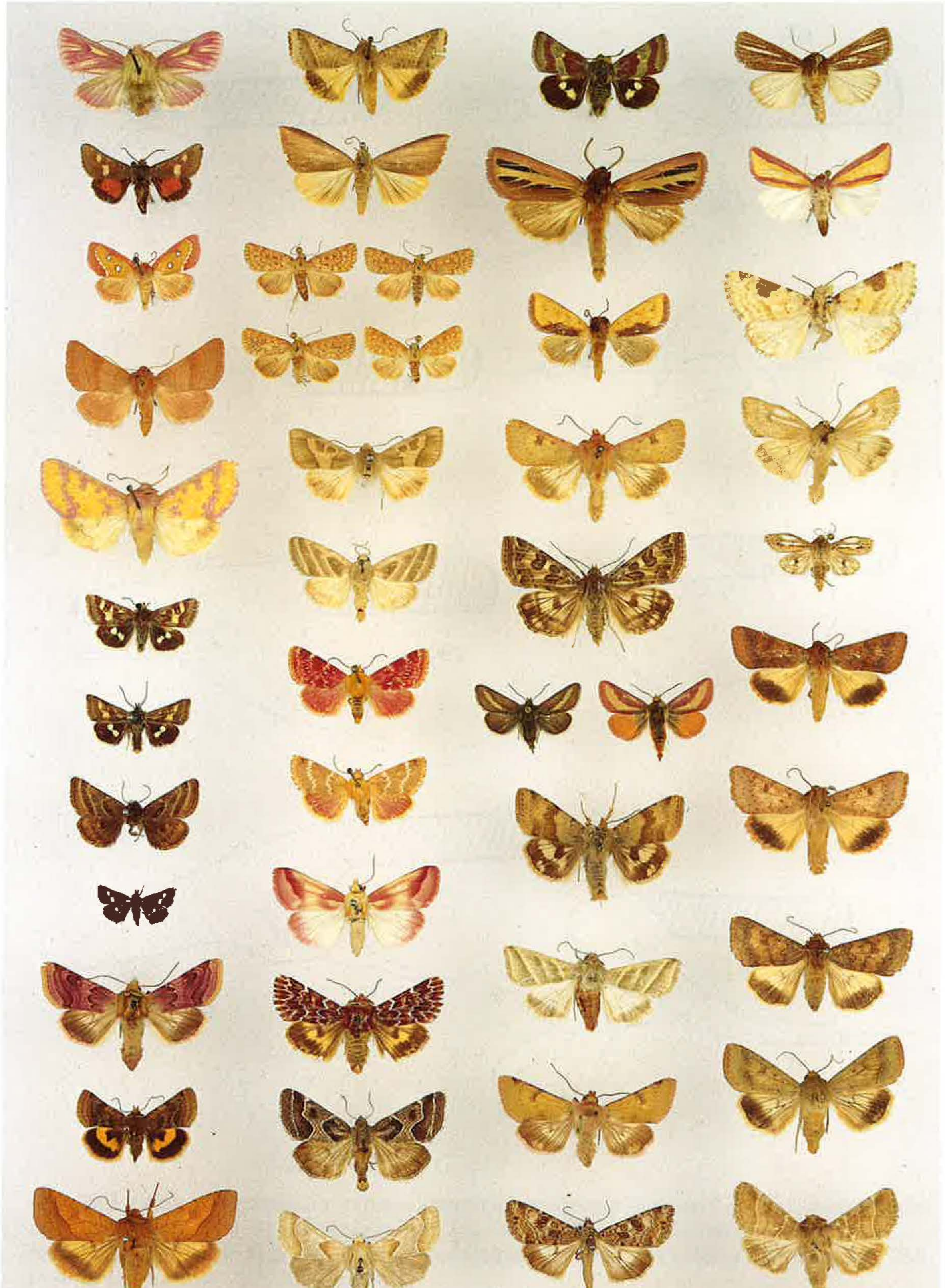
Figs. 751 - 753. Location of muscle-attachment for 'flexor of the clasper', muscle No. 5, of Forbes (1939). Fig. 751, *Helicoverpa armigera* (from Hardwick, 1970a; fig. 39); Fig. 752, *Pyrrhia umbra* (from Hardwick, 1970a; fig. 36); Fig. 753, *Basilodes chrysopis* (from Hogue, 1963; fig. 30g).



Figs. 754 - 762. Diagrammatic representation of heliothine vesicas. Fig. 754, *Aedophron phlebophora*; Fig. 755, *Aedophron rhodites*; Fig. 756, *Aedophron venosa*; Fig. 757, *Derrima stellata*; Fig. 758, *Erythrophaia suavis*; Fig. 759, *Pyrrhia treitschkei*; Fig. 760, *Pyrrhia victorina*; Fig. 761, *Eutricopis nexilis*; Fig. 762, *Baptarma felicita*.



Figs. 763 - 770. Diagrammatic representation of heliothine vesicas. Fig. 763, *Heliothodes diminutivus*; Fig. 764, *Erythroecia suavis*; Fig. 765, *Rhodoecia aurantiago*; Fig. 766, *Periphanes delphinii*; Fig. 767, *Pyrrhia purpurina*; Fig. 768, *Microhelia angelica*; Fig. 769, *Pyrrhia umbra*; Fig. 770, *Adisura bella*.

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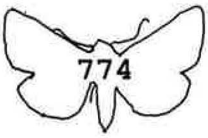
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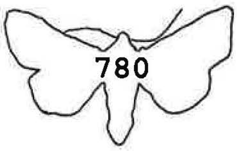
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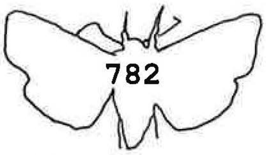
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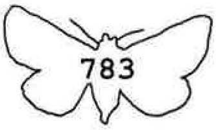
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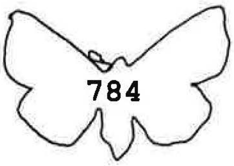
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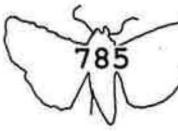
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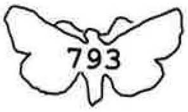
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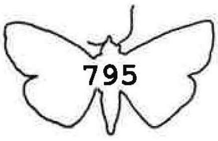
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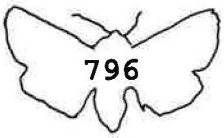
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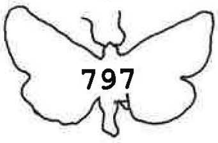
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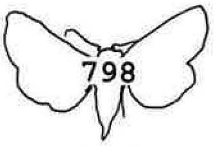
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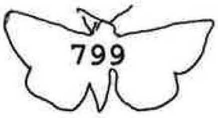
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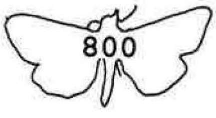
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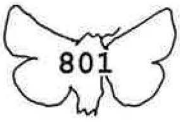
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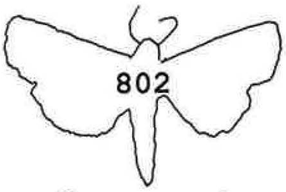
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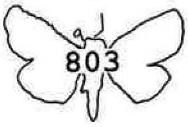
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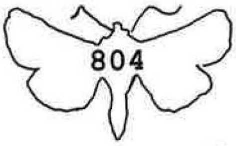
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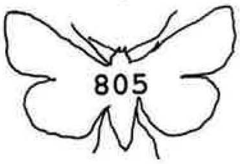
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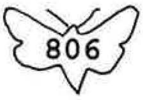
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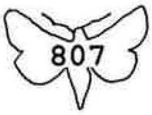
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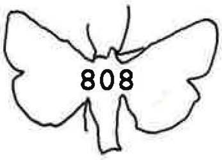
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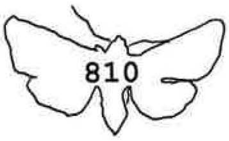
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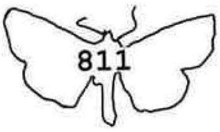
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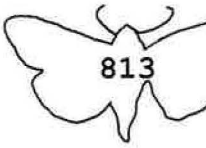
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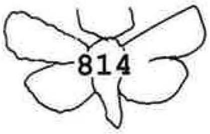
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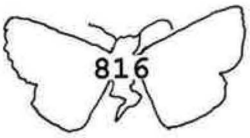
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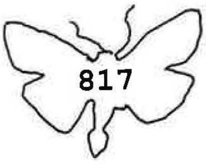
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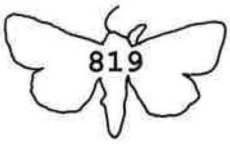
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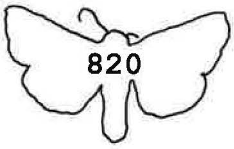
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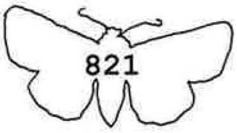
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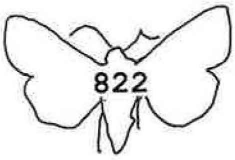
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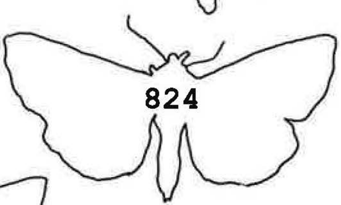
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771.	*Aedophron rhodites* USSR: Urals	Male
772.	*Baptarma felicita* USA: Utah, Beaver Creek Hills	Female
773.	*Derrima stellata* USA: Florida, Lake Placid	Male
774.	*Erythrophaia eudoxia* USSR: Aksu	Male
775.	*Erythroecia suavis* USA: Texas, near Fort Davis	Male
776.	*Eutricopis nexilis* CANADA: Alberta, Nordeg	Male
777.	*Heliothodes diminutivus* USA	Male
778.	*Melaporphyria immortua* USA: New Mexico, Gullinas Canyon	Male
779.	*Microhelia angelica* USA	Female
780.	*Periphanes delphinii* GERMANY: Berlin	Female
781.	*Pyrocleptria cora* HUNGARY: Deliblat	Female
782.	*Pyrrhia umbra* USSR	Female
783.	*Pyrrhia treitschkei* No data	Female
784.	*Rhodoecia aurantiago* USA: New York	Female
785.	*Protadisura posttriphaena* MADAGASCAR: Diego Suarez	Female
786.	*Adisura atkinsoni* INDIA: Naga Hills	Female
787.	*Adisura parva* MALI: Mourdiah	Female
788.	*Adisura parva* MALI: Mourdiah	Male
789.	*Adisura parva* MALI: Mourdiah	Female
790.	*Adisura parva* MALI: Mourdiah	Male
791.	*Adisura litarga* AUSTRALIA: Queensland, Rockhampton	Female
792.	*Schinia trifascia* USA: Texas, Houston	Male
793.	*Schinia volupia* USA: Texas, Palo Duro Canyon	Male
794.	*Schinia miniana* USA: New Mexico, Alberquerque	Male
795.	*Schinia gaurae* USA: Georgia	Female
796.	*Schinia lucens* USA: Colorado, Larima County	Male
797.	*Schinia rivulosa* USA: Virginia, Hot Springs	Male

798.	*Schinia ligae* USA: California, Providence Mts	Female
799.	*Schinia nundina* USA: New York, Long Island	Male
800.	*Schinia cumatilis* USA: Colorado	Male
801.	*Schinia imperialis* No data.	
802.	*Schinia ungemachi* ETHIOPIA: Nole Kaba	Male
803.	*Schinia xanthiata* ETHIOPIA: Addis Ababa	Male
804.	*Schinia chilensis* CHILE: Coquimbo	Holotype male
805.	*Schinia scutosa* HUNGARY: Deliblat	Female
806.	*Heliolonche modicella* USA: California, Lake County	Female
807.	*Heliolonche carolus* USA: California, 10 mi N. Adelanto	Female
808.	*Heliothis viriplaca* No data	Male
809.	*Heliothis virescens* COLOMBIA	Female
810.	*Heliothis incarnata* USSR	Female
811.	*Heliothis punctifera* No data	Female
812.	*Heliothis syrticola* No data	Female
813.	*Heliothis bivittata* INDIA: Poona	Male
814.	*Heliothis terracottoides* MALI: Mourdiah	Male
815.	*Heliothis galathae* MALI: Mourdiah	Female
816.	*Heliothis flavirufa* MALAWI: Mt Mlange	Male
817.	*Heliocheilus paradoxus* USA: Arizona, Chiricahua Mts	Male
818.	*Heliocheilus discalis* MALI: Mourdiah	Male
819.	*Australothis rubrescens* NORFOLK ISLAND	Female
820.	*Australothis rubrescens* NORFOLK ISLAND	Male
821.	*Australothis tertia* INDONESIA: Java	Female
822.	*Helicoverpa fletcheri* MALI: Mourdiah	Male
823.	*Engusanacantha bilineata* ETHIOPIA	Male
824.	*Stiria rugifrons* No data	Female

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