The systematics of Emerald Moths (Geometridae, Geometrinae): wing pigments, tympanal organs and a revision of the neotropical genus *Oospila* Warren.

by

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To Mum and Dad,
with love and thanks.

Contents

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Abstract

The monophyly of the Geometrinae is examined by investigating the green wing pigment and morphology of the tympanal (hearing) organs. The green colour of Geometrinae is caused by a single pigment, here termed geoverdin, located in the scales. Analysis of this pigment indicates that it is neither a bile pigment nor a derivative of chlorophyll. A method developed for taxonomic comparison of lepidopteran pigments and based on a chromatographic profiling technique is presented. The morphology of geometrid tympanal organs is described and an apomorphy for the Geometrinae, the distinctive shape of the ansa, is proposed. The value of the taxonomic literature on the Geometrinae is assessed in terms of its ability to identify internal monophyletic groups.

A taxonomic revision of the genus *Oospila* Warren is presented, in which the neotropical genera *Auophylla* Warren, *Auophyllodes* Prout, *Halioscia* Warren, *Oospila* Warren, *Oospiloma* Prout, *Progonodes* Warren and *Racheolopha* Warren are united into a single genus. Phylogenetic analysis is used to demonstrate the monophyly of the revised genus *Oospila* and to assess relationships between species groups within it. The revised genus *Oospila* is defined as a monophyletic group supported by two apomorphic characters: the form of the abdominal crests and the presence of an anellar complex produced by the fusion of the juxta and transtilla. Sixty-six species of *Oospila* are treated, of which three are described as new. One new subspecies is also described. Forty-eight species group names are synonymised, and 16 species are recombined with *Oospila*.

Chapter 1
Introduction

The family Geometridae has been recognised as a well defined group of Lepidoptera ever since Linnaeus (1758) who divided his genus *Phalena* into seven 'sections', including the *Geometrae*. The classification of the Geometridae into subfamilies has not, however, been so stable (the various subdivisions are reviewed by Packard, 1876 and Prout, 1910). The family is currently divided into six subfamilies, but the monophyly of these is in some doubt (Scoble, 1992).

The subfamily Geometrinae, a group of approximately 1400 species (Ferguson, 1985), although believed by Prout (1912) to be 'evidently on the whole a very natural one' has never been satisfactorily defined. Indeed, Ferguson (1969) observed that it was difficult to give a definition of the subfamily, since there are few characters that occur consistently throughout the group, or are peculiar to it. One of the aims of this work, therefore, was to determine whether or not the Geometrinae actually do form a monophyletic group. Since so few of the previously studied characters are even candidates for being autapomorphies of the subfamily, the search was extended to two additional character suites which have not been thoroughly investigated in the Geometrinae, namely the wing pigments and the tympanal (hearing) organs.

Although notable exceptions exist (Vuillaume *et al.*, 1970; Ford, 1941, 1942, 1944a, b, 1947; Shields, 1987), pigments have been used infrequently in lepidopteran systematics. Yet, potentially, pigments provide an additional, and independent, suite of taxonomic characters. Ferguson (1985) suggested that the green colour of the Geometrinae may be an apomorphy of the subfamily, since the behaviour of the pigment is different from that of green pigments found in other Lepidoptera. Certainly, its occurrence in 85% of the species (Ferguson, 1985) is a striking and unusual feature of the subfamily. Although green colour occurs in other lepidopteran groups, in no other does it pervade almost an entire subfamily of worldwide distribution. However, the geometrine green pigment system has not been studied extensively, owing to the difficulty of handling it.

Tympanal organs have, however, been more extensively used in lepidopteran systematics. Although a structure in the geometrid tympanal organ, the ansa, is a prominent apomorphy of the family (Cook and Scoble, 1992), the variation in this and other geometrid tympanal organ characters has not been investigated since Kennel and Eggers (1933). Much of the morphological variation of tympanal organs is accessible to study by light microscopy with little preparation, but tympanal organs are not routinely examined by taxonomists. Nevertheless, as with wing pigments, tympanal organs potentially provide a further suite of taxonomic characters.

The second aim of the study was to assess the value of the taxonomic literature on the Geometrinae in terms of its success in identifying internal monophyletic groups. Only a single attempt (Viidalepp, 1981) has been made at cladistic analysis of the Geometrinae, other taxonomic revisions (Ferguson, 1969, 1985; Forbes, 1948; Inoue, 1961; Prout, 1912, 1932) have not been expressly, nor even implicitly, based on cladistic methods. Moreover, these revisions have concentrated on regional faunas and their integrity and interrelationships have not been examined critically on a global scale.

The third aim of the study was to contribute to the species-level taxonomy of the subfamily by undertaking a revision of the neotropical genus *Oospila* Warren. The only revisionary works involving any neotropical Geometrinae were those of Prout (1912, 1932). If the estimate of Watson and Goodger (1986) that 50% of macrolepidopteran species occur in the Neotropics ~~,~~ is correct then the relative neglect of neotropical Geometrinae has left a large gap in our understanding of the subfamily. Moreover, the work of Prout (1912, 1932) was severly limited by its virtually exclusive use of external characters: the genitalia were not studied. Consequently, numerous synonyms were created.

The genus *Oospila* Warren was chosen for this revision, to complement the revision of the genus *Nemoria* Hübner also being undertaken at the Natural History Museum by L. M. Pitkin. The result of revising these two genera will be that the taxonomy of a significant proportion of the neotropical Geometrinae will have been thoroughly revised. The work also forms part of a broader project on the taxonomy of neotropical Geometridae being undertaken by M. J. Scoble and associates. These studies are contributing to an attempt by D. H. Janzen and colleagues at the Instituto Nacional de Biodiversidad to make an inventory of the fauna and flora of Costa Rica. In turn, this inventory will form part of a project dedicated to tropical ecological and cultural restoration in that country (e.g. Janzen, 1986).

Chapter 2
Wing pigments

INTRODUCTION

The blue and green colours of many Lepidoptera are produced by bile pigments. The occurrence of these substances in the Lepidoptera has been investigated extensively by Vuillaume *et al.* (1970), who did not find evidence of any bile pigments in green Geometridae, including *Geometra papilionaria* Linnaeus (Geometrinae). However, in later reviews from the same research group, Barbier (1972, 1981, 1984) suggested that bile pigments were indeed responsible for the green colours of geometrid caterpillars and adults; but that the bile pigment was of a different type to bile pigments found in butterflies. Later, Ferguson (1985) thought that the geometrine green pigment might be a derivative of chlorophyll.

Ferguson (1969) noted that the colour of some Geometrinae (his Hemitheini) was relatively dull and unstable, and faded or discoloured readily. The colour of other Geometrinae appeared to be brighter and much more stable, tending to discolour much more slowly. These observations led him to suggest that there might be two separate pigment systems involved. If true, this could be important to the classification of the subfamily, because it suggests either that the subfamily may not be monophyletic, or that the Geometrinae could be allocated to two monophyletic groups.

In order to assess the value of the wing pigment (or pigments) to geometrine classification, the following questions were investigated. Firstly, what is the chemical basis of the green colour? Is the same green pigment present throughout the Geometrinae or have groups within the Geometrinae evolved different green pigments? If different groups within the Geometrinae have different green pigments, are these independently derived, or can they be related to a geometrine groundplan? Lastly, is this green pigment (or pigments) an autapomorphy of the Geometrinae or does it (or do they) occur in the groundplan of a broader clade in which the Geometrinae are included?

MATERIALS AND METHODS

Extraction of pigment from Geometrinae

Following the suggestion of Barbier (1981 and 1984), the initial assumption was made here that the green pigment of Geometrinae was a bile pigment. The method developed for the extraction of bile pigments (Bois-Choussy, 1977; Rüdiger *et al.*, 1968; Vuillaume, 1968; Vuillaume and Barbier, 1969) involves the use of an acid catalyst to stabilise the extracted pigment and, presumably, also to aid in separating the pigment from the scales and its attached protein (Vuillaume and Barbier, 1969; Vuillaume *et al.*, 1970; Bois-Choussy, 1977). However, this method proved unsuitable for use on Geometrinae, because acid destroys the green pigment (e.g. Vuillaume and Barbier, 1969).

Vuillaume and Barbier (1969) found that ethyl acetate on its own failed to extract the pigment from the wings of Geometrinae. Further experiments, carried out during the course of this study, confirmed their finding and showed that a range of other solvents were also insufficient for extracting the pigment into solution. Attempts to shatter the scales using physical techniques, such as homogenisers and ultrasound, also proved ineffective. Although scales can be sliced manually with a razor-blade to expose the pigment granules, this technique is too slow and haphazard to be practical.

However, more detailed consideration of the nature of lepidopteran scales offered a solution to the problem. In most adult Lepidoptera the scales are composed of cuticulin deposited in ridges and strengthened with internal struts (Ghiradella and Radigan, 1976). Pigment granules, where present, lie in the hollow spaces between these struts. Since cuticulin is rich in lipids, it can be broken down by detergents, allowing solvents and other chemicals access to the pigments. The pigment granules consist of pigment bound to a protein, an association that can be broken by the application of a protease. Application of a protease would also be expected to help break down any protein-containing portions of the scale laminae.

Therefore, to extract pigment from the scales of Geometrinae, wings were first ground in a glass homogeniser with a solution of the detergent Sodium dodecyl sulphate (SDS, $CH_3(CH_2)_{11}OSO_3Na$, supplier Aldrich; 0.5% in cold water) and the protease trypsin (supplier Difco; 0.1 g in 5 ml water). This detergent was chosen since, unlike some others, it did not seem to alter the colour of the pigment. However, in some early trials a pink colour was formed in the slightly alkaline environment of a solution of SDS. This reversible effect was later counteracted by altering the quantity of protease used, to form a solution buffered at pH 7.0. In order to speed the extraction process, the suspension was then treated with ultrasound for 60 seconds, to break the now weakened scales and to liberate the pigment. The pigment system under examination turned out to be highly polar and soluble in cold water and so it is extracted into solution by this procedure. Owing to the extreme light lability of the free pigment, pigment solutions were protected from light by covering all glass vessels with silver foil and all procedures were carried out in a darkened room.

The quantity of material used for pigment extraction depended on the purpose to which the extract was put. Mass spectrometric, nuclear magnetic resonance spectrometric, and infra-red spectrometric analysis required wings from at least four specimens, whereas ultra-violet spectrometry usually required wings from a single specimen. For a comparative pigment profile of a specimen in good condition, using thin layer chromatography, one wing was commonly sufficient, although specimens in poor condition necessitated the use of more material.

The suspension resulting from treatment with the extracting solution consists of the pigment in solution, solid scale fragments in suspension and the extracting agents and their products. To remove the solids, the suspension was filtered through a cotton wool plug in a Pasteur pipette, under slight positive pressure. The solvent was then evaporated under vacuum, in the dark and at room temperature. The resulting dry, unpurified pigment was redissolved in the minimum quantity (a few drops) of 50: 50 methanol: water.

Previous authors working with bile pigments from butterflies stabilised them by methylation with an acid catalyst (Vuillaume and Barbier, 1969; Bois-Choussy, 1977). Following the suggestion of Barbier (1981, 1984) that, despite its acid-sensitivity, the green pigment of Geometrinae is nonetheless a bile pigment, the reagent diazomethane (Fieser and Fieser, 1967) was used here to methylate free carboxyl groups.

It is not known whether methylation confers any extra stability on geometrine pigments, although it is likely that it does, since the pigment has one or more acid groups (see section on chemical behaviour, below). However, one certain benefit of methylation was a reduction in the polarity of the pigment. This decrease in polarity increased the chromatographic mobility of the pigment, making it easier to handle and to purify. For the methylation, a freshly distilled solution of diazomethane in ether was added to the pigment solution (De Boer and Backer, 1963). Owing to the highly toxic and hazardous nature of diazomethane, all apparatus and procedures were contained within an efficient fume hood.

The crude pigment solution was allowed to stand for a few minutes, and the solvent was then evaporated under reduced pressure, at room temperature and in a darkened fume hood. The residue was dissolved in the minimum quantity of 50: 50, methanol: water (one drop, or more if required) and the pigment purified on a 20 x 20 cm silica thin layer chromatography (TLC) plate (80% Silica Hf_{254}, 20% Silica G) using the solvent system methanol: water 2: 1, with the addition of a few drops of ammonia solution (0.880). The ammonia allowed amine-containing compounds to run freely up the TLC plate by displacing them from acidic sites on the silica. This competition of the ammonia for the acidic sites on the silica also helped to neutralise the acidity of the silica, which otherwise is sufficient to destroy the pigment.

Most of the initial experiments were made using fresh, or frozen, material. However, the results reported here are based on the analysis of dried material and museum specimens. A range of geometrine species was examined (Table 1), selected to include those whose green colour Ferguson (1985) found to be intense and stable and those whose colour he found to be paler and less stable. In addition, a range of other Lepidoptera with green, blue and yellow colouration were investigated (Table 1). These were selected to assess the distribution of the geometrine green pigment system outside the subfamily. *Mantis religiosa* Linnaeus (Dictyoptera: Mantidae), *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae) and an unidentified South American species of Trichoptera (Trichoptera: Hydropsychidae) were also tested for the presence of the geometrine green pigment system, to determine whether or not it occurs outside the Lepidoptera.

Pigment profiling

Purification of the extracted pigment by thin layer chromatography also suggested a way of analysing the pigment complement of a sample by forming a 'pigment profile'. The level to which a substance travels up a TLC plate is specific under defined conditions of solvent, chromatographic support and temperature. Different pigments therefore separate out at different points on the plate and the methylated extract can be separated into characteristic bands, giving a pigment profile of the sample. Developed plates were viewed under natural and ultra-violet light to reveal the bands. Bands present on plates were catalogued according to their Rf values (Rf = distance moved by solute / distance moved by solvent; Harwood and Moody, 1989) for this solvent system.

A pigment sample analysed in this way is split into a series of bands corresponding to the individual components of the pigment complement. The pattern of banding is specific to the pigment system and therefore profiling provides a means of comparing samples from two specimens to test for the presence of the same pigment system.

Spectrometric analysis

In order to analyse the pigment using physical spectrometric techniques, further purification and preparation of the sample was required. Following chromatographic development, the purified, methylated pigment was removed from the TLC plate by scraping off the silica in the band containing the pigment. The pigment was separated from the silica by adding a solution of methanol containing a few drops of ammonia solution (0.880) and then filtering the resulting suspension through a cotton wool plug in a Pasteur pipette, applying a slight positive pressure. The solvent was then evaporated under reduced pressure, without heating and with protection from light.

Further purification of the methylated pigment was achieved by washing it with petroleum ether. The pigment was dissolved in the minimum quantity (a few drops) of methanol, and petroleum ether (30-40 fraction) was then added dropwise until the pigment was precipitated. The liquid phase was discarded and the process repeated.

Ultra-violet and visible spectra, mass spectra and nuclear magnetic resonance spectra were obtained of the pigment in solution in methanol (or equivalent). Infra-red spectra were obtained from solid pigment using potassium bromide (KBr) plates.

RESULTS

Chromatographic behaviour of the pigment

Pigment profiles of all species of Geometrinae examined (with the exception of *Prasinocyma perpulverata* Prout; Table 1) showed a single green band at Rf= 0.4 in this solvent system. This pigment is here termed geoverdin. No other coloured bands were visible to the unaided eye, although some species also gave additional bands which fluoresced under ultra-violet light.

Chemical behaviour of geoverdin

Geoverdin is unusual amongst insect pigments in being highly polar and soluble in water. The pigment also shows unusual acid-base behaviour, which is slightly different *in vivo* to the acid-base behaviour of the purified pigment in methanolic solution. *In vivo*, addition of acid to a wing wetted with acetone (in order to ensure contact between the highly hydrophobic scales and the acid) causes the green colour to turn yellowish. Addition of an alkali causes a temporary reversal of this colour change, although after a few minutes the green colour is lost again. Addition of acid to a pure solution of geoverdin in methanol destroys the green colour irreversibly, forming a yellowish solution. However, a very slight positive pH change can result in a pinkish solution developing. In its acid-base behaviour, geoverdin therefore differs from bile pigments, which show a reversible colour change with alteration of pH (Ford, 1955).

Bile pigments undergo a reaction with fuming nitric acid (i.e. very concentrated nitric acid) known as the Gmelin reaction This reaction invokes a sequence of colour changes, (brown to green to blue to violet to red to orange to yellow to colourless; Vuillaume, 1968; Vuillaume and Barbier, 1969) which can be used to demonstrate the presence of tetrapyrroles (including bile pigments). Geoverdin does not undergo this sequence of colour changes, but instead immediately discolours to pale yellow on the addition of nitric acid. The failure of geoverdin to undergo the Gmelin reaction suggests that it is not a bile pigment.

Geoverdin contains at least one acid group. This is demonstrated by the reduction in polarity resulting from its reaction with diazomethane, since the diazomethane reaction adds a methyl group to carboxylic acid groups. Geoverdin also contains at least one basic group, demonstrated by its running more freely in a slightly alkaline chromatographic solvent. The possession of a basic group may also account for the destruction of geoverdin by acids.

Spectrometric behaviour of geoverdin

Ultra-violet spectrometry

In methanolic solution, the geometrine green pigment has a peak absorption of 440-460 nm in the visible spectrum and absorbs strongly in the ultra-violet. This absorption pattern differs markedly from the spectrometric behaviour of bile pigments, which have a peak absorption (in methanol) of 590-705 nm in the visible spectrum and a second clearly identifiable peak at 380-385 nm in the ultra-violet (e.g. Vuillaume and Barbier, 1969).

Mass spectrometry

Owing to the lability of geoverdin, analysis of it by mass spectrometry was problematical, because considerable fracturing of the pigment occurred during its analysis. Although a consistent pattern of decay was observed in each trial, there was no interpretable molecular ion and thus the molecular weight of the pigment could not be determined. Nor was it possible to interpret the cause of other ions. However, since the breakdown pattern was consistent in each trial, mass spectrometry did provide a means of demonstrating the presence of geoverdin in a sample, as a check on the accuracy of TLC analysis.

Mass spectrometric analysis gave no evidence that geoverdin was a bile pigment. Tetrapyrroles, the group of substances to which bile pigments belong, give very characteristic mass spectra (McDonagh, 1979 and references therein), with a large peak corresponding to the molecular weight and two much smaller peaks, separated by the molecular weight of a $-CH_3$ group, corresponding to approximately half the molecular weight of the whole tetrapyrrole. These latter peaks are caused by the breaking of the central bridge of the tetrapyrrole, which forms two bipyrroles. No such peaks were identifiable in the mass spectra of pigment samples from Geometrinae.

Nuclear magnetic resonance (nmr) and Infra-red spectrometry

Attempts at analysis using nuclear magnetic resonance spectrometry were limited by the shortage of material available (nmr requires at least 3-4 mg of material, a quantity requiring wings from at least 10 medium-sized moths) and the extreme lability of the pigment. Impurities in the sample resulting from the decay of the pigment rendered the spectrum difficult to interpret.

Spectra obtained from nuclear magnetic resonance spectrometry were not clear enough to interpret the molecular structure of the pigment. However, the pattern of bending and stretching of bonds expected from a tetrapyrrole (see, for example, spectra published in Choussy and Barbier, 1975; Cole *et al.*, 1968 and Kuenzle, 1970) were not discernible in the spectra obtained for geoverdin.

Infra-red spectrometry indicated the presence of -OH and -C=C- groups, but this is hardly surprising in an organic compound.

Quantity of pigment in each wing

Based on the results of a single quantitative analysis, a medium sized geometrine wing contained about 70 μg of pigment. Bois-Choussy (1977) found 1-10 μg of bile pigment in wings of butterflies. However, it is not known whether Geometrinae genuinely do contain more pigment in their wings or whether the discrepancy is due to the greater efficacy of the technique used here.

Distribution of geoverdin

Geoverdin was found in the wings of all the green coloured Geometrinae examined and also in some Geometrinae with yellow areas on their wings, namely *Dysphania* sp., *Pingasa venusta* Warren and *Terpna crocina* Butler. Geoverdin was not, however, found in the wings of *Prasinocyma perpulverata* Prout which, although allocated to the Geometrinae has brown, not green wings (Table 1).

Family or Subfamily	Species	Quantity present
Geometrinae[1]	*Agathia* sp.	Primary
Geometrinae	*Comibaena pustulata* Hüfnagel	Primary
Geometrinae	*Dysphania* sp.	Primary
Geometrinae	*Geometra papilionaria* Linnaeus	Primary
Geometrinae	*Hemithea aestivaria* Hübner	Primary
Geometrinae	*Hemistola pruinata* Hübner	Primary
Geometrinae	*Nemoria* sp.	Primary
Geometrinae	*Oospila confundaria* Möschler	Primary
Geometrinae	*Pingasa venusta* Warren	Primary
Geometrinae	*Prasinocyma perpulverata* Prout	Absent
Geometrinae	*Terpna crocina* Butler	Primary
Geometrinae	*Thalassodes* sp.	Primary
Geometrinae	*Phrudocentra* sp.	Primary
Geometrinae	*Tanaorhinus* sp.	Primary
Ennominae[1]	*Catoria delectaria* Walker	Trace
Ennominae	*Cidarophanes brigatta* Thierry-Mieg	Trace
Ennominae	*Phrygionis argyostricta* Hampson	Trace?[2]
Oenoch. s.l.[1,3]	*Celerena lerne lerne* Boisduval	Primary
Oenoch. s.l.[1,3]	*Eumelea rosalia australiensis* Warren	Absent
Larentiinae[1]	*Colostigia* sp.	Trace
Sterrhinae[1]	*Traminda neptunaria neptunaria* Guenée	Trace
Archiearinae[1]	*Archiearis notha notha* Hübner	Absent
Drepanidae	*Tridrepana fasciata* Warren	Absent
Drepanidae	*Oreta stania* Watson	Absent

Family	Species	Quantity present
Noctuidae	*Pseudoips fagana* Fabricius	Trace
Noctuidae	*Trachea netuna* Guenée	Trace
Hepialidae	*Annetus* sp.	Trace
Papilionidae	*Graphium sarpedon* Linnaeus	Absent
Sphingidae	*Euchloron megarea* Linnaeus	Trace
Pyralidae	Undetermined	Trace

Table 1 Distribution of geoverdin in the Lepidoptera examined. 'Primary' indicates the presence of a large quantity of geoverdin as the primary green or yellow wing pigment. 'Trace' indicates that only a trace of geoverdin was found, as a secondary pigment.
[1] Indicates subfamilies of Geometridae. [2] A pigment extract of *Phrygionis argyostricta* showed a slight green colour which may indicate the presence of geoverdin, however, sufficient material could not be obtained to confirm the identity of the pigment.
[3] Oenochrominae *sensu lato*.

Trace quantities of geoverdin were found in the wings of species of Ennominae, Larentiinae, and Sterrhinae (Geometridae) and also in some green-coloured species of Hepialidae, Pyralidae and Sphingidae (Table 1). Although no quantitative assessment was made, it was clear from the intensity of the pigment extract and also from the colour remaining in the wings at the end of the process, that geoverdin was not the primary green pigment in these species. Geoverdin was, however, found to be the primary wing pigment of *Celerena lerne lerne* Boisduval, a species currently allocated to the Oenochrominae *sensu lato* (Geometridae).

Outside the Lepidoptera, geoverdin was not found in *Mantis religiosa*, *Chrysoperla carnea* or in an unidentified South American species of Trichoptera, despite the green or blue colouration of the wings of these insects.

DISCUSSION

The range of species examined included those in which Ferguson (1985) observed the pigment to be bright and relatively stable (e.g. *Nemoria* sp.) and those in which he observed the pigment to be duller and less stable (e.g. *Hemithea aestivaria*). Both pigment profiling and further analysis by mass spectrometry indicated that a single pigment, geoverdin, was responsible for the green colour of all species of Geometrinae examined. Therefore, the tentative suggestion (Ferguson, 1985) that two different green pigments might occur in different groups of Geometrinae may be rejected.

Although the precise identity of geoverdin was not determined, both the chemical behaviour of the pigment and the results obtained from spectrometric analysis are inconsistent with those expected from tetrapyrroles (Bois-Choussy, 1977; McDonagh, 1979 and references therein) or chlorophyll (L.M. Harwood, *pers. comm.*). Thus the suggestions that a bile pigment (Barbier, 1981, 1984) or chlorophyll (Ferguson, 1985) is responsible for the green colour of these moths can be eliminated. Moreover, the chemical and spectrometric behaviour of geoverdin is inconsistent with that expected from any known class of insect pigment (see, for example, reviews by Kayser, 1985; Needham, 1978 and Nijhout, 1985).

Ferguson (1985) noted that the green pigment of Geometrinae appeared to be different to that found in other groups of moths. This work indicates that this statement (Ferguson, 1985) needs qualifying and that the green pigment of Geometrinae, geoverdin, is different from the *primary* green pigment found in Lepidoptera outside the Geometridae. Some other species of Lepidoptera were found to contain some geoverdin

(Table 1), but only a trace of the pigment was found in these. These findings suggest that the presence of geoverdin as the primary wing pigment could be an apomorphy of a clade within the Geometridae.

Further evidence for the hypothesis that geoverdin is an apomorphy of a clade within the Geometridae comes from the absence of the pigment in closely related taxa. Certainly, *Archiearis notha notha* Hübner, thought to be a primitive geometrid by virtue of its full complement of larval prolegs, does not contain geoverdin. Visual examination of the collections of Uraniidae (included provisionally in Geometroidea by Minet, 1991), Epicopiidae (included in Uranioidea by Scoble, 1992), and Drepanoidea (proposed as the sister group of Geometroidea by Minet, 1991), in the Natural History Museum, revealed no emerald green colours in these moths. Moreover, the yellow coloured wings of two species of Drepanidae contained no geoverdin (Table 1). There is therefore good evidence that geoverdin does not occur in the groundplan of the Geometridae and has been independently derived in those Geometridae in which it occurs. Geoverdin may, of course, have been independently derived at more than one point within the Geometrinae. The consequences of these findings for the classification of the Geometrinae are discussed further in Chapter 6.

Despite their common English name of 'Emerald Moths', Geometrinae vary considerably in the tone of their green colouration and some are not green. Yellow, yellowish green, emerald green, blue green and dull greyish or brownish greens are all found in the subfamily. This variation is accounted for, at least in part, by the quantity and location of geoverdin present in the scales. Examination of a range of Geometrinae revealed that those with yellow or yellowish colours had a large number of pigment granules distributed evenly throughout the scales. Those species with a dull bluish green colour tended to have fewer pigment granules and these were clustered at the tips of the scales and along the scale midribs, leaving large areas of the scale without any pigmentation. Further evidence for this suggestion comes from the appearance of geoverdin in solution, *in vitro*, when the pigment appears yellow in concentrated solution and bluish green in dilute solution.

Although geoverdin was the only visibly green pigment found in the wings of Geometrinae, substances exhibiting ultra-violet fluorescence activity were also extracted from the wings of some Geometrinae. These represent a second potential source of colour variation, effected by modifying the visible effect of the primary pigment, through the transference of fluorescence energy to or from it (L. Harwood *pers. comm.*).

A third possible source of colour variation, which may have some modifying effect on the hue of the green colour, lies in the physical properties of the scales themselves. Light-reflecting and refracting properties of scales are responsible for producing colour in some Lepidoptera, as for example the bright metallic colours of *Morpho* Fabricius and some other butterflies (e.g. Nijhout, 1985; Ghiradella, 1974; Ghiradella and Radigan, 1976). However, it is not known whether scales of Geometrinae vary in a way which would affect their light modifying properties.

Another feature of geometrine colour variation, is the observation (Ferguson, 1985) that some species of Geometrinae (e.g. *Nemoria bistraria* Hübner) have green and brown seasonal forms. Large pH changes destroy geoverdin irreversibly, but a small increase in the pH of a solution of geoverdin can produce a pinkish colour. Although it is not known whether geoverdin is present in brown forms of these moths, the brown colour might result from this sort of modification of the geometrine green pigment system. Alternatively, the brown colour may be a melanin, since these substances are almost ubiquitous in the Lepidoptera (Kayser, 1985).

Geoverdin is absent from *Prasinocyma perpulverata*. Although allocated to the Geometrinae, this species has brown (not green) wings. Further investigation of other characters will be required to assess whether geoverdin has been secondarily lost in this species, or whether the allocation of *P. perpulverata* to the Geometrinae is doubtful.

Since the primary pigment of green-winged Geometrinae is the same despite its differential stability in museum specimens, the source of this variation must lie in the environment of the pigment. In the living organism the pigment is bound to a protein. Once separated from the protein, the pigment becomes highly unstable and it seems likely that degradation of the protein, or a loosening of its attachment to the pigment in museum specimens, allows decomposition of the pigment, and a subsequent loss of colour. Possibly, those specimens which are less prone to colour loss have a different protein, which degrades more slowly or holds the pigment more tightly.

The breaking of the association between the pigment and its protein may account for the 'green death' phenomenon (J. Rawlins, *pers. comm.*). Rawlins observed that recently acquired specimens (less than 5 years old) retained their colour under the moist conditions required for relaxing moths prior to setting for display. Older specimens (more than 5 years old) very quickly lost their colour if exposed to this regime, although specimens stored under normal conditions retained their colour. Given that geoverdin becomes highly unstable when removed from its associated protein, it seems likely that degradation of the protein over time produces the 'green death' phenomenon. It appears that about 5 years is the length of time required to loosen the pigment-protein bond sufficiently for the change of conditions to trigger decomposition of geoverdin.

The instability of geoverdin once separated from its associated protein *in vitro* was one of the major problems hampering complete chemical analysis of this pigment. The key to this problem may lie in retaining the pigment-protein complex throughout the analysis, and subtracting the effects of the protein after analysis. Investigation of the protein and its bonding to geoverdin might also provide the solution to the 'green death' problem. If it is true that degradation of the protein causes this problem, then it could be possible to encourage geoverdin to bind to another protein to enhance the longevity of the colour.

Compared with other techniques of analysis, the method of pigment profiling is a relatively simple means of comparing pigments across a wide range of taxa. The advantages of this protocol over previous approaches are firstly that it requires far less investment in time, material and cost than complete chemical analysis of pigments. Secondly, it provides a more rigorous test of homology than the chemical tests employed by Ford (1941, 1942 1944a, b, 1947) which tested only for the presence of a single functional group. In principle, thin layer chromatography is a very sensitive method for separating substances and can distinguish between different pigment molecules which have the same functional group.

The techniques of extraction and methylation described above are faster and gentler than those previously employed, and chromatographic profiling allows tests to be made for the presence of a particular substance without the need for extensive chemical analysis and identification. The protocol can be used on as little material as one wing in this system and could, with appropriate modifications, be extended to other pigment systems, to make a further, and independent, suite of characters accessible to lepidopteran taxonomists.

Chapter 3
Tympanal organs

CONTEXT

Tympanal organs of Geometridae have received little attention since the influential work of Kennel and Eggers (1933), although those of Pyralidae and Noctuidae have been more extensively researched (e.g. Fullard, 1984; Maes, 1985, 1987; Minet, 1983; 1988; Richards, 1933). The work of Kennel and Eggers (1933), although detailed and extensive, was limited by the technology of the time. Moreover, its purpose was to describe the diversity of hearing organs rather than to attempt to use these structures to formulate explicitly phylogenetic hypotheses.

An initial survey of the literature on hearing organs highlighted problems in the nomenclature. One example of this is the tympanic lacinia (Cook and Scoble, 1992; reprint bound in at the end of this section). This structure, which occurs in some Geometridae, was referred to as a *Tympanaldeckel* by Kennel and Eggers (1933). However, Sick (1937) also described a *Tympanaldeckel* in the Uraniidae, a structure which, although it is probably analogous in function, is morphologically quite different to the geometrid *Tympanaldeckel* of Kennel and Eggers (1933). In order to simplify the terminology and clarify the homologies, a review of tympanal organs and their associated structures in Geometridae was undertaken and a revised nomenclature proposed for previously described, and some new, structures (Cook and Scoble 1992).

The most striking aspect of the tympanal organs of Geometrinae is their great similarity, particularly with respect to the shape of the ansa. In all but one of the 47 species of Geometrinae examined (*Dysphania numana* Cramer: this observation is discussed in chapter 6), the ansa is narrow at the base, widens characteristically above the base and then narrows towards the apex. The apex is unmodified, in which aspect it differs from the ansa of some Sterrhinae and Larentiinae, (e.g. Figs 7 and 9g in Cook and Scoble, 1992). An ansa of similar shape to that of Geometrinae also occurs in some other Geometridae (e.g. *Abraxaphantes perampla* Swinhoe (Oenochrominae *sensu lato*), *Pareclipsis umbrata* Warren (Ennominae), *Leptomiza parableta* Prout (Ennominae) and *Lobocleta flexicosta* Warren (Sterrhinae)). Although the phylogenetic position of *A. perampla* is uncertain (in common with that of other Oenochrominae *sensu lato*, Scoble and Edwards, 1990), there is no evidence that the other species should be included in, or are sister-groups of the Geometrinae. For example, none of them are green.

Evidence for the shape of the geometrine ansa being a derived character comes from the occurrence of a differently shaped ansa in the Archiearinae, which may be the sister group of all other Geometridae (see Chapter 4). Moreover, the geometrine ansa does not occur amongst the robust-bodied Ennominae which are believed to be the more primitive members of this subfamily (Common, 1990). The characteristic shape of the ansa of the Geometrinae is therefore provisionally considered to be an apomorphy of the subfamily.

Within the Geometrinae, little variation in structure was observed using light microscopy, the chief variations being the presence or absence of a tympanic lacinia, or a lobe on the bullae tympani. The taxonomic importance of these structures is discussed in Chapter 4.

A reprint of Cook and Scoble (1992) is bound between this page and chapter 4.

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Tympanal organs of geometrid moths: a review of their morphology, function, and systematic importance

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Abstract. The basic components of the tympanal organs of Geometridae are described against the background of the relevant literature. The work is prefaced by a summary of the occurrence of hearing organs within adult Lepidoptera as a whole, and the systematic value of these structures is assessed. A Latin-based nomenclature is proposed to standardize the terminology. An assessment of the morphological variation of these organs within the Geometridae was based on the study of over 230 species representing numerous examples from all the subfamilies. Morphological variation between and within the geometrid subfamilies is discussed.

Introduction

Complex hearing organs are known from only fifteen of the 119 (Common, 1990) families of Lepidoptera. However, because some of these families (Pyralidae, Geometridae and Noctuidae) are the most speciose within the order, about half of all lepidopteran species bear such organs. Given the large number of species in which tympanal organs occur, and the morphological complexity and variation that they exhibit, it is hardly surprising that these structures are of considerable taxonomic importance; indeed their value has long been recognized. Although there have been several important studies of lepidopteran hearing organs (see below) these structures are not routinely examined by taxonomists. There are probably three main reasons for this. Firstly, most studies have made use of hearing organs at higher taxonomic levels (e.g. Börner, 1925, 1939; Kennel & Eggers, 1933; Minet, 1983). Secondly, most of the important literature is in languages other than English and seems to have been largely neglected by English speakers. Thirdly, the proper preservation of abdominal hearing organs requires special care. All too frequently, these organs are damaged or lost during routine genitalia preparation for taxonomic work.

The tympanal organs of Geometridae, a family with approximately 20,000 described species, have been less extensively studied than those of Pyralidae or Noctuidae. Here, we pay particular attention to providing a standard Latinized terminology, hoping to make the classic German paper by Kennel & Eggers (1933) more accessible to English speakers. In addition, we discuss observations from a much wider sample of geometrid species. This account is prefaced by a summary of the family-level occurrence of hearing organs in adult Lepidoptera. The purpose of this preliminary section is to update summaries by other authors and to put the work on geometrid hearing organs into perspective. The aims of this paper are to review the general morphology of these structures, provide a uniform nomenclature, and assess their systematic importance in Geometridae.

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Function of lepidopteran hearing organs

Hearing organs in adult Lepidoptera appear to function in defence against bats, or in courtship. Insectivorous bats use ultrasonics to locate their prey, and evidence suggests that a considerable reciprocal response has evolved between predator and prey (e.g. Fenton & Fullard, 1979, 1981).

Intraspecific communication by scent is well known in Lepidoptera, but some species also use sound. For example, the lesser wax moth, *Achroia grisella* (Pyralidae) uses sound signals in courtship (Dahm *et al.*, 1971; Spangler *et al.*, 1984). Other examples have also been found in the Pyralidae (e.g. Zagatti, 1981; Gwynne & Edwards, 1986) and Arctiidae (Sanderford & Conner, 1990), and there are likely to be many more. As yet, there is no evidence that sounds are produced by adult Geometridae, so there is nothing to suggest that the hearing organs in this family are used in courtship.

The function of alar hearing organs (see below) is unclear. It is unlikely that those in Nymphalidae, a family of diurnal Lepidoptera, function in defence against bats; such a function is more likely in Thyrididae, which are nocturnal. The alar organs of Hedylidae may function in defence against bats, for although some species have been observed flying by day the family is predominantly nocturnal.

The number of acoustic sense cells present in the hearing organs varies in different families of Lepidoptera. Geometridae have four acoustic sense cells, A1, A2, A3 and A4 (Kennel & Eggers 1933; Roeder, 1974), whereas most Noctuidae have only two (A1 and A2) and Notodontidae only one (Fullard, 1984). Roeder (1974) showed that the difference in sensitivity between A1 and A3 in Geometridae was approximately equivalent to that of A1 and A2 in Noctuidae. The geometrid A2 receptor, which is functionally interpolated between A1 and A3, gives better intensity discrimination in the lower range of sound intensities. Roeder (1974) suggested that whilst data on the geometrid A4 receptor is limited, its range probably overlaps that of the other receptors.

The greater overlap of the ranges of the acoustic sense cells in Geometridae would be expected to give them finer sound intensity discrimination and should confer an advantage over Noctuidae in escaping from bat predators. Tentative evidence for this suggestion comes from a perusal of the Longstaff collection of bat prey housed in the University Museum, Oxford. Remains from bat meals were collected from several sites in Dorset and in each case Geometridae seemed to be very poorly represented in the samples. There are, however, several other possible reasons for this imbalance, such as the relative abundance of Geometridae compared with other Lepidoptera, the search image and feeding preferences of bats and the methods of the collector, and the possibility that bats may eat the wings of geometrid moths, which are often relatively small, in addition to the bodies.

The occurrence of hearing organs in adult Lepidoptera

Significant general summaries of the variety of hearing organs in adult Lepidoptera have been provided by Sick (1935), Bourgogne (1951), Kiriakoff (1963), Treat (1963) and Minet (1983). In a recent review Spangler (1988) discussed the variety of these organs, mainly from a physiological standpoint.

As far as is known, all adult lepidopteran hearing organs are tympanal except for those of Sphingidae. Although variation occurs in the morphology and location of these structures, they are all composed of the same main elements and probably function essentially in the same way.

Lepidopteran tympanal organs basically consist of a tympanic membrane, or tympanum, stretched across the rim of a sclerotized casing. A mechanoreceptor (chordotonal organ) is attached to the tympanum. A large tracheal sac is closely appressed to that part of the body wall that has been transformed into the tympanum, so that, unlike the condition for other parts of the body wall, which lie against a haemolymph-filled cavity, the tympanum is backed by an air-filled chamber. Sound waves cause the tympanum to vibrate and these vibrations are sensed by the receptor, which transmits nerve impulses to the auditory nerve.

Tympanal hearing organs

Tympanal organs in all adult Lepidoptera are paired. Each organ is situated in a cavity – each cavity lying on either side of the metathorax, the base of the abdomen, or within the base of a wing vein.

Tineidae. The organs are abdominal, and occur only in *Harmaclona* Busck (Davis & Heppner, 1987), a pantropical genus with twenty species of which ten are named (Robinson & Nielsen, 1992). The morphology of the structure in *Harmaclona* has not been investigated in detail.

Dudgeoneidae. The organs are abdominal. The family includes the genus *Dudgeonea* Hampson, with three species, and, possibly, *Acritocera* Butler, with a single species (Schoorl, 1990). The superfamily relationship of the family is uncertain. Currently it is retained in the Cossoidea by Common (1990), but this placement was queried by Schoorl (1990). Structurally, the tympanal organs are not dissimilar to those of Pyralidae (Minet, 1983).

Pyralidae. In Pyralidae (including Pyraliformes and Crambiformes, Munroe, 1972) the organs are abdominal, and occur throughout the family (Kennel & Eggers, 1933; Bourgogne, 1951; Minet, 1982, 1983, 1985; Maes, 1985; Spangler, 1988). The tympanal organ exists in two distinct forms, a difference on which the primary division of the family is based. (These divisions have been variously ranked: Pyraliformes and Crambiformes (Munroe, 1972), or Pyralidae and Crambidae (Minet, 1982).)

Thyrididae. Species belonging to the subfamily Siculodinae have tympanal organs situated at the base of the forewings in vein Sc (Minet, 1983, 1988). The monophyly of the Thyrididae, including Siculodinae, is based on at least four apomorphies of the adult (Minet, 1991), but the presence of alar tympanal organs is an autapomorphy for the Siculodinae (*sensu* Minet, 1991).

Geometridae. The organs are abdominal and have a characteristic structure (Kennel & Eggers, 1933; Bourgogne, 1951; Minet, 1983; and see below). They occur throughout the family, but are secondarily reduced or lost in some flightless females.

Uraniidae (including Epipleminae). The tympanal organs are abdominal (Kennel & Eggers, 1933; Sick, 1937; Bourgogne, 1951; Minet, 1983), and occur throughout the family. In males they are located at the junction of the second and third abdominal segments and open dorsally or laterally; in females they open ventrally on the first abdominal sternum (morphologically sternum 2).

Drepanidae. In Drepanidae (including Drepaninae, Thyatirinae, Cyclidiinae, and the genus *Hypsidia* Rothschild), the organs are abdominal, occur throughout the family, and have a characteristic structure (Kennel & Eggers, 1933; Gohrbandt, 1937; Bourgogne, 1951; Minet, 1983; Scoble & Edwards, 1988). Each is derived from the tergo-sternal sclerite connecting tergum A1 with sternum A2 (the first visible sternum), and takes the form of a small oval structure composed of two interconnecting chambers, one small and one larger. The tympanum lies between these chambers, that is, inside the organ. In most species the larger chamber fuses with sternum A2, and may be mistaken for a sternal structure. The pleural chamber is always clearly formed by the dorsal part of the tergo-sternal sclerites. The structure of these organs is unique to Drepanidae and provides an autapomorphy for the family.

Nymphalidae. The organs are alar, and associated with certain veins at the base of both forewings and hindwings (Vogel, 1912; Bourgogne, 1951; Swihart, 1967). They occur in many, but by no means all, members of the family. The precise distribution of these structures within the Nymphalidae has not been determined, and their phylogenetic value has yet to be assessed.

Hedylidae. The organs of these moth-like butterflies are alar, occurring at the base of the forewing (Scoble, 1986; Minet, 1988). Present in all species, they are associated with chambers at the bases of the subcostal and cubital veins. Their position suggests that they are autapomorphies for the family, the presence of tympanal organs at the base of the wings in Siculodinae (Thyrididae) and in many Nymphalidae being independently derived.

Noctuoidea. In Noctuoidea the hearing organs (Eggers, 1911, 1925; Richards, 1933; Bourgogne, 1951; Spangler, 1988) are metathoracic, each organ lying between the epimeron and the postnotum. The morphological variation of these structures and their systematic value within the superfamily was discussed by Kiriakoff (e.g. 1963) and Kitching (1984). The metathoracic position of these tympanal organs and their morphology are unique to this superfamily.

Organs claimed to be tympanal

Axiidae. Paired organs on the seventh abdominal segment of the Axiidae, a family of about six species in a single genus (*Axia*), have frequently been considered to be tympanal (e.g. Bourgogne, 1951). Each is pleural, with a pleural pocket opening posterior to the spiracle (Minet, 1983: fig. 94). However, no associated sense organs have been discovered, and there is nothing else to suggest that they are auditory (Minet, 1983). These structures, whether or not they are actually auditory, are autapomorphic for the Axiidae.

Cossidae. 'Prototympanal organs' were said to occur in *Pseudocossus* Kenrick from Madagascar (Clench, 1959), and in the Chilean genera *Chilecomadia* Dyar and *Rhizocossus* Clench (Clench, 1957). However, Minet (1983) was unable to find any trace of tympanal organs in *Pseudocossus*. *Chilecomadia* is also devoid of tympanal organs (Schoorl, 1990; Minet, 1991).

Non-tympanal hearing organs

Sphingidae. The organs are associated with the labial palpi and the pilifers of members of the Choerocampini (a tribe of the subfamily Macroglossinae; I. J. Kitching, pers. comm.) (Roeder & Treat, 1970; Roeder, 1972). The second segment of each labial palpus is swollen and is capable of being displaced phasically by ultrasonic vibrations. This segment lies against the pilifer, the structure in which the mechanoreceptor is situated. No tympanum is present. The occurrence of these hearing organs is likely to be an autapomorphy of the Choerocampini, a group with worldwide distribution and including about 160 species (I. J. Kitching, pers. comm.).

Methods

In addition to information gained from the literature, the tympanal organs were examined in 250 species of Geometridae, representing 163 genera (see Appendix 1). These taxa were selected to represent at least one example from each tribe recognized by previous workers in an attempt to cover a substantial amount of the variation within each of the subfamilies. The material examined included slide mounted material in The Natural History Museum, London (BMNH), and preparations of dried specimens made during the course of this study.

Abdomens were removed from the thorax carefully to avoid damaging the tympanum or the accessory tympanum of the metathoracic postnotum. Tympanal organs were then mounted on stubs, coated, and viewed with an electron microscope or, alternatively, macerated in hot 10% KOH for approximately 5 min, cleaned, stained with mercurochrome and made into permanent slide preparations for viewing by light microscopy. All permanent slide preparations are housed in the collections of BMNH.

General morphology of geometrid tympanal organs

Kennel & Eggers (1933) and Minet (1983) applied different names to describe the components of geometrid tympanal organs. Kennel & Eggers' terms are German and most of Minet's are French. These are listed under the descriptions of the structures below, and a standardized English nomenclature is proposed. We have made this terminology Latin based where appropriate, following Maes (1985), who worked on the tympanal organs of Pyraloidea. In addition, we have replaced certain terms with alternatives considered more appropriate and have avoided using those which appear superfluous.

Minet (1983) suggested that the tympanal organs are essentially similar throughout Geometridae and that generally little sexual dimorphism exists in the basic structure. Examples of significant sexual dimorphism are rare, occurring mainly in wingless or vestigially winged females (e.g. *Phigalia* Duponchel and *Hybernia* Berthold) where the tympanal organs are reduced (see Heitman, 1934).

However, minor sexual dimorphism does occur in the tympanal organs of some fully winged Geometridae. For example, in *Anisozyga pieroides* (Geometrinae) the female has a lobe on each cavus tympani (see below) which is absent from the male. Essentially, the tympanal organs of Geometridae appear as a capsule with the tympanum, supported by a frame, situated medially and anteriorly.

Cavus tympani (Figs 1–4)

The *cavi tympani* (*Tympanalgrube*; *cavité tympanique*) are paired, deep, ventrolateral, walled cavities formed from a ventro-lateral invagination of the first abdominal segment. Laterally, each cavus lies against the pleuron and ventrally against sternum 2 (the first visible sternum in all Heteroneura). It opens ventrolaterally, although its aperture may be covered with scales.

The cavi tympani are not homologous with the bullae tympani (*sensu* Maes, 1985) (i.e. caisses tympaniques of Minet, 1983) of Pyralidae. Whereas the bullae tympani of Pyralidae are internal sclerites surrounding the air sacs containing the scoloparia, the cavi tympani of Geometridae are merely deep hollows, which open externally (Minet, 1983).

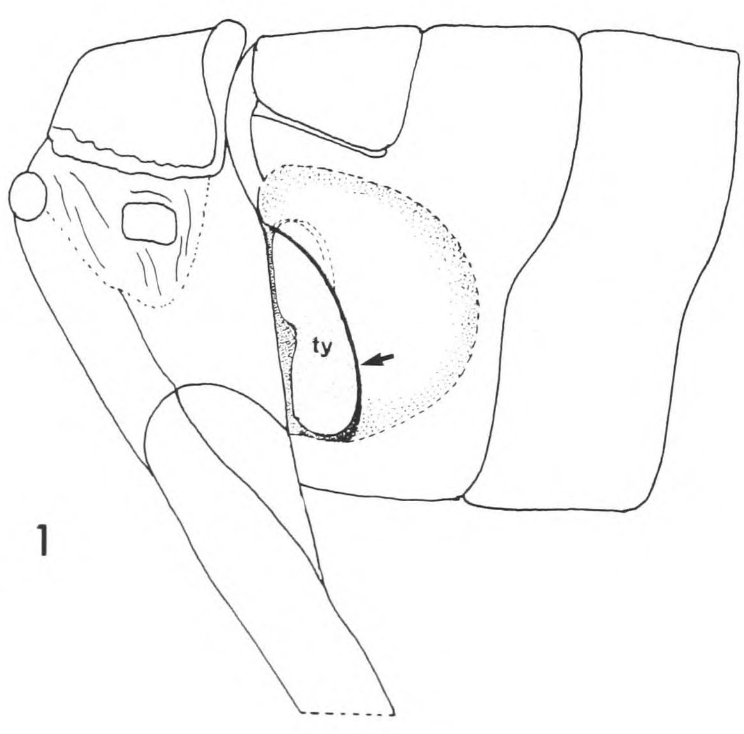
The ventral anterior edge of the cavus merges with the sternum so that there is no distinct boundary between them. The free lateral margin of the cavus is a particularly strong sclerotized brace (*Grubenrahmen*, of Kennel & Eggers (1933), see Fig. 2). On the inner wall of the cavus another sclerotized brace (*feste Trommelfelleinfassung*, *Trommelfellrahmen*, see Fig. 2) partly encircles the tympanum, forming a rigid frame across which the latter is stretched.

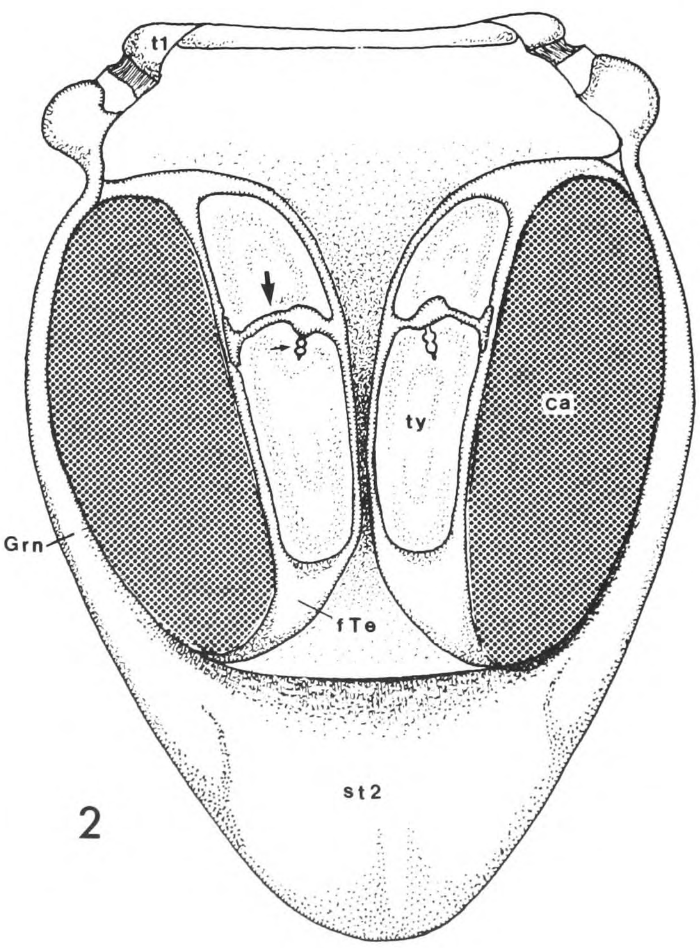
One source of variation in the cavi tympani is their relative size compared with the rest of the abodmen. In some genera they are sufficiently large, compared with the diameter of the abdomen, that their walls touch medially (e.g. as in *Sangala* Walker (Ennominae)). In others, such as *Oospila* Warren (Geometrinae), they are small compared with the diameter of the abdomen and are thus widely separated. Variation also occurs in their depth, which may be greatly elongated as in *Sangala* (Ennominae).

Occasionally, a lobe, of variable size, occurs at the posterior end of the cavus. The presence of this structure is rare and is restricted largely to the Ennominae.

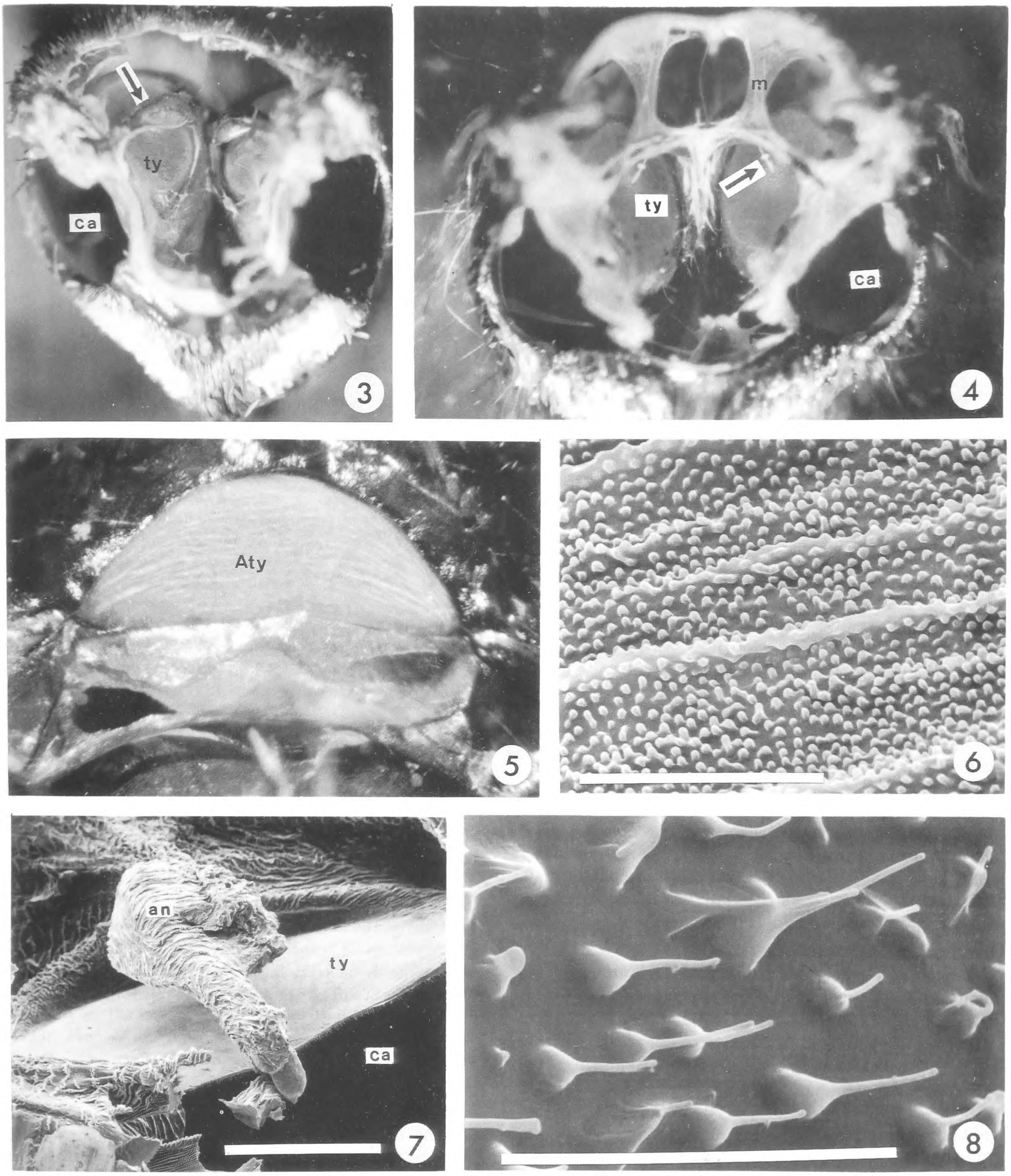
Tympanum (Figs 1–4, 7, 8, 10–12)

The tympanum (*Trommelfell*; eardrum) is an extremely thin, roughly circular, iridescent membrane (Figs 3, 4, 7). The circumference of most of the tympanum is supported by the peritympanal frame of the cavus, which allows this thin membrane to be held in shape and under tension. Where the tympanum is not supported by the frame, that





Figs 1–2. Tympanal organs of Geometridae: 1, lateral view of metathorax and base of abdomen of *Larentia tristata*. Outline of cavus tympani indicated by broken line. Sclerotized edge of cavus arrowed. Tympanal surface is that facing opening of cavus to exterior. Modified from Kennel & Eggers (1933); 2, anterior end of abdomen of *Lygris prunata* after removal from metathorax showing cavi tympani, ansa (large arrow), scoloparium (small arrow) and tympanum. After Kennel & Eggers (1933): ty, tympanum; ca, cavus tympani; st2, sternum 2; t1, tergum 1; fTe, feste Trommelfelleinfassung/Trommelfellrahmen; Grn, Grubenrahmen/weiche Trommelfelleinfassung.



Figs 3–8. Tympanal organs of Geometridae: 3, anterior end of abdomen of *Sangala beata* showing cavi tympani (ca), tympanum (ty), and ansa (arrowed); 4, as for 3 of *Archiearis parthenias*, with scoloparium arrowed, dorsal cavus muscle (m); 5, accessory tympanum of metathoracic postnotum (Aty) of *Sangala sacrata*; 6, SEM of part of surface of accessory tympanum of *Pseudoterpna pruinata atropunctaria*; 7, SEM of tympanum (ty) and ansa (curved over tympanum, an) of *Hemistola chrysoprasoria* (ca, cavus tympani); 8, SEM of part of tympanal surface of *Archiearis parthenias* showing spines (presumably microtrichia) on the surface of the tympanum which faces the cavus aperture. Scale bars: 6, 10 μm; 7, 174 μm; 8, 10 μm.

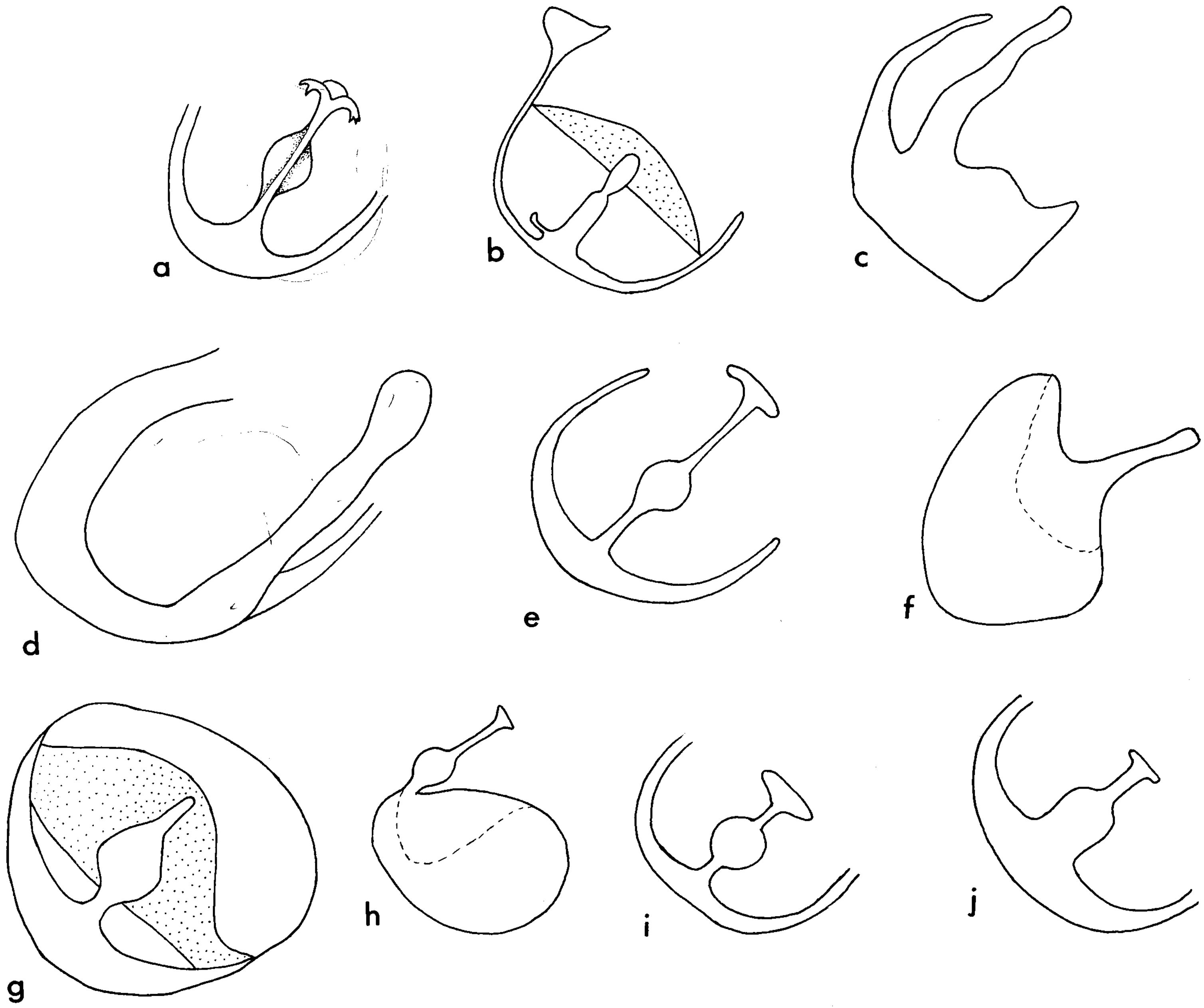


Fig. 9. Part of cavus tympani showing ansa of Geometridae: a, b, Ennominae: (a) *Oxymacaria persimilis*; (b) *Tephrina pulinda deerraria*, lacinia stippled; c–f, Oenochrominae s.l.: (c) *Antasia flavicapitata*; (d) *Celerena lerne*; (e) *Eumelea horinata*; (f) *Zeuctophlebia squalida*; (g) *Geometra papilionaria* (Geometrinae), lacinia stippled; (h) *Pleuroprucha rudimentaria* (Sterrhinae); i,j, Larentiinae; (i) *Chloroclystis hawkensi*; (j) *Eustroma elista*.

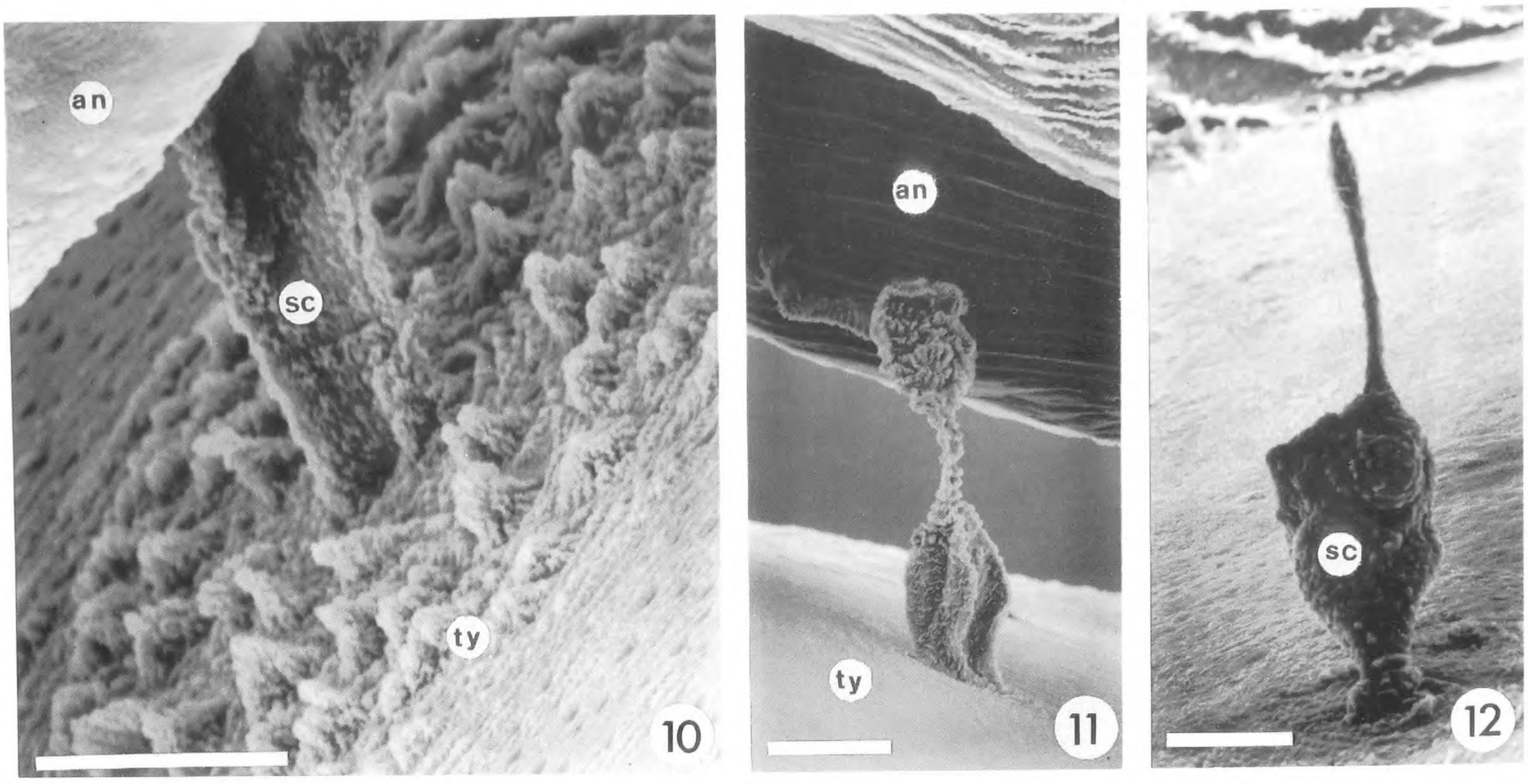
is along its morphologically anterior margin, it borders on the thoraco-abdominal membrane.

Kennel & Eggers (1933) described the surface of the tympanum as being textured and covered with fine thorns (*Dörnchen*). Also, they noted a bulge (*Randwulst des Trommelfelles*) in front of the tympanum at the aperture of the cavus. This they considered to be similar to the nodular sclerite (epaulette) in Noctuidae. The detailed structure of the surface of the tympanum to which the scoloparium is attached varies considerably within the Geometridae. In general, the surface of the tympanum around the point of attachment of the scoloparium has quite a different structure to the rest of its surface. For example, in *Oenochroma vinaria* (Oenochrominae *sensu stricto*) the scoloparium is surrounded by pointed projections raised above the surface of the tympanum (Fig. 10), although this is not so marked in other species, as, for example, in *Geometra papilionaria* (Geometrinae, Fig. 11).

The surface of the tympanum facing the aperture of the cavus (the other side from the surface to which the scoloparium is attached) is covered with small spines (presumably microtrichia). The basal third of these adornments are broad but the apical two-thirds are very narrow (Fig. 8).

Accessory tympanum (Figs 5, 6)

The accessory tympanum (*akzessorische Trommelfell*; *tympan accessoire*), a prominent membrane in all subfamilies of Geometridae except Archiearinae, was said to be formed from a thinning of the metapostnotum by Kennel & Eggers (1933), and was regarded as an enlarged fenestra media by Minet (1983) – a membrane separating the metascutellum from the crown of the first abdominal tergum. In Archiearinae, which are nevertheless tympanate, the metapostnotum is uniformly rigid, not membranous, apart from the presence of a very narrow fenestra media (Minet, 1983: 197). The function of the fenestra



Figs 10–12. 10, *Oenochroma vinaria*, surface of tympanum (ty) surrounding point of attachment of scoloparium (sc), (an, ansa); 11, scoloparium of *Geometra papilionaria* showing the two swellings (an, ansa; ty, tympanum); 12, scoloparium (sc) of *Hemistola chrysoprasoria*. Scale bars: 10, 15 μm; 11, 25 μm; 12, 15 μm.

in the acoustic system of the Geometridae is not understood, nor is it even known whether the structure actually has an acoustic function at all for it is widespread in Lepidoptera, and by no means restricted to those groups with tympanal organs.

Ansa (Figs 2–4, 7, 9, 15, 16)

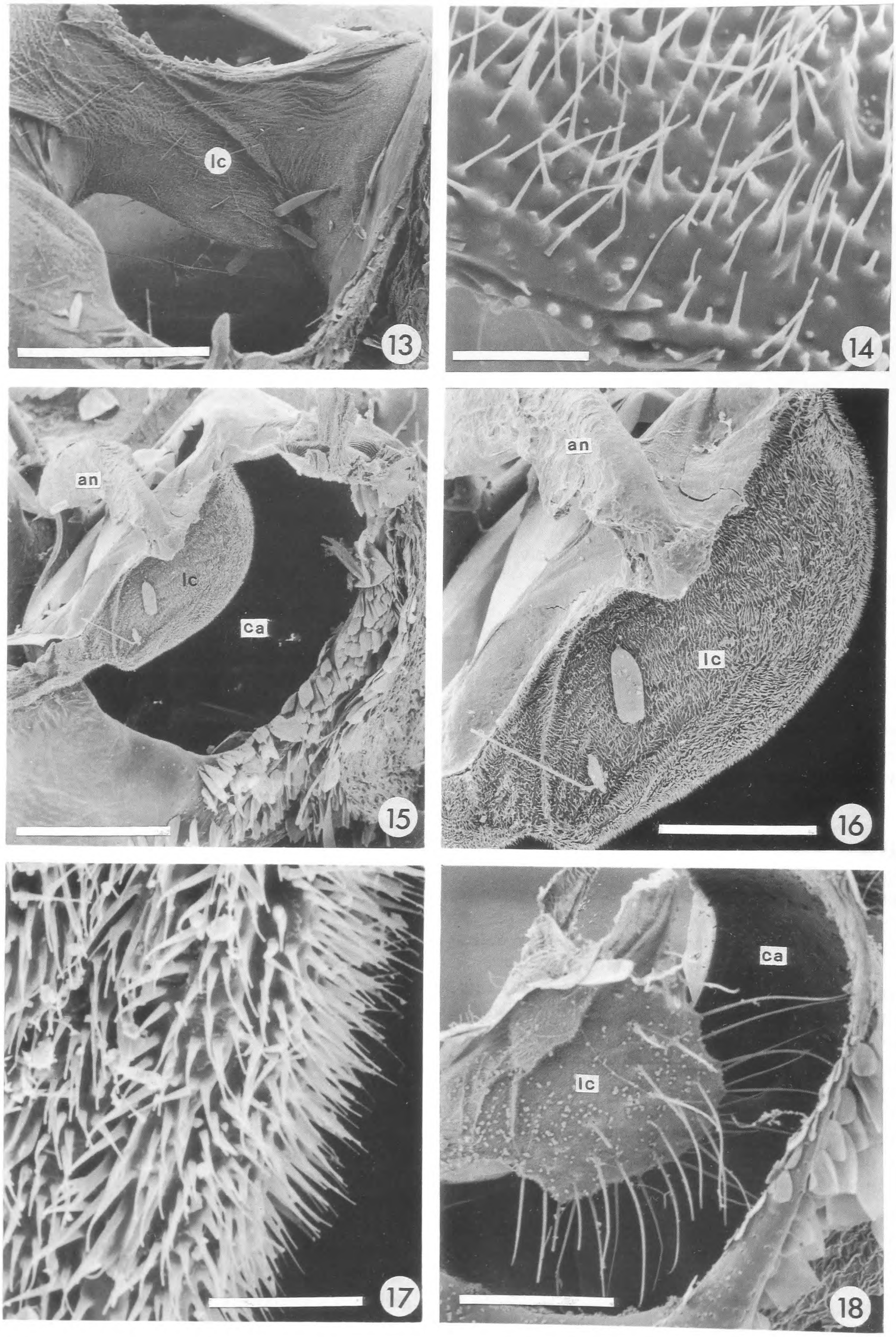
The ansa (*Bügel; anse tympanique*) is a structure unique to the Geometridae and represents a prominent autapomorphy of the family. It extends from the inner wall of the cavus and curves over the tympanum (e.g. Figs 2, 7). The ansa is hollow with an approximately circular lumen. The scoloparium (tympanal receptor) is strung between the ansa and the tympanum (Figs 2, 4). Besides acting as a point of attachment for the scoloparium, two other functions for the ansa were suggested by Kennel & Eggers (1933). Firstly, the ansa may act as a protective barrier between the delicate tympanum and the surrounding organs, particularly the oesophagus and the flight muscles, which threaten to damage the tympanum mechanically by pressure. Secondly, the ansa, particularly where it has a wide base, would appear to strengthen the edge of the inner wall of the cavus, thereby helping to maintain tension across the tympanum.

The ansa shows considerable variation in shape across the family (Fig. 9), variation that may be of some taxonomic value at the subfamily level. For example, in nearly all Geometrinae it narrows just above its base and then widens to a broad flat structure (*Bügelverbreiterung* of Kennel & Eggers, 1933) before narrowing again at the tip (Figs 7, 9g). In the Larentiinae, however, the ansa frequently broadens again at the tip to give it a hammer-headed shape (Fig. 9i, j) (*tête de marteau* of Minet, 1983). The 'free' end of the ansa is bound, by way of muscle fibres, either to the tympanic lacinia (where present) or to bands of cuticle in the thoraco-abdominal membrane. Where a tympanic lacinia (see below) is present, an additional set of muscle fibres from the tip of the ansa are attached laterally and ventrally to the abdomen. In both cases, Kennel & Eggers (1933) suggest that the function of these muscles is to bring the tympanum closer to the ansa or to the tympanic lacinia. In species where the end of the ansa is broad, the muscle fibres from its tip run almost parallel towards their other insertion. The muscles radiate out from the tip of the ansa in those species where it is narrow.

Tympanic lacinia (Figs 13–18)

Where present, the tympanic lacinia (*Tympanaldeckel* (*sensu* Kennel & Eggers, 1933), *cardo*, *sclerite cardinal*) usually lies at right angles to the ansa and hangs down inside the cavus (i.e. below the tympanum), partly (Figs 13, 15, 18) or completely obscuring its aperture. In most geometrid subfamilies it is a roughly semicircular or circular plate. However, in the Archiearinae it is a band-like structure and obscures little of the aperture of the cavus (Fig. 13). In *Oenochroma* and *Arhodia* (Oenochrominae *sensu stricto*) the lacinia is roughly circular and lies directly beneath and parallel to the tympanum, so that it hardly obscures the aperture of the cavus at all.

The surface of the lacinia facing the exterior of the animal is covered in rows of small spines (presumably



Figs 13–18. SEMs of tympanal organs of Geometridae showing laciniae (lc): 13–14, *Archiearis parthenias* L. 13, general view; 14, detail of part of surface showing the spines (presumably microtrichia) on the external surface of the lacinia; 15–17, *Pseudoterpna pruinata atropunctaria*. 15, 16, general views; 17, detail of part of surface, showing the spines (presumably microtrichia) on the external surface (an, ansa; lc, lacinia; ca, cavus tympani); 18, *Neohipparchus vallata*, general view, showing the large bristles on the lacinia (lc) which appear to be an autapomorphy of *Neohipparchus* (ca, cavus tympani). Scale bars: 13, 0.5 mm; 14, 10 µm; 15, 0.3 mm; 16, 138 µm; 17, 13.7 µm; 18, 176 µm.

microtrichia) (Figs 14, 17), which differ in appearance from those on the external surface of the tympanum. A rare modification of the lacinia occurs in *Neohipparchus vallata* (Geometrinae) which, in addition to these small spines, also bears much larger stiff bristles (Fig. 18) concentrated along the edge of the lacinia and lying across that part of the cavus aperture not obscured by the body of the lacinia. It seems likely that the lacinia and its associated structures have a protective function, probably serving to exclude any particles that might otherwise damage the delicate tympanum.

The tympanic lacinia should not be confused with the *Tympanaldeckel* described by Sick (1937), which is composed of a group of long scales partly obscuring the opening of the tympanal cavity of Uraniidae. Thus, the *Tympanaldeckel sensu* Sick is morphologically quite different from the *Tympanaldeckel* described in the Geometridae by Kennel & Eggers (1933), although the function of these structures may be similar.

Dorsal cavus muscle (Fig. 4)

This muscle, here termed the dorsal cavus muscle (*dorsaler Tympanalgrubenmuskel*), is especially conspicuous in those taxa with small tympanal organs (e.g. *Abraxas grossulariata*, *Biston* Leach (Ennominae); *Larentia* Stephens (Larentiinae)) although the extent of its occurrence in the Geometridae is unknown. The muscle runs from the posterior surface of the antecosta of abdominal tergum A2 to the posterior dorsal wall of the corresponding cavus tympani. Possible functions of this muscle include suspension of the tympanal organs, and protection of the tympanum by preventing the gonads from pushing forward (Kennel & Eggers, 1933). However, its importance has not yet been established, nor is it known whether the contraction of this muscle has any significance for the sensory performance of the tympanal organs.

Scoloparium and the tympanal nerves (Figs 2, 4, 10–12)

The tympanal receptor, or scoloparium, is a modified chordotonal organ. It runs from the middle of the ansa to its other point of attachment at the centre of the tympanum. The scoloparium is a twisted, convoluted, membranous structure.

Usually, the scoloparium has two swellings (Fig. 11), although there is only a single swelling in some species (Fig. 12). The swelling closest to the tympanum contains the main bodies of the sense cells with their nuclei. The other swelling, where present, occurs at the joint between the tympanal nerve and the scoloparium. Each tympanal organ in Geometridae has four acoustic cells. The distal dendrites from these cells, after becoming attached to the tympanum, are folded back on themselves, and since the scolopales are therefore directed away from the tympanum the scoloparium is said to be inverse (Kennel & Eggers, 1933). The tympanic nerve runs from the scoloparium, along the ansa and then anteriorly away from the tympanal organs through the constriction between the thorax and the abdomen. It enters the posterior region of the pterothoracic ganglion on either side of the connectives running between the thorax and the abdomen.

In *Archiearis parthenias* (Archiearinae) a string-like structure, loosely attached to the midpoint of the scoloparium, extends to the ansa. It is possible that this structure may be analogous to a ligament occurring in Noctuidae.

Subfamily differences in structure

Presented below is a summary of the subfamily differences in geometrid tympanal organs noted by Kennel & Eggers (1933), together with comments based on observations from the species examined in this study.

Archiearinae. Archiearinae lack an accessory tympanum, but they have a very narrow fenestra media (Minet, 1983). The medial walls of the cavi tympani often meet mesally (Fig. 4), and the entire capsule is often somewhat elongated. The ansa is commonly wide at the base and narrows towards the tip. But it may widen just above the base and narrow again towards the tip (e.g. as in Geometrinae). Where present, the tympanic lacinia is a sclerotized band (Fig. 13) obscuring very little of the aperture of the cavus. The additional ligament-like structure found in *Archiearis parthenias* (see above) has not been found in any other geometrid subfamily. Its presence may therefore be an autapomorphy for the group.

Ennominae. The tympanal organs are usually well separated, but in *Cypra delicatula* the walls of the cavi touch mesally. The organs range in size and shape from very large and round (as in *C.delicatula*, for example), to greatly elongated (as in *Sangala caelisigna*), to rather small (as in *Abraxas illuminata*). The shape of the ansa varies widely in this subfamily (compare Figs 9a and 9b) and there are some modifications unique within the Ennominae. For example, the asymmetric extension of the ansa in *Tephrina pulinda* (Fig. 9b) and the umbrella-shaped modification to the tip of the ansa of *Oxymacaria persimilis* (Fig. 9a) have not been observed outside this subfamily.

In addition, the occurrence of a lobe on the cavus wall is largely restricted to this subfamily. The tympanic lacinia is usually semicircular in shape and lies perpendicularly to the tympanum, partly obscuring the opening of the cavus.

Oenochrominae sensu stricto. The ansa of *Oenochroma* Guenée and *Parepisparis* Bethune-Baker is wide at its base and narrows towards the tip. In some species of *Parepisparis* the ansa widens again slightly at the tip (e.g. as in *P.virgatus* and *P.multicolora*). In *Oenochroma* and *Arhodia* the tympanic lacinia is a circular structure and lies directly beneath, and parallel to, the tympanum.

Oenochrominae sensu lato. The tympanal organs are rather variable, especially with regard to the shape of the ansa. This situation is not unexpected given the probable polyphyletic nature of the group (Scoble & Edwards, 1990). The form of the ansa most commonly encountered is one with a broad base which narrows evenly towards the tip, but which lacks a secondary widening. However, many forms of ansa similar to those of other subfamilies were also found (Fig. 9).

Geometrinae. The tympanal organs of this subfamily seem to be the most structurally homogeneous within the Geometridae. The diameter of the tympanum is usually about half the length of tergum A2, and the tympanal organs are usually separated from one another and do not meet mesally. The ansa usually narrows just above its base, widens to appear as a broad flat surface (*Bügelverberiterung* of Kennel & Eggers, 1933), and then narrows again to the tip (Fig. 9g). The widened section is not always symmetrical.

Sexual dimorphism in the structure of the tympanal organs is rare, occurring in only two of the forty-seven species examined. The female of *Anisozyga pieroides* has a lobe on the wall of the cavus which is not present in the male. In the male of *Aracima mucosa*, the ansa is wide at the base, narrows towards the tip, but lacks the secondary widening above the base which occurs in the female and in other Geometrinae. Also exceptional among the Geometrinae is *Dysphania numana*, where the ansa widens at its tip to give a hammer-headed shape (see Discussion).

Sterrhinae. The tympana are usually quite large compared with the diameter of the abdomen. Despite the large size of the tympanum, the tympanal organs are usually separated from one another and do not generally meet mesally. The ansa is broad or narrow at the base, widens above its base and commonly has a hammer-headed tip (Fig. 9h). A tympanic lacinia was found only in *Scopula pseudocorrivalvaria* and no species were found with a lobe on the wall of the cavus.

Larentiinae. The tympana are small but the tympanal organs in their entirety usually lie close together mesally. The larentiine ansa usually broadens out at its apex (Figs 9i, j) to give it the hammer-headed shape ('tête de marteau') noted by Minet (1983). The broadening of the apex may be rounded or angular. A tympanic lacinia occurs rarely, and none of the species examined had a lobe on the wall of the cavus.

Discussion

The structure of abdominal tympanal organs effectively characterizes, individually, as monophyletic units, superfamily Pyraloidea, family Geometridae, family Uraniidae and family Drepanidae. Also, within Pyraloidea, the primary division into Pyraliformes and Crambiformes (or Pyralidae and Crambidae) was established by tympanal organ morphology (Kennel & Eggers, 1933; Börner, 1925; Munroe, 1972; Minet, 1982; Maes, 1985). Although in Dudgeoneidae the tympanal organs are similar in structure and position to those of Pyraloidea (Minet, 1983), the family was excluded from the latter on the basis of other characters (Common, 1990; Minet, 1991).

But although abdominal tympanal organs provide a source of autapomorphic characters for particular higher taxa, they appear to have limited value in determining phylogenetic relationships between any of these taxa.

Relationships of Lepidoptera with abdominal tympanal organs

The first comprehensive use of tympanal organs was made by Börner (1939). He associated Pyralidae, Geometridae, Uraniidae, Drepanidae and 'Cymatophoridae' (= Thyatirinae and Cyclidiinae) in Pyraloidea, apparently because all have tympanal organs at the base of the abdomen. But he subdivided his Pyraloidea to distinguish the Drepanidae and 'Cymatophoridae' (Drepanina in his sense) from the other three families on the basis of structural differences of these organs. Börner's conclusions were based particularly on the detailed study of Kennel & Eggers (1933), the authors who recongized four kinds of abdominal organs (those of Pyralidae, Geometridae, Drepanidae (in their sense) and Uraniidae).

The suggestion that all these families should be united in a single group was queried by Minet (1983) who considered that the differences in structure, position, or both structure and position, between the families failed to indicate a common derivation. In the absence of other reasons for taxonomic union, Minet separated the various families into four superfamilies (Pyraloidea, Geometroidea, Uranioidea and Drepanoidea).

Prior to the study of Minet (1983), but after that of Börner (1939), a hybrid system gained general acceptance in which the Geometroidea were expanded to include Uraniidae, Drepanidae, Thyatiridae and Geometridae (and certain other families without tympanal organs) (summary in Fletcher, 1979), but the Pyralidae were still separated as Pyraloidea.

If the mere presence of abdominal tympanal organs in the families or superfamilies mentioned above indicates common ancestry, then the hybrid system, which excludes Pyraloidea from the rest, is inconsistent. But the association of all those taxa on the basis of having abdominal tympanal organs is also unsupportable. For example, the tympanal organs of *Harmaclona* (Tineidae) and, say, Geometridae, have surely developed independently, and those of Geometridae and Pyralidae exhibit many fundamental structural differences. For the abdominal tympanal organs in the different groups to be homologous, ontogenetic similarity or morphological similarity, or both of these, need to be established.

Tympanal organs situated at the base of the abdomen are likely to have a common sensory basis, namely the ventral chordotonal organs in segment A2 (Kristensen, 1984). But the presence of such chordotonal organs is extremely generalized and by no means confined to tympanal-bearing Lepidoptera. Although similarity of position (allowing for differences resulting from differential growth) of the tympanal organs is a prerequisite for homology, it does not alone establish the homology of these organs. For functional reasons, tympanal organs are likely to be restricted to those areas of the body with a chordotonal organ and an air sac. The view that these structures may be developed independently at any of the limited number of suitable body areas, such as the base of the abdomen, is therefore perfectly reasonable. The occurrence of tympanal organs on abdominal segments other than the first suggests that the organs are not homologous. Their presence on the seventh abdominal segment of Axiidae would not make them homologous with tympanal organs at the base of the abdomen in other taxa, even in the unlikely event of them being shown to be tympanal. Also, the difference in position and structure of the abdominal organs in male and female Uraniidae suggests strongly that they are not homologous. (The independent development of structures with a similar function in each sex is worthy of special consideration.)

So if a common sensory basis and a generally similar position are necessary, but not sufficient, to establish the homology of abdominal tympanal organs between the taxa under discussion, what systematic conclusions may we draw from structural comparison of these organs? Evidently, the structure of the hearing organs in Pyralidae, Geometridae and Drepanidae varies fundamentally; the derivation of the various components in these families differs (see above). For example, the bullae tympani (*caisse tympanique*) of the Pyraloidea are not homologous with the cavi tympani of Geometridae, and the double-chambered tympanal organs of Drepanidae, which are derived from tergo-sternal sclerites connecting sternum A2 with tergum A1, differ from both. The tympanal organ in male Uraniidae is apparently uniquely derived (even compared with the structure in the female), so it offers no support for a sister group relationship between this family and any other. However, that occurring in the female resembles, to some extent, the pyraloid tympanal organ. That the structural resemblance in these two groups is likely to be independently derived is supported by the absence of other synapomorphies. The suggestion (Minet, 1991) that Uraniidae should, after all, be reassigned to Geometroidea is based on two synapomorphies independent of the tympanal organs, one from the larval spinneret, and the other from the tegula of the adult.

We may conclude, with Minet (1983), that tympanal organs are of little, or no, apparent value in assessing the phylogenetic relationships between Pyraloidea, Drepanoidea, Geometroidea and Uranioidea, and nor do they support the monophyly of all Lepidoptera with abdominal tympanal organs.

Relationships of geometrid subfamilies

There is certainly some evidence that tympanal organ morphology is of systematic value at lower taxonomic levels in Pyralidae (Minet, 1982; Maes, 1985, 1987). But in Geometridae we have been able to find only limited support for the subfamily classification using information from tympanal organs. This situation merely underlines the very unsatisfactory state of geometrid classification at this taxonomic level. With the exception of Archiearinae, Oenochrominae *sensu stricto*, and the slender-bodied species of Geometrinae, the monophyly of the other subfamilies (i.e. groupings that include the great majority of geometrid species) is in doubt. Without question, there exist large groups within these subfamilies that will, with limited revision, prove to be monophyletic (e.g. many of the tribes of Ennominae). But at present a satisfactory subfamily classification of Geometridae does not exist. In the absence of a better system we continue to refer to existing subfamilies in this paper, and have listed the species examined under them in Appendix 1. To attempt to divide the Geometridae differently at present would be premature and lead to much confusion.

Although using the existing classification for purposes of communication, we were naturally mindful that tympanal organ morphology could have suggested a different, and better, classification. However, it has not, in fact, provided us with any obvious revised set of divisions.

The tympanal organs of Archiearinae differ from those of the other geometrid subfamilies in having a narrow fenestra media on the metapostnotum rather than a large, membranous, accessory tympanum. Although a fenestra media occurs elsewhere in Lepidoptera, if the accessory tympanum does indeed, as its name suggests, function in hearing, then its enlargement may prove to be a synapomorphy for the non-archiearine Geometridae. If this interpretation is indeed correct, then Archiearinae, which are very likely to be monophyletic as a group, may well be the sister taxon of all the other Geometridae. Against this argument exists the possibility that the fenestra media is a secondarily reduced accessory tympanum in Archiearinae. But if the accessory tympanum is important in hearing, it is difficult to understand why it should have become reduced in Archiearinae, all members of which are tympanate.

The classic character on which the Ennominae are defined is the absence or weakness of vein M2 in the hindwing. However, the tympanal organs are quite variable, particularly in the shape of the ansa. This subfamily, as currently composed, includes over half the species of Geometridae, but its monophyly gains no support from our survey of tympanal organ morphology, and remains in considerable doubt.

The circular form of the lacinia in Oenochrominae *sensu stricto* and its orientation parallel to the tympanum appears to be an autapomorphy of this group. Although the subfamily was greatly restricted by Scoble & Edwards (1990), the limits of the group were not established absolutely. The parallel orientation of the lacinia to the tympanum in *Sarcinodes* strongly suggests that this genus, currently left in the polyphyletic grouping Oenochrominae *sensu lato*, should be included in Oenochrominae *sensu stricto*.

The ansa of Oenochrominae (*sensu stricto*), Archiearinae and some Ennominae is generally wide at the base and narrow at the tip. This shape probably represents the primitive state of the ansa, the shapes occurring in Geometrinae, Larentiinae and Sterrhinae representing specializations, so the character fails to support a phyletic association between Oenochrominae (*sensu stricto*), Archiearinae and Ennominae.

The great range of variation in the tympanal morphology of Oenochrominae *sensu lato* is consistent with the polyphyly of this subfamily (Scoble & Edwards, 1990).

The characteristically shaped ansa of Geometrinae is probably a synapomorphic character of this subfamily. It occurs in all the species examined except for those in *Dysphania* Hübner. Species of *Dysphania* are larger than most Geometrinae and they have blue and yellow wings instead of the typically green wings of most other geometrines. (Nevertheless, the pigment responsible for the yellow in *Dysphania* and for the green in other Geometridae is the same (Cook, unpublished).) The ansa of *Dysphania* is hammer-headed, a shape characteristically occurring in Sterrhinae and Larentiinae, and the genus may be misplaced in Geometrinae.

In Sterrhinae and Larentiinae the tip of the ansa is typically hammer-headed and may be synapomorphic for these groups. But this possibility must be tempered by the rare occurrence of the feature in Ennominae. The absence of a tympanic lacinia may perhaps be construed as a loss in Sterrhinae and Larentiinae since the structure occurs in the other subfamilies and may represent a groundplan condition of the Geometridae. But if that interpretation is valid, the rare occurrence of a lacinia in both Sterrhinae and Larentiinae would have to be interpreted as a secondary gain.

We have surveyed most of the major morphological variation in the tympanal organs of the Geometridae, by careful selection of a wide range of species. However, the number of species examined accounts for little over 1% of the total number in the family, and few of these species were examined with the scanning electron microscope. Generalizations must, therefore, be treated with considerable caution. Moreover, effective systematic analysis requires that all sources of information are taken into account. But we hope that this contribution will stimulate lepidopterists to preserve adequately and to further examine the tympanal organs of Geometridae, structures that have for long been ignored as a source of taxonomic information.

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References

Börner, C. (1925) Lepidoptera, Schmetterlinge. In: Brohmer, P. (ed.), *Fauna von Deutschland*, 358–387.

Börner, C. (1939) Die Grundlagen meines Lepidopterensystems. *Verhandlungen des VII Internationalen Kongresses für Entomologie*, **2**, 1372–1424.

Bourgogne, J. (1951) Ordre des Lépidoptères. *Traité de Zoologie. Anatomie Systématique Biologie*, **10**, 174–448.

Clench, H.K. (1957) Cossidae from Chile (Lepidoptera). *Mitteilungen der Münchner Entomologischen Gesellschaft*, **47**, 122–142 + pls 4–6.

Clench, H.K. (1959) On the unusual structure and affinities of the Madagascan genus *Pseudocossus*. *Revue Française d'Entomologie*, **26**, 44–50.

Common, I.F.B. (1990) *Moths of Australia*, vi+535pp. + 32pls. E. J. Brill, Leiden.

Dahm, K.H., Meyer, D., Finn, W.E., Reinhold, V. & Röller, H. (1971) The olfactory and auditory mediated sex attraction in *Achroia grisella* (Fabr.). *Naturwissenschaften*, **58**, 265–266.

Davis, D.R. & Heppner, J.B. (1987) New discoveries concerning *Ischnuridia*, a remarkable genus of Indo-Australian Tineidae (Lepidoptera). *Tinea*, **12**, (Supplement), 145–151.

Eggers, F. (1911) Über das thoracale Tympanalorgan der Noctuiden. *Sitzungsberichte der Naturforscher-Gesellschaft bei der Universität Tartu (Dorpat)*, **20**, 139–146.

Eggers, F. (1925) Versuche über das Gehör der Noctuiden. *Zeitschrift für Vergleichende Physiologie*, **2**, 297–314.

Fenton, M.B. & Fullard, J.H. (1979) The influence of moth hearing on bat echolocation strategies. *Journal of Comparative Physiology*, **132**, 77–86.

Fenton, M.B. & Fullard, J.H. (1981) Moth hearing and the feeding strategies of bats. *American Scientist*, **69**, 266–275.

Fletcher, D.S. (1979) *The Generic Names of Moths of the World*. In: Nye, I.W.B. (ed.), **3**. xx + 243pp., 2 pls.

Fullard, J.H. (1984) External auditory structures in two species of neotropical notodontid moths. *Journal of Comparative Physiology, A: Sensory, Neural and Behavioural Physiology*, **155**, 625–632.

Gohrbandt, I. (1937) Das Tympanalorgan der Drepaniden und der Cymatophoriden. *Zeitschrift für Wissenschaft Zoologie*, **149**, 537–600.

Gwynne, D.T. & Edwards, E.D. (1986) Ultrasound production by genital stridulation in *Syntonarcha iriastis* (Lepidoptera: Pyralidae): long-distance signalling by male moths? *Zoological Journal of the Linnean Society*, **88**, 363–376.

Heitman, H. (1934) Die Tympanalorgane flugunfähiger Lepidopteren und die Korrelation in der ausbildung der Flügel und der Tympanalorgane. *Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere*, **59**, 135–200.

Kennel, J.V. & Eggers, F. (1933) Die abdominalen Tympanalorgane der Lepidopteren. *Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere*, **57**, 1–105.

Kiriakoff, S.G. (1963) The tympanic structures of the Lepidoptera and the taxonomy of the order. *Journal of the Lepidopterists' Society*, **17**, 1–6.

Kitching, I.J. (1984) An historical review of the higher classification of the Noctuidae (Lepidoptera). *Bulletin of the British Museum (Natural History) (Entomology)*, **49**, 153–234.

Kristensen, N.P. (1984) The pregenital abdomen of the Zeugloptera (Lepidoptera). *Steenstrupia*, **10**, 113–136.

Maes, K.V.N. (1985) A comparative study of the abdominal tympanal organs in Pyralidae (Lepidoptera). I. Description, terminology, preparation technique. *Nota Lepidopterologica*, **8**, 341–350.

Maes, K.V.N. (1987) Een vergelijkende, morfologisch-systematische studie van de Pyralidae (Lepidoptera) met bijzondere aandacht voor de Pyraustinae. Ph.D. thesis, Rijksuniversiteit Gent.

Minet, J. (1982) (volume dated 1981) Les Pyraloidea et leurs principales divisions systématiques. *Bulletin de la Société de Entomologique de France*, **86**, 262–280.

Minet, J. (1983) Etude morphologique et phylogénétique des organes tympaniques des Pyraloidea. 1. Généralités et homologies. (Lep. Glossata). *Annales de la Société Entomologique de France*, **19**, 175–207.

Minet, J. (1985) Etude morphologique et phylogénétique des organes tympaniques des Pyraloidea. 2. Pyralidae; Crambidae, première partie (Lepidoptera Glossata). *Annales de la Société Entomologique de France*, **21**, 69–86.

Minet, J. (1988) Structure and evolution of tympanic organs in Lepidoptera. *Proceedings of the XVIII International Congress of Entomology*, Abstracts, 78.

Minet, J. (1991) Tentative reconstruction of ditrysian phylogeny. *Entomologica Scandinavica*, **22**, 69–95.

Munroe, E. (1972) Pyraloidea: Pyralidae (part). In: Dominick, R.B. *et al.* (eds), *The Moths of America North of Mexico*, Fascicle 13.1A, 134pp.

Richards, A.G. (1933) Comparative skeletal morphology of the noctuid tympanum. *Entomologica Americana*, **13**, 1–43.

Robinson, G.S. & Nielsen, E.S. (1992) Tincid genera of Australia. *Monographs of Australian Lepidoptera* (in press).

Roeder, K.D. (1972) Acoustic and mechanical sensitivity of the distal lobe of the pilifer in choerocampine hawkmoths. *Journal of Insect Physiology*, **18**, 1249–1264.

Roeder, K.D. (1974) Responses of the less sensitive acoustic sense cells in the tympanic organs of some noctuid and geometrid moths. *Journal of Insect Physiology*, **20**, 55–66.

Roeder, K.D. & Treat, A.E. (1970) An acoustic sense in some hawkmoths (Choerocampinae). *Journal of Insect Physiology*, **16**, 1069–1086.

Sanderford, M.V. & Conner, W.E. (1990) Courtship sounds of the Polka-Dot Wasp Moth *Syntomeida epilais*. *Naturwissenschaften*, **77**, 345–347.

Schoorl, J.W. (1990) A phylogenetic study on Cossidae (Lepidoptera: Ditrysia) based on external adult morphology. *Zoologische Verhandelingen*, **263**, 1–295.

Scoble, M.J. (1986) The structure and affinities of the Hedyloidea: a new concept of the butterflies. *Bulletin of the British Museum (Natural History) (Entomology)*, **53**, 251–286.

Scoble, M.J. & Edwards, E.D. (1988) *Hypsidia* Rothschild: a review and a reassessment (Lepidoptera: Drepanoidea, Drepanidae). *Entomologica Scandinavica*, **18**, 333–353.

Scoble, M.J. & Edwards, E.D. (1990) *Parepisparis* Bethune-Baker and the composition of the Oenochrominae (Lepidoptera: Geometridae) *Entomologica Scandinavica*, **20**, 371–399.

Sick, H. (1935) Die Bedeutung der Tympanalorgane der Lepidopteren für die Systematik. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, **37**, 131–135.

Sick, H. (1937) Die Tympanalorgane der Uraniden und Epiplemiden. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **63**, 351–398.

Spangler, H.G. (1988) Moth hearing, defense and communication. *Annual Review of Entomology*, **33**, 59–81.

Spangler, H.G., Greenfield, M.D. & Takessian, A. (1984) Ultrasonic mate calling in the lesser wax moth. *Physiological Entomology*, **9**, 87–95.

Swihart, S.L. (1967) Hearing in butterflies (Nymphalidae: *Heliconius, Ageronia*). *Journal of Insect Physiology*, **13**, 469–476.

Treat, A.E. (1963) Sound reception in Lepidoptera. In: Busnel, R.G. (ed.) *Acoustic Behaviour of Animals*. Elsevier Publishing Company.

Vogel, R. (1912) Über die Chordotonalorgane in der Wurzel der Schmetterlingsflügel. *Zeitschrift für Wissenschaftliche Zoologie*, **100**, 210–244 + pls 7–8.

Zagatti, P. (1981) Comportement sexuel de la pyrale de la canne à sucre *Eldana saccharina* (Wlk.) Lié à deux phéromones émises par le mâle. *Behaviour*, **78**, 81–98.

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Appendix 1

The species examined are listed below by subfamily and in alphabetical order by genus and species.

Archiearinae

Archiearides fidenioides Butler, *Archiearides pusilla* Butler, *Archiearis infans* Möschler, *Archiearis notha notha* Hübner, *Archiearis parthenias parthenias* Linnaeus, *Leucobrephos brephoides* Walker.

Ennominae

Abaciscus figlina Swinhoe, *Abraxas fletcheri* Inoue, *Abraxas grossulariata* Linnaeus, *Abraxas illuminata* Warren, *Abraxas tricoloraria* Mabille, *Abraxas wilemani* Inoue, *Apicia cayennaria* Guenée, *Argidava subviduata* Walker, *Auaxa kaluga* Swinhoe, *Campaea dehaliaria* Wehrli, *Campaea parallela* Wherli, *Cargolia arana* Dognin, *Casbia calliorma* Turner, *Casbia impressaria* Walker, *Catoria camelaria* Guenée, *Cidariophanes ischnopterata* Warren, *Cingilia catenaria* Drury, *Cleora epiclithra* Fletcher, *Cleora psychastis* Meyr., *Colocleora simulatrix* Warren, *Crypsimetalla aurata* Warren, *Crypsimetalla flava* Warren, *Cypra delicatula* Boisduval, *Drepanulatrix unicalcaria* Guenée, *Ectropis albibasis* Hampson, *Epione alternata* Müller, *Erannis gigantea* Inoue, *Heterolocha atrivalva* Wherli, *Homochlodes fritillaria* Guenée, *Idiodes tenuicorpus* Prout, *Leptomiza bilinearia* Leech, *Leptomiza parableta* Prout, *Lomographa alba* Moore, *Lomographa bimaculata* Fabricius, *Lomographa claripennis* Inoue, *Lomographa distans* Warren, *Lomographa griseola* Warren, *Luxiaria ansorgei* Warren, *Melanolophia bostar* Druce, *Menophra subplagiata* Walker, *Nadagara xylotrema* Lower, *Nadagarodes camura* Joicey and Talbot, *Nadagarodes tentilinea* Prout, *Neogyne elongata* Warren, *Osteodes exumbrata* Walker, *Oxymacaria australiaria* Guenée, *Oxymacaria insularis* Warren, *Oxymacaria persimilis* Warren, *Paracotis hyrax* Townsend, *Pareclipsis umbrata* Warren, *Peridela curvifascia* Warren, *Pero calinaria* Poole, *Pero consimilis* Warren, *Pero pernamba* Poole, *Plagodis dolabraria dolabraria* Linnaeus, *Plutodes argentilauta* Prout, *Polyacme straminea* Warren, *Polyacme vagilinea* Warren, *Psilocerea leptosyne* Fletcher, *Psilocerea vestitaria* Swinhoe, *Sangala caelisigna* Walker, *Selenia bilunaria bilunaria* Esper, *Semiothisa arhoparia* Swinhoe, *Semiothisa berengaria* Fawcett, *Semiothisa brongusaria* Walker, *Semiothisa elvirata* Guenée, *Semiothisa epicharis* Werhli, *Semiothisa horridaria* Moore, *Semiothisa maculosa* Warren, *Semiothisa procidata* Guenée, *Semiothisa psammodes* Bastelberger, *Semiothisa sabulifera* Warren, *Semiothisa subalbataria* Swinhoe, *Semiothisa warreni* Prout, *Solomonophila vulgaris* Warren, *Sphacelodes vulneraria* Hübner, *Tephrina arizela* Fletcher, *Tephrina disputaria* Guenée, *Tephrina inaequivergaria* Mabille, *Tephrina pulinda deerraria* Walker, *Tephrina quadriplaga* Rothschild, *Tephrina sublimata* Butler, *Uranodoxa longicornis* Butler, *Xylopteryx arcuata* Walker, *Xylopteryx aucilla* Prout, *Xylopteryx protearia*, Guenée, *Zamarada townsendi* Fletcher.

Oenochrominae sensu stricto

Arhodia lasiocamparia Guenée, *Arhodia retractaria* Walker, *Monoctenia falernaria* Guenée, *Oenochroma quadrigramma* Lucas, *Oenochroma vetustaria* Walker, *Oenochroma vinaria* Guenée, *Parepisparis multicolora* Lucas, *Parepisparis virgatus* Scoble & Edwards.

Oenochrominae sensu lato

Abraxaphantes perampla Swinhoe, *Alsophila aceraria* Schiff., *Antasia flavicapitata* Guenée, *Antictenia torta* Prout, *Callipotnia multicolor* Warren, *Derambila dentiscripta* Bastelberger, *Derambila saponaria* Guenée, *Dichromodes ainaria* Guenée, *Dichromodes ophiucha* Meyr., *Dichromodes usurpatrix* Prout, *Dicyclodes hieroglyphica* Warren, *Dinophalus idiocrana* Turner, *Dolerophyle nerisaria* Warren, *Dolichoneura oxypteraria* Guenée, *Encryphia frontisignata* Walker, *Entogonia schistacea* Warren, *Epidesmia perfabricata* Walker, *Eumelea smedleyi* Prout, *Heteralex rectilineata* Guenée, *Myinodes interpunctaria* Herrich-Schäffer, *Nearcha nullata* Guenée, *Onychodes traumataria* Guenée, *Ozola acutata* Walker, *Ozola microniaria* Walker, *Ozola minor* Moore, *Phrygionis rectilineata* Warren, *Physetostege miranda* Warren, *Sarcinodes carnearia* Guenée, *Tapinogyna perichroa* Lower, *Taxeotis egenata* Walker, *Theoxena scissaria* Guenée, *Zeuctophlebia squalidata* Walker.

Geometrinae

Aeolochroma hypochromaria Guenée, *Agoschema goniata* Warren, *Anisozyga gavissima* Walker, *Anisozyga pieroides* Walker, *Aracima mucosa* Butler, *Archaeobalbis aethalia* Prout, *Cheroscelis oospila* Prout, *Chloromachia divapala* Walker, *Comibaena pustulata* Hufnagel, *Comostola flavifimbra* Warren, *Dindica subrosea* Warren, *Dysphania numana* Cramer, *Gelasma stuhlmanni* Prout, *Geometra papilionaria* Linnaeus, *Hemistola fulvimargo* Inoue, *Hemistola monotona* Inoue, *Hemistola rubrimargo* Warren, *Hemithea antigrapha* Prout, *Hemithea insularia* Guenée, *Hemithea tritonaria* Walker, *Heteresthes subaureata* Warren, *Lophochorista ockendeni ockendeni* Druce, *Merochlora graefiaria* Hulst, *Metallochlora decorata* Warren, *Metallochlora rubripuncta* Warren, *Metallochlora venusta* Warren, *Nemoria conspersa* Warren, *Neohipparchus vallata* Butler, *Oospila excrescens* Warren, *Oospila semispurcata* Warren, *Oospila trilunaria* Guenée, *Oospiloma thalassina* Warren, *Pachycopsis tridentata* Warren, *Prasinocyma discoprivata* Prout, *Prasinocyma geminipuncta* Warren, *Prognodes athena* Druce, *Prognodes nivetacta* Warren, *Pseudoterpna coronillaria* Hübner, *Pseudoterpna pruinata* Hufnagel, *Racheolopha miccularia* Guenée, *Rhomborista devexata* Walker, *Spaniocentra pannosa* Moore, *Synchlora liquoraria* Guenée, *Tanaorhinus confuciaria* Walker, *Terpna crocina* Butler, *Thalassodes grammonota* Prout, *Thalassodes pilaria* Guenée, *Timandromorpha discolor* Warren.

Sterrhinae

Acidalina proximaria Leech, *Anisephyra rufaria* Warren, *Anisodes clandestina* Prout, *Cyclophora porata* Linnaeus, *Cyclophora quercimontaria* Bastelberger, *Gnamptoloma aventiaria* Guenée, *Idaea bigladiata* Herbulot, *Idaea humiliata* Hufnagel, *Lobocleta flexicosta* Warren, *Pleuroprucha insulsaria* Kaye and Lamont, *Pleuroprucha roseipuncta* Warren, *Pleuroprucha rudimentaria* Guenée, *Problepsis crassinotata* Prout, *Rhodometra plectaria* Guenée, *Scopula addictaria* Walker, *Scopula emma* Prout, *Scopula heba* Prout, *Scopula nictata* Guenée, *Scopula nigridentata* Warren, *Scopula pseudocorrivalaria* Wehrli, *Scopula sagittilinea* Warren, *Scopula spilodorsata cosmeta* Prout, *Scopula subpulchellata* Prout.

Larentiinae

Anaitis plagiata plagiata Linnaeus, *Chloroclystis hawkinsi* Wiltshire, *Chloroclystis nigropunctata* Warren, *Cosmorhoe pustulata* Warren, *Cosmorhoe siderifera* Moore, *Dasysternica callicrena* Meyr., *Dyspteris abortivaria* Herrich-Schäffer, *Dysrhoe rhiogyra* Prout, *Electrophaes fulgidaria* Leech, *Electrophaes mesodonata* Prout, *Eois memorata* Walker, *Eudule hesperina* Burmeister, *Eudule lobula* Hübner, *Euphyia arachnitis* Turner, *Euphyia severata* Guenée, *Eupithecia obliquaria* Leech, *Eupithecia peguensis* Prout, *Eupithecia pygmaeata* Hübner, *Eupithecia subfuscata* Haworth, *Eustroma elista* Prout, *Gonanticlea aversa* Swinhoe, *Gonanticlea occlusata laetifica* Prout, *Gonanticlea sublustris* Warren, *Horisme angustealata* Stermeck, *Horisme mortuata* Guenée, *Horisme suppressaria* Walker, *Horisme teresa* Robinson, *Horisme xylinata* Warren, *Hydrelia enisaria* Prout, *Hydrelia subtestacea* Inoue, *Hydrelia undularia* Leech, *Operophtera relegata* Prout, *Papuanticlea horia* Prout, *Papuanticlea semiflava* Warren, *Poecilasthena leucydra* Prout, *Scotocyma scotopepla* Prout, *Sibatania mactata* Felder, *Sibatania mactata placata* Felder, *Stamnodes camposi* Orfila and Schajovskoy, *Thera britannica* Turner, *Thera variata* Schiff., *Xanthorhoe cadra* Debauche, *Xanthorhoe cuneosignata* Debauche, *Xanthorhoe exorista* Prout, *Xanthorhoe olbia* Prout.

Chapter 4
Systematics of the Geometrinae

INTRODUCTION

Historically, there has been some debate about the name of the Geometrinae. The subfamily, or parts of it, has been known by numerous names. The most widely used have been Chlorochromites, Dysphaniinae, Euschemidae, Geometridae, Geometridi, Geometrinae, Hazidae, Hemitheidae, Hemitheinae, Hemitheini, Nemoriinae, Nemoriae, Pseudoterpninae and Terpnae (Fletcher, 1979; Prout, 1912 and references therein). The controversy was finally settled by opinion 450 of the International Commission on Zoological Nomenclature (1957, see Fletcher, 1979) who ruled *Phalaena papilionaria* Linnaeus to be the type species of *Geometra* Linnaeus, so the nominate subfamily name Geometrinae replaced Hemitheinae.

Various divisions of groups corresponding to the Geometridae were proposed by Linnaeus and later authors (reviewed by Packard, 1876 and Prout, 1910). However, the origins of the subfamily Geometrinae appear to have been in the classification of Hübner (1816), where it is represented by Tribe I, stirps i-ii (Packard, 1876). Later authors proposed other divisions of the Geometridae, or groups corresponding to the family, but most agreed that the Geometrinae (or a taxon approximately equivalent to it) should represent one of the major divisions of the family.

The only major global taxonomic revision of the Geometrinae was that of Prout (1912, 1932). Subsequently, authors tended to concentrate on Geometrinae from particular geographic regions. The North American species were revised by Forbes (1948) and Ferguson (1969, 1985) and the Japanese Geometrinae by Inoue (1961).

Prout (1912), Forbes (1948), Inoue (1961), Ferguson (1969) and Viidalepp (1981) have all allocated genera of Geometrinae to tribes or groups. However, these supra-generic groups have not been assessed critically on a global scale and, with the exception of the revision by Viidalepp (1981), phylogenetic methods were not explicitly adopted. There is little overlap between these parochial schemes, and the integrity of the tribes and genus groups, on a global basis, and their phylogenetic positions, is therefore uncertain.

Viidalepp (1981) based his analysis of 26 Palearctic and Indo-Australian genera on 12 commonly cited characters, at least some of which have been used by other authors to diagnose tribes within the Geometrinae. The cladogram produced by Viidalepp (1981) showed the tribes Comostolini, Hemistolini, Hemitheini and Jodiini (Inoue, 1961) to be polyphletic. Viidalepp therefore revised these tribes, defining them by modified character suites, and he re-allocated genera according to his proposed phylogeny.

However, close scrutiny of this analysis (Viidalepp, 1981) cast doubt on the conclusions. Although Viidalepp did not publish the data matrix used in his analysis, he did show character states on his published cladogram. These were used to re-construct the original data set in order to assess his hypothesis, using the numerical cladistic protocol Hennig86 (Farris, 1988). A hypothetical outgroup composed of plesiomorphic states for each character was included because Viidalepp did not include any outgroups in his original analysis.

There are two problems with this analysis (Viidalepp, 1981) and its interpretation of the data. Firstly, there is much homoplasy in the data set. Analysis demonstrated that the cladogram has 90 steps and a consistency index of 0.26 (Viidalepp did not publish a consistency index for his cladogram), which is quite a low value for such a small data set (I. J. Kitching, *pers. comm.*). Moreover, Hennig86 found over 3000 shorter (length= 70 steps) cladograms than that published (Viidalepp, 1981).

In order to assess the phylogenetic content of the remaining schemes, a second data set was constructed and analysed. The first part of this chapter describes the analysis of these data, a subsidiary aim of which was to assess the phylogenetic position of *Oospila* Warren to provide a context for chapter 5. In the second part of the discussion, the structural characters of the Geometrinae are reviewed, using the literature, some personal observations and the analysis from the first part of the chapter. The value of these characters to the classification of the Geometrinae at, and below, the subfamily level is discussed.

MATERIALS AND METHODS

This study was based on characters previously used in the description of tribes or generic groups of Geometrinae. *Archiearis* Hübner was chosen as the outgroup because the presence of prolegs on segments A3-A5 of the larva suggests that the Archiearinae may represent the sister group of all other Geometridae. Since the directions of the transformation series of multi-state characters were unknown, all multi-state characters were coded as non-additive. Character states were coded as blanks when they were inconsistent within a genus, or when data were not available. Characters and descriptions of each state are given below.

The data matrix constructed from the 45 genera of Geometrinae reviewed by Inoue (1961) and Ferguson (1969, 1985) is given in Table 2. In addition, data from *Dysphania* Hübner and *Archaeobalbis* Prout, were added following suggestions (Prout, 1912, Viidalepp, 1981) that these genera should be allocated to separate groups or tribes. Data from the two neotropical genera *Oospila* Warren and *Rhodochlora* Warren were also added, in part to redress the imbalance caused by the relative neglect of neotropical species, and in part to assess the phylogenetic position of these genera.

Character coding

1. Female antenna: simple (0); pectinate (1).

2. Colour: not green (0); intense and stable green (1); faint and labile green (2); mixture of dull green and brown colouration (3); dull grey-green (4).

3. Male frenulum: present (0); absent (1).

4. Female frenulum: tuft of bristles (0); well developed (1); absent (2).

5. Forewing venation, origin of vein R_1: distinctly basal to apex of discal cell (0); at or close to apex of discal cell (1); from vein Rs, distal to apex of discal cell (2); distal to origin of vein M_1 (3).

6. Forewing venation, origin of vein M_1: from base of vein Rs, basal to origin of vein R_2 (0); independently from discal cell (1); stalked with veins R_2-R_5 (2).

7. Forewing, accessory cells: absent (0); with accessory cell formed by fusion of veins R_1 and R_2 with vein Sc (1); with accessory cell formed by fusion of veins Sc and R_1 (2); with accessory cell formed by fusion of vein R_1 with vein Sc, and vein R_1 with vein R_2 (3); with accessory cell formed by fusion of vein R_2 with vein Sc (4).

8. Forewing venation, origin of vein R_2: vein R_2 stalked with veins R_3-R_5 and arising basally to vein R_5 (0); vein R_2 independently arising from anterior edge of discal cell (1); vein R_2 stalked with veins R_3-R_5 and arising distal to vein R_5 (2).

9. Forewing venation, attachment of posterior discal cell cross-vein: joining vein M_3 (0); joining junction of veins CuA_1 and M_3 (1); joining stalk of veins M_3 and CuA_1 (2).

10. Hindwing venation, attachment of posterior discal cell cross-vein: joining junction of veins M_3 and CuA_1 (0); joining stalk of veins M_3 and CuA_1 (1); joining vein M_3 (2).

11. Hindwing venation, vein 3A: present (0); vestigial (1); absent (2).

12. Hindwing humeral lobe: not expanded (0); expanded (1).

13. Male hind tibia, with median spurs: present (0); absent (1).

14. Male hind tibia: without apical extension (0); with apical extension or process extending beyond origin of tarsus (1).

15. Male sternum A8: without extra sclerotisation (0); strongly sclerotised and with apical edge developed (1).

16. Abdominal crests: absent (0); weak (1); strongly developed (2).

17. Male uncus: extended posteriorly as slender, single spine (0); extended posteriorly as single spine, expanded at tip (1); reduced to flat plate, with or without short apical extension (2); divided into two separate elements (3); flat, with irregularly shaped sclerotised lump on each side (4); broad at base, extended posteriorly, slender over apical half and deeply forked at apex (5); broad at base, extended posteriorly, with long tapering apex (6); broad plate, extended posteriorly, slightly narrower at apex (7).

18. Male socii: absent (0); membranous or semi-membranous (1); strongly sclerotised (2).

19. Male gnathos: complete fused ring (0); not fused, as two separate elements (1); absent (2).

20. Male valva, with mesal sclerite: absent (0); present (1).

21. Male coremata: absent (0); present (1).

22. Male aedeagus: simple, cylindrical (0); long and thin (1); with 'tuning fork' shape (2); with lateral process (3).

23. Female signum: present (0); absent (1).

24. Larvae with dorsolateral protuberances: absent (0); small (1); large (2); with hooks used to attach fragments of plant material (3).

Taxon	Character number
	1 11111 11112 2222
	12345 67890 12345 67890 1234
Archiearis Hübner	00000 00000 00000 00000 0000
Agathia Guenée	01010 00002 0001- 25000 00--
Archaeobalbis Prout	03000 01102 00010 11200 10--
Aracima Butler	02010 11002 00001 04200 00--
Chetoscelis Prout	11120 22010 2110- 02200 1213
Chlorissa Stephens	02020 22011 21111 00100 00-0
Chlorochlamys Hulst	02020 22021 21110 00100 1010
Chloromachia Warren	01010 0--11 0001- 00000 00--
Chloropteryx Hulst	04020 00021 10110 -0120 1010
Chlorosea Packard	01000 12002 11101 -1100 0002
Comibaena Hübner	01012 20000 21011 03220 0103
Comostola Meyrick	01111 22021 21011 00201 00--
Culpinia Prout	02020 02011 2110- 00100 00--
Dichorda Warren	01020 02002 01001 01100 0012
Dichorophora Prout	11120 02002 01-00 -3200 0012
Dindica Moore	03010 00002 0011- 25000 00--
Diplodesma Warren	--0-2 22021 211-- -0100 00--
Dysphania Hübner	10010 20002 0-000 01100 11-0
Eueana Prout	01023 21012 21111 01101 0000
Gelasma Warren	01020 20001 01001 00100 00-0
Geometra Linnaeus	02010 10002 00011 02200 00--
Hemistola Warren	12110 22002 21010 10100 000-

Taxon	Character number
	1 11111 11112 2222
	12345 67890 12345 67890 1234
Hemithea Duponchel	02020 02021 21101 10200 00-0
Hethemia Ferguson	02020 02011 21101 00100 1010
Jodis Hübner	02112 23011 21001 00100 00-0
Lophochorista Warren	11001 22000 11111 21101 0010
Merochlora Prout	01120 21000 21000 02200 1213
Mesothea Warren	02020 24001 21101 00100 0010
Mixochlora Warren	01010 00002 00001 02000 00--
Mujiaoshakua Inoue	021-0 22021 210-- 01100 00--
Nemoria Hübner	01000 00011 01011 01100 0012
Neohipparchus Inoue	02010 10000 00101 06200 03--
Nipponogelasma Inoue	-20-0 22021 21001 00100 00--
Ochrognesia Warren	01010 00001 00011 01100 01--
Oospila Warren	11020 20021 21101 22111 000-
Parachlorissa Inoue	--0-3 22021 211-- -0100 00--
Phrudocentra Warren	01021 00002 210-1 01100 1012
Pingasa Moore	05010 24000 0001- 25000 00--
Rhodochlora Warren	01020 20002 21001 00200 000-
Rhomborista Warren	010-0 00201 2110- 00101 00--
Synchlora Guenée	01000 02011 21010 02200 1203
Tanaorhinus Butler	0101- 0--0- -000- 02000 00--
Terpna Herrich-Schäffer	10010 00002 0000- 25000 00--
Thalera Hübner	12120 10002 2110- 00100 00--

Taxon	Character number
	1 11111 11112 2222
	12345 67890 12345 67890 1234
Thalassodes Guenée	02020 20011 01001 00100 000-
Thetidia Boisduval	02120 10002 21001 03200 01--
Timandromorpha Inoue	00010 00002 00001 07200 00--
Xerochlora Ferguson	01021 20021 20110 00110 0010

Table 2 Data matrix for 47 exemplar genera of Geometrinae, and *Archiearis* (Archiearinae) (- denotes missing datum).

RESULTS

An unweighted analysis of this data produced 1964 equally parsimonious trees, with length= 173 steps, consistency index (ci)= 0.29 and retention index (ri)= 0.60. However, this is not the full set since the size of the computer's memory set the limit. The strict consensus tree derived from the set obtained is given, as a reference, in Fig. 1. In order to reduce the effect of the more homoplasious characters, successive weighting was applied to the data to produce a second set of most parsimonious trees (again, a subset of 1964 was obtained) with length= 217 steps, ci= 0.54 and ri= 0.78; the strict consensus from these is presented in Fig. 2.

DISCUSSION

Comments on the phylogenetic analysis

Using this character set, some cladistic structure is revealed in the Geometrinae. However, since any one of the 1964 or more trees is equally acceptable as a phylogenetic hypothesis, this data set is clearly insufficient to resolve the phylogeny of the Geometrinae.

Although this analysis is the most thorough that exists of the currently available data, there remain a number of weaknesses and its results must therefore be viewed with caution. One of the weaknesses results from the lack of information about the origin and outgroups of the subfamily as a whole. Although Ferguson (1985) has suggested that the Geometrinae are a specialised branch of the ennomine stem, this has not been demonstrated and what exactly constitutes the ennomine stem is uncertain. Parts of the tree are quite unstable to small changes in the root, and replacing *Archiearis* with a more appropriate outgroup could radically affect the outcome of the analysis.

A further problem exists in correctly interpreting characters and homologies when working from the literature, particularly when attempting to combine the observations of a number of different authors. This is likely to introduce extra homoplasy into the data set and thus to reduce the value of its interpretation.

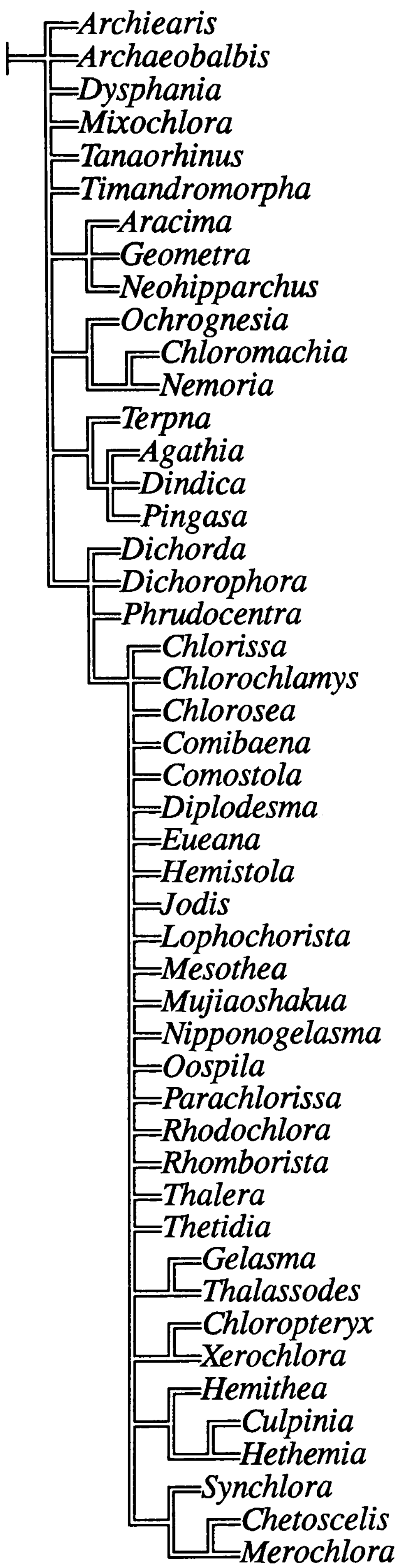

Fig. 1 Strict consensus tree from analysis of Table 2, using the unweighted data set (length = 236 steps, ci = 0.21, ri = 0.39).

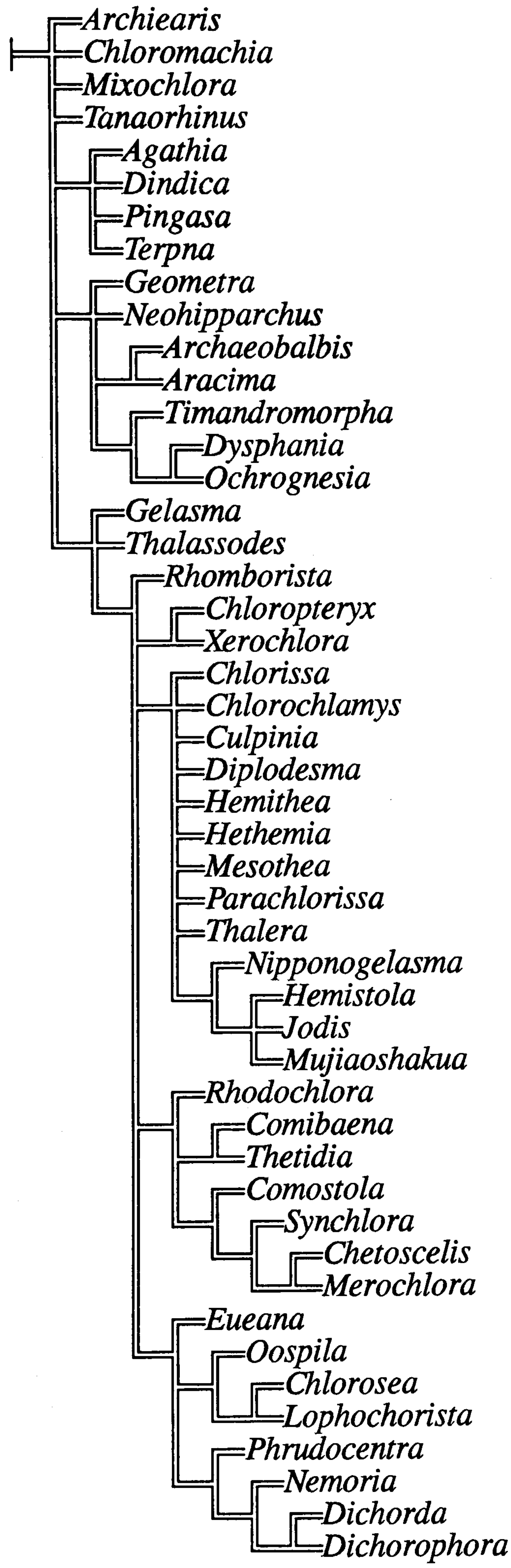

Fig. 2 Strict consensus tree from analysis of Table 2, using successive weighting (length = 229 steps, ci = 0.51, ri = 0.76).

This analysis does, however, reveal the inadequacy of most of the tribes and supra-generic groups that have been described. Many of the characters which have been used to diagnose species groups on a regional basis fail when considered at a global level. Moreover, although speculations have been made, the status of most of these characters as plesiomorphies or apomorphies, or indeed even as homologies, has not been tested by strictly parsimonious cladistic analysis. Whilst there is some cladistic information in the literature and whilst some of the generic and tribal groups are consistent with the underlying phylogeny, the character suites hitherto examined are insufficient to produce a fully resolved phylogeny of the Geometrinae.

Comments on the structural characters of Geometrinae

General appearance

The subfamily consists mainly of slender-bodied, bright green or emerald green species. However, the tone of the green varies (as discussed in chapter 2) and a group of more 'robust-bodied' species occurs in the Old World tropics with a more mottled, lichenous patterning (e.g. *Pingasa* Moore, Holloway *et al.*, 1987).

Ferguson (1985) considered dividing the Geometrinae into two groups based on the tone and relative stability of the green pigment (character 2). However, he rejected this idea because other characters did not correlate with the division. The phylogenetic analysis presented above indicated that there is no evidence to support such a division. Moreover, chemical analysis of the colour (Chapter 2) showed that a single pigment is is responsible for the green colour of Geometrinae.

Head

In common with most Geometridae, the compound eyes of Geometrinae are large and round. Little variation is observed in the size of the eyes, although some sexual dimorphism occurs, in which case the eyes of the female are smaller than those of the male (Ferguson, 1969). Eye reduction in females of *Mesothea* Warren is an important character of this genus (Ferguson, 1969). As with most Geometridae, in Geometrinae the eyes have neither interfacetal hairs nor lashes (Krüger and Scoble 1992). Chaetosemata are present and external ocelli are absent (Scoble, 1992).

The frons is rarely protuberant, which is the typical, but by no means universal, condition of Geometridae, (the frons is protuberant, for example, in Archiearinae). The frons of Geometrinae shows little structural variation. However, the colour of the frons may be an important character for identifying species.

The antennae are simple or bipectinate, although a few intermediate cases occur where they could be described as dentate or fasciculate (Ferguson, 1969). Sexual dimorphism is frequently observed and, in general, the antennae of males are bipectinate and those of females are simple. The presence or absence of pectinations on the antennae of one or both sexes is a useful character for identifying some species and genera, but the analysis presented above suggested it has little taxonomic significance at higher levels. When pectinate, the rami of the antennae of females are usually shorter than those of males (Ferguson, 1969). Ferguson (1969) used the length of the pectinations in his diagnostic key to the North American fauna. However, the value of this character at higher levels has not been assessed on a global basis.

The proboscis of Geometrinae is well developed and lacks scales at its base. The proboscis exhibits some variation in length within the subfamily, but this variation has not been used as a taxonomic character (Ferguson, 1969).

As in most macrolepidoptera, the maxillary palpi of Geometrinae are very small and one-segmented. The structure of the labial palpi differs little throughout the subfamily (Ferguson, 1969). However, they do vary in length, particularly in the length of the third segment. Where a sexual dimorphism occurs in the length of the labial palpi, those of the female are always longer. Prout (1912) used the length of the labial palpi in his generic descriptions, but this character has not been used much by other authors.

Thorax

Whilst extensive use has been made of characters of the appendages of the thorax by taxonomists, little attention has been paid to structural characters of the thorax itself. The metapostnotum has an enlarged, membranous fenestra media (which may be an accessory tympanum, Kennel and Eggers, 1933; Cook and Scoble, 1992), but this also occurs in the other geometrid subfamilies (with the exception of the Archiearinae) and many other Lepidoptera.

All Geometridae, including Geometrinae, have an epiphysis on the foreleg tibia (Scoble, 1992). The tibial spur formula of Geometrinae is commonly 0-2-4, although in some species (including most *Oospila* Warren) the proximal spurs of the hind tibia are absent (tibial spur formula 0-2-2). The tibial spur formula has been used for the diagnosis of genera and supra-generic groups (Ferguson, 1969; Inoue, 1961; Prout, 1912). However, the analysis presented above suggested that the tibial spur formula (character 13) is of little value in the higher classification of the Geometrinae on a global basis.

Ferguson (1969, 1985) noted that in some Geometrinae the hind tibia was extended beyond the origin of the tarsus, a character which he thought to be exclusive to Geometrinae (Ferguson, 1985). However, this character (character 14) did not consistently support monophyletic groups in the analysis above.

The hind tibia is dilated in many Geometrinae, and this appears to be associated with the occurrence of a recessed hair pencil (Ferguson, 1969). Hair pencils seem to be distributed widely throughout the Geometridae and, whilst useful for identifying species, are probably of little value to defining supra-specific groups.

The wings of Geometrinae are broad compared with the size of the body, and are never reduced or absent, although they may be in some other Geometridae. Eighty-five percent of species have wings which are wholly, or partly, emerald green (Ferguson, 1969). Sexual dimorphism in wing pattern is rare, although other forms of intraspecific variation occur, including brown morphs of some green species (Ferguson, 1985). Discal cell spots are often present, but these are not as pronounced as they are in Sterrhinae. Ferguson (1969) used the absence of an antemedial line to diagnose (in part) his Hemitheini from the remainder of the North American fauna, but this character is not so useful on a global basis.

In most Geometridae, the male frenulum is a composite structure (Krüger and Scoble, 1992), appearing as a single spine. Some female Geometrinae have the typical geometrid frenulum, two or more frenular bristles, but most have no frenulum. In a few species the female frenulum is a well developed single spine, like that of the male. Prout (1912), used the presence or absence of the male frenulum in his diagnosis of supra-generic groups. The analysis above demonstrated that reduction or loss of the male and female frenulum (characters 3 and 4) did not consistently support monophyletic groups.

An expansion of the humeral lobe of the hindwing appears to be associated with reduction of the frenulum (Inoue, 1961). Inoue (1961) used this character to allocate the Japanese fauna to two groups, one in which the hindwing has a reduced frenulum and a distinct expansion of the hindwing humeral lobe (character 12) and one in which the frenulum is not reduced and the humeral lobe of the hindwing is not expanded (Inoue, 1961). However, there was no evidence from this analysis such a division reflects phylogeny.

A fovea is found only in the genera *Dysphania* Hübner and *Cusuma* Moore which Prout (1912) allocated to his Group III (of Geometrinae). However, *Dysphania* and *Cusuma* may be misplaced in the Geometrinae (Cook and Scoble, 1992; also see chapter 6).

Wing venation has been used extensively in the classification of the Geometrinae, particularly by early authors (e.g. Prout, 1912). However, Ferguson (1969) found that intraspecific variation in wing structure occurred with a frequency of over 15% (Ferguson, 1969) and thereby cast doubt on the taxonomic value of wing venation characters. Certainly, in the analysis presented above, wing venation characters (characters 5-11) failed to support monophyletic groups with any degree of consistency. The wing vein nomenclature used in this work follows Scoble (1992).

In the forewing, vein R_1 usually diverges close to the apex of the discal cell, usually from the discal cell. Accessory cells occur infrequently, but in some species vein R_1 merges with veins Sc or R_2 to form an accessory cell. Vein R_2 usually diverges from vein Rs distally to the discal cell, but in rare instances, vein R_2 diverges from vein R_1. Vein R_2 usually diverges proximal to the origin of vein R_5, but occasionally it arises distally. Veins R_3, R_4 and R_5 always share a common stem. Vein M_1 arises from, or close to the base of the stalk of veins R_2-R_5.

In the hindwings, vein Rs is usually approximated to, or fused with vein Sc for a short distance (but not as far as in Larentiinae; Inoue, 1961), and diverges proximally to the apex of the discal cell. Veins Rs and M_1 are stalked, and veins M_3 and CuA_1 are also frequently stalked. In the Geometrinae, vein M_2 is always present as a tubular vein, and not reduced as it is in Ennominae. Vein M_2 also arises closer to vein M_1 than to vein M_3 and this character has been used in diagnostic keys to the subfamilies of Geometridae (e.g. by Forbes, 1948; Holloway *et al.*, 1987; Inoue, 1961; Prout, 1912). However, given observations (Ferguson, 1969) about inconsistencies in the wing venation of Geometrinae, and that therefore it may not be clear whether this vein arises closer to vein M_1 or from the mid-point of the cross-vein M_1-M_3, it seems rather an insubstantial character on which to diagnose a subfamily. Vein 3A is commonly, but not always, present.

Abdomen

The dorsal surface of the abdomen exhibits a variety of patterning, which may be taxonomically important. Abdominal crests are present in many taxa. Inoue (1961) and Prout (1912) have used the presence or absence of these structures to define tribal and supra-generic groups. However, there is no evidence from this analysis that species with, or without, abdominal crests (character 16) form a monophyletic group. Spots or stripes on the abdomen may be important for identifying species, particularly in the large neotropical genus *Nemoria* (Ferguson, 1969).

Structurally, the female pregenital abdomen is typically unspecialised, but a variety of specialisations are found in males which may be taxonomically useful.

Sternum A3 often has two fields of deciduous setae in males and these sometimes merge at the midline (Holloway *et al.*, 1987). This character occurs largely in Old World species. Setae are also found on sternum A3 of some Ennominae and Oenochrominae, where they form more comb-like fields. It is not known if the setae of Geometrinae are independently derived, although the different form of the fields suggests they may be.

Sternum A8 is strongly sclerotised in males of many species and modifications of the posterior edge are often useful for identifying species. However, this character (character 15) did not consistently support any monophyletic groups of genera in the analysis.

Tympanal organs of Geometrinae (Chapter 3) are situated at the base of abdomen, as they are in all Geometridae. The ansa of Geometrinae has a characteristic shape, broadening above its basal attachment to the bulla, and extending into a wide, flat plate, which then narrows again towards the apex. The apex of the geometrine ansa is not expanded as it is in some Larentiinae and Sterrhinae (Cook and Scoble, 1992). The shape of the geometrine ansa is probably an apomorphy of the subfamily (Cook and Scoble, 1992).

A tympanic lacinia was found in eight of the species of Geometrinae examined (*Anisozyga pierodes* Walker, *Aracima mucosa* Butler, *Dindica subrosea* Warren, *Geometra papilionaria* Linnaeus, *Neohipparchus vallata* Butler, *Pseudoterpna pruinata* Hufnagel, *Tanaorhinus confuciaria* Walker, and *Timandromorpha discolor* Warren). There is no obvious correlation between the distribution of this structure and the phylogenetic hypotheses resulting from the analysis above. Moreover, this structure was also found in some species from the other geometrid subfamilies (excluding the

Archiearinae). A small lobe was observed on the posterior of the bullae tympani only in females of *Anisozyga pierodes* Walker, although it is a fairly common feature of Ennominae (occurring in approximately 30% of the species of Ennominae examined).

Male genitalia

Both Ferguson (1969) and Inoue (1961) based their tribal classification largely on male genitalic characters. There was some evidence from the analysis above that at least some characters of the male genitalia consistently supported monophyletic groups and may define supra-generic groups.

The uncus is commonly extended as a long spine, although various degrees of reduction and modification occur throughout the subfamily and in some species the uncus is reduced to a small basal sclerite (e.g. in *Synchlora* Guenée, Ferguson, 1969). The tribe Terpnini (Inoue, 1961: *Pingasa* Moore, *Terpna* Herrich-Schäffer, *Dindica* Moore, and *Agathia* Guenée) is one of the few tribal groupings which consistently formed a monophyletic group in this analysis (as indicated by the consensus trees, Figs 1 and 2) and is based on a character of the uncus. In the Terpnini, the uncus is strongly sclerotised, extended posteriorly and has a deeply forked apex (Character 17, state 5).

Socii are present and vary chiefly in their size and degree of sclerotisation. Many Old World Geometrinae have large, strongly sclerotised socii. Both Forbes (1948) and Ferguson (1969) have used the degree of sclerotisation of the socii to diagnose tribes but there was no evidence from the analysis undertaken in this study that species with either membranous or strongly sclerotised socii (character 18) form a monophyletic group when the taxon was examined on a global basis.

The gnathos is usually a completely fused ring, although sometimes the gnathi are not fused (as in *Oospila* Warren) or are absent. The analysis above suggests that this character (Character 19), whilst useful for identifying genera or species is probably of no value to the higher classification of the subfamily.

The anellus is commonly sclerotised, and a transtilla and juxta are often present. Klots (1970) observed that the nomenclature and homologies of sclerotisations of the anellus were unclear. Until these are fully resolved, sclerotisations of the anellus probably have limited taxonomic value above that of identifying species or genera.

The valvae show numerous modifications, which are often characteristic of a genus (Ferguson, 1969). Ferguson (1969) used the presence of a medial sclerite on the valva in his tribal key to the North American fauna. However, the presence or absence of this sclerite (character 20) did not support monophyletic supra-generic groups with any consistency on a global basis in this study.

Coremata may or may not be present, and their occurrence and anatomical location may be useful for identifying species (as for example, in *Oospila* Warren). There was no evidence from this analysis that the presence or absence of coremata (character 21) supports monophyletic groups of genera in the Geometrinae.

The aedeagus shows little variation at the species level, but variations in size, shape or appendages are useful characters at the generic and tribal levels. The tribe Synchlorini (Ferguson, 1969, 1985: *Chetoscelis*, *Merochlora* and *Synchlora*) consistently formed a monophyletic group in this analysis supported by a character of the aedeagus. The aedeagus of the Synchlorini (Ferguson, 1969) has an unusual 'tuning fork' shape (character 22, state 2), which is probably an apomorphy of this tribe. There is some evidence that a character of the aedeagus also supports monophyly of the Comibaenini (*Comibaena* and *Thetidia*; Inoue, 1961) which consistently formed a monophyletic group in the analysis of the weighted data. The male aedeagus is exceptionally long and thin (character 22, state 1) in this group.

Female genitalia

Female genitalia may be important in the identification of species, particularly in those where the male genitalia are identical (Ferguson, 1969). However, female genitalia are structurally much simpler than their male counterparts, have fewer taxonomic characters and have not been used much in the higher classification of the subfamily.

The region around the ostium is often sclerotised and the form of these sclerites may be taxonomically useful at the species level. The ductus bursae varies in length, diameter and degree of sclerotisation. The corpus bursae may show little variation at the species level, but its variation, chiefly in terms of size and shape, may be of value at other levels (Ferguson, 1969). Ferguson (1969) noted that the signum, where present, varied little between closely related species, but diagnosed groups at higher taxonomic levels. In the analysis presented above, the presence or absence of a signum (character 23) did not support monophyletic groups with any consistency.

Immature stages

The eggs of Geometrinae are generally flattened, with an oval outline (Salkeld, 1983; McFarland, 1988). They are slightly truncated at the micropylar end (Forbes, 1948) and are probably always dropped freely (Scoble, 1992). They are generally exposed and not inserted into crevices (Scoble, 1992). Eggs are usually laid singly or in twos, sometimes in heaps or chains.

The head of geometrine larvae is typically bifid (Holloway *et al.*, 1987). A bifid head does not occur in any of the other geometrid subfamilies, although some Sterrhinae have a bilobed head (Scoble, 1992). The bifid head may support the monophyly of the subfamily, but this character has not been examined critically .

As with most Geometridae, geometrine larvae have prolegs only on abdominal segments A6 and A10, and thus move with the characteristic 'looping' gait which gives the family its name.

Both Forbes (1948) and Ferguson (1969) used the occurrence and size of dorsolateral protuberances (character 24) to support tribal groupings of North American Geometrinae. The Synchlorini (Ferguson, 1969) have moderately large dorsolateral protuberances bearing specialised hooks for the attachment of plant fragments. The

Nemoriini (Ferguson 1969) have large dorsolateral processes, without this specialisation. However, these groupings did not consistently form monophyletic groups in this analysis, owing to homoplasy in other characters.

Ferguson (1985) thought the behaviour of attaching plant fragments was a highly developed specialisation for a geometrid. However, he found this character distributed across the tribes he studied and concluded that it was a groundplan character of the subfamily. Given that the analysis above casts some doubt on the tribal classification of Ferguson (1969, 1985), this interpretation may not necessarily be valid.

In the Geometrinae, seta SV_4 (Stehr, 1987) is absent from segment A1, which distinguishes the subfamily from Ennominae and Oenochrominae *sensu lato* in which the seta is present on this segment. This character has been used in a diagnostic key to geometrid subfamilies (McGuffin, 1972). Seta SV_4 is, however, present on segments A3-A5, as it is in most Geometridae (except Larentiinae).

Geometrine larvae are often sluggish (McFarland, 1988) and respond to disturbance by clinging tenaciously to the substrate, or by a 'shaking' behaviour.

Pupae

The pupae of Geometrinae are obtect and adecticous. The pupal head is rounded, and has no protuberances. The cremaster bears hooked setae, which are all approximately equally sized, in contrast to those of Ennominae, Larentiinae and Sterrhinae where the hooked setae, if present, vary in size (McGuffin, 1972). Many Australian and North American species have conspicuous black (or dark) middorsal lines on the pupal abdomen (McFarland, 1988). The pupal cocoon is delicate, and usually found on the foodplant, occasionally in loose debris on the ground, and never in the soil (Ferguson, 1985; McFarland, 1988). Pupal characters of Geometrinae have received limited attention from taxonomists.

Chapter 5
Oospila Warren

Oospila Warren, 1897: 426. Type-species: *Phorodesma trilunaria* Guenée, 1857: 372.
Auophylla Warren, 1897: 423. Type-species: *Thalera includaria* Herrich-Schäffer (1856): pl. 61, fig. 341. **New synonymy.**
Anophylla Warren, 1906: 414. Incorrect subsequent spelling of *Auophylla* Warren.
Progonodes Warren, 1897: 429. Type-species: *Racheospila stagonata* Felder and Rogenhofer, 1875: pl. 127, fig. 25. **New synonymy.**
Drucia Warren, 1900: 133. Type-species: *Drucia delphinata* Warren, 1900: 133. **New synonymy.**
Halioscia Warren, 1907: 202. Type-species: *Halioscia atroviridis* Warren, 1904a: 24 [designated as the type-species by Fletcher, 1979]. **New synonymy.**
Racheolopha Warren, 1900: 137. Type-species: *Racheospila miccularia* Guenée, 1857: 374. **New synonymy.**
Auophyllodes Prout, 1912: 20 (key), 130. Type-species: *Comibaena venezuelata* Walker, 1861: 570. **New synonymy.**
Oospiloma Prout, 1916: 170. Type-species: *Oospila thalassina* Warren, 1905: 318. **New synonymy.**

Auophylla and *Oospila* were published in the same work (Warren, 1897). Although *Auophylla* was described three pages before *Oospila*, the adoption of *Auophylla* as the senior synonym would result in 32 more new combinations than the adoption of *Oospila*. Hence *Oospila* is selected here as the senior synonym (Article 24 of the

International Code of Zoological Nomenclature (1985) in line with recommendation 24a).

MATERIAL AND METHODS

This study was based largely on material from: The Natural History Museum, London, U.K. (BMNH); the National Museum of Natural History, Washington D.C., U.S.A. (NMNH); Instituto Nacional de Biodiversidad, San José, Costa Rica (INBio); Carnegie Museum of Natural History (CMNH; Pittsburgh, U.S.A); Hope Entomological Collections (HEC; Oxford); C. Herbulot (Private Collection; Paris); Den Haag Museum; Paris Museum (MNHN; Paris, France); Universidad Central de Venezuela (UCV; Maracay, Venezuela).

When material permitted, permanent slide mounts (in Euparal) of male and female genitalia were made from each locality. The method used was similar to that described in Cook and Scoble (1992) for tympanal organs. Male genitalic capsules were removed from the abdomen and mounted venter uppermost and with the inner surfaces of the valvae displayed. The aedeagus was removed from the diaphragma and mounted on the same slide. Where possible, the gnathi were also spread to display the uncus. Female genitalia were also removed from the abdomen and mounted alongside it and are illustrated in ventral view.

Wing preparations were also made for each species. Wings were bleached in a dilute solution of household bleach and then stained lightly with mercurochrome. These were also mounted as permanent slide preparations.

Locality, collection date, collector, number and sex of specimens and depository were recorded from specimen labels. These data are presented here and also stored electronically at the BMNH. Allocation of localities to provinces follows Brown (1979).

Although a key to species of *Oospila* was constructed, it is not included in this revision since it was not reckoned to be an efficient means of identifying species of this large genus. Since most species of *Oospila* can be identified from their wing markings alone, specimens should first be compared with the figures (Figs 7-81). Reference should then be made to the species descriptions which describe intraspecific variation (where it occurs) and how to differentiate a species from any other *Oospila* with which it may be confused.

SPECIES GROUPS AND A NEW DEFINITION OF *OOSPILA*

In order to redefine *Oospila* Warren as a monophyletic group it was necessary to consider the suggestion (Prout, 1932) that *Oospila*, together with the genera *Auophylla* Warren, *Auophyllodes* Prout, *Oospiloma* Prout, *Progonodes* Warren, and *Racheolopha* Warren, 'could without much difficulty be united into a single extensive genus'. Similar pattern and structural elements occur throughout this group of genera and all the species have strongly developed abdominal crests. Prout (1912 and 1916) and Warren (1897, 1900 and 1906), unaware of the value of genitalia characters, based these genera on external and wing venation characters. However, examination of the genitalia suggested a revised set of groups of species. Moreover, the occurrence of an anellar complex (see Fig. 82, and description below) in many species from all these genera strengthened the argument for uniting them into a single genus.

To assess the phylogenetic inter-relationships of the revised species groups, one species was selected to represent each of them and used to construct a data matrix of character states. Data from two species of *Lophochorista* Warren (*L. lesteraria* Grossbeck and *L. ockendi* Druce) were also included since this genus shares some important characters with the other genera (the presence of dark brown abdominal crests and modification of the mesal region of the valvae in the male genitalia). In addition, data from *Eueana niveociliaria* Herrich-Schäffer were included since Ferguson (1969) placed *Eueana* Prout in the tribe Lophochoristini (Ferguson, 1969). The analysis was rooted using a hypothetical outgroup based on other Geometrinae. All multi-state characters were coded as non-additive and the data set was analysed using Hennig86 (Farris, 1988).

Characters and states

1. Forewing venation, vein R_1 arises: basal to origin of vein M_1 (0); distal to origin of vein M_1 (1).

2. Proximal spurs on male hind tibia: present (0); absent (1).

3. Abdomen, dorsal surface with crests: absent (0); composed of long hair-like scales (1); composed of broad scales surrounding central brush of long hair-like scales (2).

4. Abdomen, male sternum A8: not strongly sclerotised, not developed (0); with apical edge a strongly sclerotised, serrated plate (1); strongly sclerotised with a bifurcate posterior extension (2); strongly sclerotised with an undivided posterior extension (3); with an emarginated apical edge (4).

5. Male genitalia, uncus: with a long, thin apical extension (0); with a short or no apical extension (1).

6. Male genitalia, gnathos: fused (0); not fused, present as two separate elements (1).

7. Male genitalia, shape of valva: without apical division (0); with apical division (1).

8. Male genitalia, sacculus of valva: not extended (0); extended into strongly sclerotised, pointed process (1).

9. Male genitalia, costal edge of valva: not strongly sclerotised (0); strongly sclerotised with short subapical extension (1).

10. Male genitalia, mesal sclerite of valva: flat and comb-like (0); a long process, i.e. an ampulla (1); absent (2).

11. Male genitalia, transtilla: a flat plate (0); fused with valvae and juxta to form anellar complex (1); absent (2); large projections from base of valvae, not fused to juxta (3); fused with juxta to form anellar complex, but not fused with valvae (4).

12. Male genitalia, juxta: a flat plate (0); a basal V-shaped sclerite (1); fused with transtilla to form anellar complex (2).

Taxon	Character No.
	1 11
	12345 67890 12
outgroup	00000 00000 00
Auophylla includaria group	01201 11102 13
Eueana niveociliaria	01000 00000 00
Lophochorista lesteraria	01130 00001 00
Lophochorista ockendi	01110 00010 00
Oospila albicoma group	01241 11101 43
Oospila asmura group	01241 10002 31
Oospila atopochlora group	01221 11101 13
Oospila marginata group	01221 11101 13
Oospila quinquemaculata group	01200 00011 -3
Oospiloma thalassina group	00200 00002 13
Oospila trilunaria group	01221 11101 13
Progonodes athena group	01221 11002 10
Racheolopha ecuadorata group	11241 11002 13
Racheolopha miccularia group	11241 11002 13

Table 3 Coding of characters (see text).

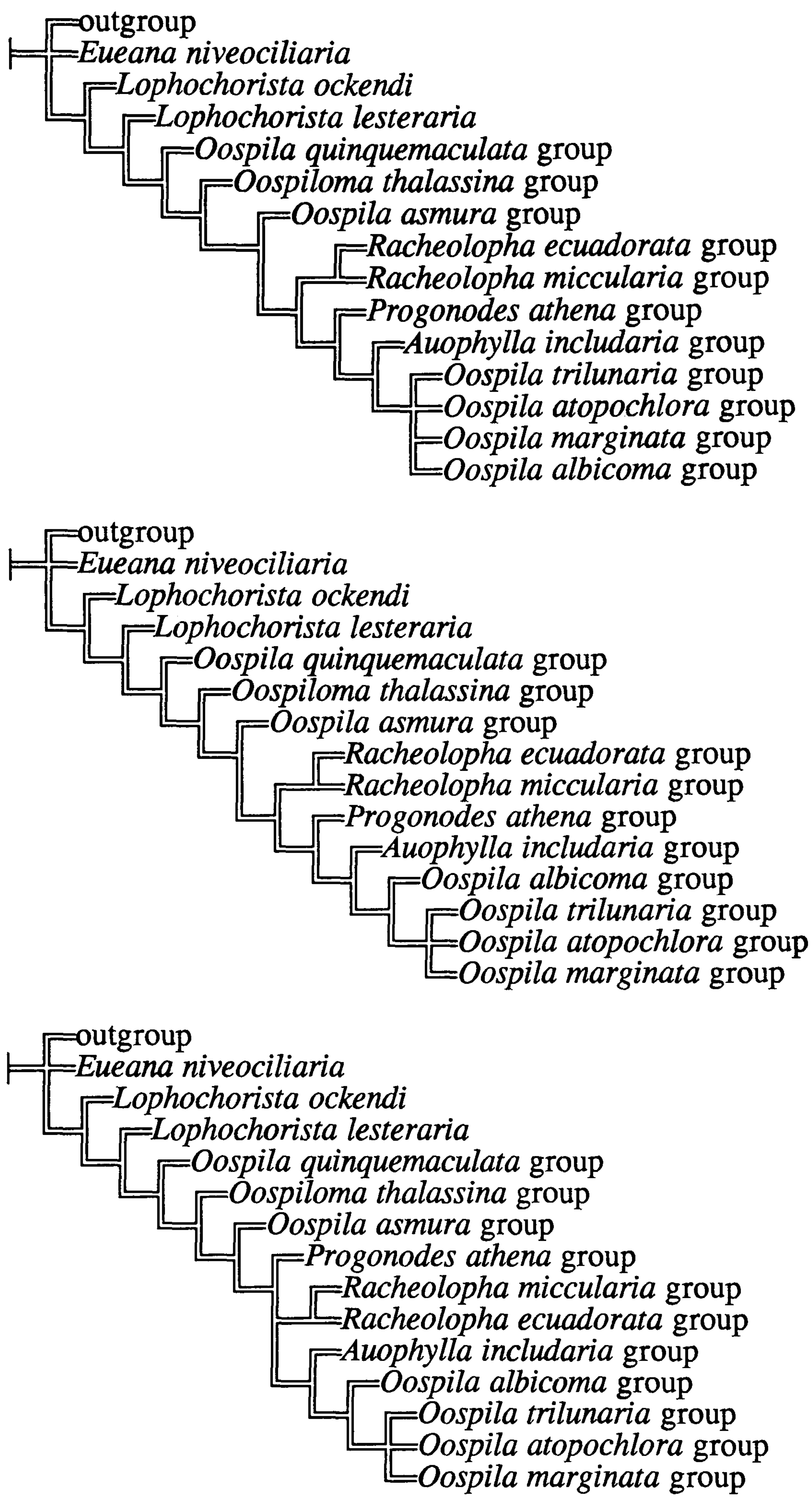

Fig. 3 Most parsimonious trees from analysis of species groups in the *Oospila* complex (length = 27 steps, consistency index = 0.77, retention index = 0.88).

Analysis of this data produced three alternative phylogenetic hypotheses (Fig. 3) and suggested a number of equally valid options for the classification of this group of genera. Given these options, it seemed prudent to draw the boundaries of *Oospila* at the points which will most facilitate identification. Since all the genera *Auophylla*, *Auophyllodes*, *Oospila*, *Oospiloma*, *Progonodes* and *Racheolopha* look much alike in external appearance, it was decided to synonymise them. The revised concept of *Oospila* is, therefore, a monophyletic group of 66 species (one of which is further subdivided into subspecies) defined by two apomorphies. These are firstly the presence of abdominal crests formed by broad scales with a central brush of long hair-like scales (character 3) and, secondly, the presence of an anellar complex, formed by the fusion of the juxta and transtilla (character 12).

A further consequence of this analysis is that the tribe Lophochoristini (*Lophochorista* plus *Eueana*; Ferguson, 1969) must be re-assessed, for there seems to be no good evidence for the monophyly of *Lophochorista* plus *Eueana*. One possible solution to this problem is to expand the tribe to include *Oospila* (in its revised sense), and base the tribe on the sclerotisation of the mesal region of the valva in the male genitalia. This would mean that it may be necessary also to include the genera *Comostola* Meyrick and *Rhomborista* Warren, unless the sclerotisation of the mesal region of the valva was shown to be independently derived in these genera.

DESCRIPTION OF THE GENUS

General appearance

Oospila species are slender-bodied Geometrinae. Their wings are typically dark green and patterned with blotches.

Head

The vestiture of the frons is typically brown, but occasionally green. The vertex is typically brown dorsally and cream ventrally, but sometimes it is entirely green. The interantennal fillet (the vestiture between the antennal bases) is usually white or, less commonly, brown. As in most Geometrinae, the chaetosemata of *Oospila* are small, external ocelli are absent and the compound eyes are large and round. The antennae of both sexes are typically bipectinate over the basal 2/3 and simple towards the apex, although the antennae of the females of some species are simple along their entire length. Where present, the rami are usually of approximately the same length in both sexes. The vestiture of the labial palpi is brown on their dorsal surface and cream ventrally; segment 3 of the labial palpi is typically short in males and longer in females. As is typical of Geometrinae, the maxillary palpi of *Oospila* are very short and one-segmented. *Oospila* has the typical geometrid proboscis which is long and without scales at the base.

Thorax

The vestiture of the thorax and patagia is typically green, in a few species it is dark- or reddish-brown.

The vestiture of the forelegs is brown on the anterior surface and cream on the lateral and posterior surfaces. In common with most Geometrinae, the fore tibia bears an epiphysis. The tibial spur formula is typically 0-2-2, but in the *thalassina* group, a pair of proximal spurs are present on the hind tibia, giving a tibial spur formula of 0-2-4. The hind tibia of some males has a recessed brush of long hair-like scales.

The wings are never reduced in size and are approximately triangular in most species. In some species, the hindwing has a short extension at the distal end of vein M_3, which is usually marked by tuft of long scales projecting beyond the fringe (e.g. *asmura*, Fig. 32). In the descriptions below, the forewing length is expressed as a range, measured along the costa from the wing base to the apex, and is typically between 7 and 26 mm. There is usually no sexual dimorphism in wing span, but the females of some species are slightly larger than their male counterparts. The hindwing frenulum is a well developed spine in males, but is absent in females.

The ground colour of the wings is dark green, except in *ciliaria* which has very pale blue-green wings. As with all Geometrinae, the wing colours of *Oospila* are prone to fading. Old specimens typically appear paler green than fresh material and in some cases (particularly in specimens of *violacea*, Fig. 9) may have faded to pale yellow, which must be borne in mind when attempting to identify museum material. The wings are typically marked with blotches although some species have bands along the termen (e.g. *pellucida*, Fig. 20), a speckled pattern (e.g. *semispurcata*, Fig. 27) or a more complex pattern (e.g. *obeliscata*, Fig. 68). The wing markings are white, cream, brown, reddish-brown or black (Figs 7-14). Most species of *Oospila* can be identified from the shape, size, position and colour of blotches, or other markings, although minor intraspecific variations may cause some confusion.

The costal edge of the forewing is usually pale brown, occasionally dark brown or white. Two blotches are typically present on the forewings, one at the apex and one at the tornus. In some species the blotch at the apex is replaced by a subapical blotch (e.g *trilunaria*, Fig. 59). In some *Oospila* species the blotches are connected by a band (usually brown) along the termen (e.g. *circumsignata*, Fig. 15). The forewing discal spot is typically small and brown, in some species it is enlarged (e.g. *altonaria*, Fig. 61) or modified to a V-shaped marking (e.g. *obeliscata*, Fig. 68).

The hindwings usually have similar markings to the forewings. In addition to blotches at the apex and tornus, a small, narrow blotch is present at the anal margin in some species (e.g. *albicoma albicoma*, Fig. 14). One or two discal spots are usually present. These are usually small and brown or white, but may be modified, as in the forewings.

The venation (Figs 4 and 5) is fairly constant throughout the genus, with minor inter- and intra-specific variation. In the forewings vein R_1 diverges at the apex of the discal cell (Fig. 4), except in the *astigma* and *miccularia* groups where it arises distally to M_1 (Fig. 5). There are no accessory cells in *Oospila*. Vein R_2 diverges proximally to vein R_5 (except in *venezuelata*). Vein M_1 diverges from Rs, distal to the discal cell. The cross-vein M_2-M_3 is often weaker than cross-vein Rs-M_1 and sometimes discontinuous at its centre.

The hindwing venation (Figs 4 and 5) is typical of Geometrinae. The only variation observed consistently in the genus is in cross-vein M_2-M_3, which is either continuous with cross-vein M_1-M_2 (e.g. *delacruzi*, Fig. 5) or displaced towards the apex of the wing (e.g. *marginata*, Fig. 4). However, this character shows some intraspecific variation and, in some species it was difficult to decide whether this vein was displaced or not. Therefore, this character is not included in individual species descriptions. Vein 3A is absent.

Abdomen

The dorsal surface of the abdomen bears distinctive crests on terga A2-A5 (see, for example, Figs 7-14); species with large abdomens also bear large, but paler, crests on terga A6 and A7; in species with smaller abdomens the crests on terga A6 and A7 are reduced or absent. Crests are dark brown with white centres and, unlike those found elsewhere in the Geometrinae, are composed of broad scales (those of other Geometrinae are composed of long, thin, hair-like scales). The most distal crest is usually smaller and paler. The remainder of the dorsal surface of the abdomen is typically cream (e.g. Figs 12 and 14), but in some species it is green, brown (e.g. Figs 7-11 and 13) or patterned. In some species, the crests are surrounded by a white area which may, in turn, be enclosed by a thin, pink line. The ventral and lateral surfaces of the abdomen are cream-coloured.

The female pregenital abdomen has no species-specific structures and all the segments are simple. However, sternum A2 is frequently modified and sternum A8 typically modified in males (Fig. 6). In males of some species, the posterior edge of sternum A2 is slightly emarginated (Fig. 6) and a small, elliptical sclerite occurs in the intersegmental membrane between sterna A2 and A3. In those species with this sclerite, sternum A2 also bears two brushes of long hair-like scales which meet over the sclerite. It therefore seems likely that this sclerite is associated with dissemination of pheromones. This sclerite does not seem to occur in other Geometrinae. The distribution within the genus is not consistent with species groups suggested by other characters and may be a groundplan character of the genus.

The male sternum A8 is a valuable character for identifying species of *Oospila* and is diagnostic in certain species where other external features are the same (e.g. *marginata*, *obsolescens* and *tricamerata*). Moreover, this structure can usually be inspected without dissecting the specimen. In males of most *Oospila*, sternum A8 is strongly sclerotised, often enlarged and typically with its posterior edge modified, either emarginated or with a bifurcate extension.

A pair of small sclerotised bands are sometimes found in the intersegmental membrane between sternum A8 and the male genitalic capsule. However, since the presence or absence and clarity of these structures varies intra-specifically they are not considered in the species descriptions below.

Male genitalia (Figs 82-142)

The uncus typically has a short apical extension, although in some species it is reduced to a narrow bar. In the *quinquemaculata* and *thalassina* groups, the uncus has a long apical extension. The socii are membranous, and usually quite large, but sometimes reduced in size. Visually, the gnathos dominates the posterior part of the genitalia of most male *Oospila* and consists of two large, strongly sclerotised horn-like processes. These structures lie across the uncus, often meeting along the midline (e.g. Fig. 82), but have been flattened in most of the drawings, to display the uncus. In the *quinquemaculata* and *thalassina* groups, the gnathos is a complete fused ring (Figs 89-97). The tegumen varies in breadth and, in some species, is strengthened by an X-shaped sclerotised brace (e.g. *excrescens*, Fig. 91).

Description of the valvae and their associated processes is aggravated by several conflicting systems of nomenclature used by taxonomists (see Klots, 1970 and Sibatani *et al.*, 1954), although Sibatani *et al.* (1954) attempted to clarify the homologies and terminology. The valvae may have a rounded or sculpted apex, and, typically the apex is divided by a cleft. In some members of the *quinquemaculata* group, the costal edge of the valva is more strongly sclerotised (e.g. in *quinquemaculata*, Fig. 89), and occasionally modified (e.g. in *continuata*, Fig. 90). A variety of processes arise from the valvae of *Oospila* species but one, a process of the mesal area of the valva, the *ampulla* (Fig. 82) (Klots, 1970) is a prominent feature of the valvae of many species of *Oospila*. The shape of this structure generally provides a clear means of identification. An ampulla also occurs in *Lophochorista lesteraria* Grossbeck, which (as mentioned above) probably belongs to an inclusive clade together with species of *Oospila* (see below). Occasionally, processes arise from the costa of the valva or close to (and in addition to) the ampulla (e.g. Figs 88, 90). Another feature of the valvae of many species of *Oospila* is an extension of the sacculus into a short, strongly sclerotised and usually pointed process (Fig. 82). Other processes, such as small spines at the apex of the valvae (e.g. *albipunctulata*, Fig. 104), are found in some species.

The term 'anellar complex' (Fig. 82) is used to describe a sclerotisation of the diaphragma which surrounds the aedeagus and which is a diagnostic feature of *Oospila*. Klots (1970) noted that the homologies and nomenclature of sclerotisations of the lepidopteran diaphragma were confused. In *Oospila*, the anellar complex has probably arisen from the fusion of the transtilla (*sensu* Pierce *in* Klots, 1970) and juxta (*sensu* Pierce *in* Klots, 1970). These two structures occur frequently in the Geometrinae, but appear to have become fused only in this genus. Typically, the anellar complex surrounds the aedeagus completely and the latter protrudes through a central hole. Functionally, the anellar complex appears to serve as a support for the aedeagus. The anellar complex may be attached to the valvae by short extensions from the medial (e.g. *O. longiplaga*, Fig. 84) or posterior regions of the sclerite (e.g. *O. trilunaria*, Fig. 121). These extensions are probably homologous with the transtillae of some other Geometrinae. In some species (e.g. *O. albicoma albicoma*, Fig. 117) the anellar complex is not attached to the valvae, but is held in position by the membrane of the diaphragma. In some species of *Oospila* the anellar complex has become secondarily reduced (e.g. *florepicta*, Fig. 92) to a V-shaped sclerite, fused with the valvae posteriorly.

Coremata are usually absent, although they are present in the *quinquemaculata* group where they arise from the base of each valva (e.g. *quinquemaculata*, Fig. 89). The vinculum has a U-, V-, or W-shaped ventral plate: this shows some intraspecific variation and is not usually of much value in identifying species.

The aedeagus is usually long, narrow and cylindrical. A small cornutus is found on the vesica of many species (e.g. *circumsignata*, Fig. 82). Additional cornuti, or other modifications, occur in a few species (e.g. *astigma*, Fig. 101).

Female genitalia (Figs. 143-191)

The anterior apophyses are exceptionally short in *Oospila*. However, this character is not unique to *Oospila* and extremely short anterior apophyses are also found in some species of the neotropical genus *Lissochlora* Warren (L.M. Pitkin, *pers. comm.*).

The area around the ostium is typically strongly sclerotised and is variously modified. The term *sterigma* is adopted for the whole complex of structures surrounding the ostium following Klots (1970) (Fig. 143). The presence and shape of the sterigma is often diagnostic for a particular species.

The bursa copulatrix typically consists of a long, relatively narrow duct, the *ductus bursae* (Klots, 1970) (Fig. 143) leading into an enlarged membranous sac, the *corpus bursae* (Klots, 1970) (Fig. 143). In some species an antrum (Fig. 152), a funnel-shaped sclerotisation of the ductus bursae, is present. The remainder of the ductus bursae is typically long, strongly sclerotised, and with longitudinal striations (e.g. *decoloraria*, Fig. 143). The corpus bursae is a membranous sac, which is either approximately spherical or bulbous in shape and varies in size between species. At 200x magnification, small teeth can be seen on the internal surface of the corpus bursae. A small signum is usually present and little structural variation occurs in this structure, although it does vary in size between species. When specimens mounted on a slide are viewed ventrally, the signum usually appears as a narrow sclerotised band. However, the signum actually consists of a narrow band of sclerotisation with a tooth at each end that protrudes into the corpus bursae (e.g. Fig. 143), which is visible if the corpus bursae is tilted a little.

Immature stages

The only species for which larval data have been recorded is *O. confundaria* Möschler, in the dry forest at 300 m elevation in the Guanacaste Conservation Area in northwestern Costa Rica. The larva (D. H. Janzen, *pers. comm.*) is light green with a slight rosy or brownish cast in a few individuals. It eats the expanding leaves of *Hymenaea courbaril* (Leguminosae) and is moderately common in the crowns of saplings 1-3 m tall at the time when they are forming new leaves (which occurs throughout the year). Mature trees of this species produce leaves only in December and January, but it is not known whether larvae are found in mature trees at this time of the year. Janzen (*pers. comm.*) has found mature larvae in March, May, June, August and December. When not feeding, the caterpillar holds itself motionless and straight, at an angle so as to look similar to a young *Hymenaea* twig or petiole (Janzen, 1988). The naked pupae are deposited in litter (Janzen, *pers. comm.*)

Distribution

The genus occurs in tropical America and has been recorded from Mexico, Cuba, Jamaica, Guatemala, Belize, Nicaragua, Costa Rica, Panamá, French Guiana, Surinam, Guyana, Trinidad, Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina, Paraguay, and Brazil. *Oospila venezuelata* has been recorded from Mexico, which seems to be the most northerly limit to the distribution of this genus, and only *O. includaria* has been recorded from Argentina, which seems to represent the southern limit of the genus. I have not examined any specimens from the Antilles, Bahamas, Chile, El Salvador, the Falkland Islands, Florida, Uruguay, the southern States of the U.S.A., or other parts of the Americas.

Diagnosis

Oospila can be distinguished from other Geometrinae by the composition of the abdominal crests. In most Geometrinae these are formed entirely of long hair-like scales, whereas in *Oospila* they are composed of much broader scales surrounding a central brush of long, thin, hair-like scales. The presence of the anellar complex in the male genitalia is also diagnostic, except in those few species where it has been secondarily reduced. Although a few other Geometrinae have blotches on their wings (e.g. *Cheroscelis oospila* Prout) these do not occur in the neotropics and the male genitalia are very different.

Habitat and biology

Oospila appears to be limited to tropical areas of Meso and South America. Species have been collected in transitional cloud forest (e.g. at Rancho Grande in the Henri Pittier National Park in Venezuela) and lowland dry forest (e.g. at Santa Rosa National

Park in Costa Rica). However, most specimens examined were collected in lowland rain forest areas of continental South America. In the rain forest, adults of most species (for which data are available) have been collected in both wet and dry seasons.

CHECKLIST OF *OOSPILA* SPECIES

Oospila Warren

Auophylla Warren **new synonymy**

Anophylla Warren (incorrect subsequent spelling)

Progonodes Warren **new synonymy**

Drucia Warren **new synonymy**

Halioscia Warren **new synonymy**

Racheolopha Warren **new synonymy**

Auophyllodes Prout **new synonymy**

Oospiloma Prout **new synonymy**

albicoma albicoma (Felder and Rogenhofer)

    minorata Warren

    deliciosa Thierry-Mieg **new synonymy**

albicoma nasuta Warren **new status**

albipunctulata (Prout) **new combination**

altonaria Jones

arpata (Schaus) **new combination**

    mionophragma (Prout) **new synonymy**

    mionophragma subruta (Prout) **new synonymy**

    similiplaga (Warren)

asmura (Druce)

    latimargo (Warren) **new synonymy**

    fumidimargo (Dognin) **new synonymy**

astigma (Warren) **new combination**

athena (Druce) **new combination**

atopochlora Prout

atroviridis Warren **new status**

dolens Druce **new synonymy**

callicula (Druce)

callicula stenobathra Prout **new synonymy**

callicula orchardae Prout **new synonymy**

camilla Schaus

carnelunata (Warren)

ciliaria (Hübner)

semialbaria (Guenée)

pallida (Warren) **new synonymy**

circumsessa Prout

circumsignata Prout

concinna Warren

eminens Schaus **new synonymy**

albicoma matura Prout **new synonymy**

confluaria (Warren)

mesocraspeda Prout **new synonymy**

confundaria (Möschler)

coerulea (Warren) **new synonymy**

coerulea aphenges Prout **new synonymy**

derasa (Warren) **new synonymy**

sesquiplaga Prout **new synonymy**

congener Warren

congener procellosa (Warren) **new synonymy**

continuata (Warren)

decoloraria (Walker)

delacruzi (Dognin)

restricta Warren **new synonymy**

delphinata (Warren)

plurimaculata (Warren) **new synonymy**

plurimaculata symmicta Prout **new synonymy**

heteromorpha (Warren) **new synonymy**

depressa Warren

semiviridis Warren **new synonymy**

dicraspeda Prout

ecuadorata (Dognin) **new combination**

sarptaria ruboris (Prout) **new synonymy**

euchlora (Prout) **new combination**

excrescens (Warren)

fimbripedata (Warren) **new combination**

florepicta (Warren)

cayennensis Herbulot **new synonymy**

holochroa (Prout) **new combination**

delicatescens (Dyar) **new synonymy**

hyalina Warren

fractimacula Prout **new synonymy**

imaculata **new species**

includaria (Herrich-Schäffer) **new combination**

magnifica (Schaus) **new synonymy**

multiplagiata (Warren) **new synonymy**

basiplaga (Warren) **new synonymy**

jaspidata (Warren)

lactecincta (Warren)

lacteguttata (Warren)

fenestrata (Bastelberger) **new synonymy**

peralta Schaus **new synonymy**

leucostigma (Warren) **new combination**

leucothalera (Prout) **new combination**

lilacina (Warren)

longipalpis (Warren)

longiplaga Warren

lunicincta (Warren)

marginata Warren

marginata sympathes Prout **new synonymy**

rufiplaga Warren **new synonymy**

miccularia (Guenée) **new combination**

imula (Dognin)

sarptaria (Möschler) **new synonymy**

nivetacta (Warren) **new combination**

obeliscata (Warren)

obsolescens **new species**

pellucida Prout

quinquemaculata (Warren)

circumdata (Warren) **new synonymy**

circumdata striolata Prout **new synonymy**

rhodophragma Prout

rosipara (Warren)

flavicincta (Warren) **new synonymy**

microspila (Warren) **new synonymy**

conversa (Dognin)

rubescens (Warren)

rufilimes (Warren) **new combination**

extensata (Warren) **new synonymy**

ruptimacula Warren

aliphera Dognin **new synonymy**

ruptimacula curtimacula Prout **new synonymy**

sellifera Warren

semispurcata (Warren)

sporadata (Warren)

curvimargo Herbulot **new synonymy**

stagonata (Felder and Rogenhofer) **new combination**

arycanda (Druce) **new synonymy**

thalassina Warren

tortuguera **new species**

tricamerata Prout

trilunaria (Guenée)

venezuelata (Walker) **new combination**

ambusta (Prout) **new synonymy**

belisama (Druce) **new synonymy**

invasata (Walker)

partita (Prout) **new synonymy**

venezuelata cellata (Prout) **new synonymy**

violacea Warren

zamaradaria Fletcher

SPECIES DESCRIPTIONS

Oospila circumsignata Prout

(Figs 15, 82)

Oospila circumsignata Prout, 1916: 171; 1932: 58. Holotype ♂, in BMNH. Type locality: BRAZIL. Label data: Fonte Boa, Upp[er] Amazon, August 1907. (S.M. Klages); Rothschild Bequest B[ritish] M[useum] 1939-1; Oospila circumsignata ♂ type Prout; Geometridae genitalia slide No. 15720 ♂. [Examined.]

♂ (Fig. 15). Forewing length 10-11 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings pale brown, with dark brown perimeters and striation. Forewing: costa pale brown; blotch at apex not extending along costa (as it does in *rubescens*, Fig. 79), connected to blotch at tornus by broad band along termen; blotch at tornus large, approximately rectangular, extending along 2/3 length of anal margin; discal spot small, brown. Hindwing: blotch at apex long, broad, extending along 1/2 length of termen, connected to blotch at tornus by narrow band along termen; blotch at anal margin absent; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: dorsal surface with crests surrounded by pink area, remainder green; sternum A2 with hair brushes and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 82). Uncus with apical extension short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: apical division deep; sacculus extended into short, strongly sclerotised, pointed process; ampulla short, curved, with denticulate apex. Anellar complex: completely surrounding aedeagus; fused to valvae posteriorly; with two large, approximately rectangular ventral plates.

Coremata absent. Vinculum with V-shaped ventral plate. Aedeagus with small cornutus on vesica.

♀ *genitalia.* Unknown.

Distribution. Only 6 specimens of this species were examined, all from the Amazonas region of Brazil.

Diagnosis. *Oospila circumsignata* is very similar in external appearance to *rubescens* (Fig. 79), but can be distinguished by the shape of the blotch at the apex of the forewing. In *circumsignata* this blotch does not extend along the costal edge as it does in *rubescens*. *Oospila circumsignata* is also slightly larger than *rubescens*. Males can be distinguished by the lack of a brush of long hair-like scales on the hind tibia of *circumsignata*.

Oospila circumsignata can be distinguished from *asmura* by the lack of a short extension of the hindwing at the apex of vein M_3 (compare Figs 15 and 32). These two species can also be distinguished by the form of the blotch at the tornus of the hindwing which is extended along the anal margin in *asmura*.

The male genitalia of *circumsignata* can be recognised by the curved form of the ampulla and the large ventral plates of the anellar complex (Fig. 82).

Material examined.

BRAZIL: *Amazonas*: Sao Paulo de Olivença, 2 ♂. Fonte Boa, 1 ♂, vii.1907 (*Klages*); 1 ♂ [holotype] viii.1907 (*Klages*); Nova Olinda, Rio Purus, 2 ♂, v.1922 (*Klages*). *Depositories:* BMNH, CMNH, NMNH.

Oospila decoloraria (Walker)

(Figs, 16, 83, 143)

Iodis decoloraria Walker, 1861: 541. Holotype ♀ [see remarks], in BMNH. Type locality: JAMAICA. Label data: Jamaica; Type, 45 110; 7. IODIS DECOLORARIA; Geometridae genitalia slide No. 15703 ♀. [Examined.]

Oospila decoloraria (Walker); Prout, 1912: 133; 1932: 56.

♂, ♀ (Fig. 16). Forewing length 8-11 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent. Forewing: costa pale brown; unmarked except for minute brown spot at tornus. Hindwing: small brown spot at tornus; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: dorsal surface with crests surrounded by narrow white line, remainder green; sternum A2 with hair brushes and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 83). Uncus with apical extension short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: divided apically; sacculus extended into long spine-like process; ampulla short, apex weakly curved and denticulate. Anellar complex: completely surrounding aedeagus; with ventro-lateral extensions fused to valvae. Vinculum with ventral plate rounded, with short, anterior extension. Coremata absent. Aedeagus: with short cornutus on vesica, specimen illustrated with 90° curve (this unusual feature may be a deformity, but only one male specimen was available).

♀ *genitalia* (Fig. 143). Sterigma a semicircular plate, with shallow emargination of posterior edge (not as deep as in *ruptimacula*, Fig. 148). Bursa copulatrix: ductus bursae narrow posteriorly, widening anteriorly, strongly sclerotised and striated, antrum absent; corpus bursae large, approximately spherical; signum small. Anterior apophyses, unusually, quite long.

Distribution. The nine specimens examined were collected in Cuba and Jamaica.

Diagnosis. *Oospila decoloraria* is recognisable from most other species by having only very small wing markings. Males can be distinguished from those of *confundaria* by the absence of a brush of long hair-like scales on the hindleg of *decoloraria.* In the females of *decoloraria* the antenna is bipectinate, whereas in *confundaria* it is simple.

Oospila decoloraria can be distinguished from *imaculata* by the presence of small markings at the tornus of both fore- and hindwings (compare Figs 16 and 76).

The male genitalia of *decoloraria* can be recognised by the shape of the valvae, ampullae and anellar complex (Fig. 83) and the female genitalia by the form of the sterigma (Fig. 143).

Remarks. The sex of the holotype was incorrectly given as male in the original description (Walker, 1861: 541).

Material examined.

CUBA: 3 ♀. Baracoa, 1 ♂. Cayamas, 2 ♀. Santiago, 1 ♀.

JAMAICA: 1 ♀ [holotype]. Newcastle, 1 ♀, viii.93.

Depositories: BMNH, NMNH.

Oospila jaspidata (Warren)

(Figs 17, 144)

Racheospila (?) jaspidata Warren, 1897: 430. Holotype ♀, in BMNH. Type locality: GUYANA. Label data: Type; Rio Demerara British Guiana; Racheospila jaspidata type ♀ ? Warr[en]; Racheolopha; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15049 ♀. [Examined.]

Racheolopha jaspidata (Warren), 1900: 137.

Drucia jaspidata (Warren), 1906: 416.

Oospila jaspidata (Warren); Prout, 1912: 133; 1932: 59.

♀ (Fig. 17). Forewing length 10-12 mm. Antenna unknown. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings reddish brown. Forewing: costa pale brown; blotch at apex large, extending to costa, extended posteriorly along termen to abut blotch at tornus; blotch at tornus smaller; discal spot small, brown. Hindwing: blotch at apex large, extending along 1/2-2/3 of termen, connected to blotch at tornus by narrow band along termen; blotch at tornus small, not connected to blotch at anal margin; blotch at anal margin narrow; discal spot small, brown. Hindleg with proximal spurs absent. Abdomen: dorsal surface reddish around crests; sterna simple.

♂ *genitalia.* Unknown.

♀ *genitalia* (Fig. 144). Sterigma absent. Bursa copulatrix: ductus bursae very short, weakly sclerotised, not striated, antrum absent; bursa copulatrix large and bulbous; signum small. Anterior apophyses, unusually, quite long.

Distribution. Only two females were examined, one from French Guiana and one from Guyana.

Diagnosis. *Oospila jaspidata* is similar in appearance to *excrescens*, from which it can be distinguished by the absence of a brick-red marking at the base of the forewing (compare Figs 7, 17 and 25).

Oospila jaspidata may be distinguished from *continuata* by the redder colour of the wing markings and by the shape of the blotch at the apex of the forewing, which is rounded in *jaspidata* and lacks the distinct apical emargination of that of *continuata* (compare Figs 17 and 24).

Material examined.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♀.

GUYANA: *East Demerara-West Coast Berbice:* Demerara River, 1 ♀ [holotype].

Depositories: BMNH, NMNH.

Oospila longiplaga Warren

(Figs 18, 84, 145)

Oospila longiplaga Warren, 1909: 83; Prout, 1912: 134; 1932: 57. Lectotype ♀, here designated, in BMNH. Type locality: BRAZIL. Label data: Type; Fonte Boa, Amazonas, September 06. (S.M. Klages); Oospila longiplaga type ♀ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15717 ♀. [Examined.]

♂, ♀ (Fig. 18). Forewing length 12-13 mm. Female antenna bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings pale brown, with perimeters darker and with dark brown striations. Forewing: costa pale brown; blotch at apex large, approximately circular, extending to costa, not connected to blotch at tornus; blotch at tornus large, extending to cover discal spot, extending along 2/3 of anal margin, wedge-shaped, wider towards centre of wing, gradually tapering towards termen; discal spot absent. Hindwing: blotch at apex large, quite narrow, approximately rectangular, although narrower where extended along costa, extending along 1/2 of termen, not connected to blotch at tornus; blotch at tornus large, approximately rectangular, extending along 2/3 of anal margin; blotch at anal margin absent; discal spot small, white or absent. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: dorsal surface cream around crests; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 84). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: apical division absent; sacculus not extended; costal edge with small, pointed, subapical extension; ampulla short, with pointed apex. Anellar complex: completely surrounding aedeagus; with ventro-lateral extensions fused to valvae. Vinculum with ventral plate broad, V-shaped. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia* (Fig. 145). Sterigma absent. Bursa copulatrix: ductus bursae long, strongly sclerotised and striated, antrum absent; corpus bursae large, approximately spherical; signum small. Anterior apophyses short.

Distribution. The three specimens examined were examined, all from the Amazonas region of Brazil.

Diagnosis. The size and shape of the blotches distinguish *longiplaga* from most other species. *Oospila longiplaga* can be distinguished from *lunicincta* and *ruptimacula* by the large blotch at the tornus of the forewing, which extends to the discal cell in *longiplaga* (compare Figs 18, 19 and 21).

Oospila longiplaga may be distinguished from *albicoma albicoma*, *albicoma nasuta*, *concinna* and *depressa* by the absence of a blotch on the anal margin of the hindwing in *longiplaga* and by the long, rectangular blotch at the tornus of the hindwing (compare Figs 14, 18, 54-56, 78).

The male genitalia of *longiplaga* can be recognised by the presence of a small subapical extension of the costal edge of the valvae (Fig. 84).

Material examined.

BRAZIL: *Amazonas:* Fonte Boa, 1 ♀ [lectotype] ix.06 (*Klages*); 1 ♀ [paralectotype] ix.06 (*Klages*); Alto Paraiso, 100m, 1 ♂, 4.x.1985 (*Becker*).

Depositories: BMNH, V.O. Becker Collection.

Oospila lunicincta (Warren)

(Figs 19, 85, 146)

Racheolopha lunicincta Warren, 1909: 85. Holotype ♂, in BMNH. Type locality: PARAGUAY. Label data: Type; Sapucay, Paraguay, 16.ix.03 (W. Foster); fi[g] in Seitz 8; Racheolopha lunicincta type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15724 ♂. [Examined.]

Auophyllodes lunicincta (Warren); Prout, 1912: 131.

Oospila lunicincta (Warren); Prout, 1932: 58.

♂ (Fig. 19). Forewing length 12-13 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings cream, with thin, dark perimeters and some dark striation. Forewing: costa pale brown; subapical blotch small, not extending to costa, not connected to blotch at tornus; blotch at tornus small; discal spot absent. Hindwing: blotch at apex large, not connected to blotch at tornus by band along termen; blotch at tornus small, not connected to blotch at anal margin; blotch at anal margin very narrow; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: dorsal surface around crests cream with pink and brown flecks; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 85). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen broad, with X-shaped sclerotised brace absent. Valvae: apical division absent; ampulla broad, robust, with denticulate margin. Anellar complex with posterior part broadly fused with valvae, distinctively shaped (Fig. 85). Vinculum with broad W-shaped ventral plate. Coremata absent. Aedeagus with small cornutus on vesica.

♀ *genitalia* (Fig. 146). Sterigma absent. Ostium with pocket on each side. Bursa copulatrix: ductus bursae strongly sclerotised, not striated, antrum absent; corpus bursae small, bulbous; signum small. Anterior apophyses short.

Distribution. The 6 specimens examined were collected in Peru, Paraguay, and Brazil.

Diagnosis. In general, *lunicincta* can be distinguished from other species with cream or pale brown blotches by the smaller size of its blotches. It can be distinguished from *albicoma albicoma*, *concinna* and *longiplaga* by the small size of the blotch at the tornus of the forewing, which does not extend to cover the discal spot in *lunicincta* (compare Figs 14, 18, 19, 54 and 56). *Oospila lunicincta* can be distinguished from *albicoma nasuta* by the absence of a short, digitate extension of the blotch at the tornus of the forewing (compare Figs 19 and 55).

The shape of the blotch at the apex of the forewing distinguishes *lunicincta* from *depressa*: in *lunicincta* this blotch is approximately triangular, tapers towards the costa and does not fill the apex as it does in *depressa* (compare Figs 19 and 78).

The male genitalia of *lunicincta* can be recognised by the shape of the valvae and ampullae (Fig. 85). The female genitalia can be recognised by the presence of a pocket on each side of the ostium (Fig. 146).

Material examined.

PERU: Divisoria, 5200 ft, 1 ♂, 20-23.vi.1982 (*Covell*).

PARAGUAY: *Paraguarí:* Sapucay, 1 ♂ [holotype] 16.ix.03 (*Foster*).

BRAZIL: Minas Geraes, Uberaba, 3 ♂ (*Le Moult*). Rio de Janeiro, 1 ♀, xi. (*Smith*).

Depositories. BMNH, CMNH, C. V. Covell Jr. collection.

Oospila pellucida **Prout**

(Figs 20, 86, 147)

Oospila pellucida Prout, 1916: 170; 1932: 56. Lectotype ♂, here designated, in BMNH. Type locality: PERU. Label data: type; La Oroya, R[ío] Inambari, Peru, Sept[ember] 1904. 3100 ft., dry seas[on] (G. Ockenden); Oospila pellucida ♂ Prout type; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15707 ♂. [Examined.]

♂, ♀ (Fig. 20). Forewing length 11-14 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent; markings brown. Forewing: costa pale brown; with band along termen narrow; not expanded into blotches; discal spot small, brown. Hindwing: as forewing; anterior discal spot small, white; posterior discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: dorsal surface with white area around crests enclosed by pink line, remainder cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with bifurcate posterior extension, apices enlarged.

♂ *genitalia* (Fig. 86). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: apical division absent; sacculus extended into short, pointed projection; ampulla large, robust with lateral projection, margin toothed. Anellar complex: with ventral V-shaped part fused to valvae; posterior part modified into an approximately rectangular plate with posterior margin denticulate, lying dorsal of aedeagus. Vinculum with ventral plate squarish. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia* (Fig. 147). Sterigma large, expanded at apical edges. Bursa copulatrix: ductus bursae long, strongly sclerotised and striated, with large lateral appendix anterior to ostium, antrum absent; corpus bursae large, bulbous; signum small. Anterior apophyses short.

Distribution. Four specimens were examined from Peru and two from Colombia.

Diagnosis. The band along the termen of *pellucida* is uniformly narrow and not expanded into blotches, which distinguishes it from *confluaria* and *dicraspeda* (compare Figs 20, 57 and 62). Males can also be distinguished from those of *confluaria* by the absence of a brush of long hair-like scales on the hind tibia.

Oospila pellucida can be distinguished from *lacteguttata* by the absence of blotches and by the absence of the proximal pair of spurs on the hind tibia.

The darker ground colour of the wings and the presence of a brown, not reddish, band along the termen distinguishes *pellucida* from *ciliaria*.

The male genitalia of *pellucida* can be recognised by the modification of the posterior part of the anellar complex into a rectangular plate with a denticulate margin and by the shape of the ampulla (Fig. 86). The female genitalia of *pellucida* can be recognised by the presence of an appendix at the posterior of the ductus bursae (Fig. 147).

Material examined.

COLOMBIA: *Risaralda:* Siató, Rio Siató, slopes of Chocó, 5200 ft, 2 ♀, ix.09. **PERU:** *Puno:* La Oroya, Río Inambari, 3100 ft, 1 ♂ [lectotype], 1 ♂ [paralectotype] dry season, ix.1904 (*Ockenden*). Carabaya: Tinguri, 3400 ft, 1 ♂ [paralectotype] dry season, viii.1904 (*Ockenden*). La Unión, Río Huacamayo, 2000 ft, 1 ♀ [paralectotype] wet season, xi.1904 (*Ockenden*).

Depository: BMNH.

Oospila ruptimacula **Warren**

(Figs 21, 87, 148)

Oospila ruptimacula Warren, 1901: 448; Prout, 1912: 133; 1932: 58. Holotype ♂, in BMNH. Type locality: ECUADOR. Label data: Type; Paramba [3500 ft II.97 struck out]; 8b IIX IX; Oospila ruptimacula type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15723 ♂. [Examined.]

Oospila aliphera Dognin, 1923: 20. Holotype ♂, in NMNH. Type locality: BOLIVIA. Label data: Bolivia: Río Songo, 750 m (*Fassl*); Genitalia slide By MAC 57762 USNM. [Examined.] **New synonymy.**

Oospila ruptimacula aliphera Dognin; Prout, 1932: 58.

Oospila ruptimacula curtimacula Prout, 1932: 58. Lectotype ♂, here designated, in BMNH. Type locality: COLOMBIA. Label data: Type; Gorgona Island, Colombia, at light, 200 ft. 15.10:24. S[ain]t George Exped[itio]n. C. L. Collenette; Brit[ish] Mus[eum] 1925-488; Seitz VIII; Oospila ruptimacula curtimacula ♂ type Prout; Geometridae genitalia slide No. 15721 ♂. [Examined.] **New synonymy.**

♂, ♀ (Fig. 21). Forewing length 15-20 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour very dark green; markings cream, with brown perimeters and brown striation. Forewing: costa pale brown; blotch at apex rounded, connected to blotch at tornus by thin brown line along termen; blotch at tornus approximately rectangular or wedge-shaped, usually narrower distally; discal spot absent. Hindwing: blotch at apex large, extending along 1/2 termen, dark at anterior, connected to blotch at tornus by dark brown line along termen; blotch at tornus long, thin, extending along 2/3 of anal margin; blotch at anal margin absent; anterior discal spot small, white; posterior discal spot sometimes small, white, sometimes absent (as in specimens previously allocated to *curtimacula*). Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: dorsal surface green around crests; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge in male.

♂ *genitalia* (Fig. 87). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: apical division deep; sacculus extended into long, narrow, sclerotised process; ampulla thin, digitate, with denticulate apex. Anellar complex: completely surrounding aedeagus; fused to valvae posteriorly; posterior part extended to deeply emarginated plate with denticulate margin. Vinculum with broad, V-shaped ventral plate. Coremata absent. Aedeagus with cornutus on vesica.

♀ *genitalia* (Fig. 148). Sterigma semicircular, deeply emarginated medially (deeper than *decoloraria*, Fig. 143). Bursa copulatrix: ductus bursae long, strongly sclerotised and striated, widening distally; corpus bursae small, spherical; signum small. Anterior apophyses short.

Distribution. This species is widely distributed throughout Central and South America and specimens have been collected from Belize, Costa Rica, Colombia, Ecuador, Peru, Bolivia and Brazil.

Diagnosis. *Oospila ruptimacula* can be distinguished from other species with cream blotches by the presence of patches of concentrated dark brown colour within these blotches. Thus, the blotches of *ruptimacula*, particularly the blotch at apex of the hindwing, are much darker than those of other species with cream or pale brown blotches. The shape of the blotch at the tornus of the forewing distinguishes *ruptimacula* from *albicoma albicoma*, *concinna*, and *longiplaga*: in *ruptimacula* this blotch does not extend to cover the discal spot as it does in the others (compare Figs 14, 18, 21, 54, and 56). *Oospila ruptimacula* can be distinguished from *albicoma nasuta*, *depressa*, and *lunicincta* by the size of the blotch at the tornus of the hindwing, which is much larger in *ruptimacula* (compare Figs 19, 21, 55, 78).

The male genitalia of *ruptimacula* can be recognised by the shape of the valvae and the modified form of the anellar complex (Fig. 87). The female genitalia can be recognised by the shape of the sterigma (Fig. 148).

Material examined.

BELIZE: *Stann Creek:* Stann Creek Valley, 1 ♀ (*Bilaux*).

COSTA RICA: *Alajuela:* Estacion Pitilla, 9 km South of Santa Cecilia, 700 m, 1 ♀, 18.v.1988 (*Janzen & Hallwachs*). *Puntarenas:* Fila Esquinas, 35 km South of Palmar Norte, 8°45'x83°20', 150 m, 2 ♂, 1 ♀, 7-8.i.1983 (*Janzen & Hallwachs*). *San José:* Estacion Carrillo, Parque Nacional Braulio Carrillo, 700 m, 1 ♂, viii.1984 (*Chacon & Chacon*); 1 ♂, iv.1985 (*Chacon & Chacon*).

COLOMBIA: *Cauca:* Gorgona Island, 200 ft, 1 ♂ [lectotype of *ruptimacula curtimacula*] 15.x.24 (*Collenette*); 1 ♀ [paralectotype of *ruptimacula curtimacula*] 17.x.24 (*Collenette*); 1 ♂ [paralectotype of *ruptimacula curtimacula*] 21.xi.24 (*Collenette*); 1 ♂ [paralectotype of *ruptimacula curtimacula*] [28].x.24 (*Collenette*).

ECUADOR: *Imbabura:* Paramba, 1 ♂ [holotype of *ruptimacula*]. *Chimborazo:* Chimbo, 1 ♀ (*Mathan*) 1.[ix].1892.

PERU: *Huánuco:* Pozuzo, 1 ♀. *Madre de Diós:* Tambopata Reserve, 30 km South

West of Peurto Maldonado, 300 m, 1 ♂, 16-22.x.1983 (*Covell*). *Puno:* South East Peru, La Oroya, Río Inambari, 3000 ft, 1 ♂, dry season, v.1905 (*Ockenden*); 3100 ft, 2 ♂, wet season, iii.05 (*Ockenden*); South East Peru, Santo Domingo, 6000 ft, 1 ♂, xi.1904 (*Ockenden*); South East Peru, 1 ♂; Yahuarmayo, 1200 ft, 1 ♀, v-vii.1912 (*Watkins*). **BOLIVIA:** Río Songo, 750 m, 1 ♂ [holotype of *aliphera*] (Fassl). **BRAZIL:** *Amazonas:* Fonte Boa, 1 ♂, v.1906 (*Klages*); Sao Paulo de Olivença, 1 ♂; Hyntanahan, Rio Purus, 2 ♂, iii.1922 (*Klages*).

Depositories: BMNH, CMNH, C. V. Covell Jr. collection, INBio, NMNH.

Oospila venezuelata (Walker) new combination

(Figs 22, 88, 149)

Comibaena venezuelata Walker, 1861: 570. Lectotype ♂, here designated, in BMNH. Type locality: VENEZUELA. Label data: 47 g; Venezuela; 7. Comibaena venezuelata; South America; Type; Geometridae genitalia slide No. 15782 ♂. [Examined.]

Comibaena venezuelata Walker; Druce, 1892: 87.

Auophyllodes venezuelata (Walker); Prout, 1912: 131; 1932: 53.

[*Auophyllodes venezuelata* ab. *connexa* Prout, 1932: 53 Infra-subspecific name.]

Auophyllodes venezuelata cellata Prout, 1932: 53. Holotype ♀, in BMNH. Type locality: MEXICO. Label data: Mexique oriental Tabasco W. Gugelmann, 1er trimestre 1914; Ex Oberthür Coll[ection] Brit[ish] Mus[eum] 1927-3; Auophyllodes venezuelata cellata ♀ type Prout; Geometridae genitalia slide No. 15786 ♀. [Examined.] **New synonymy.**

Comibaena invasata Walker, 1866: 1611; Druce, 1892: Table 49, Fig.18. Holotype ♂, in BMNH. Type locality: COLOMBIA. Label data: 65 86; S[an]ta Marta; Comibaena invasata; Type. [Examined.] Synonymised by Prout, 1932: 53.

Auophyllodes invasata (Walker); Prout, 1912: 131.

[*Auophyllodes venezuelata* ab. *invasata* Prout, 1932: 53. Infra-subspecific name.]

[*Auophylla invasata* ab. *perrupta* Warren, 1900: 132. Infra-subspecific name].

Comibaena belisama Druce, 1892: 87. Holotype ♂, in BMNH. Type locality: PANAMA. Label data: Type; V[olcan] de Chiriqui, 2-3000 ft. Champion; Godman-Salvin Col[lection] 1903-4. B[iologia] C[entrali] A[mericana] Lep[idoptera] Het[erocera]. Comibaena belisama, Druce; Comibaena belisama ♂ type Druce; Geometridae genitalia slide No. 15779 ♂ [Examined.] **New synonymy.**

Auophyllodes belisama (Druce); Prout, 1912: 131; 1932: 53.

Auophylla ambusta Warren, 1900: 131. Holotype ♂, in BMNH. Type locality: VENEZUELA. Label data: Type; Palma Sola, Venezuela. 96 (Whytmann); Rothschild Bequest B[ritish] M[useum] 1939-1; auophylla ambusta type ♂ Warr[en]; Geometridae genitalia slide No. 15785 ♂. [Examined.] **New synonymy.**

Auophyllodes ambusta (Warren); Prout, 1912: 131; 1932: 53.

Auophyllodes partita Prout, 1912, 131; 1932: 53. Holotype ♀, in BMNH. Type locality: PANAMA. Label data: La Choerra. Panama. 1 IV to 15 V 98. C.H. Dolby-Tylor. 98-146; Auophyllodes partita type Prout; Geometridae genitalia slide No. 15780 ♀. [Examined.] **New synonymy.**

♂, ♀ (Fig. 22). Forewing length 9-12 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent, markings cream or dark brown. Forewing: costa pale brown; with band of varying width along termen, often expanded at tornus; often band is cream along entire length (as in most specimens formerly allocated to *venezuelata*), sometimes cream proximally and dark brown distally, sometimes wholly dark brown (as in specimens previously allocated to *belisama*); discal spot usually a short brown line surrounded by cream area; cream area around discal spot may be continuous with cream area at tornus, sometimes discal spot reduced, occasionally absent. Hindwing: with broad band along termen, coloured as forewing; discal spot usually absent, occasionally a short brown line surrounded by a small white area. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: dorsal surface cream around crests; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 88). Uncus a narrow bar, not extended apically. Socii reduced. Gnathos not fused, components exceptionally large. Valvae: apical division absent; sacculus not extended; costa with large curved projection; apex sometimes with short process (in larger specimens) or rounded (Fig. 88); ampulla absent. Anellar complex: V-shaped; fused to valvae posteriorly. Vinculum with V- or U-shaped ventral plate. Coremata absent. Aedeagus with small cornutus on vesica.

♀ *genitalia* (Fig. 149). Ostium displaced anteriorly and intersegmental membrane between sternum A7 and A8 extended. Sterigma a rectangular bar with a short anteriorly-directed projection on each side. Bursa copulatrix: ductus bursae wide, weakly sclerotised and not striated, antrum absent; corpus bursae bulbous; signum small. Anterior apophyses short.

Distribution: Widely distributed throughout Central and South America, this species has been collected in Mexico, Guatemala, Nicaragua, Costa Rica, Panamá, Trinidad, Venezuela, Colombia, Peru and Bolivia.

Diagnosis. *Oospila venezuelata* is unlikely to be confused with any other species, but may be distinguished from *astigma* by the broader band along the termen of its hindwings (compare Figs 22 and 37). Males of these two species can also be distinguished by the shape of the anellar complex (compare Figs 88 and 101).

The female genitalia of *venezuelata* can be recognised by the displacement of the ostium and extension of the intersegmental membrane between sternum A7 and A8 (Fig. 149). The displacement of vein R_2 in the forewings, so that its origin is distal to that of vein R_5, also distinguishes *venezuelata* from other species.

Material examined.

MEXICO: Tabasco, 1 ♀ [holotype of *venezuelata cellata*] 1^er trimestre, 1914 (*Gugelmann*). *Veracruz:* Huatuxco, 1 ♀. 1 ♂.

GUATEMALA: South Geronimo, 2 ? (*Champion*). *Santa Rosa:* Barberena, 1 ♂. *Izabel:* Cayuga, 1 ♂ (*Schaus & Barnes*); *Sacatepéquez:* Duenas, 1 ? (*Champion*).

NICARAGUA: *Rio San Juan:* Chontales, 1 ♂.

COSTA RICA: *Alajuela:* Cerro Campana, 650 m East side Volcan Cacao, 6 km North West Dos Rios, 1 ♂, 15.i.1988 (*Janzen & Hallwachs*). Finca San Gabriel, 2 km South West of Dos Rios, 600 m, 7 ♂, v.1989 (*GNP Biodiversity Survey*). *Guanacaste:* Estacion Mengo, South West side of Volcan Cacao, W85°28'10" N10°55'43", 1100 m, 1 ♂, ii.1988 (*Janzen & Hallwachs*); 4 ♂, 10.ii.1988 (*Janzen & Hallwachs*); 2 ♂, vi.1988 (*Janzen & Hallwachs*). Casa Roberto, Estacion Pitilla, 7 km South of Santa

Cecilia, W85°25'33" N11°00'18", 500 m, 2 ♂, v.1988 (*GNP Biodiversity Survey*); 2 ♂, i.1989 (*GNP Biodiversity Survey*). Estacion Pitilla, 9 km South of Santa Cecilia, 700 m, 1 ♂ (*Moraga & Rios*). *Limón:* Sixola River, 1 ♂. *San José:* San José, 2 ♂, 2 ♀ (*Schmidt*).

PANAMA: La Choerra, 1 ♀ [holotype of *partita*] 1.iv-15.v.98 (*Dolby-Tylor*). *Canal Zone:* Corozal, near Balboa, 1 ♀, 20.vi.24 (*Collenette*). *Chiriquí:* Volcan de Chiriquí, 2-3000 ft, 1 ♂ [holotype of *belisama*] (*Champion*). 1 ♂ (*Walker*).

TRINIDAD: *Saint George East:* Caparo, 1 ♀ (*Birch*). 1 ?, 10.vi-2.vii (*Kaye*).

VENEZUELA: 1 ♂ [lectotype of *venezuelata*]. Cucuta, 2 ♂, 1 ♀. Palma Sola: 1 ♂ [holotype of *ambusta*] 1896 (*Whytmann*); 1 ♂ [lectotype of *venezuelata*]; 1 ♀ 1896 (*Whytmann*); 1 ♀ (*Whytmann*); 1 ♂, 4 ♀. *Carabobo:* Valencia, 1 ♂; San Esteban, near Pueno-Cabello, 1 ♂ (*Sagan*). *Distrito Federal:* Caracas, 1 ♂.

COLOMBIA: *Boyacá:* Muzo, 400-800 m, 5 ♂ (*Fassl*). *Magdalena:* Santa Marta, 1 ♂ [holotype of *invasata*]; Suert Cabel, 1 ?, 76 (*Smith*); Minca, 2000 ft, 1 ♂ (*Smith*); Don Amo, 2000 ft, 1 ♂ (*Smith*); 1 ♂. Bonda, 0 ft, 1 ♂ (*Smith*). *Meta:* East Colombia, Upper Río Negro, 800 m, 6 ♂ (*Fassl*).

PERU: 1 ♂.

BOLIVIA: *Santa Cruz:* East Bolivia, Buenavista, 750 m, 1 ♂, viii.06-iv.07 (*Steinbach*). *Cochabamba:* Charaplaya, 65°W 16°S, 1300 m, 1 ♂, iv.01 (*Simons*); 1 ♂ (*Germain*).

Depositories: BMNH, INBio.

The *quinquemaculata* group

The *quinquemaculata* group is characterised by three characters of the male genitalia. The uncus has a long apical extension, the gnathos is fused and coremata are present (except in *florepicta*). This group is distinguished from the *thalassina* group by the absence of a proximal pair of spurs on the hind tibia.

Oospila quinquemaculata (Warren)

(Figs 23, 89, 150)

Drucia quinquemaculata Warren, 1906: 416. Holotype ♀, in NMNH. Type locality: FRENCH GUIANA. Label data: S[ain]t Jean, Maroni, F[rench] Guiana; Drucia quinquemaculata type ♀; Type No. 9177 U.S.N.M; Collection Wm Schaus; Genitalia Slide By MAC 57765 USNM. [Examined.]

Oospila quinquemaculata (Warren); Prout, 1912: 134; 1932: 58.

Drucia circumdata Warren, 1907: 202. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; La Oroya, R[ío] Inambari, S[outh] E[ast] Peru, 3100 ft, wet season, Oct[ober] 1904. (G. Ockenden); Drucia circumdata type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15685 ♂. [Examined.] **New synonymy.**

Oospila circumdata (Warren); Prout, 1912: 134; 1932: 58.

Oospila circumdata striolata Prout, 1918a: 118; 1932: 58. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type H[olo]T[ype], Río Ampiyacu, Putomayo, Peruv[ian] Amaz[onas]; Det[ermined] by L.B. Prout; Joicey Bequest. Brit[ish] Mus[eum] 1934-120; Oospila circumdata striolata ♂ type Prout; Geometridae genitalia slide No. 15686 ♂. [Examined.] **New synonymy.**

♂, ♀ (Fig. 23). Forewing length 12-14 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings reddish brown or pale brown with darker brown centres. Forewing: costa pale brown; blotch at apex large, extending to costa, connected to blotch at tornus by narrow band along termen; blotch at tornus small; discal spot small, brown. Hindwing: blotches at apex and tornus connected by thin band along termen, sometimes joined to blotch at anal margin by thin band along anal margin; blotch at anal margin small, narrow; discal spot usually small, brown, occasionally absent. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: dorsal surface around crests brown or reddish brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 89). Uncus long, with long, pointed apical extension. Socii large. Gnathos fused. Tegumen with X-shaped sclerotised brace absent. Valvae: apical division absent; costa more strongly sclerotised; sacculus not extended; ampulla short, digitate, with pointed apex. Anellar complex: completely surrounding aedeagus, fused to valvae posteriorly. Vinculum with broad, ventral plate, sometimes W-shaped, sometimes U-shaped. Coremata present. Aedeagus with large cornutus on vesica.

♀ *genitalia* (Fig. 150). Sterigma absent, but membrane below ostium with extra sclerotisation and folded to form pouch. Bursa copulatrix: complex of ductus bursae and corpus bursae large, with short striations, with convoluted folds, antrum absent; signum small. Anterior apophyses quite long.

Distribution. Recorded in and south of Costa Rica, in French Guiana, Peru, Bolivia, and northern parts of Brazil.

Diagnosis. Although rather similar to *continuata* in external appearance, *quinquemaculata* can be distinguished by the distinct separation of the blotches at the apex and tornus of the forewing. In *continuata*, these blotches are connected by a broad band along the termen (compare Figs 23 and 24). Moreover, *quinquemaculata* has a rounded blotch at the apex; that of *continuata* is indented at the apex.

The absence of an extension of the hindwing at the apex of vein M_3 of the hindwing distinguishes *quinquemaculata* from *asmura* (compare Figs 23 and 32). The form of the anellar complex distinguishes males of *quinquemaculata* from those of *asmura* and *continuata* (compare Figs 89, 90 and 98).

The female genitalia can be recognised by the unusual shape and convoluted folds of the bursa copulatrix (Fig. 150).

Material examined.

COSTA RICA: *Guanacaste:* Derrumbe, Estacion Mengo, West side Volcan Cacao, 1400 m, 1 ♀, 5.vi.1988 (*Janzen & Hallwachs*); Estacion Pitilla, 9 km South of Santa Cecilia, 700 m, 1 ♀, xi.1989 (*Moraga & Rios*).

FRENCH GUIANA: *Guyane:* Godebert-Maroni, 1 ♂ (*Le Moult*); Saint Jean du Maroni, 1 ♀ [holotype of *quinquemaculata*].

PERU: *Loreto:* Río Ampiyacu, 1 ♂ [holotype of *circumdata striolata*]. *Puno:* South East Peru, La Oroya, Río Inambari, 3100 ft, 1 ♀, wet season, x.1904 (*Ockenden*); 1 ♂ [holotype of *circumdata*] wet season, x.1904 (*Ockenden*); 1 ♂, ix.05 (Ockenden); 2 ♂, wet season, xi-xii.1905 (*Ockenden*).

BOLIVIA: *Santa Cruz:* Provincia del Sara, 450 m, 1 ♂ vii.1914 (*Steinbach*).

BRAZIL: *Amazonas:* Upper Amazon, Codajas, 1 ♀ [paratype of *circumdata striolata*] iv.1907 (*Klages*).

Depositories: BMNH, CMNH, INBio, NMNH.

Oospila continuata (Warren)

(Figs 24, 90, 151)

Racheolopha continuata Warren, 1906: 422. Holotype ♀, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: S[ain]t Laurent du Maroni, xii.1904; Schaus Coll[ection]; USNM Type no. 9190 [Examined.]

Oospila continuata (Warren); Prout, 1932: 58.

♂, ♀ (Fig. 24). Forewing length 9-10 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings brown. Forewing: costa pale brown; blotch at apex indented at apex, connected to blotch at tornus by broad band along termen; blotch at tornus quite small; discal spot small, brown. Hindwing: blotch at apex long, thin, extending along 1/2 termen, connected to blotch at tornus by narrower band along termen; blotch at tornus connected to blotch at anal margin by narrower band along anal margin; blotch at anal margin short, narrow; discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales present. Abdomen: dorsal surface around crests brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 90). Uncus with apical extension long, with expanded, rounded apex. Socii large. Gnathos fused. Tegumen, with X-shaped sclerotised brace absent. Valvae: apical division absent; costa with shallow cleft towards apex; with short, digitate projection close to costa below apex; ampulla short, with cleft tip; sacculus not developed. Anellar complex: completely surrounding aedeagus; connected to valvae by short ventro-lateral extensions; extended posteriorly to broad tongue-shaped plate (broader than *depressa*, Fig. 139). Vinculum with broad, rounded, U-shaped ventral plate. Coremata present. Aedeagus short, squat, without cornutus on vesica.

♀ *genitalia* (Fig. 151). Sterigma absent. With shallow internally-directed pocket each side of ostium. Bursa copulatrix: ductus bursae quite short, not strongly sclerotised or striated, antrum absent; corpus bursae large, bulbous; signum small. Anterior apophyses quite long.

Distribution. Five specimens were examined, four from the Guyane region of French Guiana and a single specimen from the Amazonas region of Brazil.

Diagnosis. *Oospila continuata* is rather similar in external appearance to *quinquemaculata*, from which it may be distinguished by the broad band along the termen connecting the blotches at the apex and tornus (compare Figs 23 and 24). Also, *continuata* has a distinct apical indentation of the blotch at the apex of the forewing, whereas the blotch is more rounded in *quinquemaculata*.

The narrower and more uniform band of brown along the termen of the wings and the absence of a brick-red marking at the base of the forewing distinguish *continuata* from *excrescens* (compare Figs 7, 24 and 25).

Oospila continuata may be distinguished from *circumsessa* by the extension of the brown markings along the anal margin of the hindwing and by the absence of a short extension of the hindwing at the apex of vein M_3 (compare Figs 24 and 33).

The male genitalia of *continuata* can be recognised by the extension of the posterior part of the anellar complex into a broad, tongue-shaped plate, and by the shape of the valvae (Fig. 90).

Material examined.

BRAZIL: *Amazonas:* Fonte Boa, 1 ♂, viii.1907 (*Klages*).

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♀, 1 ? (*Le Moult*); Saint Laurent du Maroni, 1 ♀ [holotype] xii.1904; 1 ?

Depositories: BMNH, NMNH.

***Oospila excrescens* (Warren)**

(Figs 7, 25, 91, 152)

Drucia excrescens Warren, 1906: 415. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: Maroni R[iver], Saint Jean, vii.1904 (Schaus Coll); USNM Type No. 9176; NMNH. [Examined.]

Oospila excrescens (Warren); Prout, 1912: 134; 1932: 59.

♂, ♀ (Figs 7, 25). Forewing length 9-10 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface reddish brown. Wings: ground colour dark green; markings reddish brown. Forewing: costa pale brown; blotch at apex large, extending to costa, connected to blotch at tornus by narrower band along termen; with additional blotch at wing base or 1/3 along anal margin; discal spot small, reddish. Hindwing: with blotches at apex and tornus connected by narrower band along termen, extended along anal margin and connected to blotch at anal margin;

blotch at anal margin, small, narrow; discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests reddish-brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 91). Uncus with apical extension long, widened at apex. Socii large. Gnathos fused, shape resembles that of uncus. Tegumen with X-shaped sclerotised brace. Valvae: with apical division absent; sacculus not extended; ampulla short, triangular; with large curved, denticulate sclerite occurring basal to ampulla; sacculus not developed. Anellar complex: completely surrounding aedeagus, fused to valvae posteriorly. Vinculum with U-shaped ventral plate and medial projection. Coremata present. Aedeagus with long cornutus on vesica.

♀ *genitalia* (Fig. 152). Sterigma absent. Membrane around ostium with convoluted folds. Bursa copulatrix: ductus bursae long, with small antrum, strongly sclerotised and striated below antrum; corpus bursae large, bulbous; signum small. Anterior apophyses quite long.

Distribution. Most of the specimens examined were collected from French Guiana and Brazil, 2 males were also collected in Peru.

Diagnosis. *Oospila excrescens* is easily recognised by the presence of a brick-red blotch at the base of the forewing (Figs 7 and 25). The male genitalia of *excrescens* can be recognised by the sclerites of the valva (Fig. 91).

Material examined.

FRENCH GUIANA: *Guyane:* Haut Maroni, La Forestière, 1 ♀ (*Le Moult*); Nouveau Chantier, 1 ♀; Saint Jean du Maroni, 1 ♂ [holotype]; 2 ♂; Saint Laurent du Maroni, 1 ♂, 1 ♀; 1 ♂.

PERU: *Madre de Diós:* Tambopata Reserve, 30 km South West of Peurto Maldonado, 300 m, 2 ♂, 16-22.x.1983 (*Covell*).

BRAZIL: *Amazonas:* Fonte Boa, 1 ♂, v.06 (*Klages*); 4 ♂, ix.06 (*Klages*); Teffe, Egas, 1 ♂.

Depositories: BMNH, C. V. Covell Jr. collection, NMNH.

Oospila florepicta (Warren)

(Figs 26, 92, 153)

Racheolopha florepicta Warren, 1906: 424. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: Maroni, Saint Jean, iv.1904; Schaus Coll[ection]; Type No. 9194, U.S.N.M. [Examined.]

Oospila florepicta (Warren); Prout, 1932: 57.

[*Oospila florepicta ab. pulchripicta* Prout, 1918b: 82. Infra-subspecific name.]

Oospila cayennensis Herbulot, 1991: 108. Holotype ♂, in C. Herbulot collection. Type locality: FRENCH GUIANA. Label data: Piste Nancibo Pk 6 28-III-1990; Guyane Francaise environs de Cayenne H. de Toulgoët; Pr. N°6646 C. Herbulot; Oospila cayennensis H[e]rb[u]l[o]t Holotype. [Examined.] **New synonymy.**

♂, ♀ (Fig. 26). Forewing length 13-16 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings brown, orange-brown (as in specimens formerly allocated to *cayennensis*), reddish brown (described by Prout (1932) as *florepicta* ab. *pulchripicta*) or with dark brown centres surrounded by paler brown or yellow.

Forewing: costa pale brown; blotches at apex and tornus approximately circular, not connected by band along termen; discal spot small, dark, same colour as blotches. Hindwing: subapical blotch and blotch at tornus approximately circular, not connected by band along termen, not connected to blotch at anal margin; blotch at anal margin small, thin; discal spot small, dark, same colour as blotches. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests dark coloured (same colour as wing markings); sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 92). Uncus with apical extension long. Socii quite large. Gnathos fused, resembles shape of uncus. Tegumen with X-shaped sclerotised brace absent. Valvae: apical division absent; costa more strongly sclerotised, with small subapical extension; sacculus not extended, typically without denticulate margin, sometimes irregularly shaped with denticulate margin; usually with shallow notch just below ampulla; ampulla broad, square, with denticulate apex. Anellar complex: V-shaped; fused to valvae posteriorly. Vinculum typically with shallow W-shaped ventral plate, sometimes with U-shaped ventral plate. Coremata absent. Aedeagus with large cornutus on vesica.

♀ *genitalia* (Fig. 153). Sterigma absent. Bursa copulatrix: ductus bursae with short, narrow antrum, below antrum ductus widens distally and is strongly sclerotised and striated; corpus bursae large, bulbous; signum small. Anterior apophyses quite long.

Distribution. Specimens were examined from French Guiana and northern areas of Brazil.

Diagnosis. The intricate colour of the blotches makes most specimens of *florepicta* instantly recognisable. However, some colour variants of this species are close to *rosipara*, from which they can be distinguished by the presence of blotches at the tornus of both the fore- and hindwings (compare Figs 26 and 34). The male genitalia of *florepicta* can be recognised by the shape of the ampulla (Fig. 92).

Material examined.

FRENCH GUIANA: *Guyane:* Godebert Maroni, 1 ♀ (*Le Moult*); Saint Jean du Maroni, 1 ♂ (*Le Moult*); 1 ♂ [holotype of *florepicta*] iv.1904; Environs de Cayenne, piste Nancibo PK 6, 1 ♂ [holotype of *cayennensis*] 28.iii.1990 (*Toulgoët*); Piste Changement PK 1, 1 ♀ [paratype of *cayennensis*] 27.iv.1989 (*Toulgoët, Navatte & Lalanne-Cassou*).

BRAZIL: *Amazonas:* Fonte Boa, 2 ♂, v.1906 (*Klages*); 1 ♀, vi.1907 (*Klages*).

Amapá: Para, 1 ♂ (*Moss*).

Depositories: BMNH, C. Herbulot collection.

***Oospila semispurcata* (Warren)**

(Figs 27, 93, 154)

Drucia semispurcata Warren, 1906: 416. Holotype ♀, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: Maroni R[iver], Saint Jean, vii.1904 (Schaus Coll[ection]); Type No. 9179 U.S.N.M. [Examined.]

Oospila semispurcata (Warren); Prout, 1912: 134; 1932: 59.

♂, ♀ (Fig. 27). Forewing length 12-14 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; speckled with brown except at apex of forewing and wing base of fore- and hindwings; blotches absent; discal spot of fore- and hindwings small, brown;

forewing with costa pale brown. Hindleg: proximal spurs absent; with brush of long hair-like scales on male tibia. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 93). Uncus with apical extension long, slightly expanded at apex. Socii large. Gnathos fused, with single, posteriorly directed spine. Tegumen with X-shaped sclerotised brace absent. Valvae: costa with large notch on margin just below apex; ampulla quite short, digitate, expanded to spinulose apex. Anellar complex: not surrounding aedeagus completely, V-shaped, with two separate ventral plates; not fused to valvae. Coremata present. Vinculum with broad W-shaped ventral plate. Aedeagus with small cornutus on vesica.

♀ *genitalia* (Fig. 154). Sterigma forms ring around ostium with broad medial pocket and smaller pocket on each side of this. Bursa copulatrix: ductus bursae with small antrum; ductus below antrum narrow at apex, broadening distally, strongly sclerotised and striated; corpus bursae large, bulbous; signum small. Anterior apophyses short.

Distribution. All the specimens examined were collected in the Guyane region of French Guiana.

Diagnosis. The speckled brown wing patterning (Fig. 27) is unique to *semispurcata* and unlikely to be confused with any other species. The male genitalia of *semispurcata* can be recognised by the shape of the ampulla and the anellar complex (Fig. 93). The female genitalia can be recognised by the arrangement of pockets surrounding the ostium (Fig. 154).

Material examined.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♂, 1 ♀ (*Le Moult*); 1 ♂, 1 ♀ [holotype] vii.1904; 3 ♀; Saint Laurent du Maroni, 1 ♂.

Depositories: BMNH, NMNH.

Oospila rhodophragma Prout

(Figs 28, 94)

Oospila rhodophragma Prout, 1916: 170; 1932: 59. Holotype ♂, in BMNH. Type locality: BRAZIL. Label data: Type; Codajas, Upper Amazon, April 1907 (S.M. Klages); Rothschild Bequest B[ritish] M[useum] 1939-1; fig [d] in Seitz VIII; Oospila rhodophragma ♂ type Prout; Geometridae genitalia slide No. 15731 ♂. [Examined.]

♂ (Fig. 28). Forewing length 12 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent. Forewing: costa white, with brown line inside and parallel to costa; with narrow white band along termen, marked with small brown patches at ends of veins; with parallel brown line inside white band; discal spot small, brown. Hindwing: with narrow white band along termen, with small brown patches at ends of veins; with parallel brown line inside white band; discal spot small, brown. Abdomen: with dorsal surface around crests green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 94). Uncus with apical extension long. Socii large. Gnathos fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with shallow subapical cleft; sacculus not extended; ampulla long, thin, digitate; with rounded sclerotisation basal to ampulla, with denticulate apex. Anellar complex: completely surrounding aedeagus. Coremata present. Vinculum with ventral plate broad, U-shaped. Aedeagus with vesica striated; without cornutus on vesica.

♀ *genitalia*. Unknown.

Distribution. Only known from one specimen, which was collected in Brazil.

Diagnosis. The white colour of the costa and absence of other markings distinguishes *rhodophragma* from other *Oospila*. The male genitalia of *rhodophragma* can be recognised by the shape of the ampulla and the sclerite basal to it on the valva (Fig. 94).

Material examined.

BRAZIL: *Amazonas:* Upper Amazon, Codajas, 1 ♂ [holotype] iv.1907 (*Klages*). *Depository:* BMNH.

Oospila tortuguera new species

(Figs 29, 95)

Holotype ♂, in INBio. Type locality: COSTA RICA. Label data: Cerro Tortuguero P[arque] N[acional] Tortuguero. Prov[ince] Limon COSTA RICA. 100 m. April 1989. R. Aguillar & J. Solano 285000, 588000; COSTA RICA INBIO CR1001 067006; Geometridae genitalia slide No. 15766 ♂. [Examined.]

♂ (Fig. 29). Forewing length 11 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent; markings dark brown. Forewing: costa pale brown; broad, dark brown band along distal 1/2 of wing, parallel to tornus; discal spot small, brown. Hindwing: broad band along distal 1/2 of wing, parallel to tornus, continuous with narrow band along remainder of anal margin; with small distal yellow marking between veins M_3 and CuA_1; discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 95). Uncus with apical extension long, slightly expanded at apex. Socii large. Gnathos fused, with long medial projection. Tegumen with X-shaped sclerotised brace absent. Valvae: apical division absent; ampulla with distinctive shape (Fig. 95); sacculus not extended. Anellar complex: with distinctive shape (Fig. 95); with posterior extensions fused to dorsal area of valvae and anterior extensions fused to ventral area. Vinculum with ventral plate broad, U-shaped. Coremata present. Aedeagus with short cornutus on vesica.

♀ *genitalia*. Unknown.

Distribution. Only known from one specimen, which was collected in the Tortuguero National Park in Costa Rica.

Diagnosis. *Oospila tortuguera* may be distinguished from *zamaradaria* by the paler and less extensive brown wing markings (compare Figs 29 and 44). The lighter and redder colour of the markings also distinguishes *tortuguera* from *atroviridis*, as does the smaller size of the brown discal spots and the absence of a white discal spot on the hindwing (compare Figs 10, 29 and 74). The male genitalia of *tortuguera* can be recognised by the form of the ampullae and anellar complex (Fig. 95).

Material examined.

COSTA RICA: *Limón:* Cerro Tortuguero, Parque Nacional Tortuguero, 100 m, 1 ♂ [holotype] iv.1989 (*Aguillar & Solano*).

Depository: INBio.

The *thalassina* group

The *thalassina* group is distinguished by a suite of characters. Firstly, there are of two pairs of spurs on the male hind tibia. Secondly, the male sternum A8 is not strongly sclerotised, and the posterior of this sternum is not extended. Thirdly, a suite of characters in the male genitalia is typical of the group: the uncus has a long apical extension, the gnathos is fused; the valvae are simple, without an ampulla, and without any extension of the sacculus.

Oospila thalassina Warren

(Figs 30, 96)

Oospila thalassina Warren, 1905: 318; Prout, 1912: 134. Holotype ♂, in BMNH. Type locality: PERU. Label data: Cuzco, Peru, April 1901. (Garlepp); Rothschild Bequest B[ritish] M[useum] 1939-1; Oospila thalassina type ♂ Warr[en]; Geometridae genitalia slide No. 16309 ♂. [Examined.]

Oospiloma thalassina (Warren); Prout, 1916: 170; 1932: 55.

♂ (Fig. 30). Forewing length 13-16 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings dark brown. Forewing: costa dark brown; subapical blotch and blotch at tornus small, joined by narrow band along termen; discal spot large, brown. Hindwing: blotches absent; with narrow band along termen; anterior discal spot small, white; posterior discal spot small, brown. Hindleg: proximal spurs present; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 96). Uncus with apical extension long, slightly expanded at apex. Socii large. Gnathos fused. Tegumen with X-shaped sclerotised brace absent. Valvae: apical division absent; sacculus slightly expanded into membranous lobe at apex; ampulla absent. Anellar complex: with distinctive shape (Fig. 96); completely surrounding aedeagus; fused to valvae posteriorly; posterior extended into short tongue-like process (obscured by gnathos in Fig. 96). Vinculum with ventral plate broad, U-shaped, with short medial projection. Coremata present. Aedeagus small, short and squat; with cornutus absent.

♀ *genitalia*. Unknown.

Distribution. Material examined from Peru and Bolivia.

Diagnosis. *Oospila thalassina* has similar wing markings to *confluaria* and *dicraspeda* (Figs 30, 57, 62), from which it may be distinguished by the presence of a proximal pair of spurs on the hind tibia. The simple sternum A8, long apical extension of the uncus, the fused gnathos and the presence of coremata distinguish males of *thalassina* from the other two species (compare Figs 96, 119 and 124). The wing markings distinguish *thalassina* from *lacteguttata*, the only other species of *Oospila* with proximal spurs on the hind tibia (compare Figs 30 and 31).

Material examined.

PERU: 2 ♂ (*Le Moult*). *Amazonas:* Huambo, 7 ♂, IVer Trimestre 1989 (*Mathan*). *Cuzco:* 1 ♂ [holotype] iv.1901 (*Garlepp*). *Puno:* La Oroya, Río Inambari, 3100 ft, 1 ♂, dry season, ix.01 (*Ockenden*).

BOLIVIA: 1 ♂ (*Germain*).

Depository: BMNH.

Oospila lacteguttata (Warren)

(Figs 31, 97)

Racheolopha lacteguttata Warren, 1909: 85. Lectotype ♂, here designated, in BMNH. Type locality: PERU. Label data: Huancabamba, Cerro de Pasco (E. Boettger); Rothschild Bequest B[ritish] M[useum] 1939-1; Racheolopha lacteguttata type ♂ Warr[en]; Geometridae genitalia slide No. 16308 ♂. [Examined.]

Oospila lacteguttata (Warren); Prout, 1912: 134.

Oospiloma lacteguttata (Warren); Prout, 1916: 170; 1932: 54.

Progonodes fenestrata Bastelberger, 1911: 54; Prout, 1912: 132. Holotype ♂, in Senckenberg Museum. Type locality: PERU. Label data: fenestrata Bastelb[erger]; Typus; Coll[ection] Bastelberger. [Not examined]. **New synonymy.**

Oospiloma fenestrata (Bastelberger); Prout, 1932: 54.

Oospila peralta Schaus, 1912b: 287. Lectotype ♂, here designated, in NMNH. Type locality: COSTA RICA. Label data: Feb[ruary] 07; Peralta 2000 ft C[osta]R[ica];

Collection Wm Schaus; Type No. 17720 U.S.N.M; Oospila peralta type Sch[au]s; Genitalia Slide By MAC 57761 USNM. [Examined.] **New synonymy.**

Oospiloma (?) peralta (Schaus); Prout, 1916: 170; 1932: 55.

♂ (Fig. 31). Forewing length 11-13 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent. Forewing: costa pale brown; with cream band along termen, brown band inside and parallel to this, with white spots marking apices of veins; discal spot small, brown. Hindwing: markings on termen as forewings; discal spot small, white. Hindleg: proximal spurs present on tibia; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 97). Uncus with apical extension long, slightly expanded at apex. Socii large. Gnathos fused. Tegumen with X-shaped sclerotised brace absent. Valvae: apical division absent; with subapical thinning; sacculus not extended; ampulla absent. Anellar complex: with distinctive bell-shape (Fig. 97); posterior extensions fused to valvae. Vinculum with ventral plate broad, W-shaped. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia.* Unknown.

Distribution. Occurs in Costa Rica, and the North Western area of South America, namely Colombia and Peru.

Diagnosis. The presence of proximal spurs on the hind tibia distinguishes *lacteguttata* from other species of *Oospila* (with the exception of *thalassina*, which is easily distinguished from the wing markings). *Oospila lacteguttata* may be distinguished from *imaculata* by the presence of a brown discal spot on the forewings (compare Figs 31 and 76) and from *holochroa* by the presence of a single discal spot only on the hindwings. The long apical extension of the uncus, the fused gnathos and the form of the anellar complex also distinguish males of *lacteguttata* from the two other species (compare Figs 97, 113 and 137).

Material examined.

COSTA RICA: *Cartago:* Peralta, 2000 ft, 1 ♂ [lectotype of *peralta*] ii.07.

COLOMBIA: *Meta:* East Colombia: Upper Río Negro, 1 ♂ (*Fassl*).

PERU: *Cajamarca:* Huancabamba, Cerro de Paseo, 1 ♂ [lectotype of *lacteguttata*] (*Boettger*); 1 ♂ [paralectotype of *lacteguttata*] (*Boettger*); 1 ♂ (*Boettger*). 1 ♂ (*Le Moult*).

Depositories: BMNH, NMNH.

The *asmura* group

The *asmura* group is distinguished by two characters: a short extension of the hindwing at the distal end of vein M_3, terminating in a tuft of scales projecting beyond the fringe, and by the form of the transtillae in the male genitalia.

Oospila asmura (Druce)

(Figs 32, 98, 155)

Racheospila (?) asmura Druce, 1892: 92. Holotype ♂, in Berlin Museum. Type locality: PANAMA. Label data: 715; Origin; Zool. Mus[eum] Berlin; Chiriqui; Typus; Racheospila asmura ♂ type Druce. [Examined.]

Drucia asmura (Druce); Warren, 1900: 133.

Oospila asmura (Druce); Prout, 1912: 133; 1932: 59.

Drucia latimargo Warren, 1904a: 20. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; S[anto] Domingo, Carabaya, 6000 ft., XII.01. wet seas[on] (Ockenden); Oospila latimargo type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15730 ♂. [Examined.] **New synonymy.**

Oospila latimargo (Warren); Prout, 1912: 133; 1932: 59.

Drucia fumidimargo Dognin, 1911b: 162. Holotype ♂, in NMNH. Type locality: COLOMBIA. Colombia: [Valle,] near Cali, Alto de las Cruces, 2200 m, iii.1909 (*Fassl*). [Examined.] **New synonymy.**

Oospila fumidimargo (Dognin); Prout, 1912: 134; 1932: 59.

♂, ♀ (Fig. 32). Forewing length 10-16 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet brown. Thorax: dorsal surface green. Wings: ground colour dark green; markings reddish brown. Forewing: costa pale brown; blotch at apex large, usually connected by narrow band along termen to blotch at tornus; discal spot small, brown. Hindwing: with blotch at apex large, connected by thin band along termen to blotch at tornus; blotch at tornus smaller, connected to blotch at anal margin by thin band along anal margin; blotch at anal margin small, narrow; discal spot small, brown; usually with short extension of wing at distal end of vein M_3, marked by one or two tufts of dark brown scales projecting beyond wing fringe. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests reddish brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge in male.

♂ *genitalia* (Fig. 98). Uncus not extended apically. Socii small. Gnathos not fused. Tegumen very narrow, with X-shaped sclerotised brace absent. Valvae: with apical division absent; with shallow constriction below apex and wider, rounded apex; sacculus not extended; ampulla absent. Transtillae: large curved projections, not fused to each other, membranous in smaller specimens (as in *rosipara*, Fig. 100), strongly sclerotised and with denticulate apex in larger specimens (Fig. 98). Anellar complex: V-shaped. Vinculum with ventral plate formed by two strongly sclerotised rods, joined by more weakly sclerotised plate. Aedeagus with small cornutus on vesica.

♀ *genitalia* (Fig. 155). Sterigma absent; but with weakly sclerotised convoluted folds around ostium. Bursa copulatrix: ductus bursae short, with wide antrum, strongly sclerotised but not striated below antrum; corpus bursae large, approximately spherical; signum small. Anterior apophyses short.

Distribution. Widely distributed in Central and South America: this species has been collected in Guatemala, Costa Rica, Panamá, French Guiana, Venezuela, Colombia, Ecuador, Peru, and Bolivia.

Diagnosis. *Oospila asmura* is similar to *camilla* in external appearance, but can be distinguished by the absence of a green patch enclosed within the red-brown markings of the forewings (compare Figs 32 and 36). The female genitalia of these two species can be distinguished by the absence of a pocket posterior to the ostium in *asmura* (compare Figs 155 and 157).

Oospila asmura may be distinguished from *circumsessa* by the separation of the blotches at the apex and the tornus of the forewings, by the absence of small yellow markings within the brown markings of the hindwings, and by the extension, along the anal margin, of the blotch at the tornus of the hindwing (compare Figs 32 and 33). The male genitalia of *asmura* and *circumsessa* are quite similar, but the sacculus of the valva of *asmura* is not extended, whereas it is in *circumsessa* (compare Figs 98 and 99).

The extension of the blotch at the tornus of the hindwing along the anal margin and the extension of the hindwing at the apex of vein M_3 distinguish *asmura* from *jaspidata* (compare Figs 17 and 32).

The male genitalia of *asmura* are distinguished from those of *rosipara* and *delphinata* by the absence of small spines at the tip of the valvae (compare Figs 98 and 100). These three species also have distinctive wing markings (compare Figs 32 and 34) and the female genitalia of *asmura* can be distinguished from those of *rosipara* by the absence of striation of the ductus bursae in *asmura* (compare Figs 155 and 156).

Material examined.

GUATEMALA: *Quezaltenago:* Volcan Santa Maria, 1 ♂.

COSTA RICA: *Cartago:* Cachi, 1 ♀. Moravia de Chirripo, 1000 m, 1 ♀, 10.v.1983 (*Janzen & Hallwachs*); Juan Vinas, 2500 ft, 1 ♂, v. (*Schaus*); 2 ♂, 3 ♀; Orosi, 1200 m, 2 ♂ (*Fassl*); Sitio, 1 ♂. *Puntarenas:* Monteverde, 1 ♂, 1 ♀ (*Covell*); 1 ♀.

PANAMA: *Chiriquí:* Bogava, Chiriquí, 800 ft, 1 ♀ (*Watson*); Chiriquí, 1 ♂ [holotype of *asmura*].

FRENCH GUIANA: *Guyane:* Saint Laurent du Maroni, 1 ♂.

VENEZUELA: *Aragua:* Rancho Grande, 1100 m, Parque Nacional Henri Pittier, 1 ♂, 25.vi.74 (*Pilske*); 1 ♀. *Lara:* Yacambu National Park, 13 km South East Sanare, 4800 ft, 3 ♂.

COLOMBIA: *Meta:* East Colombia: Upper Río Negro, 800 m, 4 ♂ (*Fassl*). *Tolima:* Rio Toche, Quindiu, 2400 m, 1 ♂; 4 ♂. *Valle:* Near Cali, Alto de las Cruces, 2200 m, 1 ♂ [holotype of *fumidimargo*], iii.1909 (*Fassl*).

ECUADOR: 1 ♂, 1920 (*Hammond*). *Bolívar:* Balzapamba, 1 ♀, ix.1883-ii.1884

(*Mathan*). *Chimborazo:* Huigra, 1 ♀. *Loja:* Environs de la Loja, 1 ♂, 1891; 2 ♂, 1 ?; Loja, 1 ♂.

PERU: 1 ♂ (*Mathan*); Río Bamba, Hacienda Cayandeled, Versant Quest Cordillières, 4200 [ft], 1 ♂, 1 ♀, ii.1883 (*Stolzmann*). *Amazonas:* Chachapoyas, 15 ♂, 1889 (*Mathan*); Huambo, 1 ♂, 1889 (*Mathan*). *Cajamarca:* Huancabamba, Cerro de Paseo, 6-1000 ft, 1 ♂ (*Boettger*); Huancabamba, Cerro de Paseo, 2 ♂ (*Boettger*). *Cuzco:* Caradoc, Marcapata, 4000 ft, 1 ♀, ii.01 (*Ockenden*); *Huánuco:* Pozuzo, 5000-6000 ft, 1 ♂ (*Native collector*). *Puno:* La Oroya, Río Inambari, 3100 ft, 1 ♂, dry season, ix.04 (*Ockenden*); 1 ♂, wet season, ix.04 (*Ockenden*); 1 ♂, 1 ♀, wet season, iii.05 (*Ockenden*); 1 ♀, ix.05 (*Ockenden*); 1 ♂, wet season, xi-xi.1905 (*Ockenden*); 1 ♀, wet season, xii.05 (*Ockenden*). La Unión, Río Huacamayo, 2000 ft, 2 ♂, wet season, xi.04 (*Ockenden*); 1 ♂, wet season, xii.1904 (*Ockenden*); Oconeque, 7000 ft, 1 ♀, dry season, vii.1904 (*Ockenden*). Santo Domingo, 6000 ft, 1 ♂ [holotype of *latimargo*] wet season, xii.01 (*Ockenden*); 1 ♂, xi.1904 (*Ockenden*); Tinguri, 3400 ft, 5 ♂, dry season, viii.1904 (*Ockenden*).

BOLIVIA: *Cochabamba:* Charaplaya, 65°W 16°S, 1300 m, 1 ♂, vi.01 (*Simons*); Yunga del Espiritu Santo, 11 ♂, 1888-1889 (*Germain*); Incachaca, 1 ♀. *La Paz:* Balzapamba, 2 ♂, 1 ♀; Río Songo, 750 m, 1 ♂. *Sud Yugas:* Puente Villa, 1 ♂ (*Covell*). River Tamampaya, 1 ♂ (*Garlepp*); 3 ♂ (*Germain*).

Depositories: Berlin Museum, BMNH, CMNH, C. V. Covell Jr. collection, INBio, NMNH.

Oospila circumsessa Prout

(Figs 33, 99)

Oospila circumsessa Prout, 1918a: 119; 1932: 59. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; Contamana Rio Ucayali, Peru, Nov[ember]-Dec[ember] 1912; Oospila circumsessa ♂ type Prout; Joicey Bequest. Brit[ish] Mus[eum] 1934-120. [Examined.]

♂ (Fig. 33). Forewing length 10 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings reddish brown. Forewing: costa pale brown; with red-brown band along termen, not extending along costa, widest at tornus, yellowish towards termen; discal spot small, brown. Hindwing: blotches at apex and tornus joined by narrow band along termen, with small yellow patch 1/3 along termen; blotch at anal margin absent; discal spot small, brown; wings with short extension at distal end of vein M_3, marked by small tuft of scales projecting beyond fringe. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge.

♂ *genitalia* (Fig. 99). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: divided apically; sacculus extended to short, robust apical process; ampulla absent. Transtillae: large outwardly curving membranous lobes with pointed tips. Anellar complex: not surrounding aedeagus completely, V-shaped. Vinculum with broad, W-shaped ventral plate. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia*. Unknown.

Distribution. Only two males were examined, both from the Loreto region of Peru.

Diagnosis. *Oospila circumsessa* may be distinguished from *asmura* and *jaspidata* by the merging of the blotches at the apex and the tornus of the forewings, by the presence of small yellow markings within the brown markings of the hindwings and by the smaller size of the blotch at the tornus of the hindwing (compare Figs 17, 32 and 33). The male genitalia of *circumsessa* and *asmura* are quite similar, but the sacculus of *asmura* is not extended as it is in *circumsessa* (compare Figs 98 and 99).

Material examined.
PERU: *Loreto:* Contamana, Río Ucayali, 1 ♂ [holotype] xi-xii.1912; Pumayacu, 1 ♂.
Depositories: BMNH, NMNH.

***Oospila rosipara* (Warren)**

(Figs 34, 100, 156)

Racheospila rosipara Warren, 1897: 431. Holotype ♂, in BMNH. Type locality: VENEZUELA. Label data: Type; Palma Sola, Venezuela; Racheolopha; Racheospila rosipara type ♂ Warr[en]; Racheolopha; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15040 ♂. [Examined.]

Oospila rosipara (Warren); Prout, 1912: 133; 1932: 57.

Racheolopha flavicincta Warren, 1900: 137. Holotype ♀, in BMNH. Type locality: VENEZUELA. Label data: Type; Palma Sola, Venezuela; Rothschild Bequest B[ritish]

M[useum] 1939-1; Racheolopha flavicincta type ♀ Warren; Geometridae genitalia slide No. 15039 ♀. [Examined.] **New synonymy.**

Oospila flavicincta (Warren); Prout, 1932: 57.

Racheolopha microspila Warren, 1909: 86. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; La Union, R[ío] Huacamayo, Carabaya, 200 ft., wet season, Dec[ember] 1904. (G. Ockenden); Racheolopha microspila type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15041 ♂. [Examined.] **New synonymy.**

Oospila microspila (Warren); Prout, 1932: 57.

Racheolopha conversa Dognin, 1908: 264. Holotype ♀, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: S[ain]t Laurent du Maroni. [Examined.] Synonymised by Prout, 1932: 57.

Oospila conversa (Dognin); Prout, 1912: 134.

[*Oospila rosipara* ab. *conversa* Prout, 1932: 57. Infra-subspecific name.]

♂, ♀ (Fig. 34). Forewing length 12-18 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet brown. Thorax: dorsal surface green. Wings: ground colour dark green; markings dark brown, or pale brown with darker perimeters. Forewing: costa pale brown; blotch at apex large; blotch at tornus absent; discal spot, small, brown. Hindwing: blotch at apex large; blotch at tornus absent; blotch at anal margin large, narrow; discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests dark brown or green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge in male.

♂ *genitalia* (Fig. 100). Uncus completely reduced to broad, flat plate. Socii small, thin. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: apical division absent; narrowing about halfway along, with several rows of small spines at apex; ampulla absent. Transtillae large, crescent-shaped projections, with spines at apex and along facing edges in larger specimens (as in *asmura*, Fig. 98), membranous in smaller specimens (as illustrated, Fig. 100); not fused to anellus. Anellar complex V-shaped. Vinculum with broad, shallow W-shaped ventral plate. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia* (Fig. 156). Sterigma absent. Bursa copulatrix: ductus bursae short, strongly sclerotised, striated, antrum absent; corpus bursae quite small, bulbous; signum small. Anterior apophyses short.

Distribution. This species is widely distributed in Central and South America. Specimens were examined from: Guatemala, Costa Rica, Panamá, French Guiana, Venezuela, Colombia, Ecuador, Peru, and Brazil.

Diagnosis. *Oospila rosipara* can be distinguished from other species by the arrangement of blotches on the wings: no other species of *Oospila* has large blotches only at the apex and tornus of the fore- and hindwings.

The male and female genitalia are indistinguishable from those of *delphinata*. However, the two species can be distinguished by the wing markings: the blotches of *rosipara* are larger and darker (compare Figs 34 and 35). Furthermore, *rosipara* does not have a blotch at the tornus of the hindwing and also lacks an extension of the hindwing at the apex of vein M_3.

The male genitalia of *rosipara* may be distinguished from those of *asmura* by the presence of small spines towards the apex of the valvae in *rosipara* (compare Figs

98 and 100). The female genitalia can be distinguished by the striation of the ductus bursae in *rosipara* (compare Figs 155 and 156).

Material examined.

GUATEMALA: *Izabel:* Cayuga, 4 ♂, 1 ♀; 1 ♀, v. (*Schaus & Barnes*).

COSTA RICA: *Limón:* Guapiles, 1 ♂; Sixola River, 1 ♂; 1 ♂, iii. *Osa Peninsula:* Sirena, Corcovado National Park, 2 ♂, 11.i.1981 (*Janzen & Hallwachs*).

PANAMA: La Choerra, 1 ♀.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 4 ♂, iii. (*Le Moult*); Nouveau Chantier, 1 ♂, iii. (*Le Moult*); 1 ♂, vii (*Le Moult*); Cayenne, 1 ♂; Saint Laurent du Maroni, 1 ♂, 1 ♀ [holotype of *conversa*]; 2 ♀.

VENEZUELA: Palma Sola, 1 ♂ [holotype of *rosipara*]; 1 ♀ [holotype of *flavicincta*]; 1 ♂; 1 ♀, vi.1909 (*Klages*). *Aragua:* El Limón, 450 m, 1 ♀. *Barinas:* Barinas, Rio Caparo Research Station, 32 km East El Canton, 1 ♂. *Carabobo:* San Esteban, 1 ♂, 1 ♀, vi.1909 (*Klages*); Las Quiguas, Esteban Valley, 1 ♂, 1914; 1 ♂, 1 ♀. *Miranda:* Miranda Parque Nacional, Guatopo Agua Blanca, 500 m, 1 ♀, 7.v.1975.

COLOMBIA: *Boyacá:* River Cantinero, Muzo, 400 m, 1 ♂ (*Fassl*). Minca, 2000 ft, 1 ♀ (*Smith*); Muzo, 400-800 m, 2 ♂ (*Fassl*). *Cauca:* Popayan, 2 ♂. *Meta:* Upper Río Negro, Ost Colombia, 800 m, 1 ♂ (*Fassl*).

ECUADOR: Bulim, 160 ft, 1 ♀, xii.00 (*Fl. & M.*).

PERU: *Huánuco:* Tingo Maria, 1 ♂. *Junín:* Lima-Charchamayo, 1 ♂ (*Moss*); La Merced, C. Peru, 3000-4500 ft, 1 ♂, i-ii.20 (*Watkins*). *Puno:* La Unión, Río Huacamayo, Carabaya, 200 ft, 1 ♂ [holotype of *microspila*], wet season, xii.1904 (*Ockenden*).

BRAZIL: *Amazonas:* Sao Paulo de Olivença, 1 ♂; Hyntanahan, Rio Purus, 1 ♂, ii.1922 (*Klages*); Fonte Boa, 1 ♂, vi.1906 (*Klages*). *Pará:* Unt. Amaz. Taperhina, below Santarem, 1 ♂, 1-10.vii.27 (*Zerny*).

Depositories: BMNH, CMNH, INBio, NMNH, UCV.

***Oospila delphinata* (Warren)**

(Figs 35, 100, 156)

Drucia delphinata Warren, 1900: 133. Holotype ♂, in BMNH. Type locality: BRAZIL. Label data: Sao Paulo, Drucia delphinata type ♂ Warr[en]; Type; Geometridae genitalia slide No. 15728 ♂. [Examined.]

Oospila delphinata (Warren); Prout, 1912: 133; 1932: 59.

Racheolopha plurimaculata Warren, 1907: 208. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; Pozuzo, Huánuco, 800-1000 m. (W. Hoffmann); Racheolopha plurimaculata type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15727 ♂. [Examined.] **New synonymy.**

Oospila plurimaculata (Warren); Prout, 1912: 134; 1932: 59.

Oospila plurimaculata symmicta Prout, 1932: 59. Holotype ♂, depository unknown. Type locality: BRAZIL. Label data: Brazil: Minas Geraes, 4.ii (coll[ection] Seitz). [Not examined.] **New synonymy.**

Racheospila heteromorpha Warren, 1909: 84. Lectotype ♂, here designated, in BMNH. Type locality: PARAGUAY. Label data: Type; Sapucay, Paraguay, 16.x.01. (W. Foster); Racheolopha heteromorpha type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15729 ♂. [Examined.] **New synonymy.**

Oospila heteromorpha (Warren); Prout, 1912: 134.

Oospila delphinata heteromorpha (Warren); Prout, 1932: 59.

♂, ♀ (Fig. 35). Forewing length 9-13 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings cream or pale brown, with dark brown perimeters and brown striae. Forewing: costa pale brown; blotch at apex small (very small in specimens previously allocated to *plurimaculata symmicta*), not extending to costa, connected to blotch at tornus by very thin, dark band along termen; blotch at tornus small; discal spot small, brown. Hindwing: usually extended at distal end of vein M_3, often with tuft of long brown scales marking extension; often also with smaller tuft posterior to this; blotch at apex large, extending along 1/2 termen, connected to blotch at tornus by thin, dark line along termen; blotch at tornus small, connected to blotch at anal margin by thin, dark line along anal margin; blotch at anal margin narrow. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests dark brown or green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge in male.

♂ genitalia (Fig. 100). As for *rosipara*.

♀ genitalia (Fig. 156). As for *rosipara*.

Distribution. Unlike *rosipara*, this species does not occur in Central America, but specimens have been collected in Colombia, Ecuador, Peru, Bolivia, Paraguay, and Brazil.

Diagnosis. The male and female genitalia of *delphinata* are indistinguishable from those of *rosipara*. However, these species can be distinguished by the wing markings: the blotches of *delphinata* are smaller, and paler (compare Figs 34 and 35). Furthermore, the hindwings of *delphinata* have a blotch at the tornus, and a short extension at the apex of vein M_3.

Material examined.

COLOMBIA: *Cundinamarca:* Mediana, 1 ♂.

ECUADOR: *Pastaza:* Huigra, 7000 ft, 1 ♂, 3.vi.1931 (*Coxey*).

PERU: *Huánuco:* Pozuzo, Huánuco, 800-1000 m, 1 ♂, [holotype of *plurimaculata*] (*Hoffmann*); 2 ♂.

BOLIVIA: *Santa Cruz:* Central Bolivia: Santa Cruz de la Sierra, 450 m, 1 ♂, ix.1909 (*Steinbach*).

PARAGUAY: Itape, 1 ♂, 27.xi,24 (*Schade*). *Paraguarí:* Sapucay: 1 ♂ [lectotype of *heteromorpha*] 16.x.01 (*Foster*); 1 ♂ [paralectotype of *heteromorpha*] 16.x.04 (*Foster*); 1 ♀ [paralectotype of *delphinata heteromorpha*] x.04 (*Foster*); 1 ♂ (*Foster*).

BRAZIL: Serra de Baturlité, Ceara, 1 ♂, i.1985 (*Gounelle*). Rio Grande do Sul, 1 ♂. Uberaba, Minas Geraes: 1 ♂; 1 ♀ (*Le Moult*). *Mato Grosso:* Burity, Mato Grosso, 20 miles North East of Cuyaba, 2250 ft, 1 ♂, 6-21.ix.27 (*Collenette*); Chapada, near Cuyaba, Mato Grosso, 4 ♂ (*Smith*). *Pará:* Unt. Amaz. Taperhina, below Santarem, 1 ♂, 10.vii.27 (*Zerny*). *Paraná:* Castro, 2900 ft, 1 ♂ (*Jones*). Iguassu, 1 ♂, 1 ?, xi.1922. *Rio de Janeiro:* Itatiaia, 700 m, Estado do Rio Brasil, 1 ♂; Nova Friburgo, 1 ♀. *Santa Catarina:* Santa Catarina, Nova Brémen, Rio Laeiss, 1 ♂, iv.1936 (*Hoffmann*); Rio Laeiss, Blumenau 2 ♂, x.1934 (*Hoffmann*); Blumenau, 2 ♂, 29.iv.29 (*Schade*); Jaraguá do Sul, 1 ♂, xi.27 (*Hoffmann*); Hansa Humbolt, 60 m, 1 ♂, vii.1936 (*Maller*); Rio Natal, vic. Sâo Beuto do Sul, 1 ♂, 15.viii.1985 (*Mielke & Casegrande*). *Sao Paulo:* South East Brazil, Sao Paulo, 1 ♂ [holotype of *delphinata*]; 3 ♂, 1 ♀; 2300 ft, 2 ♂ (*Jones*).

Depositories: BMNH, CMNH, C. V. Covell Jr. collection, NMNH.

Oospila camilla Schaus

(Figs 36, 157)

Oospila camilla Schaus, 1913: 350; Prout, 1932: 58. Holotype ♀, in NMNH. Type locality: COSTA RICA. Label data: March; Sixola Riv[er] C[osta] R[ica]; Oospila; Type No. 17979 U.S.N.M; Oospila camilla type Sch[au]s; Genitalia Slide By MAC 57759 USNM. [Examined.]

♀ (Fig. 36). Forewing length 12 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent, markings reddish brown. Forewing: costa pale brown; with very broad red-brown band along termen interrupted by small subapical green patch and two yellow spots halfway along termen; discal spot small, red-brown. Hindwing: with broad red-brown band along termen, extended along anal margin as a narrow band, expanded at wing base; discal spot red-brown; wing extended to short tail where vein M_3 meets termen. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia.* Unknown.

♀ *genitalia* (Fig. 157). Sterigma ring-shaped with central depression around ostium. With small pocket posterior to ostium. Bursa copulatrix: ductus bursae reduced, not strongly sclerotised or striated, antrum absent; corpus bursae quite small, bulbous; signum small. Anterior apophyses short.

Distribution. Only a single specimen is known, from Costa Rica.

Diagnosis. The wing markings of *camilla* are similar to those of *asmura*, but the two species can be distinguished by the broader extent of the red-brown markings and by the presence of the green subapical marking and the yellow spots within the red-brown area of the forewings of *camilla* (compare Figs 32 and 36). The female genitalia of *camilla* can be recognised by the presence of a pocket posterior to the ostium (Fig. 157).

Material examined.
COSTA RICA: *Limón:* Sixola River, 1 ♀, [holotype] iii.
Depository: NMNH.

The *astigma* group

The *astigma* group is characterised by an apomorphic character of the forewing venation: vein R_1 arising distally of the origin of vein M_1. These species are rather similar in external appearance and, whilst they can often be distinguished by their wing markings do exhibit some intraspecific variation. The genitalia are, however, quite distinctive.

Oospila astigma (Warren) new combination

(Figs 37, 101)

Racheolopha astigma Warren, 1907: 206. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; La Oroya, R[ío] Inambari, S[outh] E[ast] Peru 3100 ft., wet s[eason], Oct[ober] 1904 (G. Ockenden); Rothschild Bequest B[ritish] M[useum] 1939-1; Racheolopha astigma type ♂ Warr[en]; Geometridae genitalia slide No. 15798 ♂. [Examined.]

Auophyllodes astigma (Warren); Prout, 1912: 131.

Racheolopha astigma (Warren); Prout, 1932: 54.

♂ (Fig. 37). Forewing length 9-11 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent; markings cream or pale brown, with dark brown perimeters. Forewing: costa pale brown; with narrow band along termen and distal 1/2 of anal margin; discal spot absent. Hindwing: with similar band along termen and distal 1/3 of costal and anal margins; discal spot absent. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge in male.

♂ *genitalia* (Fig. 101). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus not extended; ampulla absent; with short projection from base of valva. Anellar complex: completely surrounding aedeagus, with distinctive shape (Fig. 101); with two posterior processes, not fused with valvae. Vinculum with ventral plate W-shaped. Aedeagus: denticulate at base of vesica, but without prominent cornutus.

♀ *genitalia*. Unknown.

Distribution. Only known from Colombia and Peru.

Diagnosis. The wing markings of *astigma* (Fig. 37) are similar to those of *albipunctulata*, *delacruzi* and *leucostigma* (Figs 38, 39 and 40), but can be distinguished by the absence of discal spots on the wings of *astigma*. *Oospila astigma* can be distinguished from *miccularia* by the paler colour of the markings and by the blotch at the apex of the forewing which is narrow at its anterior and does not extend along the costa in *astigma* (compare Figs 37 and 45). The male genitalia of *astigma* can be recognised by the form of the anellar complex, the small, pointed extension of the base of the valva and the denticulate aedeagus (Fig. 101).

Material examined.

COLOMBIA: *Meta:* East Colombia, Upper Río Negro, 800 m, 9 ♂ (*Fassl*).
PERU: *Puno:* La Oroya, Río Inambari, 3100 ft, 1 ♂ [holotype] wet season, x.1904 (*Ockenden*); 1 ♂, wet season, ix.05 (*Ockenden*); 1 ♂, wet season, xii.05 (*Ockenden*); La Unión, Río Huacamayo, Carabaya, 2000 ft, 1 ♂, xi.1904 (*Ockenden*); Oconeque, Carabaya, 7000 ft, 1 ♂, dry season, vi.1904 (*Ockenden*); Tinguri, Carabaya, 3400 ft, 2 ♂ dry season, viii.1904 (*Ockenden*); 1 ♂ [paratype] wet season, i.05 (*Ockenden*).
Depository: BMNH.

Oospila leucostigma (Warren) new combination

(Figs 38, 102)

Racheolopha leucostigma Warren, 1907: 207; Prout, 1932: 54. Lectotype ♂, here designated, in BMNH. Type locality: PERU. Label data: Type; Tinguri, Carabaya, 3400 ft., wet s[eason], Jan[uary] 1905. (G. Ockenden); Rothschild Bequest B[ritish] M[useum] 1939-1; Racheolopha leucostigma type ♂ Warr[en]; Geometridae genitalia slide No. 15799 ♂. [Examined.]

Auophyllodes leucostigma (Warren); Prout, 1912: 131.

♂ (Fig. 38). Forewing length 8-10 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches cream coloured. Forewing: costa pale brown; subapical blotch triangular, sometimes connected to blotch at tornus by narrow band along termen; discal spot small, brown. Hindwing: blotch at apex large, extending along 1/2 of termen, not connected to blotch at tornus; blotch at tornus small; discal spot small, white. Hindleg: proximal spurs absent; with brush of long hair-like scales on tibia. Abdomen: with dorsal surface around crests brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge.

♂ *genitalia* (Fig. 102). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; apical part with costa more strongly sclerotised; sacculus with short, blunt apical and subapical extensions; ampulla short, thin, curved. Anellar complex: completely surrounding aedeagus, approximately cuboid, with central hole; not fused with valvae. Coremata absent. Vinculum usually with V-shaped, sometimes with W-shaped, ventral plate. Aedeagus with two short cornuti on vesica.

♀ *genitalia.* Unknown.

Distribution. Only known from the North West of South America, namely Ecuador, Colombia and Peru.

Diagnosis. The cream wing markings of *leucostigma* are usually larger than those of *delacruzi* (compare Figs 38 and 39). However, intraspecific variation does occur in the extent of the markings of both species, so the wing markings may not be sufficient to identify the species. The presence of a small, white discal spot on the hindwing distinguishes *leucostigma* from *astigma*. *Oospila leucostigma* can be distinguished from *albipunctulata* and *miccularia* by the apical blotch of the forewing which does not extend to the costa in *leucostigma* (compare Figs 38, 40 and 45). The wing markings of *leucostigma* are also paler than those of *miccularia*. Males of *leucostigma* can be distinguished from all these species by the presence of a brush of long hair-like scales on the hind tibia. The male genitalia of *leucostigma* can be recognised by the shape of the ampulla and the anellar complex (Fig. 102).

Material examined.

ECUADOR: *Tungurahua:* Or de Bañosa Canelos, 1 ♂, ix-x.1984 (*Mathan*).

COLOMBIA: *Meta:* Upper Río Negro, 800 m, 3 ♂ (*Fassl*).

PERU: *Puno:* Tinguri, Carabaya, 3400 ft, 2 ♂, dry season, viii.1904 (*Ockenden*); 1 ♂ [lectotype] wet season, i.1905 (*Ockenden*); 1 ♂, [paralectotype], wet season, i.1905 (*Ockenden*); La Oroya, Río Inambari, 3100 ft, 1 ♂, dry season, viii.1904 (*Ockenden*); 1 ♂ [paralectotype] wet season, iii.1905 (*Ockenden*); 1 ♂, ix.05 (*Ockenden*); 1 ♂, wet season, xi-xii.1905 (*Ockenden*); 1 ♂, wet season, i.1906 (*Ockenden*). South East Peru, 1 ♂.

Depository: BMNH.

Oospila delacruzi (Dognin)

(Figs 5, 39, 103, 158)

Comibaena delacruzi Dognin, 1898: 218. Holotype ♂, in NMNH. Type locality: ECUADOR. Label data: Environs de Loja Equateur 1890; Dognin Collection; Comibaena Delacruzi type ♂ D[o]g[ni]n; close to Comibaena callicula Druce pl 49 fig 19 [page] 88; [raisus] de Comibaena invasata
W[a]lk[er] [Biologia centrali-Americana] 49 fig 18; Type No. 32757 U.S.N.M. Genitalia slide No. MAC 022. [Examined.]

Oospila delacruzi (Dognin); Warren, 1904b: 505.

Auophyllodes delacruzi (Dognin); Prout, 1912: 131.

[*Racheolopha delacruzei* (Dognin); Prout, 1932: 54. Incorrect spelling of *delacruzi*.]

Oospila restricta Warren, 1904b: 504; Prout, 1912: 133. Holotype ♀, in BMNH. Type locality: PERU. Label data: Type; S[anto] Domingo, Carabaya, 6500 ft. Dec[ember] 02. Wet s[eason] (G. Ockenden); Oospila restricta type ♀ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15801 ♀. [Examined.] **New synonymy.**

Racheolopha restricta (Warren); Prout, 1932: 54.

♂, ♀ (Fig. 39). Forewing length 8-11 mm. Antenna of female unknown. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches, where present, cream, with dark brown perimeters and some brown striation. Forewing; subapical blotch usually small, never extending to costa, sometimes connected to blotch at tornus by thin line along termen; blotch at tornus small; sometimes unmarked except brown band along termen and very small cream marking at tornus; discal spot small, brown. Hindwing: blotch at apex small, large or absent, typically extending along 2/3 of termen, sometimes connected to blotch at tornus by thin band along termen; wings often unmarked except brown band along termen; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream or brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge in male.

♂ *genitalia* (Fig. 103). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus with blunt apical extension; inner margin of valva with broad, rounded extension with serrated edge; ampulla absent. Anellar complex: completely surrounding aedeagus; with distinctive shape (Fig. 103). Vinculum with ventral plate V-shaped. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia* (Fig. 158). Sterigma absent. Bursa copulatrix: ductus bursae long, thin, with long, thin antrum; strongly sclerotised and striated below antrum; corpus bursae quite large; signum long. Anterior apophyses very short.

Distribution. Occurs in the North West of South America, namely in Colombia, Ecuador and Peru.

Diagnosis. Although the wing markings of *delacruzi* are usually less extensive than those of *leucostigma* (compare Figs 38 and 39), intraspecific variation in both species means that this character is not always reliable. Males can be distinguished by the absence of a brush of long hair-like scales on the hind tibia of *delacruzi*.

A similar problem occurs with distinguishing between *delacruzi* and *astigma* (compare Figs 37 and 39), but these two species can be distinguished by the presence of a white discal spot on the hindwing of delacruzi. *Oospila delacruzi* can be distinguished from *albipunctulata* by the lesser extent of the cream markings: if present, the subapical blotch on the forewing of *delacruzi* never extends to the costa, as it does in *albipunctulata*.

The male genitalia of *delacruzi* can be recognised by the shape of the valvae and anellar complex (Fig. 103).

Material examined.

COLOMBIA: *Meta:* East Colombia, Upper Río Negro, 800 m, 1 ♂, 1 ? (*Fassl*).
ECUADOR: Environs de Loja, 1 ♂ [holotype of *delacruzi*] 1890.
PERU: *Puno:* La Oroya, Río Inambari, 3100 ft, 2 ♂, wet season, xii.05 (*Ockenden*); Tinguri, Carabaya, 3400 ft, 4 ♂, 1 ♀, dry season, viii.1904 (*Ockenden*); 1 ♂, i.1905; Santo Domingo, Carabaya, 6000 ft, 1 ♀, iv.02 (*Ockenden*); 1 ♂, dry season, vi.02 (*Ockenden*); 1 ♀ [holotype of *restricta*] xii.02 (*Ockenden*); Oconeque, Carabaya, 7000 ft, 2 ♂, dry season, vii.1904 (*Ockenden*).
Depository: BMNH.

Oospila albipunctulata (Prout) new combination

(Figs 40, 104, 159)

Racheolopha albipunctulata Prout, 1932: 54. Holotype ♂, in BMNH. Type locality: COLOMBIA. Label data: Type; Muzo. Colombia 400-800 m Coll[ection] Fassl; Seitz VIII p54 (1932); Racheolopha albipunctulata ♂ type Prout; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15797 ♂. [Examined.]

♂, ♀ (Fig. 40). Forewing length 7-9 mm. Antenna of female unknown. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings cream, with small brown patches and dark brown perimeters. Forewing: costa pale brown; blotch at apex approximately rectangular, extending to costa, connected to blotch at tornus by narrow band along termen; blotch at tornus small; discal spot absent. Hindwing: blotch at apex approximately rectangular, extending along 1/2 termen, connected to blotch at tornus by narrow band along termen; blotch at anal margin absent; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream, with pink and brown flecks; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge in male.

♂ *genitalia* (Fig. 104). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus extended, with pointed apex; apex with small spines; ampulla absent. Anellar complex: not completely surrounding aedeagus; with distinctive shape; not fused to valvae. Vinculum with ventral plate W-shaped. Coremata absent. Aedeagus short, squat, without cornutus on vesica.

♀ *genitalia* (Fig. 159). Sterigma absent. Bursa copulatrix: with antrum wide at ostium, narrowing distally; ductus bursae below antrum short, wide, weakly sclerotised, not striated; corpus bursae large, bulbous; signum long. Anterior apophyses very short.

Distribution. Material was examined from Panamá, Colombia and Peru.

Diagnosis. The wing markings of *albipunctulata* are similar to those of *astigma*, *delacruzi*, *leucostigma* and *miccularia*. Whilst these species can be distinguished on the basis of external characters, it is recommended that they are dissected, because intraspecific variation can cause confusion. *Oospila albipunctulata* can be distinguished from *astigma* and *miccularia* by the presence of a small, white discal spot on the hindwing: *astigma* has no discal spot and *miccularia* a small reddish or no discal spot. The markings of *albipunctulata* are also paler than those of *miccularia*. The greater extent of the cream markings distinguishes *albipunctulata* from *delacruzi* (compare Figs 38 and 40). *Oospila albipunctulata* can be distinguished from *leucostigma* by the apical blotch of the forewing which extends to the costa in *albipunctulata* (compare Figs 38 and 40).

The male genitalia of *albipunctulata* can be recognised by shape of the valvae and the arrangement of small spines towards the apex of the valvae (Fig. 104).

Material examined.

PANAMA: *Chiriquí:* 3 ♂ [paratypes].

COLOMBIA: *Boyacá:* Muzo, 400-800 m, 1 ♂ [holotype] (*Fassl*); 4 ♂ [paratypes]; 1 ♂, 1 ♀. *Meta:* Upper Río Negro, 800 m, 1 ♂ (*Fassl*).

PERU: *Puno:* Río Huacamayo, Carabaya, 3100 ft, 1 ♂, vi.04 (*Ockenden*).

Depository: BMNH.

Oospila rufilimes (Warren) new combination

(Figs 41, 105, 160)

Racheolopha rufilimes Warren, 1905: 319; Prout, 1912: 129; 1932: 53. Holotype ♀, in BMNH. Type locality: ECUADOR. label data: Type; R[iver] Cayapas, N[orth] W[est] Ecuador (Fl. & Mik.); Rothschild Bequest B[ritish] M[useum] 1939-l; Racheolopha rufilimes type ♀ Warr[en]; Geometridae genitalia slide No. 15788 ♀ [Examined.]

Racheolopha extensata Warren, 1906: 423. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. French Guiana, Maroni R[iver], S[ain]t Jean, vii. 1904; Schaus Coll[ection]; USNM Type No. 9193. [Examined.] **New synonymy.**

Auophyllodes extensata (Warren); Prout, 1912: 131; 1932: 53.

♂, ♀ (Fig. 41). Forewing length 7-8 mm. Antenna of female simple. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour green; markings reddish brown. Forewing: costa pale brown; blotch at apex long, narrow, connected to blotch at tornus by band along termen; discal spot small, brown. Hindwing: blotch at apex long, narrow, connected to blotch at tornus by band along termen; blotch at tornus extending along 1/3 of costal and anal margins; discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests reddish brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ genitalia (Fig. 105). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus extended into robust, strongly sclerotised process, serrated at tip; ampulla

absent. Anellar complex: not surrounding aedeagus completely; with very distinctive form; with pair of long processes on each side of aedeagus. Coremata absent. Vinculum with W-shaped ventral plate. Aedeagus short, squat; with small cornutus on vesica.

♀ *genitalia* (Fig. 160). Sterigma absent. Bursa copulatrix: ductus bursae wide, with apical part not strongly sclerotised nor striated, antrum absent, towards corpus bursae, ductus becomes more strongly sclerotised; corpus bursae large, bulbous; signum very small, reduced to single tooth. Anterior apophyses short.

Diagnosis. *Oospila rufilimes* can be distinguished from *arpata* by the greater extent of the brown wing markings (compare Figs 41 and 42); although *arpata* sometimes has a small subapical blotch, this never extends right to the costa as the brown markings do in *rufilimes*. Females may also be distinguished by the absence of pectinations on the antennae of *rufilimes*. *Oospila rufilimes* can be distinguished from *fimbripedata* by the absence of a distinctive triangular blotch just posterior to the apex (compare Figs 41 and 43). The male genitalia of *rufilimes* can be recognised by the very distinctive form of the anellar complex (Fig. 105).

Distribution. Specimens were examined from French Guiana, Guyana, Ecuador, Peru, Brazil.

Material examined.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♂ [holotype of *extensata*] vii.1904; 8 ♀ (*Le Moult*).

GUYANA: *Mazaruni-Potaro:* Potaro, 1 ♀, ii.1908 (*Klages*).

ECUADOR: North West Ecuador, Cayapas, 1 ♀ [holotype of *rufilimes*] (*Fl. & Mik.*).

BRAZIL: *Amapá:* Para, 2 ♂. *Amazonas:* Fonte Boa, 2 ♂, v.1906 (*Klages*); Teffe, 1 ♂, viii.1935 (*Moss*).

Depository: BMNH.

Oospila arpata (Schaus) new combination

(Figs 42, 106, 161)

Racheospila arpata Schaus, 1897: 161. Holotype ♀, in NMNH. Type locality: BRAZIL. Label data: Rio Janeiro; Racheospila arpata Type Sch[au]s; Type No. 11898 U.S.N.M; Collection Wm Schaus; Genitalia Slide No. MAC 016. [Examined.]

Auophyllodes arpata (Schaus); Prout, 1912: 131.

Racheolopha arpata (Schaus); Prout, 1932: 54.

Racheolopha similiplaga Warren, 1900: 137, Lectotype ♂, here designated, in BMNH. Type locality: unknown. Label data: Type; Racheolopha similiplaga type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15792 ♂. [Examined.] Synonymised with *Racheolopha arpata* by Prout, 1932: 54.

Auophyllodes similiplaga (Warren); Prout, 1912: 131.

Racheolopha mionophragma Prout, 1932: 53. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; Pérou Huambo; M. de Mathan IV^{e} Trim[estre] 1889; Ex Oberthür Coll[ection] Brit[ish] Mus[eum] 1927-3; Racheolopha mionophragma ♂ type Prout; Geometridae genitalia slide No. 15790 ♂. [Examined.] **New synonymy.**

Racheolopha mionophragma subruta Prout, 1932: 53. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; Chanchamayo Peru; not matched in coll[ection]

D[ogni]n; L. B. Prout Coll[ection] B[ritish] M[useum] 1939-643; Seitz VIII p53; Racheolopha mionophragma subruta ♂ type Prout; Geometridae genitalia slide No. 15802 ♂. [Examined.] **New synonymy.**

♂, ♀ (Fig. 42). Forewing length 8-9 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings brown. Forewing: costa pale brown; blotch at apex absent; sometimes with small subapical blotch, which may be joined to blotch at tornus by band along termen; discal spot small, brown. Hindwing: blotch at apex small, sometimes joined to blotch at tornus (if present) by narrow band along termen; blotch at anal margin absent; discal spot small, brown. Hindleg: proximal spurs absent; with brush of long hair-like scales on male tibia. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with deep medial cleft.

♂ *genitalia* (Fig. 106). Uncus not extended apically. Socii small. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus extended into short, digitate process; ampulla absent. Anellar complex: not surrounding aedeagus completely; V-shaped, supporting aedeagus ventrally; fused to valvae posteriorly. Vinculum with V-shaped ventral plate, with short medial projection. Coremata absent. Aedeagus short, squat; without cornutus on vesica.

♀ *genitalia* (Fig. 161). Sterigma absent. Bursa copulatrix: ductus bursae short, strongly sclerotised, not striated, antrum absent; corpus bursae large, elongated; signum small. Anterior apophyses very short.

Distribution. Material was examined from Colombia, Ecuador, Peru, Bolivia and Brazil.

Diagnosis. *Oospila arpata* can be distinguished from *rufilimes* by the lesser extent of the brown markings in *arpata*. In *arpata* these are usually restricted to the tornus of the forewing and the apex of the hindwing; occasionally there is a small subapical blotch but this never extends right to the costa as the markings do in *rufilimes* (compare Figs 41 and 42). Males can be distinguished by the absence of a bifurcate posterior extension of sternum A8 in *arpata* (compare Figs 105 and 106). Females can be distinguished by the presence of pectinations on the antennae and by the thinner ductus bursae of *arpata* (compare Figs 160 and 161).

Oospila arpata can usually be distinguished from *fimbripedata* by the lesser extent of the brown markings (compare Figs 42 and 43) although in specimens where the markings of *arpata* are more extensive, this character is unreliable. Males of these two species can be distinguished by the shape of sternum A8, the absence of an ampulla and by the extension of the sacculus of the valva in *arpata* (compare Figs 106 and 107).

Material examined.

COLOMBIA: *Boyacá:* Muzo, 400-800 m, 1 ♂ (*Fassl*). *Cauca:* N[elle] Grenade, Juntas, 1 ♂, end 1897-1898 (*Mathan*). *Meta:* Upper Río Negro, 400-800 m, 2 ♂ (*Fassl*).
ECUADOR: *Pastaza:* El Topo, Río Pastaza, 4200 ft, 1 ♂ (*Palmer*). Canelos, [Riohacha], 2100 ft, 1 ♂ (*Palmer*).
PERU: *Amazonas:* Huambo, 1 ♂ [holotype of *mionophragma*] IV[er] Trimestre 1889 (*Mathan*). *Junín:* Chanchamayo, 1 ♂ [holotype of *mionophragma subruta*]. La Merced, 2000-3000 ft, 2 ? (*Watkins*). *Puno:* La Oroya, Río Inambari, 3100 ft, 2 ♂, wet season, iii.05 (*Ockenden*). La Unión, Río Huacamayo, Carabaya, 2000 ft, 1 ♂, 1 ♀, 1 ?, wet season, xi.1904 (*Ockenden*). Yahuarmayo, 1200 ft, 1 ♂, iv.1912.
BOLIVIA: *Cochabamba:* Charaplaya, 65°W 16°S, 1300 m, 1 ♂, vi.01 (*Simons*).
BRAZIL: Rio Grande du Sol, 1 ♀. *Paraná:* Castro, 2900 ft, 1 ? (*Jones*). *Rio de Janeiro:* Rio Janeiro, 1 ♂ [holotype of *arpata*]; Novo Friburgo, 1 ♀ [paralectotype of *similiplaga*]. *Sao Paulo:* Alto da Serra, Santos, 800 m, 1 ♂, 28.ii.1913 (*Jones*); 1 ♂,

4.iii.1913 (*Jones*); 1 ♂, 5.iv.1913 (*Jones*). South East Brazil, 1 ♂. Sao Paulo, 1 ?.
UNKNOWN: 1 ♂ [lectotype of *similiplaga*].
Depositories: BMNH, NMNH.

Oospila fimbripedata (Warren) new combination

(Figs 43, 107)

Racheolopha fimbripedata Warren, 1907: 207; Prout, 1932: 53. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; La Oroya, R[ío] Inambari, S[outh] E[ast] Peru, 3100 ft, wet s[eason], March 05. (G. Ockenden); Racheospila fimbripedata type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15791 ♂ [Examined.]

Auophyllodes fimbripedata (Warren); Prout, 1912: 131.

♂ (Fig. 43). Forewing length 9-10 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings brown. Forewing: costa pale brown; subapical blotch small, triangular, connected to blotch at tornus by thin band along termen; blotch at tornus small; discal spot small, brown. Hindwing: blotch at apex connected to blotch at tornus by thin brown line along termen; blotch at anal margin absent; discal spot small, brown. Hindleg: proximal spurs absent; with brush of long hair-like scales on tibia. Abdomen: with dorsal surface around crests brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised, with deeply emarginated posterior edge and two posterior extensions with slightly expanded, rounded apices.

♂ *genitalia* (Fig. 107). Uncus not extended apically. Socii small. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: not divided; with distinctive field of short bristles at apex; ampulla short, digitate, curved; sacculus not extended. Anellar complex: V-shaped, not completely surrounding aedeagus. Vinculum with ventral plate approximately square with short medial projection. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia*. Unknown.

Distribution. Material was examined from Colombia and Peru.

Diagnosis. *Oospila fimbripedata* can be distinguished from *rufilimes* by the distinctive triangular subapical blotch on the forewings (compare Figs 41 and 43). The greater extent of the brown markings usually distinguishes *fimbripedata* from *arpata* (compare Figs 42 and 43) although in specimens where the markings of *arpata* are more extensive, this character is unreliable. Males of these two species can be distinguished by the shape of sternum A8, by the presence of an ampulla and by the absence of an extension of the sacculus in *fimbripedata* (compare Figs 106 and 107).

Material examined.

COLOMBIA: *Risaralda:* Siató, Rio Siató, Slopes of Chocó, 5200 ft, 1 ♂, ix.09.
PERU: *Puno:* La Oroya, Río Inambari, 3100 ft, 1 ♂ [holotype] wet season, iii.05 (*Ockenden*); 1 ♂, ix.05 (*Ockenden*).
Depository: BMNH.

Oospila zamaradaria Fletcher

(Figs 44, 108)

Oospila zamaradaria Fletcher, 1951: 103. Holotype ♂, in BMNH. Type locality: VENEZUELA. Label data: Type; Rancho Grande n[ea]r Maracay, Ven[ezuela] May 24 1946; Oospila zamaradaria Fletcher Holotype ♂; Geometridae genitalia slide No. 15725 ♂. [Examined.]

[*Oospila zamaradensis* Fletcher, 1951: figs 6,7; pl. 1, fig. 1. Incorrect spelling.]

♂ (Fig. 44). Forewing length 8-9 mm. Frons and vertex black. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings black. Forewing: with blotches at apex and tornus enlarged and merged to give broad black band over distal 1/2 of wing; Hindwing: with blotches at apex and tornus merged to give broad band along termen, band narrower than that of forewing; discal spot small, black, or absent. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests black; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 108). Uncus with apical extension short, approximately rectangular. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with shallow apical division; costa extended as broad process with spinulose apex; ampulla absent. Anellar complex: completely surrounding aedeagus; with very distinctive form (Fig. 108); not fused to valvae. Vinculum with ventral plate thin, weak, U-shaped. Aedeagus: unusually long and thin; with short cornutus on vesica.

♀ *genitalia*. Unknown.

Distribution. Only known from the transitional forest surrounding the Rancho Grande field station in the Henri Pittier National Park in northern Venezuela.

Diagnosis. *Oospila zamaradaria* can be distinguished from *atroviridis* by the absence of a white discal spot on the hindwings of *zamaradaria*. In addition, *atroviridis* usually has separate blotches at the apex and the tornus, whereas *zamaradaria* has a continuous dark brown band along the termen (compare Figs 10, 44 and 74). The darker colour and greater extent of the wing markings distinguishes *zamaradaria* from *tortuguera* (compare Figs 29 and 44). The male genitalia can be recognised by the shape of the valvae, anellar complex and aedeagus (Fig. 108).

Material examined.
VENEZUELA: *Aragua:* Rancho Grande, near Maracay: 1 ♂ [holotype], 24.v.1946; 1 ♂ [paratype] 16.vii.1946; 2 ♂ [paratypes]; 1 ♂, vi.1991 (*Cook*).
Depository: BMNH.

The *miccularia* group

The *miccularia* group is a monophyletic group of three species. This group is defined by the presence of a field of large spines towards the apex of the dorsal (outer) surface of the male valva. The group shares a wing venation character with the *astigma* group, namely that in the forewing vein R_1 arises distally to the origin of vein M_1.

Oospila miccularia (Guenée) new combination

(Figs 45, 109, 162)

Racheospila miccularia Guenée, 1857: 374. Holotype ♂, in BMNH. Type locality: FRENCH GUIANA. Label data: Ex Musaeo Ach. Guenée; Typicum Specimen; Racheospila miccularia Guenée sp G. n° 599: specimen typicum; 3242 [fig.]; Ex Oberthür Coll[ection] Brit[ish] Mus[eum] 1927-3; Geometridae genitalia slide No. 15795 ♂. [Examined.]

Racheolopha miccularia (Guenée); Warren, 1900: 137; Prout, 1912: 129; 1932: 54.

Racheolopha imula Dognin, 1911a: 23. Lectotype ♂, here designated, in NMNH. Type locality: FRENCH GUIANA. Label data: Saint-Jean du Maroni, French Guiana (Le Moult). [Examined.] Synonymised with *Racheolopha miccularia* by Prout, 1932: 54.

Phorodesma sarptaria Möschler, 1881: 402. Holotype ♂, depository unknown. Type locality: SURINAM. Label data: Surinam: Paramaribo. [Not examined.] **New synonymy.**

Comibaena sarptaria (Möschler); Dognin, 1892: 186.

Auophylla sarptaria (Möschler); Warren, 1900: 132.

Auophyllodes sarptaria (Möschler); Prout, 1912: 131.

Racheolopha sarptaria (Möschler); Prout, 1932: 54.

♂, ♀ (Fig. 45). Forewing length 6-9 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches pale brown, with dark brown perimeters and brown striation. Forewing: costa pale brown; blotch at apex large, extending along costa, connected to blotch at tornus by narrow or broad band along termen; discal spot absent. Hindwing: with blotch at apex long, narrow, connected to blotch at tornus by band along termen; blotch at anal margin absent; discal spot small, reddish brown, or absent. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests pink; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge in male.

♂ *genitalia* (Fig. 109). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace present. Valvae: with apical division; with field of large, distinctive spines at apex; sacculus extended into short process with serrated edge; ampulla absent. Anellar complex: completely surrounding aedeagus; with distinctive shape, with medial large, square, anterio-dorsally directed projection and two pointed lateral processes, not connected to valvae. Vinculum with ventral plate V-shaped, with short, medial projection. Coremata absent. Aedeagus: short, squat, without cornutus on vesica.

♀ *genitalia* (Fig. 162). Sterigma absent. Bursa copulatrix: ductus bursae long, thin, weakly sclerotised and not striated, antrum absent; corpus bursae large, bulbous; signum exceptionally large. Anterior apophyses very short.

Distribution. Widely distributed throughout the north and central regions of South America, namely: French Guiana, Guyana, Venezuela, Ecuador, Colombia, Peru, Bolivia and Brazil.

Diagnosis. *Oospila miccularia* can be distinguished from *albipunctulata* by the darker colour of the wing markings and by the lack of a white discal spot on the hindwings: *miccularia* has a small red or no discal spot. The pale brown colour of the blotches and the absence of a discal spot on the forewings distinguishes *miccularia* from *ecuadorata*.

The more extensive markings on the forewings distinguish *miccularia* from *astigma*, *delacruzi* and *leucostigma*. In miccularia the blotch at the apex of the forewing extends right to the costa (compare Figs 37, 38, 39 and 45).

The male genitalia of *miccularia* are very similar to those of *euchlora*, but can be distinguished by the presence of an X-shaped sclerotised brace on the tegumen of *miccularia* (compare Figs 109 and 110). Moreover, the wing markings of these two species are quite distinctive (compare Figs 45 and 46).

Material examined.

FRENCH GUIANA: *Guyane:* Cayenne, 1 ♂ [Holotype of *miccularia*]; 3 ♂; Godebert Maroni, 1 ♂ (*Le Moult*); Saint Jean du Maroni, 2 ♂, 3 ♀ (*Le Moult*); 1 ♂, vii. (*Le Moult*); 1 ♂, viii. (*Le Moult*); Saint Laurent du Maroni, 2 ♂ (*Le Moult*); 1 ♂, x. (*Le Moult*); Nouveau Chantier, 1 ♀ [paralectotype of *imula*] ix. (*Le Moult*); 1 ♂ [lectotype of *imula*] (*Le Moult*); 1 ♂ [paralectotype of *imula*] (*Le Moult*); 1 ? (*Rodway*).

GUYANA: *East Demerara-West Coast Berbice:* Demerara River, 1 ♂, 2 ♀, vii.97. *Mazaruni-Potaro:* Potaro, 1 ♀, ii.1908 (*Klages*); Kartabo, 1 ♀, 27.vii.1925.

VENEZUELA: 2 ♂, 1905 (*Schaus*).

COLOMBIA: *Boyacá:* Muzo, 400-800 m, 1 ♂ (*Fassl*). *Meta:* Upper Río Negro, 800 m, 3 ♂ (*Fassl*).

ECUADOR: Bulim, 160 ft, 1 ♀; 1 ♂, xii.00 (*Fl & M*).

PERU: *Amazonas:* Huambo, 1 ♂, IV^{er} Trimestre 1889 (*Mathan*). *Puno:* Chaquimayo, 2500-3000 ft, 3 ♂ (*Watkins*): 1 ♂, viii-x.10 (*Watkins*); La Oroya, Río Inambari, Carabaya, 3100 ft, 1 ♂, wet season, x.04 (*Ockenden*); 3 ♂, wet season, iii.05

(*Ockenden*); 1 ♂, dry season, v.05 (*Ockenden*); 4 ♂, wet season, xi-xii.1905 (*Ockenden*); 1 ♂, 1 ? wet season, xii.05 (*Ockenden*); South East Peru: Tinguri, Carabaya, 3400 ft, 1 ♂, dry season, viii.04 (*Ockenden*); 1 ♀ (*Ockenden*); Río Huacamayo, Carabaya, 3100 ft, 1 ♂, dry season, vi.04, 1 ♂ (*Ockenden*).

BOLIVIA: Saampioni, 800 m, 1 ♂, 1 ♀. *Santa Cruz:* Río Suruta, 400 m, 1 ♂.

BRAZIL: Santa Cruz de la Sierra, 450 m, 2 ♂ (*Steinbach*); River Yapacani, 600 m, 6 ♂, 1 ♀ (*Steinbach*). *Amapá:* Para, 3 ♂ (*Moss*). *Amazonas:* Sao Paulo de Olivença, 1 ♂; 2 ♂; 1 ♂ (*Germain*). *Mato Grosso:* 1 ♂, 1886 (*Germain*). *Minas Geraes:* Caraça, 1300 m, 1 ♀, 2-4.i.1895 (*Becker*). *Pará:* Unt. Amaz. Taperhina, below Santarem, 1 ♀, 21-31.viii.27 (*Zerny*).

UNKNOWN: No data, 1 ♂ [holotype of *miccularia*].

Depositories: BMNH, CMNH, NMNH.

Oospila euchlora (Prout) new combination

(Figs 46, 110)

Racheolopha euchlora Prout, 1932: 54. Holotype ♂, in BMNH. Type locality: BRAZIL. Label data: Type; 39, 27, Burity, 30 miles N[orth] E[ast] of Cuyaba 2250 ft. 1-14.vii.27 Mato Grosso C.L. Collenette; 515; On damp sand; Joicey Bequest. Brit[ish] Mus[eum] 1934-120; Seitz VIII p54, fig 8g; racheolopha euchlora ♂ type Prout; Geometridae genitalia slide No. 15800 ♂. [Examined.]

♂ (Fig. 46). Forewing length 8-9 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent; markings pink. Forewing: costa pale brown; with narrow pink band along termen; discal spot pink. Hindwing: narrow pink band along termen; anterior discal spot small, white; posterior discal spot small, pink. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 110). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus extended into short, pointed process; with large spines over distal 1/2 of dorsal surface; ampulla absent. Anellar complex: completely surrounding aedeagus; distinctively shaped, with two narrow anterio-dorsal processes. Coremata absent. Vinculum with ventral plate V-shaped. Aedeagus long, thin, without cornutus on vesica.

♀ *genitalia*. Unknown.

Distribution. The only specimen of this species examined was collected in the Mato Grosso province of Brazil.

Diagnosis. *Oospila euchlora* may be distinguished from *restricta* by the colour of the band along the termen: this is pink in *euchlora* and brown in *restricta*. In addition, *restricta* lacks a second, pink discal spot on the hindwing. The male genitalia of *euchlora* are very similar to those of *miccularia*, from which they can be distinguished by the absence of an X-shaped sclerotised brace on the tegumen of *euchlora* (compare Figs 109 and 110). Moreover, the wing markings of these two species are quite distinctive (compare Figs 45 and 46).

Material examined.

BRAZIL: *Mato Grosso:* 30 miles North East of Cuyaba, Burity, 2250 ft, 1 ♂ [holotype] 1-14.vii.27 (*Collenette*).

Depository: BMNH.

***Oospila ecuadorata* (Dognin) new combination**

(Figs 47, 111)

Comibaena ecuadorata Dognin, 1892: 186. Lectotype ♂, here designated, in NMNH. Type locality: ECUADOR. Label data: Zamora Equateur; Comibaena ecuadorata type ♂ [Dognin]; [pas des Druce un] Brit[ish] M[useum] Mar[ch] 92; dans sarptaria l'abdomen [?]; Dognin Collection; Type No. 32756 U.S.N.M; Genitalia Slide By MAC 57760 USNM. [Examined.]

Auophyllodes ecuadorata (Dognin); Prout, 1912: 131.

Racheolopha sarptaria ecuadorata (Dognin); Prout, 1932: 54.

Racheolopha sarptaria ruboris Prout, 1932: 54. Lectotype ♂, here designated, in BMNH. Type locality: COLOMBIA. Label data: Muzo, Colombia 400-800 m Coll[ection] Fassl; Racheolopha sarptaria ruboris type ♂ Prout. [Examined.] **New synonymy.**

♂ (Fig. 47). Forewing length 7-9 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings orange-brown, with reddish perimeters and brown striation. Forewing: costa pale brown; with blotches at apex and tornus joined by narrower band along termen; discal spot small, red-brown. Hindwing: with band along termen, extending along distal 1/3 of costal and anal margins; blotch at anal margin absent; discal spot small, red-brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests pink; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge.

♂ *genitalia* (Fig. 111). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus extended into short, pointed process; with field of large spines towards apex of dorsal surface; ampulla absent; with distinctive, long process from base of valva, where joins anellar complex. Anellar complex: surrounding aedeagus completely, with three anterio-dorsal extensions; fused to valvae posteriorly. Vinculum with V-shaped ventral plate. Coremata absent. Aedeagus short, squat; without cornutus on vesica.

♀ *genitalia*. Unknown.

Distribution. Distributed in Central America and northern and central areas of South America, namely Panamá, Colombia, Ecuador, Peru, Bolivia and Brazil.

Diagnosis. *Oospila ecuadorata* can be distinguished from *miccularia* and *albipunctulata* by the presence of reddish discal spots on both fore- and hindwings and by the redder colour of the blotches. The male genitalia of *ecuadorata* can be recognised by the presence of long processes at the base of the valvae and peg-like sclerites at the apex of their dorsal surface (Fig. 111).

Material examined.

PANAMA: *Chiriquí:* Chiriquí, 1 ♂.

COLOMBIA: *Boyacá:* Muzo, 400-800 m, 1 ♂ [lectotype of *ruboris*] (*Fassl*); 3 ♂ (*Fassl*); Upper Río Negro, 800 m, 2 ♂ (*Fassl*); Muzo, River Cantinero, 400 m, 1 ♂ (*Fassl*).

ECUADOR: *Pastaza:* El Topo, Río Pastaza, 4200 ft, 1 ♂ (*Palmer*); *Zamora-Chinchipe:* Zamora, 1 ♂ [lectotype of *ecuadorata*]; 6 ♂ [paralectotypes of *ecuadorata*].

PERU: *Amazonas:* Huambo, 2 ♂, IV^{er} Trimestre 1889 (*Mathan*); *Puno:* Oconeque, Carabaya, 7000 ft, 1 ♂, dry season, vii.1904 (*Ockenden*); Carabaya: Tinguri, 3400 ft, 3 ♂, dry season, viii.1904 (*Ockenden*); 3 ♂, wet season, i.1905 (*Ockenden*); Carabaya: Río Huacamayo, 3100 ft, 3 ♂, dry season, vi.04 (*Ockenden*); La Oroya, Río Inambari, 3100 ft, 2 ♂, dry season, ix.04 (*Ockenden*); 1 ♂, wet season, x.04 (*Ockenden*); 2 ♂, iii.05 (*Ockenden*); 1 ♂, wet season, xi-xii.1905 (*Ockenden*); South East Peru, Santo Domingo, 6000 ft, 1 ♂, xi.1904 (*Ockenden*).

BOLIVIA: Salampioni, 600 m, 2 ♂, dry season, viii.01 (*Simons*). *La Paz:* Chimate, 760 m, 1 ♂, ix.00 (*Simons*); San Ernesto, 68°W 15°S, 1000 m, 6 ♂, viii.-ix.00 (*Simons*). *Santa Cruz:* Río Sunta, 400 m, 1 ♂, v. (*Steinbach*).

BRAZIL: *Amazonas:* Upper Amazon: Sao Paulo de Olivença, 1 ♂, i.1932 (*Wucherpfennig*). *Pará:* Unt. Amaz. Taperhina, below Santarem, 1 ♂; 1 ♂, 10.vi.27 (*Zerny*).

Depositories: BMNH, NMNH.

The *athena* group

The *athena* group is a group of two species, formerly assigned to *Progonodes*, characterised by the form of the anellar complex, which is a flat plate, not surrounding the aedeagus.

Oospila athena (Druce) new combination

(Figs 12, 48, 112, 163)

Racheospila athena Druce, 1892: 89. Holotype, ♂ in Staudinger Museum. Type locality: PANAMA. Label data: Panama: Chiriqui (Tr?tsch) (mus[eum] Stau[dinger]). [Not examined.]

Progonodes athena (Druce); Prout, 1912: 135.

♂, ♀ (Figs 12, 48). Forewing length 17-19 mm. Antenna of female bipectinate. Frons green, vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour white, speckled with dark green; blotches absent. Forewing: costa pale brown; with large white patch 1/3 along costal edge; also with large white patch at apex; discal spot absent. Hindwing: with solid white areas at base and apex; discal spot absent. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with deeply emarginated posterior edge and two curved, posterior extensions, with serrated margins.

♂ *genitalia* (Fig. 112). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with costa developed into long curved process; sacculus not extended into process, but with lobe; ampulla absent. Anellar complex: a flat plate; not surrounding aedeagus; V-shaped at posterior. Vinculum with ventral plate broad, shallow W-shape. Aedeagus short, without cornutus on vesica.

♀ *genitalia* (Fig. 163). Sterigma absent. Bursa copulatrix: ductus bursae long, quite narrow, weakly sclerotised and not striated, antrum absent; corpus bursae large, bulbous; signum very small. Anterior apophyses very short.

Distribution. Specimens were examined from Panamá, Costa Rica, Venezuela, Colombia and Peru.

Diagnosis. *Oospila athena* can be distinguished from *lactecincta, nivetacta* and *sporadata* by the presence of large white apical patches on the wings (compare Figs 12, 48, 50 and 51). The absence of large, brown discal spots on the fore- and hindwings distinguishes *athena* from *nivetacta* (compare Figs 12, 48 and 81). The male genitalia of *athena* can be recognised from the unusual shape of the valvae and the anellar complex (Fig. 112). The shape of sternum A8 is also distinctive in this species (Fig. 112).

Material examined.

PANAMA: 1 ♀.

COSTA RICA: *Cartago:* Cachi, 1 ?; 1 ♀ (*Underwood*); Sitio, 4000 ft, 3 ♀ (*Schaus*); 1 ♀; Tuis, 1 ♀ (*Schaus*); 1 ♀ (*Underwood*); *Puntarenas:* Finca Cafrosa, Estacion Las Mellitzas Parque Nacional Amistad, 1300 m, 1 ♀, xi.1989 (*Ramirez & Mora*).

VENEZUELA: Tachira Río Frio, 600 m, 1 ♂, 2.x.1981 (*Fernandez, Clavijo & Chacon*).

COLOMBIA: *Boyacá:* Muzo, 400-600 m, 1 ♀ (*Fassl*); 1 ♂ (*Pratt*).

PERU: *Cajamarca:* Huancabamba, Cerro de Pasco, 1 ♂ (*Boettger*); North Peru: River Tabaconas, 6000 ft, 1 ?, 1912 (*Pratt & Pratt*). *Junín:* Chanchamayo, 1 ♂, 1898 (*Schuncke*); Central Peru: La Merced, 3000-4500 ft, 1 ♀, xi-xii.19 (*Watkins*). *Loreto:* North Peru: Rentema Falls, Upper Marañón, 1000 ft, 1 ♀ (*Pratt & Pratt*). *Pasco:* Oxapampa, 6400 ft, 1 ♀. *Puno:* Carabayo: La Unión, Río Huacamayo, 2000 ft, 3 ♂, 1

♀, 1 ?, wet season, xi-xii.1904 (*Ockenden*).

Depositories: BMNH, INBio, UCV.

Oospila holochroa (Prout) new combination

(Figs 49, 113)

Progonodes holochroa Prout, 1912: 417. Holotype ♂, in BMNH. Type locality: PANAMA. Label data: Type; Chiriqui S.K.B; L.B. Prout Coll[ection] B[ritish] M[useum] 1939-643; Progonodes holochroa Prout N.Z. p.417 ♂ type; [?]; Geometridae genitalia slide No. 15768 ♂. [Examined.]

Progonodes stagonata holochroa Prout, 1932: 60.

Racheospila delicatescens Dyar, 1914: 229. Holotype ♀, in NMNH. Type locality: PANAMA. Label data: Panama: Panama Canal Zone, Porto Bello, iii.1911 (Busck); Type No. 16056 U.S.N.M. [Not examined.] **New synonymy.**

Oospila delicatescens (Dyar); Prout, 1932: 56.

♂ (Fig. 49). Forewing length 15 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent; markings pale brown. Forewing: costa pale brown; termen with beige fringe; thin brown line inside fringe, interrupted by small white dots where veins meet termen; discal spot small, brown. Hindwing: as forewing; anterior discal spot large, white; posterior discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised with deep medial groove and two short posterior processes.

♂ *genitalia* (Fig. 113). Uncus with two short apical extensions. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; with distinctive shape; sacculus a blunt lobe; ampulla absent. Anellar complex: a flat plate, not completely surrounding aedeagus, fused to valvae posteriorly. Vinculum with ventral plate broad, W-shaped. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia*. Unknown.

Diagnosis. *Oospila holochroa* can be distinguished from *lacteguttata* by the presence of two white discal spots on the hindwings and by the absence of a proximal pair of spurs on the hind tibia. The presence of a brown discal spot on the forewings distinguishes *Oospila holochroa* from *imaculata* (compare Figs 49 and 76). The male genitalia of *holochroa* can be recognised by the unusual shape of the uncus and the valvae (Fig. 113).

Remarks. The type specimen of *delicatescens* Dyar has not been located in the NMNH. However, the descriptions suggest that it is synonymous with *holochroa*.

Distribution. Only a single specimen was examined, from Chiriquí in Panamá.

Material examined.

PANAMA: *Chiriquí:* 1 ♂ [holotype]

Depository: BMNH.

Oospila lactecincta (Warren)

(Figs 50, 114, 164)

Racheolopha lactecincta Warren, 1909: 85. Lectotype ♂, here designated, in BMNH. Type locality: BRAZIL. Label data: Fonte Boa, Upp[er] Amazon, July 1907 (S.M. Klages); Racheolopha lactecincta type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15732 ♂. [Examined.]

Oospila lactecincta (Warren); Prout, 1912: 134; 1932: 59.

♂, ♀ (Fig. 50). Forewing length 13-16 mm. Antenna of female bipectinate. Frons and vertex green. Interantennal fillet white. Thorax: dorsal surface white. Wings: ground colour white; blotches absent; markings dark green. Forewing: with costa pale brown; green band along distal part of costa and termen, white bands inside this enclose a central greenish triangle which is irregularly streaked with white; discal spot, small, dark brown, surrounded by white area. Hindwing: as forewing but green colour more mottled and diffuse; discal spot extended, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge in male.

♂ *genitalia* (Fig. 114). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace present. Valvae: short, not divided; with subapical constriction and rounded, denticulate apex; sacculus not extended; ampulla absent. Anellar complex: completely surrounding aedeagus; fused to valvae posteriorly. Vinculum with ventral plate broad, V-shaped. Coremata absent. Aedeagus with two large cornuti on vesica.

♀ *genitalia* (Fig. 164). Sterigma elliptical, with posterior edge emarginated. Bursa copulatrix: ductus bursae long, with large antrum, strongly sclerotised and striated below antrum; corpus bursae large, approximately spherical; signum small. Anterior apophyses short.

Distribution. Specimens were examined from Peru and the Amazonas region of Brazil.

Diagnosis. *Oospila lactecincta* can be distinguished from *athena* and *sporadata* by the position of solid areas of white on the forewings (compare Figs 12, 48, 50 and 51). The male genitalia of *lactecincta* can be recognised by the shape of the valvae (Fig. 114).

Material examined.

PERU: *Loreto:* North Peru: Rentema Falls, Upper Marañón, 1000 ft, 1 ♀ (*Pratt & Pratt*).

BRAZIL: *Amazonas:* Fonte Boa, Upper Amazon, 1 ♂ [lectotype] vii.1907 (*Klages*); 1 ♀ [paralectotype] v.1906; 1 ♀, [paralectotype] vii.1906; 2 ♀, viii.1907.

Depository: BMNH.

Oospila sporadata (Warren)

(Figs 51, 115, 165)

Racheolopha sporadata Warren, 1906: 426. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. French Guiana: Maroni, S[ain]t Jean, iii.1904; USNM Type No. 9199. [Examined.]

Oospila sporadata (Warren); Prout, 1932: 59.

Progonodes curvimargo Herbulot, 1991: 110. Holotype ♂, in C. Herbulot collection. Type locality: Ecuador. Label data: Ecuador Km 17 de la route Limon Méndez 900 m - 12 et 13.i.1975 C. Herbulot; Progonodes curvimargo H[e]rb[u]l[o]t Holotype. [Examined.] **New synonymy.**

♂, ♀ (Fig. 51). Forewing length 14-20 mm. Antenna of female bipectinate. Frons and vertex green. Interantennal fillet white. Thorax: dorsal surface white. Wings: ground colour white; blotches absent; with dark green speckling, spots joined to give small patches of solid green in some areas. Forewing: with costa pale brown; green speckling concentrated to form mainly green areas along termen and at centre of wings; discal spot absent. Hindwing: as forewing but with large white area along costa and anal margin; discal spot absent. Hindleg: proximal spurs absent; brush of long hair-like scales present on tibia of male. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised, in male, with short bifurcate apical extension.

♂ *genitalia* (Fig. 115). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: divided apically; sacculus extended into long, strongly sclerotised, pointed process; ampulla short, robust, with flat, denticulate apex. Anellar complex: completely surrounding aedeagus; distinctively shaped, with long anterio-dorsal extension. Vinculum with ventral plate large, W-shaped. Coremata absent. Aedeagus long, thin, with cornutus on vesica forked; base of vesica strongly sclerotised, denticulate.

♀ *genitalia* (Fig. 165). Sterigma absent, but with ring of slightly stronger sclerotisation around ostium and with shallow membranous pouch on each side. Bursa copulatrix: ductus bursae quite long, narrow just below ostium, widening distally, strongly sclerotised and striated; bursa copulatrix large, bulbous; signum small. Anterior apophyses short.

Distribution. Distributed throughout most of South America, except the far South, this species has been collected in French Guiana, Surinam, Guyana, Colombia, Ecuador, Peru and Brazil.

Diagnosis. *Oospila sporadata* can be distinguished from *athena* and *lactecincta* by the more speckled appearance of the wing markings; *sporadata* does not have the solid patches of green and white which are found in the others (compare Figs 12, 48, 50 and 51). The male genitalia of *sporadata* can be recognised by the short, robust ampulla, the long anterior extension of the anellar complex and the denticulate aedeagus (Fig. 115).

Material examined.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 7 ♂, 1 ♀ (*Le Moult*); 1 ♂, x. (*Le Moult*); 4 ♂, 1 ♀ (*Le Moult*); 1 ♂ [holotype of *sporadata*], 2 ♂, 2 ♀; Nouveau Chantier, 1 ♂, 1 ♀ (*Le Moult*).

SURINAM: *Marowijne:* Aroewarwa Creek, Maroewym valley, 1 ♂, iv.05 (*Klages*): 1 ♂, v.05 (*Klages*).

GUYANA: *Mazaruni-Potaro:* Omai, 1 ♂, 1 ?.

COLOMBIA: *Amazonas:* Leticia, 1 ♂ [paratype of *curvimargo*] viii.1977 (*Moinier*).

ECUADOR: *Pasatza:* Sarayacu, 1 ♂ (*Buckley*). 17 km de La route Limón, 900 m, 1 ♂ [holotype of *curvimargo*] 12-13.i.1975 (*Herbulot*); 1 ♀ [paratype of *curvimargo*] (*Herbulot*).

PERU: *Junín:* River Chuchurras, River Palcazu, 320 m, 1 ♂ (*Hoffmann*). *Puno:* Yahuarmayo, 2000 ft, 1 ♂, iv.1912.

BRAZIL: *Amapá:* Para, 1 ♂, 1 ♀ (*Moss*). *Amazonas:* Fonte Boa, 7 ♂, 2 ♀, vii.06 (*Klages*); 1 ♂ ix.06 (*Klages*); 1 ♂, 1 ♀, vii.07 (*Klages*); 1 ♂, viii.06 (*Klages*); 1 ♂, xi.06 (*Klages*).

Depositories: BMNH, C. Herbulot collection, NMNH.

The *includaria* group

The *includaria* group is a group of 2 similar-looking species which were formerly assigned to the genus *Auophylla*.

Oospila includaria (Herrich-Schäffer) new combination

(Figs 52, 116, 166)

Thalera includaria Herrich-Schäffer, 1855, fig. 341; 1856: 36, 62, 82. Holotype ♂, in mus[eum] Staudinger. Type locality: GUATEMALA. [Not examined.]

Phorodesma (?) inclusaria Guenée, 1857: 371. [Incorrect spelling.]

Comibaena inclusaria (Guenée); Druce, 1892: 88.

Comibaena (?) inclusaria (Guenée); Walker, 1861: 570.

Auophylla includaria (Herrich-Schäffer); Warren, 1897: 423-424; Prout, 1912: 130; 1932: 52.

Comibaena magnifica Schaus, 1901: 252. Lectotype ♂, here designated, in NMNH. Type locality: BRAZIL: Sao Paulo. [Examined.] **New synonymy.**

Auophylla magnifica (Schaus); Prout, 1912: 130; 1932: 52.

Auophylla multiplagiata Warren, 1897: 424; Prout, 1912: 130; 1932: 52. Holotype ♂, in BMNH. Type locality: PARAGUAY. Label data: Paraguay Dr Bohls; Rothschild Bequest B[ritish] M[useum] 1939-1; Anophylla multiplagiata type ♂ Warr[en]; Geometridae genitalia slide No. 15806 ♂. [Examined.] **New synonymy.**

Auophylla basiplaga Warren, 1907, 201; Prout, 1912, 130; 1932: 52. Holotype ♂, in BMNH. Type locality: PARAGUAY. Label data: Type; Sapucay, Paraguay, 9.vii.02

(W. Foster); Rothschild Bequest B[ritish] M[useum] 1939-1; Oospila basiplaga type ♂ Warr[en]; Geometridae genitalia slide No. 15805 ♂. [Examined.] **New synonymy.**

♂, ♀ (Fig. 52). Forewing length 9-14 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings cream, with brown detail. Forewing: with costa pale brown; with band along termen, often expanded at apex and tornus, often containing a narrow, parallel brown band; where cream band extends along distal 1/3-1/2 of anal margin it may have a short digitate anterior extension which may be continuous with the discal spot (as in Fig. 52); with additional cream blotch at wing base; discal spot a short white band containing a brown line. Hindwing: as forewing except cream band along apex of discal cell extends from apex only along 1/2 wing length; discal spot absent. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♂ *genitalia* (Fig. 116). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus extended into long, strongly sclerotised, pointed process, with denticulate margin at basal end; with pointed subapical extension; apex of valva with row of small spines; ampulla absent. Anellar complex: completely surrounding aedeagus; with medial extensions fused to valvae. Vinculum with ventral plate V-shaped. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia* (Fig. 166). Sterigma approximately elliptical; with a shallow pocket on each side. Bursa copulatrix: ductus bursae long, wide, weakly sclerotised and not striated, antrum absent; corpus bursae large, bulbous; signum small. Anterior apophyses short.

Distribution. Distributed in South America, namely, Peru, Argentina, Paraguay and Brazil.

Diagnosis. The wing markings of *Oospila includaria* are rather similar to those of *obeliscata*. However, *includaria* is smaller than *obeliscata* and may be distinguished by the smaller size of the discal spots (compare Figs 52 and 68). The presence of a white blotch at the base of the wings and the absence of a constriction of the anterior of the green area at the middle of the forewing distinguishes *includaria* from *leucothalera* (compare Figs 52 and 53). The male genitalia of *includaria* can be recognised by the extension of the middle part of the valva into a pointed process (Fig. 116).

Material examined.

PERU: *Puno:* Carabaya: La Unión, Río Huacamayo, 2000 ft, 1 ♂, wet season, xii.1904 (*Ockenden*).

ARGENTINA: Sierra de la Ramada, 650 m, 1 ♂ (*Schreiter*); Ocampo, El Chaco, 1 ♂, i.1906 (*Venturi*). *Misiones:* Haut Parana, San Ignacio Missions, 4 ♂. *Salta:* North Argentina: Salta, 1 ♀, ii.05 (*Steinbach*). *Tucuman:* 1 ♂, 1 ♀, 1 ? (*Steinbach*); Cuidad Tucuman, 1 ♀, iii.1903 (*Monetti*).

PARAGUAY: *Paraguarí:* Sapucay, 1 ♂ [holotype of *basiplaga*] 9.vii.02 (*Foster*); 1 ♀, 2.xi.03 (*Foster*); 1 ♂, 19.vi.03 (*Foster*); 1 ♀, 15.xi.03 (*Foster*); 1 ♀, 30.xi.04; 1 ♂ [holotype of *multiplagiata*] (*Bohls*).

BRAZIL: Brazilia, 1 ♂ (*Dohrn*); Rio Grande do Sul, 2 ♂ (*[Stgr]*). *Bahia:* Iguassu, 1 ♀. *Mato Grosso:* 1 ♂, 1886 (*Germain*); 1 ♂, 1886. *Minas Geraes:* Uberaba, 1 ♂, 1 ♀ (*Le Moult*). *Paraná:* Castro, 2900 ft, 1 ♂, 1 ♀ (*Jones*). *Sao Paulo:* Sao Paulo, 2300 ft, 1 ♂ [lectotype of *magnifica*], 1 ♀; South East Brazil: Sao Paulo, 2300 ft, 1 ♀ (*Jones*). *Santa Catarina:* Blumenau, 1 ♂, 1 ♀, 26.iv.29 (*Schade*); Rio Vermehlo, 1 ♀, i.1937

(*Hoffmann*); Jaraguá do Sul, 1 ♀, xi.1934 (*Hoffmann*).

UNKNOWN: Guerica ?, 1 ♀.

Depositories: BMNH, NMNH.

Oospila leucothalera (Prout) new combination

(Figs 53, 167)

Auophylla leucothalera Prout, 1932: 52. Holotype ♀, in BMNH. Type locality: BRAZIL. Label data: Bresil Caraca P. Germain 2° Semestre 1884; Ex. Oberthür Coll[ection] Brit[ish] Mus[eum] 1927-3; Auophylla leucothalera ♀ type Prout; Geometridae genitalia slide No. 15807 ♀. [Examined.]

♀ (Fig. 53). Forewing length 9-10 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent; markings cream with brown detail. Forewing: costa pale brown; cream band along termen, with broken brown line inside this; small triangular green patch at wing base; larger solid green area in centre of wing, constricted abruptly anteriorly and sometimes separating into two separate green patches; discal spot a short brown line. Hindwing: with broad band along termen, extending along costal edge and along 1/2 anal margin; discal spot absent. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 not strongly sclerotised, simple.

♀ *genitalia* (Fig. 167). Sterigma large, crescent-shaped, with shallow pocket on each side. Bursa copulatrix: ductus bursae short, wide, with large antrum, strongly sclerotised and striated below antrum; corpus bursae large, bulbous; signum absent. Anterior apophyses quite long.

Distribution. Only known from southern areas of Brazil.

Diagnosis. *Oospila leucothalera* can be distinguished from *includaria* by the absence of a white blotch at the base of the wings and by the shape of the green marking at the centre of the forewing. In *leucothalera* this marking is either narrower at the apex, or the apical part of the marking is separate; in *includaria*, this marking is continuous and wider at the apex (compare Figs 52 and 53).

Material examined.

BRAZIL: Queluz, 1 ♀, [paratype] (*Germain*). *Minas Geraes:* Caraça, 1 ♀ [holotype] 2° Semestre 1884 (*Germain*). *Sao Paulo:* Alto de Serra, 1 ♀ [paratype] xi.1922 (*Spitz*); Serra do Mar, 1 ♀, iv.1927 (*Wucherpfennig*).

Depository: BMNH.

The *albicoma* group

The *albicoma* group is a monophyletic group of 4 species defined by the form of the male anellar complex. The transtilla and juxta are fused to form a sclerite completely surrounding and supporting the aedeagus. The anellar complex of this group has a distinctive shape and lacks any processes or extensions; the anellar complex of these species is not connected to the valvae.

Oospila albicoma (Felder & Rogenhofer)

Two subspecies with identical male genitalia, but with distinctive wing markings. One of these, *albicoma nasuta*, is confined to Trinidad.

Oospila albicoma albicoma (Felder & Rogenhofer)

(Figs 14, 54, 117, 168)

Racheospila albicoma Felder & Rogenhofer, 1875: pl 127, fig. 22. Holotype ♂, in BMNH. Type locality: AMAZONAS. Label data: Holotype; 146; Novara CXXVII p 22, Racheospila albicoma Amaz[onas] m[ale]. Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15713 ♂. [Abdomen incorrectly associated, see Remarks.] [Examined.]

Oospila albicoma (Felder & Rogenhofer); Warren, 1900: 136; Prout, 1912: 133; 1932: 57.

Oospila minorata Warren, 1909: 83. Lectotype ♂, here designated, in BMNH. Type locality: BRAZIL. Label data: Type; Fonte Boa, Upp[er] Amazonas, May 1906. (S.M. Klages); Oospila minorata type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15715 ♂. Synonymised with *albicoma* by Prout, 1932: 57. [Examined.]

Oospila deliciosa Thierry-Mieg, 1916: 42. Prout, 1932: 57. Lectotype ♂, here designated, in MNHN. Type locality: FRENCH GUIANA. Label data: Type; Guyane

Française St-Jean du Maroni Collection Le Moult; 1917 Coll[ection]. P. Thierry-Mieg Museum Paris; Oospila deliciosa t.m. misc. ent., XXIII, n°10-11, p[4]2, 1916. type original. [Examined.] **New synonymy.**

♂, ♀ (Figs 14, 54). Forewing length 14-19 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches cream or pale brown, with dark brown perimeters and some dark brown striation. Forewing: with costa pale brown; blotch at apex large, extending along costa, not connected to blotch at tornus by band along termen; blotch at tornus large, circular towards middle of wing, narrowing abruptly towards termen (not wedge-shaped as in *depressa*, compare Figs 8, 14, 54 and 78), extending to cover discal spot; discal spot small, dark brown. Hindwing with blotches at apex and tornus large, occasionally connected by band along termen; blotch at anal margin small, narrow; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 with emarginated posterior margin in male.

♂ *genitalia* (Fig. 117). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace present. Valvae: deeply divided at apex; sacculus extended into short, blunt process; apex sculpted; ampulla narrow, digitate, with denticulate apex. Anellar complex: completely surrounding aedeagus; not connected to valvae. Vinculum with ventral plate V-shaped. Coremata absent. Aedeagus with long, thin cornutus on vesica.

♀ *genitalia* (Fig. 168). Sterigma absent. Bursa copulatrix: ductus bursae long with large antrum; strongly sclerotised and striated below antrum; corpus bursae fairly small, approximately spherical; signum small. Anterior apophyses very short.

Distribution. Widely distributed in Central and South America in and south of Costa Rica, in French Guiana, Surinam, Guyana, Venezuela, Colombia, Peru and Brazil.

Diagnosis. *Oospila albicoma albicoma* can be distinguished from most other species with cream blotches by the size of the blotch at the tornus of the forewing. In *albicoma albicoma* this blotch is large and extends to cover the discal spot, but is usually much smaller in other species. *Oospila albicoma albicoma* can also be distinguished from *depressa* and *longiplaga* by the shape of the blotch at the tornus of the forewing. In *albicoma albicoma* this blotch is large and rounded towards the inside of the wing but has an abrupt constriction towards the termen. In *depressa* and *longiplaga* this blotch tapers gradually towards the termen (compare Figs 8, 14, 18, 54 and 78).

Oospila albicoma albicoma can be distinguished from *concinna* by its smaller size, and by the presence of brushes of long hair-like scales and a small elliptical sclerite on sternum A2; these are absent from *concinna*. The shape of the distal end of the valva distinguishes males, also the aedeagus of *albicoma albicoma* bears a short cornutus, which is absent from *concinna* (compare Figs 117 and 118). In the female, a sterigma is absent from *albicoma albicoma* but present in *concinna* (compare Figs 168 and 169).

The shape of the blotch at the apex of the forewing distinguishes *albicoma albicoma* from *lunicincta*. This blotch extends along the costa in *albicoma albicoma* but not in *lunicincta* (compare Figs 14, 19 and 54).

Oospila albicoma albicoma can be distinguished from *albicoma nasuta* by the larger size of the blotch at the tornus of the forewing and also by the lack of a short digitate extension of this blotch in *albicoma albicoma* (compare Figs 14, 54 and 55).

Remarks. The holotype has an incorrectly associated abdomen (the genitalia of this abdomen belong to a species of *Semiothisa* Hübner (Geometridae: Ennominae)).

Material examined.

COSTA RICA: *Alajuela:* Finca San Gabriel, 2 km South West of Dos Rios, 630 m, 1 ♂, 8.ii.1983 (*Janzen & Hallwachs*); 1 ♂, 5.v.1984 (*Janzen & Hallwachs*); Finca Campana, 5 km North West Dos Rios, 750 m, 1 ♂, 21.iii.1985 (*Janzen & Hallwachs*); Finca San Gabriel, 630 m, 16 km East of Quebrada Grande, 3 ♂, 1 ♀; Estacion Pitilla, 700 m, 9 km South of Santo Cecilia, 1 ♀, i.1988 (*Chacon & Espinosa*); 4 ♂, vii.1988 (*Scoble & Brooks*); Finca San Gabriel, 16 km East North East of Quebrada Grande, 650 m, 2 ♂, 8.ii.1983 (*Janzen & Hallwachs*); 2 ♂, 12.iii.1983 (*Janzen & Hallwachs*); 1 ♀, 11.xi.1983 (*Janzen & Hallwachs*); 1 ♂, 5.v.1984 (*Janzen & Hallwachs*); 1 ♂, vii.1988 (*Gauld & Mitchell*). *Cartago:* I.I.C.A. Grounds, 600 m, 1 ♂, 24-26.vi.1974 (*Watson*); Orosi, 1200 m, 2 ♀ (*Fassl*); Tuis, 2 ♂; 3 ♂. *Guanacaste:* Estacion Pitilla, 700 m, 9 km South of Santa Cecilia, 3 ♂, 1 ♀; Finca Biesnan, Colonia Refug., Los Angeles, 11 km East of Quebrada Grande, 500 m, 1 ♂, 13.vi.1985 (*Janzen & Hallwachs*); 4 km East Casetilla Rincon National Park, 750 m, 1 ♂, 22.v.1982 (*Janzen & Hallwachs*). *Heredia:* Chilamate, 100 m, 3 ♂, 1 ♀, 11.viii.1986 (*Covell*); Finca La Selva Biological Station, Puerto Viejo Sarapiqui, 40 m, 3 ♂, 14-15.xi.1982 (*Janzen & Hallwachs*); 1 ♂, 6-9.iii.1985 (*Janzen & Hallwachs*); 1 ♂, ii.1986 (*Chavarria & Chacon*); 2 ♂, iii.1986 (*Chavarria*); 2 ♂, 1 ♀, vii.1986 (*Chavarria*); 3 ♂, 1 ♀, xi.1986 (*Chavarria*); 1 ♂, iii.1987 (*Chavarria*); 6 ♂, iv.1987 (*Chavarria*); 1 ♂, v.1987 (*Chavarria*); 3 ♂, x.1987 (*Chavarria*); 1 ♂, xii.1987 (*Chavarria*). *Limón:* Cerro Tortuguero, Parque Nacional Tortuguero, 0-100 m, 3 ♂, 27.iii.1981 (*Janzen & Hallwachs*); 2 ♂, 30.v.1984; Sixola river: 1 ♂, 1 ♀. *Osa Peninsula:* Sirena, Corcovado National Park, 3 ♂, 19-27.iii.1981 (*Janzen & Hallwachs*). *Puntarenas:* Fila Esquinas, 35 km South of Palmar Norte, 8°45' x 83°20', 150 m, 3 ♂, 7-8.i.1983 (*Janzen & Hallwachs*). *San José:* Estacion Carrillo, Parque Nacional Braulio Carrillo, 700 m, 1 ♂, 1 ♀, ix.1984 (*Chacon*); 1 ♂, x.1984; Cario, 1 ♂; La Fuente, Turrialba, 1 ♂.
FRENCH GUIANA: *Guyane:* Mana River, 3 ♂, v.1917; Saint Jean du Maroni, 1 ♂ [lectotype of *deliciosa*]; 2 ♂, 1 ♀; Saint Laurent du Maroni, 1 ♀ (*Le Moult*); 1 ♂.

SURINAM: *Marowijne:* Aroewarwa Creek, Maroewym valley, 1 ♂, v.1905 (*Klages*).

GUYANA: *East Demerara-West Coast Berbice:* Rio Demerara, 1 ♀. *Mazaruni-Potaro:* Omai, 1 ♂; Rockstone, Essequebo, 1 ♂. Potaro River, 1 ♀, 1904 (*Roberts*); Tumatumari, 1 ♂, xii.1907 (*Klages*); Potaro, 2 ♂, 1 ♀, ii.1908 (*Klages*).

VENEZUELA: Briceno, 5 ♂. *Amazonas:* Parque Nacional Dida, 1 ♂; Río Baria, dept Río Negro, 1 ♂. San Carlos de Río Negro, 1 ♂, 2 ♀. *Bolívar:* El Boninche Reserve, Forestal Imataca, 200 m, 1 ♂. El Dorado, 1 ?; El Dorado, Santa Elena, 125 km, 1100 m, 1 ♂. *Carabobo:* Las Quignas, Esteban Valley, 3 ♂; San Esteban, 3 ♂; Campo Bello, Río Zoikan, 2 ♂. *Mérida:* 7 ♂.

COLOMBIA: *Boyacá:* Muzo, 400-800 m, 8 ♂ (*Fassl*). *Cauca:* Gorgona Island, 200 ft, 1 ♀, 17.x.24 (*Collenette*). *Meta:* Buena Vista, 1 ♂; Cundinamarca, La Mesa, 1 ♂; Upper Río Negro, 800 m, 2 ♂ (*Fassl*).

AMAZONAS: 1 ♂ [holotype of *albicoma*].

PERU: *Cajamarca:* Charape River, Tabaconas, 2 ♂. *Junín:* Utcuyacu, 1 ♂. *Loreto:* Río Ampiyacu, Putomayo, 1 ♂. *Madre de Diós:* Tambopata Reserve, 30 km South West of Puerto Maldonado, 1 ♂, 16-22.x.1983 (*Covell*). *Puno:* Yahuarmayo, 1200 ft, 1 ♂, iv.1912; La Unión, Río Huacamayo, 2000 ft, 2 ♂, wet season, xi.1904 (*Ockenden*); 1 ♂, wet season, xii.1904 (*Ockenden*); 2 ♂, xi-xii.1904 (*Ockenden*); Río Huacamayo, 3100 ft, 3 ♂, dry season, vi.04 (*Ockenden*); Oconeque, 3 ♂; Quinton, 3 ♂; Santo Domingo, 6000 ft, 1 ♀, wet season, iii.02 (*Ockenden*); 2 ♂, xi.1904 (*Ockenden*); 1 ♀; Tinguri, 3400 ft, dry season, 3 ♂, 2 ♀, viii.1904 (*Ockenden*); La Oroya, Río Inambari, 3100 ft, 5 ♂, dry season, ix.1904 (*Ockenden*); 5 ♂, 1 ♀, wet season, iii.05, 5 ♂, 1 ♀ (*Ockenden*); 3 ♂, ix.05 (*Ockenden*); 4 ♂, wet season, xi-xii.1905 (*Ockenden*); 2 ♂, wet season, xii.05 (*Ockenden*); 1 ♂, 1 ♀, wet season, i.1906 (*Ockenden*).

BRAZIL: San Joas, Solimoes, 1 ♂. *Amapá:* Para, 1 ♀ (*Moss*). *Amazonas:* Fonte Boa, 1 ♂ [lectotype of *minorata*], v.1906 (*Klages*); 4 ♂, vii.06 (*Klages*); 2 ♂, ix.06 (*Klages*); 1 ♂, vii.07 (*Klages*); Teffe, 1 ♂, viii.1935 (*Moss*); 3 ♂; Sao Paulo de Olivença, 2 ♂; 1 ♀, i.1932 (*Wucherpfennig*); Rio Purus, 1 ♂, xii.1921 (*Klages*);

Rondônia: Calama, River Madeira, below River Machados, 1 ♂, viii-x.07 (*Hoffmann*).
Depositories: BMNH, CMNH, C.V. Covell Jr. collection, INBio, MNHN, NMNH, UCV.

Oospila albicoma nasuta **Warren new status**

(Figs 55, 117)

Oospila nasuta Warren, 1909: 83; Prout, 1912: 134; 1932: 58. Lectotype ♂, here designated, in BMNH. Type locality: TRINIDAD. Label data: Type; Caparo, Trinidad, Dec[ember] 1905. (S. M. Klages); Rothschild Bequest B[ritish] M[useum] 1939-1; Oospila nasuta type ♂ Warr[en]; Geometridae genitalia slide No. 15718 ♂. [Examined.]

♂ (Fig. 55). Forewing length 12 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches cream, with dark brown perimeters and striation. Forewing: with costa pale brown; blotch at apex large, rounded, extending to costa, not connected to blotch at tornus by band along termen; blotch at tornus quite large, but not extending as far as discal cell, with short digitate extension; discal spot absent. Hindwing: blotch at apex large; blotch at tornus smaller; blotch at anal margin narrow; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present; sternum A8 with emarginated posterior edge.

♂ *genitalia* (Fig. 117). As for *albicoma albicoma*.

♀ *genitalia*. Unknown.

Distribution. Only known from Trinidad.

Diagnosis. *Oospila albicoma nasuta* can be distinguished from other species with cream blotches by the form of the blotch at the tornus of the forewing: *albicoma nasuta* has a short, digitate extension of this blotch which does not occur in other species (compare Figs 14, 54 and 55).

Material examined.

TRINIDAD: *Saint George East:* Caparo, 1 ♂ [lectotype] xii.1905 (*Klages*); 1 ♂.
Depository: BMNH.

Oospila concinna **Warren**

(Figs 56, 118, 169)

Oospila concinna Warren, 1900: 136; Prout, 1912: 133; 1932: 57. Lectotype ♂, here designated, in BMNH. Type locality: VENEZUELA. Label data: Type; Merida 1630 m 97 Briceno; Rothschild Bequest B[ritish] M[useum] 1939-1. Oospila concinna ♂ Warr[en]; Geometridae genitalia slide No. 15710 ♂. [Examined.]

Oospila eminens Schaus, 1912a: 428. Lectotype ♂, here designated, in BMNH. Type locality: COSTA RICA. Label data: Paratype; Juan Vinas Costa Rica June W. Schaus; Oospila eminens Sch[aus]; Oospila eminens Sch[au]s (cotype); L.B. Prout Coll[ection] B[ritish] M[useum] 1939-643; Geometridae genitalia slide No. 15711 ♂. [Examined.] **New synonymy.**

Oospila concinna eminens Schaus; Prout, 1932: 57.

Oospila albicoma matura Prout, 1932: 57. Lectotype ♀, here designated, in BMNH. Type locality: BRAZIL. Label data: Paratype; 8.4.24 Zikau Itatiaya (Zicht); Oospila albicoma matura Prout ♀ parat[ype]; L.B. Prout Coll[ection] B[ritish] M[useum] 1939-643; Geometridae genitalia slide No. 15712 ♀. [Examined.] **New synonymy.**

♂, ♀ (Fig. 56). Forewing length 19-26 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches cream or pale brown (as in specimens formerly allocated to *eminens* and *matura*), with dark brown perimeters and striation. Forewing: with costa pale brown; blotch at apex large, sometimes connected to blotch at tornus by thin band along termen; blotch at tornus very large centrally, extending to include discal spot, with abrupt constriction towards termen (not wedge-shaped as in *depressa*, compare Figs 56 and 78); discal spot large, brown. Hindwing: blotches at apex and tornus not connected by band along termen; blotch at anal margin small, narrow; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 with emarginated posterior edge in male.

♂ *genitalia* (Fig. 118). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus extended into long, thin, weakly sclerotised process; apex rounded; ampulla short, spinulose. Anellar complex: completely surrounding aedeagus, not fused to valvae. Vinculum with strongly sclerotised, W-shaped ventral plate. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia* (Fig. 169). Sterigma approximately rectangular, with posterior edge emarginated. Bursa copulatrix: ductus bursae long, with large antrum, thin, strongly sclerotised and striated below antrum; bursa copulatrix, large, bulbous; signum small. Anterior apophyses short.

Distribution. Widely distributed in Central and South America, including Guatemala, Nicaragua, Costa Rica, Venezuela, Colombia, Peru, Bolivia and Brazil.

Diagnosis. *Oospila concinna* can be distinguished from other species with cream blotches (except *albicoma albicoma*) by the size and shape of the blotch at the tornus of the forewing. In *concinna* and *albicoma albicoma* this blotch is large towards the centre of the wing, extending over the discal spot and has an abrupt constriction towards the edge of the wing (Fig. 56). In other species with cream blotches this blotch is smaller, does not extend to cover the discal spot and is wedge-shaped, tapering evenly towards the termen and does not have an abrupt constriction.

Oospila concinna and *albicoma albicoma* are indistinguishable using their wing markings alone, although *concinna* is larger. Males of *concinna* can be distinguished by the absence of a small elliptical sclerite and brushes of long hair-like scales on sternum A2. The male genitalia of these two species are also very similar, but can be distinguished by the lack of a cornutus on the aedeagus of *concinna* and by the shape of the apex of the valva which is rounded in *concinna*, but is sculpted in *albicoma albicoma* (compare Figs 117 and 118). The female genitalia can be distinguished by the presence of a sterigma in *concinna* (compare Figs 168 and 169).

The larger size and absence of a short, digitate extension of the blotch at the tornus of the forewing distinguishes *concinna* from *albicoma nasuta* (compare Figs 55 and 56).

Material examined.

GUATEMALA: Chejel, 1 ♂, 1 ♀. *Guatemala:* Guatemala City, 1 ♀ (*Rodriguez*). *Izabel:* Cayuga, 1 ♂.

NICARAGUA: *Zelaya:* Eden, 14°0'N 84°26'W, 1 ♀, 28.v.1922 (*Wharton Huber*).

COSTA RICA: Recu de Janson, 1 ♂, 1 ♀, iv.1924. *Alajuela:* Río San Lorencito, Reserve Forestal de San Ramon, 5 km North Col. Palmarena, 800 m, 1 ♂, xi.1986 (*Chacon*). *Cartago:* Moravia de Chirripo, 100 m, 1 ♀; Tapanti, Río Grande de Orosi, 1300-1400 m, 9°46'x83°50', 1 ♂, 23.i.1985 (*Janzen & Hallwachs*); Moravia de Chirripo, 1000 m, 1 ♀, 10.v.1983 (*Janzen & Hallwachs*); Sitio, 1 ♀; Cachi, 1 ♀, 23.v.17; Juan Vinas, 1 ♂ [lectotype of *eminens*] vi. (*Schaus*); 3500 ft, 1 ♂ [paralectotype of *eminens*]; 2500 ft, ii.1911 (*Schaus*); v.1911, 1 ♀ (*Schaus*); 1 ♂ [lectotype of *eminens*]; 3 ♂ (*Schaus*); 1 ♂, i. (*Schaus*); Juan Vinas, 1 ♂, xi; 1 ♂ [paralectotype of *eminens*] (*Schaus*). *Cartago:* Sitio, 1 ♂, v. *Heredia:* La Selva Biological Station, Puerto Viejo de Sarapiqui, 40 m, 1 ♂, 1 ♀, iii.1986 (*Chavarria*); 1 ♂, ix.1987 (*Chavarria*); 2 ♂, ii.1986 (*Chavarria & Chacon*); El Angel waterfall, 1350 m, 8.2 km downhill Vara Blanca, 1 ♂, 3.i.1981 (*Janzen & Hallwachs*); 1 ♂, 22.iv.1984 (*Janzen & Hallwachs*). *Limón:* Cuatro Esquinas, Parque Nacional Tortuguero, 0 m, 1 ♂, set 1989 (*Solano*); 1 ♀, iv.1989 (*Aguillar & Solano*); Cerro Tortuguero, Parque Nacional Tortuguero, 0-100 m, 1 ♀, 30.v.1984 (*Janzen & Hallwachs*); 100 m, 1 ♂, x.1989 (*Solano*); 100 m, 1 ♂, iv.1989 (*Aguillar & Solano*); Guapiles, 1 ♂. *Puntarenas:* Fila Esquinas, 35 km South of Palmar Norte, 150 m, 8°45'x83°20', 2 ♂, 1 ♀, 7-8.i.1983 (*Janzen & Hallwachs*). *San José:* Estacion Carrillo, Parque Nacional Braulio Carrillo, 700 m, 1 ♀, vii.1984 (*Chacon*); 1 ♂, x.1984 (*Chacon*); 1 ♀, ix.1984 (*Chacon*); 1 ♂, iii.1985 (*Chacon*); 2 ♂, vi.1985 (*Chacon*); La Montura, Braulio Carrillo National Park, 1100 m, 3 ♂, 17.xii.1981 (*Janzen & Hallwachs*); Estacion Bijagual, 500 m, Reserve Biologica Carara, 1 ♂, xi.1989 (*Zuniga*); Carrillo, 1 ♀; La Fuente, Turrialba, 3 ♂. *Osa Peninsula:* Corcovado National park, 1 ♂, 13-22.iii.1980 (*Janzen & Hallwachs*).

VENEZUELA: Hotel La Mantana, La Grita, Tachira, 2040 m, 1 ♀. San Esteban, 3 ♂, vi.1909 (*Klages*). *Aragua:* Rancho Grande, 1100 m, 2 ♂, 2 ♀; 1 ♂, 22-23.vi.1984 (*Covell*); 1 ♂, 12.vii-16.viii.1976 (*Watson*); 1 ♂, 14.vii.1975 (*Pliske*). *Bolívar:* Ptari-tepui, 1 ♂. *Mérida:* Mérida, 1630 m, 1 ♂ [lectotype of *concinna*] 1897 (*Briceno*); 1 ♂, iv.99 (*Briceno*); 4 ♂ [paralectotypes of *concinna*] (*Briceno*); 4 ♂, 1 ♀ (*Briceno*);

Mérida: 7 ♂, 1 ♀. *Carabobo:* Las Quignas, Esteban Valley: 1 ♂, xi-iii.10; 2 ♂, 1914; 1 ♂ (*Klages*); 2 ♂, vi.19 (*Klages*); 1 ♂, 2 ♀.

COLOMBIA: *Cundinamarca:* La Mesa, 4000 ft, 1 ♂, v-vi.1920 (*Hall*). *Meta:* Upper Río Negro, 800 m, 1 ♂ (*Fassl*). *Nariño:* West Colombia, Altaquer, 500 m, 1 ♀, iii-vi.1927.

PERU: *Cajamarca:* River Tabaconas, North Peru, 6000 ft, 3 ♂, 1 ♀, 1912 (*Pratt & Pratt*); Charapo River, Tabaconas, 4000 ft, 1 ♂, 1912 (*Pratt*); 600 ft, 1 ♂, 1912 (*Pratt & Pratt*). *Junín:* Utcuyacu, 5000 ft, 1 ♂, xii.ii.1920 (*Watkins*). *Puno:* La Oroya, Río Inambari, S.E Peru, 3100 ft, 1 ♂, 1 ♀, dry season, ix.1904 (*Ockenden*); 3 ♂, 1 ♀, wet season, iii.05 (*Ockenden*); 1 ♂, v.1905 (*Ockenden*); San Gaban, 2500 ft, 2 ♂, iii-iv.1913; Oconeque, 7000 ft, 1 ♂, ii.1905 (*Ockenden*); 1 ♂, dry season, vii.1904 (*Ockenden*); 3 ♂, ii.1905 (*Ockenden*); Santo Domingo: 6000 ft, 1 ♂, wet season, xi.01 (*Ockenden*); 4500 ft, 1 ♂, dry season, vi.02 (*Ockenden*); 6000 ft, 2 ♀, dry season, vi.02 (*Ockenden*); 1 ♂, 1 ♀, dry season, vii.02 (*Ockenden*); 6500 ft, 1 ♀, viii.02 (*Ockenden*); 1 ♂, xi.1904 (*Ockenden*); Tinguri, 3400 ft, 1 ♂, wet season, i.1905 (*Ockenden*); Quinton, 5000 ft, 2 ♂, 1905 (*Ockenden*).

BOLIVIA: *La Paz:* Chulumani, 2000 m, 2 ♂, wet season, 1.i (*Simons*); Río Songo, 3 ♂.

BRAZIL: Espirito Santo, 4 ♂, 1 ♀; 1 ♀ (*Smith*); Campo Bello, Rio Zikan, 3 ♂. *Amazonas:* Fonte Boa, 1 ♀, vii.1906 (*Klages*); Hyntanahan, Rio Purus, 1 ♂, ii.1922 (*Klages*); 1 ♀, iv.1922 (*Klages*). *Rio de Janeiro* Zikau, Itatiaia, 1 ♀ [lectotype of *albicoma matura*] 8.iv.24 (*Zicht*). *Santa Catarina:* Jaraguá do Sul, 1 ♂, ix.1932 (*Hoffmann*); 1 ♂, xii.1933 (*Hoffmann*); 1 ♂, xii.1934 (*Hoffmann*); Rio Laeiss, Blumenau, 3 ♂, xii.1933 (*Hoffmann*). *Sao Paulo:* Alto da Serra, 800 m, 1 ♀ (*Jones*); 1 ♂, 3.xii.1912 (*Jones*); Alto da Serra, Sao Paulo, 1 ♂, xi.1922 (*Spitz*); 2 ♂, i.1923 (*Spitz*); 1 ♂, xii.1923 (*Spitz*); 1 ♀, iii.1924 (*Spitz*); 1 ♀, xii.1924 (*Spitz*); 1 ♀, ii.1928

(*Spitz*); Serra do Mar, 1 ♀ (*Wucherpfennig*); Boraceia, 1 ♂, 3.xi.1984 (*Ebert*).
UNKNOWN: 1 ♂, 1 ♀.
Depositories: BMNH, CMNH, INBio, NMNH, UCV.

Oospila dicraspeda Prout

(Figs 57, 119, 170)

Oospila dicraspeda Prout, 1932: 56. Lectotype ♂, here designated, in BMNH. Type locality: BRAZIL. Label data: Type; Brésil Prov[ince]. Mato Grosso. P. Germain 1886; Ex. Oberthür Coll[ection] Brit[ish] Mus[eum] 1927-3; Oospila dicraspeda ♂ Prout type; Geometridae genitalia slide No. 15705 ♂. [Examined.]

♂, ♀ (Fig. 57). Forewing length 9-10 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches brown, slightly paler at centres. Forewing: with costa pale brown; subapical blotch small, connected to blotch at tornus by band along termen; blotch at tornus small; discal spot small, brown. Hindwing: with blotches at apex and tornus small, connected by band along termen; blotch at anal margin absent; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 119). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: divided apically; sacculus extended into large, robust projection with pointed tip; ampulla absent. Anellar complex: completely surrounding aedeagus, not fused to valvae.

Vinculum with V-shaped ventral plate. Coremata absent. Aedeagus with small cornutus on vesica and larger, blunt medial extension.

♀ *genitalia* (Fig. 170). Sterigma approximately triangular. Bursa copulatrix: ductus bursae long, with long antrum; strongly sclerotised, and striated below antrum; corpus bursae large, approximately spherical; signum small. Anterior apophyses short.

Distribution. Specimens were examined from Costa Rica, Peru and Brazil.

Diagnosis. *Oospila dicraspeda* is very similar in external appearance to *confluaria* from which it may be distinguished by the absence of a brown discal spot on the hindwings (compare Figs 57 and 62). Males can also be distinguished by the absence of a brush of long hair-like scales on the hind tibia and the absence of an ampulla in the genitalia (compare Figs 119 and 124). Females may be distinguished by the shape of the sterigma (compare Figs 170 and 174). The presence of small blotches at, or posterior to, the apex and tornus of the fore- and hindwings distinguish *dicraspeda* from *pellucida* (compare Figs 20 and 43).

Material examined.

COSTA RICA: *Guanacaste:* Casa Oeste, Cerro El Hacha, 12 km South East La Cruz, 300 m, 1 ♂, i.1988 (*Chacon*); Santa Rosa National Park, 1 ♀, 2-11.iii.1980 (*Janzen & Hallwachs*); 1 ♂, 9-11.v.1980 (*Janzen & Hallwachs*); 1 ♂, 8-10.vi.1980 (*Janzen & Hallwachs*); 2 ♂, 1-15.i.1982 (*Janzen & Hallwachs*); 1 ♀, 10-20.iii.1982 (*Janzen & Hallwachs*); 2 ♂, 1 ♀, xii.1982 (*Janzen & Hallwachs*); 300 m, 4 ♂, 6 ♀, i.1983 (*Janzen & Hallwachs*); 1 ♂, 30.vi.1983 (*Janzen & Hallwachs*); 1 ♂, i.1984 (*Janzen & Hallwachs*); 4 km E Casetilla, Rincon National Park, 750 m elevation, 1 ♂, 11.iv.1983 (*Janzen & Hallwachs*).

PERU: 1 ♂ (*Mathan*).

BRAZIL: *Mato Grosso:* 1 ♂ [lectotype] 1886 (*Germain*); 7 ♂ [paralectotypes].

Depositories: BMNH, INBio.

Oospila ciliaria (Hübner)

(Figs 58, 120, 171)

[*Phalaena Geometra marginaria* Stoll (1787-1790, title page dated 1791): 156, pl. 34, fig. 8. Homonym of *marginaria* Fabricius; Prout, 1912: 133.]

[*Phalena marginaria* (Stoll); Verloren, 1837: 269.]

[*Comibaena (?) marginaria* (Stoll); Walker, 1861: 570.]

Eucrostes ciliaria Hübner, 1823: 283. Holotype: unknown. [Not examined.]

Oospila ciliaria (Hübner); Prout, 1912: 133; 1932: 56.

Phorodesma ? semialbaria Guenée, 1857: 372. Holotype: sex and depository unknown. Type locality: Brazil. [Not examined.] Synonomised with *Oospila ciliaria* (Hübner) by Guenée, 1857: 372.

Racheolopha pallida Warren, 1906: 426. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. French Guiana: Maroni R[iver], Saint Jean, viii.1904; Schaus coll[ection]; Type No. 9198 U.S.N.M; Genitalia Slide By MAC 57726 USNM. [Examined.] **New synonymy.**

Oospila pallida (Warren); Prout, 1912: 133.

Oospila ciliaria pallida (Warren); Prout, 1932: 56.

♂, ♀ (Fig. 58). Forewing length 12-15 mm. Antenna of female bipectinate. Frons and vertex red. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour pale bluish green; blotches absent; markings pink. Forewing: with narrow band along termen; discal spot small, faint, brown. Hindwing: as forewing. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male, unusually, also with deciduous setae in male; sternum A8 with emarginated posterior edge in male.

♂ *genitalia* (Fig. 120). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: narrow, digitate; sacculus extended into short, pointed process; ampulla short, thin and spinulose at apex. Anellar complex: completely surrounding aedeagus, not fused to valvae. Vinculum with ventral plate squarish. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia* (Fig. 171). Sterigma absent. Bursa copulatrix: ductus bursae long, strongly sclerotised and striated, antrum absent; corpus bursae medium sized, approximately spherical; signum small. Anterior apophyses short.

Distribution. Only known from the north west of South America, this species has been collected in French Guiana, Guyana and Brazil.

Diagnosis. Although the pattern of the wing markings is somewhat similar to that of *euchlora* and *pellucida*, *ciliaria* can be distinguished by the colour of its wings and markings. The wings of *ciliaria* have a very pale blue-green ground colour and brick-red markings. The red colour of the frons, vertex and abdominal crests also distinguishes *ciliaria* from other species of *Oospila*.

Material examined.

BRAZIL: *Amazonas:* Fonte Boa, 1 ♂, vii.1906 (*Klages*).

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♂ [holotype of *pallida*]; 1 ♂, vii (*Le Moult*); 5 ♂, 1 ♀ (*Le Moult*); 2 ♂; Mana River, 1 ♀, v.1917.

GUYANA: *Mazaruni-Potaro:* Kartabo, Bartica District, 1 ♂; Omai, 2 ♂, vi.1908 (*Klages*); Potaro, 4 ♂, ii.1908 (*Klages*); 3 ♂, v.1908 (*Klages*); Potaro, 1 ♀; Tumatumari, 1 ♂, ii.1907 (*Klages*); 1 ♂ ii.1908 (*Klages*).

Depositories: BMNH, NMNH.

The *trilunaria* group

The *trilunaria* group is a monophyletic group defined by the form of the anellar complex. In the *trilunaria* group, the transtillae are short arms, fused with the posterior of the anellar complex. The juxta forms a long, strongly sclerotised support to the aedeagus. The basal part of the anellar complex usually has a short dorsal projection which also supports the aedeagus. Two smaller groups, the *marginata* group and the *atopochlora* group are recognised within the *trilunaria* group.

Oospila trilunaria (Guenée)

(Figs 59, 121, 172)

Phorodesma trilunaria Guenée, 1857: 372. Holotype ♂, in BMNH. Type locality: BRAZIL. Label data: B[razil]; Ex Musaeo Ach Guenée; Typicum Specimen; Phorodesma trilunaria guenée. Sp. G. no [5]94. type; 3238 [Figure]; Ex Oberthür Coll[ection] Brit[ish] Mus[eum] 1927-3; Geometridae genitalia slide No. 15756 ♂. [Examined.]

Comibaena trilunaria (Guenée); Walker, 1861: 570.

Oospila trilunaria (Guenée); Warren, 1897: 426; Prout, 1912: 132; 1932: 56.

♂, ♀ (Fig. 59). Forewing length 15-22 mm. Antenna of female bipectinate. Frons green, vertex green dorsally, cream ventrally. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches cream, with dark brown perimeters and some dark striation. Forewing: with costa pale brown; subapical blotch approximately circular, not connected to blotch at tornus by line along termen; blotch at tornus large, approximately circular; discal spot large, brown. Hindwing: blotch at apex absent; blotch at tornus approximately circular; blotch at anal margin absent; anterior discal spot small, white; posterior discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 deeply emarginated in male, with two posterior extensions, serrated on facing margins.

♂ *genitalia* (Fig. 121). Uncus with apical extension short, pointed. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace. Valvae: with shallow apical division; sacculus not extended; ampulla broad and flattish, robust, with denticulate apex. Anellar complex: completely surrounding aedeagus, with posterior extensions fused to valvae. Vinculum with narrow W-shaped ventral plate. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia* (Fig. 172). Sterigma approximately circular. Bursa copulatrix: ductus bursae quite broad, quite long, with short, narrow antrum, weakly sclerotised, not striated below antrum; corpus bursae large and bulbous; signum small. Anterior apophyses short.

Distribution. Only known from Brazil.

Diagnosis. *Oospila trilunaria* can be distinguished by the approximately circular shape of its blotches and by their distribution on the wings (Fig. 59). The male genitalia of *trilunaria* can be recognised by the shape of the ampulla (Fig. 121). The male sternum A8 also has a distinctive shape in this species.

Remarks. Type-species of the genus.

Material examined.

BRAZIL: Friburgo, 1 ♀. 1 ♂ [holotype]. Campo Bello, Rio Zilcan, 4 ♂, 1 ♀. Rio, 1 ?. *Rio de Janeiro:* Corcovado, 1 ♀, ii.1910; Rio de Janeiro: 2 ♂. *Santa Catarina:* Nova Brémen, Rio Laeiss, 1 ♂, 1 ♀, iii.1936 (*Hoffmann*); Nova Brémen, 250 m, 1 ♂, x.37 (*Hoffmann*); Blumenau, 1 ♂, 26.iv.29 (*Schade*); Rio Vermehlo, 850 m, 1 ♂, iii.37 (*Hoffmann*); 1 ♂, iv.37 (*Hoffmann*);

Depositories: BMNH, NMNH.

Oospila carnelunata (Warren)

(Figs 6, 60, 122, 173)

Racheolopha carnelunata Warren, 1906: 421. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. Label data: S[ain]t Jean, Maroni, F[rench] Guiana; Racheolopha carnelunata type ♂; Type No. 9187 U.S.N.M; Collection Wm Schaus; Genitalia Slide By MAC 57756 USNM. [Examined.]

Oospila carnelunata (Warren); Prout, 1932: 56.

♂, ♀ (Fig. 6, 60). Forewing length 11-12 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches cream, with dark brown perimeters and some brown striation. Forewing: with costa pale brown; blotch at apex not extending to costa, not connected to blotch at tornus by band along termen; blotch at tornus small; discal spot small, brown. Hindwing: blotch at apex dark brown anteriorly, paler where expanded posteriorly; blotch at tornus small; anterior discal spot small, white; posterior discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales present on male tibia. Abdomen: with cream area around crests enclosed by thin pink line, remainder of dorsal surface green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 122). Uncus with apical extension short, blunt. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: divided apically; sacculus extended slightly into short, pointed process; ampulla narrow, with short, blunt, subapical process. Anellar complex: completely surrounding aedeagus; posterior extensions fused to valvae. Vinculum with ventral plate V-shaped. Coremata absent. Aedeagus with two apical cornuti on vesica.

♀ *genitalia* (Fig. 173). Sterigma with two short, stubby, posteriorly directed pockets. Bursa copulatrix: ductus bursae short, weakly sclerotised, not striated, antrum absent; corpus bursae large, bulbous; signum small. Anterior apophyses, unusually, absent.

Distribution. Material was examined from French Guiana, Surinam, Venezuela, Peru, Bolivia and Brazil.

Diagnosis. The wing markings of *carnelunata* are fairly distinctive. This species can be distinguished from *marginata*, *obsolescens* and *tricamerata* by the larger size of the blotch at the apex of the hindwing in *carnelunata* (compare Figs 11, 13, 60, 69, 70 and 71). *Oospila carnelunata* can be distinguished from *confluaria* by the paler colour of its markings (compare Figs 60 and 62). The male genitalia of *carnelunata* can be recognised by the shape of the ampulla (Fig. 122). The female genitalia can be recognised by the distinctive arrangement of pockets surrounding the ostium and by the absence of anterior apophyses (Fig. 173).

Remarks. A specimen in the BMNH collection was labelled by Prout as the type of *Oospila vetita*. However, this name was never published.

Material examined.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♂ [holotype].

SURINAM: Geldersland, Surinam River, 1 ♀.

VENEZUELA: 1 ♀.

PERU: *Loreto:* Lago Yarina-Cocha, Loreto, 1 ♂

BOLIVIA: Río Songo, 750 m, 1 ♂.

BRAZIL: *Amazonas:* Fonte Boa, 1 ♂, ix.06 (*Klages*).

Depositories: BMNH, NMNH.

Oospila altonaria Jones

(Figs 61, 123)

Oospila altonaria Jones, 1921: 349; Prout, 1932: 56. Holotype ♂, in BMNH. Type locality: BRAZIL. Label data: Type; Alto da Serra Santos 800 m. 10 Mar[ch] 1913 E.D. Jones; Oospila altonaria Type ♂ D. Jones; E.D. Jones Coll[ection] Brit[ish] Mus[eum] 1919-295; Geometridae genitalia slide No. 15706 ♂. [Examined.]

♂ (Fig. 61). Forewing length 14-16 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent. Forewing: with costa pale brown; unmarked, except for large, prominent, brown discal spot. Hindwing: unmarked, except discal spots; anterior discal spot small, white; posterior discal spot large, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with cream area around crests enclosed by thin pink line, remainder of dorsal surface green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised, with bifurcate apical extension.

♂ *genitalia* (Fig. 123). Uncus with apical extension short, blunt. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: divided apically; sacculus extended into short, pointed process; costal margin bearing a pointed projection at base; ampulla short, robust, with denticulate apex. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with V-shaped ventral plate, with medial extension. Coremata absent. Aedeagus with small cornutus on vesica.

♀ *genitalia*. Unknown.

Distribution. Only known from the Sao Paulo province of Brazil.

Diagnosis. The large, brown discal spots on all the wings distinguish *altonaria* from other species of *Oospila* with little marking on their wings (Fig. 61). The male genitalia of *altonaria* can be recognised by the pointed extension of the base of the costal edge of the valva and by the shape of the ampulla (Fig. 123).

Material examined.

BRAZIL: *Sao Paulo:* Alto da Serra, Santos, 800 m, 1 ♂ [holotype] 10.iii.1913 (*Jones*); 2 ♂, xi.1922 (*Spitz*); 1 ♂, 31.viii.24 (*Spitz*).

Depository: BMNH.

Oospila confluaria (Warren)

(Figs 62, 124, 174)

Racheolopha confluaria Warren, 1906: 422. Holotype ♂, in NMNH. Type locality; FRENCH GUIANA. Label data: French Guiana: Maroni R[iver], Saint Jean, iii.1904; Schaus Coll[ection]; USNM Type No. 9189; Genitalia slide by MAC No. 57720. [Examined.]

Oospila confluaria (Warren); Prout, 1932: 56.

Oospila mesocraspeda Prout, 1912: 134. Holotype ♀, in BMNH. Type locality: PANAMA. Label data: Type; La Choerra. Panama. 1 IV to 15 V 98. C.H. Dolby-

Tylor 98-146; Oospila mesocraspeda type Prout; Geometridae genitalia slide No. ♀ 15696. [Examined.] **New synonymy.**

Oospila confluaria mesocraspeda Prout, 1932: 56.

♂, ♀ (Fig. 62). Forewing length 11-14 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches dark brown, with paler centres. Forewing: with costa pale brown; subapical blotch small, connected to apex and to blotch at tornus by band along termen; blotch at tornus small; discal spot small, brown. Hindwing: blotch at apex narrow, connected to blotch at tornus by band along termen, blotch at tornus small; blotch at anal margin absent; anterior discal spot small, white; posterior discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales present on male tibia. Abdomen: with pink area around crests, remainder of dorsal surface green or cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 124). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: divided apically; sacculus extended into short, pointed process; ampulla long, thin, digitate. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate V-shaped. Coremata absent. Aedeagus with large cornutus on vesica.

♀ *genitalia* (Fig. 174). Sterigma distinctively shaped (Fig. 174). Bursa copulatrix: ductus bursae with large antrum, wide, strongly sclerotised and striated below antrum; corpus bursae large, squarish; signum small. Anterior apophyses short.

Distribution. Specimens were examined from Costa Rica, Panamá, French Guiana, Surinam, Guyana, Colombia and Brazil.

Diagnosis. *Oospila confluaria* can be distinguished from *sellifera* by its much narrower brown band along the termen, especially in the hindwings (compare Figs 62 and 64). Females can be distinguished from *sellifera* by the antennae which are bipectinate in *confluaria*.

The presence of a brown discal spot on the hindwings distinguishes *confluaria* from *dicraspeda* (compare Figs 57 and 62). Males can also be distinguished by the presence of a brush of long hair-like scales on the hind tibia of *confluaria*.

The expansion of the brown markings into blotches distinguishes *confluaria* from *pellucida* (compare Figs 20 and 62) and the uniformly dark colour of the markings distinguishes *confluaria* from *carnelunata* (compare Figs 60 and 62).

The female genitalia of *confluaria* can be recognised by the distinctive shape of the sterigma (Fig. 174).

Material examined.

COSTA RICA: 1 ♂, 2 ♀. *Guanacaste:* 4 km West Santa Cecilia, 250 m, 1 ♂, 25.ii.1985 (*Janzen & Hallwachs*).

PANAMA: La Choerra, 1 ♀ [holotype of *mesocraspeda*] 1.iv-15.v.98 (*Dolby-Tylor*). *Canal Zone:* Barro Colorado Island, 1 ♀.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♂, v. (*Le Moult*); 6 ♂, 1 ♀ (*Le Moult*); Saint Jean du Maroni, 1 ♂ [holotype of *confluaria*] iii.1904; 3 ♂, 2 ♀; Saint Laurent du Maroni, 1 ♀; Maroni river, 1 ♂. 1 ♂, 1916 (*Knudsen*).

SURINAM: *Marowijne:* Aroewarwa Creek, Maroewym Valley, 1 ♂, v.05 (*Klages*).

GUYANA: *Mazaruni-Potaro:* Potaro, 1 ♀, ii.1908 (*Klages*).

COLOMBIA: *Meta:* Upper Río Negro, 800 m, 1 ♀ (*Fassl*).

BRAZIL: *Amapá:* Para, 1 ♂ (*Moss*).

Depositories: BMNH, INBio, NMNH.

Remarks. One of the specimens in the NMNH bears a printed label with "Orizaba, Mex" and a handwritten label with "S[ain]t Jean, FRENCH GUIANA". Since only one other species of *Oospila* occurs in Mexico and there have been no other records of *confluaria* occurring north of Costa Rica, the Mexican record seems rather unlikely.

Oospila longipalpis (Warren)

(Figs 63, 125, 175)

Racheolopha longipalpis Warren, 1906: 425. Holotype ♀, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: Maroni R[iver], S[ain]t Jean; Schaus Coll; Type No. 9196 U.S.N.M. [Examined.]

Oospila longipalpis (Warren); Prout, 1912: 134; 1932: 55.

♂, ♀ (Fig. 63). Forewing length 13-20 mm. Antenna of female unknown. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches absent; markings dark brown. Forewing: with costa pale brown; with band along termen narrow at apex, not extending to costa, broadening posteriorly, widest at tornus; discal spot very small, dark brown. Hindwing; with band along termen, widest at apex and tornus; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales present in male. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 125). Uncus with apical extension very short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: divided apically; sacculus with very short, pointed extension; ampulla short, forked at apex. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum: ventral plate U-shaped; with short ventral projection. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia* (Fig. 175). Sterigma square with central hole surrounding ostium. Bursa copulatrix: ductus bursae long, with long antrum; thin, strongly sclerotised and striated below antrum; corpus bursae quite small, bulbous; signum small. Anterior apophyses short.

Distribution. Only known from two specimens, both from French Guiana.

Diagnosis. *Oospila longipalpis* can be distinguished from *sellifera* by its exceptionally long labial palpi, by the shape of the brown markings (compare Figs 63 and 64) and by the absence of a brown discal spot on the hindwings. The absence of white speckling within the brown markings distinguishes *longipalpis* from *lilacina* (compare Figs 63 and 65). The male genitalia of *longipalpis* can be recognised by the shape of the ampulla (Fig. 125).

Material examined.

FRENCH GUIANA: 1 ♂; *Guyane:* Saint Jean du Maroni, 1 ♀ [holotype].

Depositories: BMNH, NMNH.

Oospila sellifera Warren

(Figs 64, 126, 176)

Oospila sellifera Warren, 1906: 420; Prout, 1912: 134; 1932: 55. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: Maroni R[iver], S[ain]t Jean, vii.1904; Schaus Coll[ection]; Type No. 9186, USNM. [Examined.]

♂, ♀ (Fig. 64). Forewing length 10-13 mm. Antenna of female simple. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings dark brown. Forewing: with costa pale brown; subapical blotch large, connected to blotch at tornus by broad band along termen; blotch at tornus large, extending along 1/2 of anal margin; discal spot small, brown. Hindwing: blotch at apex large, connected to blotch at tornus by broad band along termen; blotch at tornus large, extending along approximately 1/2 of anal margin; blotch at anal margin small, narrow; anterior discal spot small, white; posterior discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales present in male. Abdomen: with white area around crests enclosed by thin pink line, sometimes with pink or white spot anterior of crests, remainder of dorsal surface green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised in male, with bifurcate posterior extensions.

♂ *genitalia* (Fig. 126). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with deep apical division; sacculus extended into pointed process; ampulla double, as two long, thin, pointed projections on each valva. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate squarish. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia* (Fig. 176). Sterigma with posterior edge bearing two pointed extensions. Bursa copulatrix: ductus bursae long, with short antrum; wide, strongly sclerotised and striated below antrum; corpus bursae squarish, marginally wider than ductus; signum small. Anterior apophyses quite long.

Distribution. Material was examined from French Guiana, Guyana, Venezuela, Peru and Brazil.

Diagnosis. *Oospila sellifera* can be distinguished from *lilacina* by the absence of white dots within the brown areas of the wings (compare Figs 64 and 65). The presence of a single discal spot on the hindwings of *sellifera*, and the simple antennae of the females also distinguish these two species.

The presence of distinct blotches on the hindwings of *sellifera*, distinguish it from *violacea* in which the blotches are merged and the brown colour is more suffuse (compare Figs 64 and 66).

The male genitalia of *sellifera* can be recognised by the presence of a double ampulla on each valva (Fig. 126). The female genitalia can be recognised by the shape of the sterigma (Fig. 176).

Material examined.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♂, 1 ♀ (*Le Moult*); Maroni River, Saint Jean du Maroni, 1 ♂ [holotype]; 1 ♀.

GUYANA: 1 ♂.

VENEZUELA: Río Baria, 140 m, 0°55'N 66°10'W, 1 ♂, 25.xii.xi-4.1984 (*Osuna & Chacon*); Cerro de la Neblina, Basecamp, 4 ♂, 3 ♀. *Amazonas:* San Carlos de Río Negro, 125 m, 1 ♂, 19-31.viii.1976 (*Salcedo & Fernandez*). *Lara:* Guárico, Hato Masaguaral, 45 km South of Calabozo, 1 ♂.

PERU: *Loreto:* Contamana, Río Ucayali, 2 ♂, x-xii.1912.

BRAZIL: *Amapá:* Para: Cachimbo, Altitude 400 m, 1 ♀, 13/20.vii.55 (*Travossos, Olivera & Pearson*). *Distrito Federal:* Planaltina, 15°35'S 47°42'W, 1000 m, 1 ♀, 25.ix.1985, 1 ♀.*Goiás:* Formosa, Goiás, 800 m, 1 ♂, 15.x.1976; *Pará:* Unt. Amaz. Taperhina, below Santarem, 1 ♂, 21-31.vii.27 (*Zerny*).
Depositories: BMNH, NMNH, UCV, V. O. Becker collection.

Oospila lilacina (Warren)

(Figs 65, 127, 177)

Racheolopha lilacina Warren, 1906: 424. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: Maroni R[iver], S[ain]t Jean, vii. 1904; Schaus Coll[ection]; Type No. 9195 U.S.N.M. [Examined.]

Oospila lilacina (Warren); Prout, 1912: 134; 1932: 55.

♂, ♀ (Fig. 65). Forewing length 14-22 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings dark brown with white flecks. Forewing: with costa pale brown; subapical blotch large, connected to blotch at tornus by broad band along termen; blotch at tornus large, extending along 2/3 of anal margin; discal spot small, brown. Hindwing: blotch at apex large, connected to blotch at tornus by broad band along termen; blotch at tornus large, extending along 1/2 anal margin; blotch at anal margin absent; wing base white; anterior discal spot small, white; posterior discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales present on male tibia. Abdomen: with dorsal surface around crests cream or green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male;

sternum A8 strongly sclerotised in male, with bifurcate posterior extension, with expanded, rounded apices.

♂ *genitalia* (Fig. 127). Uncus with apical extension short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace present. Valvae: with shallow apical division; sacculus extended into short, thin, pointed projection; ampulla broad, rounded, with denticulate apex and extending just beyond edge of valva. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate V-shaped. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia* (Fig. 177). Sterigma squarish, denticulate at anterior end. Bursa copulatrix: ductus bursae with short, cone-shaped antrum, strongly sclerotised and striated below antrum; corpus bursae approximately spherical; signum small. Anterior apophyses short.

Distribution. Specimens were examined from Guatemala, Nicaragua, Costa Rica, French Guiana, and Brazil.

Diagnosis. *Oospila lilacina* can be distinguished from *longipalpis*, *sellifera* and *violacea* by the presence of white flecks within the brown markings (compare Figs 9, 63, 64, 65 and 66). *Oospila lilacina* also has two white discal spots on the hindwing, whereas *sellifera* only has one. *Oospila lilacina* is also distinguished from *violacea* by its larger size and by its more extensive brown areas. The female genitalia of *lilacina* can be recognised by the shape of the sterigma (Fig. 176).

Material examined.

GUATEMALA: 2 ♂, 1 ♀.

NICARAGUA: *Zelaya:* Eden, 14°0'N 84°26'W, 1 ♂, 24.iii.1922 (*Wharton-Huber*).

COSTA RICA: 3 ♂, 4 ♀. *Alajuela:* Finca Campana, 5 km North West Dos Rios, 750

m, 1 ♂, 21.iii.1985 (*Janzen & Hallwachs*). Finca San Gabriel (16 km East North East Quebrada Grande); 650 m, 1 ♂, 11.ix.1988 (*Janzen & Hallwachs*). *Guanacaste:* Estacion Pitilla, 700 m, 9 km South of Santa Cecilia, 1 ♂. *Heredia:* La Selva Biological Station, Peurto Viejo de Sarapiqui, 1 ♂, iv.1987 (*Chavarria*). *Puntarenas:* Fila Esquinas, 35 km South of Palmar Norte, 150 m elevation, 8°45' x 83°20', 3 ♀, 7-8.i.1983 (*Janzen & Hallwachs*); 2 ♂ (*Janzen & Hallwachs*). *San José:* Estacion Carrillo, Parque Nacional Braulio Carrillo, 700 m, 1 ♀, ix.1984 (*Chacon*); 1 ♂.
FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♂ [holotype]; 2 ♂, ix. (*Le Moult*); 1 ♂. Nouveau Chantier, 2 ♂ (*Le Moult*); 2 ♂.
BRAZIL: *Amazonas:* Nova Olinda, Rio Purus, 1 ♂, v.1922 (*Klages*).
Depositories: BMNH, CMNH, INBio, NMNH.

Oospila violacea Warren

(Figs 9, 66, 128, 178)

Oospila violacea Warren, 1897: 427; Prout, 1912: 133. Holotype ♀, in BMNH. Type locality: GUYANA. Label data: Type; Rio Demerara; Rothschild Bequest B[ritish] M[useum] 1939-1; Oospila violacea type ♀ Warren; Geometridae genitalia slide No. 15709 ♀. [Examined.]

♂, ♀ (Figs 9, 66). Forewing length 13-15 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green in fresh specimens, rapidly fading to yellow. Forewing: with costa pale brown; subapical blotch small, not connected to blotch at tornus by band along termen; blotch at tornus small; discal spot small, brown. Hindwing: largely brown, but with green area at base of wings; anterior discal spot small, white; posterior discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised with bifurcate posterior extension.

♂ *genitalia* (Fig. 128). Uncus completely reduced. Socii reduced. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus extended into blunt process; ampulla with origin close to base of valva, long, thin, digitate, with denticulate apex. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum: ventral plate V-shaped; with short ventral projection. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia* (Fig. 178). Sterigma: large, rectangular, with central raised section. Bursa copulatrix: ductus bursae long, with large antrum, strongly sclerotised and striated below antrum; corpus bursae large, bulbous; signum small. Anterior apophyses short.

Distribution. This species occurs in French Guiana, Surinam, Guyana, Peru and Brazil.

Diagnosis. *Oospila violacea* can be distinguished from *lilacina* by the absence of white flecks in the brown markings (compare Figs 9, 65 and 66). The absence of distinct blotches on the hindwings and the more suffuse brown markings distinguish *violacea* from *sellifera* (compare Figs 9, 64 and 66). The female genitalia of *violacea* can be recognised from the shape of the sterigma (Fig. 178).

Material examined.

FRENCH GUIANA: *Guyane:* Saint Laurent du Maroni, vi.1915, 1 ♂. Saint Jean du Maroni, 8 ♂, 7 ♀; 2 ♂, 3 ♀ (*Le Moult*); 1 ♀, vi. (*Le Moult*); 2 ♀, 1 ?, ii. (*Le Moult*); 1 ♂, x. (*Le Moult*); Nouveau Chantier, 1 ♂, vii. (*Le Moult*); 1 ♀.

SURINAM: *Marowijne:* Aroewarwa Creek, Maroewym valley, 1 ♀, vii.1905 (*Klages*).

GUYANA: *Mazaruni-Potaro:* Essequebo River, Moraballi Creek, 1 ♀, 28.vii.29 (*Oxford University Expedition*). Potaro River, 1 ♀, 9-13.vii.1912 (*Rendall*); Omai, 1 ♀; Rockstone, Essequebo, 1 ♀. *East Demerara-West Coast Berbice:* Demerara River, 1 ♀ [holotype]; Potaro, 2 ♂, 2 ♀, v.1908 (*Klages*).

PERU: 1 ♂ (*Mathan*).

BRAZIL: Rio Madeira, 1 ♂. 1 ♂ (*Germain*). *Amazonas:* Fonte Boa, 1 ♀, vi.06 (*Klages*); 1 ♀, vii.06 (*Klages*); 4 ♀, viii. (*Klages*). *Mato Grosso:* 5 ♂, 1886 (*Germain*); 4 ♂ (*Germain*); Burity, 30 miles North East of Cuyaba, 1 ♂, 16-22.x.27 (*Collenette*). *Puno:* Monte Cristo, Tapajós, 1 ♂; Nova Olinda, Rio Purus, 2 ♀, vi.1922 (*Klages*). *Depositories:* BMNH, NMNH.

Oospila callicula (Druce)

(Figs 67, 129, 179)

Comibaena callicula Druce, 1892: 88. Holotype ♂, in Staudinger museum. Type Locality: PANAMA. Label data: Panama: Chiriqui (Trötsch). [Not examined.]

Oospila callicula (Druce); Prout, 1912: 133; 1932: 58.

Oospila callicula stenobathra Prout, 1932: 58. Holotype ♂, in BMNH. Type locality: BOLIVIA. Label data: Type; 39. 27. Mutum, 20 miles W[est] of Porto Saurez, 1500 ft., 7-14.xi.27. Bolivia C. L. Collenette; 2982; Oospila callicula stenobathra ♂ type Prout; At light; Joicey Bequest. Brit[ish] Mus[eum] 1934-120; Geometridae genitalia slide No. 15692 ♂. [Examined.] **New synonymy.**

Oospila callicula orchardae Prout, 1932: 58. Holotype ♀, in BMNH. Type locality: BRAZIL. Label data: Type; Maranhao, N[orth] E[ast] Brazil. (Miss Orchard); Rothschild Bequest B[ritish] M[useum] 1939-1; Oospila callicula orchardae ♀ Prout type; Geometridae genitalia slide No. 15693 ♀. [Examined.] **New synonymy.**

♂, ♀ (Fig. 67). Forewing length 15-17 mm. Antenna of female bipectinate. Frons brown, vertex green. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green, markings cream. Forewing: with costa pale brown; blotch at apex variable in size, never extending to costa, not usually connected to blotch at tornus by band along termen; blotch at tornus quite small; sometimes with additional blotch at wing base (absent in specimens previously allocated to *callicula stenobathra*); discal spot a short brown line, or V-shape, surrounded by white area. Hindwing: blotch at apex long, thin, usually extending along 1/2 of termen, but variable in size; blotch at tornus small; blotch at anal margin often absent, occasionally short, narrow; sometimes with blotch at wing base; anterior discal spot small, white; posterior discal spot a short brown V-shape, surrounded by white area. Hindleg: proximal spurs absent; brush of long hair-like scales present in male. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised, with bifurcate posterior extension, with serrated apical margins.

♂ *genitalia* (Fig. 129). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus extended into short, blunt, process; ampulla short, curved, with rounded, denticulate apex. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate squarish. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia* (Fig. 179). Sterigma dumbbell-shaped, with pocket on each side. Bursa copulatrix: ductus bursae long, quite strongly sclerotised, but not striated, antrum absent, with large appendix close to corpus bursae; corpus bursae large, bulbous; signum small. Anterior apophyses short.

Distribution. This species is only known from Bolivia and Brazil.

Diagnosis. *Oospila callicula* can be distinguished from other species with cream markings by the forewing discal spot which is a short brown line or V-shape in *callicula*. The genitalia of *callicula* (Figs 129 and 179) are indistinguishable from those of *obeliscata*, but the less extensive pale markings and the absence of brown bands parallel to the termen distinguish these two species (compare Figs 67 and 68). The male genitalia of *callicula* and *obeliscata* can be recognised by the distinctive form of the ampulla (Fig. 129). The female genitalia can be recognised by the distinctive form of the sterigma and by the appendix at the anterior of the ductus bursae (Fig. 179).

Material examined.

BOLIVIA: *Santa Cruz:* Mutum, 20 miles West of Peurto Suárez, 1500 ft, 1 ♂ [holotype of *callicula stenobathra*], 7-14.xi.27 (*Collenette*).

BRAZIL: *Gioás:* Maranhao, North East Brazil, 1 ♀ [holotype of *callicula orchardae*] (*Orchard*). *Mato Grosso:* Urucum, 15 miles South of Corumba, 650 ft, 1 ♂ [paratype of *callicula stenobathra*] 26.iv.27 (*Collenette*); 1 ♂ (*Germain*); Chapada, near Cuyaba, 4 ♂ (*Smith*).

Depositories: BMNH, CMNH.

Oospila obeliscata (Warren)

(Figs 68, 129, 179)

Anophylla obeliscata Warren, 1906: 414. Holotype ♂, in NMNH. Type locality: GUYANA. Label data: Guyana: Omai; Type No. 9174 U.S.N.M. [Examined.]

Oospila obeliscata (Warren); Prout, 1912: 134; 1932: 58.

♂, ♀ (Fig. 68). Forewing length 18-26 mm (female usually slightly larger than male). Antenna of female bipectinate. Wings: ground colour dark green; markings cream, yellow and brown. Forewing: with costa pale brown; with broad white band from just below apex, extending along termen to tornus, with two brown bands parallel to termen within this, yellowish between these bands; cream area connected by thin white line along distal 1/2 of anal margin to white blotch at wing base, this blotch with brown striation concentrated to give small brown patches; discal spot large, W-shaped brown marking surrounded by white patch. Hindwing: with white band parallel to wing edges, surrounding central green area; white band along termen contains two brown bands parallel to termen, coloured yellowish between; white area along anal margin with striations concentrated to give small brown patches; anterior discal spot large, with brown central marking surrounded by white area; posterior discal spot similar, but larger. Hindleg: proximal spurs absent; brush of long hair-like scales present on male tibia. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised, with bifurcate posterior extension, with serrated apical margins.

♂ *genitalia* (Fig. 129). As for *callicula*.

♀ *genitalia* (Fig. 179). As for *callicula*.

Diagnosis. The wing markings of *obeliscata* are rather similar to those of *includaria*. However, *obeliscata* is larger than *includaria* and may be distinguished by the larger size of the discal spots (compare Figs 52 and 68) and also by the genitalia (compare Figs 116, 129, 166 and 179).

The genitalia of *obeliscata* are indistinguishable from those of *callicula* (Figs 129 and 179), but the more extensive pale markings and the presence of brown bands parallel to the termen distinguish *obeliscata* from *callicula* (compare Figs 67 and 68).

The male genitalia of *callicula* and *obeliscata* can be recognised by the distinctive form of the ampulla (Fig. 129). The female genitalia can be recognised by the distinctive form of the sterigma and by the appendix at the anterior of the ductus bursae (Fig. 179).

Distribution. This species is more widely distributed than *callicula* and has been collected in French Guiana, Guyana, Venezuela, Peru, Bolivia and Brazil.

Material examined.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 3 ♂, 1 ♀ (*Le Moult*); 1 ♀ (*Le Moult*); Cayenne, 1 ♂; Saint Laurent du Maroni, 1 ♀; Pied Saut, Oyapek River, 1 ♀, ii.1908 (*Klages*).

GUYANA: *Mazaruni-Potaro:* Potaro, 1 ♂, ii.1908 (*Klages*); Omai, 1 ♂ [holotype]; 1 ♀.

VENEZUELA: *Bolívar:* El Boninche Reserve, 200 m, 1 ♀; El Dorado, Santa Elena, 107 km, Bolívar, 520 m, 1 ♀.

PERU: *Cuzco:* Upper Amazon, Santo Antonio de Javary, 1 ♂, v.07 (*Klages*). *Puno:* La Unión, Río Huacamayo, Carabaya, 2000 ft, 1 ♂, wet season, xi.1904 (*Ockenden*).

BOLIVIA: *Santa Cruz:* Mutum, near Puerto Suárez, 1 ♂; Provincia del Sara, 450 m, 1 ♂, xi. (*Steinbach*).

BRAZIL: Hyntanahan, Rio Purus, 1 ♂, iii.1922 (*Klages*). *Amapá:* Para, 12 ♂, 1 ♀ (*Moss*). *Amazonas:* Manicore, Rio Madeira, 2 ♂; River Madeira, 1 ♂ (*Moss*). *Mato*

Grosso: Urucum, near Corumba, 1 ♂; 1 ♀. *Rondônia:* Calama, River Madeira, below River Machados, 1 ♂, x.07 (*Hoffmann*).

Depositories: BMNH, CMNH, NMNH, UCV

The *marginata* group

The *marginata* group is a group of three species within the *trilunaria* group. These species are very similar in external appearance. Males can be identified from the shape of sternum A8, which can be inspected without dissecting the specimen. Females, however, must usually be dissected to confirm their identity.

Oospila marginata Warren

(Figs 4, 13, 69, 130, 180)

Oospila marginata Warren, 1897: 427; Prout, 1912: 133. Prout, 1932: 56. Holotype ♀, in BMNH. Type locality: GUYANA. Label data: Type; Brit[ish]. Guiana; Rothschild Bequest B[ritish] M[useum] 1939-1. Oospila marginata Type ♀ Warr[en]; Geometridae genitalia slide No. 15030 ♀. [Examined.]

Oospila rufiplaga Warren, 1904b: 505; Prout, 1912: 133. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; S[anto] Domingo, Carabaya, 600 ft., VI. 02 Dry seas[on] (Ockenden); Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15033 ♂. [Examined.] **New synonymy.**

Oospila marginata sympathes Prout, 1932: 56. Holotype ♂, in BMNH. Type locality: COLOMBIA. Label data: Type; Ob[erer] Rio Negro, Ost Colombia 800 m Coll[ection] Fassl; [?]; L.B. Prout Coll[ection] B[ritish] M[useum] 1939-643; Seitz VIII. 56; Oospila marginata sympathes ♂ type Prout; Geometridae genitalia slide No. 15029 ♂. [Examined.] **New synonymy.**

♂, ♀ (Figs 13, 69). Forewing length 13-16 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches brown. Forewing: with costa pale brown; subapical blotch small, or absent; blotch at tornus small, or absent (blotches at apex and tornus absent in specimens previously allocated to *marginata sympathes*); discal spot large, brown. Hindwing: blotch at tornus small or absent; blotch at anal margin short, narrow or absent; anterior discal spot small, white; posterior discal spot large, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with posterior edge with bifurcate posterior extension.

♂ *genitalia* (Fig. 130). Uncus with apical extension short, blunt. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace. Valvae: divided apically; sacculus extended into short, pointed process; ampulla long, thin, digitate, with origin close to base of valva, with denticulate apex. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with broad V- or W-shaped ventral plate. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia* (Fig. 180). Sterigma absent. Bursa copulatrix: ductus bursae with antrum thickened, with convoluted folds, below antrum quite short, not strongly sclerotised or striated, corpus bursae large, bulbous; signum small. Anterior apophyses short.

Distribution. Apparently confined to South America and collected in French Guiana, Guyana, Colombia, Peru, Bolivia, and Brazil.

Diagnosis. *Oospila marginata* cannot always be distinguished from *tricamerata* and *obsolescens* using external characters alone. The markings of *marginata* are paler and less reddish brown than those of *obsolescens* (compare Figs 11 and 13), although this may not always be very clear. Males can be distinguished by the shape of sternum A8 and by the genitalia (compare Figs 130, 131 and 132). Females can only be distinguished from their genitalia: *marginata* has no sterigma, although this structure is present in both *tricamerata* and *obsolescens* (compare Figs 180, 181 and 182). *Oospila marginata* can be distinguished from *carnelunata* by the brown colour of the subapical blotch on the forewing (if present); *carnelunata* has a large, cream subapical blotch. The female genitalia of *marginata* can be recognised by the distinctive thickened and convoluted form of the antrum (Fig. 180).

Material examined.

FRENCH GUIANA: *Guyane:* Saint Laurent du Maroni, 1 ♀, 1923 (*Aymès*); Saint Jean du Maroni, 1 ♀.

GUYANA: 1 ♀ [holotype of *marginata*].

COLOMBIA: *Meta:* East Colombia: Upper Río Negro, 800 m, 1 ♂ [holotype of *marginata sympathes*] (*Fassl*); 4 ♂ [paratypes of *marginata sympathes*] (*Fassl*); Buena Vista, 1 ♀.

PERU: San Groan, 1 ♂; 4 ♂ (*Mathan*). *Loreto:* Contamana, Río Ucayali, 1 ♂, xi-xii.1912. *Madre de Diós:* Tambopata Reserve, 30 km South West Puerto Maldonado, 1 ♂ (*Covell*). *Puno:* Yahuarmayo, 1200 ft, 1 ♂, iv-v.1912; San Gaban, 2500 ft, 1 ♂, iii.-iv.1913; La Oroya, Río Inambari, 3100 ft, 1 ♂, ix.05 (*Ockenden*); 1 ♂, wet season, x.1904 (*Ockenden*); Santo Domingo, 6000 ft, 1 ♂ [holotype of *rufiplaga*] dry season, vi.02 (*Ockenden*); Tinguri, 3400 ft, 1 ♂, wet season, i.1905 (*Ockenden*).

BOLIVIA: Río Songo, 750 m, 1 ♀. *Santa Cruz:* East Bolivia: Buenavista, 750 m, 1 ♂,

viii.06-iv.07 (*Steinbach*); Buenavista, 400 m, 1 ♂, xi.1914 (*Steinbach*); Provincia del Sara, 450 m, 2 ♂, xi.1912 (*Steinbach*); 2 ♂, xii.1912 (*Steinbach*); 1 ♂, i.1913 (*Steinbach*); 1 ♂, ii. (*Steinbach*); 1 ♂, x. (*Steinbach*); 1 ♂, xi. (*Steinbach*); 1 ♂, xii. (*Steinbach*); River Yapacani, East Bolivia, 600 m, 2 ♂, ii.1915 (*Steinbach*).
BRAZIL: River Yapacani, 600 m, 2 ♂. *Mato Grosso:* 4 ♂, 1886 (*Germain*); 1 ♂. *Amazonas:* Fonte Boa, Upper Amazon: 1 ♂; 1 ♂, viii.1906 (*Klages*); 5 ♀, vii.1907 (*Klages*); 3 ♀, viii.1907 (*Klages*); Sao Paulo de Olivença, 2 ♂, 2 ♀; Nova Olinda, Rio Purus, 3 ♂, v.1922 (*Klages*); 2 ♀, vi.1922 (*Klages*); Hyantanahan, Rio Purus, 1 ♂, ii.1922 (*Klages*); 1 ♂, iv.1922 (*Klages*); 1 ♂ (*Germain*).
Depositories: BMNH, CMNH, C. V. Covell Jr. collection, NMNH,

Oospila tricamerata Prout

(Figs 70, 131, 181)

Oospila tricamerata Prout, 1916: 171; 1932: 56. Holotype ♂, in BMNH. Type locality: BRAZIL. Label data: Type; Fonte Boa, Amazonas, May 1906 (S.M. Klages); Oospila tricamerata ♂ type Prout; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15036 ♂. [Examined.]

♂, ♀ (Fig. 70). Forewing length 12-13 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches, where present, dark brown, slightly paler at centres. Forewing: with costa pale brown; subapical blotch small, or absent, not connected to blotch at tornus by band along termen; blotch at tornus small, or absent; discal spot small, brown. Hindwing: blotch at apex usually small, narrow, touching or continuous with small subapical blotch, not connected to blotch at tornus by band along termen;

blotch at tornus small; blotch at anal margin absent; anterior discal spot small, white; posterior discal spot small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with short posterior extension, with shallowly emarginated posterior edge.

♂ *genitalia* (Fig. 131). Uncus with apical extension short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: divided apically; sacculus not extended; ampulla broad, flat, approximately same shape as valva, usually with dorsally directed projection close to base (absent from Costa Rican specimens), dorsal margin denticulate towards apex. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate quite broad, U-shaped. Coremata absent. Aedeagus with large cornutus on vesica.

♀ *genitalia* (Fig. 181). Sterigma approximately rectangular, slightly expanded apically on each side. Bursa copulatrix: ductus bursae wide, moderately long, weakly striated, antrum absent; corpus bursae quite large, bulbous; signum small. Anterior apophyses short.

Distribution. Material was examined from Belize, Costa Rica, French Guiana, Surinam, Colombia, Peru and Brazil. A record from Guyana may be spurious since the specimen was bought, although it would be surprising if *tricamerata* did not occur there.

Diagnosis. Owing to intraspecific variation, *tricamerata* cannot always be distinguished from *marginata* or *obsolescens* from the wing markings alone. Males can be distinguished by the shape of sternum A8 and by the genitalia (compare Figs 130, 131 and 132). Females can only be distinguished reliably from the genitalia: the presence and shape of the sterigma is diagnostic (compare Figs 180, 181 and 182). The male genitalia of *tricamerata* can be recognised by the shape of the ampulla (Fig. 131).

Material examined.

BELIZE: Río Grande, 1 ♂ (*White*). *Toledo:* Punta Gorda, 1 ♀, vii.1932 (*White*); 1 ♂, ix.1932 (*White*); 1 ♂, x.1932 (*White*); 1 ♂, ii.1932 (*White*); 1 ♂, vi.1933 (*White*); 1 ♀ (*White*); 1 ?, vii.1933 (*White*); 1 ♂, iv.1934 (*White*); 1 ♂, viii.1934 (*White*); 1 ♂, v.1935 (*White*).

COSTA RICA: *Guanacaste:* 4 km West Santa Cecilia, 1 ♂.

FRENCH GUIANA: *Guyane:* Godebert-Maroni, 1 ♂ [paratype] (*Le Moult*); Saint Jean du Maroni, 2 ♂ (*Le Moult*); 2 ♂; Saint Laurent du Maroni, 1 ♂, 1 ♀; Mana River, 3 ♂, v.1917; Nouveau Chantier, 1 ♂ (*Le Moult*).

SURINAM: Sipalawini District, Thibiti area, Kabo Creek (partly swampy, primary forest on hilly slopes circa 2 km from river); 1 ♂. *Suriname:* Geldersland, Surinam River, 1 ♂.

GUYANA: Bought at Georgetown, 1 ♂.

COLOMBIA: Magdalena Valley, 1 ♂, v-viii.1920 (*Hall*). *Meta:* Upper Río Negro, East Colombia, 800 m, 1 ♂, 1 ♀ (*Fassl*).

PERU: 1 ♂ (*Mathan*). *Amazonas:* Cavallo-Cocho, 1 ♂, v-vii.1884 (*Mathan*). *Loreto:* Río Pacaya, Lower Ucayali, 1 ♂, viii-ix.1912; Río Ampiyacu, Putomayo, 1 ♂.

BRAZIL: Rio Topajoz, 1 ♂. *Amapá:* Para, 1 ♂ (*Moss*); 1 ♂. *Amazonas:* Codajas, Upper Amazon, 1 ♂ [paratype] iv.1907 (*Klages*); Fonte Boa, 1 ♂ [holotype] v.1906 (*Klages*); 2 ♂ [paratypes] viii.1907 (*Klages*); Boa Fé, 1 ♂; Amazonas, 1 ♂; Above Manaos, 1 ♀ (*Moss*). *Mato Grosso:* 1 ♂ (*Germain*).

Depositories: BMNH, CMNH, Den Haag museum, INBio, NMNH.

Oospila obsolescens new species

(Figs 11, 71, 132, 182)

[*Racheolopha trilunaria Guenée ab. obsolescens* Warren, 1909: 86. Infra-subspecific name.]

[*Oospila rufiplaga* ab. *obsolescens*; Prout, 1932: 56. Infra-subspecific name.]

Holotype ♂, in BMNH. Type locality: BRAZIL. Label data: Type; Fonte Boa, Amazonas, August 1906. (S.M. Klages); Racheolopha trilunaria Guen[ée] ab. obsolescens type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-l; Geometridae genitalia slide No. 15035 ♂. [Examined.]

♂, ♀ (Figs 11, 71). Forewing length 12-14 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches with pale orange-brown centres with dark brown crescent-shaped marking and dark brown perimeters. Forewing: with costa pale brown; blotch at apex absent, sometimes with small subapical blotch, not connected to blotch at tornus by band along termen; blotch at tornus small, approximately circular; discal spot large, brown. Hindwing: blotch at apex absent; blotch at tornus small; blotch at anal margin absent; anterior discal spot small, white; posterior discal spot large, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with cream area around crests enclosed by thin pink line, remainder of dorsal surface green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised, with bifurcate posterior extension.

♂ *genitalia* (Fig. 132). Uncus with apical extension short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace present. Valvae: with shallow apical division; sacculus not extended; ampulla short, broad, robust, spinulose, characteristically shaped. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate broad, flattened. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia* (Fig. 182). Sterigma approximately elliptical; basal part with irregularly arranged small projections. Bursa copulatrix: ductus bursae quite long, weakly sclerotised, not striated, antrum absent. Bursa copulatrix large, bulbous; signum small. Anterior apophyses short.

Diagnosis. Although the wing markings of *O. obsolescens* are darker and more reddish than those of *marginata* and *tricamerata* (compare Figs 11 and 13), these species cannot always be distinguished from the wing markings alone. However, males can be distinguished by the genitalia and by the shape of sternum A8 (compare Figs 130, 131 and 132). Females can only reliably be distinguished from the genitalia: the presence of an elliptical sterigma distinguishes *obsolescens* from the other two species (compare Figs 181, 182 and 183). The absence or smaller size and brown colour (if present) of the subapical blotch of the forewing and the absence of a blotch at the apex of the hindwing distinguishes *obsolescens* from *carnelunata* (compare Figs 11, 60 and 71). The male genitalia of *obsolescens* can be recognised by the shape of the ampulla (Fig. 132).

Distribution. Material was examined from Surinam, Peru, Bolivia, Brazil.

Remarks. The infra-subspecific (Warren, 1909; Prout, 1932) name is used as the basis of the new specific name of this species.

Material examined.

SURINAM: Sipalawini District, Thibiti area, Kabo Creek (partly swampy, primary forest on hilly slopes circa 2 km from river) 2 ♂.

PERU: *Amazonas:* Cavallo-Cocho, 1 ♂, v-vii.1884 (*Mathan*).

BOLIVIA: *Santa Cruz:* Provincia del Sara, 450 m, 1 ♂; East Bolivia, River Yapacani, 600 m, 1 ♂, ii.1914 (*Steinbach*); 2 ♂, ii.1915 (*Steinbach*).

BRAZIL: *Amazonas:* Fonte Boa, 1 ♂ [holotype] viii.1906 (*Klages*); 1 ♂, vii.1906 (*Klages*); 1 ♂, 1 ♀ viii.1906 (*Klages*); 1 ♀ (*Klages*); 1 ♀, ix.06 (*Klages*); 1 ♀, viii.1907 (*Klages*). *Amazonas:* Sao Paulo de Olivença, 1 ♂, i.1933 (*Waehner*).

Depositories: BMNH, CMNH, Den Haag museum.

The *atopochlora* group

The *atopochlora* group is a group of four species within the *trilunaria* group. These four species are very similar in external appearance.

Oospila atopochlora Prout

(Figs 72, 133, 183)

Oospila atopochlora Prout, 1932: 57. Holotype ♂, in BMNH. Type locality: COLOMBIA. Label data: Type; Muzo, Colombia 400-800 m Coll[ection] Fassl; Seitz VIII 57; Oospila atopochlora Prout ♂ type; L.B. Prout Coll[ection] B[ritish] M[useum] 1939-643; Geometridae genitalia slide No. 15047 ♂. [Examined.]

♂, ♀ (Fig. 72). Forewing length 16-21 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface dark brown or black. Wings: ground colour dark green; blotches dark brown or black. Forewing: with costa pale brown; blotch at apex large, but not extending to costa, not connected to blotch at tornus by band along termen; blotch at tornus large; discal spot large, dark brown or black. Hindwing: blotch at apex large, enclosing smaller subapical green area on termen, not connected to blotch at tornus by band along termen; blotch at tornus large; blotch at anal margin absent; anterior discal spot small, dark brown or black; posterior discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests dark brown or black at anterior, green at posterior; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 133). Uncus with apical extension short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: without apical division; sacculus extended into very short, pointed process; ampulla quite short, digitate, with denticulate apex. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with V-shaped ventral plate. Coremata absent. Aedeagus with two large cornuti, and one small cornutus, on vesica.

♀ *genitalia* (Fig. 183). Sterigma absent. Bursa copulatrix: ductus bursae short, not strongly sclerotised or striated; corpus bursae large, bulbous, not distinct from ductus, more strongly sclerotised than in most *Oospila*, with wavy folds; signum small. Anterior apophyses short.

Distribution. Material was examined from Nicaragua, Costa Rica, Panamá, Guyana, Venezuela, Colombia, Ecuador and Brazil. There is also a record of one male from San Gaban in Peru (Prout, 1932), although the identity of the specimen has not been confirmed.

Diagnosis. *Oospila atopochlora* can be distinguished from *congener* by its larger size and by the presence of a small subapical green area on the termen of the hindwing; this area is dark brown or black in *congener* (compare Figs 72 and 75). The male genitalia of the two species are very similar but *atopochlora* can be identified by the presence of two large cornuti towards the base of the aedeagus (compare Figs 133 and 136). The female genitalia of *atopochlora* are distinguished by the absence of a sterigma (compare Figs 183 and 185).

The large blotch at the apex of the forewing distinguishes *atopochlora* from *hyalina* (compare Figs 72 and 73). Furthermore, *hyalina* has two separate dark brown or black markings at the apex of the hindwing, joined by a dark brown or black band along the termen whereas *atopochlora* has a single blotch.

Material examined.

NICARAGUA: *Zelaya:* Eden, 14°0'N 84°26'W, 1 ♂, 24.iii.1922 (*Wharton Huber*); 1 ♂, 24.iv.1922 (*Wharton Huber*); 1 ♂, 17.v.1922 (*Wharton Huber*).

COSTA RICA: *Heredia:* La Selva Biological Station, Puerto Viejo de Sarapiqui, 40 m, 1 ♂, x.1986 (*Chavarria*); 1 ♂, iv.1987 (*Chavarria*). *Limón:* Cerro Tortuguero, North edge Tortuguero National Park, 0-100 m, 1 ♀, 30.v.1984 (*Janzen & Hallwachs*); 9.4 km West of Bribi, Suretka, 200 m, 1 ♂, 9-11.vi.1983 (*Janzen & Hallwachs*); 1 ♂, iv.1989 (*Aguillar & Solano*). *Puntarenas:* Estacion Quebrada Bonita, 50 m R.B. Carara, 1 ♂, ix.1989 (*Zuniga*); 1 ♂, x.1989 (*Zuniga*); Fila Esquinas, 35 km South of Palmar Norte, 8°45' x 83°20', 4 ♂, 1 ♀, 7-8.i.1983 (*Janzen & Hallwachs*); Manuel Antonio National Park Quepos, 30 m, 1 ♂, v.1987 (*Chacon*); 1 ♂, vi.1987 (*Chacon*); Las Cruces Biological Station, San Vito, 1200 m, 1 ♀, 16-20.xi.1987 (*Chacon*); *Osa Peninsula:* Sirena Corcovado National Park, 1 ♂, 10-12.viii.1980 (*Janzen & Hallwachs*); 1 ♂, 1 ♀, 5-11.i.1981 (*Janzen & Hallwachs*); 1 ♂, 1.v.1984 (*Janzen & Hallwachs*); Sirena Corcovado: 1 ♀, iv.1989 (*Blanco & Fonseca*); 1 ♀, ii.1990 (*Fonseca*); Finca Cafrosa, Estacion Las Mellitzas, Parque Nacional Amistad, 1300 m, 1 ♂, 20.viii-4.ix.1989 (*Ramirez & Mora*).

PANAMA: *Canal Zone:* Barro Colorado Island, 1 ♀.

GUYANA: *Mazaruni-Potaro:* Omai, 2 ♂.

VENEZUELA: *Bolívar:* Forestal Imataca, El Boninche Reserve, Bolívar, 200 m, 1 ♂, 6-13.xii.74.

COLOMBIA: *Boyacá:* Muzo, 400-800 m, 1 ♂ [holotype] (*Fassl*); 3 ♂ [paratypes]. *Meta:* Buena Vista, 2 ♂, 1 ♀.

ECUADOR: Tung Banos (39 km East) 1 ♀.

BRAZIL: *Amazonas:* Sao Paulo de Olivença, 2 ♂; Hyntanahan, Rio Purus, 3 ♂, ii.1922 (*Klages*); 2 ♂, iii.1922 (*Klages*).

Depositories: BMNH, CMNH, INBio, NMNH, UCV.

Oospila hyalina Warren

(Figs 73, 134, 184)

Oospila hyalina Warren, 1897: 427; Prout, 1912: 133; 1932: 56. Holotype ♀, in BMNH. Type locality: COLOMBIA. Label data: Type; Bogota; Rothschild Bequest B[ritish] M[useum] 1939-1; Oospila hyalina Warr[en] type ♀; Geometridae genitalia slide No. 15042 ♀. [Examined.]

[*Halioscia ruptimacula* Warren, 1909: 77. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; La Union, Huacamayo, Carabaya, 2000 ft., wet season, Dec[ember] 1904. (G. Ockenden); Halioscia ruptimacula type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; find in Seitz vol 8; Oospila fractimacula Prout nom. nov; ruptimacula Warr[en] nom. praeocc; Geometridae genitalia slide No. 15044 ♂. [Examined.] Homonym of *Oospila ruptimacula* Warren, 1901: 448.]

Oospila fractimacula Prout, 1912: 134. Prout, 1932: 56. [Prout replaced *Halioscia ruptimacula* with *Oospila fractimacula*]. **New synonymy.**

Halioscia atroviridis Warren, 1907: 202. Lectotype ♂, here designated, in BMNH. Type locality: PERU. Label data: La Oroya, R[ío] Inambari, S[outh] E[ast] Peru, 3100 ft., wet season, March 1905 (G. Ockenden); Rothschild Bequest B[ritish] M[useum] 1939-1. Geometridae genitalia slide No. 14046 ♂; Geometridae slide No. 14607. [Examined.] Synonymised by Prout, 1912: 133.

♂, ♀ (Fig. 73). Forewing length 12-20 mm (females generally slightly larger than males). Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches dark brown or black. Forewing: with costa pale brown; blotch at apex small, thin, approximately rectangular, not extending to costa, not connected to blotch at tornus by band along termen; blotch at tornus larger; discal spot large, round, dark brown or black. Hindwing: blotch at apex split into two small markings with central green patch between, not connected to blotch at tornus by band along termen; blotch at tornus small; blotch at anal margin absent; anterior discal spot small, white; posterior discal spot large, dark brown or black. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 134). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen thin, with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus not extended; ampulla short, thin, with pointed apex; also with similar short sclerotised process where valva widens. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with V-shaped ventral plate. Coremata absent. Aedeagus with short cornutus on vesica.

♀ *genitalia* (Fig. 184). Sterigma large, approximately elliptical, with posterior edge emarginated. Bursa copulatrix: ductus bursae long, strongly sclerotised, and striated, antrum absent; corpus bursae moderately small, sclerotised with some striation; signum small. Anterior apophyses short.

Remarks. Warren (1907) incorrectly identified one paralectotype of *Halioscia atroviridis* Warren: the specimen is *hyalina*.

Distribution. Only known from Colombia, Ecuador and Peru.

Diagnosis. *Oospila hyalina* can be distinguished from *atopochlora* and *congener* by the small, narrow subapical blotch of the forewing, which never extends to the costa in *hyalina* (compare Figs 72, 73 and 75). *Oospila hyalina* can also be distinguished by the form of the blotch at the apex of the hindwing, which is split into two small, completely separate, dark brown or black patches. The male genitalia of *hyalina* can be recognised by the presence of a second short, pointed process (in addition to the ampulla) on the valvae (Fig. 134).

Material examined.

COLOMBIA: *Cundinamarca:* Bogota, 1 ♀ [holotype of *hyalina*]; 1 ♀. *Antioquia:* El Cerro, Frontino, Dept di Antioquia, 6000 ft, 1 ♂, 17.vi.1938.

ECUADOR: Carchi, Chical, 0°56'N 78°11'W, 1250 m, 1 ♂, 31.vii.78 (*Rawlins*); 1 ♀, 18.vii.1983 (*Rawlins & Davidson*). *Morona-Santiago:* 40 km North North East Macas, 2°05'S 78°01'W, 1020 m, 1 ♂, 13.vi.1983 (*Rawlins & Thompson*).

PERU: *Puno:* La Unión, Río Huacamayo, 2000 ft, 1 ♂ [holotype of *Halioscia ruptimacula*] wet season, xii.04 (*Ockenden*); South East Peru: La Oroya, Río Inambari, 3100 ft, 1 ♀, wet season, iii.05 (*Ockenden*).

Depositories: BMNH, CMNH, NMNH.

Oospila atroviridis Warren new status

(Figs 10, 74, 135)

Oospila atroviridis Warren, 1904a: 24; Prout, 1912: 133. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; S[anto] Domingo, Carabaya, 6000 ft., XII.01. wet seas[on] (Ockenden); Rothschild Bequest B[ritish] M[useum] 1939-1; Oospila atroviridis type ♂ Warr[en]; Geometridae genitalia slide No. 15043 ♂. [Examined.]

Oospila hyalina atroviridis Warren; Prout, 1932: 59.

[*Halioscia ruptimacula* Warren, 1909: 77, *sensu* Prout, 1912: 134 [incorrect identification.]]

Oospila dolens Druce, 1911: 293; Prout, 1932: 59. Holotype ♂, in BMNH. Type locality: COLOMBIA. Label data: Type; La Maria Dagua Valley W[est] Colombia, 4700 ft May' 08; Joicey Bequest. Brit[ish] Mus[eum] 1934-120; Oospila dolens type Druce; Det[ermined] by L.B. Prout; Geometridae genitalia slide No. 15726 ♂. [Examined.] **New synonymy.**

♂ (Figs 10, 74). Forewing length 13-14 mm. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches dark brown or black. Forewing: with costa pale brown; blotches merged to give broad band along termen, sometimes broken by small green patch or patches within the dark brown or black band, usually towards apex or termen; discal spot large, brown. Hindwing: with dark brown blotches at apex and tornus, these usually separate, but occasionally merged along termen; anterior discal spot small, white; posterior discal spot large, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests dark brown or black; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised, with bifurcate apical extension.

♂ *genitalia* (Fig. 135). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; sacculus developed into short, pointed process; ampulla short, curved, with short basal projection. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate elongated, V-shaped. Aedeagus with short cornutus on vesica.

♀ *genitalia*. Unknown.

Distribution. Only known from Colombia and Peru.

Diagnosis. *Oospila atroviridis* can be distinguished from *atopochlora, congener* and *hyalina* by its smaller size and by the more extensive brown markings (compare Figs 10, 72, 73, 74 and 75). In *atroviridis* the brown markings on the forewing are continuous: the other species have separate blotches with green patches between them.

Most specimens can be distinguished from *zamaradaria* by the presence of two separate dark brown blotches on the hindwings: *zamaradaria* has a continuous dark brown line along the termen of the hindwing (compare Figs 10, 44 and 74). The presence of an anterior white discal spot and a posterior dark brown or black discal spot also distinguishes *atroviridis* from *zamaradaria*, which has a single, or no discal spot.

The darker, blacker colour of the markings and the presence of large, prominent, discal spots distinguish *atroviridis* from *tortuguera* (compare Figs 10, 29 and 74).

Material examined.

COLOMBIA: *Antioquia:* El Cerro, Frontino, 1 ♂. *Valle:* La Maria, Dagua Valley, 4700 ft, 1 ♂ [holotype of *dolens*] v.08.

PERU: *Puno:* Santo Domingo, 6000 ft, wet season, 1 ♂ [holotype of *hyalina atroviridis*] xii.01 (*Ockenden*); 1 ♂, wet season, i.02 (*Ockenden*); 2 ♂, wet season, iv.02 (*Ockenden*); 1 ♂, dry season, vii.02 (*Ockenden*); 1 ♂, dry season, x.02 (*Ockenden*); 1 ♂, wet season, xi.02 (*Ockenden*); 1 ♂, wet season, xii.02 (*Ockenden*); La Oroya, Río Inambari, 3100 ft, 1 ♂, dry season, ix.04 (*Ockenden*); 1 ♂, wet season, x.04 (*Ockenden*); 1 ♂, wet season, iii.05 (*Ockenden*); Quinton, 5000 ft, 1 ♂, i.1905 (*Ockenden*).

Depository: BMNH.

Oospila congener Warren

(Figs 75, 136, 185)

Oospila congener Warren, 1900: 136; Prout, 1912: 133; 1932: 57. Holotype ♂, in BMNH. Type locality: GUYANA. Label data: Type; Rio Demerara. VII.97; Rothschild Bequest B[ritish] M[useum] 1939-1; Oospila congener type ♂ Warr[en]; Geometridae genitalia slide No. 15045 ♂. [Examined.]

Halioscia congener Warren, 1907: 203.

Halioscia procellosa Warren, 1907: 202. Holotype ♂, in BMNH. Type locality; PERU. Label data: Type; La Oroya, R[ío] Inambari, Peru, Sept 1904 3100 ft., dry seas[on] (G. Ockenden); Halioscia procellosa type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15046 ♂. [Examined.] **New synonymy.**

Oospila procellosa (Warren); Prout, 1912: 134.

Oospila congener procellosa (Warren); Prout, 1932: 57.

♂, ♀ (Fig. 75). Forewing length 12-19 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches dark brown or black. Forewing: with costa pale brown; blotch at apex large, approximately circular, but not extending to costa, not connected to blotch at tornus by band along termen; blotch at tornus large; discal spot large, diffuse, dark brown or black. Hindwing: with blotch at apex large, not broken by internal green markings (as it is in *atroviridis* and *atopochlora*); anterior discal spot large, diffuse, dark brown or black; posterior discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests dark brown, or black; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 136). Uncus with apical extension short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with shallow apical division; sacculus extended into very short, pointed process; ampulla short, thin, digitate. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate squarish. Coremata absent. Aedeagus long, thin, with small cornutus on vesica.

♀ *genitalia* (Fig. 185). Sterigma somewhat variable; with two apical pockets of varying size; often with smaller central apical projection (as in Fig. 185). Bursa copulatrix: ductus bursae moderately long, not strongly sclerotised, or striated, but with wavy folds, antrum absent; corpus bursae slightly wider than ductus, moderately long; signum small. Anterior apophyses short.

Distribution. Material was examined from French Guiana, Guyana, Colombia, Peru, Bolivia and Brazil.

Diagnosis. *Oospila congener* can be distinguished from *hyalina* by its smaller size and by the large and approximately circular blotch at the apex of the forewings. Also, the blotch at the apex of the hindwing is not split into two smaller markings in *congener* as it is in *atopochlora* and *hyalina* (compare Figs 72, 73 and 75). The separation of blotches at the apex and tornus of all wings distinguishes *congener* from *atroviridis*, in which these blotches are merged (compare Figs 10, 74 and 75). Females of *congener* can be recognised by the distinctive form of the sterigma (Fig. 185).

Material examined.

FRENCH GUIANA: *Guyane:* Nouveau Chantier, 1 ♀, ii. (*Le Moult*); Saint Laurent du Maroni, 1 ♂; Mana River, 1 ♂, v.1917.

GUYANA: *East Demerara-West Coast Berbice:* Demerara River, 1 ♂ [holotype of *congener*] vii.97. *Mazaruni-Potaro:* Potaro, 1 ♀, ii.1908 (*Klages*).

COLOMBIA: Mérida, 500 m, 1 ♂. *Meta:* East Colombia, Upper Río Negro, 800 m, 4 ♂ (*Fassl*).

PERU: *Puno:* La Oroya, Río Inambari, 3100 ft, 1 ♂ [holotype of *procellosa*] dry season, ix.1904 (*Ockenden*); 3 ♂, dry season, ix.1904 (*Ockenden*); 7 ♂, wet season, iii.1905 (*Ockenden*); 2 ♂, dry season, v.1905 (*Ockenden*); 1 ♂, ix.05 (*Ockenden*); 2 ♂, xi-xii.1905 (*Ockenden*); 2 ♂, xii.05 (*Ockenden*); La Oroya, South East Peru, 3000 ft, 1 ♂, 1 ♀ (*Ockenden*); Carabaya, Tinguri, 3400 ft, 1 ♂, dry season, viii.1904 (*Ockenden*); 1 ♀ [paratype of *procellosa*] viii.1904 (*Ockenden*); San Gaban, 2500 ft, 1 ♂, iii-iv.1912.

BOLIVIA: Río Songo, 1 ♂.

BRAZIL: *Amazonas:* Fonte Boa, 2 ♂, v.1906 (*Klages*); 4 ♂, vi.1906 (*Klages*); 2 ♂,

viii.1906 (*Klages*); 1 ♂, vii.1907 (*Klages*); 1 ♀ (*Klages*); Hyntanahan, Rio Purus, 1 ♂, i.1922 (*Klages*); 1 ♂, ii.1922 (*Klages*); 1 ♂, iii.1922 (*Klages*); 1 ♂, vi.1922 (*Klages*). *Amapá:* Para, 13 ♂, 3 ♀ (*Moss*). *Pará:* Unt. Amaz. Taperhina, below Santarem, 1 ♂, 21-31.vii.27 (*Zerny*); Monte Cristo, Tapajós, 1 ♂.
Depositories: BMNH, CMNH, NMNH.

Oospila imaculata **new species**

(Figs 76, 137, 186)

Holotype ♂, in V.O. Becker collection. Type Locality: BRAZIL. Label data: Col Becker 58355; Planaltina D[istrito] F[ederal], BRASIL - 1000m, 15°35'S 47°42'W, 3.viii.1986, V.O. Becker col; Geometridae genitalia slide No. 14684 ♂. [Examined.]

♂, ♀ (Fig. 76). Forewing 13-14 mm. Antenna of female bipectinate. Frons and vertex green. Interantennal fillet white. Thorax: dorsal surface green. Wings: unmarked. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with cream area around crests enclosed by pink line, remainder of dorsal surface green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 137). Uncus with apical extension short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with apical division; ampulla absent; sacculus extended into robust, pointed process. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate broad, robust, W-shaped. Coremata absent. Aedeagus with large, cornutus and denticulate vesica.

♀ *genitalia* (Fig. 186). Sterigma absent. Bursa copulatrix with antrum long, strongly striated; ductus bursae below antrum very long, unusually, with U-bend, strongly sclerotised, striated; corpus bursae, large, bulbous; signum absent. Anterior apophyses short.

Diagnosis. *Oospila imaculata* can be distinguished from *holochroa* and *stagonata* by the absence of a discal spot on the forewings (compare Figs 49, 76 and 80). The absence of a small marking at the tornus of the fore- and hindwings distinguishes *imaculata* from *decoloraria* (compare Figs 16 and 76). The female genitalia of *imaculata* can be recognised by the unusual U-bend of the ductus bursae (Fig. 186).

Distribution. The two specimens examined were collected in Brazil.

Material examined.

BRAZIL: RJ Cach. do Macacu, 600 m, 1 ♀ [paratype] 13.x.1985 (*Becker*) (V.O. Becker collection). *Distrito Federal:* Planaltina, 15°35'S 47°42'W, 1000 m, 1 ♂ [holotype] 3.viii.1986 (*Becker*).

Depository: V. O. Becker Collection.

Oospila confundaria (**Möschler**)

(Figs 77, 138, 187)

Racheospila confundaria Möschler, 1890: 242. Lectotype ♀, here designated, in Berlin Museum. Type locality: Unknown. Type; Portorico, Mus[eum] Krug. 87; Typus; Zool. Mus[eum] Berlin; Confundaria Moschl[er]; MAC genitalia slide No. 018; [Examined.]

Oospila confundaria (Möschler); Prout, 1912: 133; 1932: 55.

Racheolopha coerulea Warren, 1906: 421. Holotype ♂, in NMNH. Type locality: GUYANA. Label data: British Guiana: Omai; Schaus Coll[ection]; Type No. 9188, USNM; Genitalia Slide By MAC No. 57731 U.S.N.M. [Examined.] **New synonymy.**

Oospila coerulea (Warren); Prout, 1912: 134; 1932: 55.

Oospila coerulea aphenges Prout, 1932: 55. Holotype ♂, in BMNH. Type locality: BRAZIL. Label data: Type H[olo]t[ype]; 39. 27. Urucum, 15 miles S[outh] of Corumba. 650 ft., 16-23.xi.27. Mato Grosso. C.L. Collenette; 3174; Oospila coerulea aphenges ♂ type Prout; Joicey Bequest. Brit[ish] Mus[eum] 1934-120; Geometridae genitalia slide No. 15695. [Examined.] **New synonymy.**

Racheolopha derasa Warren, 1906: 422. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: Maroni R[iver], S[ain]t Jean, vii. 1904; Schaus Coll[ection]; Type No. 9191, USNM; Genitalia Slide By MAC No. 57730 U.S.N.M. [Examined.] **New synonymy.**

Oospila derasa (Warren); Prout, 1912: 134; 1932: 55.

Oospila sesquiplaga Prout, 1912: 135; 1932: 55. Holotype ♀, in Hope Entomological Collections, Oxford. Type locality: BRAZIL. Label data: [type]; Oospila sesquiplaga Prout type; [ns]; t., 1910, L.B. Prout; Type Lep[idoptera]: No. 2519 Oospila sesquiplaga Prout Hope Dep[ar]t[ment] Oxford; 647. [Examined.] **New synonymy.**

♂, ♀ (Fig. 77). Forewing length 10-15 mm. Antenna of female simple. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings dark brown. Forewing: with costa pale brown; blotch at apex sometimes very small (as in specimen formerly allocated to *sesquiplaga*), usually absent; blotch at tornus often small (as in specimens formerly allocated to *derasa*), sometimes absent; sometimes with thin brown band along termen; sometimes unmarked; discal spot brown. Hindwing: blotch at apex absent; blotch at tornus sometimes very small, usually absent; blotch at anal margin absent; anterior discal spot usually absent, sometimes small, white; posterior discal spot usually absent, sometimes small, brown. Hindleg: proximal spurs absent; brush of long hair-like scales on male tibia. Abdomen: with cream area surrounding crests, remainder of dorsal surface green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised in male, with bifurcate apical extension.

♂ *genitalia* (Fig. 138). Uncus with apical extension short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: divided apically; sacculus with very short, pointed apical extension; ampulla thin, curved, articulating close to base of valva, lacking teeth. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate V-shaped. Coremata absent. Aedeagus with small cornutus on vesica.

♀ *genitalia* (Fig. 187). Sterigma large, elliptical. Bursa copulatrix: ductus bursae long, not strongly sclerotised, with a little striation, antrum absent; corpus bursae large, bulbous; signum quite large. Anterior apophyses quite long.

Distribution. The most widely distributed species of *Oospila*, *O. confundaria* has been collected in Cuba, Jamaica, Trinidad, West Indies, Dominican Republic, Guatemala, Costa Rica, Panamá, French Guiana, Surinam, Guyana, Venezuela, Colombia, Peru, Bolivia, Paraguay and Brazil. Prout (1932) recorded a specimen in the Naturhistorisches Museum Wien, from Recife, Pernambuco, Brazil, said to be *confundaria*, however the identity of the specimen has not been confirmed and the specimen appears to be missing (M. Lödl, *pers. comm.*).

Diagnosis. *Oospila confundaria* has similar wing markings to *decoloraria* (compare Figs 16 and 77) from which males can be distinguished by the presence of a hair pencil on the hind tibia of *confundaria* and females can be distinguished by the simple antennae of *confundaria*. *Oospila confundaria* can be distinguished from *marginata*, *tricamerata*, and *obsolescens* by the smaller size, or lack of blotches in *confundaria* and by the absence of large brown discal spots on the hindwings (compare Figs 11, 13, 69, 70, 71 and 77).

Remarks. The holotype of *O. sesquiplaga* has a glued and incorrectly associated abdomen.

Material examined.

CUBA: *Matanzas:* Cienaga, Zapata, near Playa Larga, 1 ♀.

JAMAICA: Baron Hill, Trelawny, 1 ♀.

TRINIDAD: Curepe, 9.i.1980, 1 ♂ (*Cock*).

WEST INDIES: Santa Lucia, 1 ♀ (*Br[a]nch*).

DOMINICAN REPUBLIC: La Vega, 15 km North Jarabacoa, 240 m, 1 ♀, 21.vii.1987 (*Rawlins & Davidson*).

GUATEMALA: Chejel, 1 ♂. *Izabel:* Cayuga, 2 ♀.

COSTA RICA: Avangarez, 2 ♂. *Alajuela:* Finca San Gabriel, 2 km South West of

Dos Rios, 600 m, W85 23'50" N10 53'19" 1 ♀, i.1988 (*Janzen & Hallwachs*); Estacion Pitilla, 700 m, 9 km South Santa Cecilia, 1 ♂, 18.vi.1988 (*Janzen & Hallwachs*); 1 ♀, vi.1988 (*Espinosa*); 1 ♀, vii.1988 (*Espinosa & Chaves*); 3 ♂, 1 ♀, viii.1988 (*Scoble & Brooks*); Finca La Campana, El Ensayo, 7 km West Dos Rios, 1 ♂. *Cartago:* Juan Vinas, 1 ♀. *Guanacaste:* Las Canas, Río Carobici, 1 ♀. Casa Oeste, Cerro El Hacha, 12 km South East La Cruz, 300 m, 2 ♀, x.1987 (*Chacon*); 1 ♂, 2 ♀, xi.1987 (*Chacon*); Cerro El Hacha, 300 m, 12 km South East La Cruz, 1 ♂, 1 ♀; Derrumbe, Estacion Mengo, 1400 m, West side Volcan Cacao, 1 ♀; Estacion Mengo, 1100 m, South West side of Volcan Cacao, W85°28'10" N10°55'43" 1 ♂, vi.1988 (*Janzen & Hallwachs*); 1 ♂, 3 ♀ (*Janzen & Hallwachs*); Finca Jenny, 300 m, 31 km North Liberia, 2 ♂, 3 ♀; Santa Rosa National Park, 300 m, 3 ♀, 6.vi.1978 (*Janzen*); 1 ♂, 12.vi.1978 (*Janzen*); 2 ♂, 1 ♀, 2.vii.1978 (*Janzen*); 1 ♂, 12.xii.1978-10.i.1979 (*Janzen*); 1 ♀, 18-20.v.1979 (*Janzen & Hallwachs*); 1 ♀, 19-21.vi.1979 (*Janzen & Hallwachs*); 1 ♀, 22-24.vi.1979 (*Janzen*); 1 ♂, 27-30.vi.1979 (*Janzen*); 1 ♂, 10-12.xi.1979 (*Janzen*); 1 ♂, 1♀, 23-25.xi.1979 (*Janzen & Hallwachs*); 1 ♂, 26-28.xi.1979 (*Janzen*); 1 ♀, 7-9.xii.1979 (*Janzen & Hallwachs*); 1 ♀, 21-24.xii.1979 (*Janzen*); 2 ♂, 2-11.iii.1980 (*Janzen & Hallwachs*); 2 ♀, 1.v.1980 (*Janzen & Hallwachs*); 1 ♀, 5-6.v.1980 (*Janzen & Hallwachs*); 1♂, 1 ♀, 9-11.v.1980 (*Janzen & Hallwachs*); 2 ♀, 16-18.vii.1980 (*Janzen & Hallwachs*); 1 ♀, 9-17.iii.1981 (*Janzen & Hallwachs*); 1 ♀, 1-5.i.1982 (*Janzen & Hallwachs*); 1 ♂, 1-15.i.1982 (*Janzen & Hallwachs*); 2 ♀, 10-20.iii.1982 (*Janzen & Hallwachs*); 1 ♂, xii.1982 (*Janzen & Hallwachs*); 300 m, 6 ♂, 1 ♀, i.1983 (*Janzen & Hallwachs*); 1 ♂, ii.1983 (*Janzen & Hallwachs*); 2 ♀, iii.1983 (*Janzen & Hallwachs*); 1 ♀, 3.vi.1983 (*Janzen & Hallwachs*); 1 ♂, 1 ♀, iv.1984 (*Janzen & Hallwachs*); 1♂, 2 ♀, v.1984 (*Janzen & Hallwachs*); 1 ♂, 15-17.iii.1986 (*Janzen & Hallwachs*); 4 km East Casetilla Rincon National Park, 1 ♀, 14.ii.1983 (*Janzen & Hallwachs*); Estacion Maritza, 600 m, West side Volcan Orosi, 1 ♂, v.1988 (GNP Biodiversity Survey); Finca Jenny, 30 km north Liberia, W85 34'272 N10 51'55", 1 ♂, xii.1987 (GNP Biodiversity Survey); 1 ♂, i.1988 (GNP Biodiversity Survey); 1 ♂, 3 ♀, viii.1988 (GNP Biodiversity Survey). *Heredia:* Chilamate, Heredia, 2 ♂, 1 ♀, 9.viii.1986 (*Covell*). *Limón:* Sixola River, 2 ♂; Cerro Tortuguero, Parque Nacional Tortuguero, 100 m, 3 ♂, 2 ♀ iv.1989 (*Aguillar & Solano*); 1 ♂, x.1989 (*Solano*); *Puntarenas:* Fila Esquinas, 35 km South of Palmar Norte, 150 m, 8°45' x 83°20', 1 ♂, 7-8.i.1983 (*Janzen & Hallwachs*).

PANAMA: *Veraguas:* Veragua, 1 ♂.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♂ [holotype of *derasa*]; 12 ♂, 13 ♀ (*Le Moult*); Saint Laurent du Maroni, 1 ♂, 1923 (*Aymès*); 7 ♂, 3 ♀; Nouveau Chantier, 1 ♂; 1 ♀ (*Bar*).

SURINAM: *Sipalawini:* Thibiti area, Kabo Creek (partly swampy, primary forest on hilly slopes circa 2 km from river), 2 ♀.

GUYANA: Bought at Georgetown, 1 ♂. *Mazaruni-Potaro:* Omai: 1905, 1 ♂ [holotype of *coerulea*] 1 ♂, 11 ♀; Tumatumari, 1 ♂, xii.1907 (*Klages*); Kartabo Point, 1 ♂, 1 ♀. *East Demerara-West Coast Berbice:* Rockstone, Essequebo, 1 ♀.

VENEZUELA: *Bolívar:* Maripa, Caura River, 1 ♂ (*Klages*). Anacoco, 60 m, 1 ♂. Guririo Caroni, 100 m, 1 ♂. 88 km South El Dorado, 1 ♂, 26-28.vi.1984, 1 ♂ (*Covell*); Las Clarita, 1 ♂, 1 ♀, 28.vi.1984 (*Covell*). *Lara:* Canoñ Panzacola, Guárico, 1 ♂. Guárico, Hato Masaguaral, 45 km South Calabozo, 1 ♂, 1 ♀.

COLOMBIA: *Meta:* East Colombia: Upper Río Negro, 800, 1 ♂; 1 ♂.

PERU: *Madre de Diós:* Tambopata Reserve, 300 m, 30 km South West Peurto Maldonado, 6 ♂, 16-22.x.1983 (*Covell*).

BOLIVIA: *Santa Cruz:* River Yapacani, 600 m, 1 ♂.

PARAGUAY: *Amambay:* Parque Nacional Cerro Cora, 1 ♂. *Paraguai:* Sapucay, 1 ♂, 6.ix.02 (*Foster*); 1 ♂, 30.x.04 (*Foster*); 26.2 km South East Ybycui, Parque Nacional Ybycui, 3 ♂.

BRAZIL: Minas Geraes, Uberaba, 1 ♂ (*Le Moult*); East Brazil: Tutaya, 2 ♂ (*Moss*); 1 ♀ [holotype of *sesquiplaga*]; Perambuca, 4 ♂. *Acre:* Rio Juruá, 4°40'S 666°40'W, 1 ♂, 20.x.74. *Amazonas:* Humayta, River Madeira, 1 ♂; Sao Paulo de Olivença, 1 ♂.

Bauru, Sao Paulo, 1 ♂. *Mato Grosso do Sul:* 15 miles South Corumba, Urucum, 650 ft, 1 ♂ [holotype of *coerulea aphenges*] 23.xi.27 (*Collenette*); Burity, 30 miles North East of Cuyaba, 2250 ft, 2 ♂, 1-14.vii.27 (*Collenette*); 6 ♂, 1886 (*Germain*); Tombador, 16 miles South of Diammantino, 1500 ft, 1 ♂, 20-27.viii.27 (*Collenette*). *Pará:* Unt. Amaz. Taperhina: below Santarem, 1 ♂, 21-31.viii.1927 (*Zerny*); 1 ♂, 1 ♀, 1-7.ix.27. *Rondônia:* Calama, River Madeira, below River Machados, 1 ♂, viii-x.07 (*Hoffmann*). *Rio de Janeiro:* Rio de Janeiro, 1 ♂, x. *Santa Catarina:* Santa Catarina, Nova Brémen, 850 m, 1 ♂, xi.37 (*Hoffmann*). *Sao Paulo:* Alto de Serra, Santos, 800 m, 1 ♀, 3.xii.12.

UNKNOWN: Portorico, 1 ♀ [lectotype].

Depositories: Berlin museum, BMNH, CMNH, C. V. Covell Jr. collection, Den Haag museum, HEC, INBio, NMNH, UCV.

Oospila depressa Warren

(Figs 8, 78, 139, 188)

Oospila depressa Warren, 1905: 45; Prout, 1912: 133; 1932: 57. Lectotype ♀, here designated, in BMNH. Type locality: COSTA RICA. Label data: Type; Tuis, Costa Rica; Oospila depressa type ♀ Warr[en]; isthoxia; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15719 ♀. [Examined.]

Oospila semiviridis Warren, 1909: 84; Prout, 1912: 134. Holotype ♂, in BMNH. Type locality: PERU. Label data: Type; La Oroya R[ío] Inambari, S[outh] E[ast] Peru, 3100 ft., wet s[eason], March 05. (G. Ockenden); Oospila semiviridis type ♂ Warr[en]; Rothschild Bequest B[ritish] M[useum] 1939-1; Geometridae genitalia slide No. 15716 ♂. [Examined.] **New synonymy**

♂, ♀ (Figs 8, 78). Forewing length 11-15 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; blotches cream or pale brown, with dark brown striations and perimeters. Forewing: with costa pale brown; blotch at apex variable in size, rounded, extending to costa, not connected to blotch at tornus by band along termen; blotch at tornus variable in size, but never large enough to cover discal spot, wider at centre, tapering gradually towards termen, without abrupt constriction; discal spot small, brown. Hindwing: with blotch at apex large; blotch at tornus smaller, approximately circular; blotch at anal margin small, narrow; discal spot white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with pink and brown flecks around crests, remainder of dorsal surface cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 139). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace present. Valvae: with deep apical cleft; sacculus extended into long, thin sclerotised process; ampulla short, with denticulate apical margin. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae; with posterior extended into tongue-shaped process. Vinculum with ventral plate V-shaped. Coremata absent. Aedeagus usually without, rarely with small cornutus on vesica.

♀ *genitalia* (Fig. 188). Sterigma rectangular. Bursa copulatrix: ductus bursae strongly sclerotised and striated, antrum absent; corpus bursae small, spherical; signum small. Anterior apophyses short.

Distribution. Material was examined from Guatemala, Belize, Costa Rica, Panamá, Venezuela, Peru and Bolivia.

Diagnosis. *Oospila depressa* can be distinguished from *albicoma albicoma* and *concinna* by the shape and extent of the blotch at the tornus of the forewing. In *depressa* this blotch is smaller, never extends to cover the discal spot and is wedge-shaped, tapering gradually towards the termen, and never with an abrupt constriction (compare Figs 8, 14, 54, 56 and 78). The absence of a digitate extension of the blotch at the tornus of the forewing distinguishes *depressa* from *albicoma nasuta* (compare Figs 8, 55 and 78).

The small, approximately circular blotch at the tornus of the hindwing distinguishes *depressa* from *longiplaga* in which this blotch is longer and approximately rectangular (compare Figs 8, 18 and 78). The large blotch at the apex of the forewing distinguishes *depressa* from *lunicincta* (compare Figs 8, 19 and 78).

The male genitalia of *depressa* can be recognised by the small tongue-shaped posterior extension of the anellar complex. The female genitalia can be recognised by distinctive shape of the sterigma (Fig. 188).

Material examined.

GUATEMALA: *Izabel:* Cayuga, 1 ♀, vi. (*Schaus and Barnes*); 1 ♂, 3 ♀; 1 ♂, v. (*Schaus & Barnes*); Chejel, 1 ♂, 1 ♀; near Matias de Galvez, 1 ♀; Quirigua, 1 ♀. **BELIZE:** Belize, 1 ♀; Río Grande, 1 ♂, xii.1932 (*White*); 1 ♀. *Toledo:* Punta Gorda, 1 ♀ x.1935 (*White*).

COSTA RICA: Canta Rana, 300 m, 1 ♀ (*Herbulot*). *Cartago:* Tuis, 1 ♀ [lectotype of *depressa*]; 2 ♀; Sitio 1 ♀, v; Juan Vinas, 2500 ft, 1 ♂, v. (*Schaus*); 3 ♂, 1 ♀; Moravia de Chirripo, 1000 m, 1 ♀, 10.v.1983 (*Janzen & Hallwachs*). *Guanacaste:* Rincon National Park, 4 km East Casetilla, 750 m, 1 ♀, 22.v.1982 (*Janzen & Hallwachs*); 1 ♂, 8.x.1982 (*Janzen & Hallwachs*); 4 km East Casetilla 750 m, 1 ♂, 11.iv.1983 (*Janzen & Hallwachs*); Mirador Ad., 900 m, 1 ♀, 29.iii.1984 (*Janzen & Hallwachs*); 4 km West Station Cecilia, 250 m, 1 ♂, 25.ii.1985 (*Janzen & Hallwachs*); 2 km South-West Station Cecilia, 300 m, 1 ♂, 25.xii.1984. *Heredia:* La Selva Biological Station, Puerto Viejo de Sarapiqui, 40 m, 1 ♀, iv.1987 (*Chavarria*). *Limón:* Cerro Tortuguero, North edge Tortuguero National Park, 0-100 m, 2 ♀, 30.v.1984 (*Janzen & Hallwachs*); Guapiles, 1 ♀. *Osa Peninsula:* Sirena Corcovado National Park, 2 ♂, 5-11.i.1981 (*Janzen & Hallwachs*). *Puntarenas:* San Vito, 1 ♀; Fila Esquinas, 35 km South of Palmar Norte, 8°45' x 83°20', 1 ♀, 7-8.i.1983 (*Janzen & Hallwachs*). *San José:* Estacion Carrillo, Parque Nacional Braulio Carrillo, 700 m, 1 ♀, ix.1984 (*Chacon & Chacon*); 2 ♂, x.1984 (*Chacon & Chacon*); 1 ♂, i.1985 (*Chacon & Chacon*); 1 ♂, iii.1985 (*Chacon & Chacon*); 1 ♂, 1 ♀; Fila Esquinas, 35 km South of Palmar Norte, 150 m, 1 ♀, 7-8.i.1988 (*Janzen & Hallwachs*).

PANAMA: *Chiriquí:* Volcan de Chiriquí, 200-300 ft, 1 ♀ (*Champion*); Lino, 1 ♀; Oja de Agua, 1600 m, 1 ♀ (*Herbulot*); Environs de Estacion Clara, 1 ♂ (*Herbulot*); 15 km Norte Oeste de El Hato del Volcan, 1400 m, 1 ♀ (*Herbulot*). *Canal Zone:* Barro Colorado Island, 2 ♀.

VENEZUELA: *Aragua:* Rancho Grande, 1 ♀, 28.vi-18.vii.1974 (*Watson*); 1 ♂, 12.vii-16.viii.1976 (*Watson*). *Bolívar:* 88 km South El Dorado, Estado Bolívar, 150 m, 1 ♂, 26-28.vi.1984 (*Covell*).

PERU: *Puno:* La Oroya, Río Inambari, 3100 ft, 1 ♂, dry season, ix.04 (*Ockenden*); 1 ♀, wet season, x.1904 (*Ockenden*); 1 ♂ [holotype of *semiviridis*] wet season, iii.05 (*Ockenden*); Carabaya, Río Huacamayo, 3100 ft, 1 ♂, dry season, vi.04 (*Ockenden*).

BOLIVIA: *Santa Cruz:* East Bolivia: Buenavista, 1 ♀, vii-x.1906 (*Steinbach*); Provincia del Sara, 450 m, 1 ♀, xi.1909 (*Steinbach*).

Depositories: BMNH, C. Herbulot collection, CMNH, INBio, NMNH.

Oospila rubescens (Warren)

(Figs 79, 140, 189)

Racheolopha rubescens Warren, 1906: 423. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: Maroni R[iver], S[ain]t Jean; Schaus Coll[ection]; Type No. 9192 U.S.N.M; Genitalia slide by MAC 57763 USNM. [Examined.]

Oospila rubescens (Warren); Prout, 1932: 58.

♂, ♀ (Fig. 79). Forewing length 8-10 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour dark green; markings reddish brown. Forewing: with costa pale brown; blotch at apex large, extending to costa, connected to blotch at tornus by broad band along termen; blotch at tornus large; discal spot small, brown. Hindwing: blotches at apex and tornus large, connected by broad band along termen; discal spot small, white. Hindleg: proximal spurs absent; brush of long hair-like scales present on male tibia. Abdomen: with dorsal surface around crests cream or brown; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior present in male; sternum A8 strongly sclerotised in male, with bifurcate posterior extension.

♂ *genitalia* (Fig. 140). Uncus with apical extension very short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace. Valvae: deeply divided at apex; with sacculus extended into short, robust, spinulose process; ampulla long, thin, digitate, articulating close to base of valva. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with V-shaped ventral plate. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia* (Fig. 189). Sterigma dumbbell shaped. Large, shallow pocket present on each side of sterigma. Bursa copulatrix: ductus bursae broad, quite long, with short antrum, strongly sclerotised but weakly striated below antrum; corpus bursae squarish; signum small. Anterior apophyses short.

Distribution. Only known from French Guiana and Surinam.

Diagnosis. *Oospila rubescens* can be distinguished from *circumsignata* by the blotch at the apex of the forewing which extends to the costa in *rubescens* (compare Figs 15 and 79). Males can also be distinguished by the presence of a brush of long hair-like scales on the hind tibia of *rubescens*. The female genitalia of *rubescens* can be recognised by the distinctive dumbbell-shaped sterigma and the pocket on each side of the sterigma (Fig. 189).

Material examined.
FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♂ [holotype]; 8 ♂, 4 ♀ (*Le Moult*); 1 ♂ (*Le Moult*); 1 ♂ (*Bar*); 8 ♂, 4 ♀; Roches de Kourou, 1 ♂.
SURINAM: *Marowijne:* Areowarwa Creek, Maroewym Valley, 1 ♀, iv.05 (*Klages*).
Depositories: BMNH, NMNH.

***Oospila stagonata* (Felder and Rogenhofer) new combination**

(Figs 80, 141, 190)

Racheospila stagonata Felder and Rogenhofer, 1875: pl. 127, fig 25. Holotype ♀, in BMNH. Type locality: COLOMBIA. Label data: Bogota; Blechroma arycanda Druce; Rothschild Bequest B[ritish] M[useum] 1939-1. [Examined.]

Progonodes stagonata (Felder & Rogenhofer); Warren, 1897: 430; Prout, 1912: 135; 1932: 60.

Racheospila arycanda Druce, 1892: 89 Holotype ♂, in BMNH. Type locality: COSTA RICA. Label data: Type; R[iver] Sucio, Costa Rica, H. Rogers; Godman-Salvin Coll[ection] 1903-4 B[iologia] C[entrali-] A[mericana]. Lep[idoptera-]Het[erocera]. Racheospila arycanda Druce; Racheospila arycanda ♂ type Druce; Geometridae genitalia slide No. 15772 ♂. [Examined.] **New synonymy.**

Progonodes arycanda (Druce); Prout, 1912: 135.

Progonodes stagonata arycanda (Druce); Prout, 1932: 60.

♂, ♀ (Fig. 80). Forewing length 12-17 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour pale green (may be dark green in fresh material); speckled with white. Forewing: with costa pale brown; discal spot usually absent, occasionally small, brown. Hindwing: anterior and posterior discal spots small, white. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests cream; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with bifurcate apical extension.

♂ *genitalia* (Fig. 141). Uncus with apical extension short. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace present. Valvae: short, thin, digitate; costa with small subapical projection; sacculus not extended; ampulla absent. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae. Vinculum with ventral plate broadly W-shaped. Coremata absent. Aedeagus without cornutus on vesica.

♀ *genitalia* (Fig. 190). Sterigma absent. Segment A8 enlarged and strongly sclerotised. Bursa copulatrix: ductus bursae and corpus bursae form large, bulbous, weakly sclerotised complex with some striation, antrum absent; signum small. Anterior apophyses absent.

Distribution. Specimens were examined from Costa Rica, Colombia, Ecuador, and Venezuela.

Diagnosis. *Oospila stagonata* can be distinguished from *holochroa* and *imaculata* by the presence of white speckling on its wings (compare Figs 49, 76 and 80). *Oospila stagonata* has a more mottled appearance than, and lacks the solid green and white patches found in *lactecincta*, *sporadata*, *athena* and *nivetacta* (compare Figs 12, 48, 50, 51, 80, 81). The female genitalia of *stagonata* can be recognised by the enlargement and strong sclerotisation of sternum A8 (Fig. 190).

Material examined.

COSTA RICA: *Cartago:* Orosi, 1200 m, 2 ♀ (*Fassl*). *Limón:* Río Sucio, 1 ♀ [holotype of *arycanda*] (*Rogers*).

COLOMBIA: *Cundinamarca:* Bogota, 1 ♀ [holotype of *stagonata*].

ECUADOR: Ita[i], 1 ♂ (*Buckley*).

VENEZUELA: *Bolívar:* Carret Caicara, San Juan de Manapiare km 170, 300 m, 1 ♀, 4-9.iv.1977 (*Bordon*); Carret Bramor Delicias, 1800 m, 1 ?, 16-17.vii.1980.

Depositories: BMNH, UCV.

Oospila nivetacta (Warren) new combination

(Figs 81, 142, 191)

Racheolopha nivetacta Warren, 1906: 425. Holotype ♂, in NMNH. Type locality: FRENCH GUIANA. Label data: French Guiana: Maroni R[iver], S[ain]t Jean, iv. 1904 (Sch Colombial); Type No. 9199 U.S.N.M. [Examined.]

Progonodes nivetacta (Warren); Prout, 1912: 135; 1932: 60.

♂, ♀ (Fig. 81). Forewing length 10-16 mm. Antenna of female bipectinate. Frons and vertex brown. Interantennal fillet white. Thorax: dorsal surface green. Wings: ground colour white, marked with dark green speckling, concentrated at distal areas of wings leaving central white patch. Forewing: with costa dark brown; discal spot large, brown. Hindwing: with discal spot large, brown. Hindleg: proximal spurs absent; brush of long hair-like scales absent. Abdomen: with dorsal surface around crests green; sternum A2 with brushes of long hair-like scales and elliptical sclerite at posterior absent; sternum A8 strongly sclerotised in male, with very short, bifurcate posterior extension.

♂ *genitalia* (Fig. 142). Uncus not extended apically. Socii large. Gnathos not fused. Tegumen with X-shaped sclerotised brace absent. Valvae: with deep apical division; sacculus extended into long, pointed process; ampulla absent. Anellar complex: completely surrounding aedeagus; with posterior extensions fused to valvae.

Vinculum with ventral plate broad, W-shaped. Coremata absent. Aedeagus long, thin, with small cornutus on vesica.

♀ *genitalia* (Fig. 191). Sterigma absent. Bursa copulatrix: ductus bursae short, strongly sclerotised, not striated; corpus bursae large, bulbous; signum small. Anterior apophyses short.

Distribution. Apparently confined to the North West of South America, this species has been collected in French Guiana, Guyana, Venezuela and Brazil.

Diagnosis. *Oospila nivetacta* can be distinguished from other species of *Oospila* with green and white speckled wing markings by the dark brown colour of the costa, and the large, brown discal spots (compare Figs 12, 48, 50, 51, 80 and 81). The male genitalia of *nivetacta* can be recognised by the shape of the valva (Fig. 142).

Material examined.

FRENCH GUIANA: *Guyane:* Saint Jean du Maroni, 1 ♂ [holotype]; 1 ♂ (*Le Moult*).
GUYANA: *Mazaruni-Potaro:* Rio Potaro, 1 ♂, i.1908 (*Klages*); 1 ♀. Potaro, 1 ♂, ii.1908 (*Klages*). Tumatumari, 1 ♂, xii.1907 (*Klages*).
VENEZUELA: El Boninche res, Forestal Imataca, 200 m, 2 ♂, 6-13.xii.74. *Bolívar:* El Horniguero Meseta de Nuria, 500 m, 1 ♂, 13-17.xii.74.
BRAZIL: *Amazonas:* Upper Amazonas: Fonte Boa, 2 ♂, v.1906 (*Klages*); 1 ♂, vii.07; Sao Paulo de Olivença: 1 ♂, i.1932 (*Wucherpfennig*); 1 ♂, vi-vii.1933 (*Moss*); 1 ♀, vii.1934 (*Waehner*); Nova Olinda, Rio Purus, 1 ♂, v.1922 (*Klages*). *Amapá:* Para, 2 ♂ (*Moss*).
Depositories: BMNH, CMNH, UCV.

INDEX TO SPECIES OF *OOSPILA*

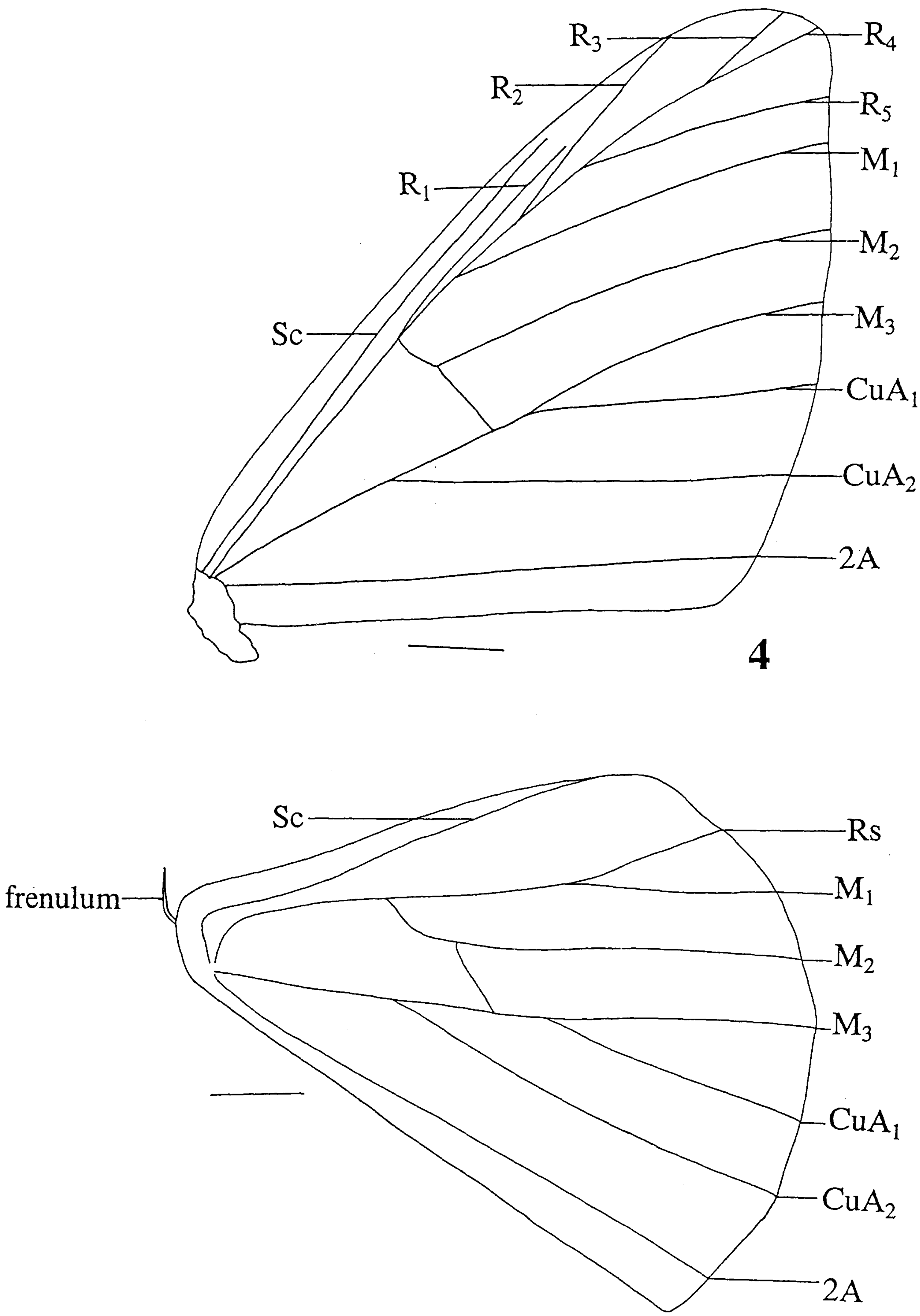

Fig. 4 Wing venation of *Oospila marginata* ♂. Scale bar 2 mm.

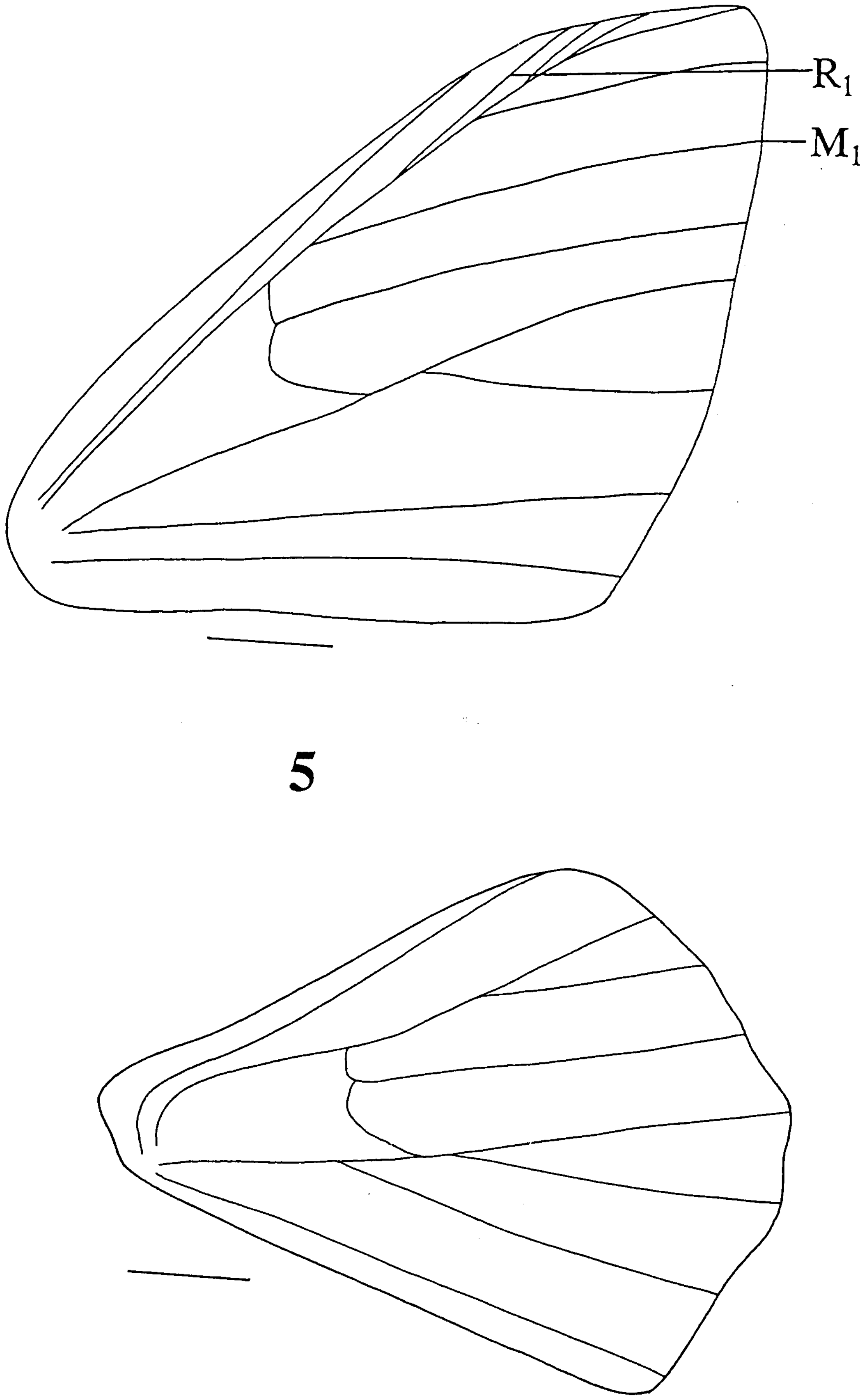

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Fig. 5 Wing venation of *Oospila delacruzi* ♀. Scale bar 2 mm.

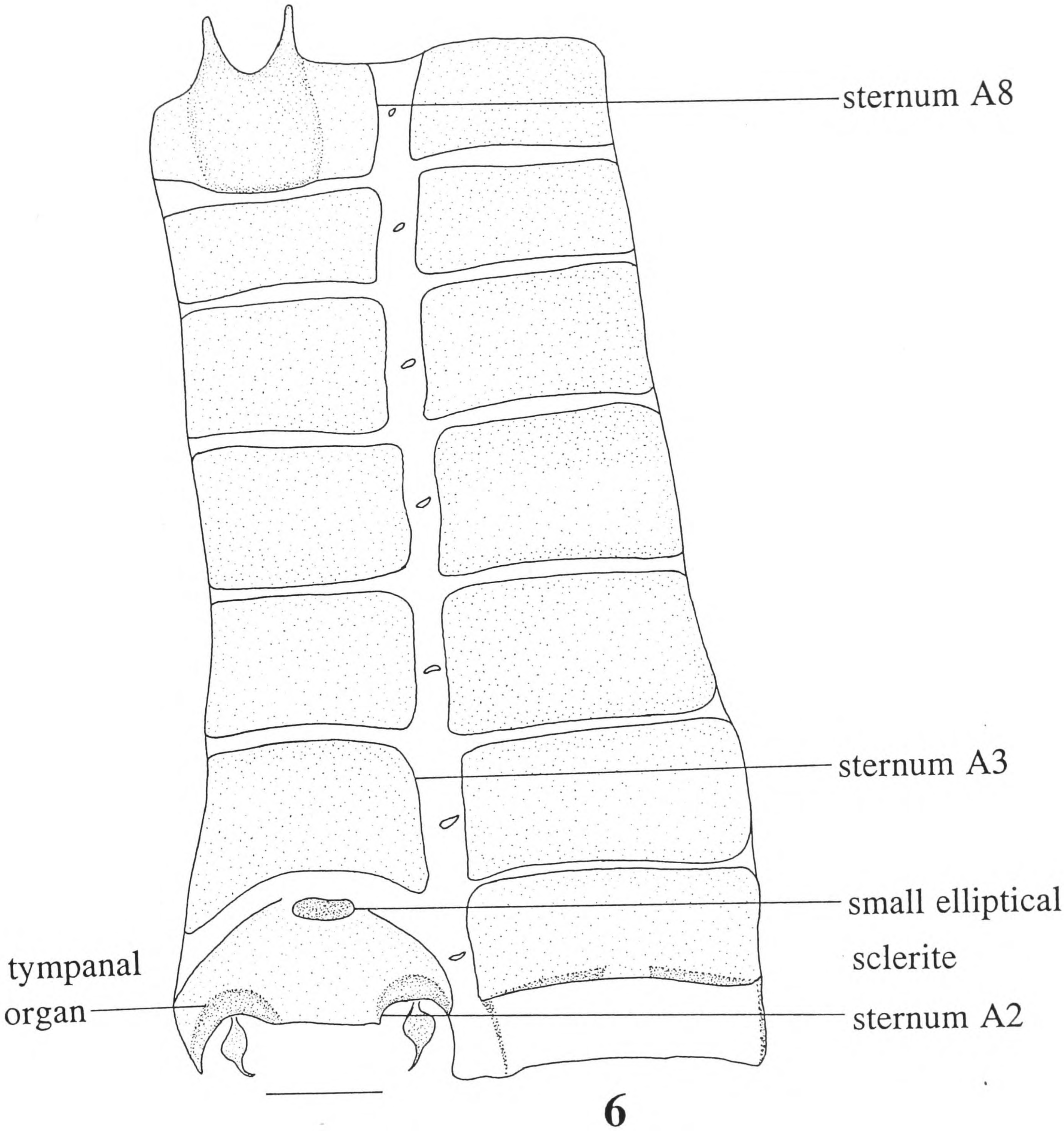

Fig. 6 Pregenital abdomen of *O. carnelunata* ♂. Scale bar 1 mm.

Figs 7-14 (overleaf). *Oospila* species, showing range of variation within the genus. 7, *O. excrescens*; 8, *O. depressa*; 9, *O. violacea*; 10, *O. atroviridis*; 11, *O. obsolescens*; 12, *O. athena*; 13, *O. marginata*; 14, *O. albicoma albicoma*. Scale 1: 2.

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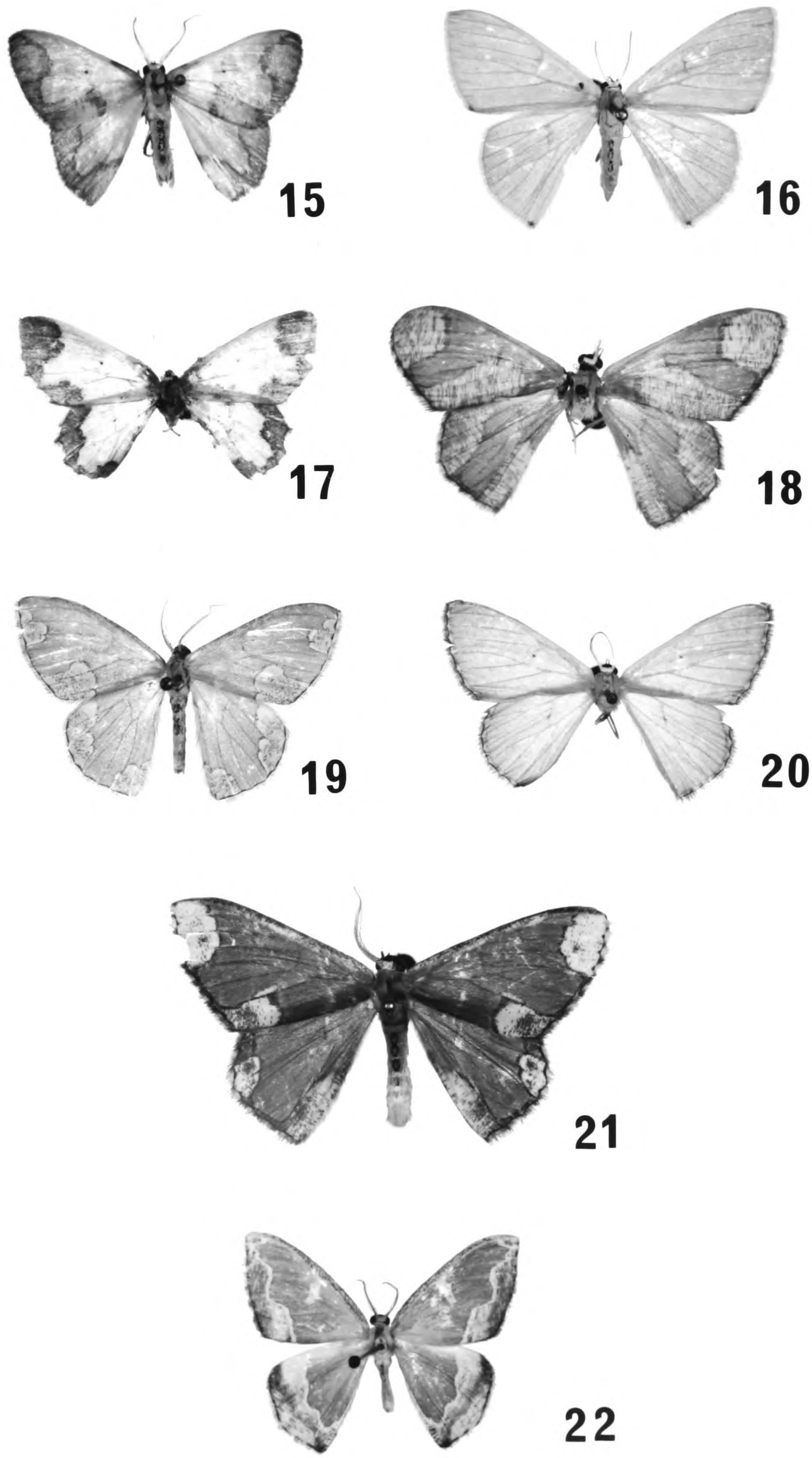
Figs 15-22 (overleaf). *Oospila* species. 15, *O. circumsignata*; 16, *O. decoloraria*; 17, *O. jaspidata*; 18, *O. longiplaga*; 19, *O. lunicincta*; 20, *O. pellucida*; 21, *O. ruptimacula*; 22, *O. venezuelata*. Scale 1: 2.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Figs 23-29 (overleaf). *Oospila* species. 23, *O. quinquemaculata*; 24, *O. continuata*; 25, *O. excrescens*; 26, *O. florepicta*; 27, *O. semispurcata*; 28, *O. rhodophragma*; 29, *O. tortuguera*. Scale 1: 2.

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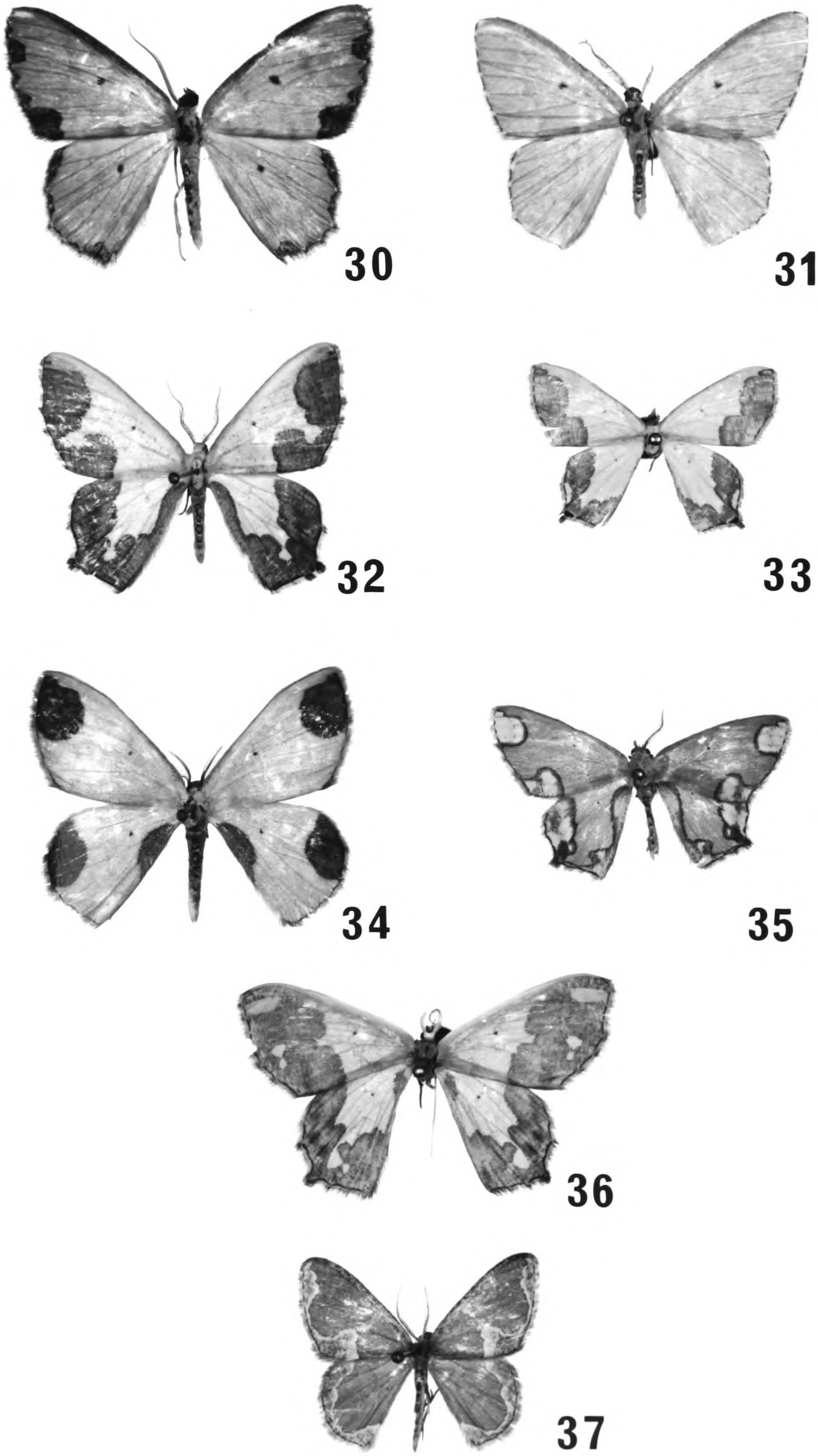
Figs 30-37 (overleaf). *Oospila* species. 30, *O. thalassina*; 31, *O. lacteguttata*; 32, *O. asmura*; 33, *O. circumsessa*; 34, *O. rosipara*; 35, *O. delphinata*; 36, *O. camilla*; 37, *O. astigma*. Scale 1: 2.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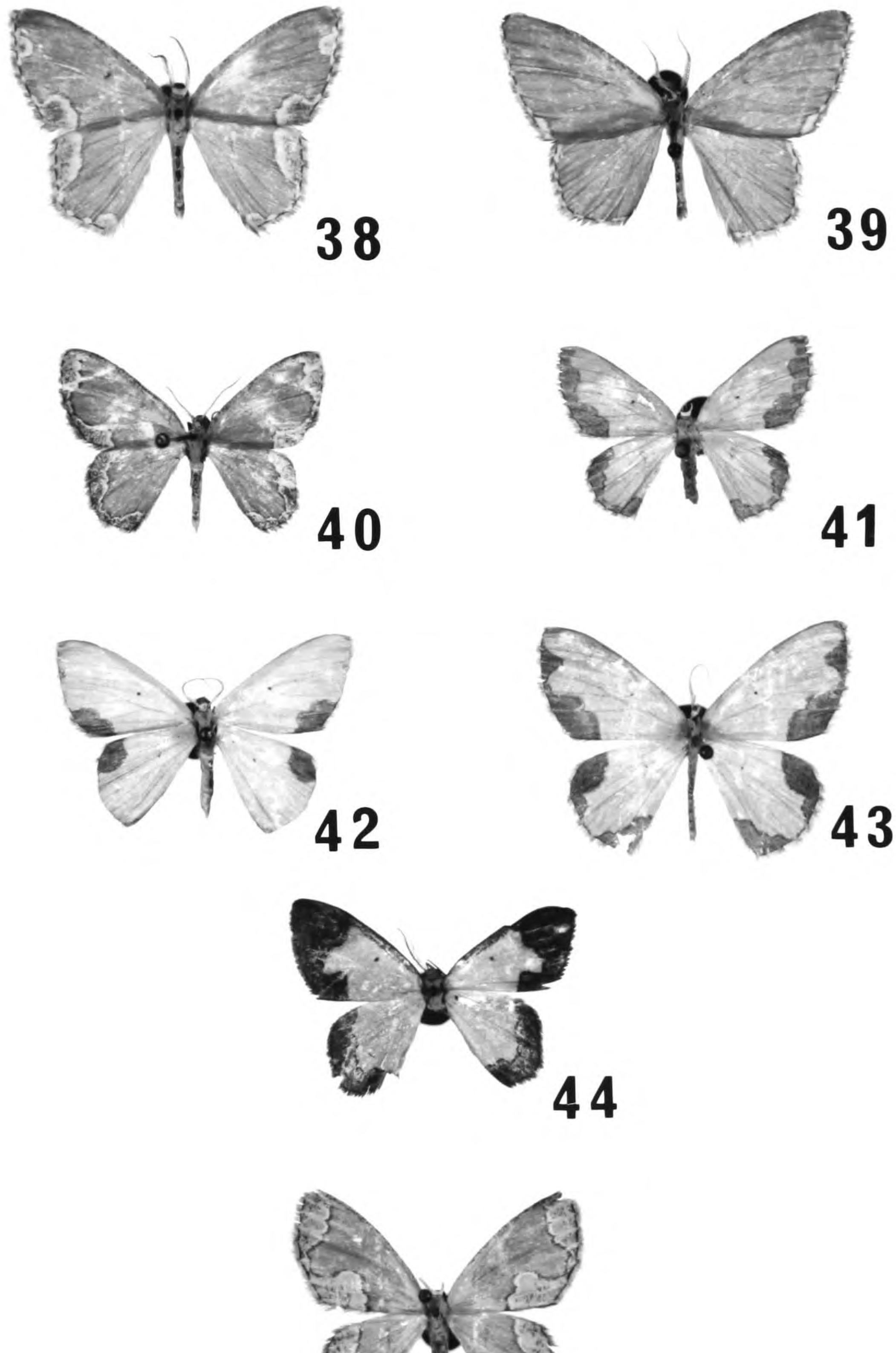
Figs 38-45 (overleaf). *Oospila* species. 38, *O. leucostigma*; 39, *O. delacruzi*; 40, *O. albipunctulata*; 41, *O. rufilimes*; 42, *O. arpata*; 43, *O. fimbripedata*; 44, *O. zamaradaria*; 45, *O. miccularia*. Scale 1: 2.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Figs 46-53 (overleaf). *Oospila* species. 46, *O. euchlora*; 47, *O. ecuadorata*; 48, *O.athena*; 49, *O. holochroa*; 50, *O. lactecincta*; 51, *O. sporadata*; 52, *O. includaria*; 53, *O. leucothalera*. Scale 1: 2.

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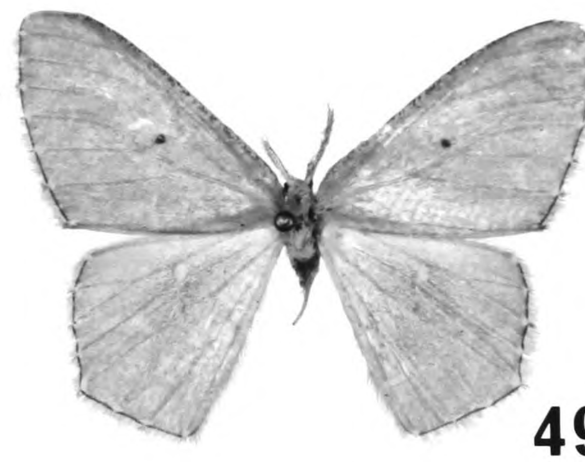

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Figs 54-61 (overleaf). *Oospila* species. 54, *O. albicoma albicoma*; 55, *O. albicoma nasuta*; 56, *O. concinna*; 57, *O. dicraspeda*; 58, *O. ciliaria*; 59, *O. trilunaria*; 60, *O. carnelunata*; 61, *O. altonaria*. Scale 1: 2.

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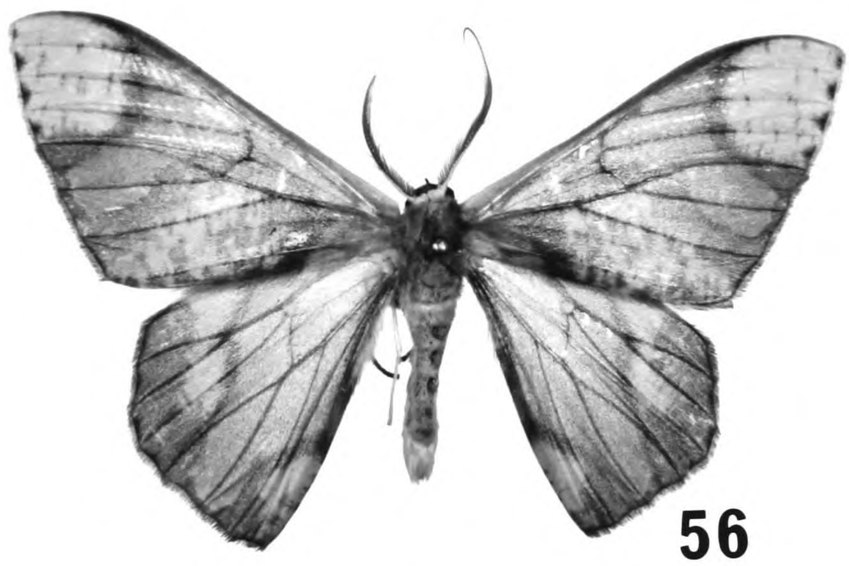

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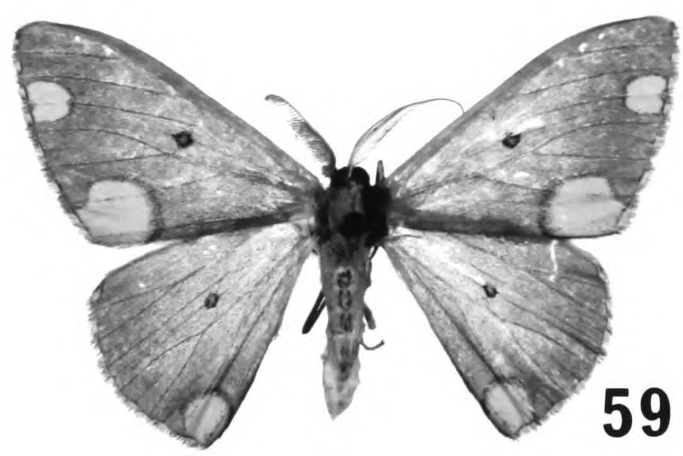

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Figs 62-69 (overleaf). *Oospila* species. 62, *O. confluaria*; 63, *O. longipalpis*; 64, *O. sellifera*; 65, *O. lilacina*; 66, *O. violacea*; 67, *O. callicula*; 68, *O. obeliscata*; 69, *O. marginata*. Scale 1: 2.

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Figs 70-77 (overleaf). *Oospila* species. 70, *O. tricamerata*; 71, *O. obsolescens*; 72, *O. atopochlora*; 73, *O. hyalina*; 74, *O. atroviridis*; 75, *O. congener*; 76, *O. imaculata*; 77, *O. confundaria*. Scale 1: 2.


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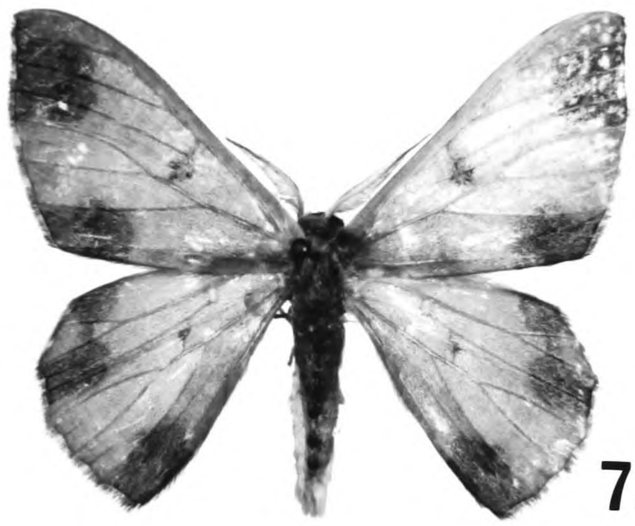
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Figs 78-81 (overleaf). *Oospila* species. 78, *O. depressa*; 79, *O. rubescens*; 80, *O. stagonata*; 81, *O. nivetacta*. Scale 1: 2.


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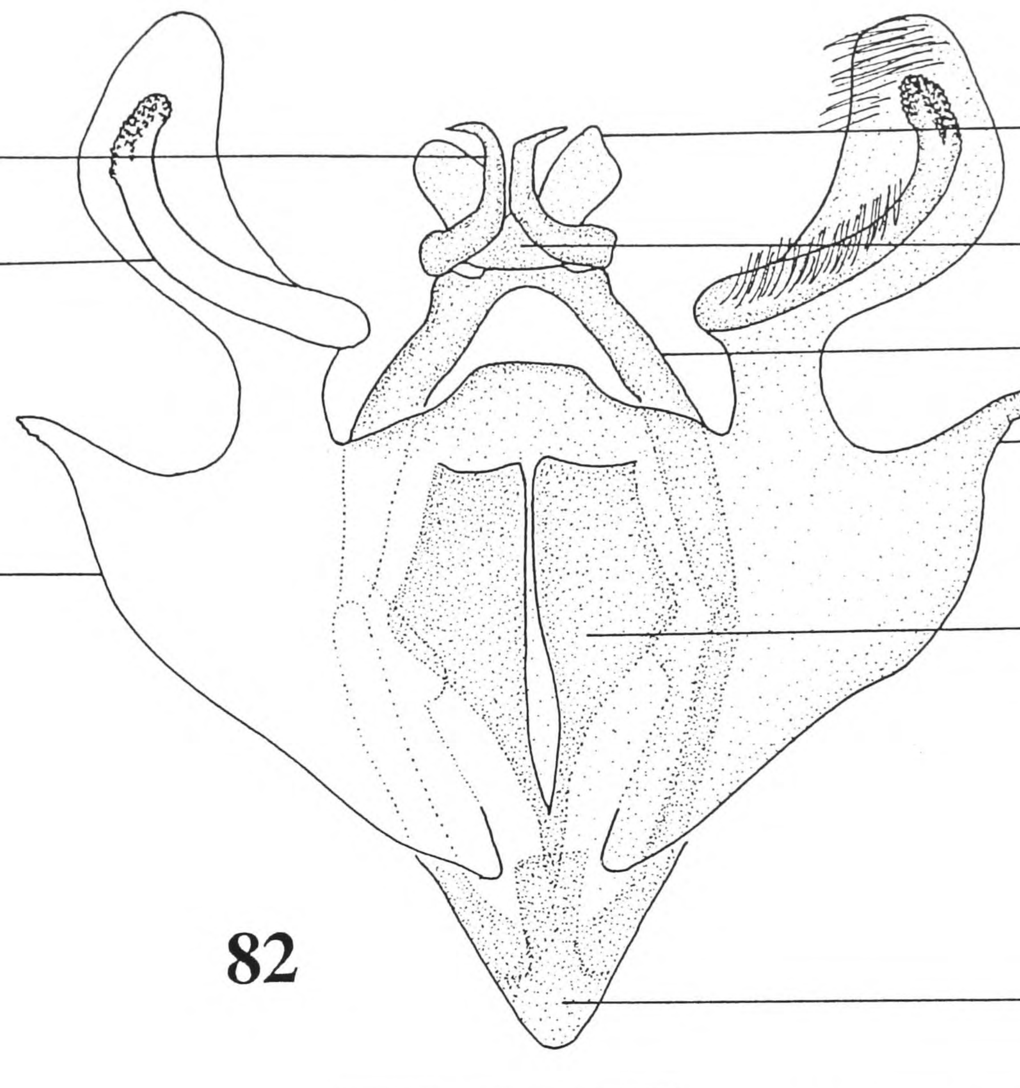
Figs 82-142 (on following pages). Male genitalia and sternum A8 of *Oospila species*. Scale bar 1 mm.



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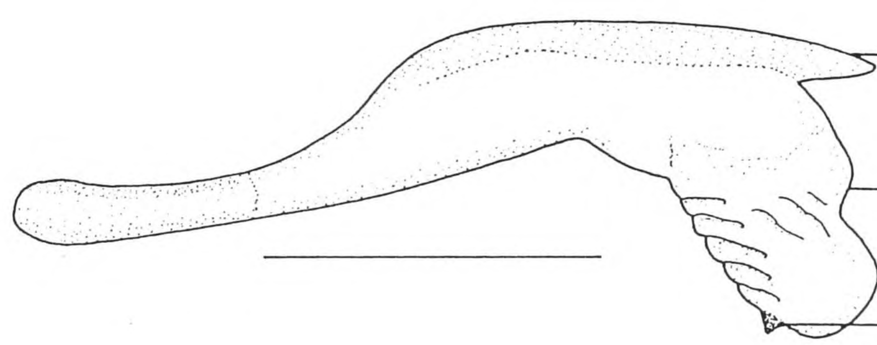
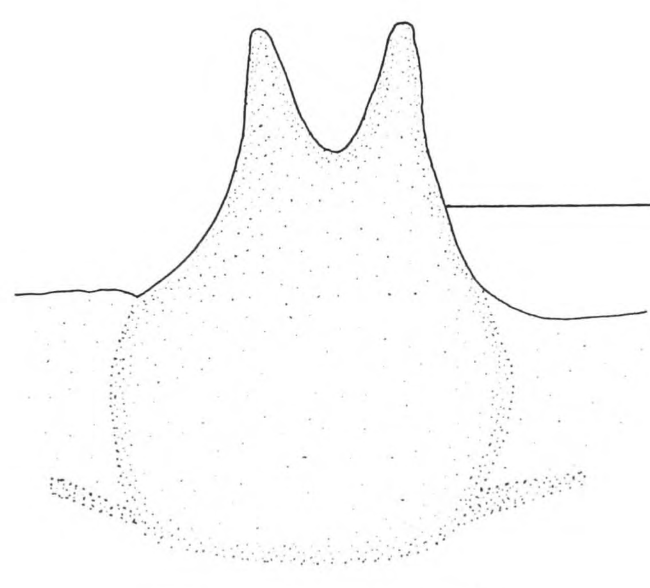
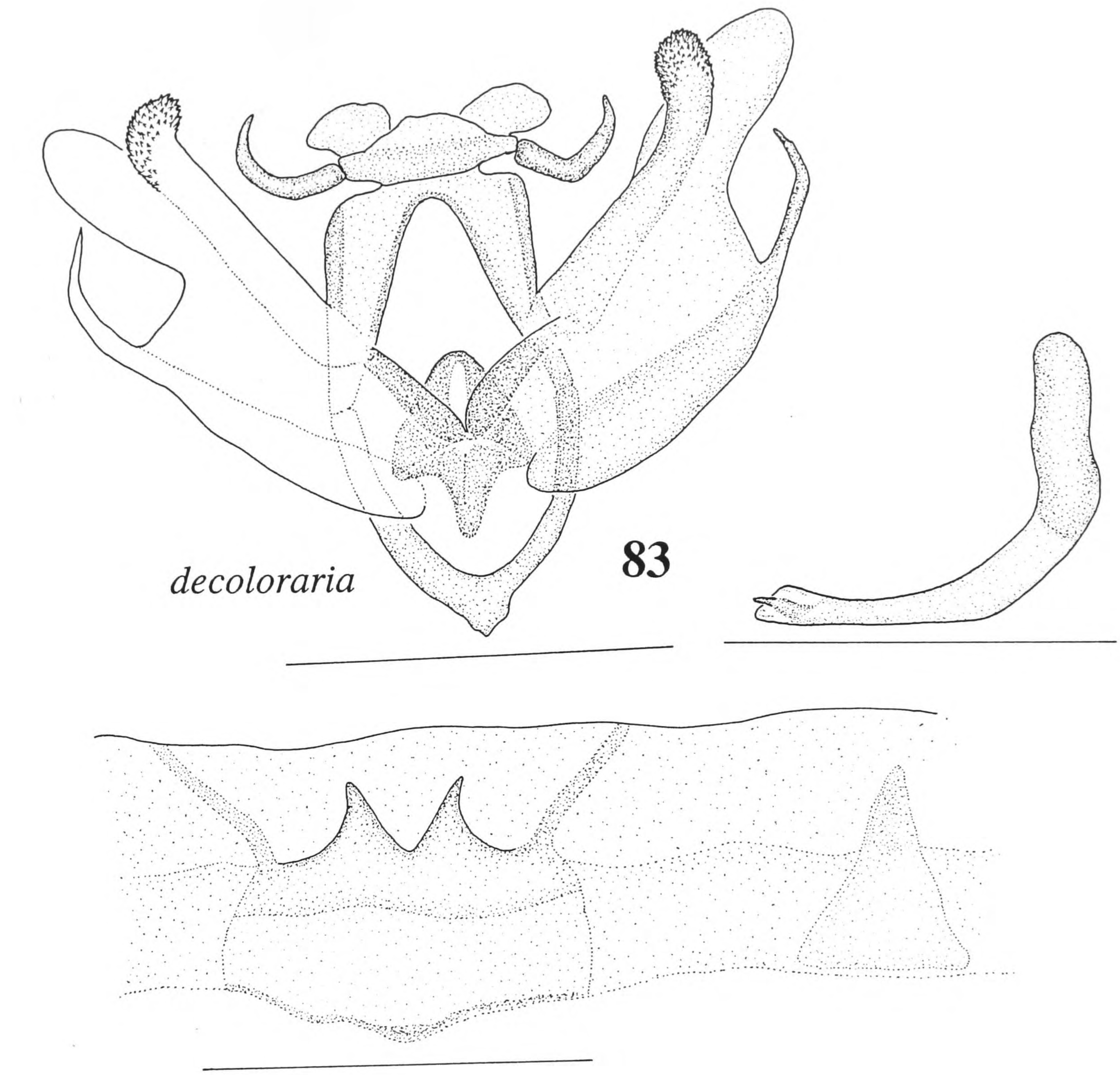
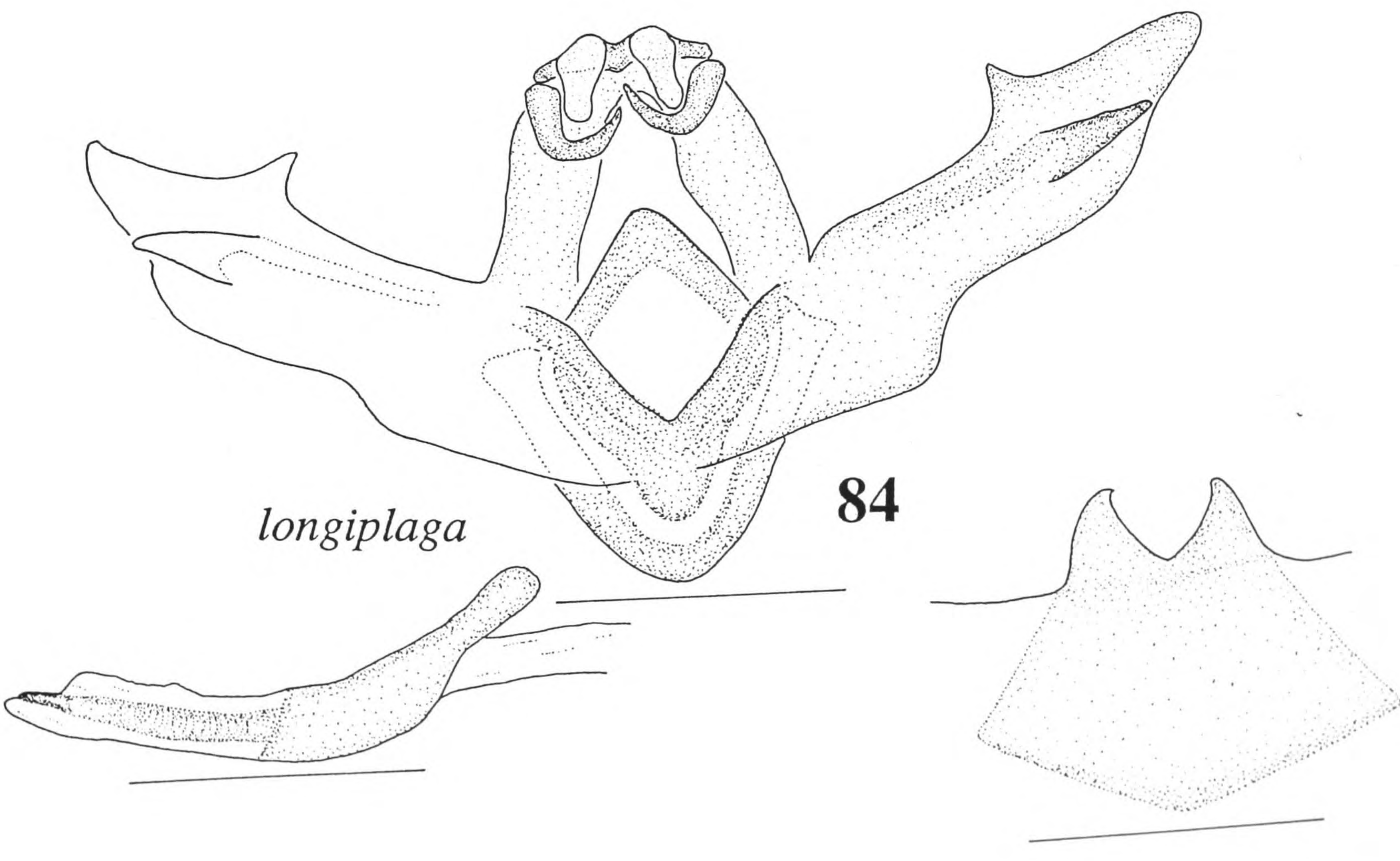
circumsignata



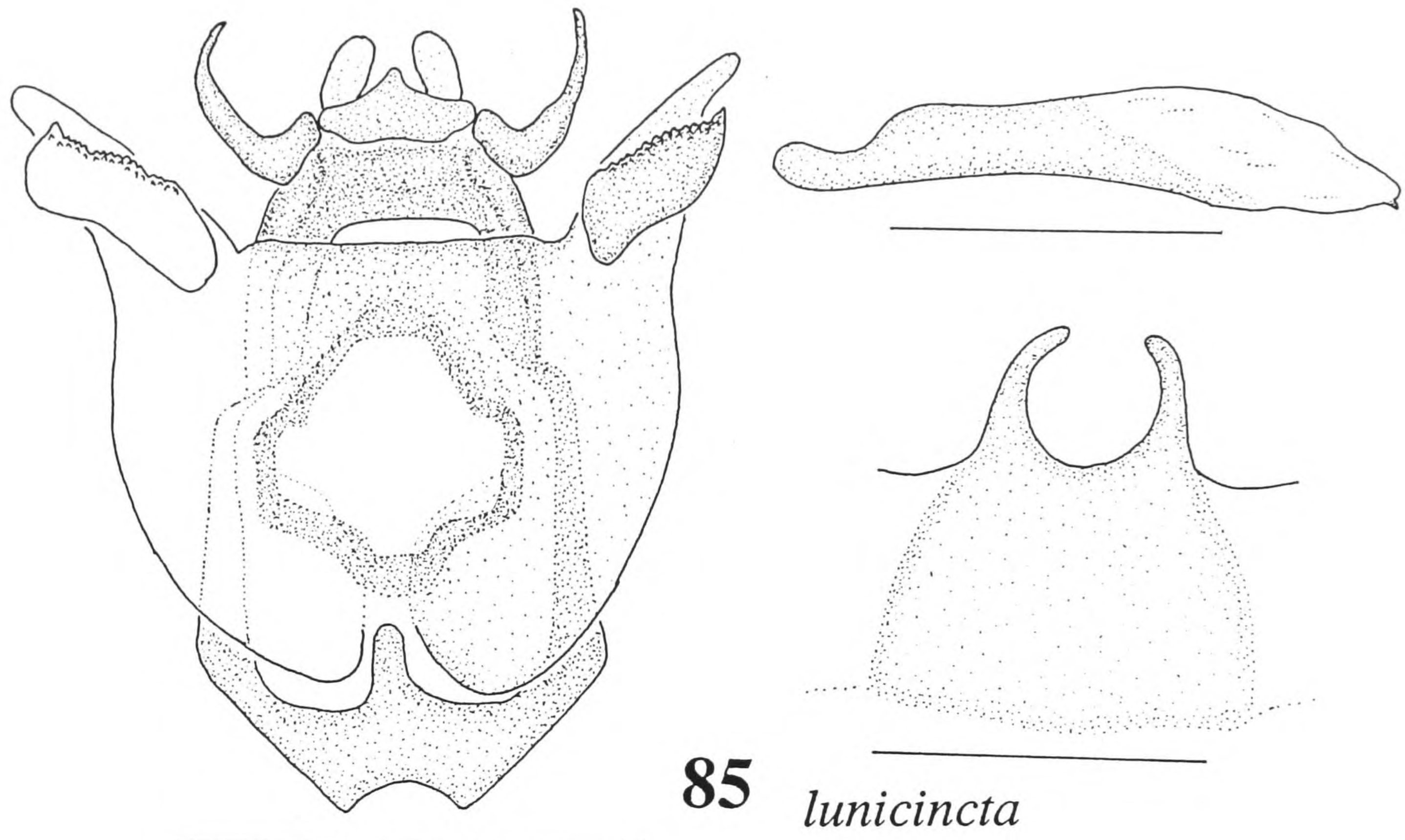




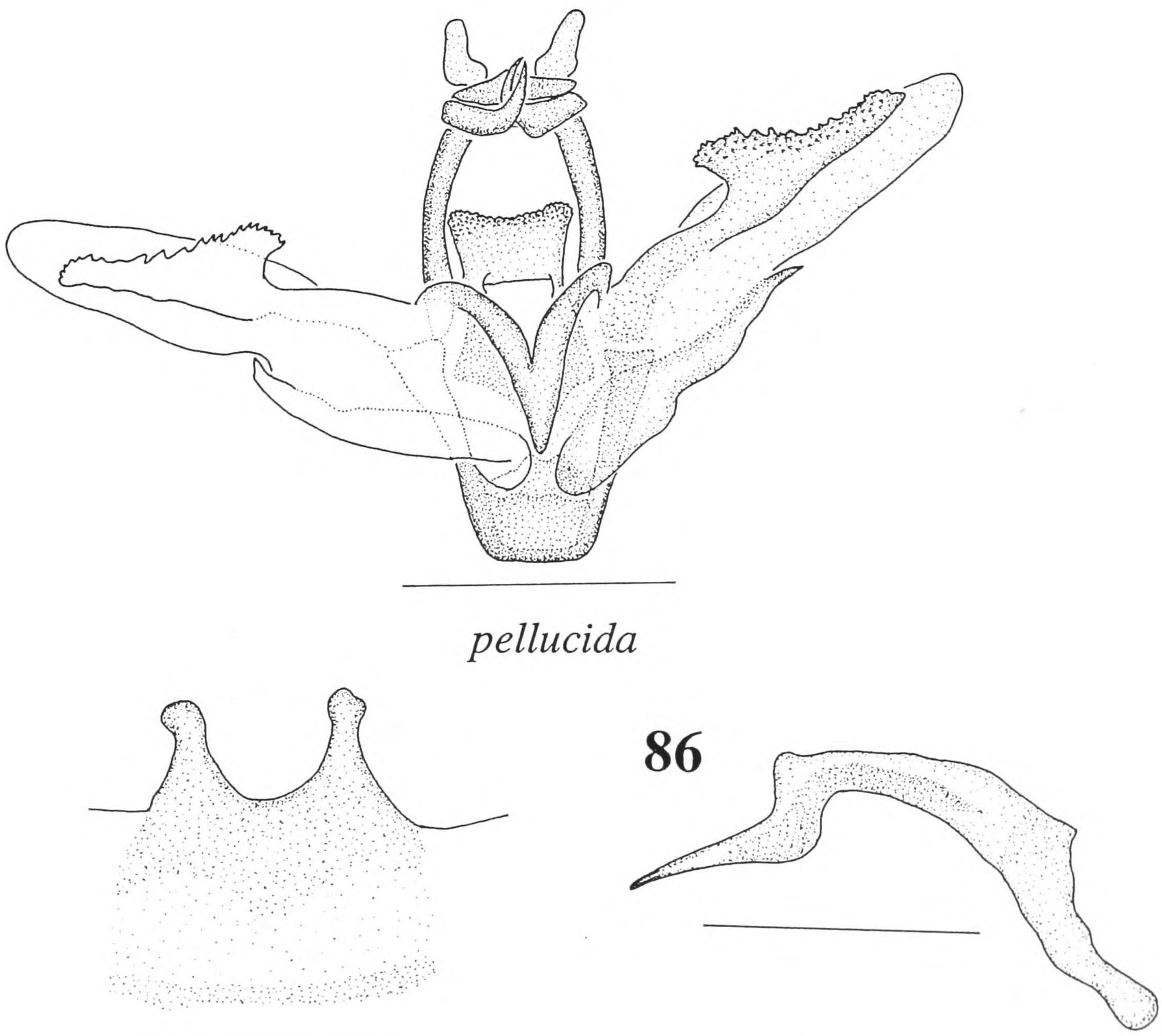
decoloraria **83**



longiplaga **84**



85 *lunicincta*



pellucida

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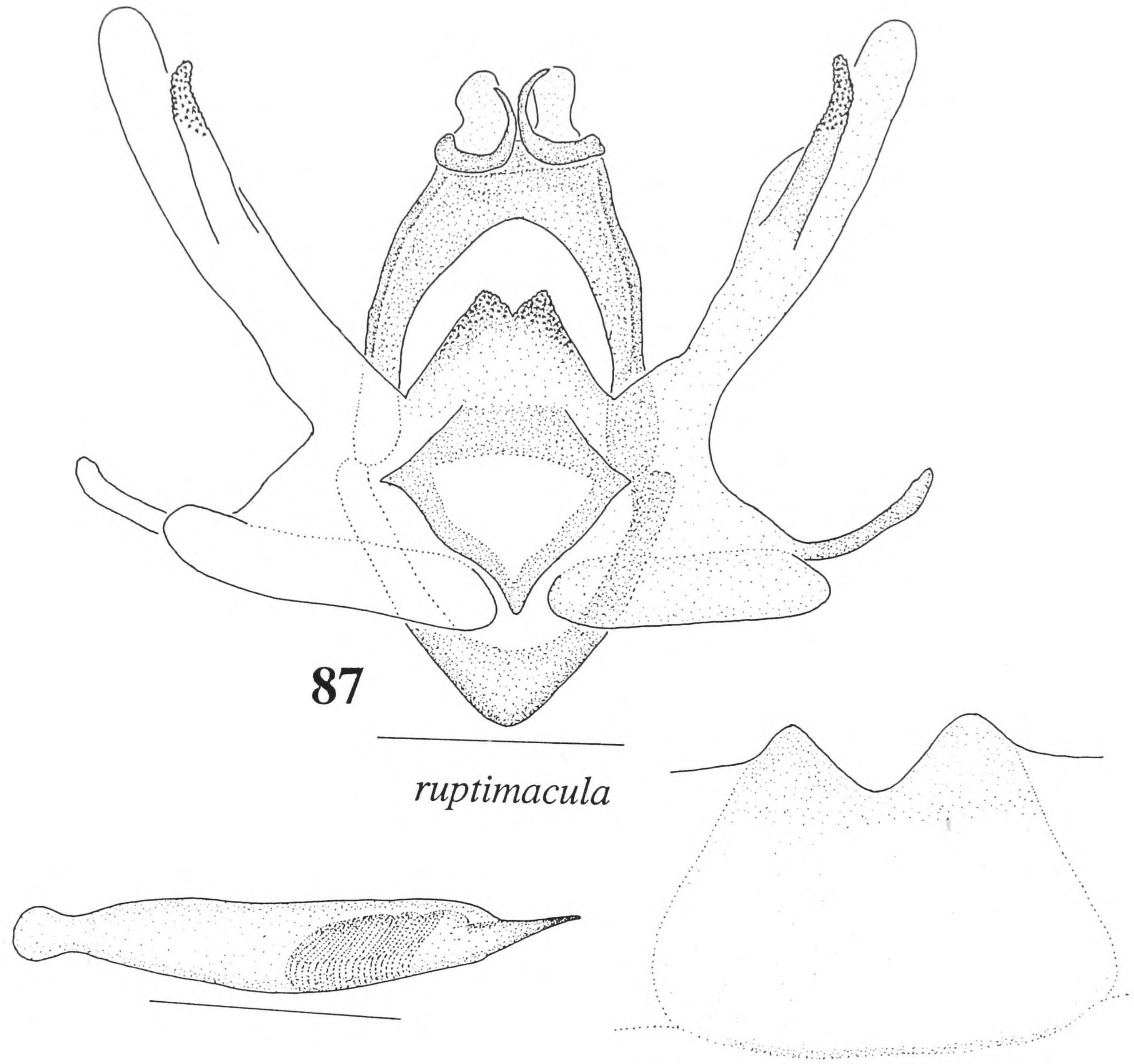
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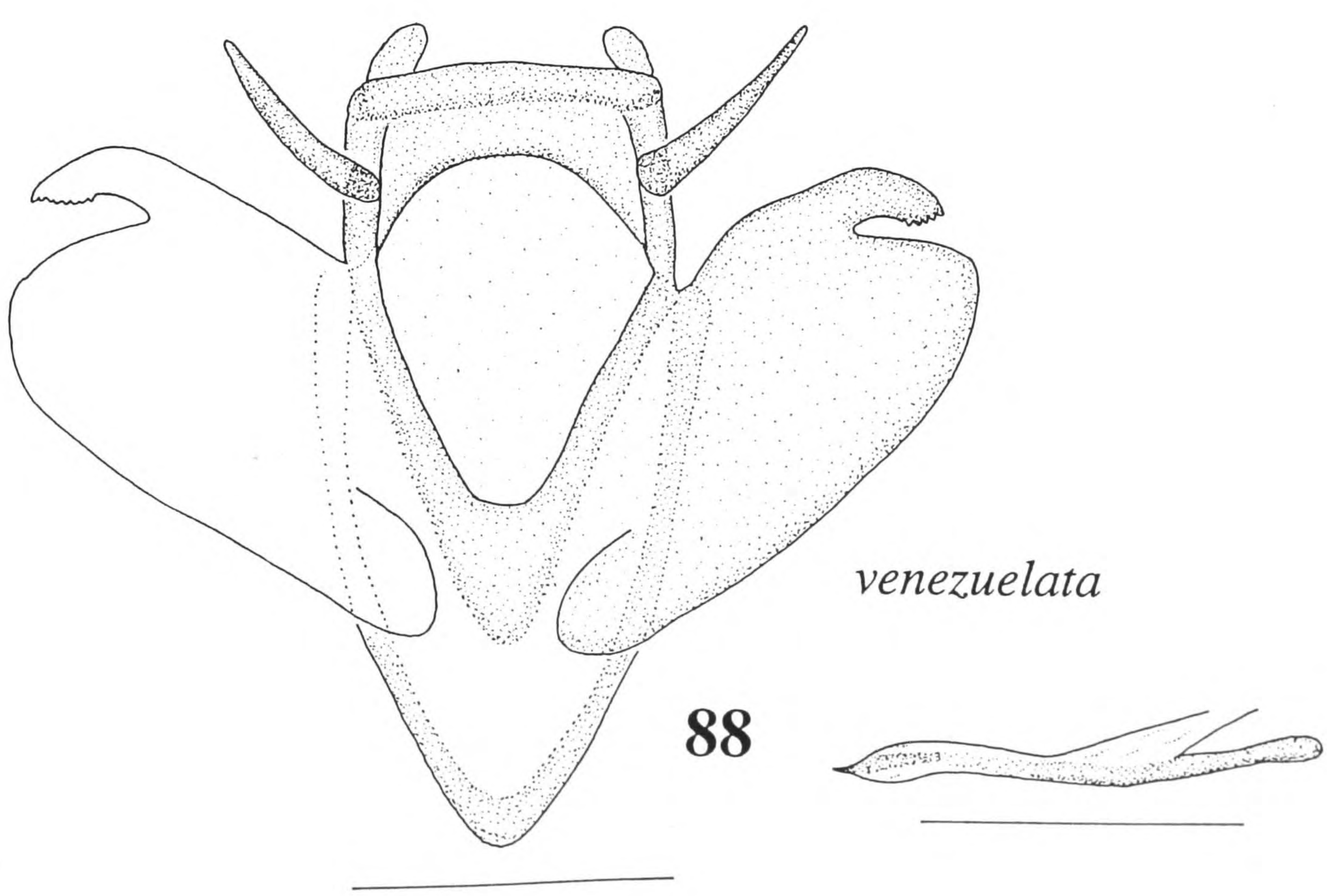
ruptimacula


venezuelata
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quinquemaculata

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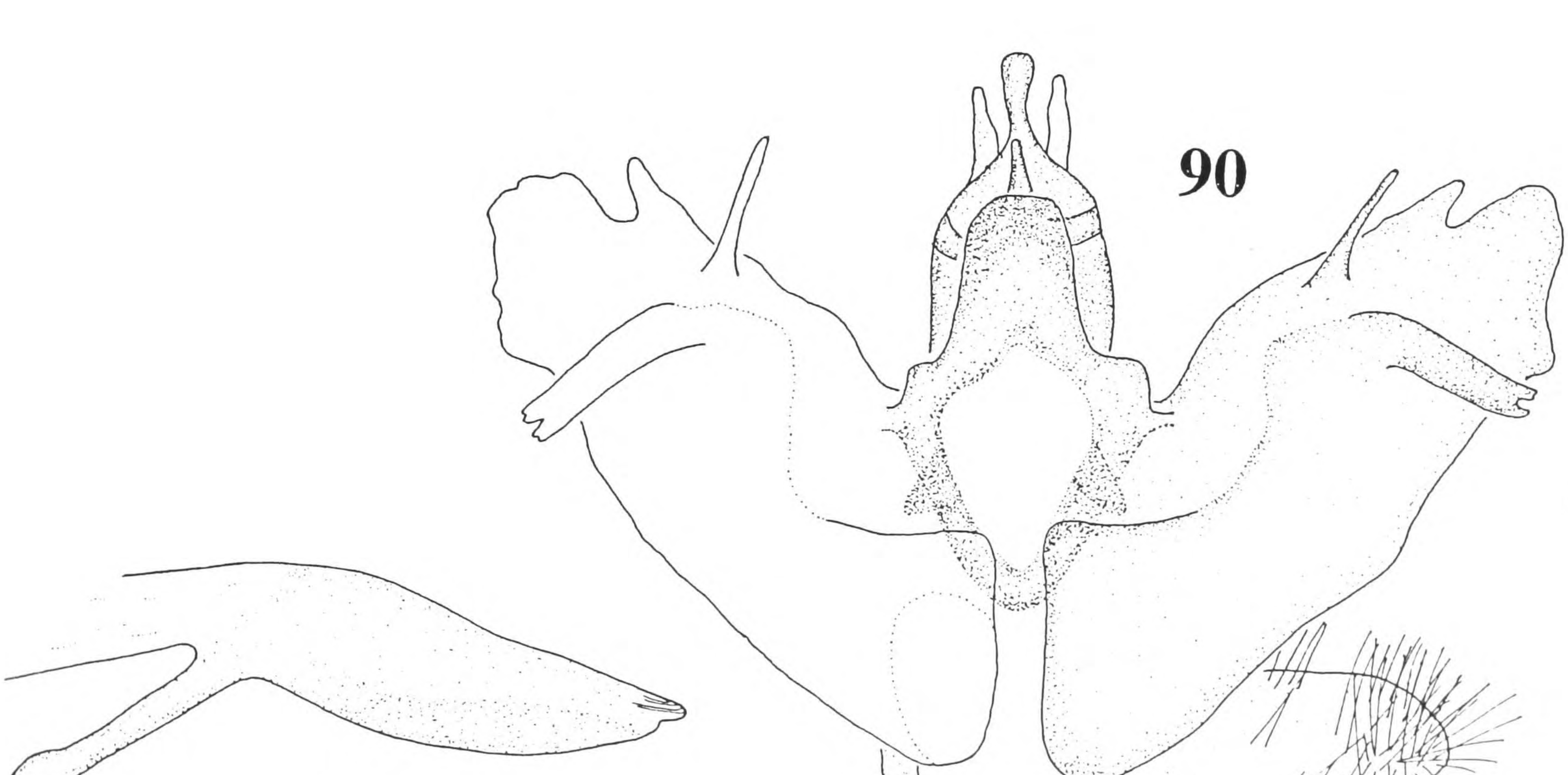
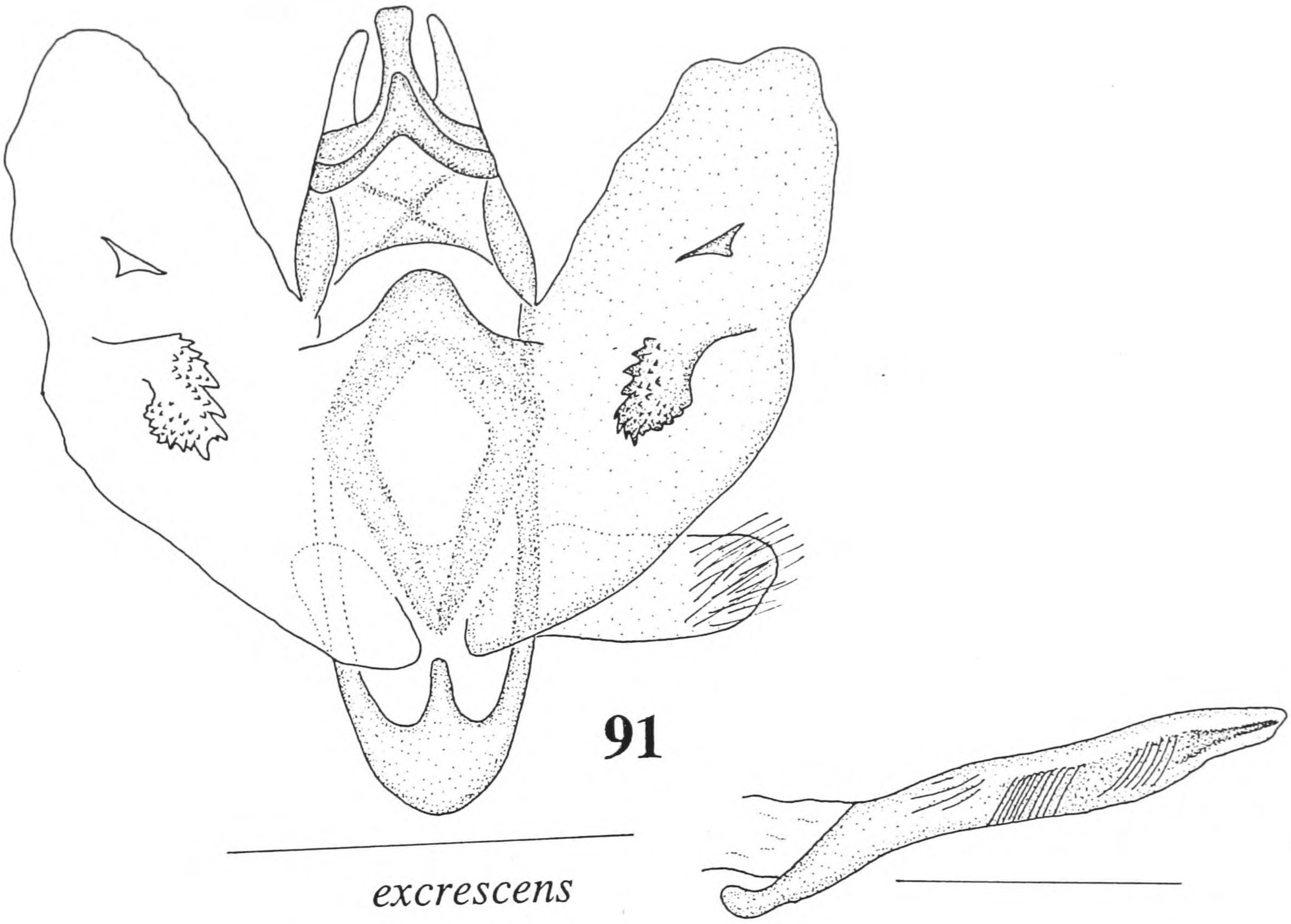


continuata



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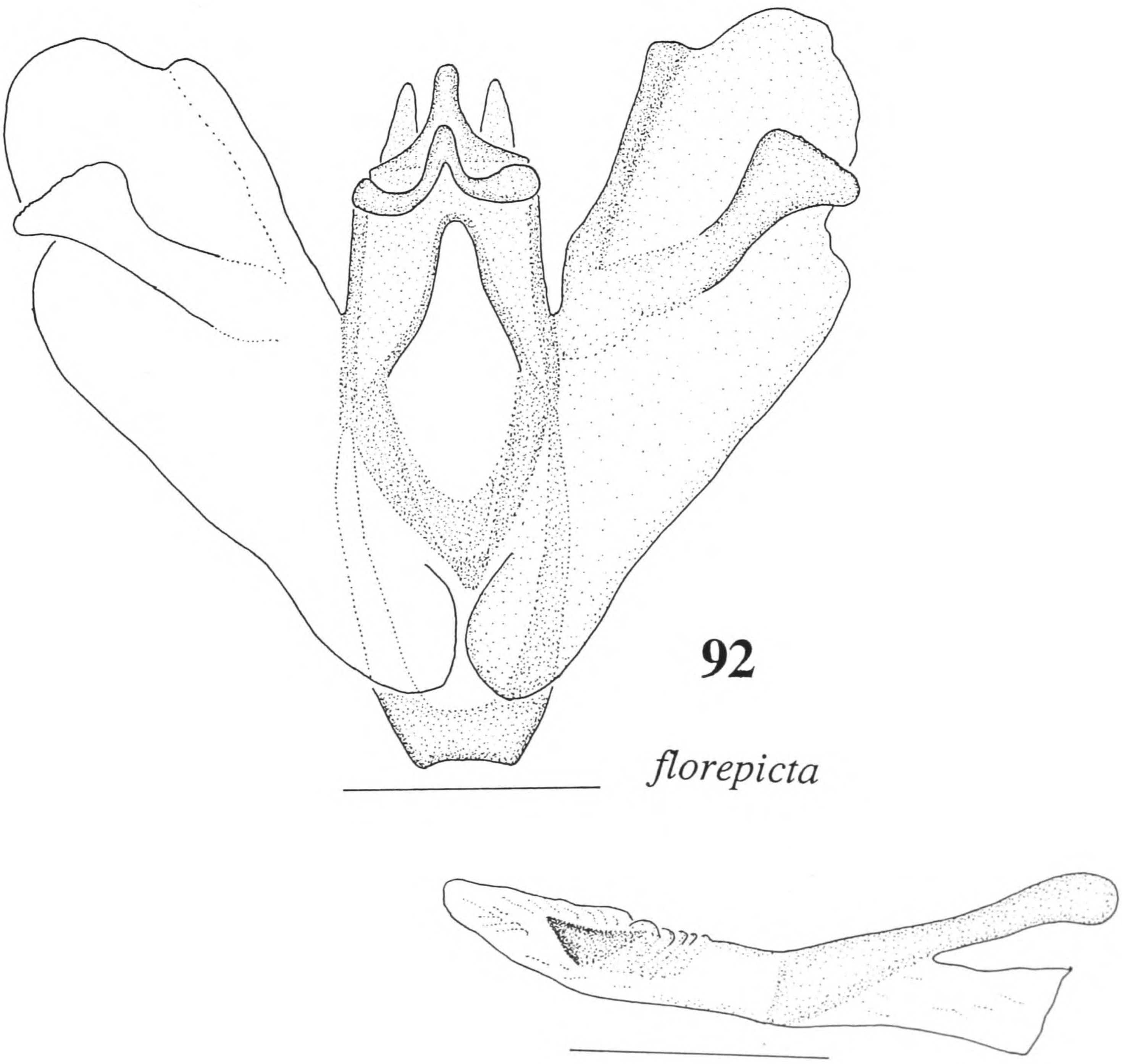
excrescens



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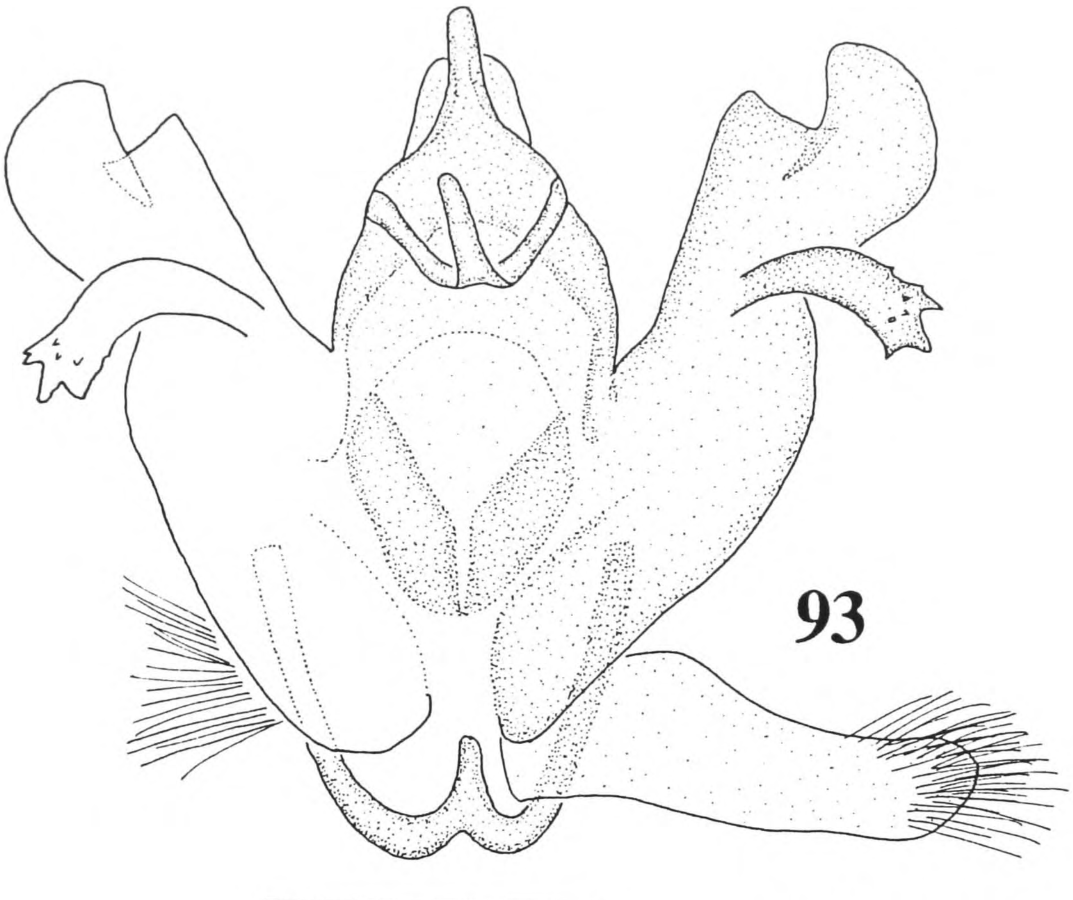
florepicta



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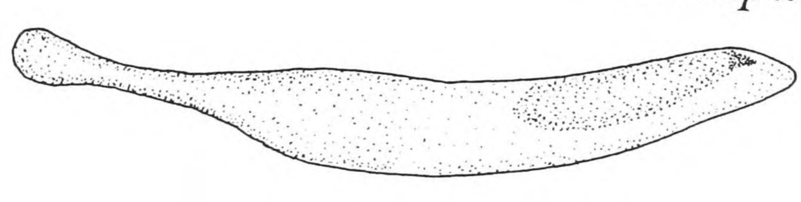
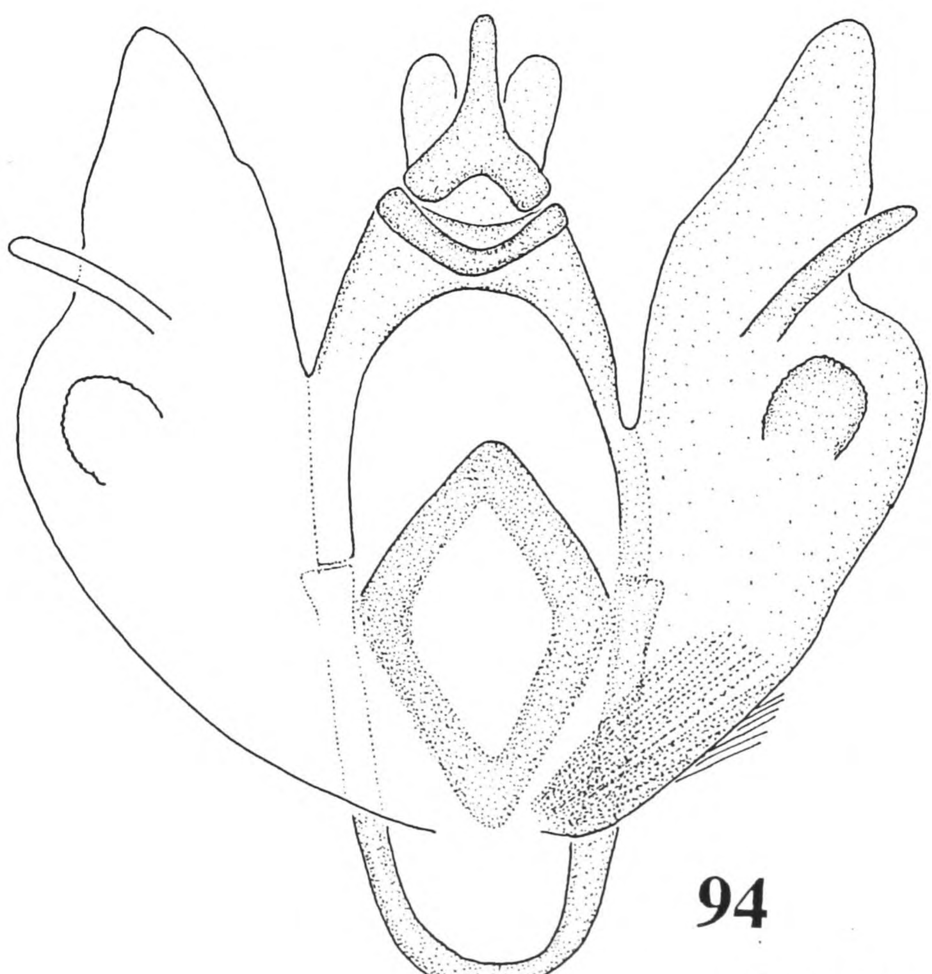
semispurcata





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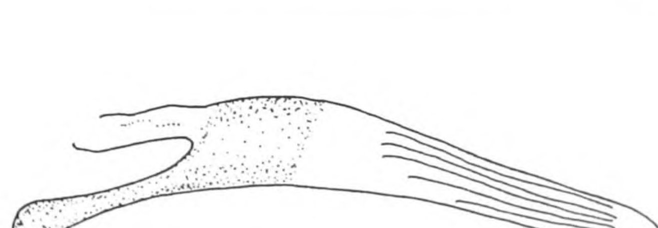
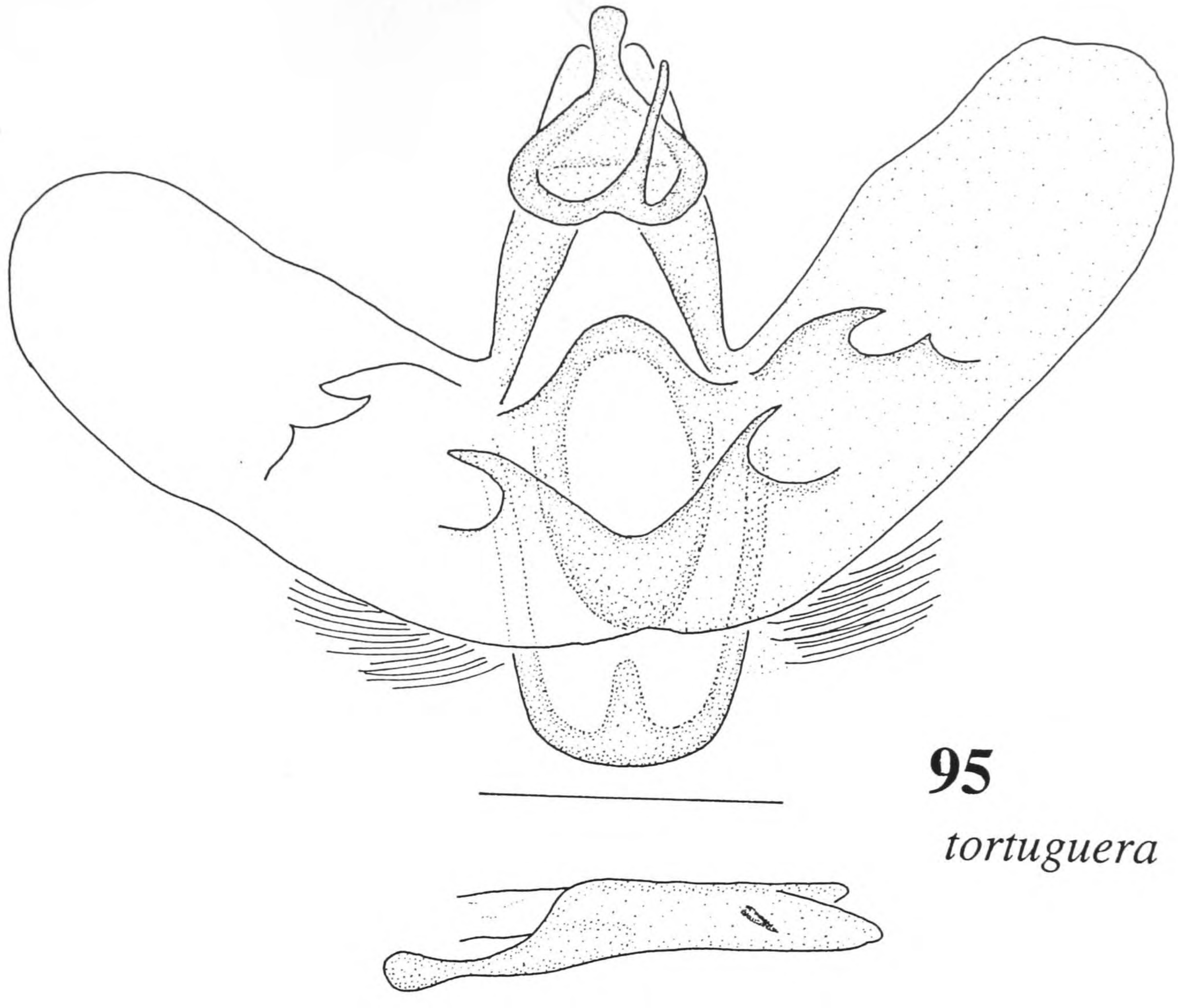
rhodophragma





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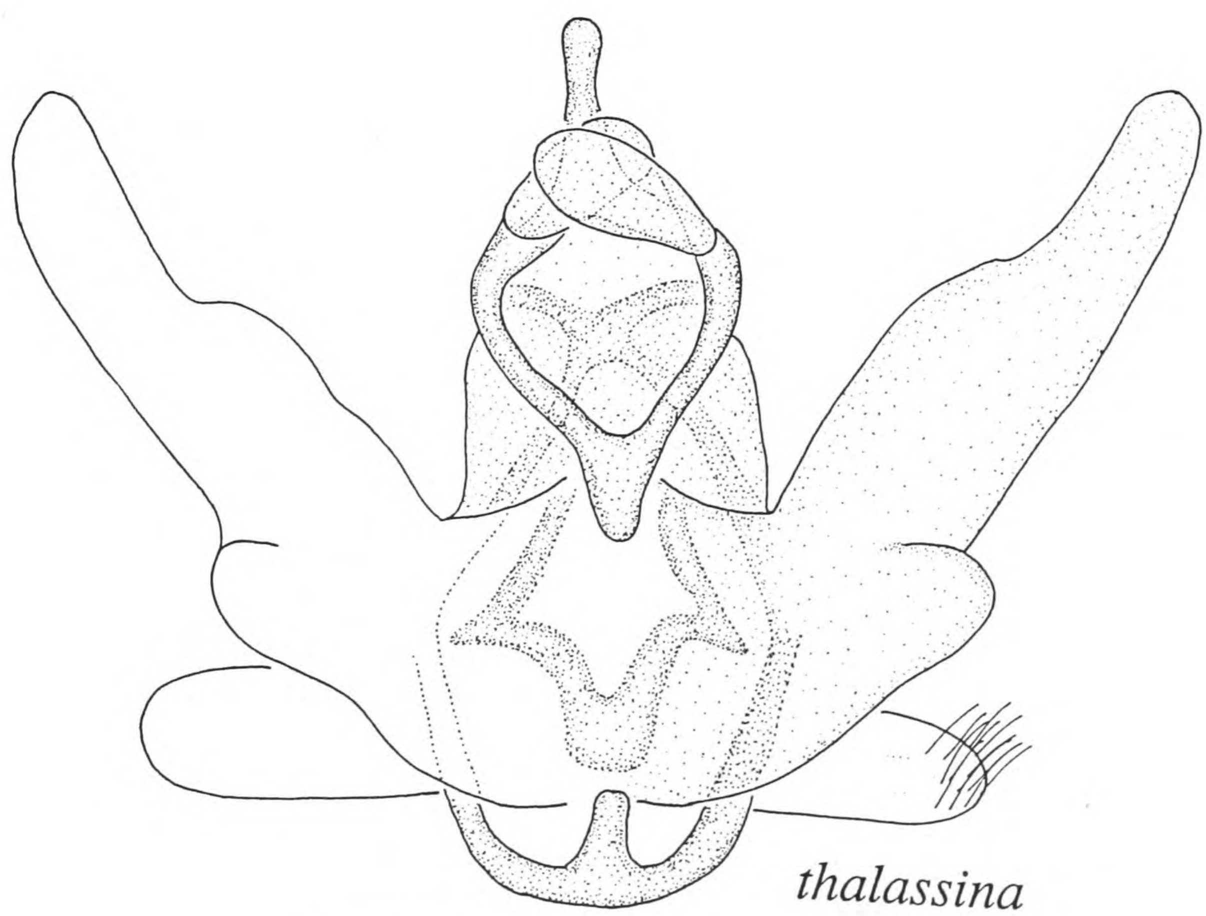
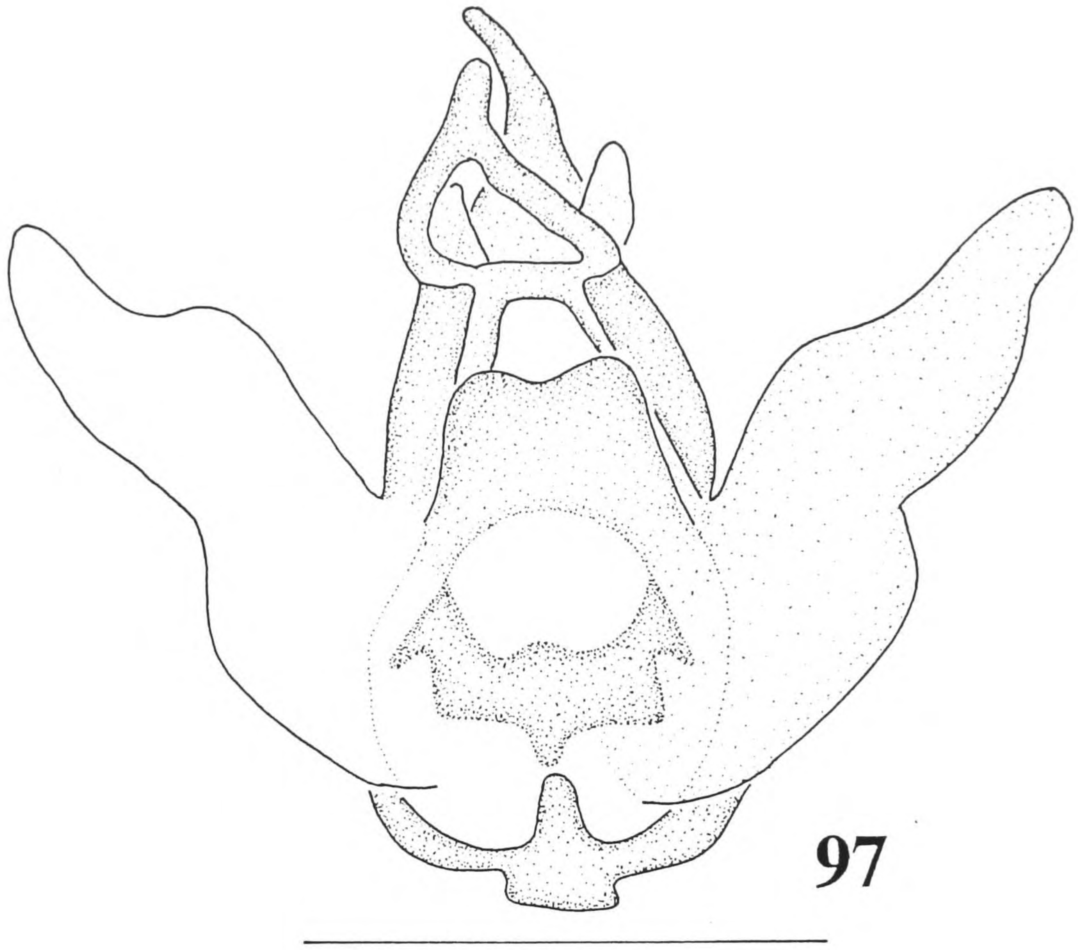
tortuguera



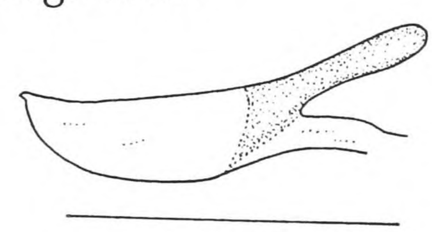
thalassina

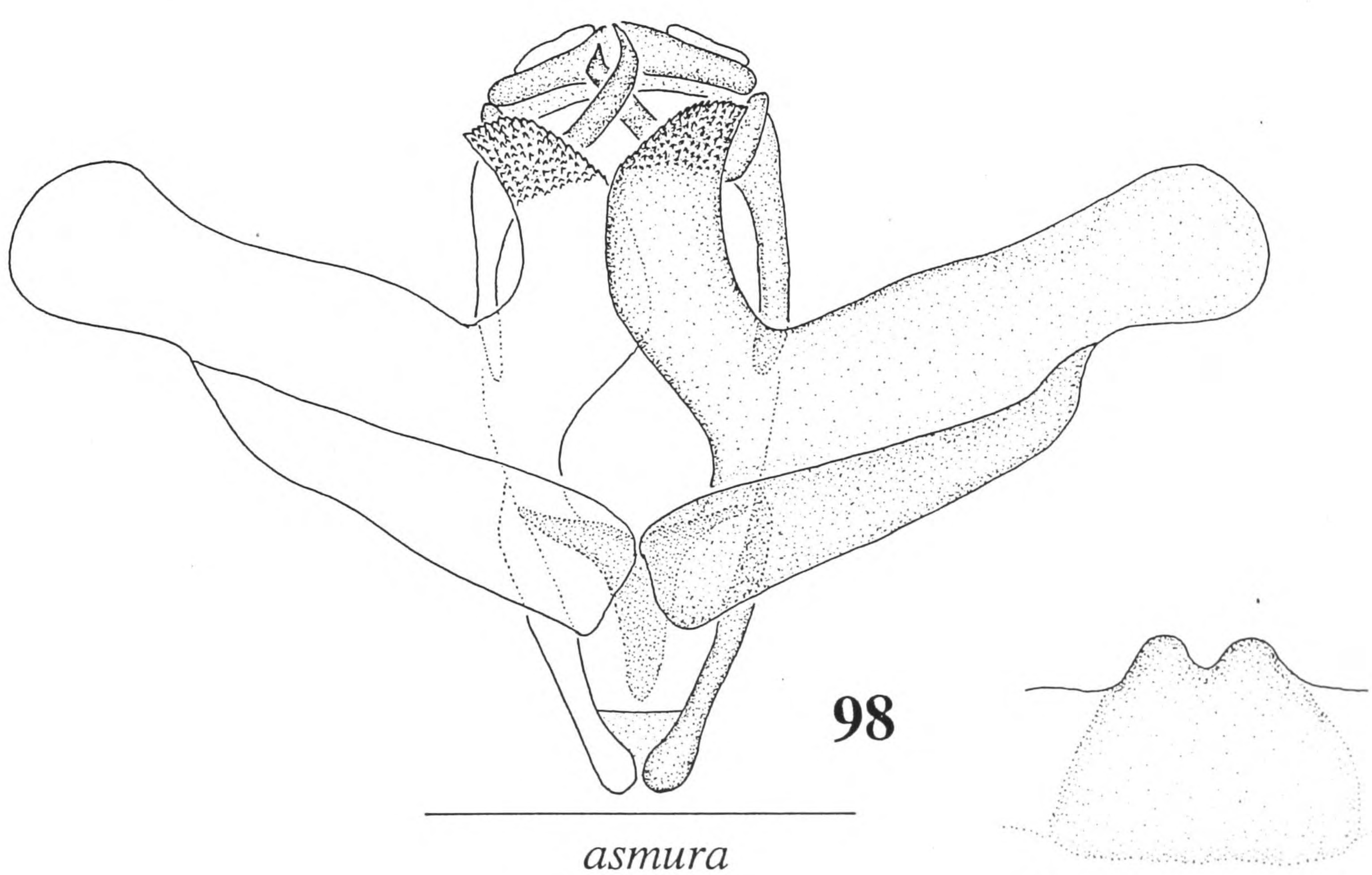
96



97

lacteguttata





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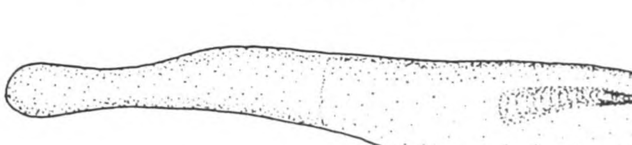

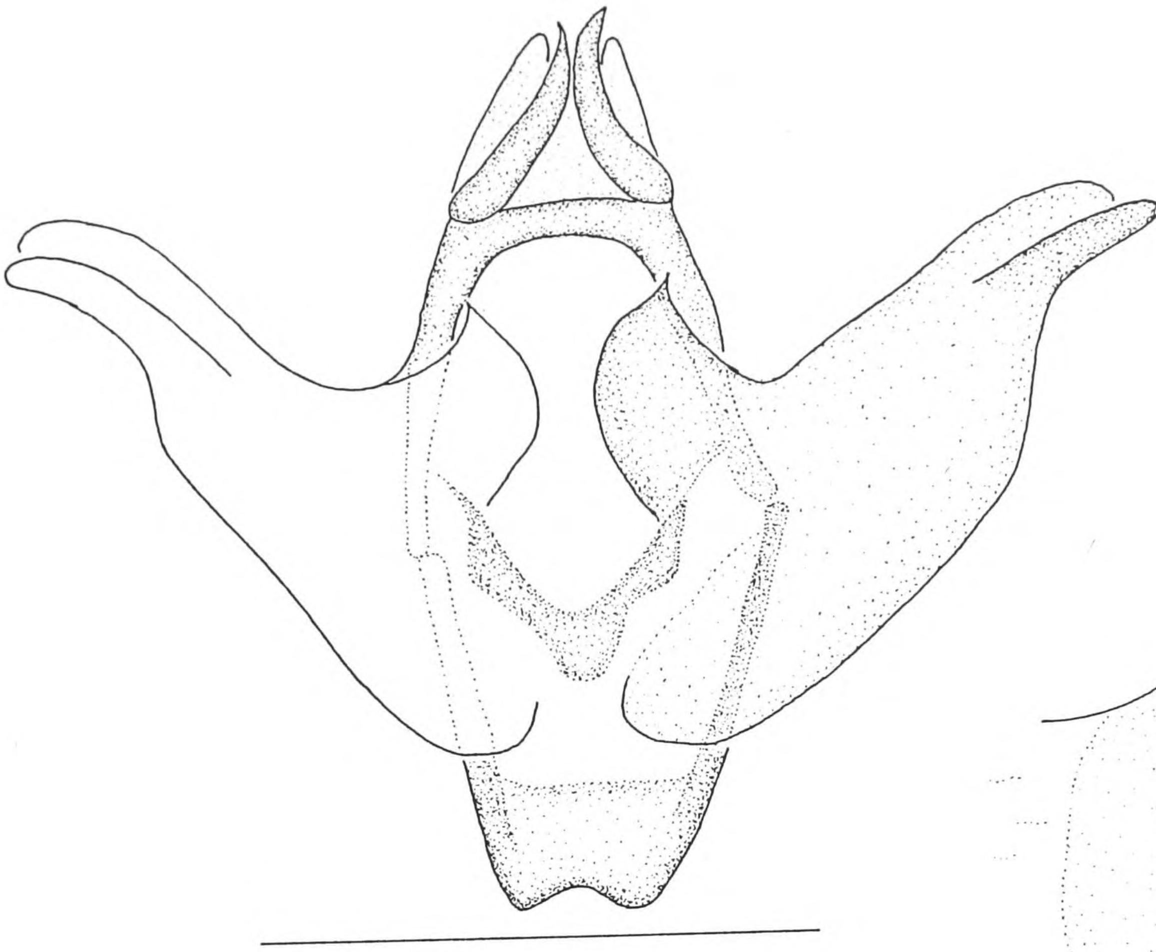

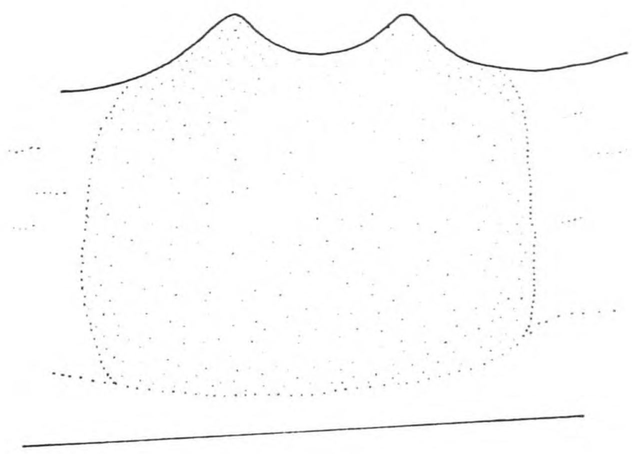

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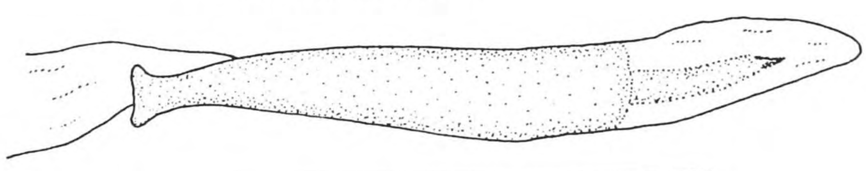

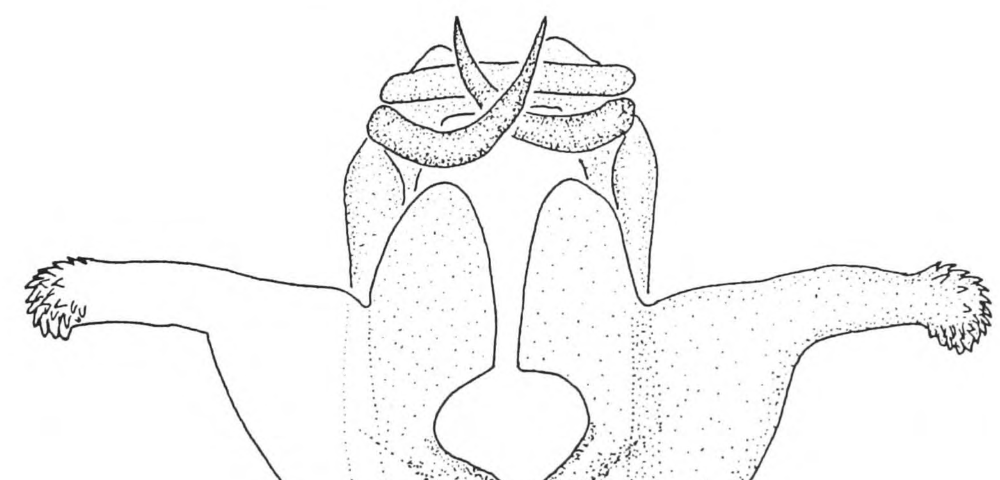

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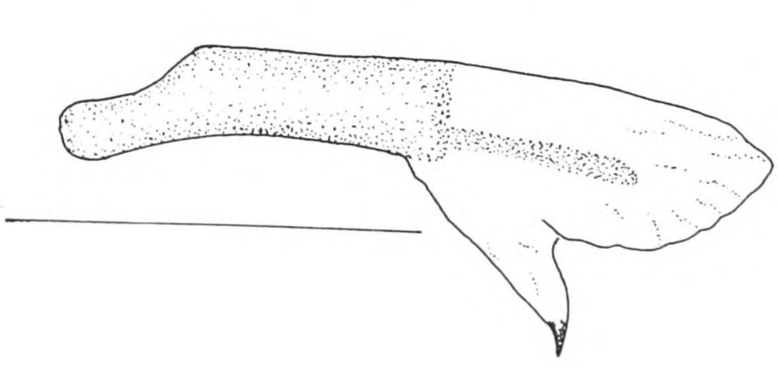
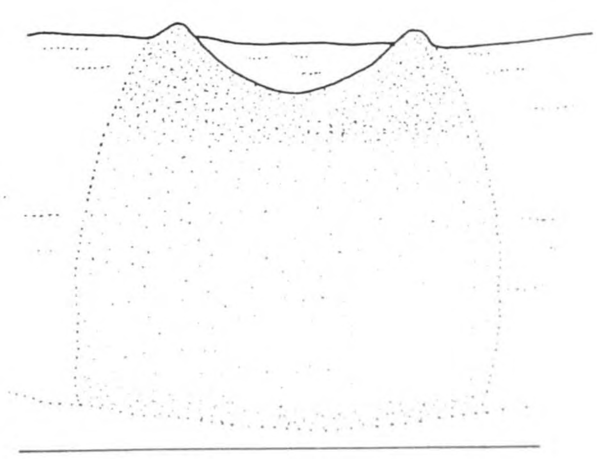
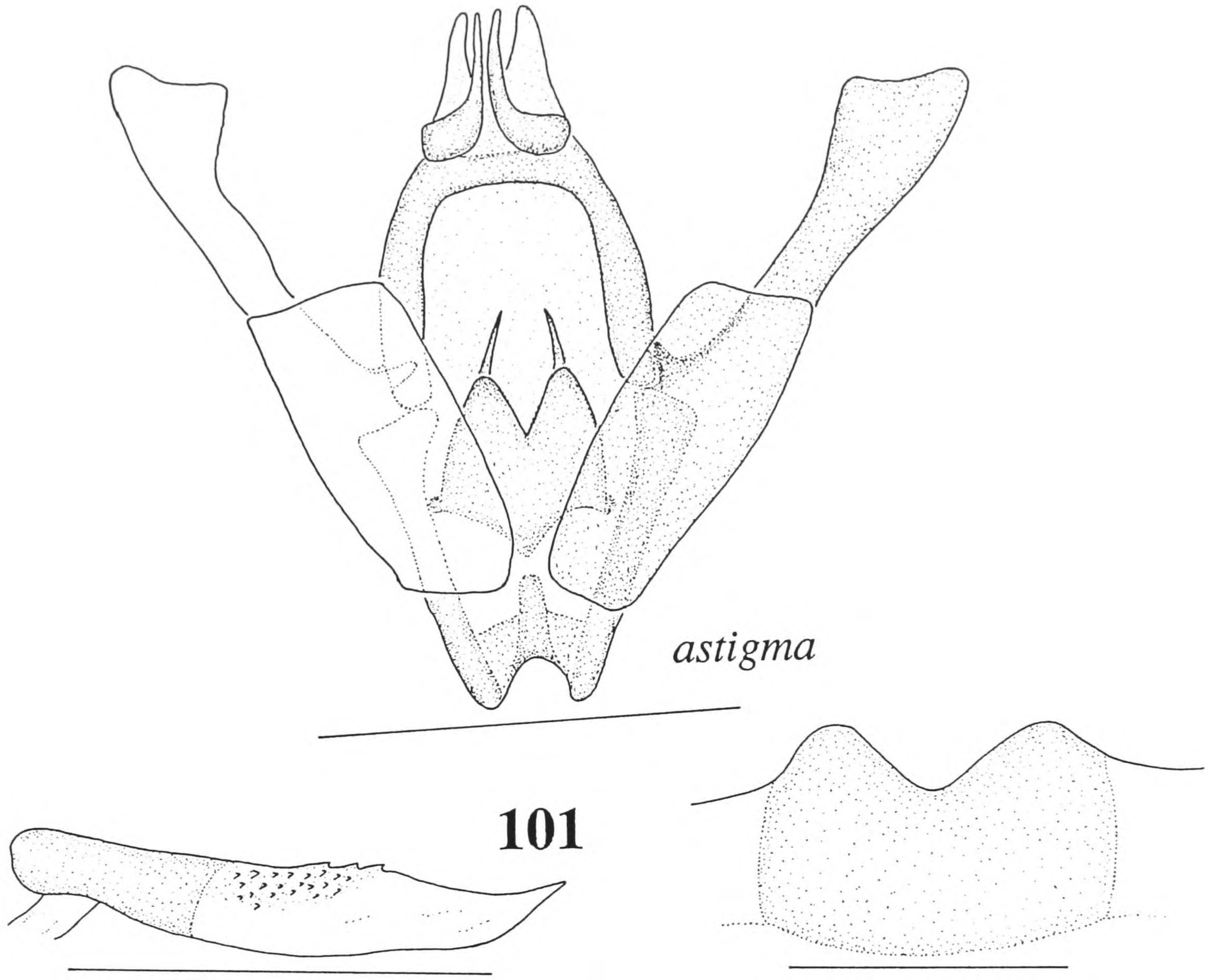
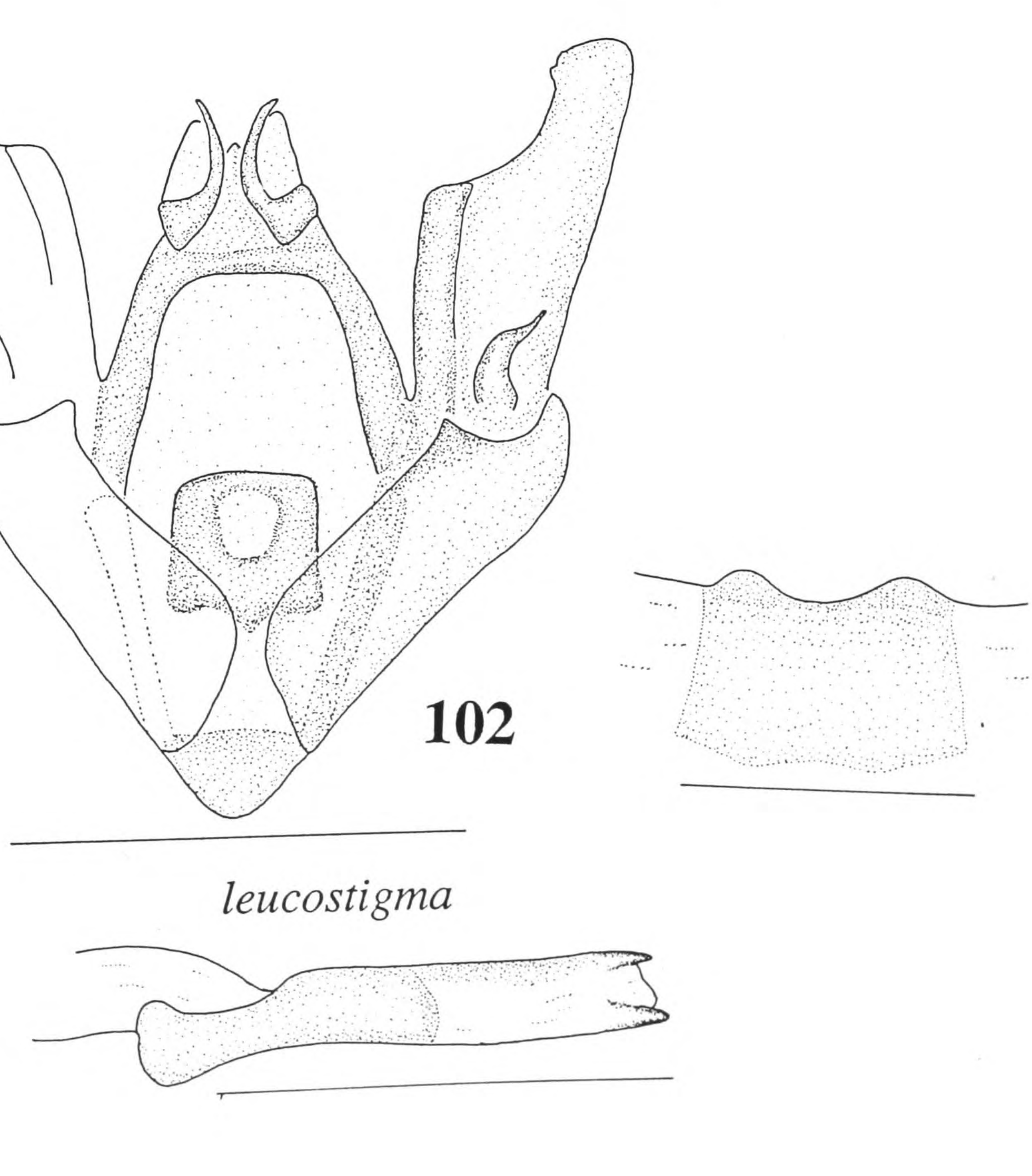






astigma

101



102

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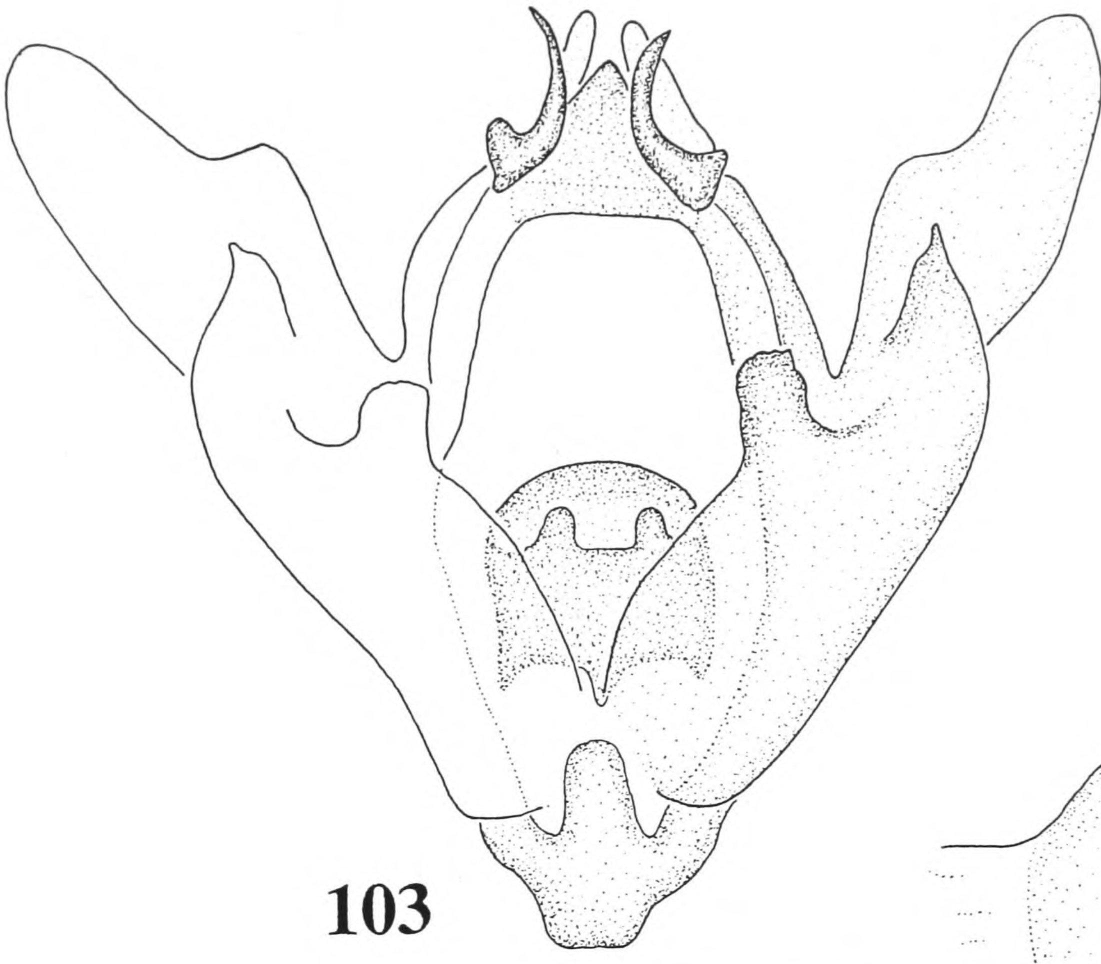
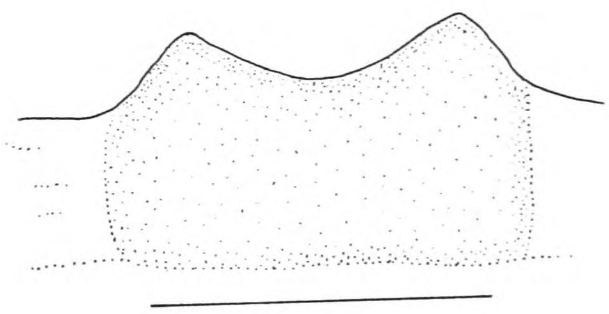
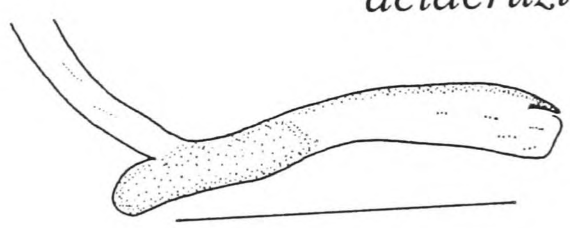
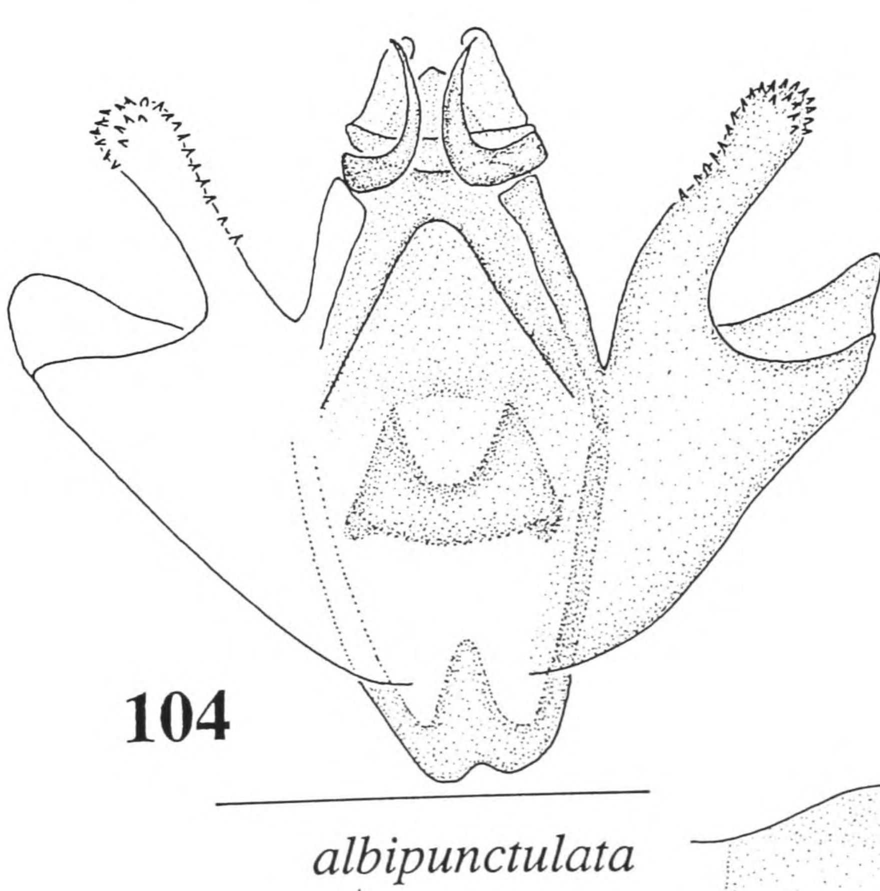




103

delacruzi





104

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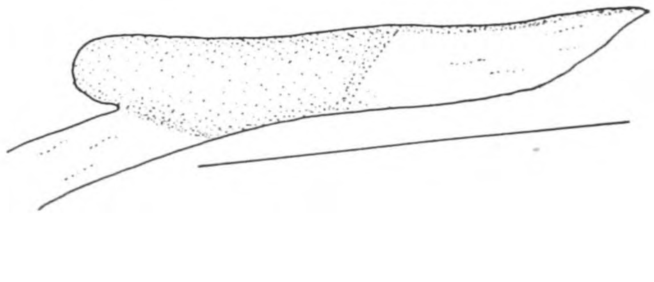

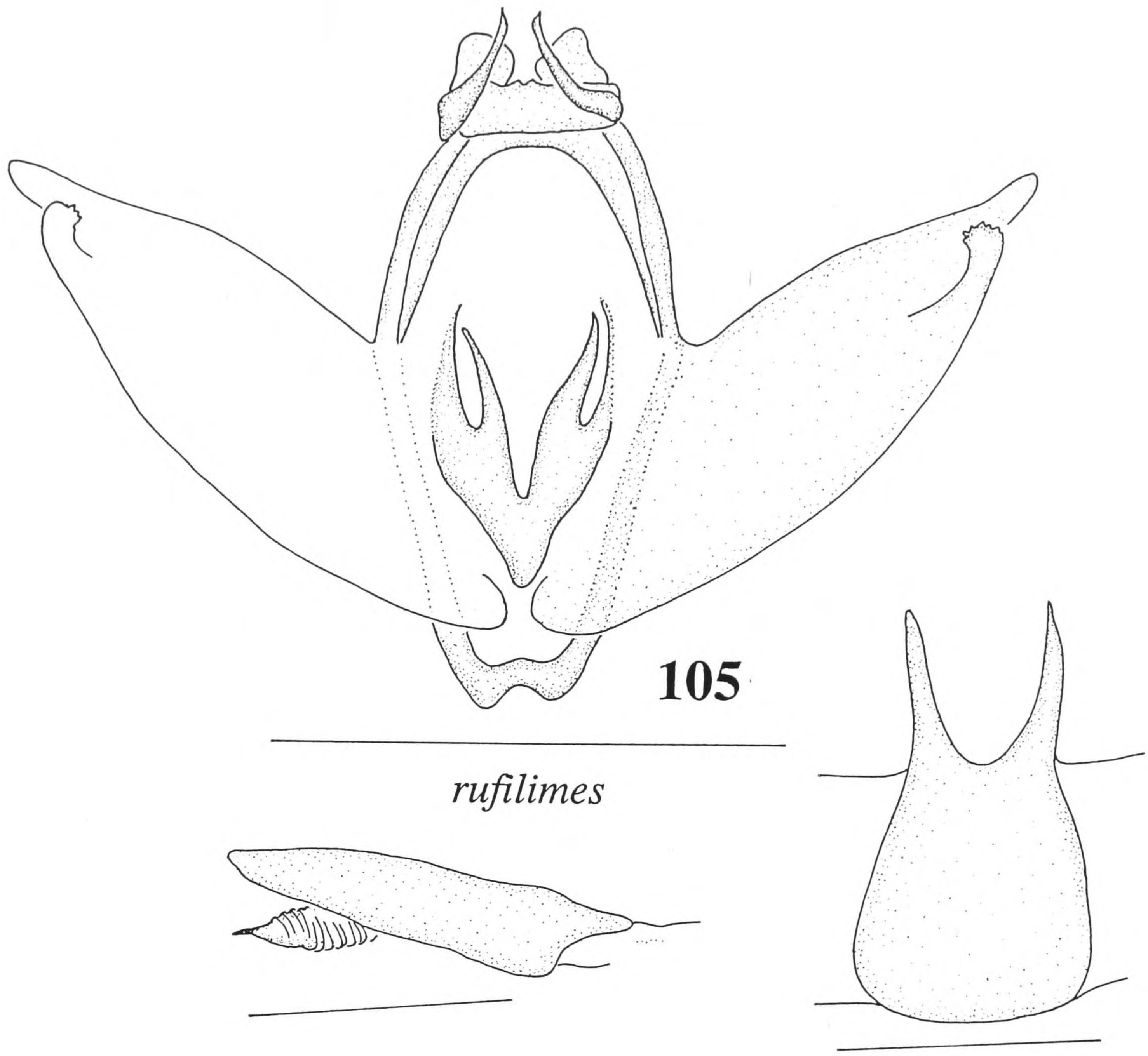

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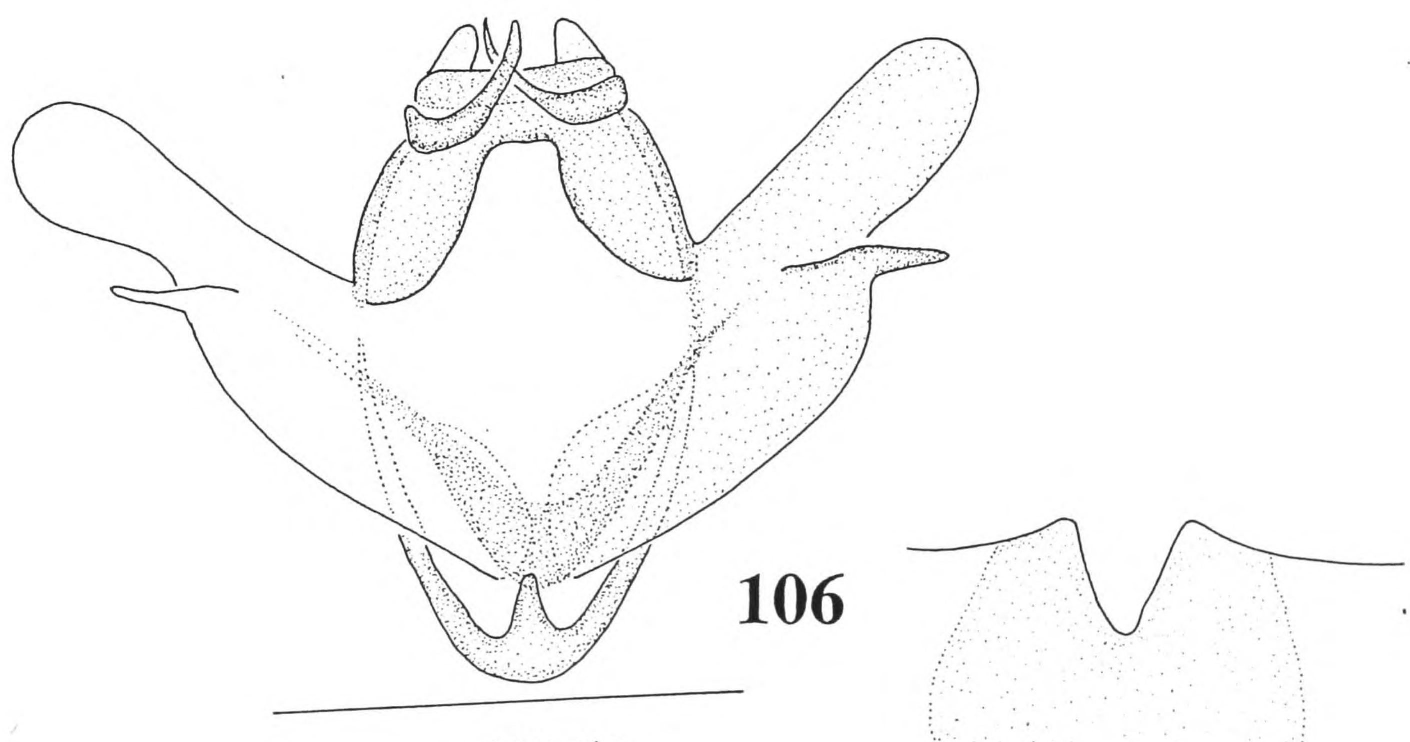

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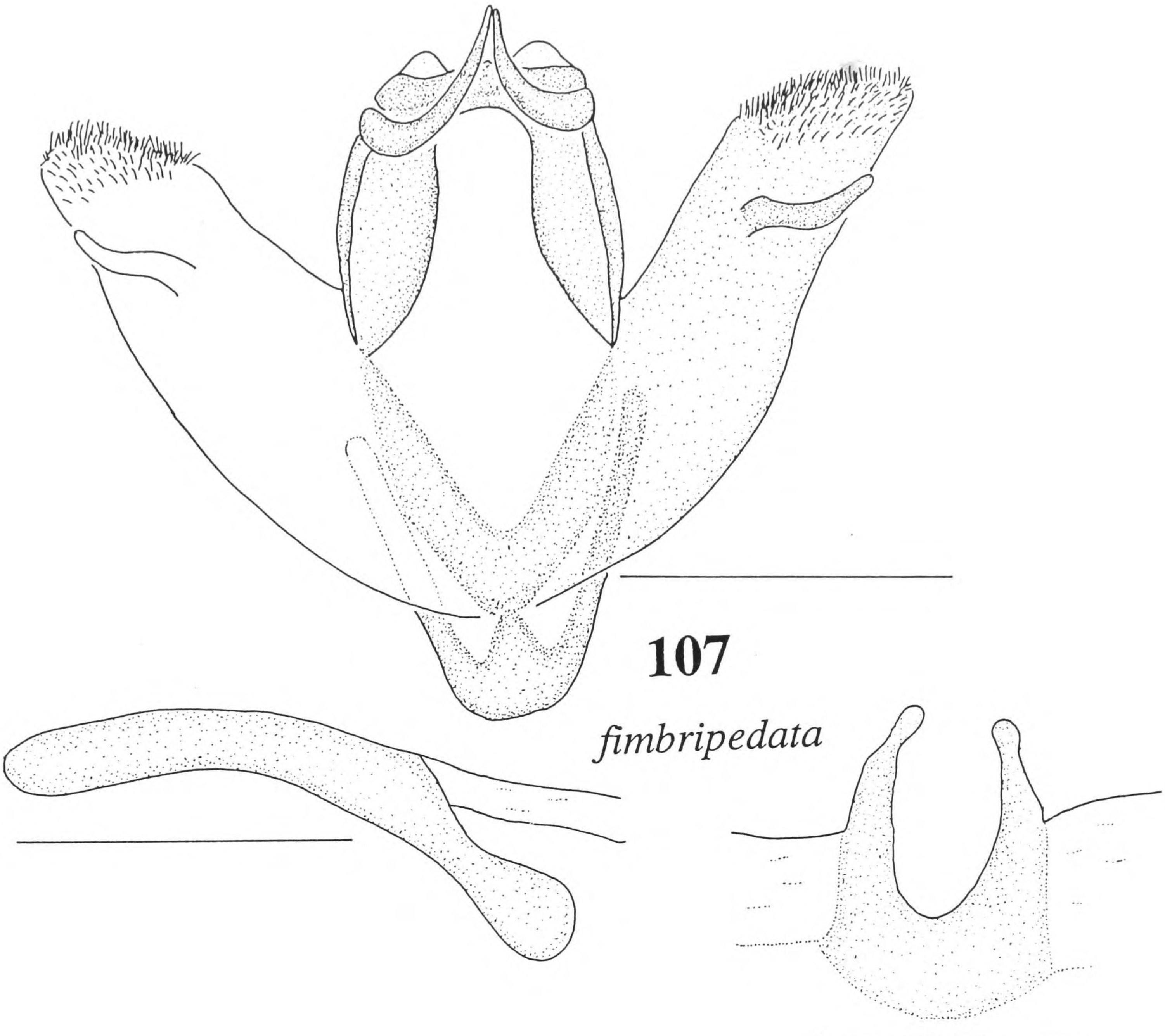

107

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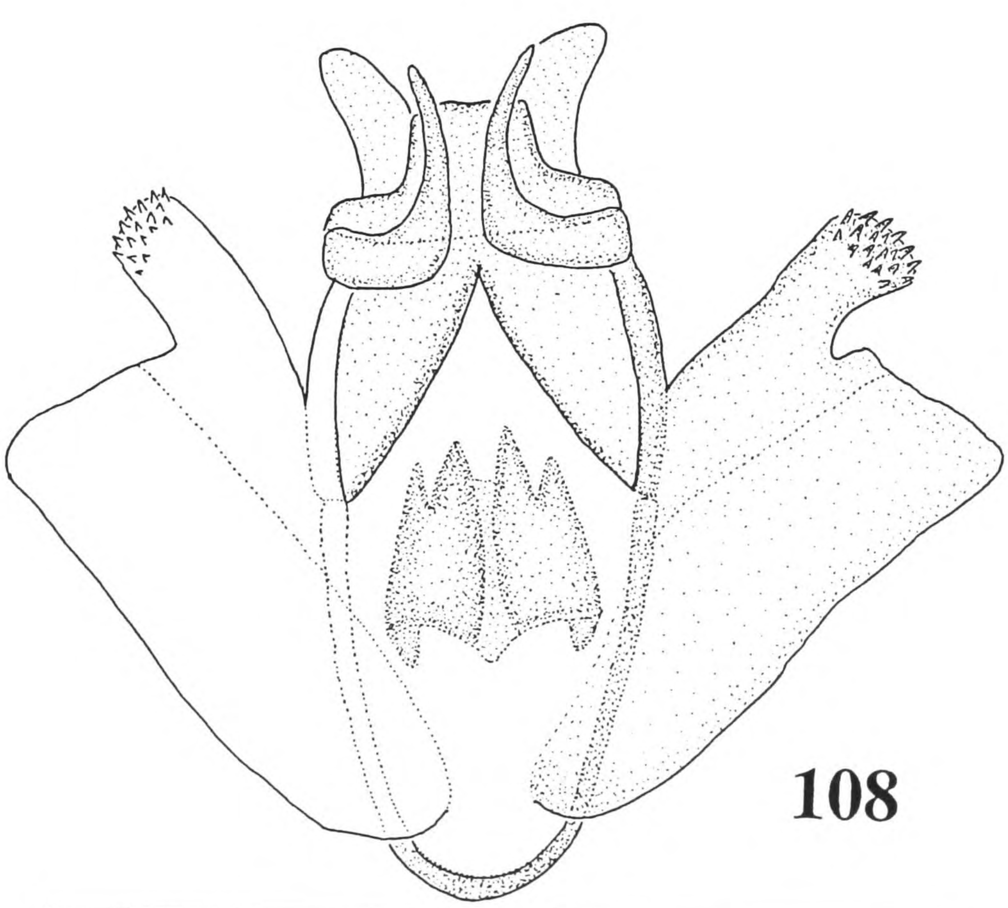
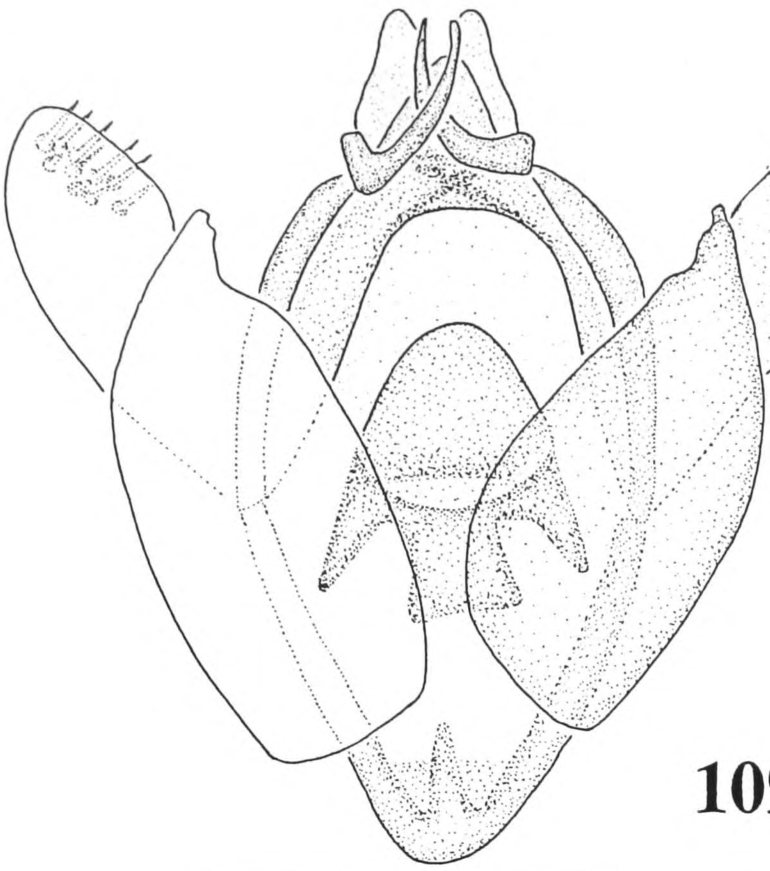


108

zamaradaria



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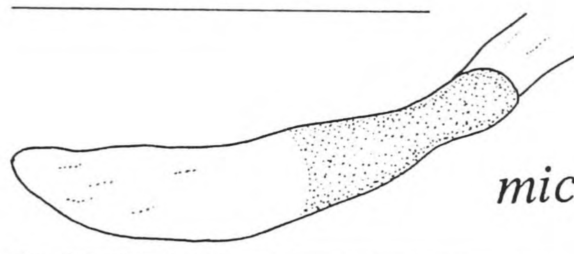

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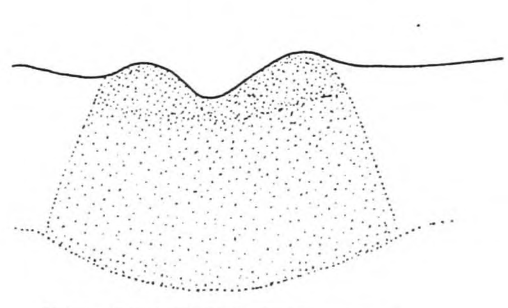
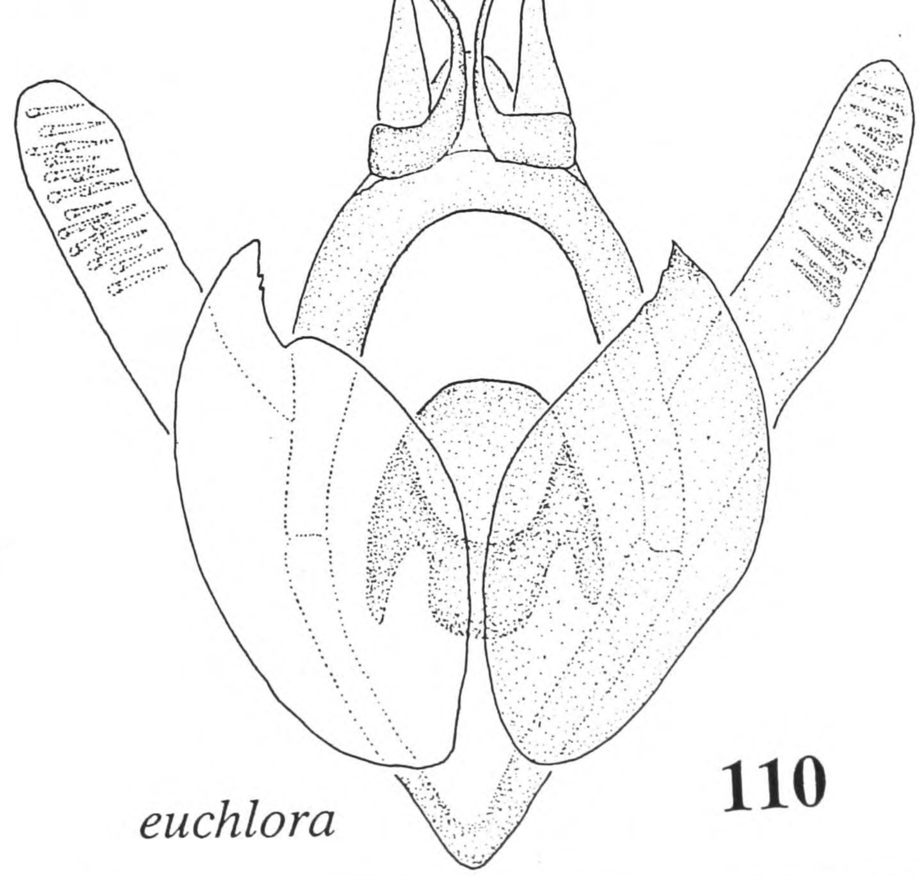
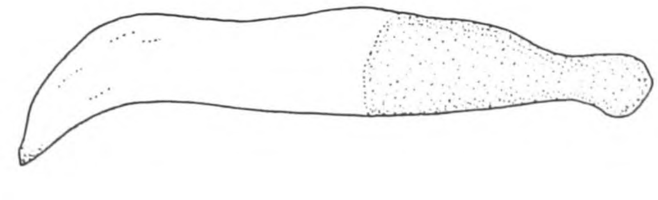
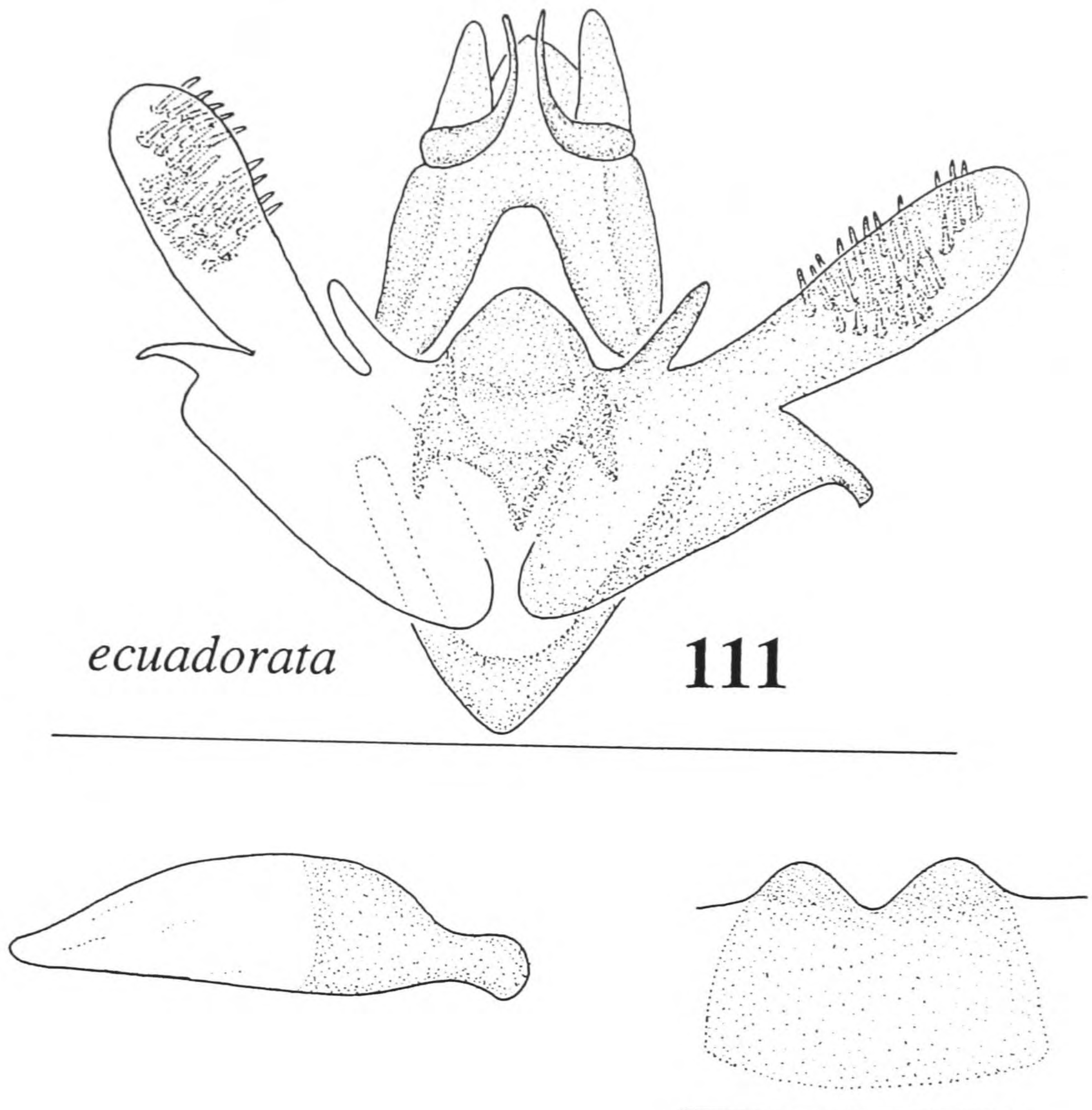


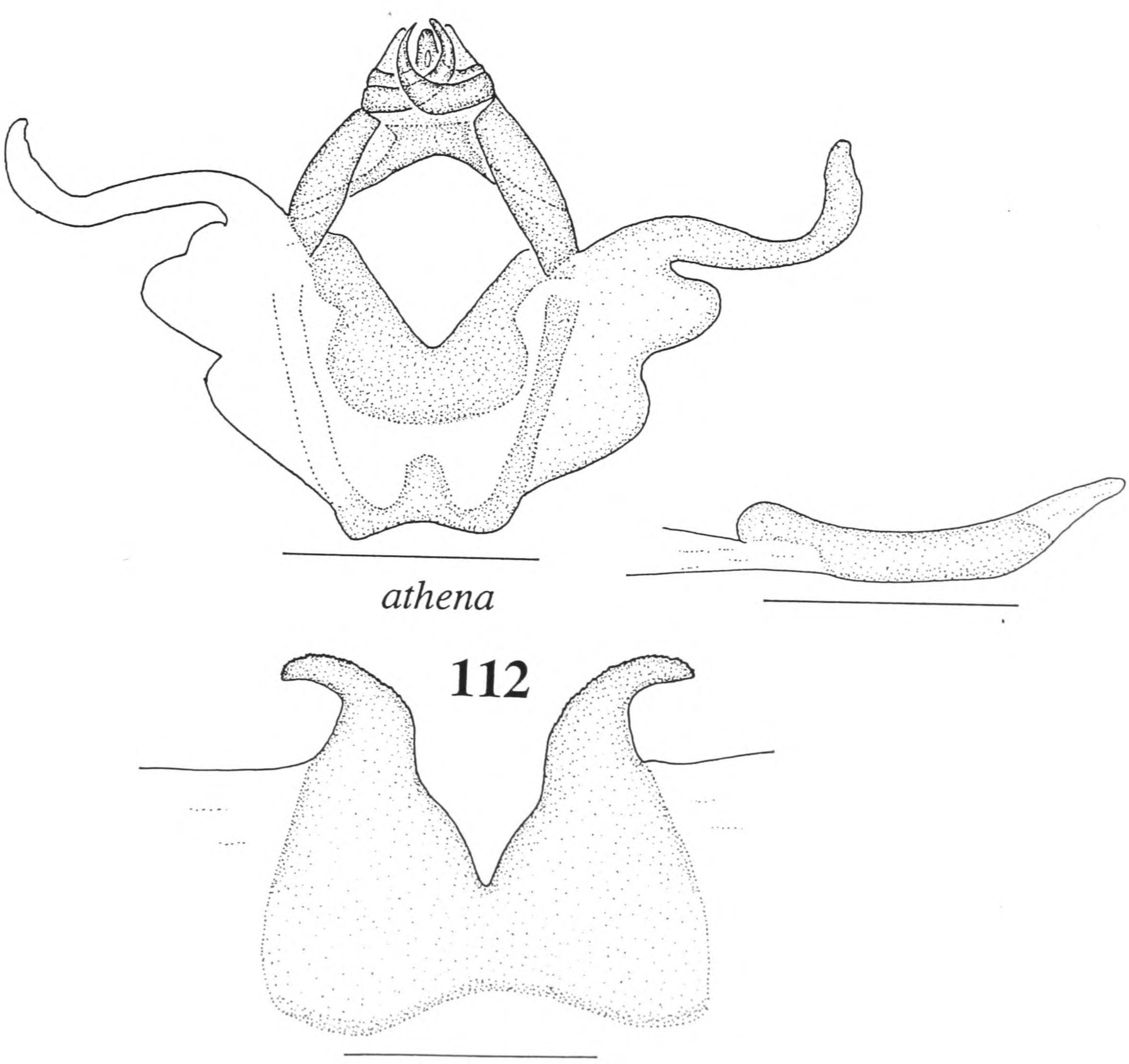


euchlora **110**



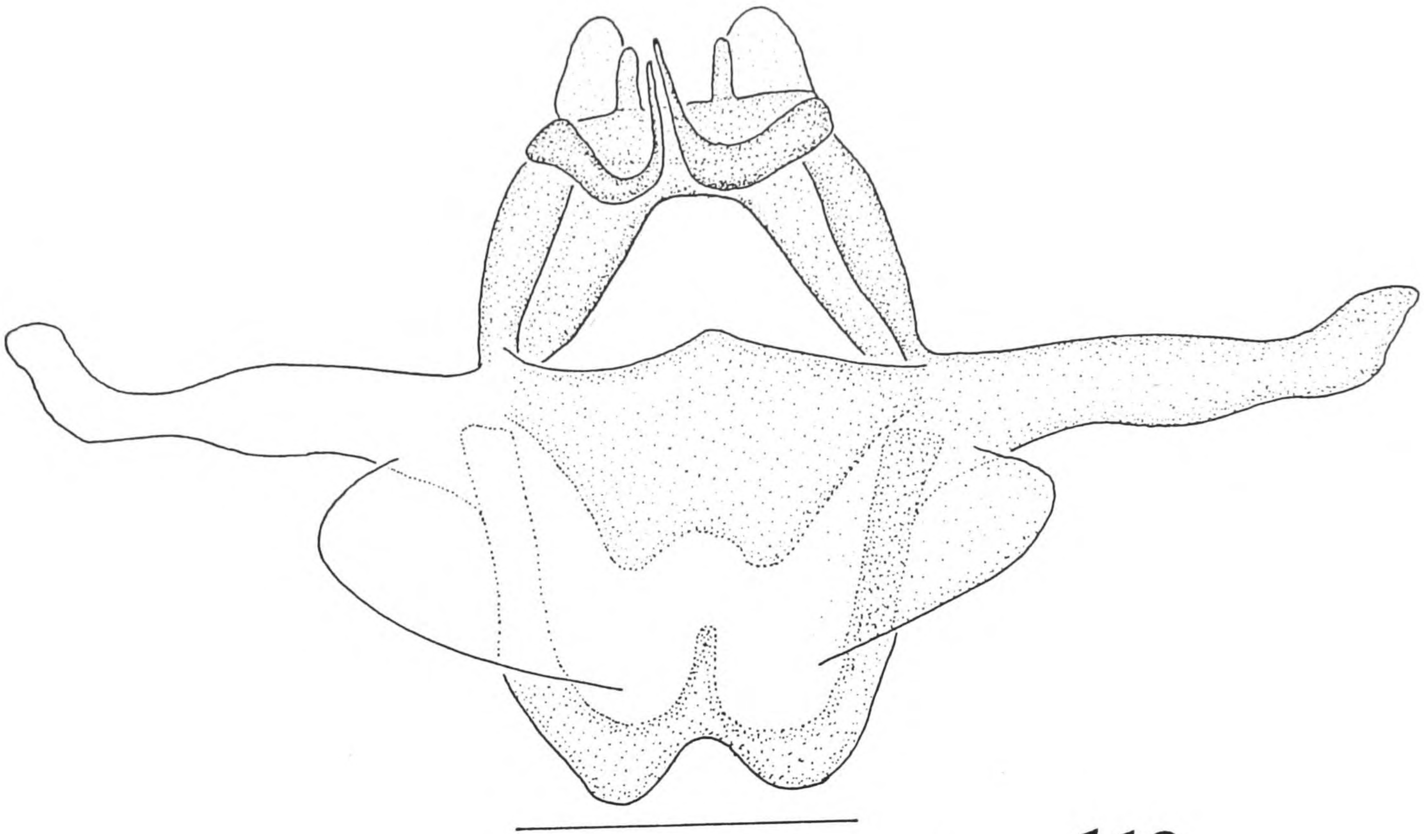


ecuadorata **111**



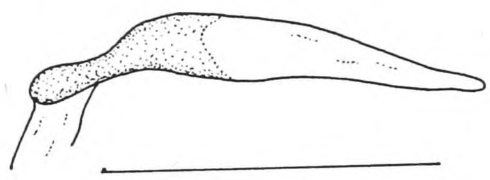
athena

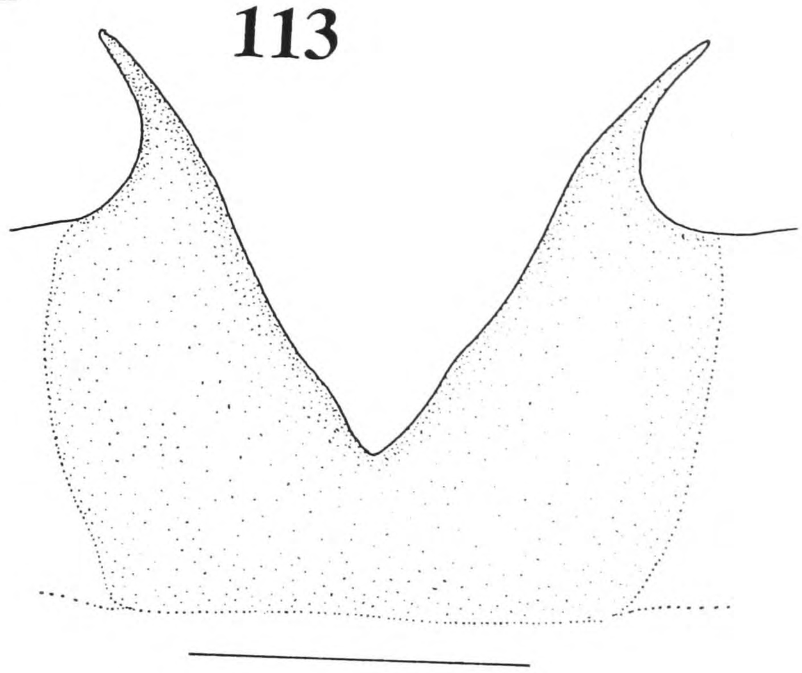
112

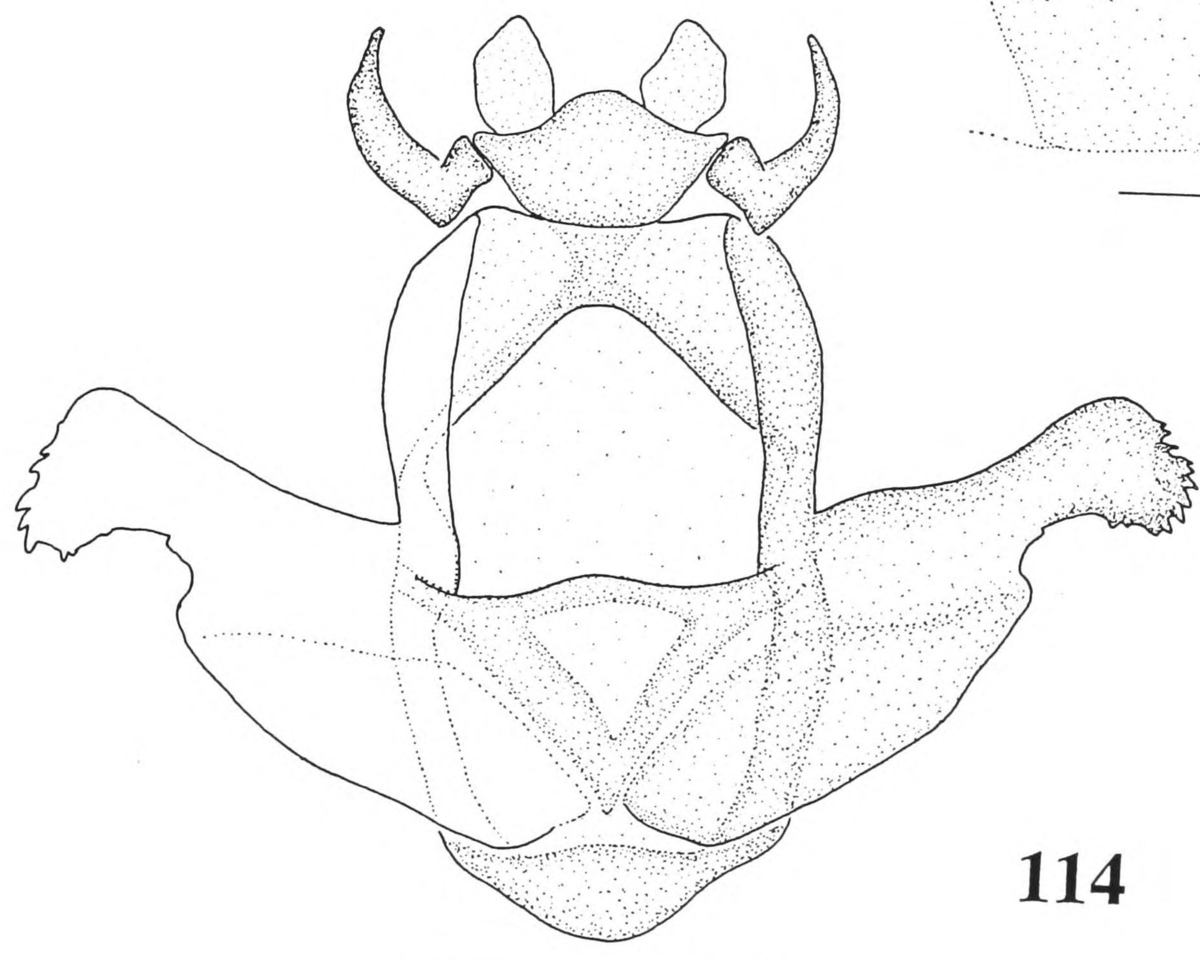


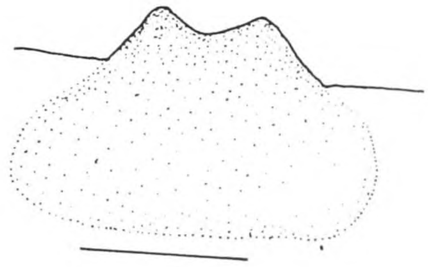
holochroa

113



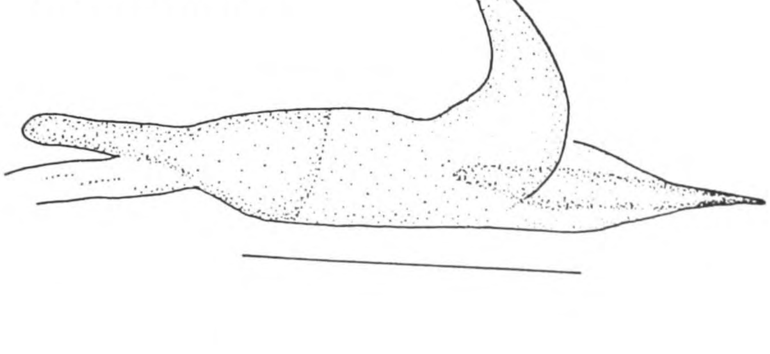


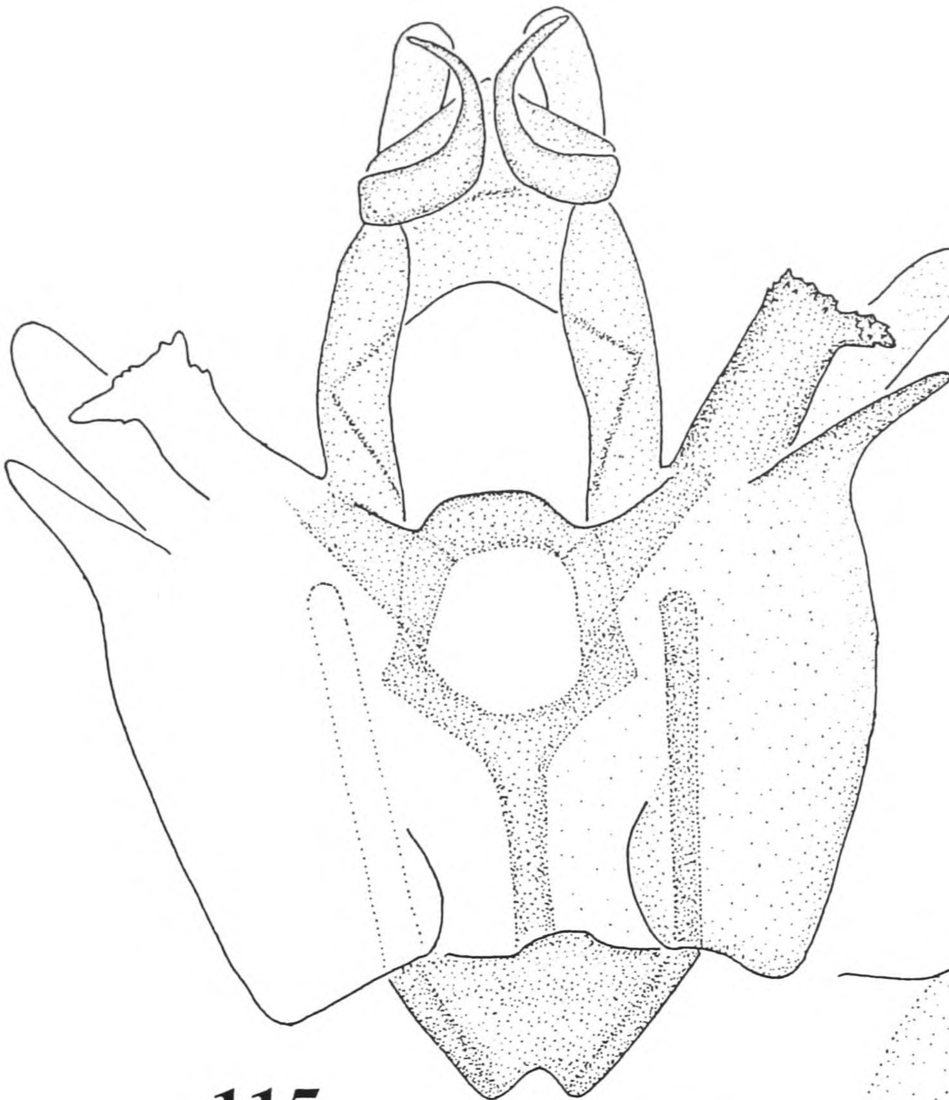


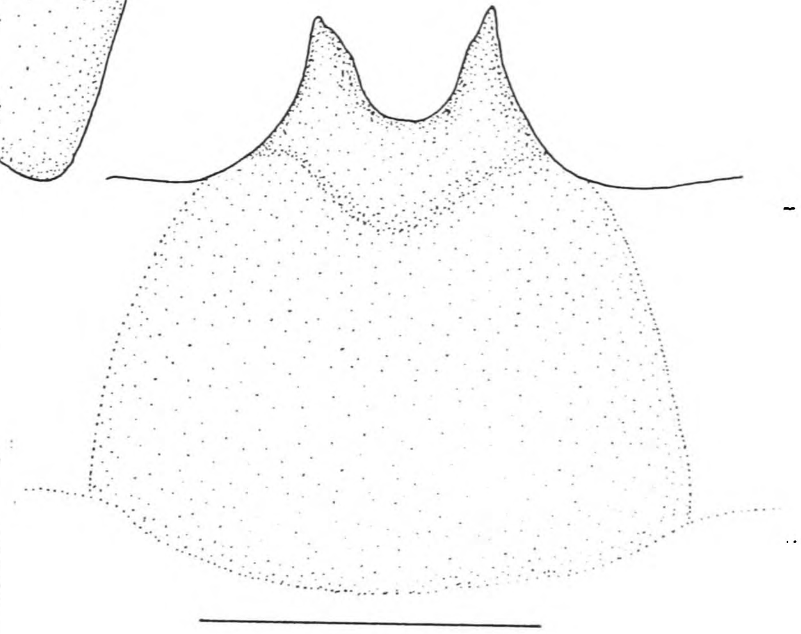


114

lactecincta

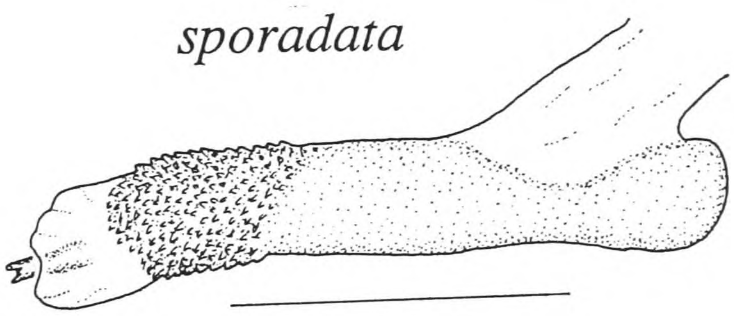


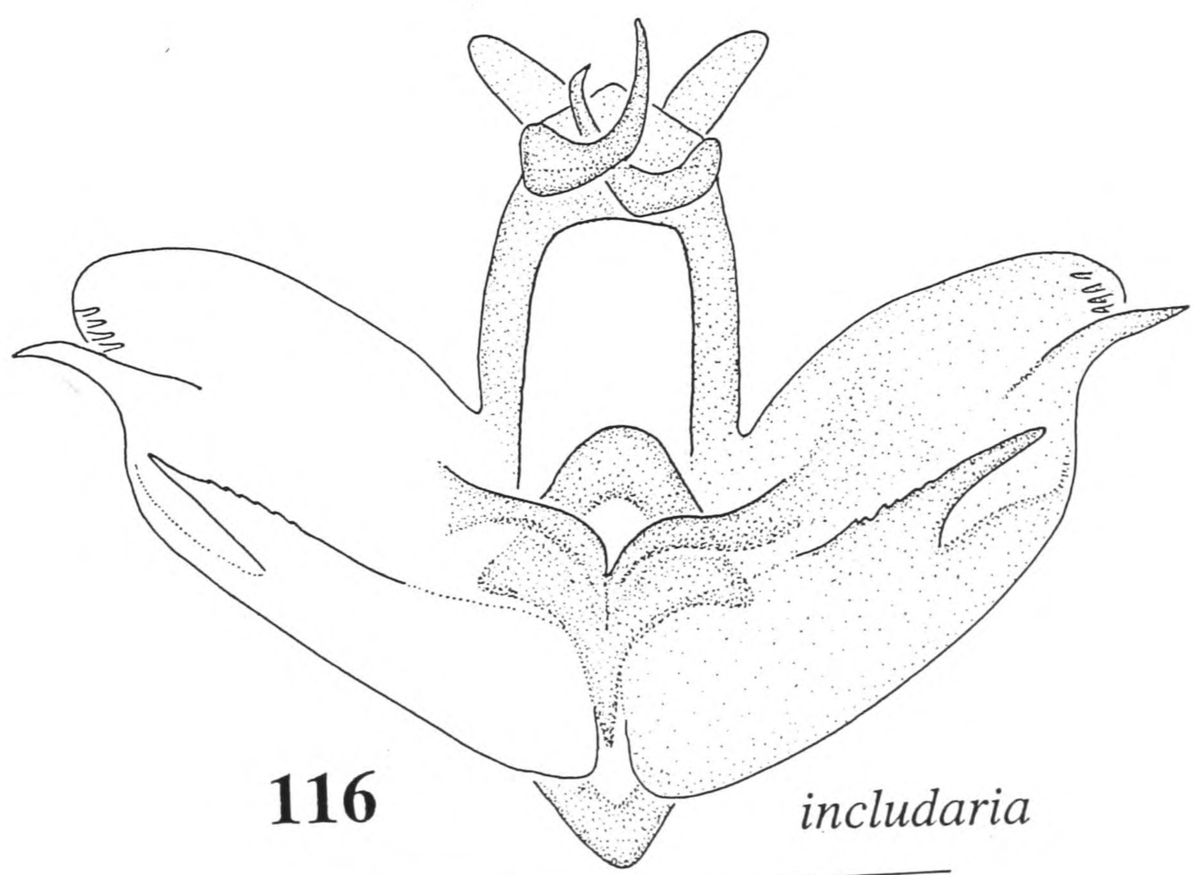




115

sporadata





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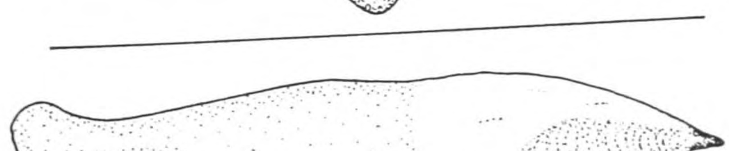
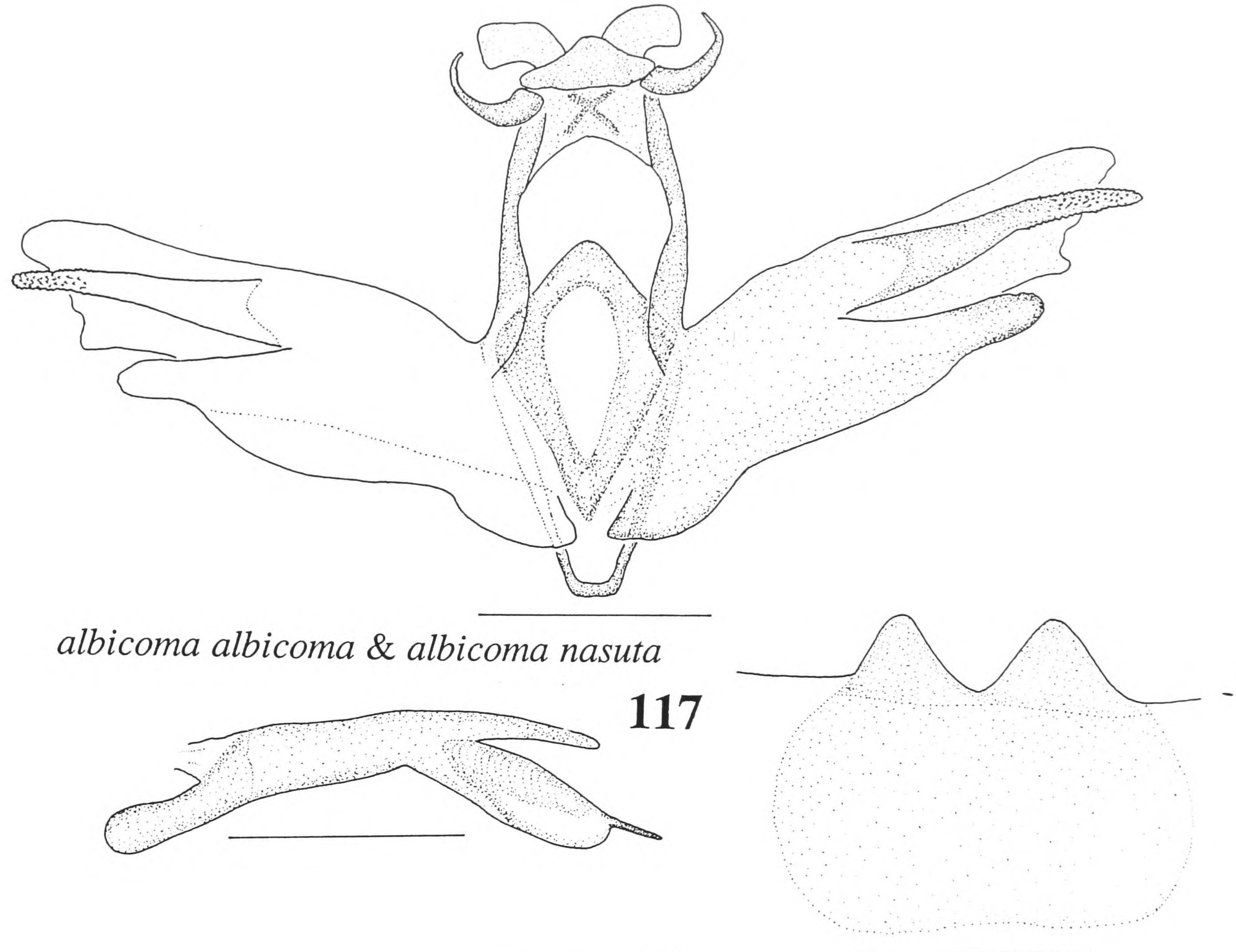
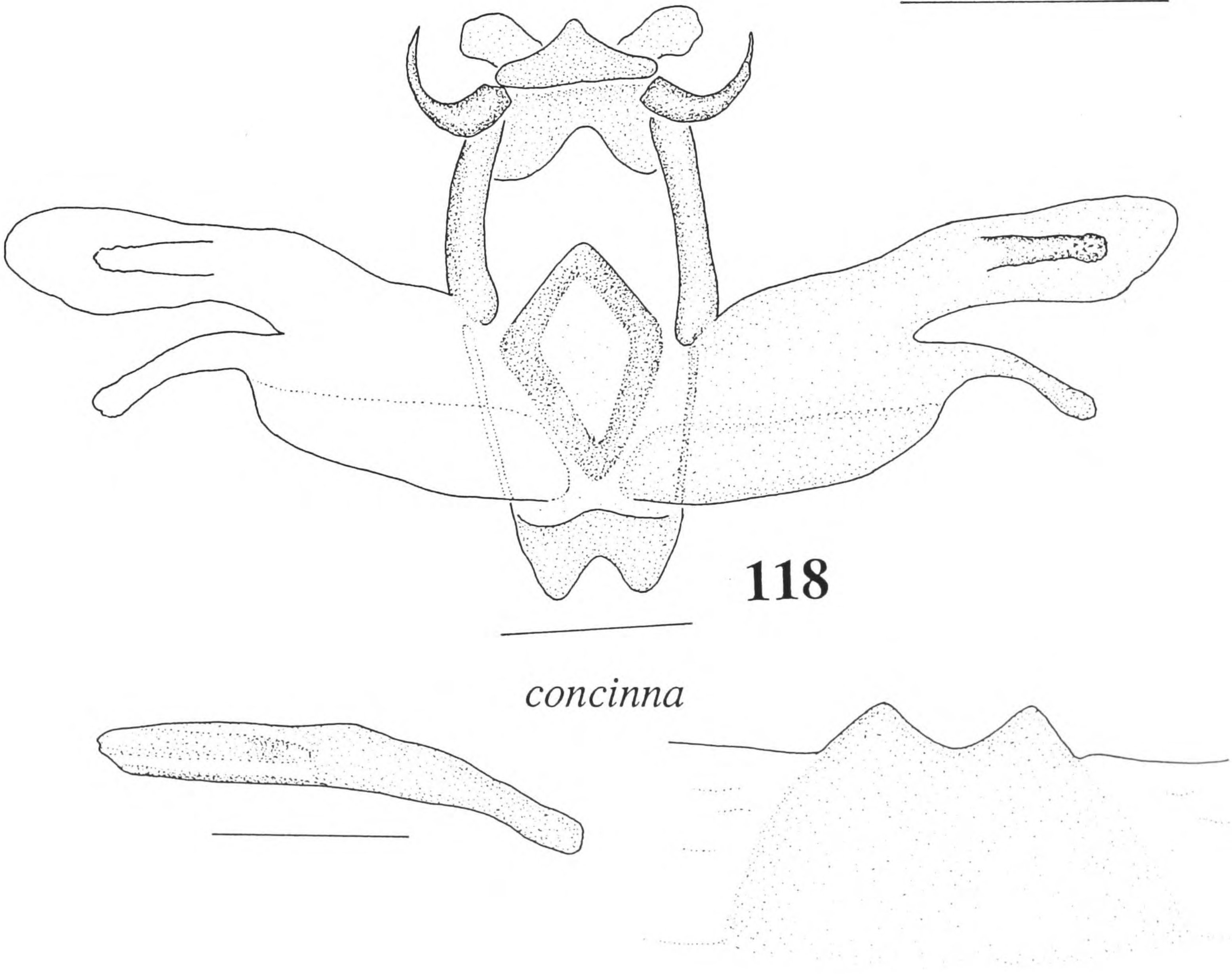




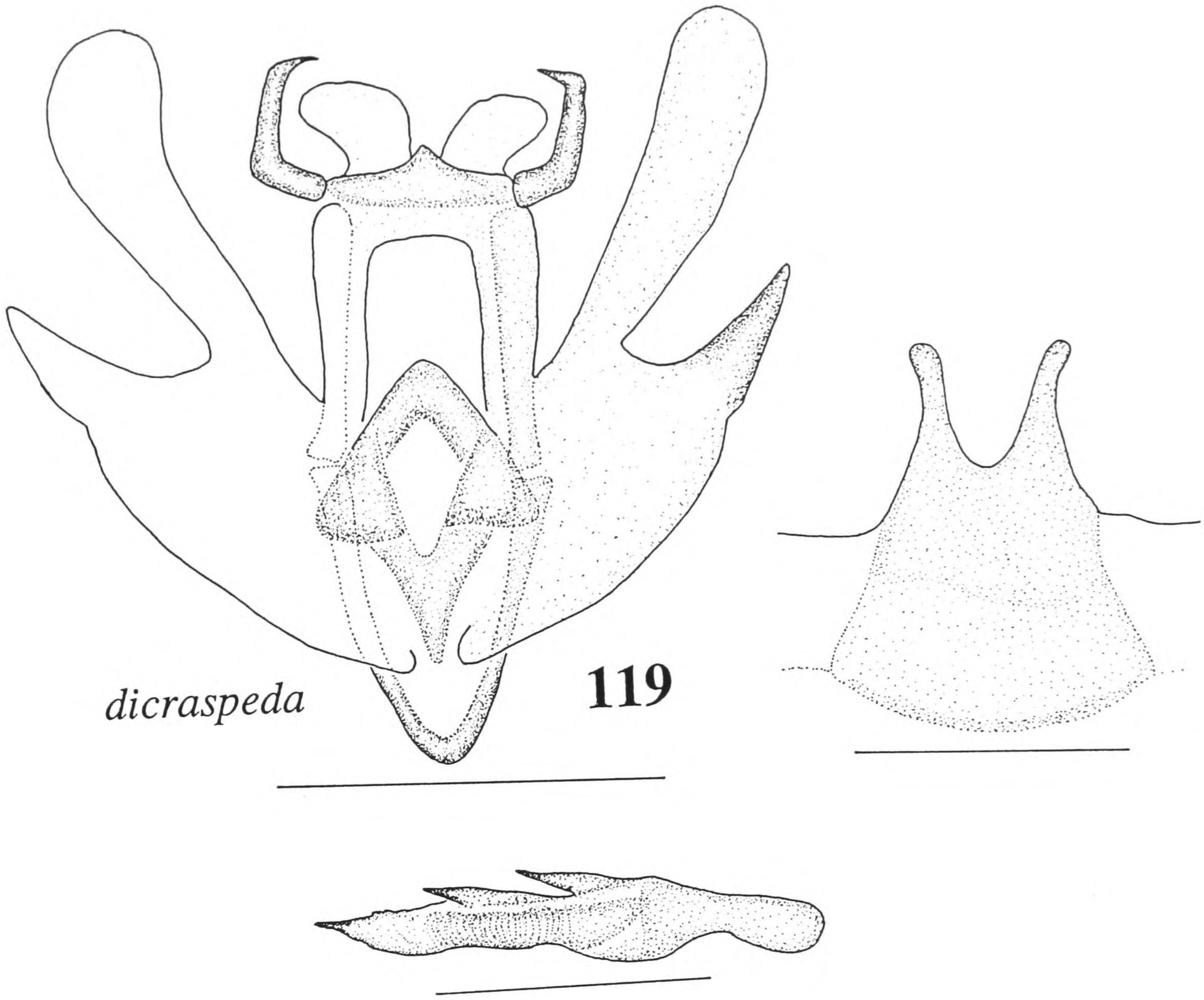
albicoma albicoma & albicoma nasuta

117

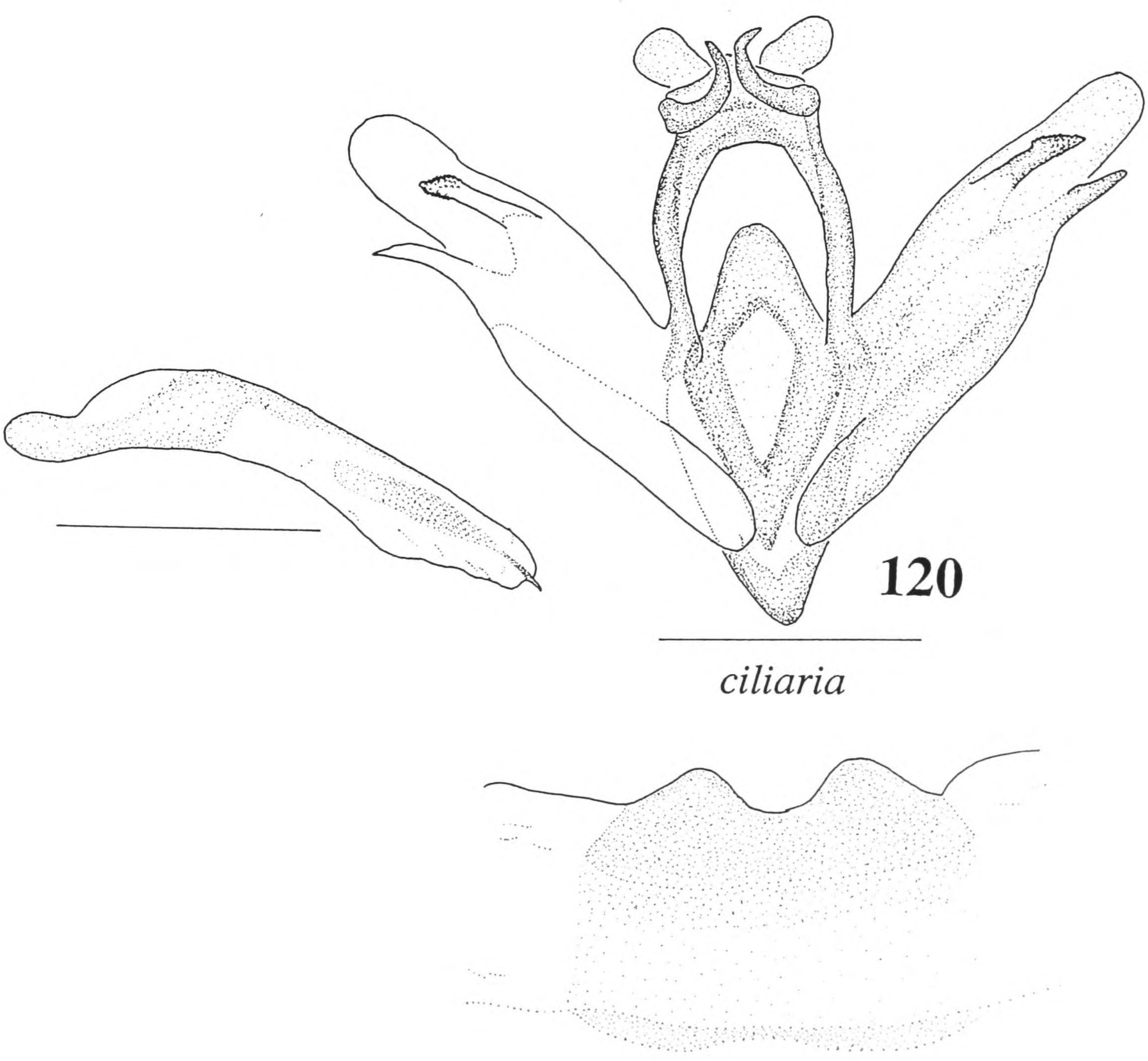


118

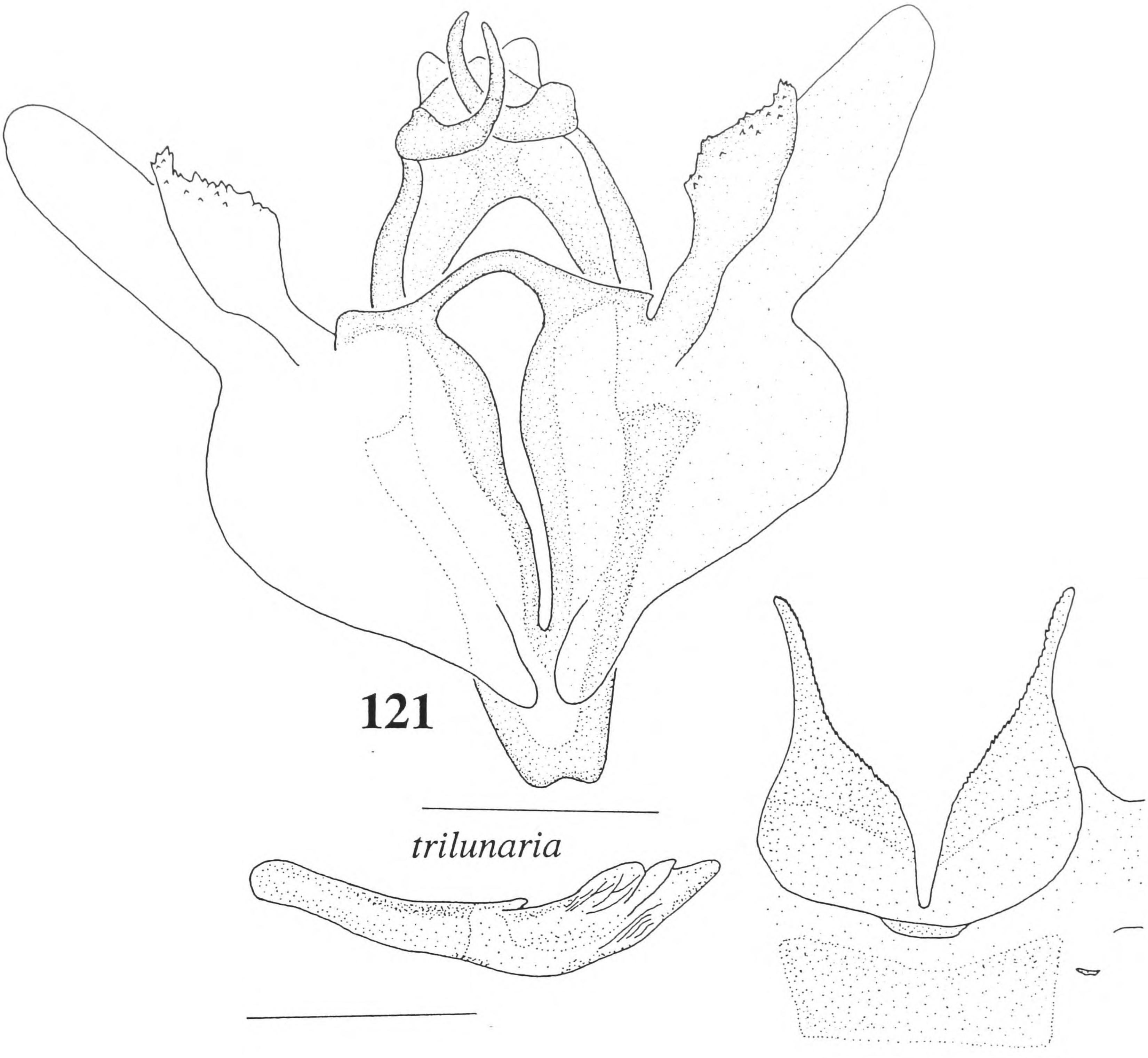
concinna



dicraspeda **119**



120 *ciliaria*



121

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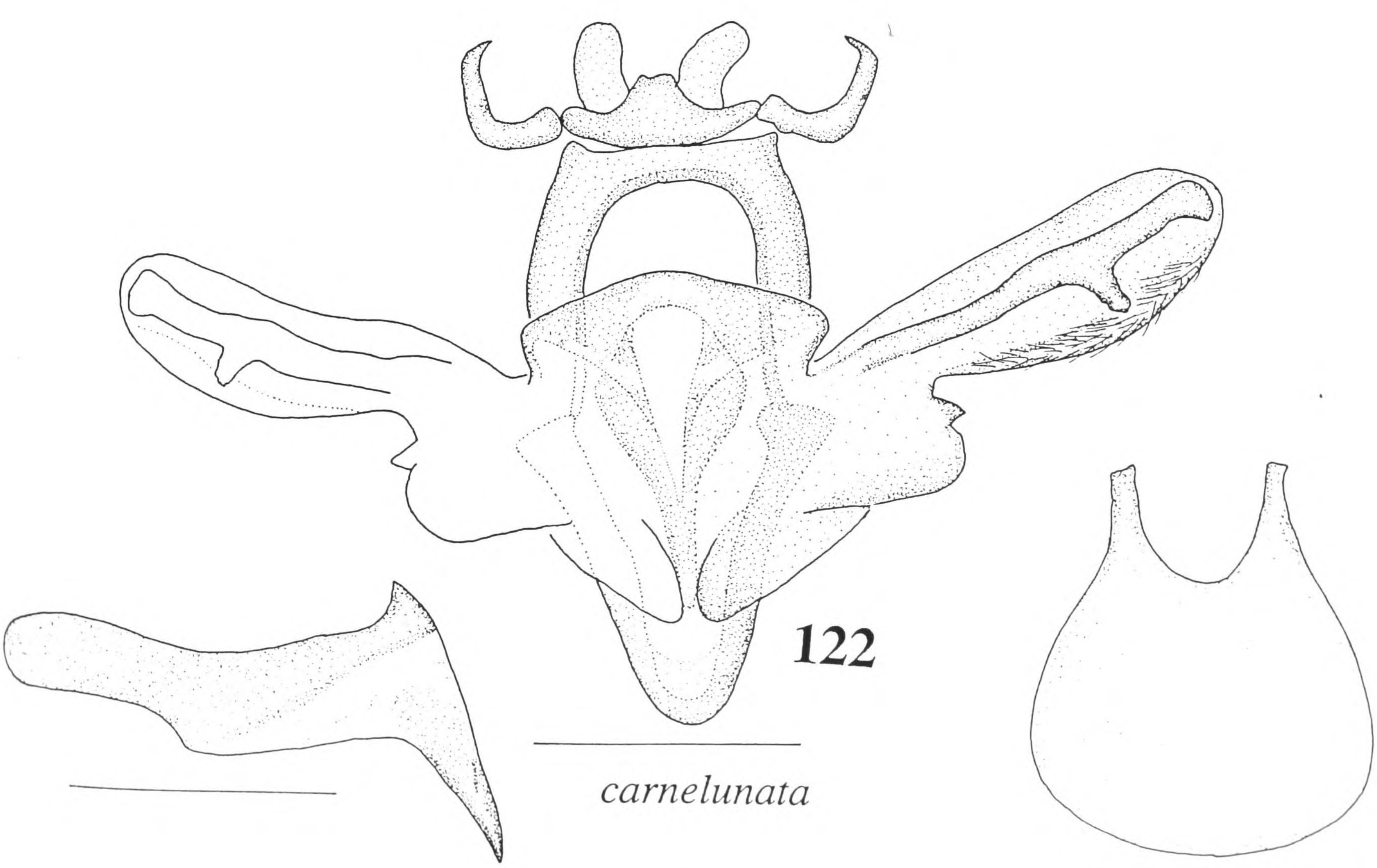
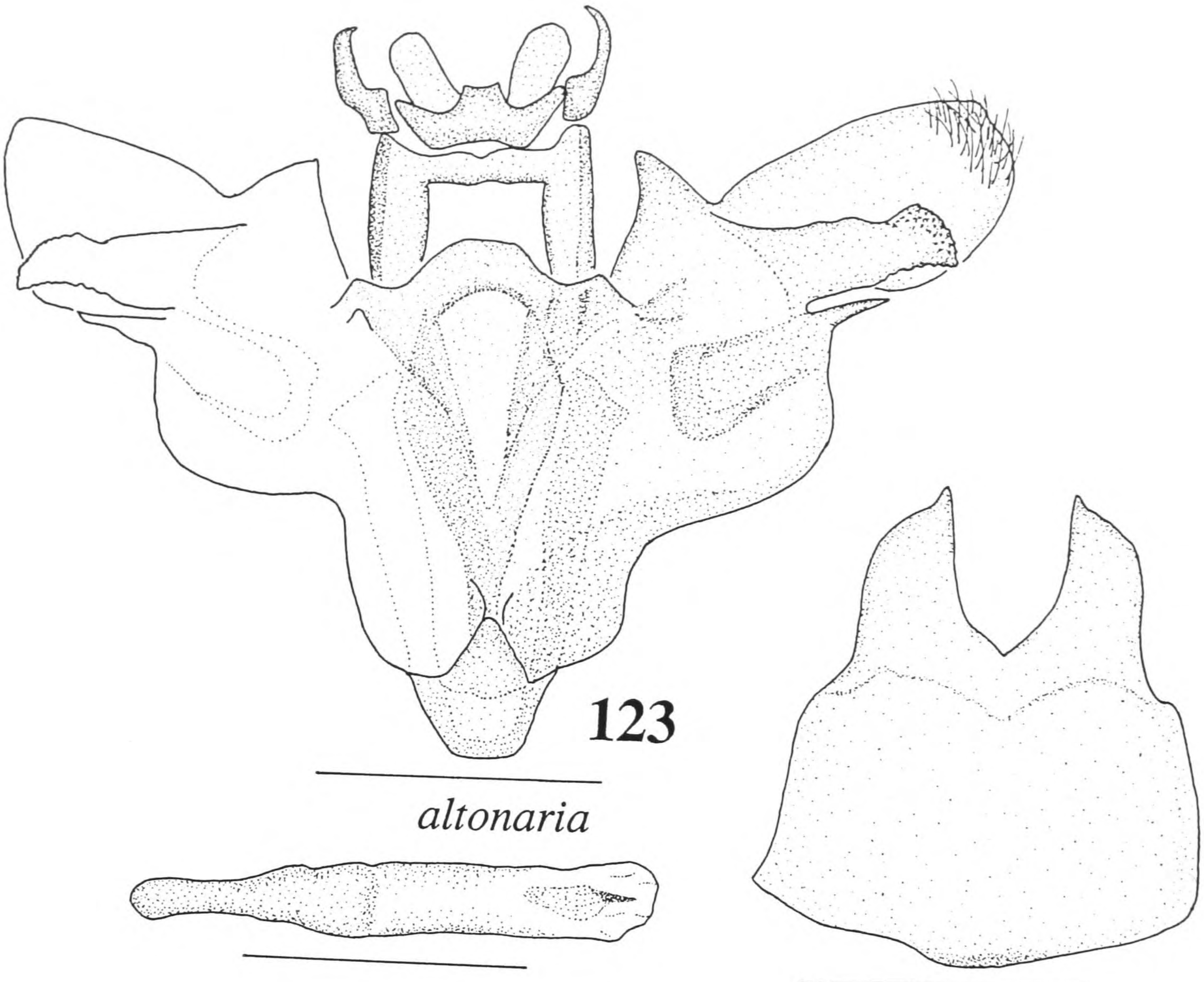


122

carnelunata



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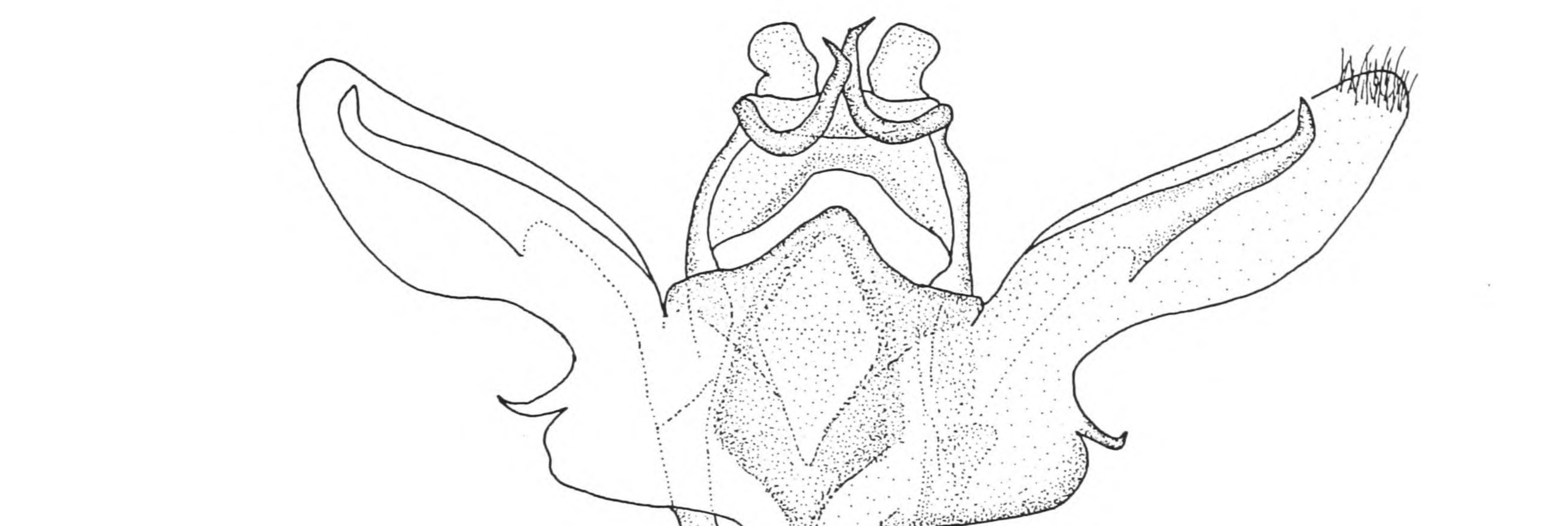
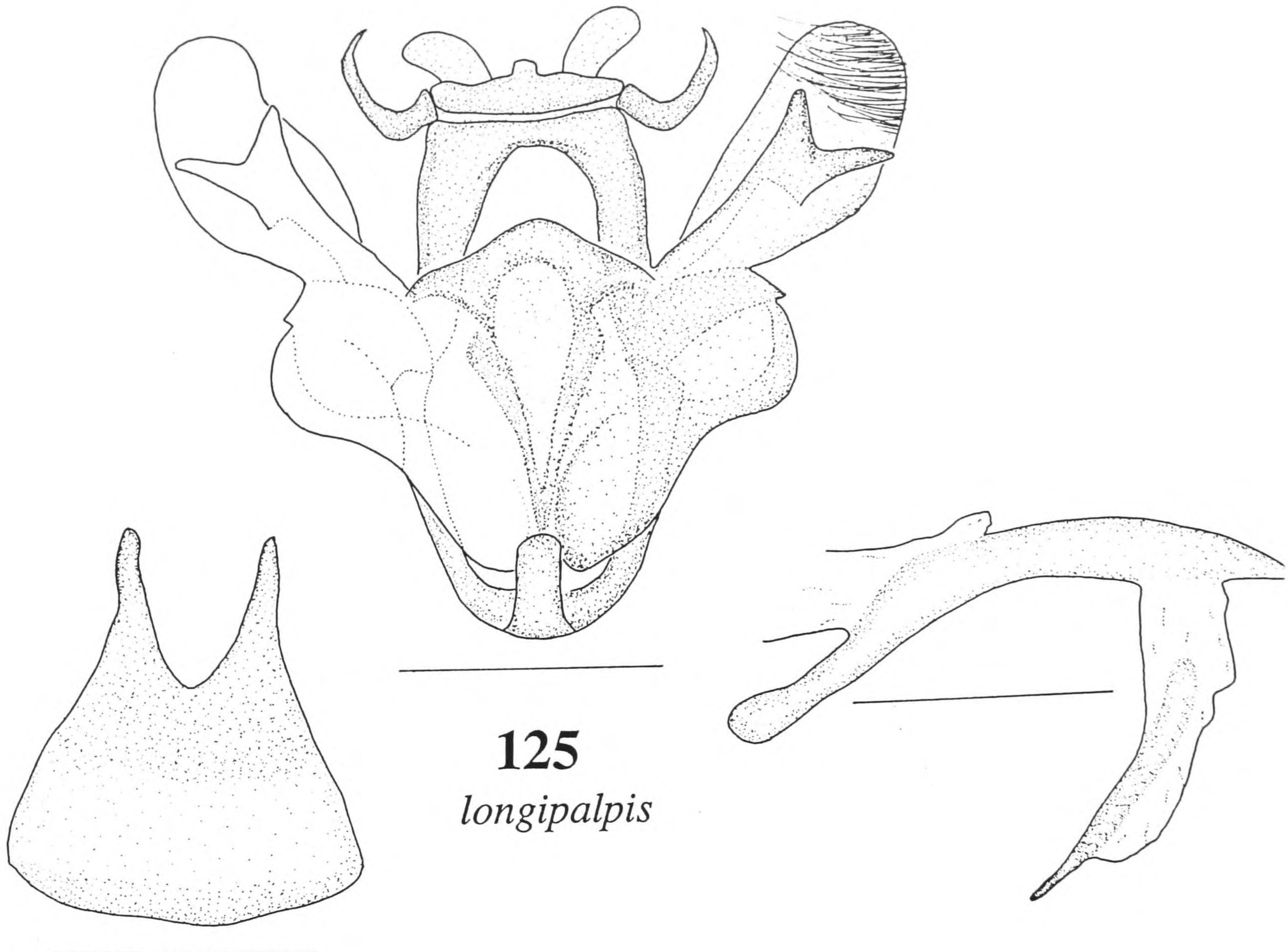
altonaria

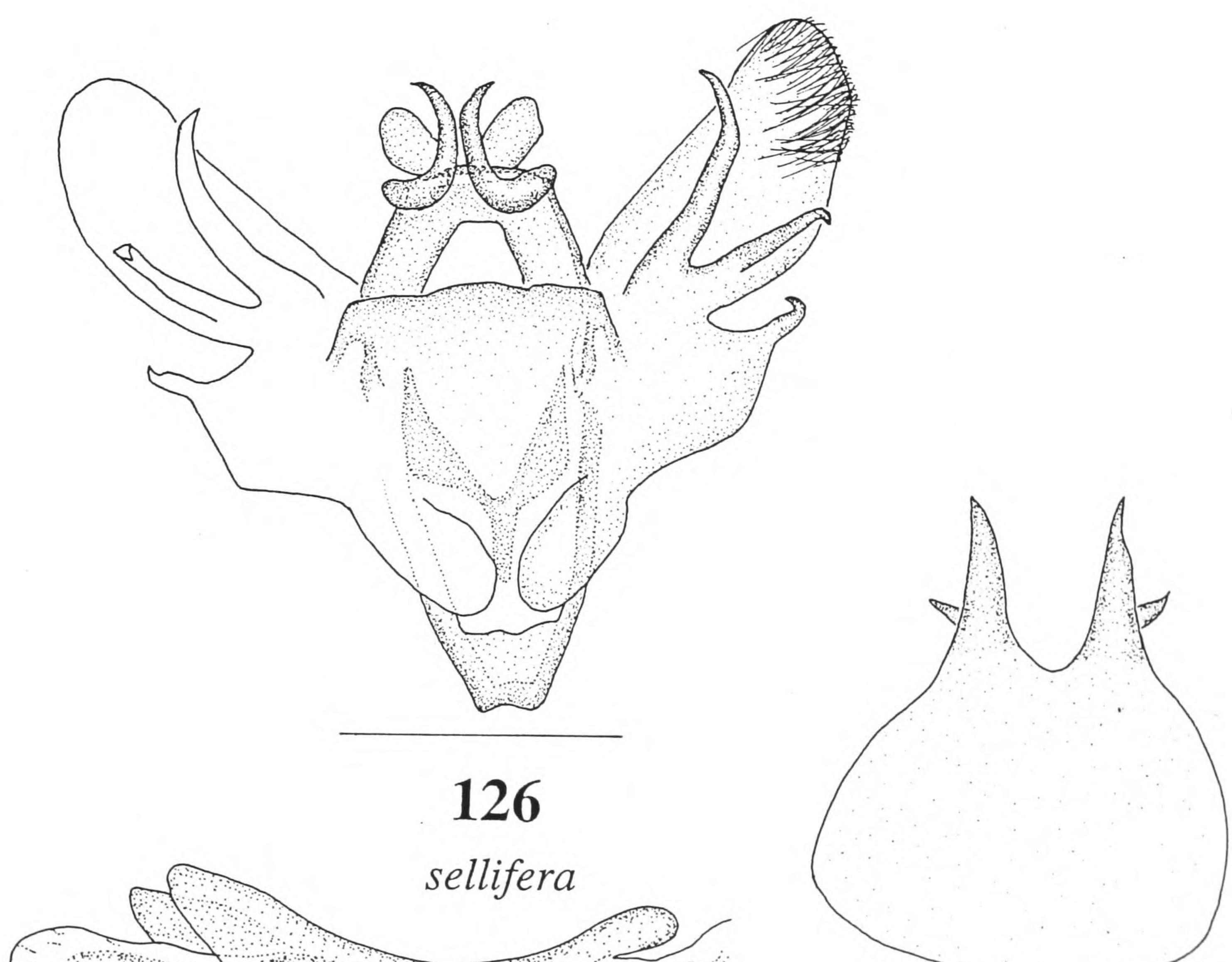


confluaria

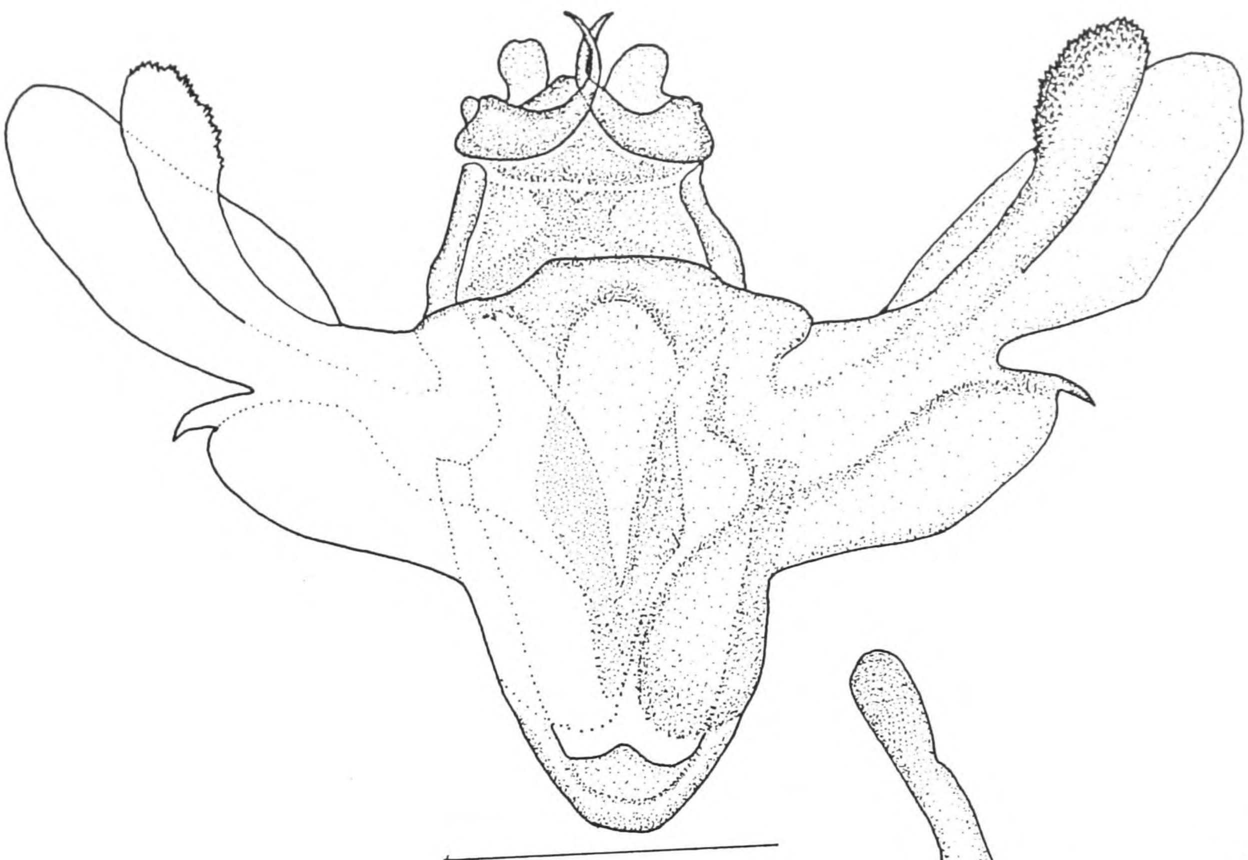
124

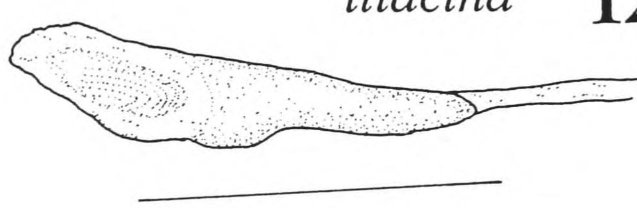


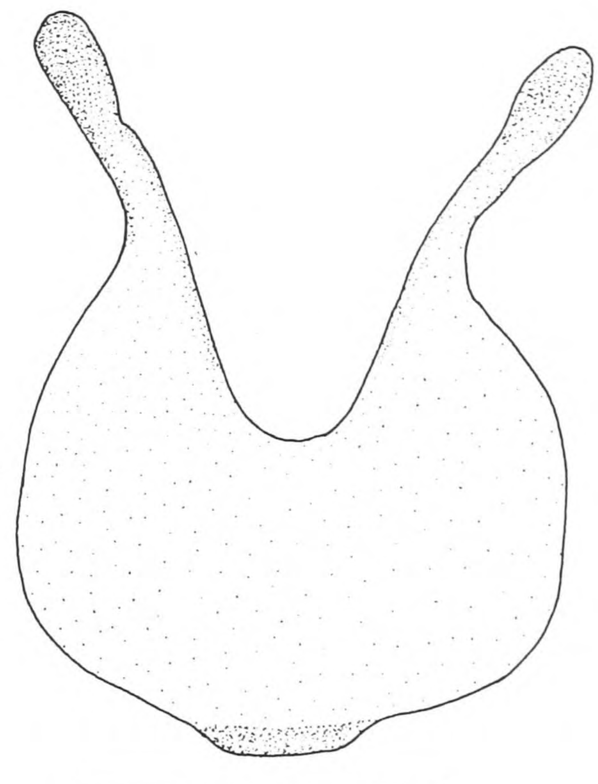
125
longipalpis



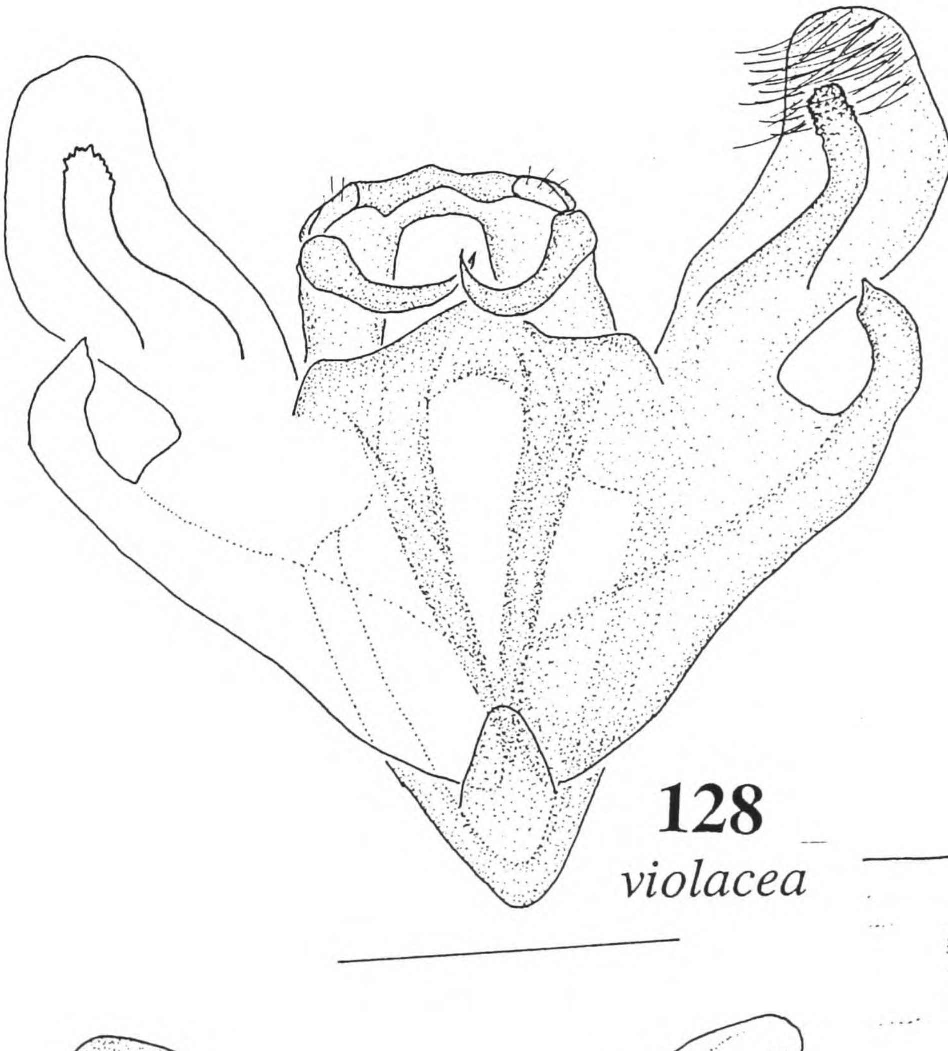
126
sellifera







lilacina **127**



128
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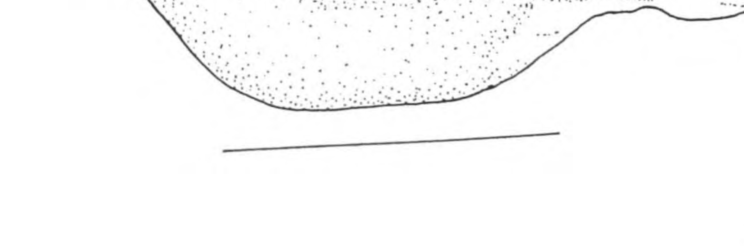
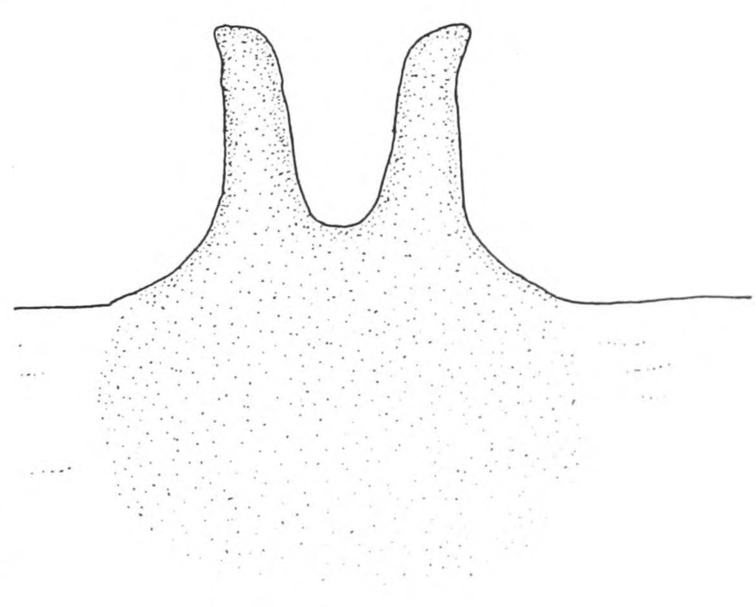
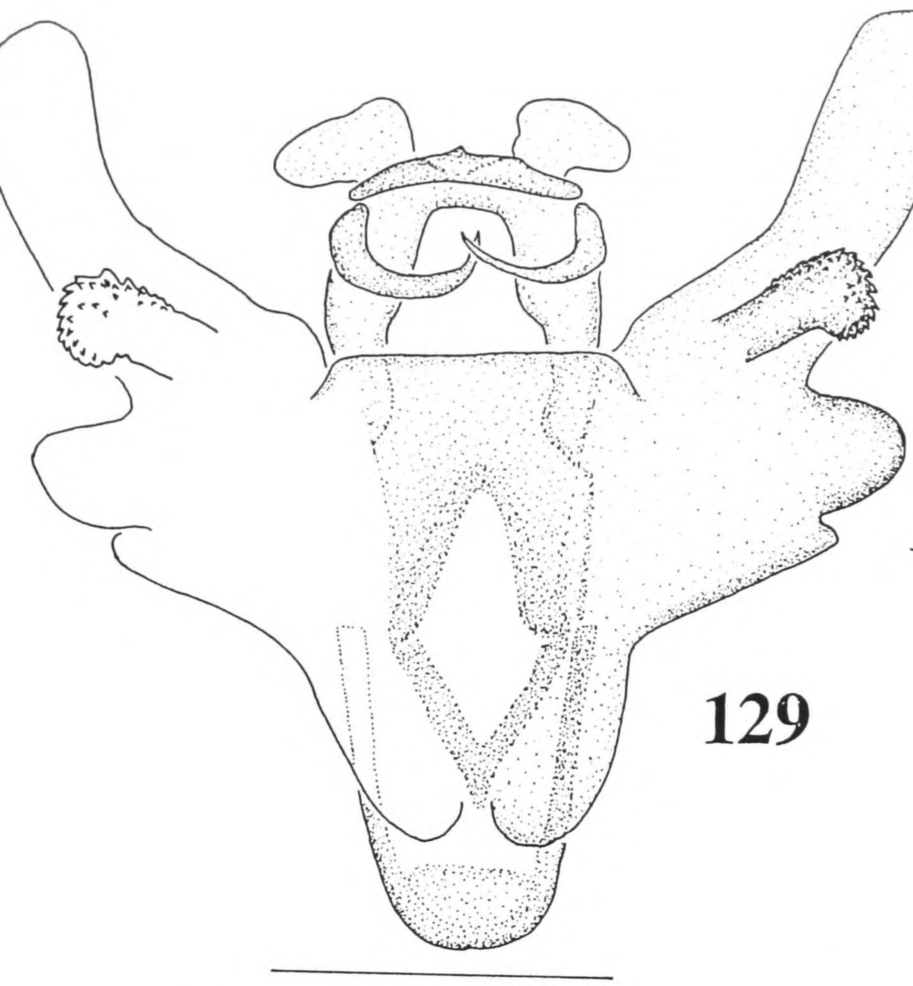
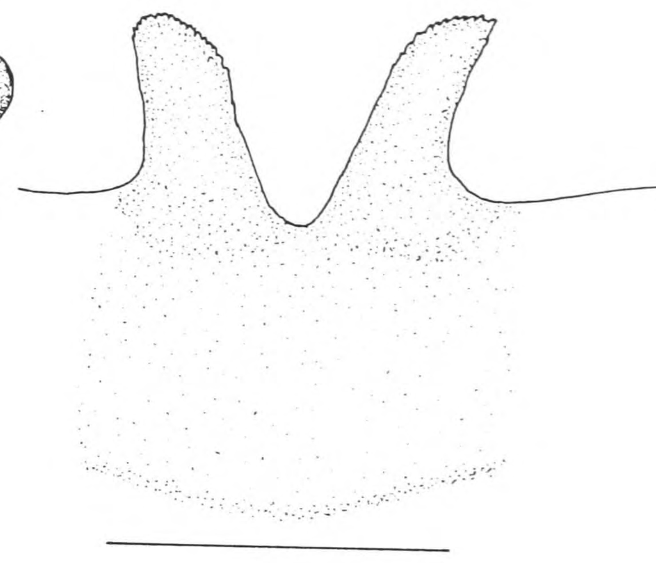


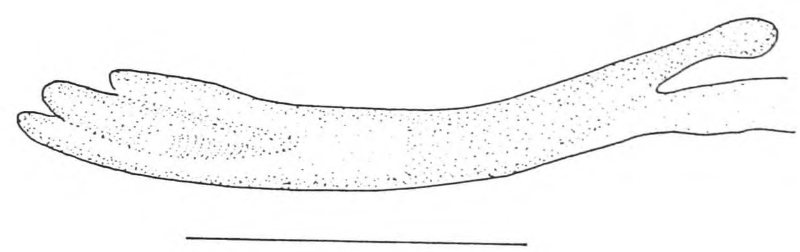


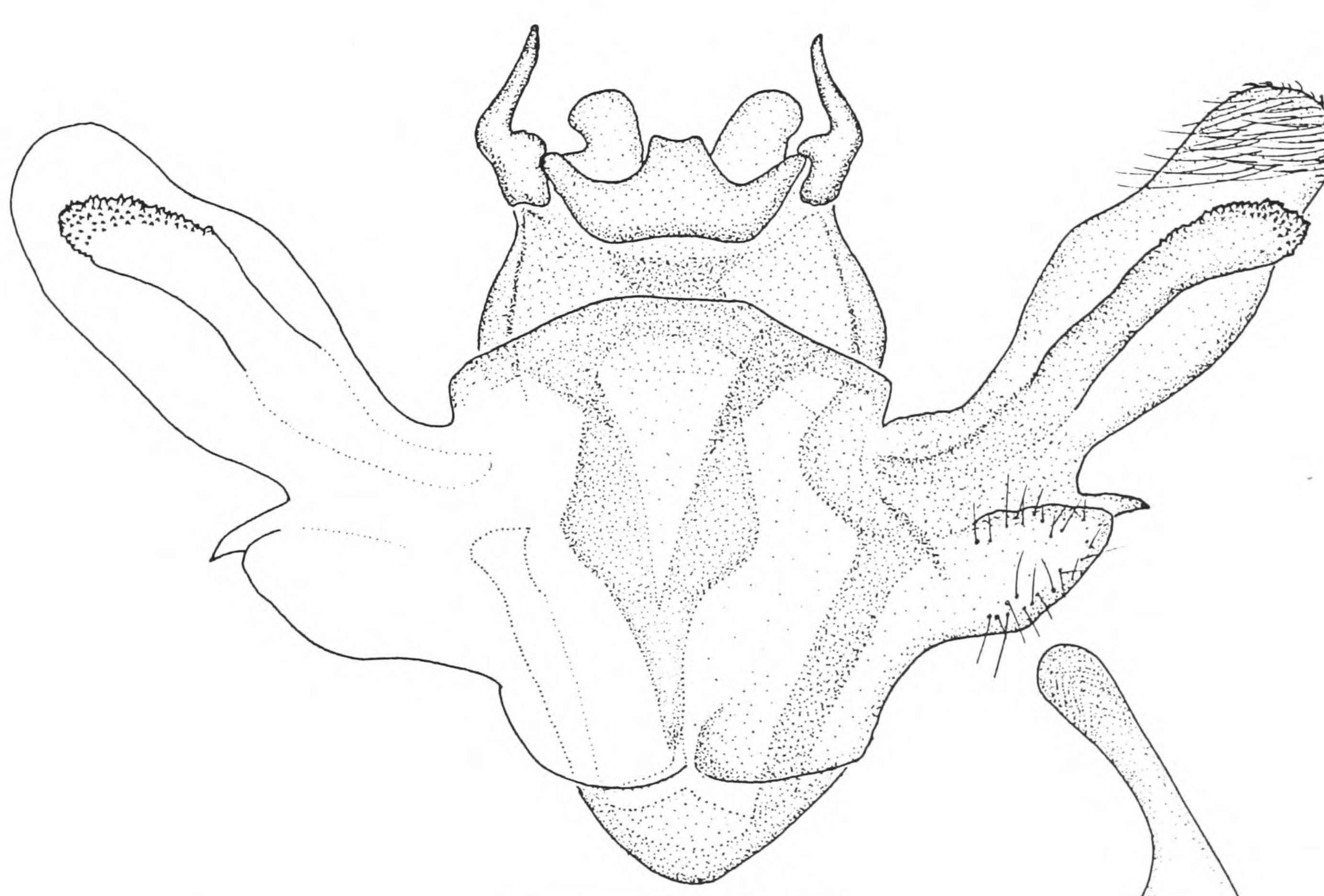


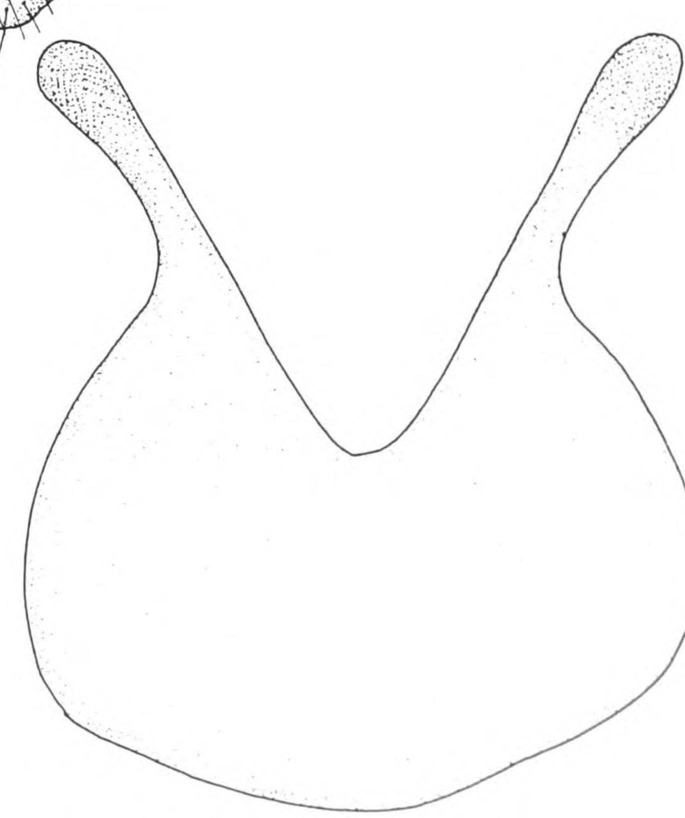


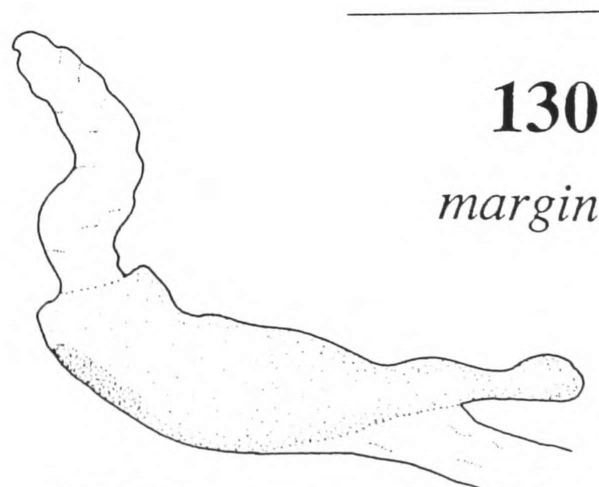
129

callicula & obeliscata



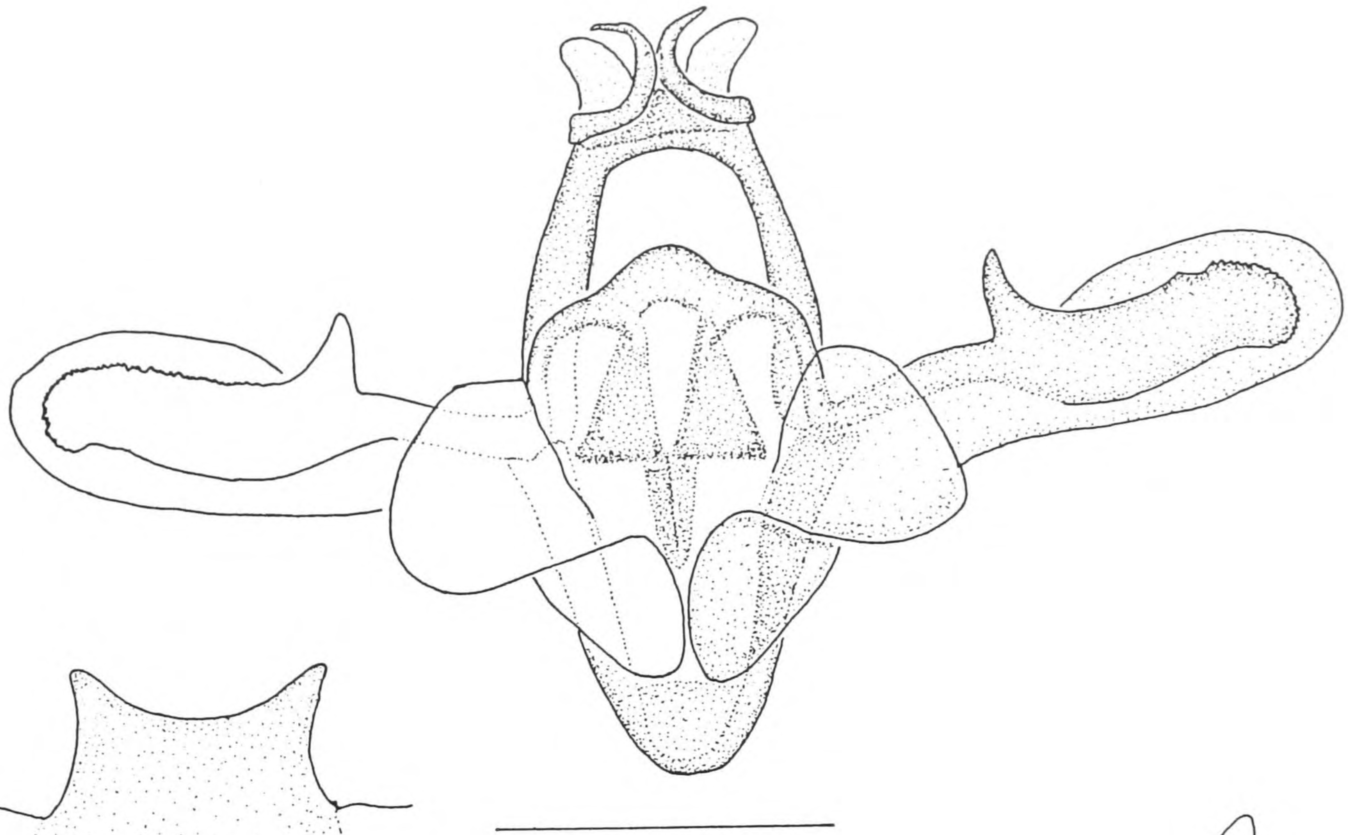


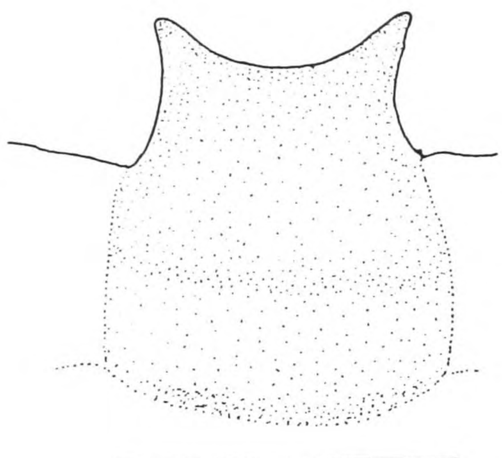




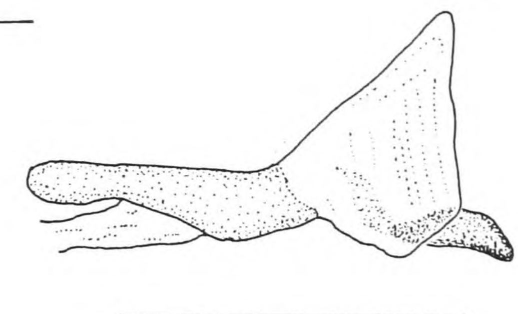
130

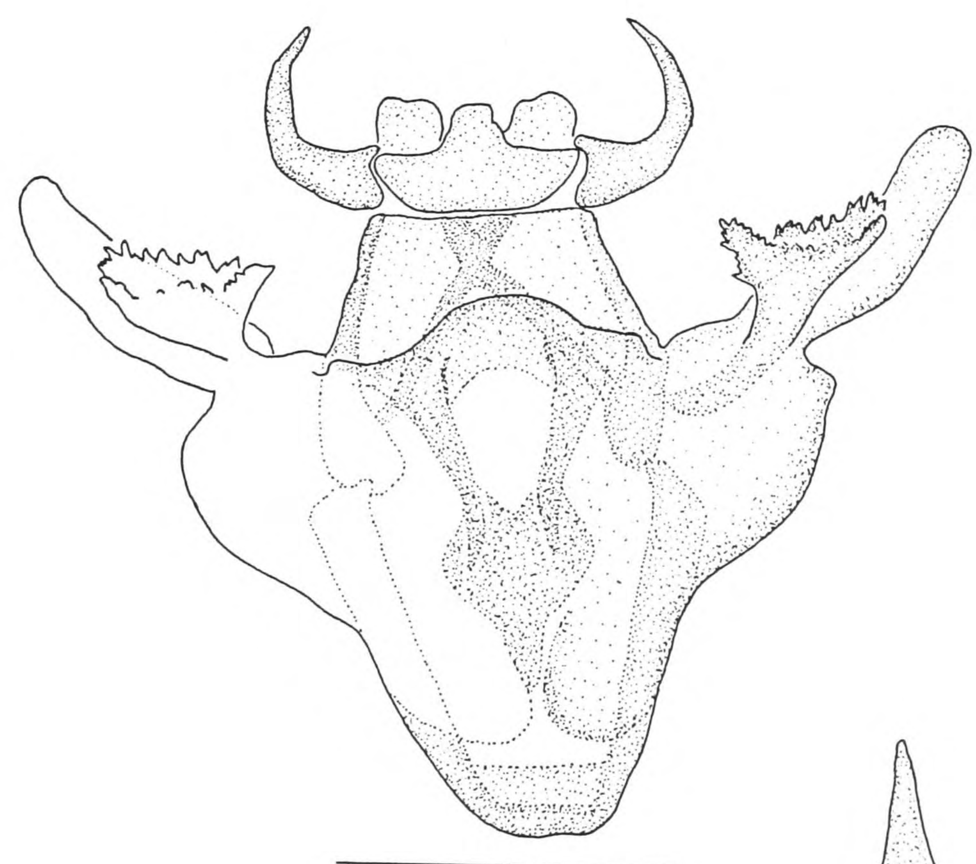
marginata



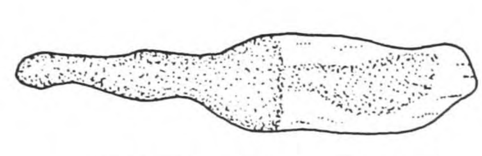


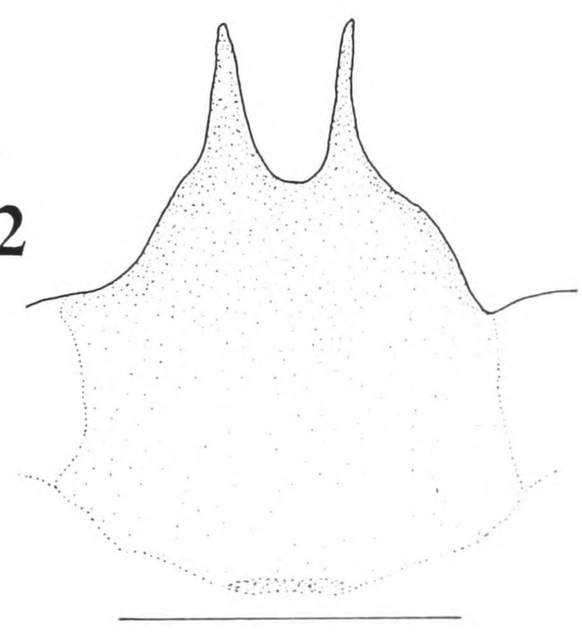
131
tricamerata

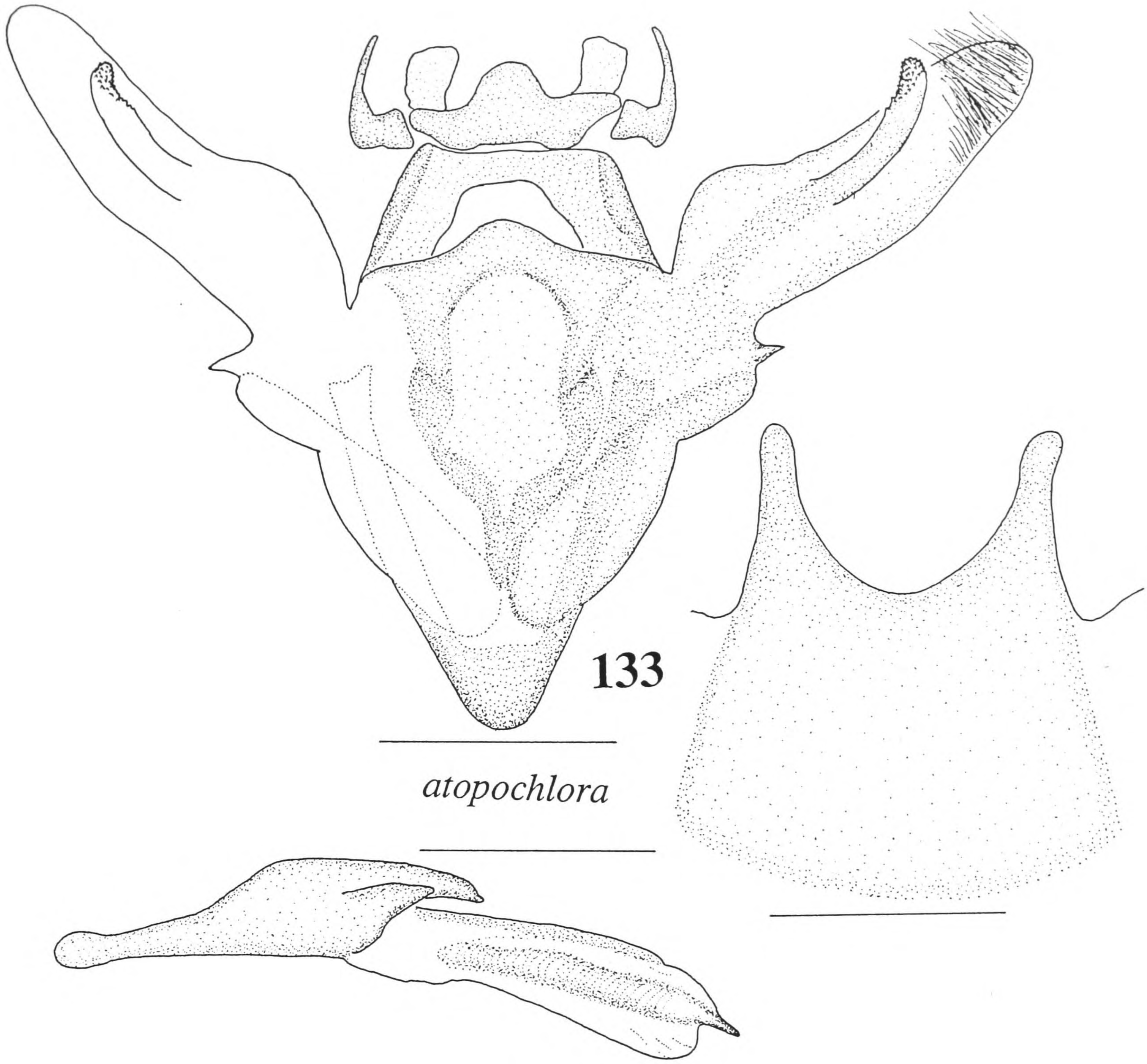




obsolescens **132**

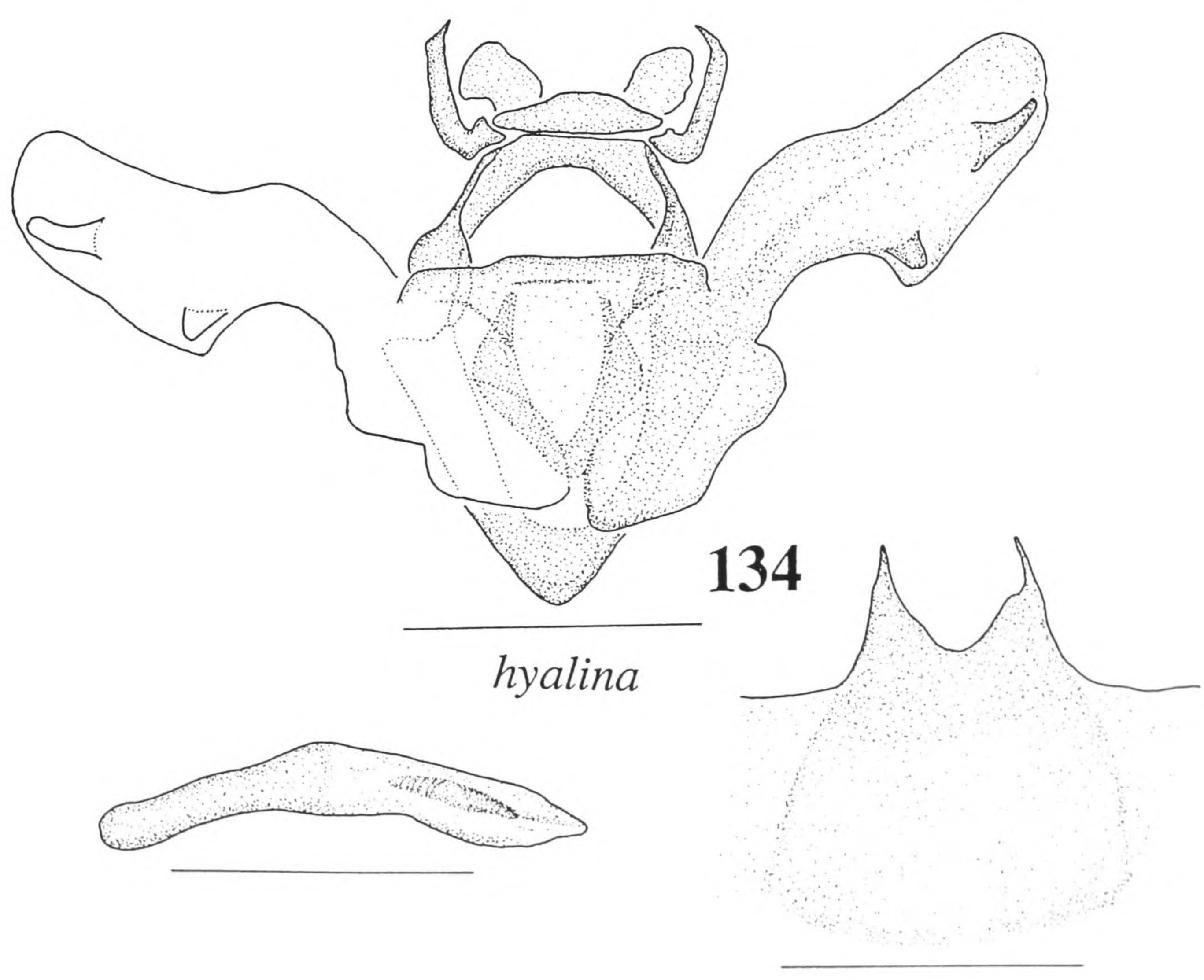






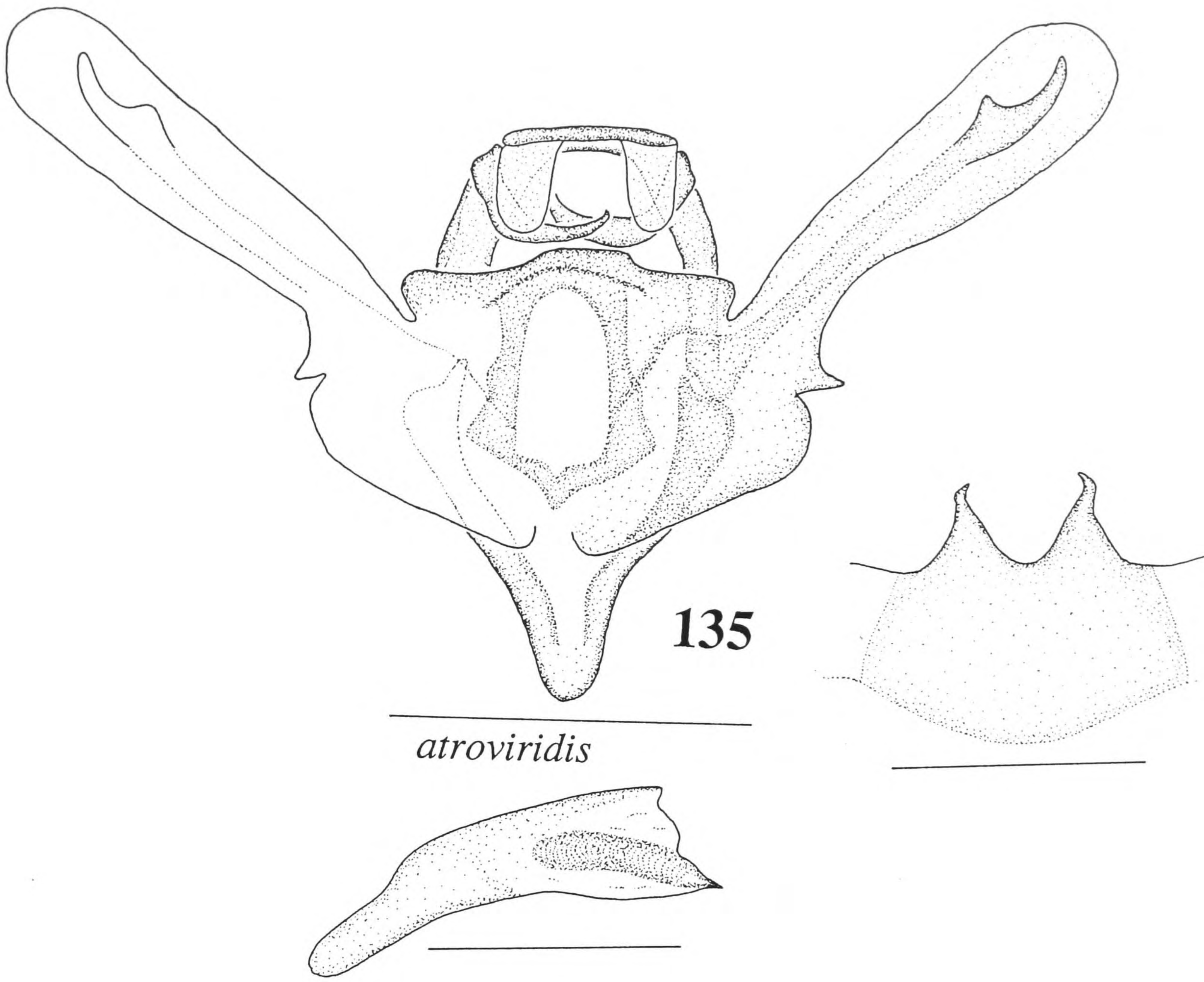
133

atopochlora



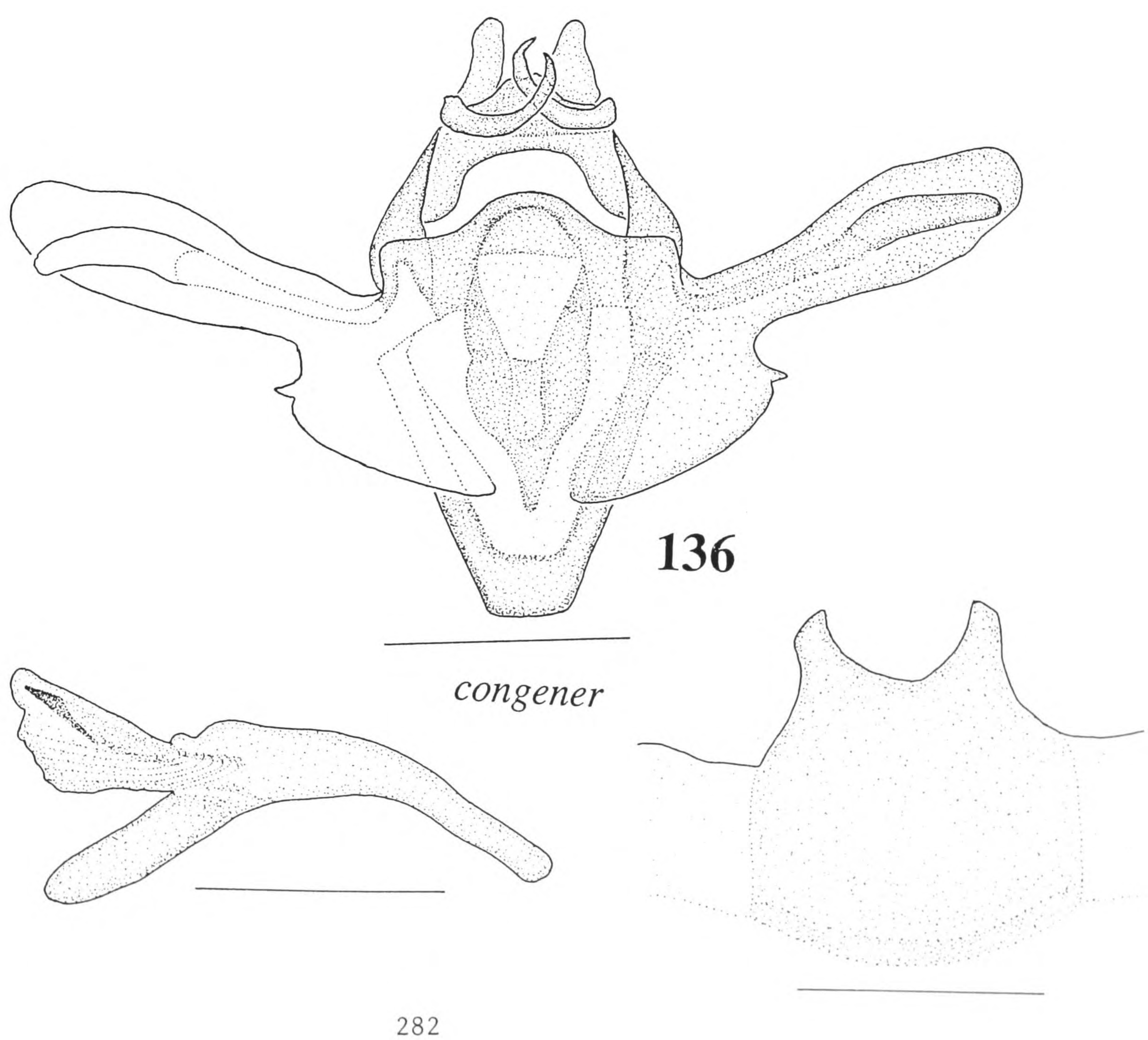
134

hyalina



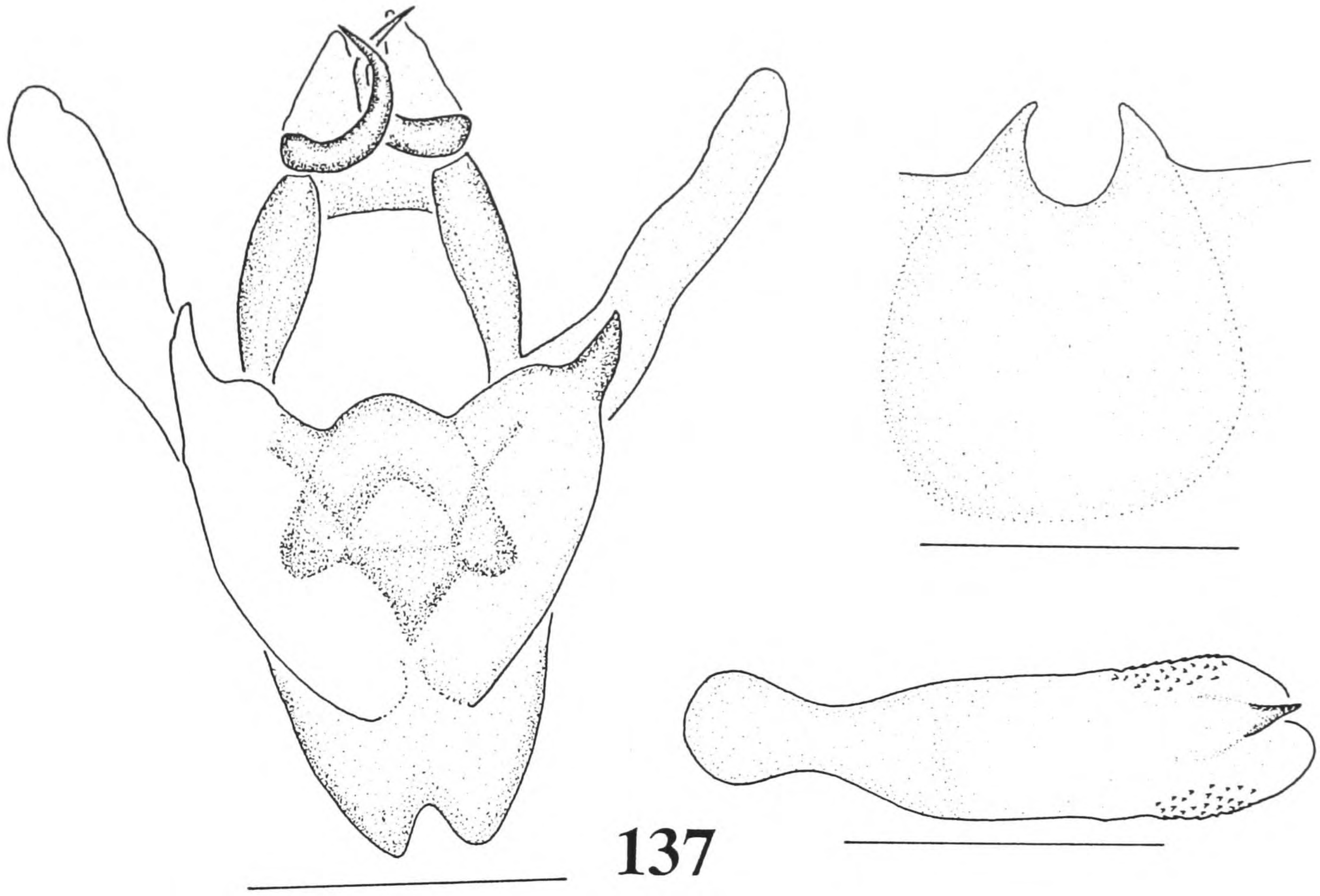
135

atroviridis



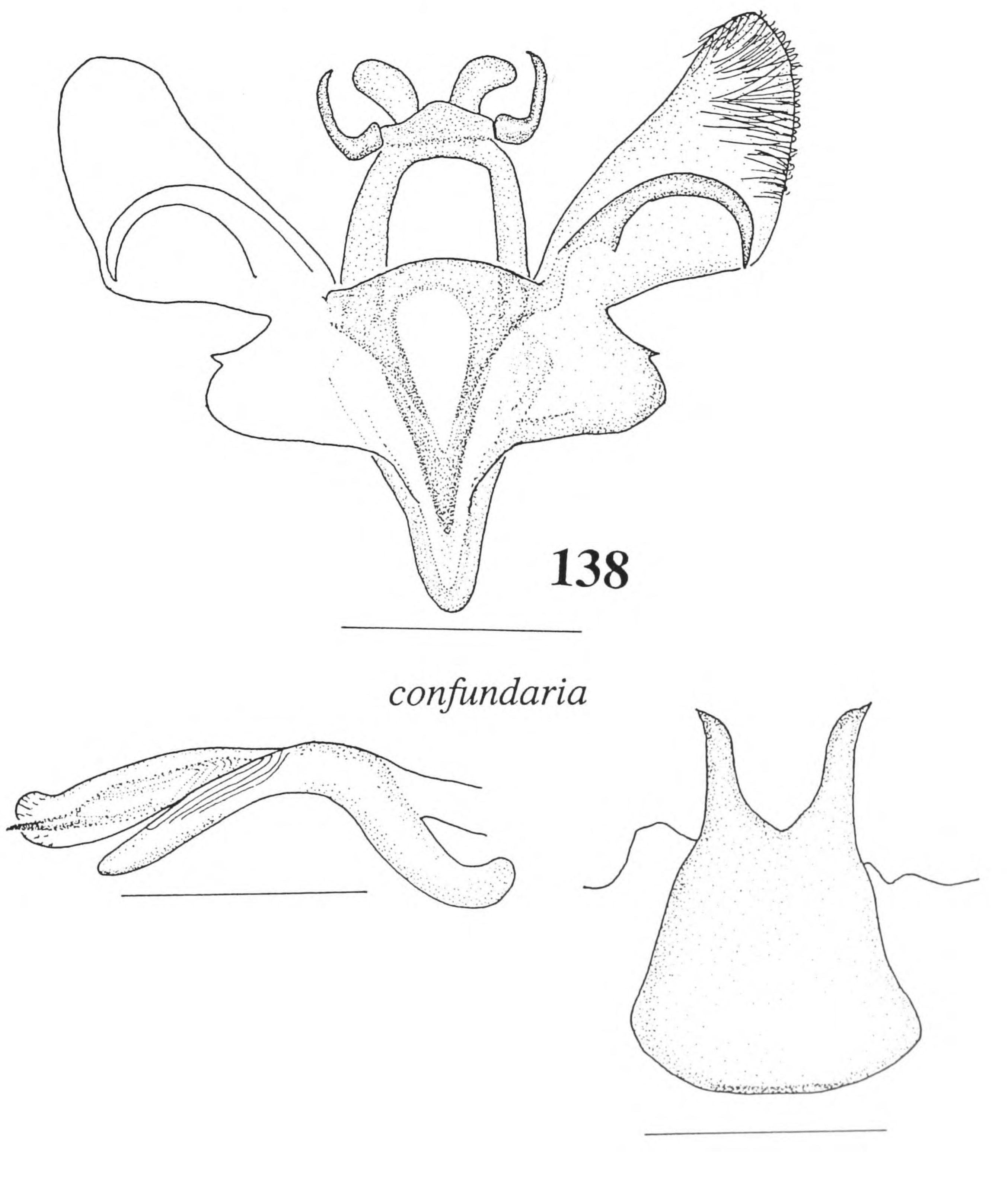
136

congener



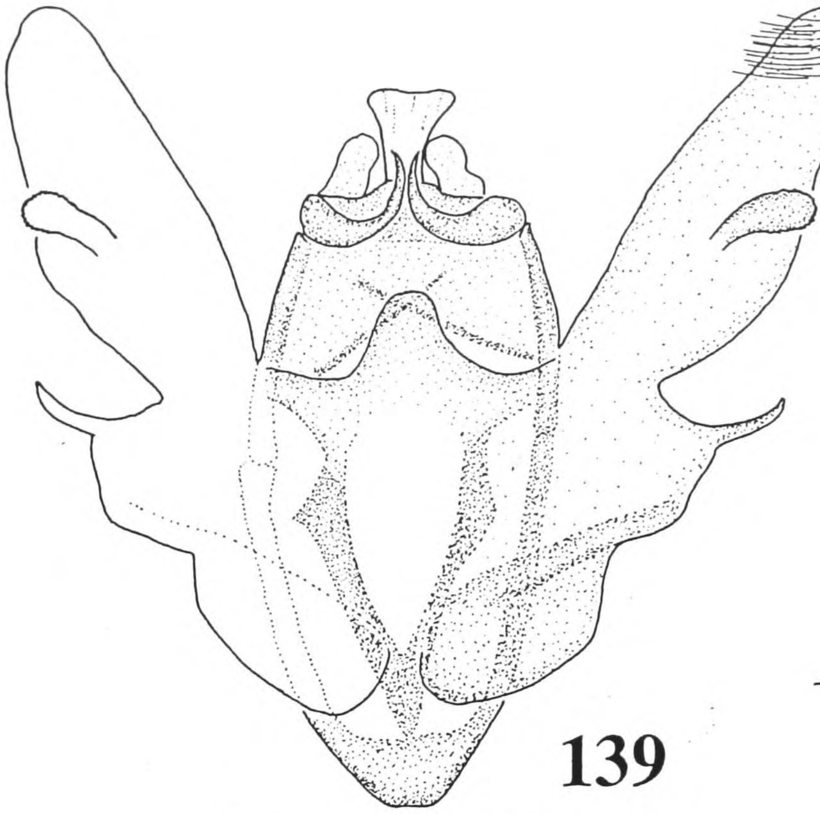
137

imaculata



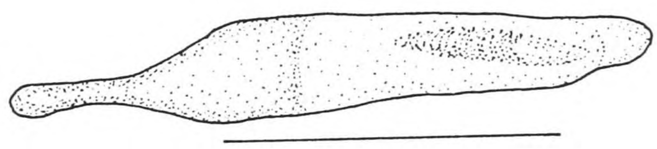
138

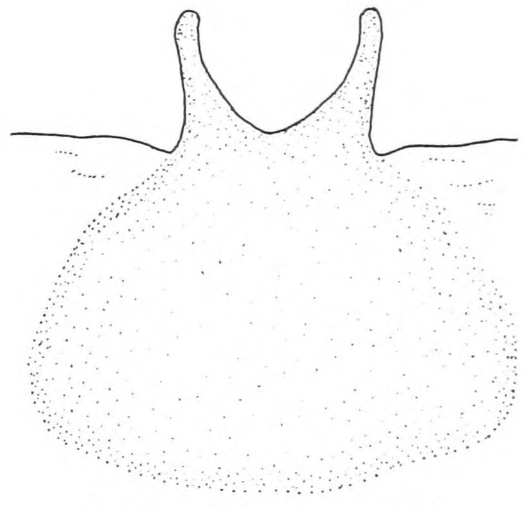
confundaria

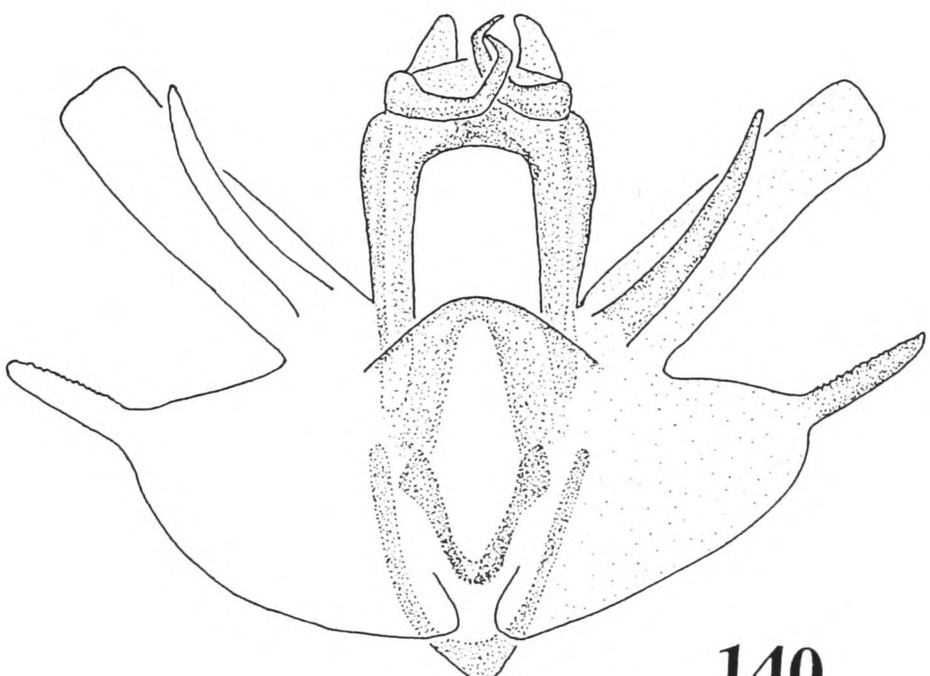


139

depressa







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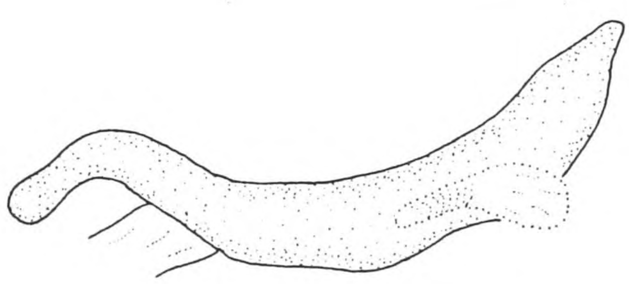
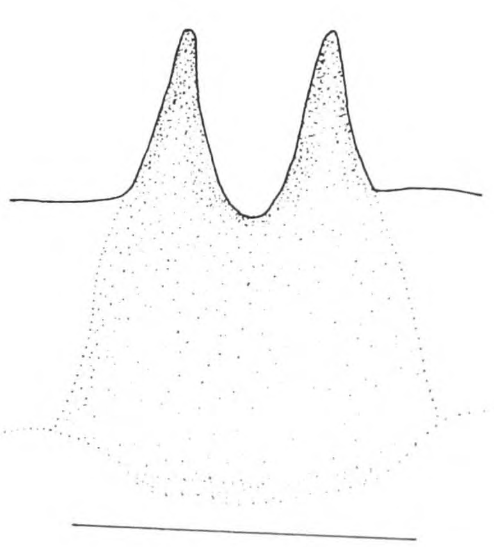
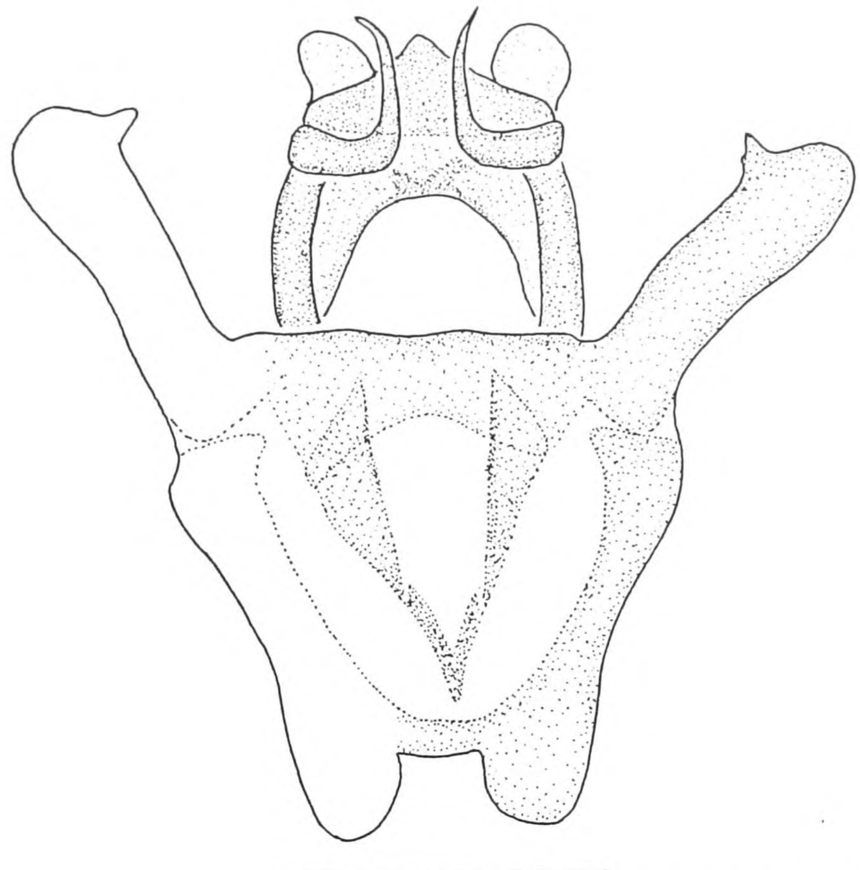
rubescens







stagonata

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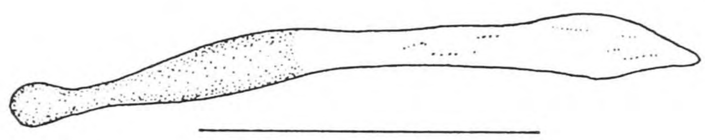

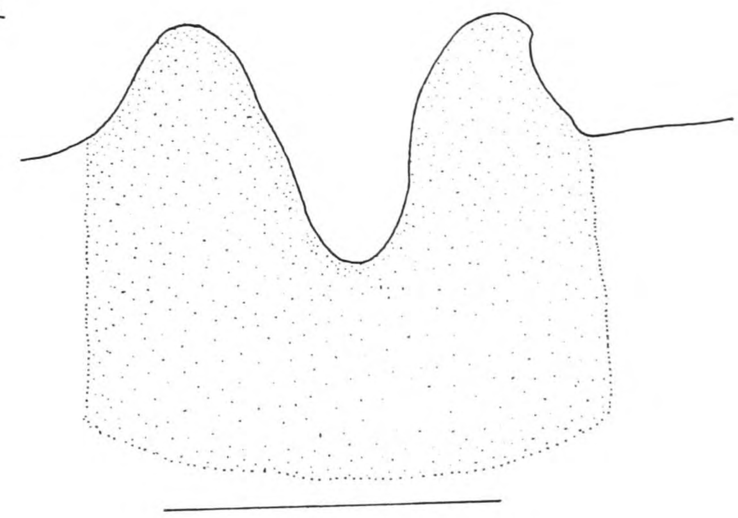

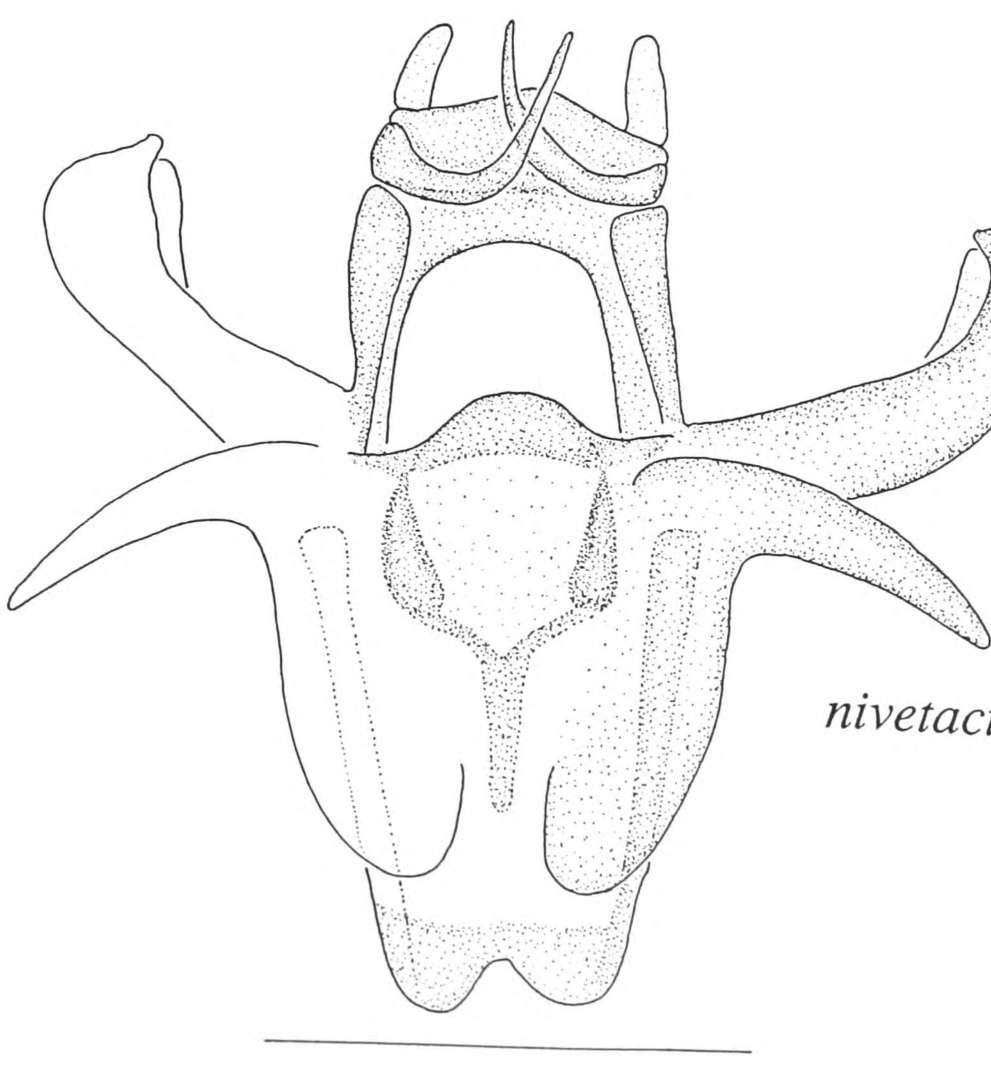

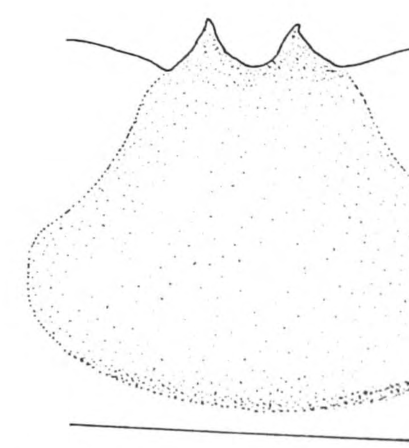

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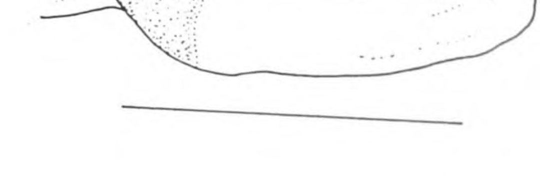
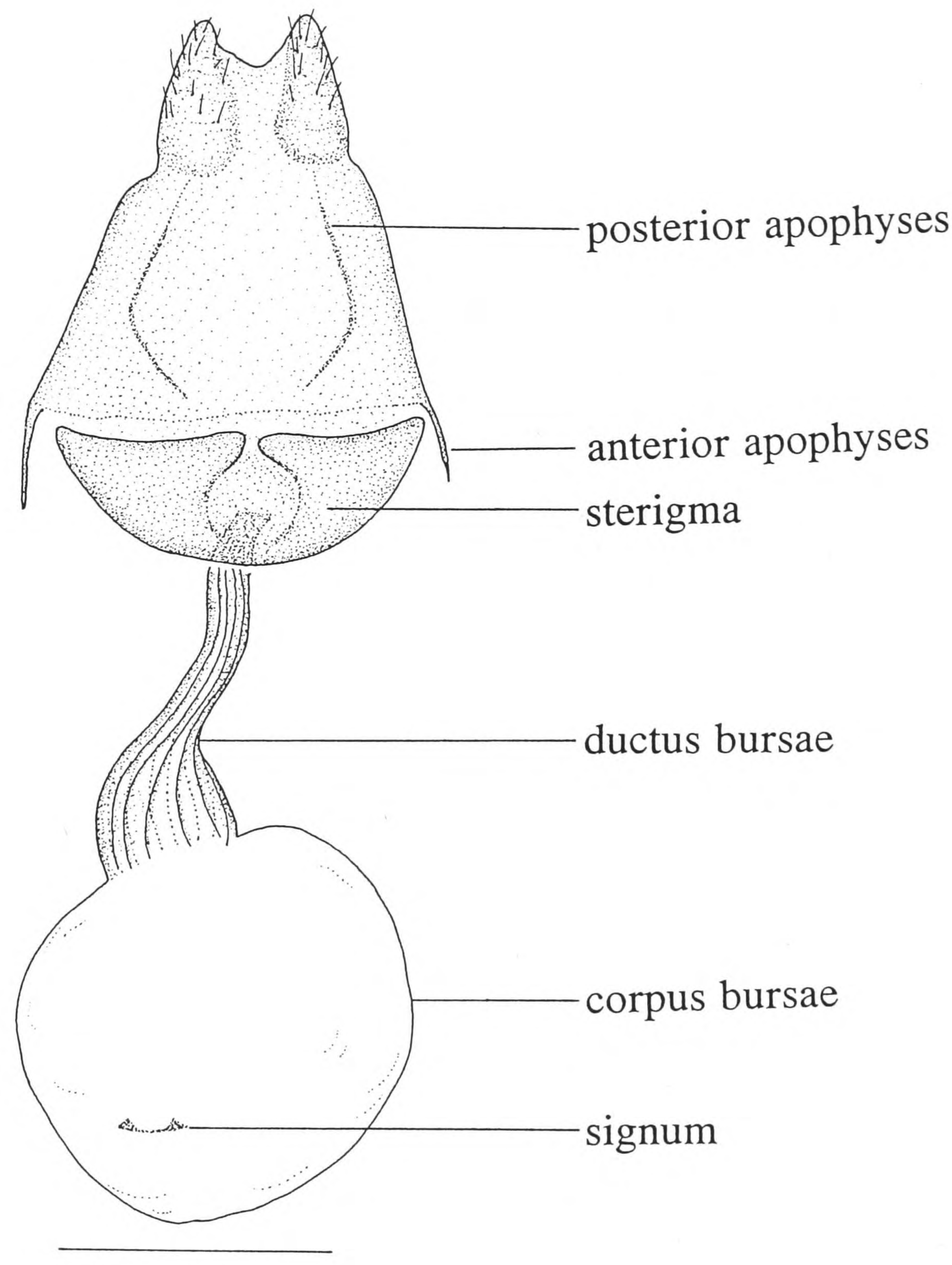
nivetacta



Figs 143-191 (on following pages). Female genitalia of *Oospila species*.

Scale bar 1 mm.



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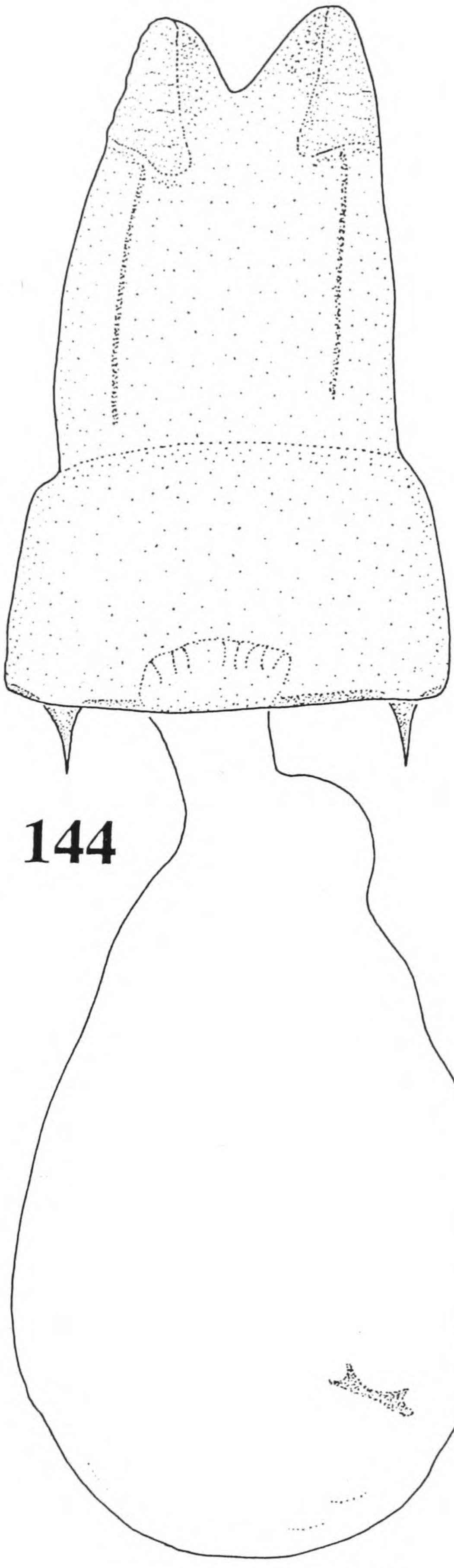
decoloraria



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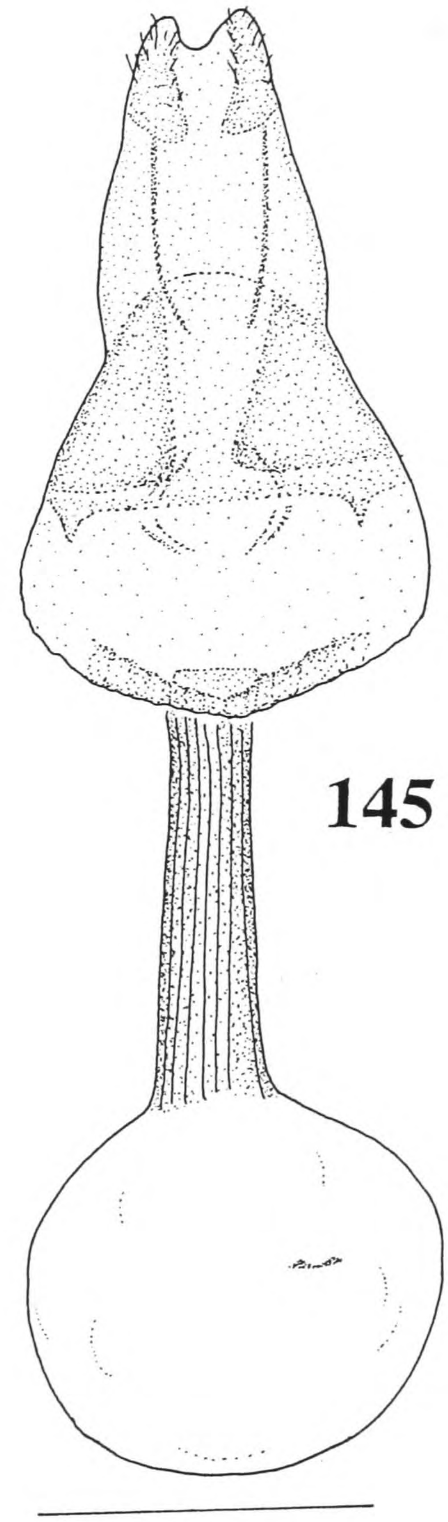
jaspidata



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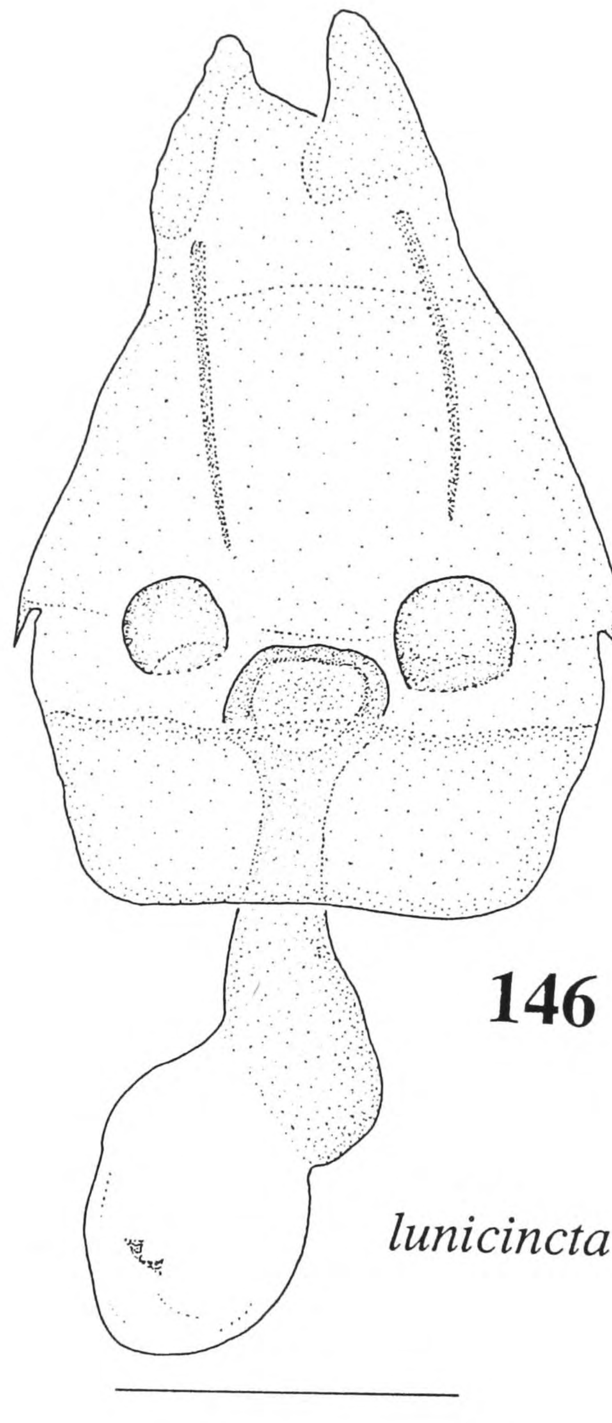
longiplaga



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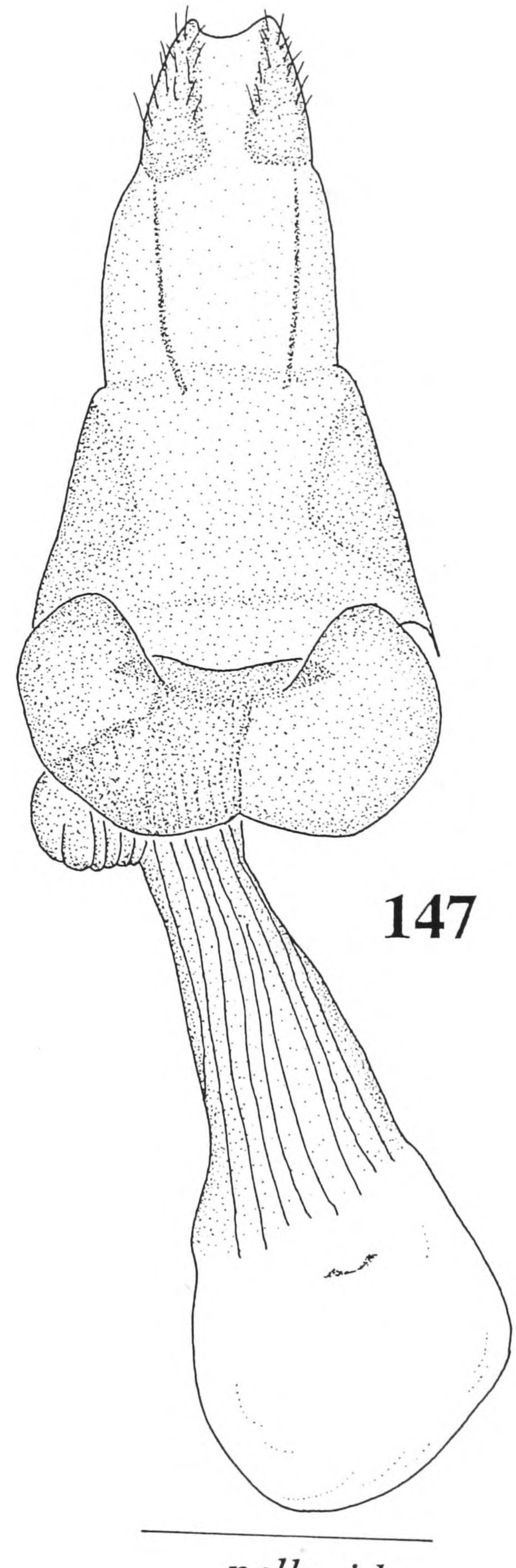
lunicincta



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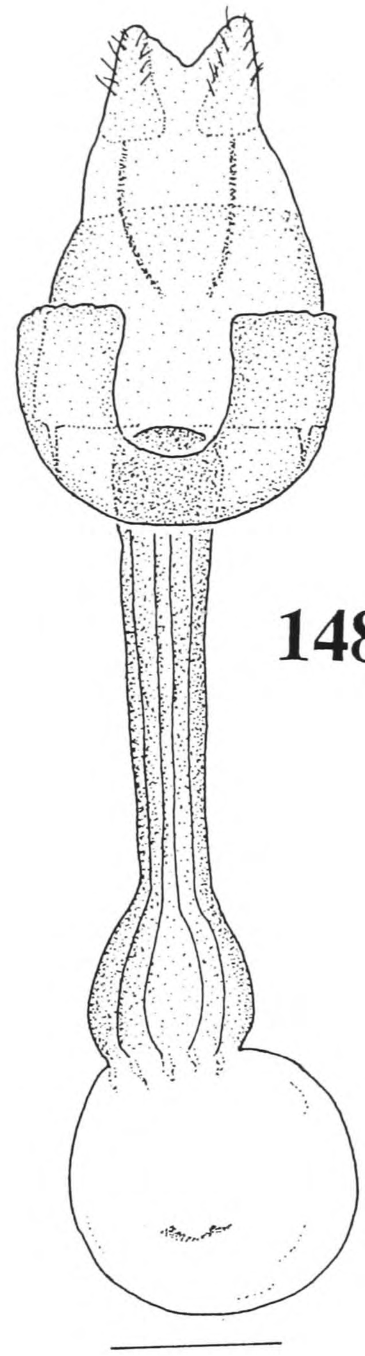
pellucida



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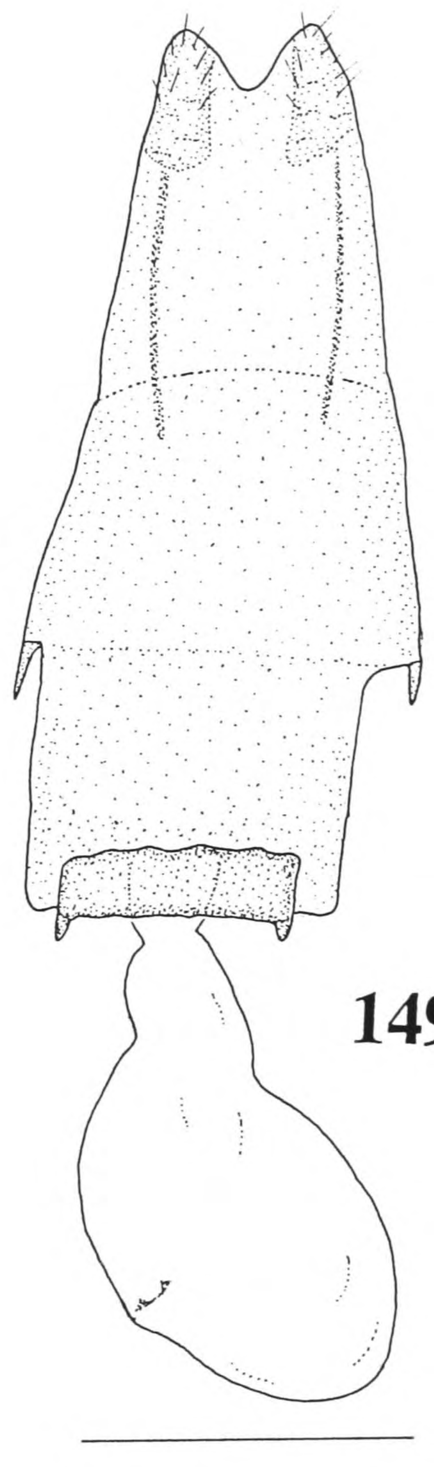
ruptimacula



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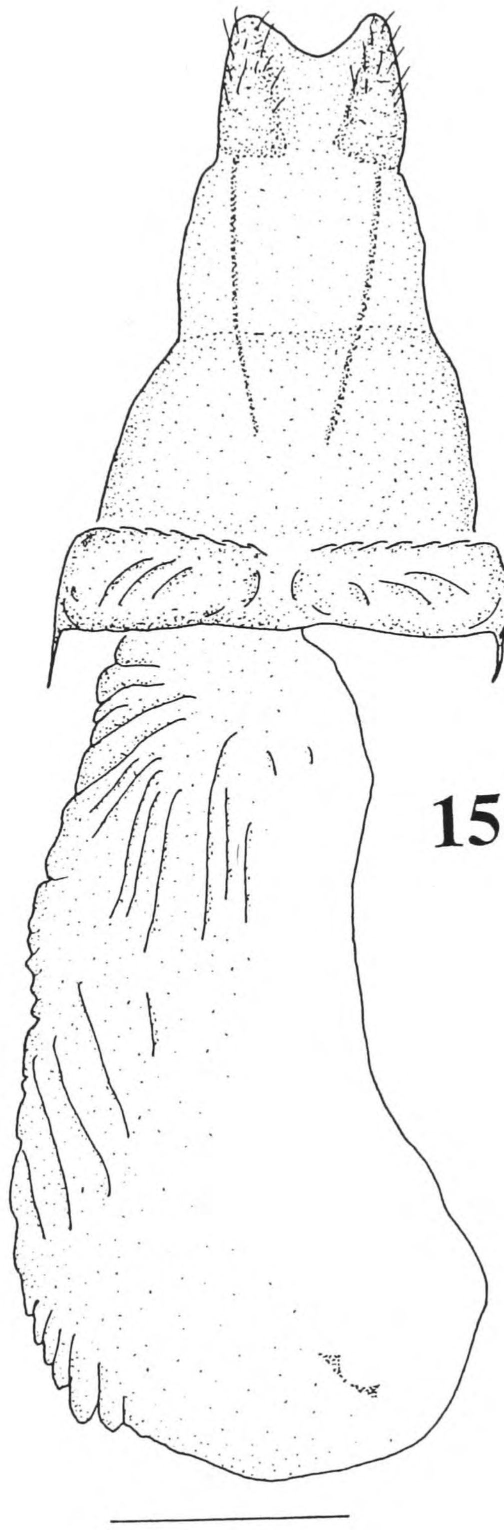
venezuelata



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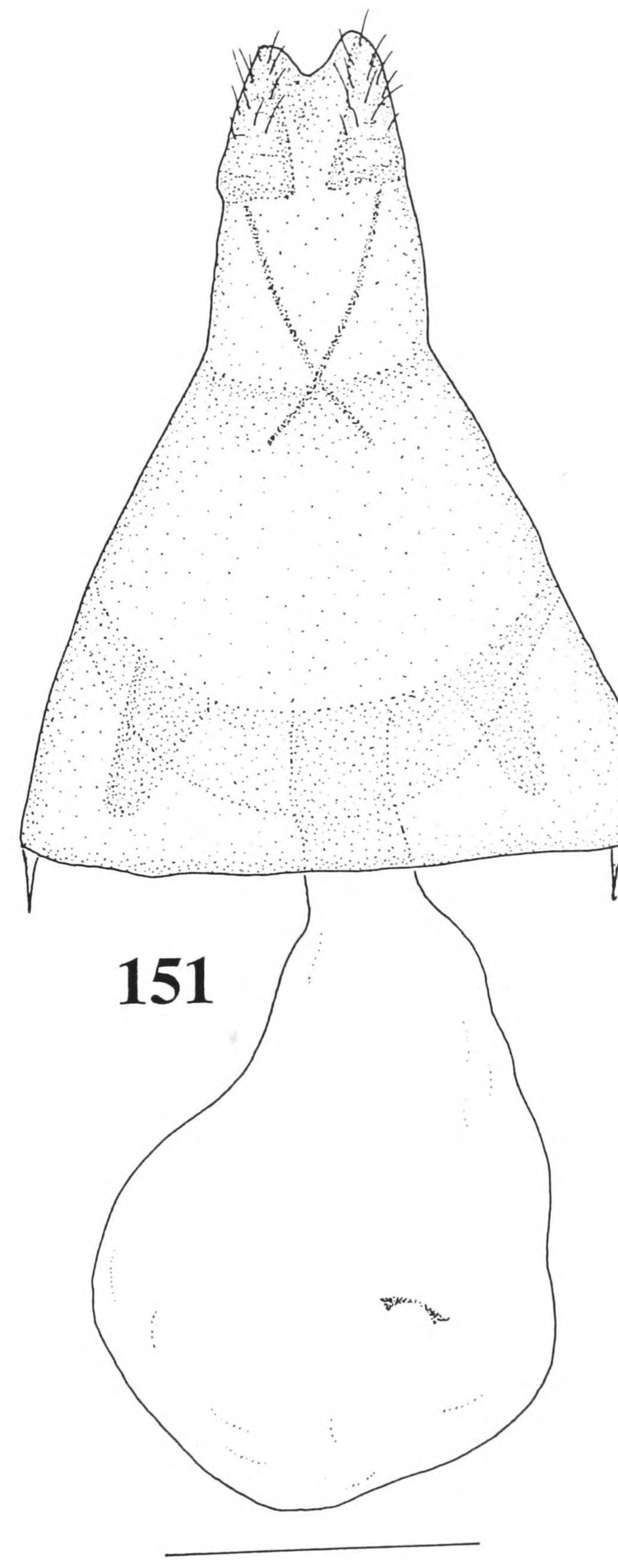
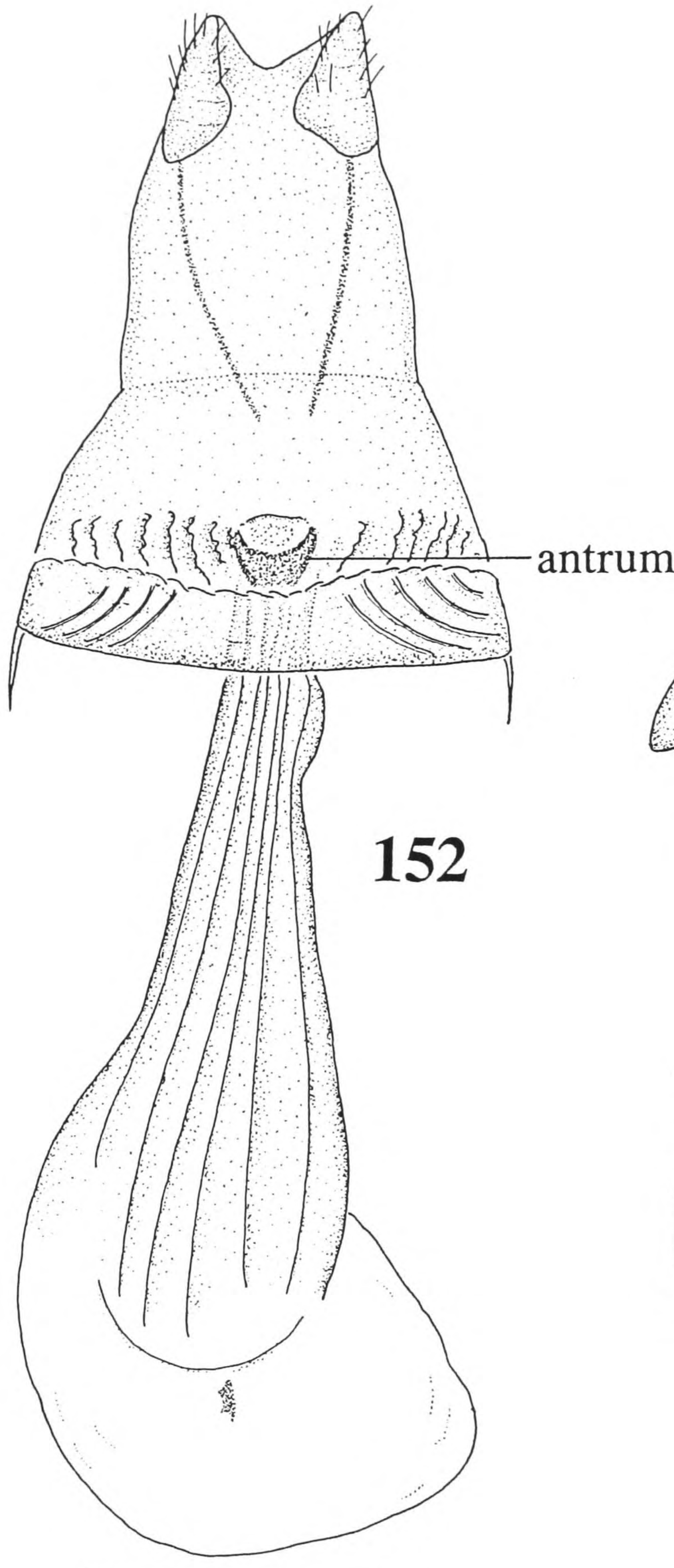
quinquemaculata



151

continuata



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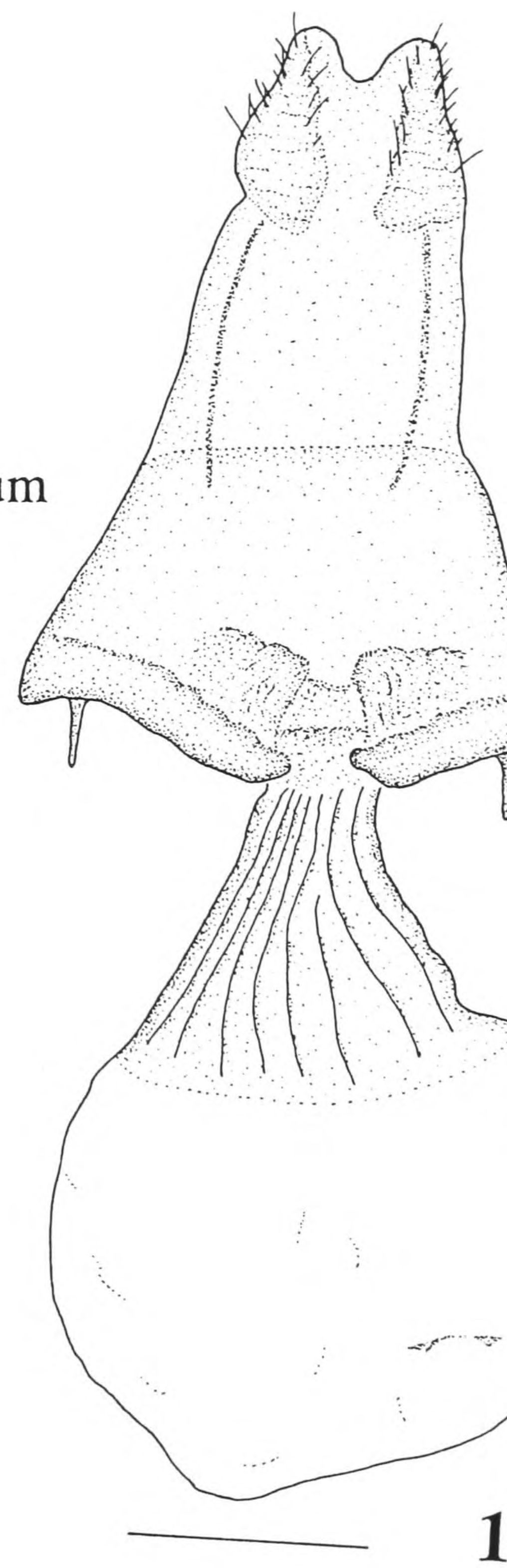
excrescens



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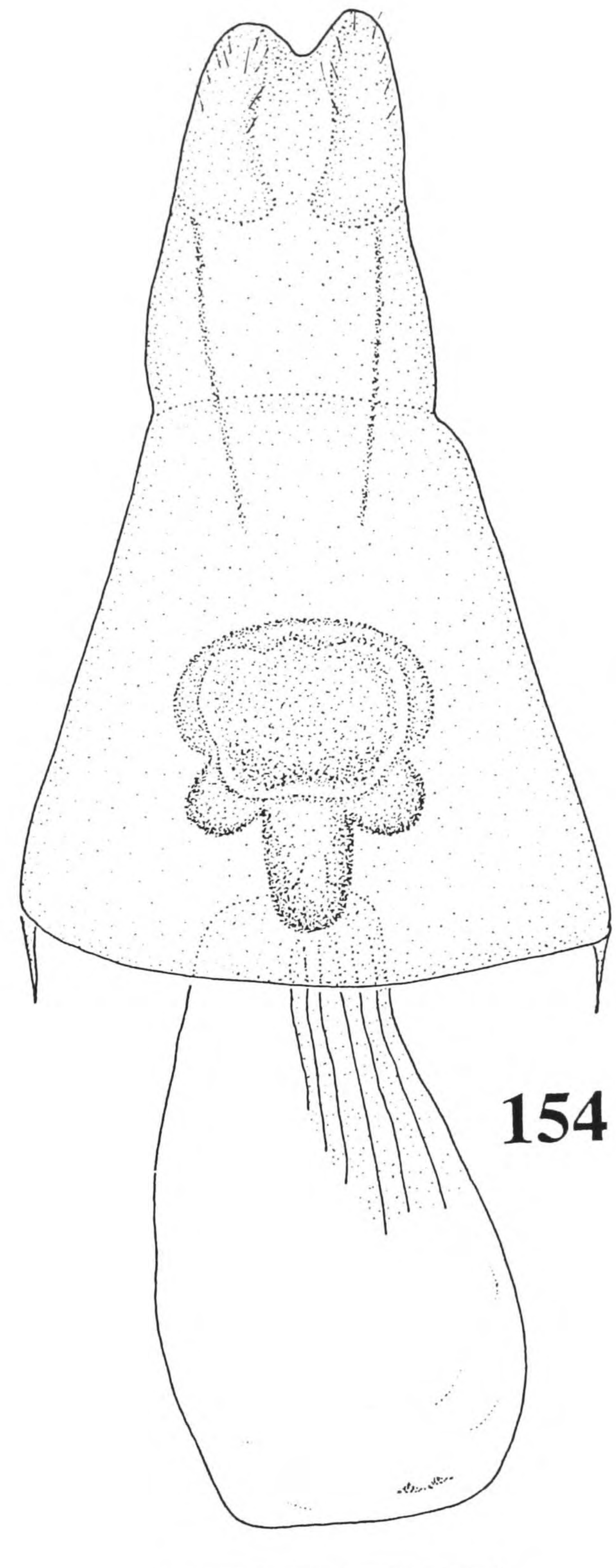
florepicta



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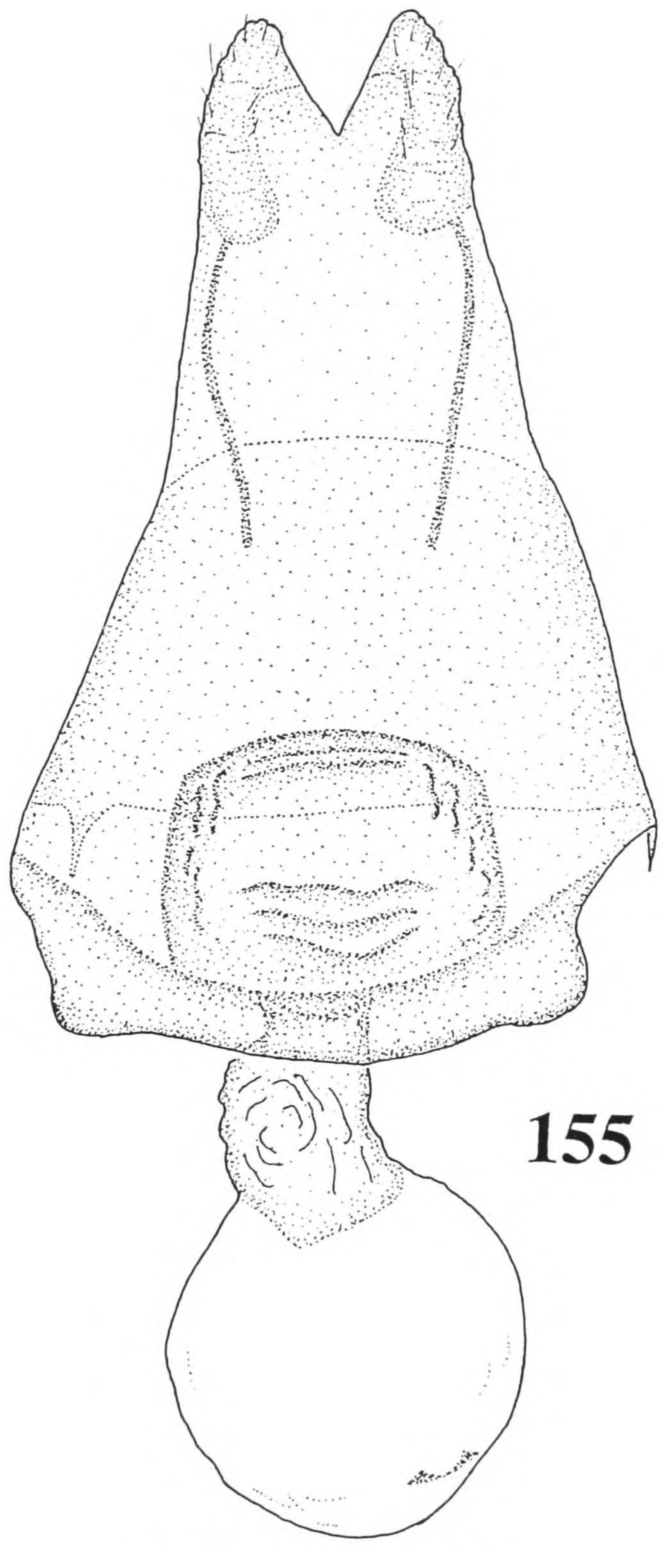
semispurcata



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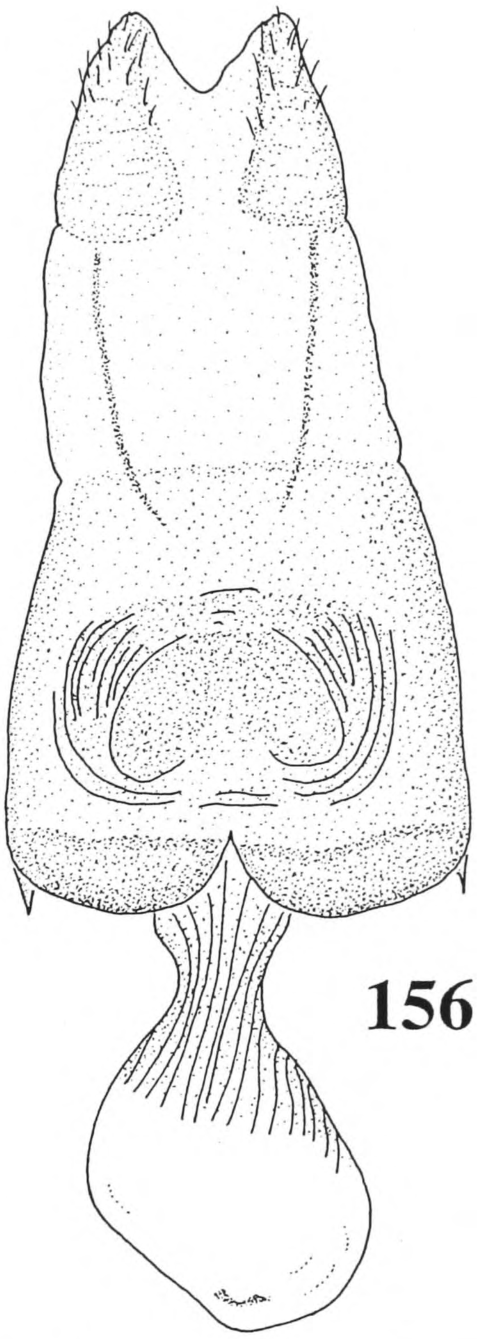
asmura



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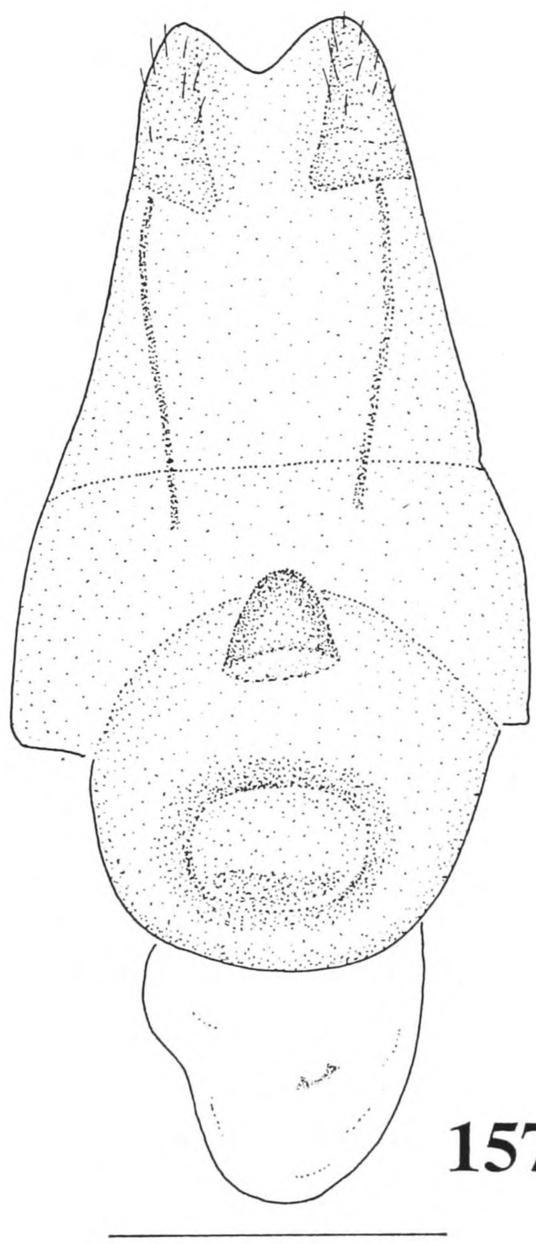
rosipara & delphinata



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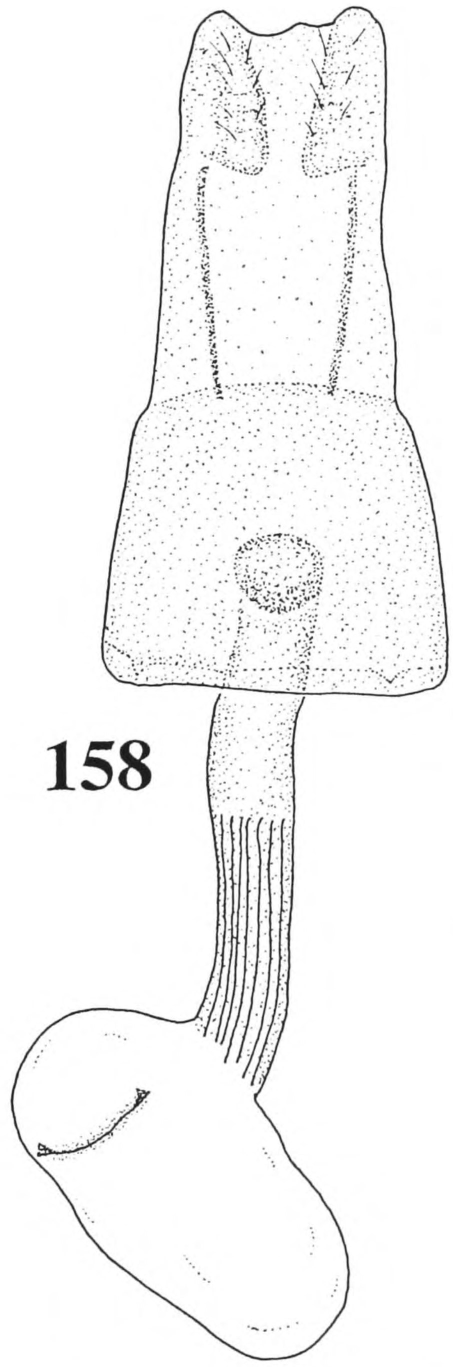
camilla



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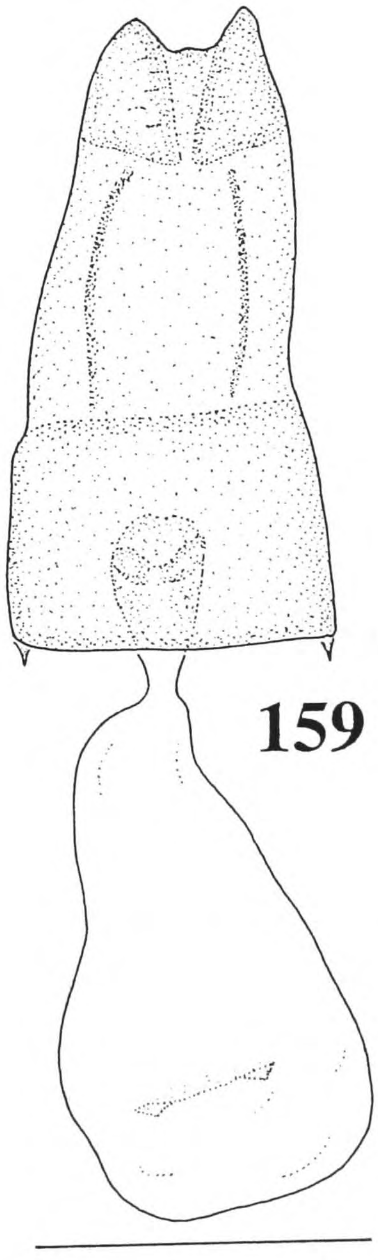
delacruzi



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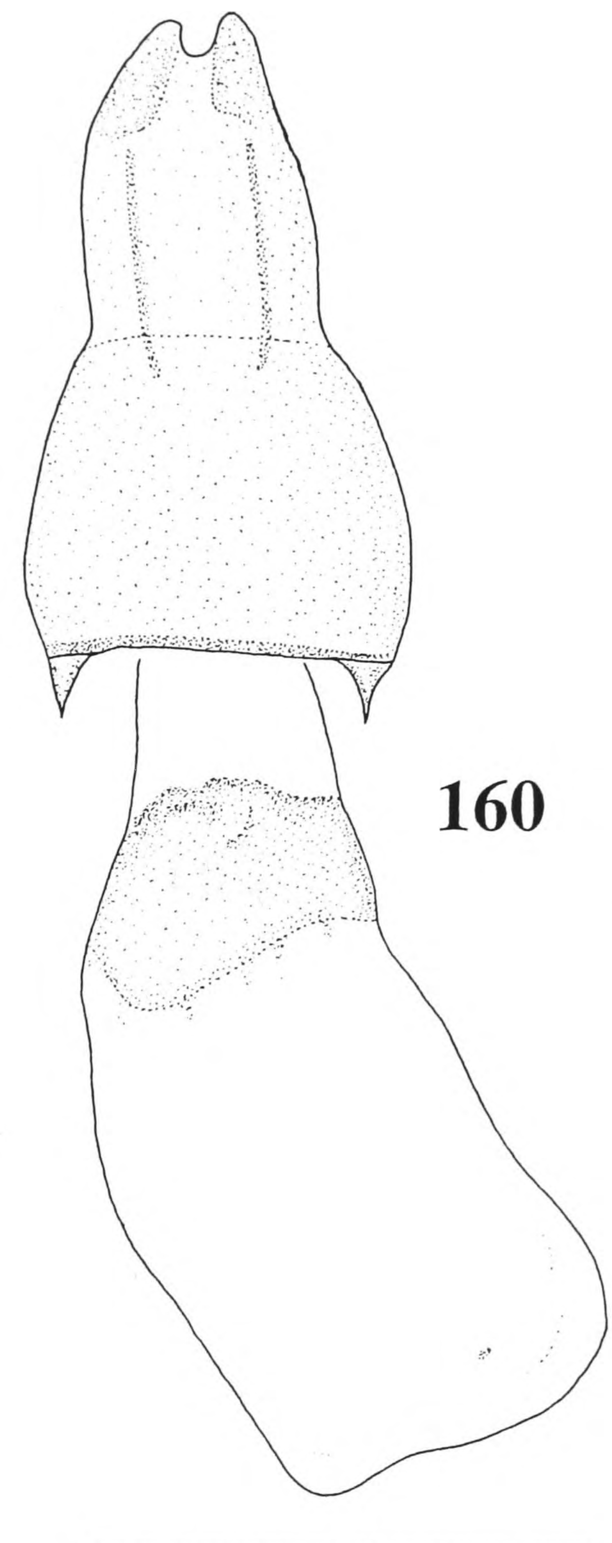
albipunctulata



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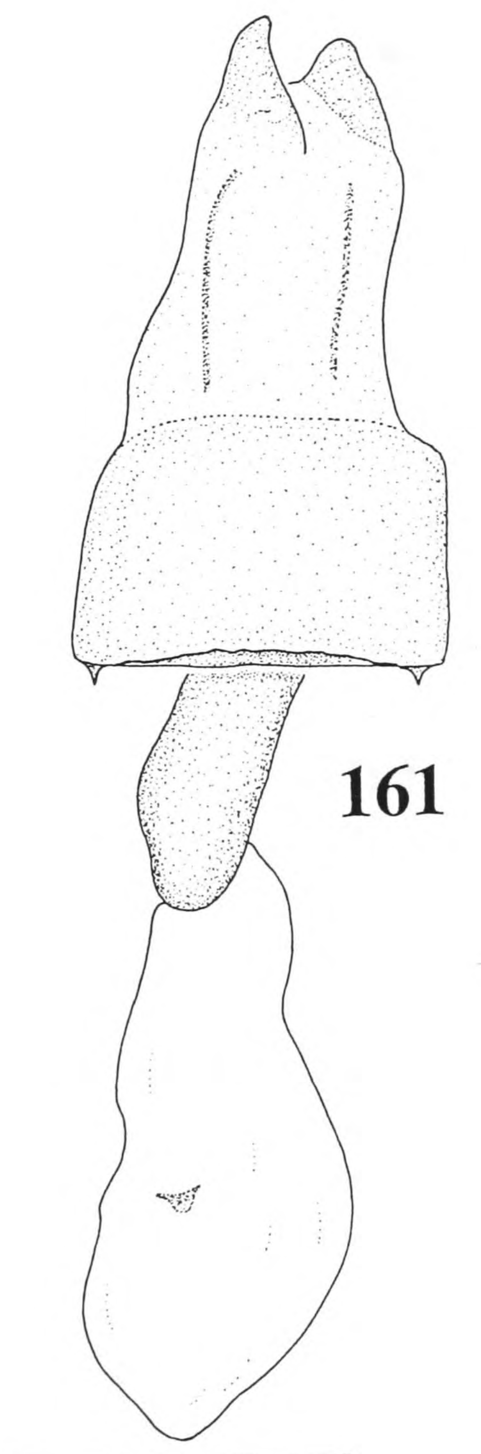
rufilimes



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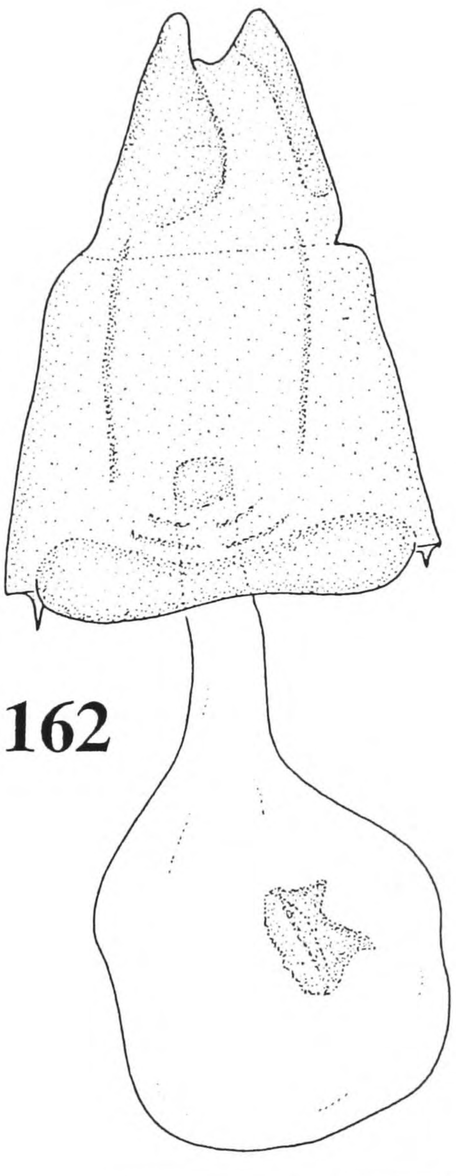
arpata



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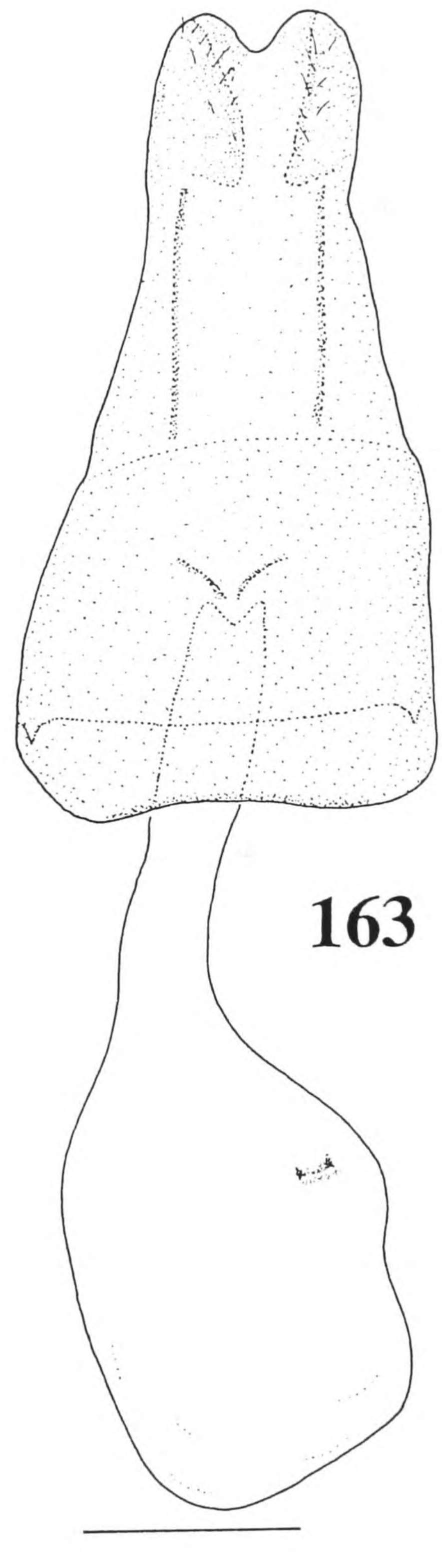
miccularia



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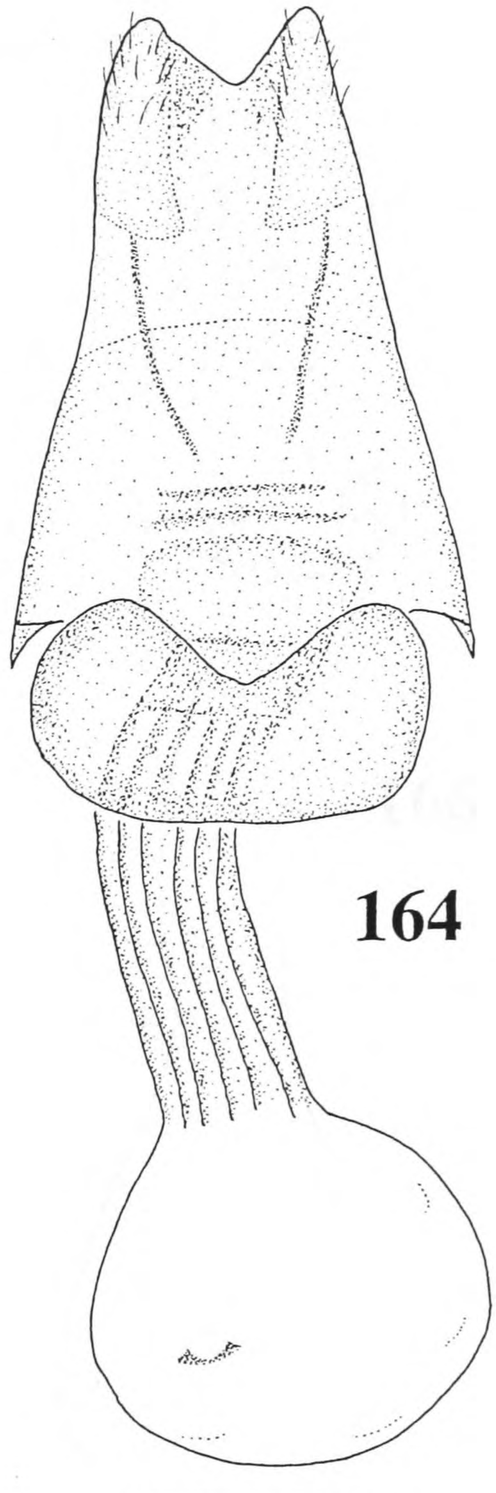
athena



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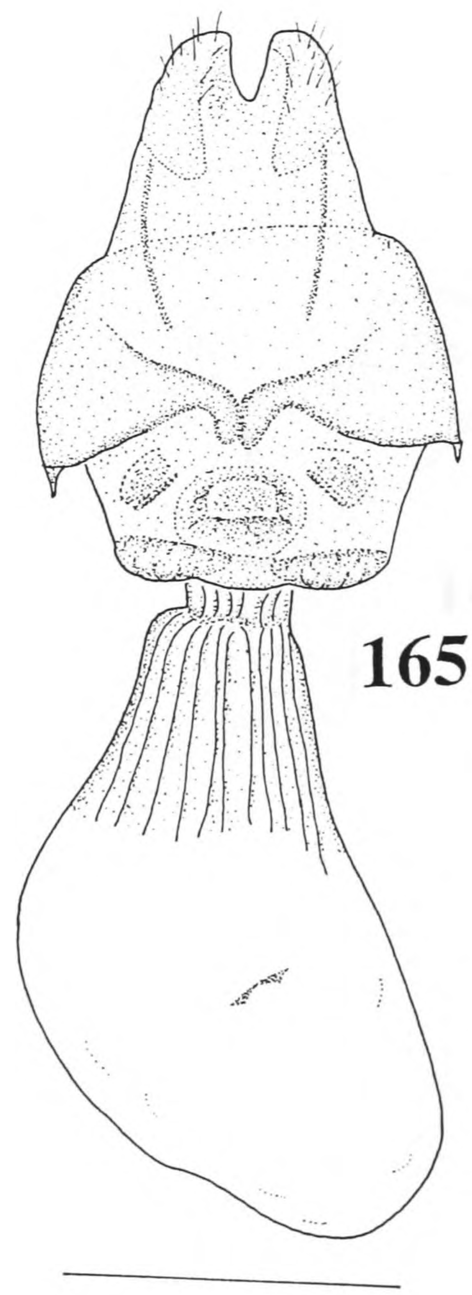
lactecincta



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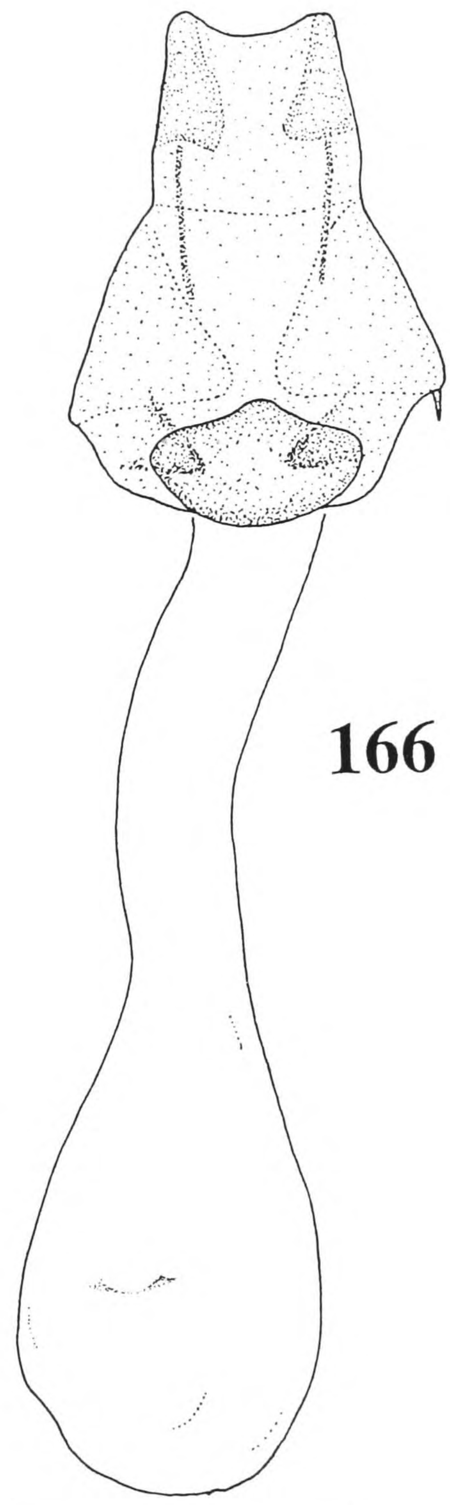
sporadata



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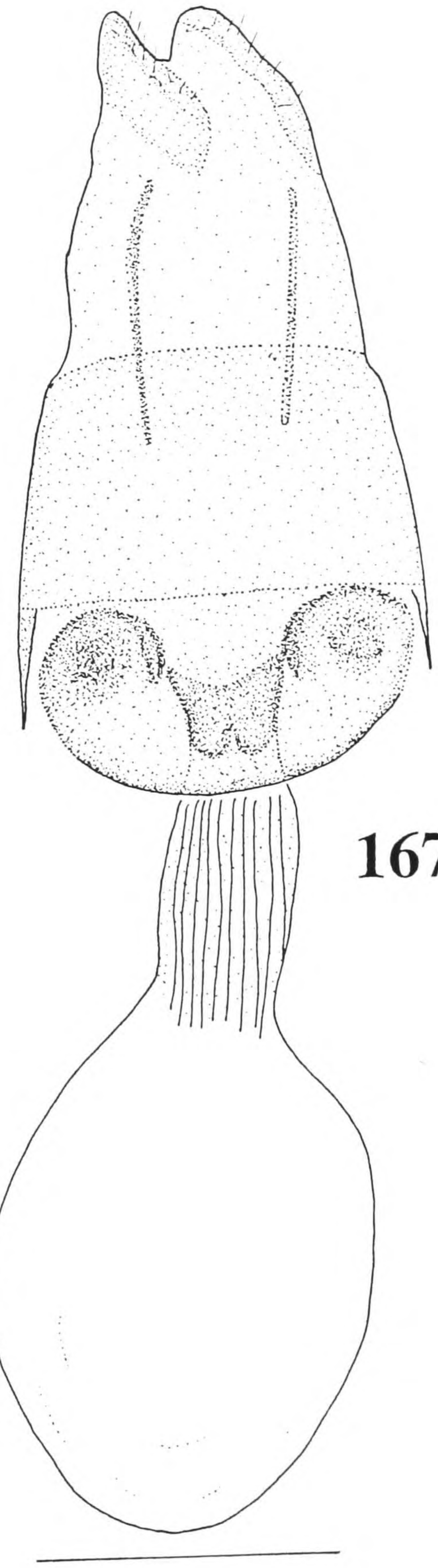
includaria



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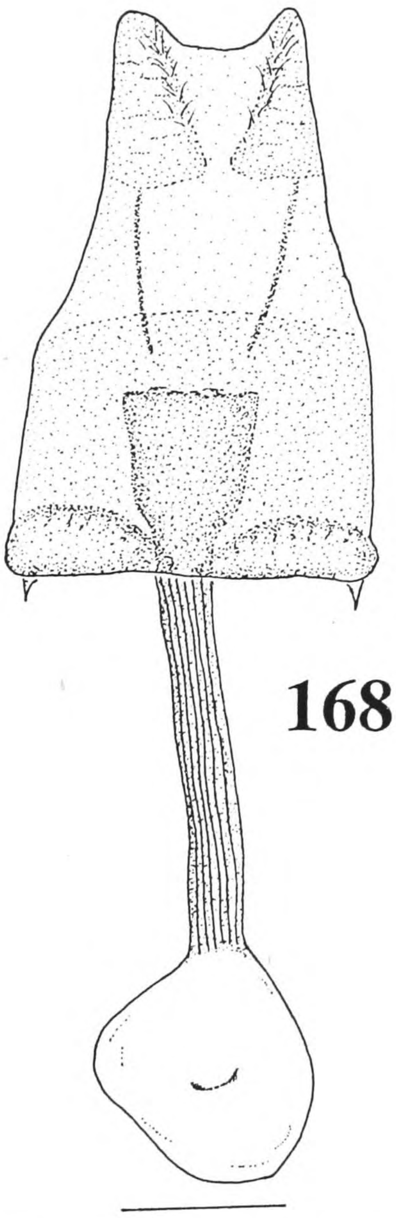
leucothalera



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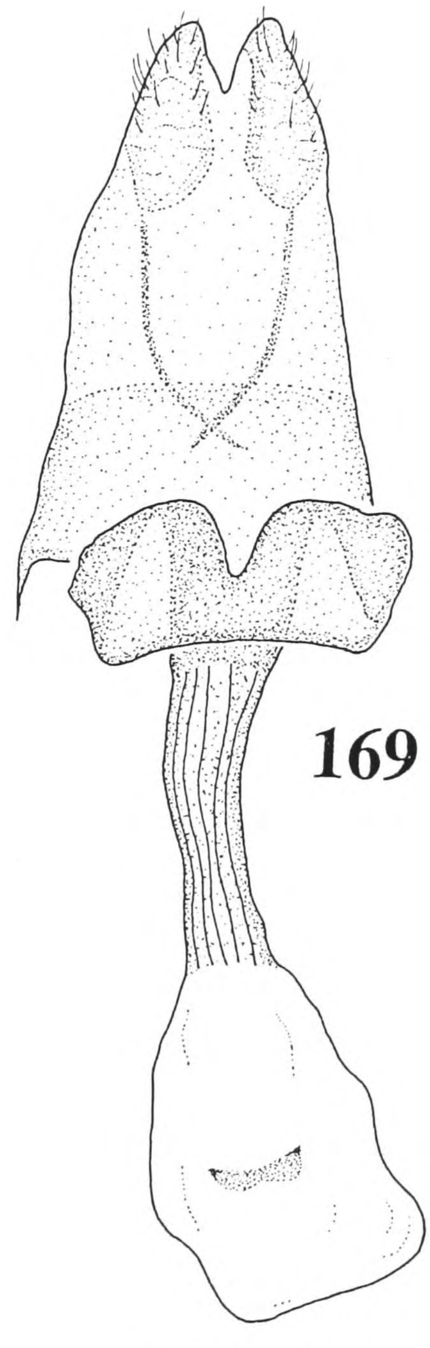
albicoma albicoma



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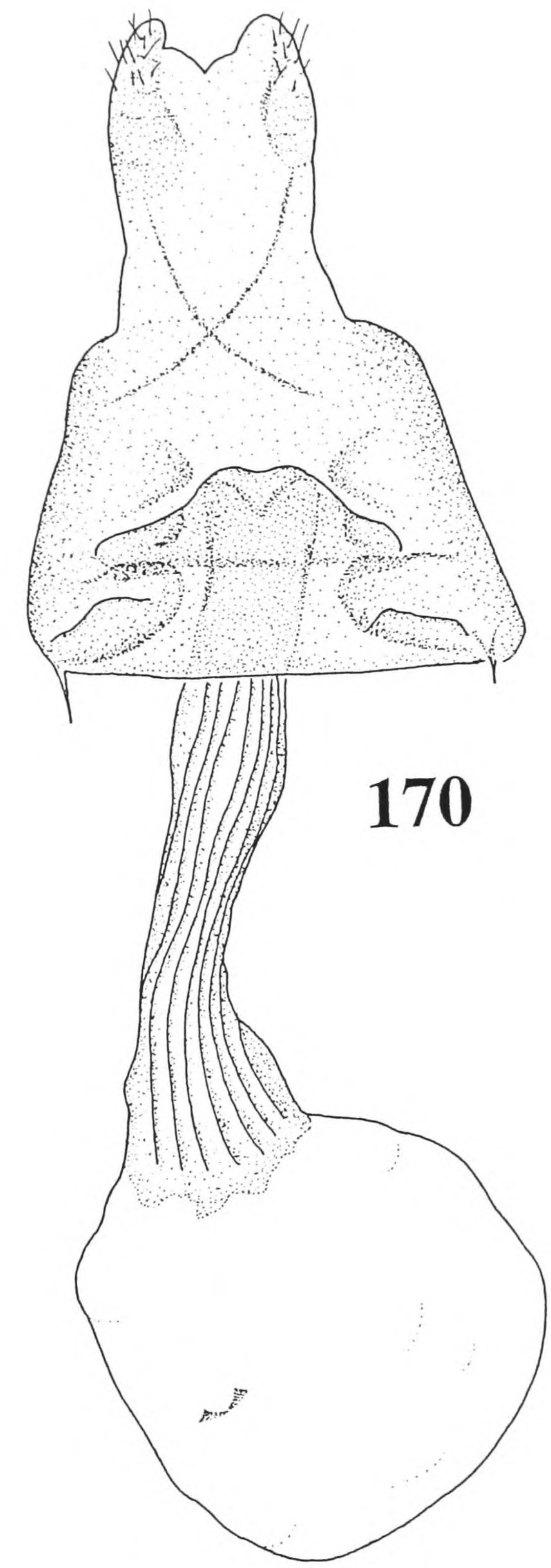
concinna



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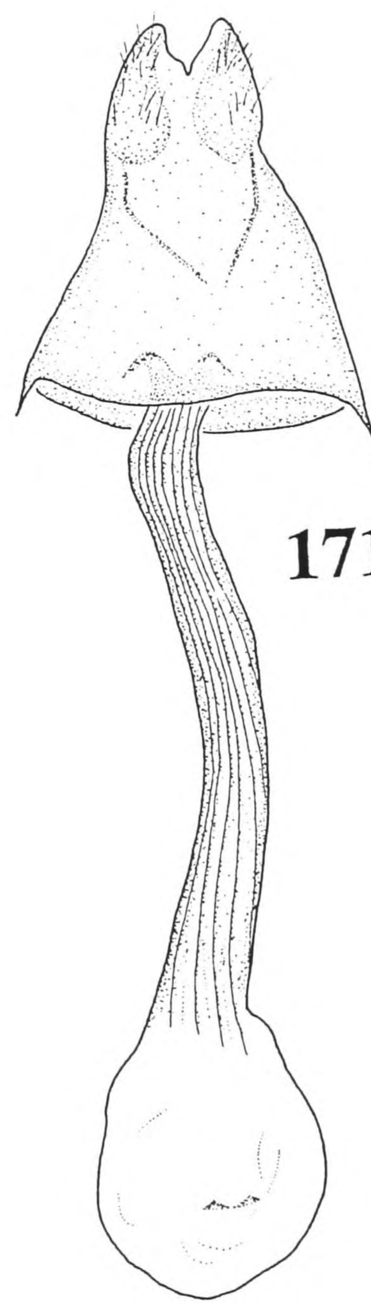
dicraspeda



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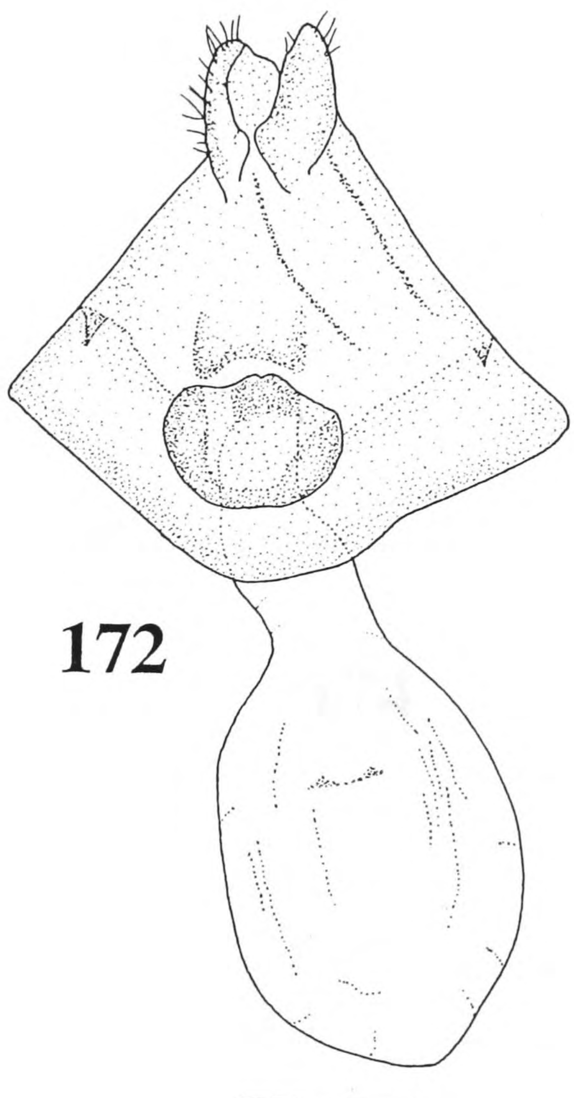
ciliaria



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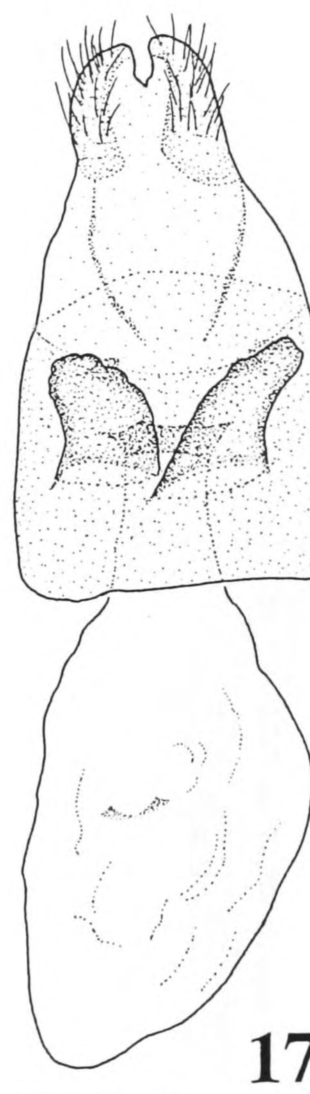
trilunaria



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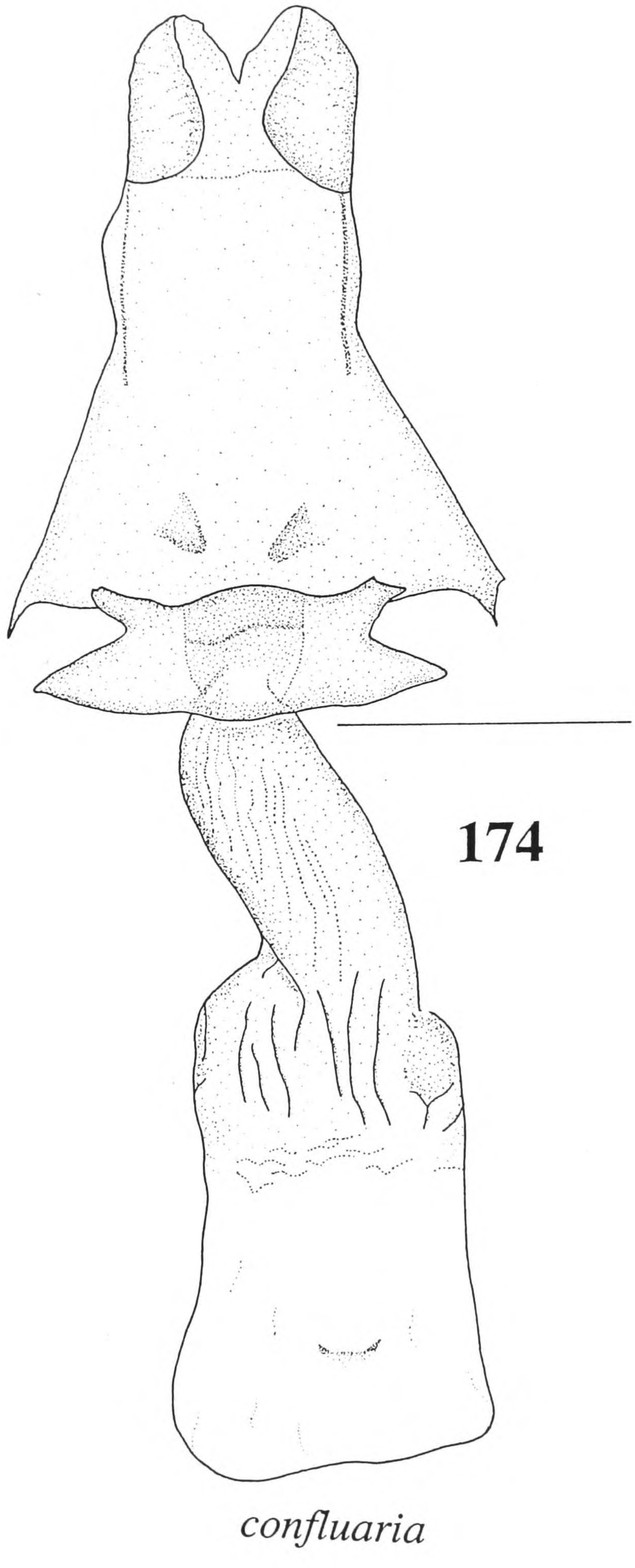
carnelunata



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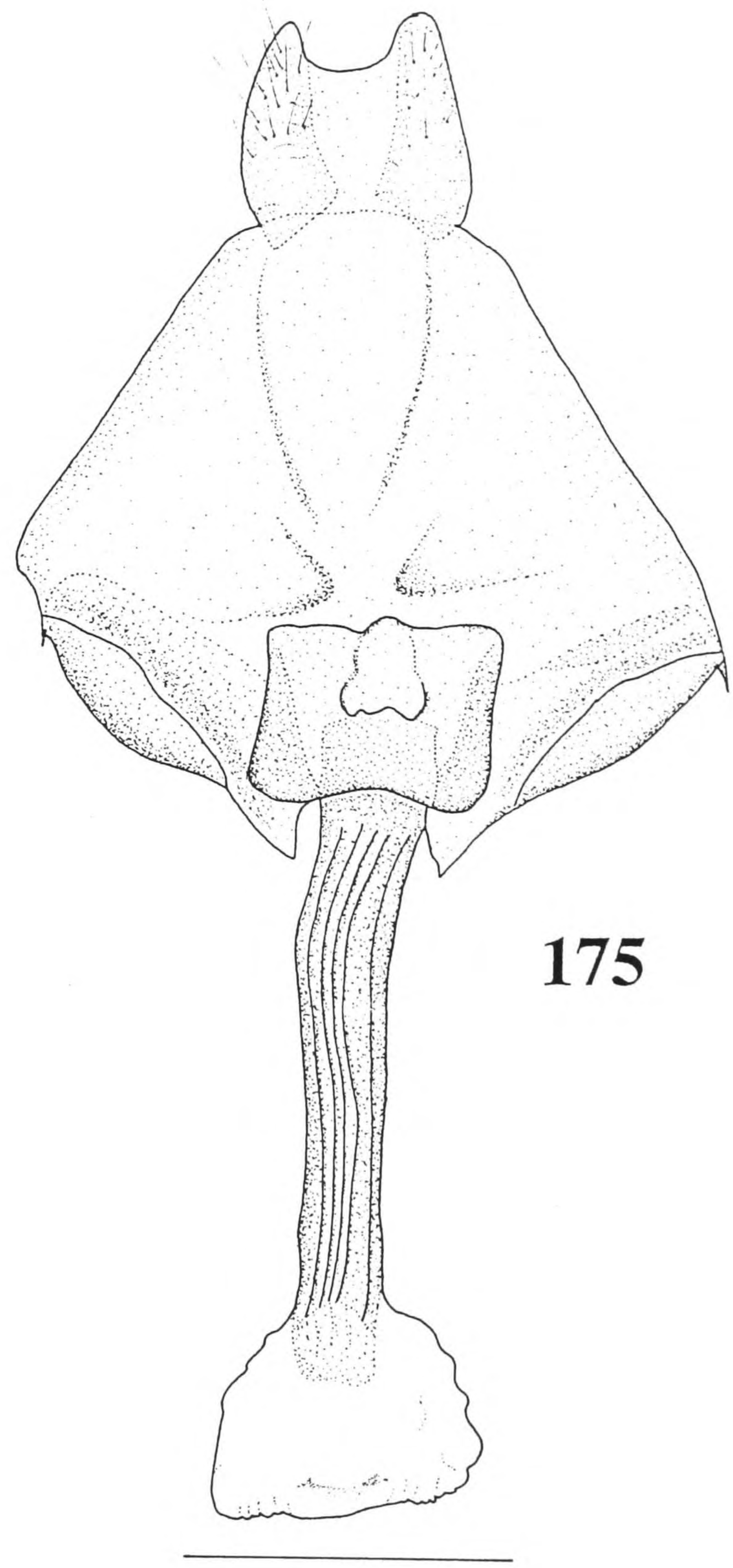
confluaria



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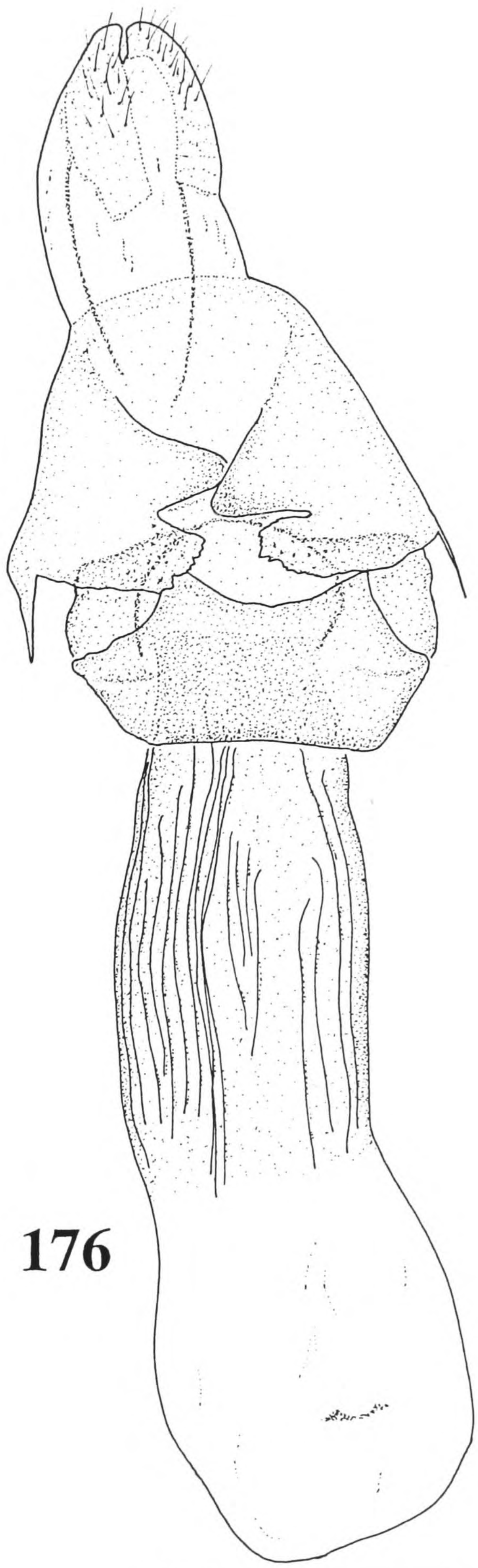
longipalpis



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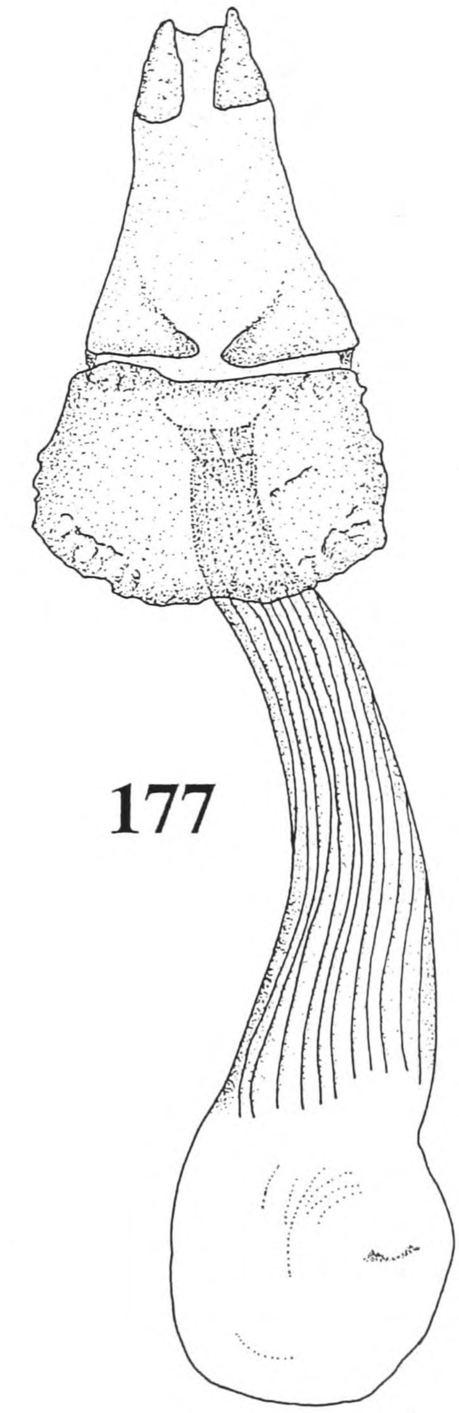
sellifera



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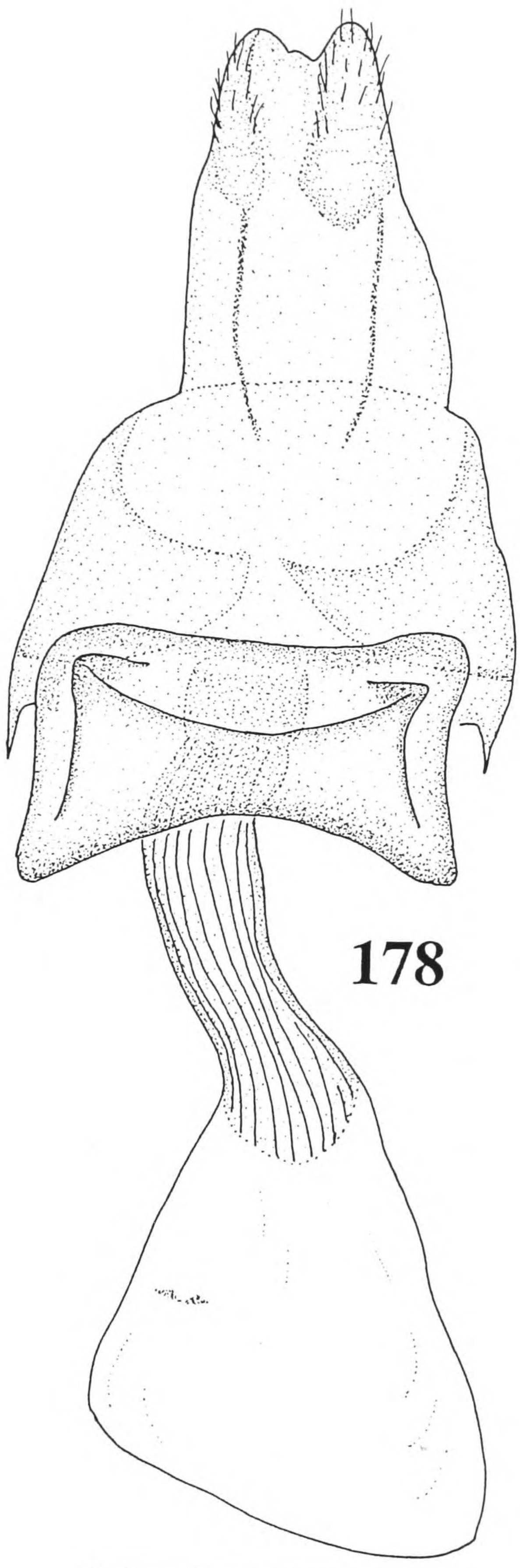
lilacina



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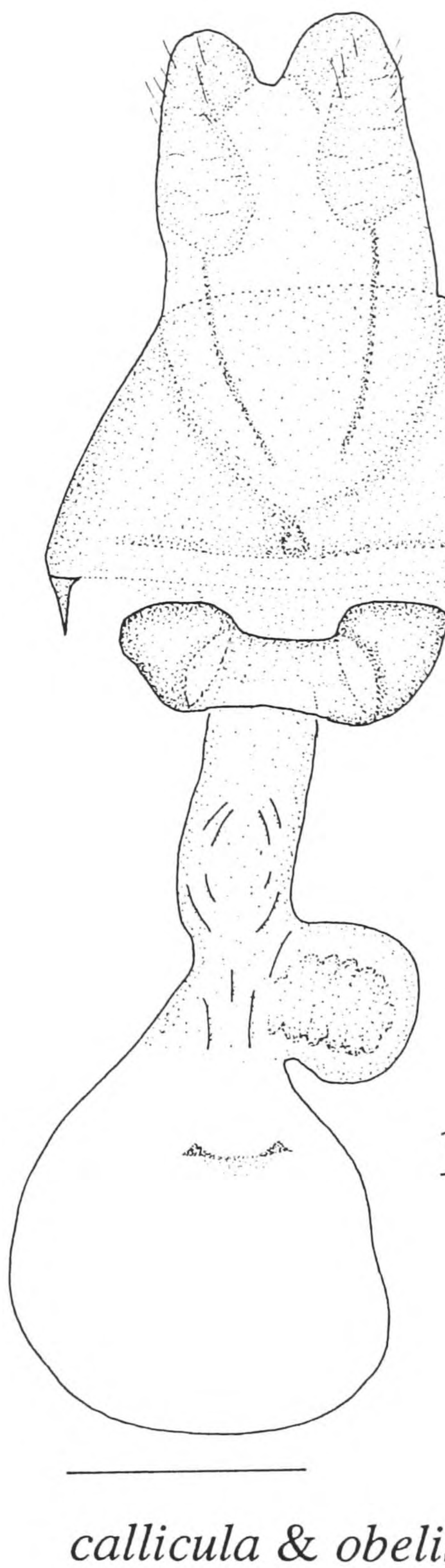

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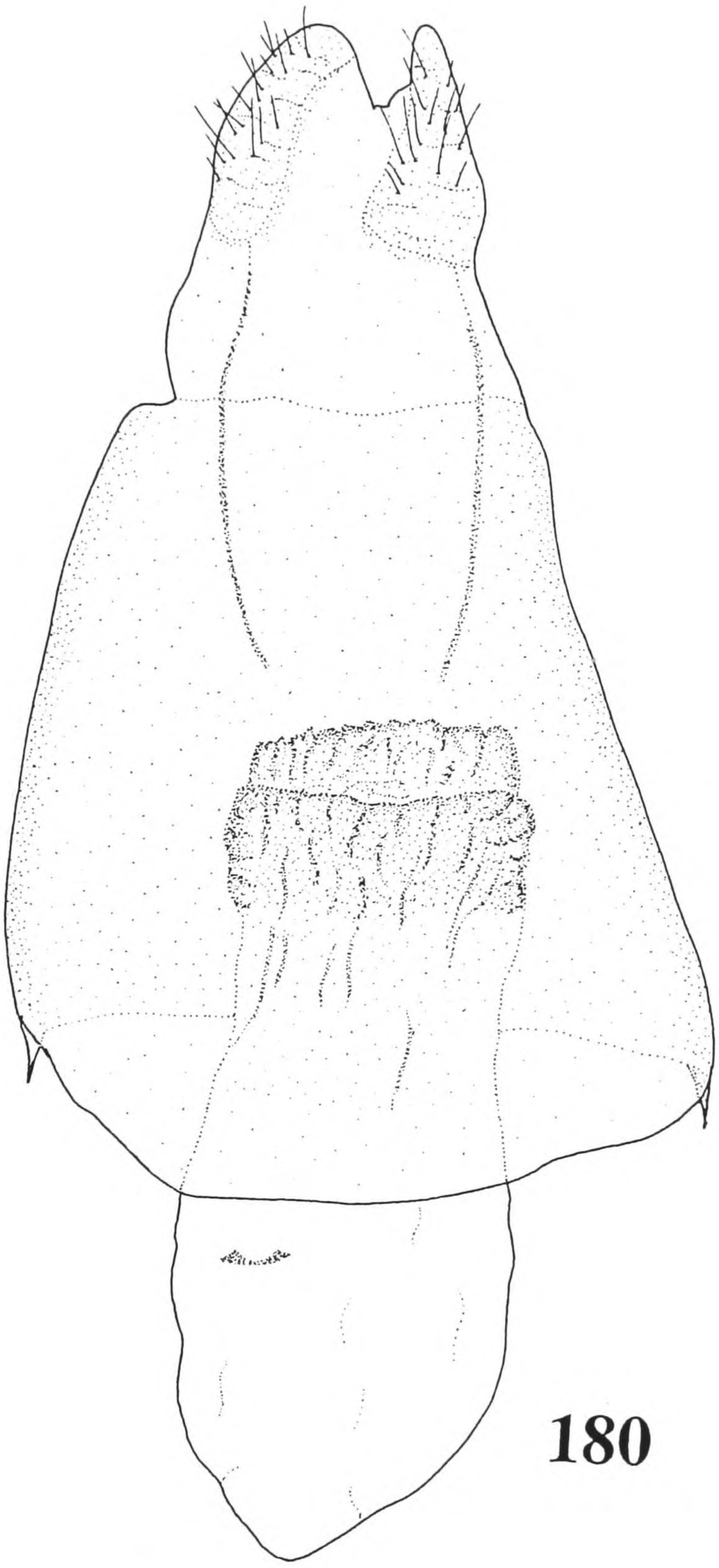
callicula & obeliscata



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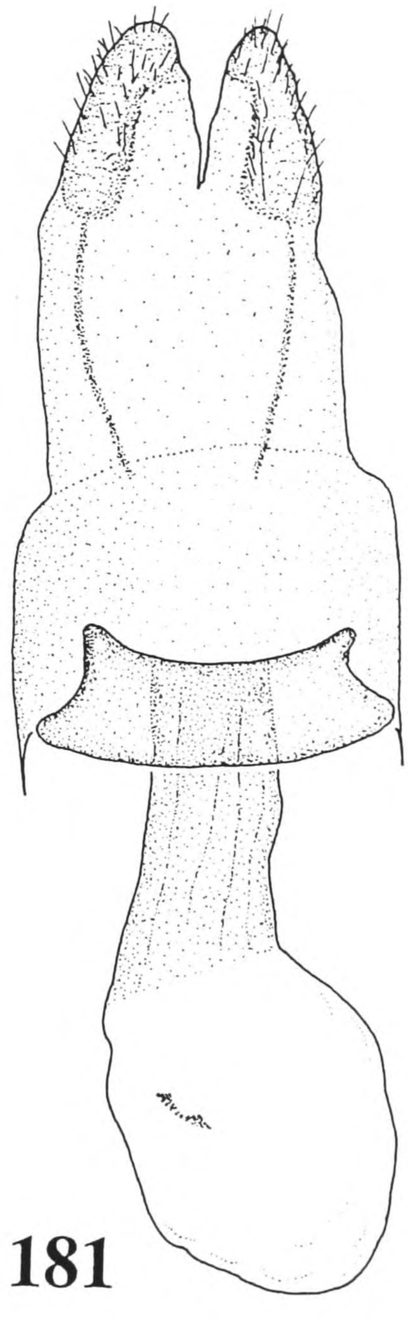
marginata



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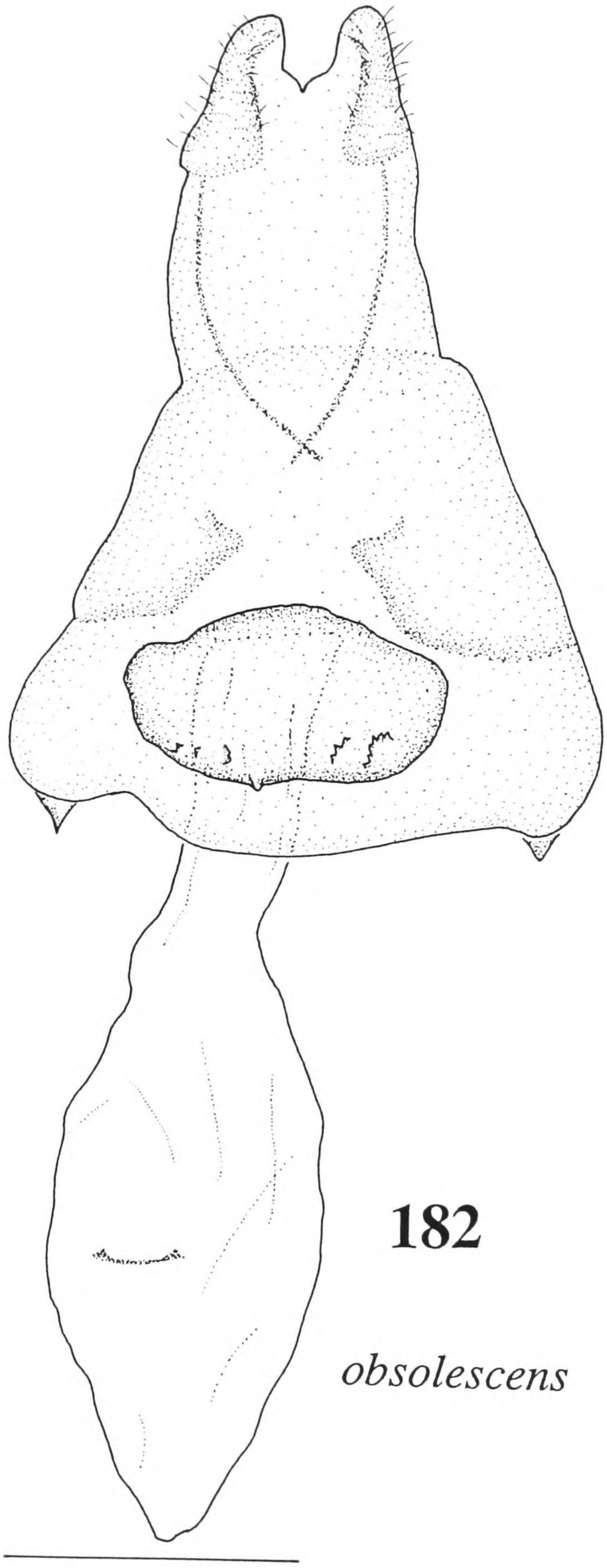
tricamerata



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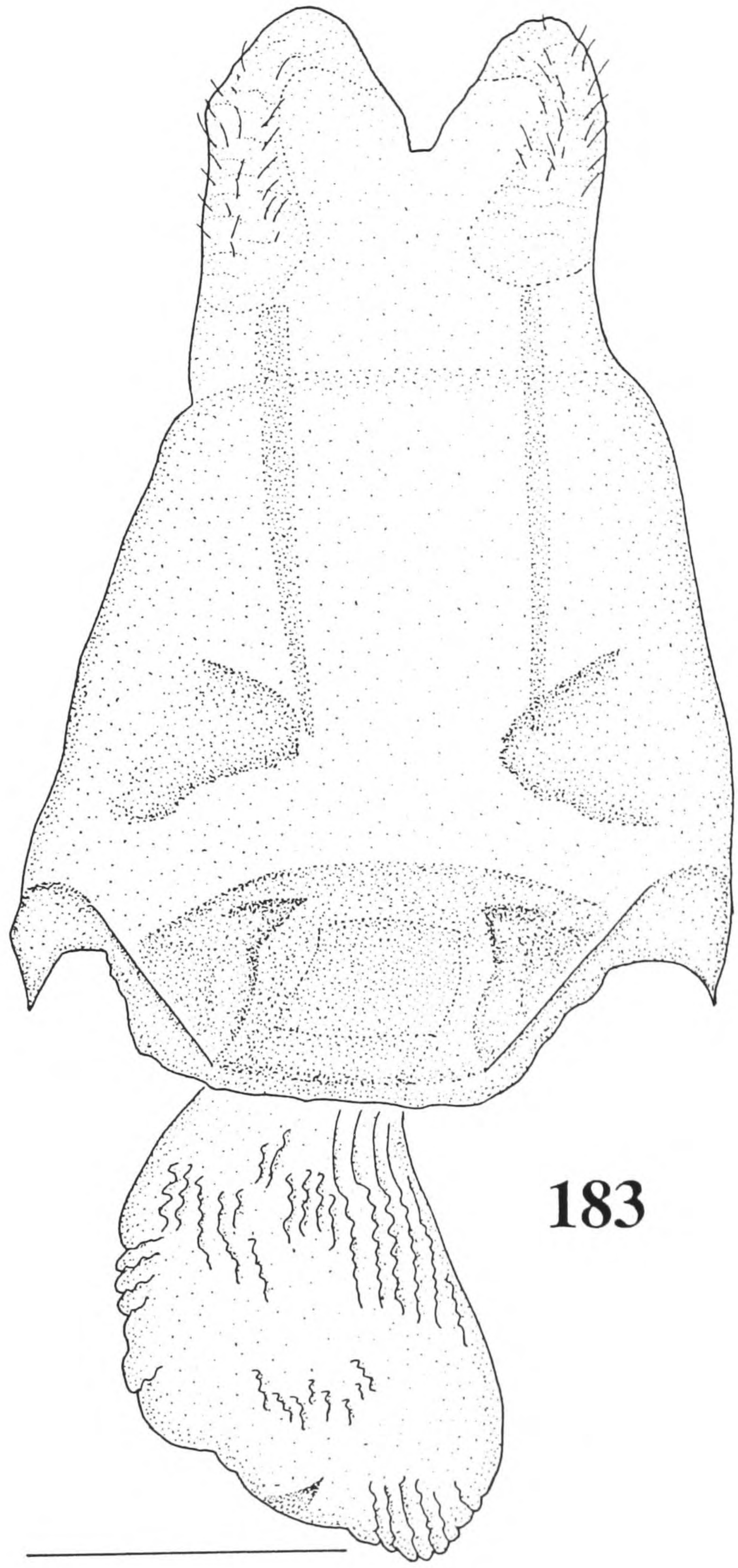
obsolescens



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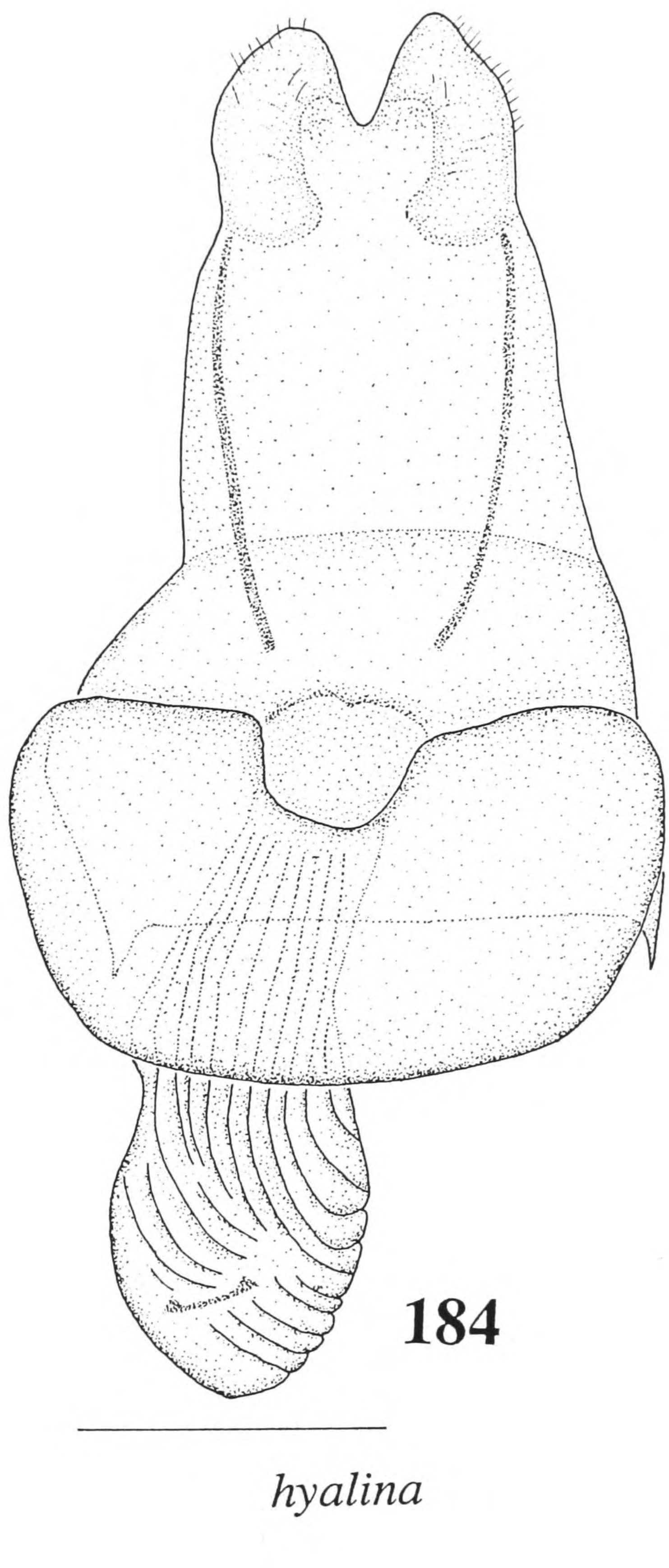
atopochlora



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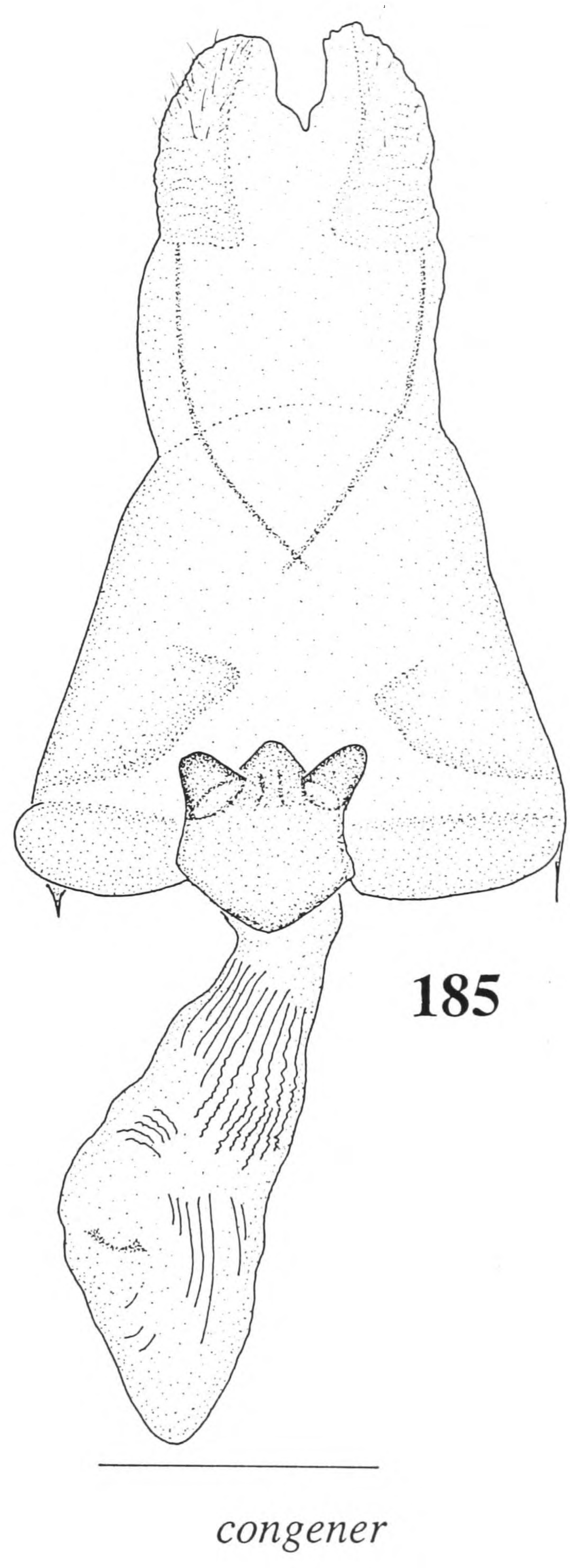
hyalina



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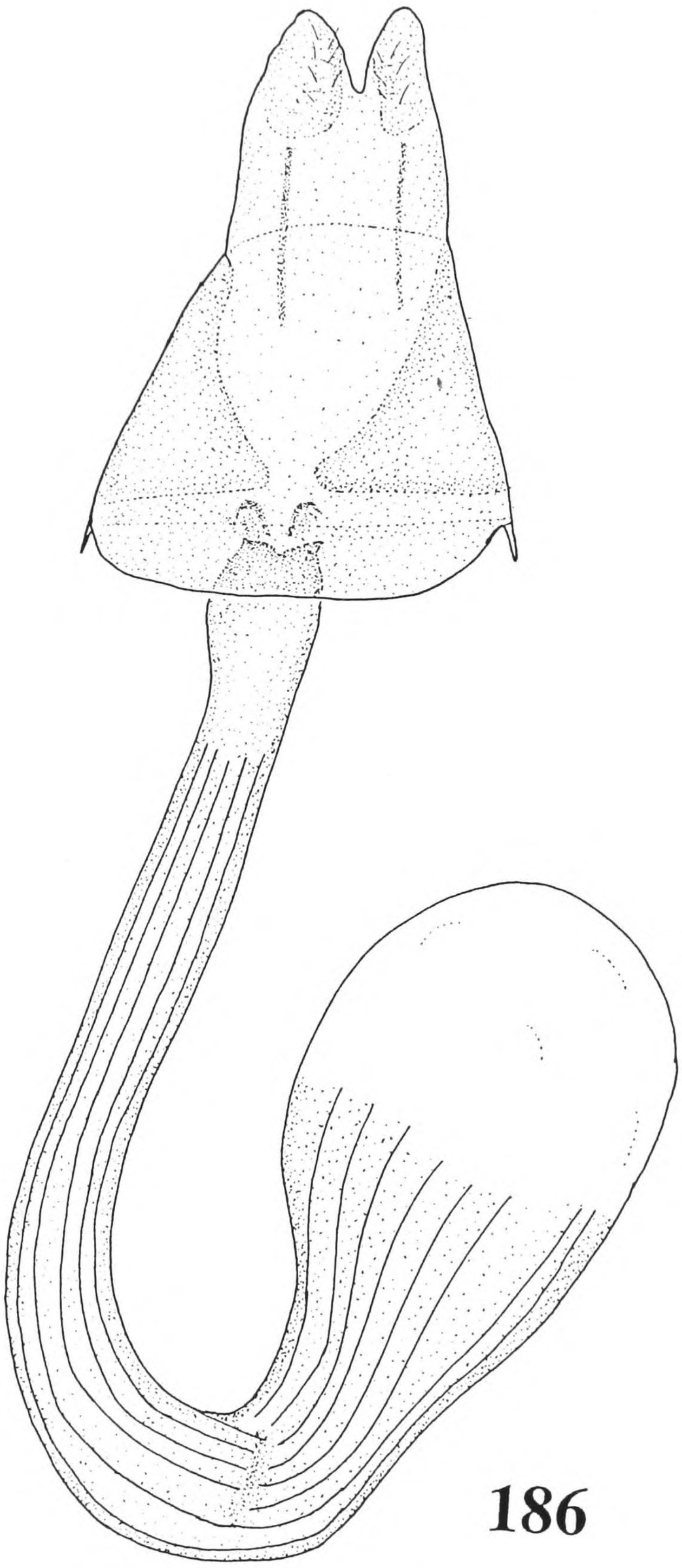

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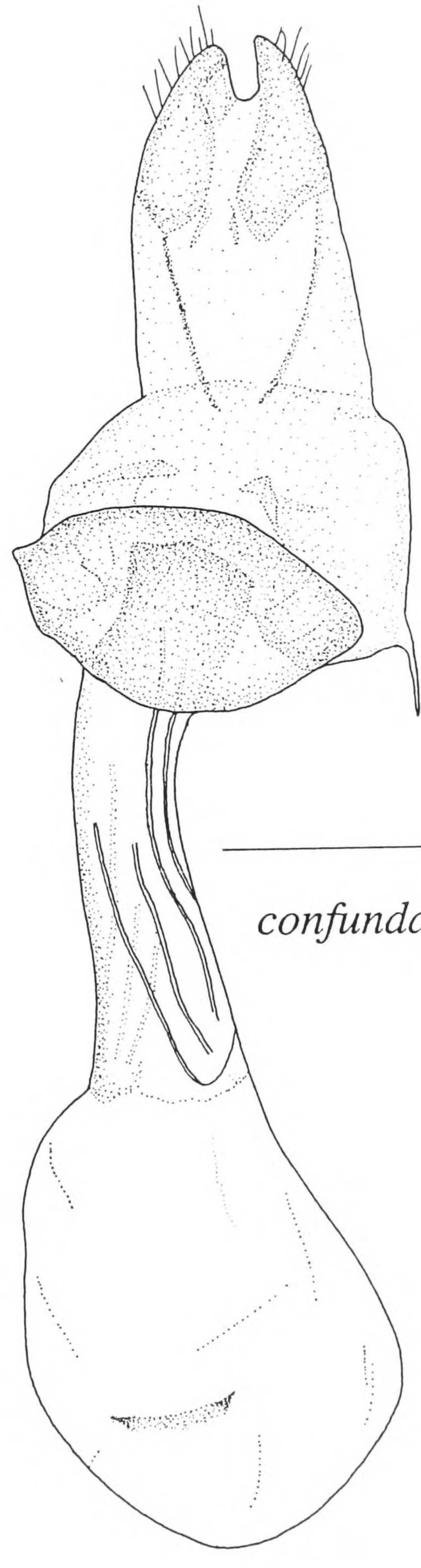
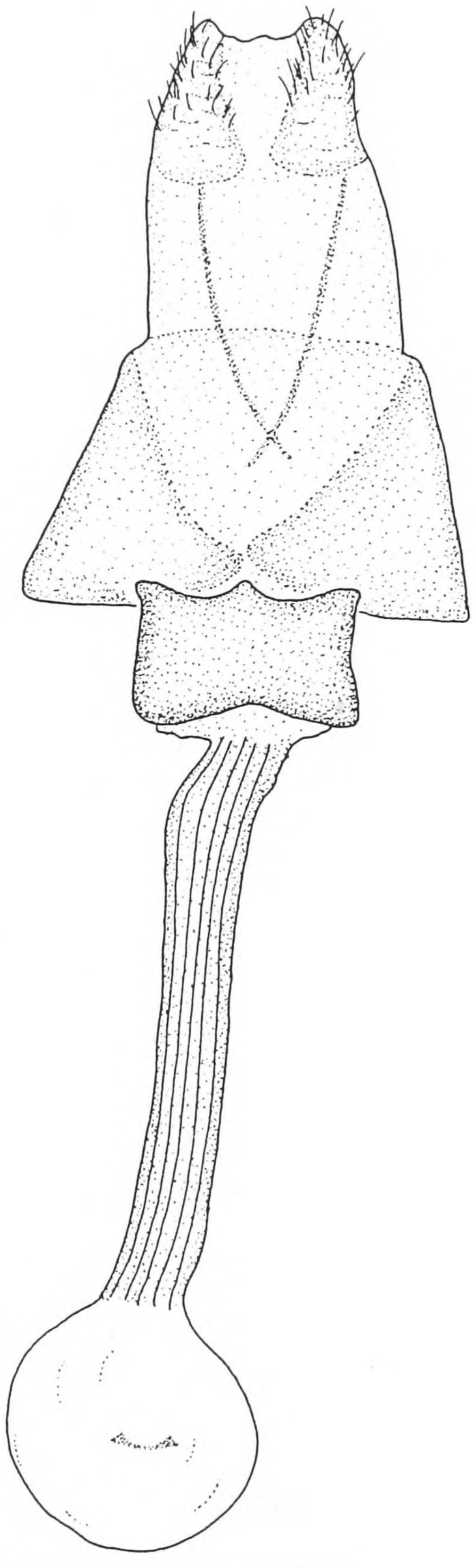


confundaria

187



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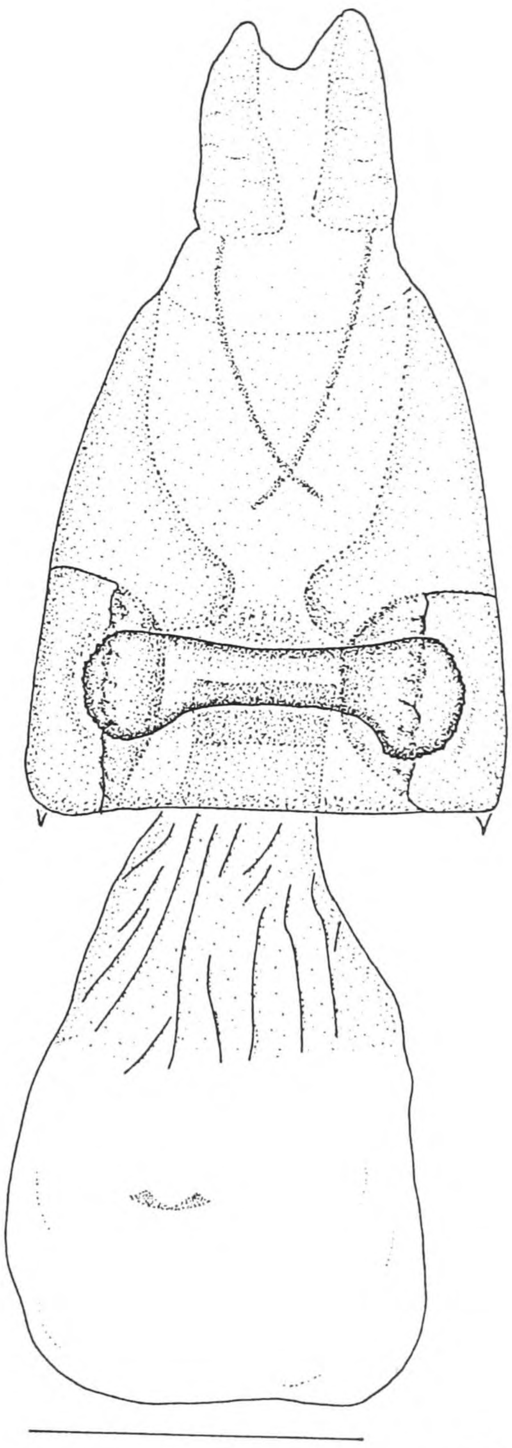
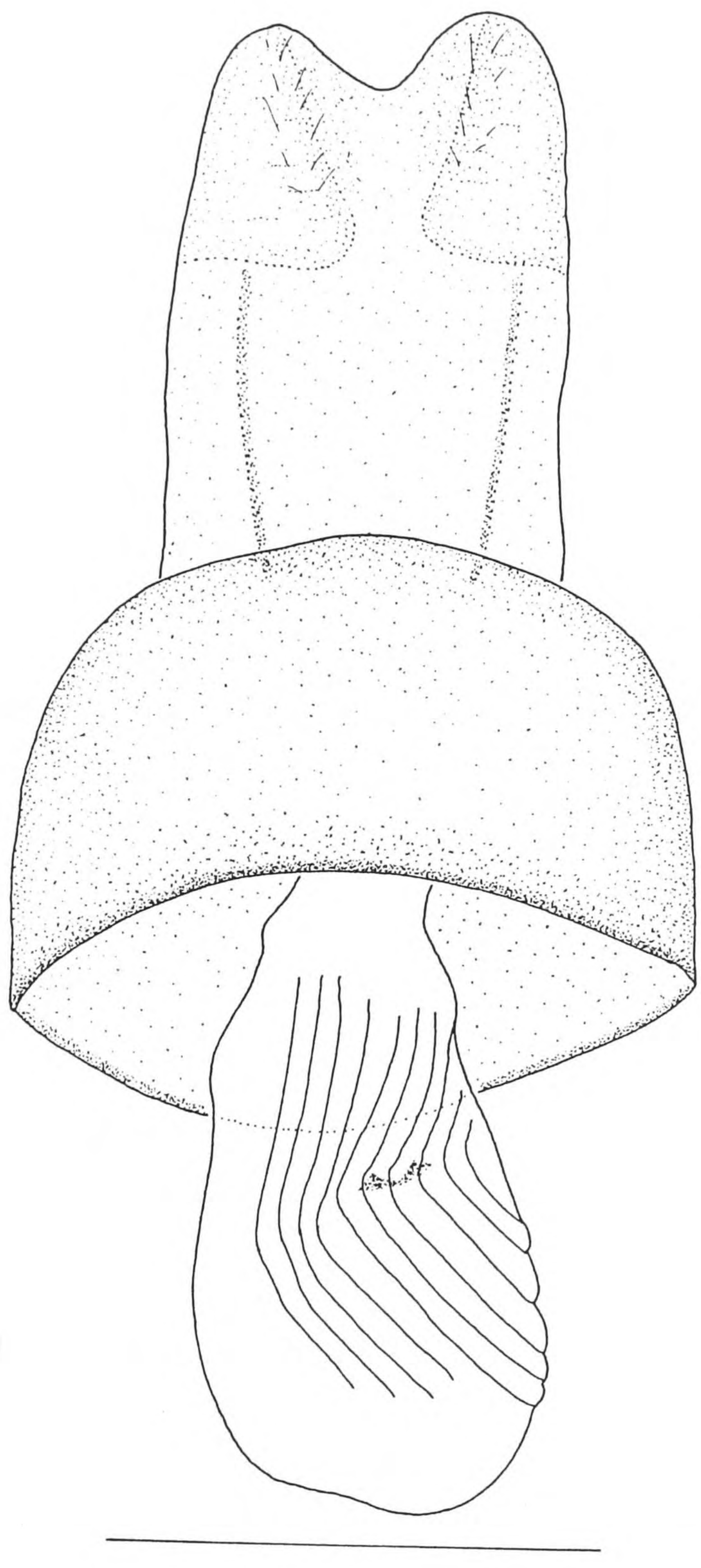
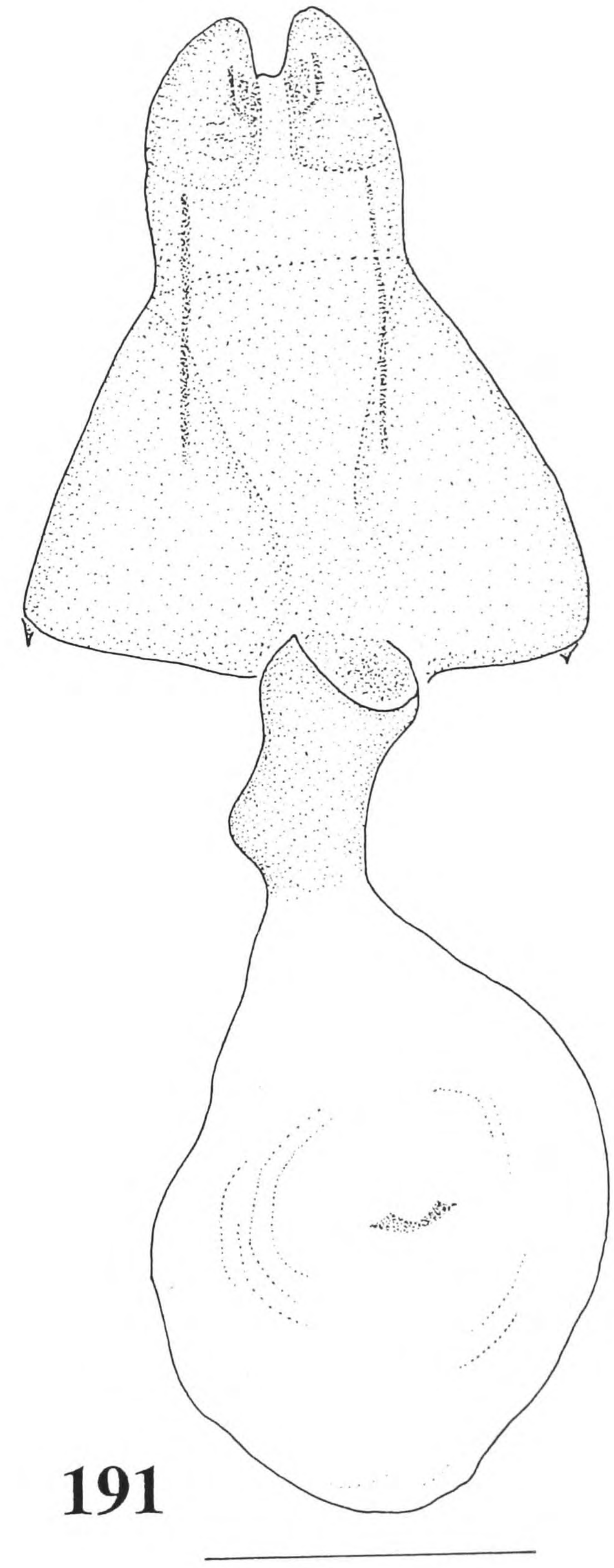
depressa



rubescens **189**



190
stagonata



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nivetacta

Chapter 6
Concluding remarks

Two apomorphies have been proposed here to define the Geometrinae, namely the occurrence of a large quantity of geoverdin as the primary wing pigment (Chapter 2) and the shape of the ansa in the tympanal organs (Chapter 3). However, there are two genera whose position inside or outside the subfamily is not fully resolved by these characters, namely *Celerena* Walker and *Dysphania* Hübner. The options for classifying these two genera, and the implications of these for the taxonomy of the Geometrinae are discussed below.

Although *Celerena* has been allocated to the Oenochrominae *sensu lato* (Fletcher, 1979), its phylogenetic position, as with most members of this group (Scoble and Edwards, 1990) is unresolved. The presence of geoverdin as the primary wing pigment of *C. lerne lerne* Boisduval (other species of *Celerena* have similar wing colouration, and presumably contain the same pigment) suggests that it should be allocated to the Geometrinae. However, the tympanal organs and wing venation contradict such a placement. The ansa of *Celerena* is wide at the base and narrows towards the apex; it does not have the distinctive medial widening that is probably an apomorphy of the Geometrinae. Moreover, vein M_2 in the hindwing of *Celerena* does not arise closer to vein M_1 than to M_3 (which has been cited as a character of the Geometrinae, e.g. by Inoue, 1961; Holloway *et al.*, 1987 and Prout, 1912).

These observations suggest two hypotheses regarding the phylogenetic position of *Celerena*. The first is that geoverdin has been independently derived in *Celerena*, a hypothesis supported by the other morphological characters mentioned above. The second is that the presence of a large quantity of geoverdin as the primary wing pigment is an apomorphy of a clade including both *Celerena* and the Geometrinae. This latter hypothesis may be preferable since it does not postulate two independent derivations of geoverdin as the primary wing pigment.

Such a clade might also include *Dysphania*. Although this genus is currently allocated to the Geometrinae, a number of characters suggest that it may not belong there. Firstly, species of *Dysphania* are much larger than most Geometrinae and have blue and yellow, not green, wing markings. Secondly, as with *Celerena*, the ansa of *Dysphania* does not exhibit the characteristic shape of other Geometrinae (Chapter 3). Thirdly, the larva (illustrated in Barlow, 1982) does not have a bifid head (which may also be an apomorphy of the Geometrinae). Finally, a fovea is present in the forewing of *Dysphania*, a structure which apparently occurs in only one other geometrine genus (*Cusuma* Moore; Prout, 1912), a genus that looks superficially very similar to *Dysphania*.

Yet, *Dysphania* does have a number of characters in common with most Geometrinae. Firstly, the wings of *Dysphania* do contain a large quantity of geoverdin as the primary wing pigment and, in the hindwings of many species of *Dysphania*, vein M_2 does arise closer to vein M_1 than to vein M_3 (even if in some species it is really not clear that this is the case). Furthermore, in the weighted cladistic analysis described in Chapter 4, *Dysphania* was located within, not as an outgroup of, the Geometrinae.

In terms of classifying these two genera, these character suites present a number of possible options. One option is to include both *Celerena* and *Dysphania* in the Geometrinae and to define the subfamily on the basis of the presence of a large quantity of geoverdin as the primary wing pigment. A second option is to exclude *Dysphania* from the Geometrinae and define the subfamily by the shape of the ansa. A third option would be to retain *Dysphania* within the Geometrinae, and *Celerena* within the Oenochrominae *sensu lato*, continuing to diagnose the subfamily Geometrinae on the basis of the location of vein M_2 in the hindwing and assuming that the presence of geoverdin as the primary wing pigment of *Celerena* is independently derived. The fourth possible combination, that of including *Celerena* in the Geometrinae and displacing *Dysphania* from this subfamily, does not, on present evidence, seem to be the most parsimonious solution.

Further characters will have to be assessed before a firm decision is made. However, I favour the second option. The revised Geometrinae *sensu stricto* would then be a monophyletic group supported by the shape of the ansa, a common green colouration and, possibly, by the bifid head of the larva. The Geometrinae *sensu lato* would be a larger monophyletic group including both *Celerena* and *Dysphania* (and probably *Cusuma*) and supported by the presence of a large quantity of geoverdin as the primary wing pigment.

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References

References quoted in Chapter 3 (Tympanal organs) are given in the reprint.

Bastelberger, M. J. (1911) Sechs neue Hemitheinae aus meiner Sammlung. *Internationale Entomologische Zeitschrift*, **5:** 53-57.

Barbier, M. (1972) Les coleurs bleues et vertes des Lépidoptères, naissance et évolution d' un thème de recherche. *Alexanor*, **7:** 312-315.

Barbier, M. (1981) The status of blue-green pigments of butterflies, and their phototransformations. *Experientia*, **137:** 1060-1062.

Barbier, M. (1984) Progrès des recherches sur les colorations bleues et vertes des Lépidoptères et leurs significations biologiques. *Alexanor*, **13:** 235-237.

Barlow, H. S. (1982) *An Introduction to the Moths of South East Asia.* Malayan Nature Society.

Bois-Choussy, M. (1977) *Ptérobiline, phorcabiline et sarpédobiline pigments biliaires IXy isolés de Lepidoptères, biosynthèses, réactivitiés et structures.* Doctoral Thesis (L'Universite de Paris Sud, Centre D'Orsay).

Brown, K.S. (1979) *Ecologia Geográfica e evoluçanas florestas neotropicais.* PhD Thesis. Universidade Estadual de Campinas.

Choussy, M. and Barbier, M. (1975) Ptérobiline et néoptérobilines, réactivité et structures. *Helvetica Chimica Acta*, **58:** 2651-2661.

Cole, W. J., Chapman, D. J. and Siegelman, H. W. (1968) The structure and properties of phycocyanobilin and related bilatrienes. *Biochemistry*, **7:** 2929-2935.

Common, I. F. B. (1990) *Moths of Australia*. Melborne University Press.

Cook, M. A. and Scoble, M. J. (1992) Tympanal organs of geometrid moths: a review of their morphology, function and systematic importance. *Systematic Entomology*, **17:** 219-232.

De Boer, Th. J. and Backer, H. J. (1963) Diazomethane. *Organic Synthesis Collective*, **4:** 250-253. John Wiley and Sons, Inc.

Dognin, P. (1892) Descriptions de Lépidoptères nouveaux. *Le Naturaliste*, **14:** 185-186.

Dognin. P. (1898) Hétérocères nouveaux de l'Équateur. *Annales de la Société Entomologique de Belgique*, **42:** 212-219.

Dognin, P. (1908) Hétéroèceres nouveaux de l'Amerique du Sud. *Annales de la Société Entomologique de Belgique*, **52:** 264-270.

Dognin, P. (1911a) *Hétéroèceres nouveaux de l'Amerique du Sud.* Oberthür, Rennes. **3:** 1-66.

Dognin, P. (1911b) Hétéroèceres nouveaux de l'Amerique du Sud. *Mémoirs de la Société Entomologique de Belgique*, **18:** 151-188.

Dognin, P. (1923) *Hétérocères nouveaux de l'Amérique du Sud.* Oberthür, Rennes. **23:** 1-34.

Druce, H. (1891-1900) *Biologia centrali-Americana. Insecta. Lepidoptera-Heterocera*, **2:** 1-622.

Druce, H. (1911) New species of Heterocera. *The Annals and Magazine of Natural History including Zoology, Botany and Geology.* Series 8, **7:** 288-294.

Dyar, H. G. (1914) Report on the Lepidoptera of the Smithsonian Biological Survey of the Panama Canal Zone. *Proceedings of the United States National Museum*, **47:** 139-350.

Farris, J. S. (1988) Hennig86. Version 1.5.

Felder, C., Felder, R. and Rogenhofer, A. F. (1875) *Reise der österrichischen Fregatte Novara um die Erde* (Zoologischer Theil). Band 2 (Abtheilung 2).

Ferguson, D. C. (1969) A revision of the moths of the subfamily Geometrinae of America north of Mexico (Insecta, Lepidoptera). *Peabody Museum of Natural History Yale University Bulletin*, **29**.

Ferguson, D. C. (1985) *The moths of North America north of Mexico. Fascicle 18.1. Geometroidea, Geometridae (part)*. The Wedge Entomological Research Foundation.

Fletcher, D. S. (1951) Four new species of Geometridae (moths) from Rancho Grande, North-central Venezuela. *Zoologica*, 37: 101-104.

Fletcher, D. S. (1979) *in* Nye, I. W. B. *The Generic Names of Moths of the World*, volume 3 Geometroidea 243pp. Trustees of the British Museum (Natural History), London.

Fieser, L. F. and Fieser, M. (1967) *Reagents for Organic Synthesis*, **1**. John Wiley and Sons, Inc.

Forbes, W. T. M. (1948) *Lepidoptera of New York and Neighbouring States*. Part 2. *Memoirs of Cornell University Agricultural Experimental Station*, **274:** 1-263.

Ford, E. B. (1941) Studies on the Chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 1. The Anthoxanthins. *Proceedings of the Royal Entomological Society, London* (A), **16:** 65-90.

Ford, E. B. (1942) Studies on the Chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 2. Red pigments in the genus *Delias* Hübner. *Proceedings of the Royal Entomological Society, London* (A), **17:** 87-92.

Ford, E. B. (1944a) Studies on the Chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 3. The red pigments of the Papilionidae. *Proceedings of the Royal Entomological Society, London* (A), **19:** 92-106.

Ford, E. B. (1944b) Studies on the Chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 4. The classification of the Papilionidae. *Transactions of the Royal Entomological Society, London*, **94:** 201-223.

Ford, E. B. (1947) Studies on the Chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 5. *Pseudopontia paradoxa* Felder. *Proceedings of the Royal Entomological Society, London (A)*, **22:** 77-78.

Ford, E. B. (1955) *Moths*. The New Naturalist. Collins, London. (Third Edition).

Ghiradella, H. (1974) Development of ultraviolet-reflecting butterfly scales: how to make an interference filter. *Journal of Morphology*, **142:** 395-410.

Ghiradella, H. and Radigan W. (1976) Development of Butterfly Scales. II Struts, Lattices and Surface Tension. *Journal of Morphology*, **150:** 279-298.

Guenée, A. (1857) Uranides et Phalénites 1. *In:* Boisduval, M. & Guenée, A. *Histoire Naturelle des Insectes, Species Général des Lépidoptères*, **9:** 1-514.

Harwood, L. M. and Moody, C. J. (1989) *Experimental Organic Chemistry. Principles and Practice*. Blackwell Scientific Publications.

Herbulot, C. (1991) Trois nouveaux Geometrinae d'Amerique du Sud (Lepidoptera: Geometridae). *Lambillionea*, **91:** 108-112.

Herrich-Schäffer, G. A. W. [1853-1869] Sammlung neuer oder wenig bekannter aussereuripäischer Schmetterlinge (subsequently titled *Lepidopterorum exoticorum species novae aut minus cognitae* and *Collections de nouvelles espèces de Papillons exotiques*). Vol 1. [later issue of part Volume 1; bound together in BMNH].

Holloway, J. D., Bradley, J. D. and Carter, D. J. (1987) *CIE Guides to insects of importance to man. 1. Lepidoptera.* CAB International Institute of Entomology. British Museum (Natural History).

Hübner, J. [1816-1926] *Verzeichniss bekannter Schmettlinge* [sic.].

Inoue, H. (1961) *Insecta Japonica Series 1 Part 4 Lepidoptera: Geometridae [1].* Horuyukan Publishing Co. Ltd Tokyo.

International Commission on Zoological Nomenclature (1957) Opinion 450. *Opinions and declarations rendered by the International Commission on Zoological Nomenclature*, **15:** 251-328.

International Commission on Zoological Nomenclature (1985) *International Code of Zoological Nomenclature.* Third Edition. xx + 388pp. University of California Press, Berkeley and Los Angeles.

Janzen, D. H. (1986) *Guanacaste National Park: tropical ecological and cultural restoration.* Universidad estadal a distancia. San José, Costa Rica.

Janzen, D. H. (1988) Ecological Characterization of a Costa Rican Dry Forest Caterpillar Fauna. *Biotropica*, **20:** 120-135.

Jones, E. D. (1921) New moths from South-East Brazil. *Proceedings of the Zoological Society of London*, 323-356.

Kayser, H. (1985) *Pigments*. In Kerkut, G.A. and Gilbert, L.I. (Executive Eds) *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. Volume 10. Biochemistry. Pergamon Press.

Kennel, J. V. and Eggers, F. (1933) Die abdominalen Tympanalorgane der lepidopteren. *Zoologische Jahrbücher Abteilung für anatomie und ontogenie der Tiere*, **57**: 1-105.

Klots, A. B. (1970) Lepidoptera. In *Taxonomist's Glossary of Genitalia in Insects*. Edited by Tuxen, S.L. Munksgaard. Copenhagen (Second Edition).

Kristensen, N. P. (1984) Studies on the morphology and systematics of primitive Lepidoptera (Insecta). *Steenstrupia*, **10:** 141-191.

Krüger, M., and Scoble, M. J. (1992) Neotropical red-brown Ennominae in the genera *Thysanopyga* Herrich Schäffer and *Perissopteryx* Warren (Lepidoptera: Geometridae). *Bulletin of the British Museum (Natural History). Entomology Series*, **61:** 77-148.

Kuenzle, C. C. (1970) Bilirubin Conjugates of Human Bile Nuclear- magnetic-resonance, Infrared and optical spectra of model compounds. *Biochemical Journal*, **119**: 395-409.

Linnaeus, C. (1758) Systema naturae per regna tria naturae secundum classes, ordines, genera, species cum characteribus, diferentiis, synonymis, locis Ed. decima reformata. Silvius, Holmiae.

McDonagh, A. F. (1979) Bile pigments: Bilatrienes and 5,15- Biladienes. In Dolphin, D. (Ed.) *The Porphyrins, Part A*. Academic Press.

McFarland, N. (1988) *Portraits of South Australian Geometrid Moths*. Allen Press Inc.

McGuffin, W. C. (1972) Guide to the Geometridae of Canada (Lepidoptera) II. Subfamily Ennominae I. *Memoirs of the Entomological Society of Canada*, **86**.

Minet, J. (1991) Tentative reconstruction of the ditrysian phylogeny (Lepidoptera: Glossata). *Entomologica Scandinavia*, **22:** 69-95.

Möschler, H. B. (1881) Beträge zur Schmetterlings-Fauna von Surinam. IV. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, **31:** 393-442. [Volume dated 1881, paper dated 1882, volume title page dated 1882].

Möschler, H. B. (1890) Die Lepidopteren-fauna der Insel Portorico. *Abhandlungen hrsg. von der Senckenbergischen Naturforschenden Gesellschaft. Frankfurt a.M.*, **16:** 69-360.

Needham, A. E. (1978) *Insect Biochromes. Their chemistry and role*. In Rockstein, M. *Biochemistry of Insects*. Academic Press.

Nijhout, H. F. (1985) The Developmental Physiology of Colour patterns in Lepidoptera. *Advances in Insect Physiology*, **18:** 181- 247.

Packard, A. S. (1876) *A monograph of the Geometrid Moths or Phalaenidae of the United States*. Washington: Government Printing Office.

Prout, L. B. (1910) Lepidoptera Heterocera Fam. Geometridae Subfam. Brephinae. In Wytsman, P. *Genera Insectorum*, 103^{me} Fascicule: 1-16.

Prout, L. B. (1912) Lepidoptera Heterocera fam. Geometridae subfam Hemitheinae. In Wytsman, P. *Genera Insectorum*, 129me Fascicule: 1-274.

Prout, L. B. (1916) New Neotropical Geometridae. *Novitates Zoologicae*, **23:** 151-190.

Prout, L. B. (1918a) New Geometridae in the Joicey Collection. *The Annals and Magazine of Natural History including Zoology, Botany and Geology* Series 8, **20:** 108-128.

Prout, L. B. (1918b) New Species and forms of Geometridae. *Novitates Zoologicae*, **25:** 76-89.

Prout, L. B. (dated 1931, published in 1932) In Seitz, A. *The Macrolepidoptera of the World*. Volume 8. The American Geometridae.

Rüdiger, W., Klose, W., Vuillaume, M. and Barbier, M. (1968) On the structure of Pterobilin, the blue pigment of *Pieris brassicae*. *Experientia*, **24:** 1000.

Salkeld, E. H. (1983) A catalogue of the eggs of some canadian Geometridae (Lepidoptera), with comments. *Memoirs of the Entomological Society of Canada*, **126**.

Schaus, W. (1897) New species of Geometridae from Tropical America. *Journal of the New York Entomological Society*, **5:** 161-166.

Schaus, W. (1901) New species of Geometridae from tropical America. Part II. *Transactions of the American Entomological Society*, **27:** 241-276.

Schaus, W. (1912a) New Species of Heterocera from Costa Rica - XV. *Annals and Magazine of Natural History including Zoology, Botany, and Geology.* Eighth Series, **9:** 423-433.

Schaus, W. (1912b) New species of Heterocera from Costa Rica-XVII. *Annals and Magazine of Natural History including Zoology, Botany, and Geology.* Eighth Series, **10:** 286-311.

Schaus, W. (1913) New species of Heterocera from Costa Rica- XXI. *Annals and Magazine of Natural History including Zoology, Botany, and Geology.* Eighth Series, **11:** 342-357.

Scoble, M. J. and Edwards, E. D. (1990) *Parepisparis* Bethune-Baker and the composition of the Oenochrominae (Lepidoptera: Geometridae) *Entomologica Scandinavia*, **20:** 371-399.

Scoble, M. J. (1992) *The Lepidoptera: form, function and diversity*. Natural History Museum Publications. Oxford University Press.

Shields, O. (1987) Presence of pterin pigments in wings of Libytheidae butterflies. *Journal of Chemical Ecology*, **13:** 1843-1848.

Sibatani, A., Ogata, M., Okada, Y. and Okagaki, H. (1954) Male genitalia of Lepidoptera: Morphology and Nomenclature. I. Divisions of the valvae in Rhopalocera, Phalaenidae (=Noctuidae) and Geometridae. *Annales of the Entomological Society of America*, **47:** 93-106.

Stehr, F. W. (1987) *Immature Insects*. Kendall / Hunt Publishing Company.

Stoll, C. (1787-1790, title page dated 1791) *in* Cramer, P. *Aanhangsel van het Werk, de Uitlandsche Kapellen (Supplément à l'Ouvrage intitulé les Papillons exotiques.)*

Thierry-Mieg, P. (1916) Descriptions de Lépidoptères nouveaux. *Miscellanea Entomologica*, **23:** 41-52.

Verloren, H. (1837) *Catalogus systematicus ad Cramerum.* Academiae typographum.

Viidalepp, J. (1981) To the systematics of geometrid moths above the generic level. *Horae Societatis Entomologicae Unionis Soleticae*, **58:** 90-95.

Vuillaume, M. (1968) Pigmentations et Variations Pigmentaires de trois insects: *Mantis religiosa* (L.), *Sphodromantis viridis* (F) et *Locusta migratoria* (L). *Bulletin Biologique de la France et de la Belgique*, **102:** 147-232.

Vuillaume, M. and Barbier, M. (1969) Sur les pigments tétrapyrroliques des Lépidoptères. *Compte Rendu de l' Académie des Sciences. Paris, t (Série D)*, **268:** 2286-2289.

Vuillaume, M., Choussy, M. and Barbier, M. (1970) Pigments tétrapyrroliques verts et bleus des ailes de lépidoptères pterobiline et néoptérobilines. *Bulletin de la Société Zoologique de France*, **95:** 19-29.

Walker, F. (1861) *List of the specimens of Lepidopterous insects in the collection of the British Museum*, **22**.

Walker, F. (1866) *List of the specimens of Lepidopterous insects in the collection of the British Museum*, **35**.

Warren, W. (1897) New genera and species of *Thyrididae, Epiplemidae,* and *Geometridae*, from South and Central America and the West Indies, in the Tring Museum. *Novitates Zoologicae*, **4:** 408-507.

Warren, W. (1900) New genera and species of American *Drepanulidae, Thyrididae, Epiplemidae* and *Geometridae. Novitates Zoologicae*, **7:** 117-225.

Warren, W. (1901) New American Moths. *Novitates Zoologicae*, **8:** 435-492.

Warren, W. (1904a) New American Thyrididae, Uraniidae, and Geometridae. *Novitates Zoologicae*, **11:** 1-173.

Warren, W. (1904b) New American Thyrididae, Uraniidae, and Geometridae. *Novitates Zoologicae*, **11:** 493-582.

Warren, W. (1905) New American Thyrididae, Uraniidae and Geometridae. *Novitates Zoologicae*, **12:** 307-379.

Warren, W. (1906) Descriptions of new genera and species of South American Geometrid Moths. *Proceedings of the United States National Museum*, **30:** 399-557.

Warren, W. (1907) American Thyrididae, Uranidae and Geometridae in the Tring Museum. *Novitates Zoologicae*, **14:** 187-323.

Warren, W. (1909) New American Uraniidae and Geometridae. *Novitates Zoologicae*, **16:** 69-109.

Watson, A. & Goodger, D. T. (1986) Catalogue of the Neotropical tiger-moths. *Occasional Papers on Systematic Entomology*, **1:** 1-71.