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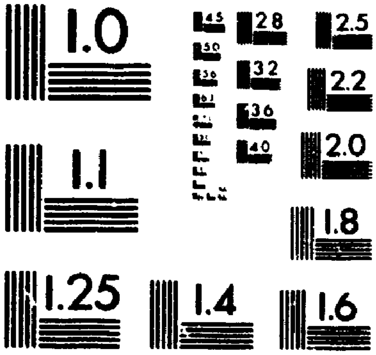

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A PHYLOGENETIC ANALYSIS OF THE MAJOR LINEAGES OF THE CRAMBINAE AND OF THE GENERA OF CRAMBINI OF NORTH AMERICA (LEPIDOPTERA: PYRALIDAE)

by

BERNARD LANDRY

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of
Doctor of Philosophy

Department of Biology
Carleton University
Ottawa, Ontario
February 1992

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A PHYLOGENETIC ANALYSIS OF THE MAJOR LINEAGES OF THE
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(LEPIDOPTERA: PYRALIDAE)

submitted by

Bernard Landry

in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

Chairman, Department of Biology

Stewart B Peck

Thesis Supervisor

Eugene Munroe

External Examiner

Carleton University

1992

ABSTRACT

This study is a cladistic analysis of the tribes of Crambinae (sod-webworm moths) and the genera of Crambini of America north of Mexico (Lepidoptera: Pyralidae). Forty-three characters were utilized. The morphology of the tympanal organs and microsculpture of the antennae were analysed in detail for the first time in this group of Lepidoptera. The morphology of the genitalia and the wing venation were also studied. The cladistic analysis was made with PAUP and Hennig86. The monophyly of the Crambinae was supported by three synapomorphies. Of the five previously recognized North American tribes of Crambinae, two (Crambini, Diptychophorini) were supported by new synapomorphies. The Chilonini is not recognized although five genera formerly placed in this taxon formed a monophyletic group (Haimbachiini, **new tribe** [type genus: Haimbachia Dyar, 1909]) which is supported by a newly discovered synapomorphy. The taxon called Ancylolomiini is dismantled and its North American taxa placed in a new taxon (Prionapterygini, **new tribe** [type genus Prionapteryx Stephens, 1834]). The Argyriini is not supported by any synapomorphy but its status is left unchanged. The relationships between the tribes remain unresolved while those between the genera of Crambini are partly resolved. Nineteen genera of Crambini in North America are recognized and two species described in Crambus are left unassigned to any genus. Descriptions and a key to these taxa are provided. The genera are redefined, most often on the basis of newly discovered synapomorphies. The status of Crambus Fabricius, Fissicrambus Bleszynski, Loxocrambus Forbes, Parapediasia Bleszynski and Thaumatopsis Morrison is revised to include species formerly placed in other genera or to exclude species. Two genera of Crambini are described as new: Almita **new genus** (type species: Almita texana n. sp.); Neodactria **new genus** (type species: Crambus luteolellus Clemens). The Neotropical genus La Bleszynski is newly reported in North America from a new species (La cerveza n. sp.). Two more species are described as new (Almita portalia n. sp. and Parapediasia torquatella n. sp.). A study of the primary types of the North American Crambinae in the British Museum (Natural History) is presented, and 35 lectotypes are designated.

ACKNOWLEDGMENTS

Any long-term study like this one cannot be succesfully achieved without the precious help of many people.

I would especially like to thank the members of my advisory committee who first believed in my potential to do a PhD. at Carleton University and supported me in many ways. They are S.B. Peck, J.D. Lafontaine, H.F. Howden, J.T. Arnason and D.M. Wood (as a replacement of H.F. Howden for a short period).

Most of my research time was spent at the Biosystematics Research Division of Agriculture Canada (now part of the Centre for Land and Biological Resources Research). It is appropriate that I thank again Don Lafontaine for providing space and equipment and Drs. Robert Trottier and Richard Asselin, directors, for allowing my presence there. The following members of staff at the CLBRR (BRD) were also extremely helpful in many ways: Suzanne Allison-Morello, Ed Becker, Klaus Bolte, Jacques Cayouette, P.T. Dang, Louise Dumouchel, Bill Forrest, Barb Grey, Lise Guilbault, Marie Israel, Eugenie Krelina, Doug Kritsch, Marie Labelle, Jean-François Landry, Josée Poirier, Amalia Pucat, Lise Robillard, Michael Schwartz, Michael Sharkey, Ales Smetana and Larry Speers. Drs. Schwartz, Landry and Sharkey were especially helpful with the cladistic analysis. Dr. Landry allowed me to work on his MacIntosh computer. Also from the Research Branch of Agriculture Canada, I wish to acknowledge the excellent work and support of Bill Lukey and his colleagues of the

Biographics Unit, and A. F. Yang and colleagues of the Electron Microscopy Unit. Kauri Mikkola and André Larochelle, visitors at the CLBRR, helped with decisions on zoological nomenclature. From the Biology Department of Carleton University I must thank Karen McLauchlan-Hamilton, Lew Ling, Tessa MacKechnie and Janet Wilson for their always friendly welcome and assistance. Several graduate students at Carleton and Ottawa University made the social life there sometimes quite enjoyable and were always there to discuss problems and solutions; they are Anne-Christine Bonfils, Cliff Benninger, John Heraty, Gary Humphrey, Dominique Lainet, Luc Leblanc and Brad Sinclair. Dr. John Heraty brought considerable help with the cladistic analyses. The support and hospitality of Dr. Jarmila Kukalová-Peck will always be remembered with warmth.

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Field trips are improved by companionship and I salute the following people who went with me several times and provided assistance in numerous ways; Robert S. Anderson, Yves Bousquet, Terry S. Dickel, Cees Gielis, Raymond Hutchinson, Peter M. Jump, Jacques Koster, J. Donald Lafontaine,

Jean-François Landry, Serge Laplante, Noel MacFarlane, Tou Fadua Malick, Daniel Néron, Stewart B. Peck, Simon Rainville, Ed D. Riley, P. Michael Sanborne, Brad J. Sinclair, and Hugo van der Wolf. Special thanks are extended to Ms. Ellen Peck for her hospitality during a field trip to Florida.

Again I wish to acknowledge the always kind assistance of several collection managers and amateur collectors for their loans of specimens. They are identified on the first pages of the Material and Methods section.

In order to financially survive through the last four years I received money from several organisations. The Natural Sciences and Engineering Research Council of Canada provided financial support for three years in the form of a postgraduate scholarship. Financial support also came from Dr. S.B. Peck's NSERC operating grant and from the Government of Québec. The Entomological Society of Canada awarded me a Research Travel Grant to study the types of North American Crambinae in the British Museum of Natural History in London, England. The American Museum of Natural History, New York, also awarded me a small grant to study their collection of Crambinae.

Finally, I consider that without the moral support provided by the following people, this project could not have been undertaken and completed. They are my father, Yvan Landry, my mother, Madeleine Marois, my brother, Vincent Landry, the Mazur-Goulet family and my friends Daniel

Néron, Andrée Éthier, Sophie Turcot, Michel Robert, Anne Lasalle, Jean-Marc Léveillée, Simon Rainville and Jacques Lemieux.

To those that I have forgotten while these lines are written I ask forgiveness for such a poor memory.

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FOREWORD

I have been collecting Lepidoptera since the age of 12, but until six years ago, I never really paid much attention to the smaller moths (Microlepidoptera). Nevertheless, I decided to do my M.Sc. thesis on a group of Microlepidoptera, because I thought they would offer more potential for discovery. I chose the Pterophoridae, the plume-moths, because they showed obvious strange structural features, such as their cleft wings and others, which I found appealing.

Three years later, I still had only a vague idea of the diversity of the so-called Microlepidoptera other than my plume-moths. Thus, I was ready to continue to work on pterophorid systematics. However, I asked Dr. J.D. Lafontaine of the Centre for Land and Biological Resources Research, Agriculture Canada, Ottawa, to make a suggestion for a group that would represent a good challenge for Ph.D. work. He proposed the crambines as a group to be worked on. Of them I knew little, except that they could be quite abundant in my parents' front yard during the warmer weeks of summer. My collection then contained only five species of Crambinae. Soon I learned to like them. They have introduced me to some of nature's marvels.

1.1 Pyralidae

The Crambinae belong to family Pyralidae, the sister-group of which was believed to be the Dudgeonidae (Minet 1982) until he more recently (1991) abandoned this idea on the basis that the Dudgeonidae share the following two synapomorphies with the Cossidae: the haustellum is reduced and the lower part of the fronto-clypeus bears a pair of asymmetrical pits. All adult pyralids can be identified by the presence of "pyraloid-type" abdominal tympanal organs and a scaled haustellum (proboscis). Minet (1991) also proposed two more synapomorphies of the wing venation for the Pyralidae. The scaled haustellum is shared by the Gelechioidea, a group of Microlepidoptera distinguishable by their falciform palpi, and the Choreutidae (Choreutoidea, Minet 1991). This character is missing in some pyralid genera where the haustellum is absent (Munroe 1972). The presence of abdominal tympanal organs is shared by all Pyralidae but they can be somewhat reduced as in the subfamily Midilinae. The Geometroidea, Drepanoidea and Dudgeonidae (Cossoidea) also have abdominal tympanal organs. However, these are structurally different from those of the Pyralidae and are generally thought to have originated independently (Minet 1983, 1991). The Geometroidea can be distinguished by their generally broader wings and by their hindwing subcostal vein which is anastomosed with the Radius at the base while it is stalked with the Radius beyond the cell in the Pyraloidea (Munroe 1972). The Pyralidae have a worldwide distribution and contain about 1500 genera and 20000 species (Munroe 1982). The family is the second largest of the order.

1.2 Crambiformes

The subfamily Crambinae was recently given family status based on five synapomorphies of their tympanal organs (Minet, 1985) (fig. 1 and table 1). The most striking of these is the development of a praecinctorium, a ventral projection of the thoraco-abdominal membrane which protects the tympanum. Minet's decision was to unite one group of pyralid subfamilies (i.e. the Crambinae, Midilinae, Schoenobiinae, Cybalomiinae, Scopariinae, Pyraustinae, Spilomelinae and eight others) under the family Crambidae and to retain the other subfamilies (i.e. Pyralinae, Chrysauginae, Galleriinae, Epipaschiinae, Phycitinae and four others) in the family Pyralidae *s. str.* This has been accepted by the North American specialists, but not by the non-specialists because, I think, these groups of subfamilies cannot be separated by external diagnostic characters, while any Pyralidae *sensu lato* can easily be recognized as such on the basis of the scaled haustellum and the presence of abdominal tympanal organs. Minet's decision is consistent with phylogenetic principles since the two groups of subfamilies seem to be monophyletic and sister taxa. However, I don't think it is necessary to call the two groups families. Usefulness of the current taxonomy should prevail over Minet's decision. Thus, the group of pyralid subfamilies with a preacinctorium is here called Crambiformes following Munroe (1972) and the group of pyralid subfamilies without a praecinctorium is referred to as the Pyraliformes. Previous hypotheses of relationship of Crambiformes subfamilies are illustrated in figure 1.

1.3 Crambinae

Prior to this study, the Crambinae were not defined as a monophyletic group. The moths of the subfamily are often characterized by their long palpi, narrow forewings, hairy hindwing cubital stem and by their behavior of wrapping their wings around their body in repose. Some characters for the recognition of the subfamily at the larval stage were given by Hasenfuss (1960), Capps (1963) and Allyson (1986) but the distribution of the characters used by these authors is not known for many crambine genera and they have not been analysed within the framework of the whole Crambiformes. Some of these characters are: only one lateral seta on abdominal segment IX (A9) and setae V1 on A10 half as far apart as on A9. There are 21 "genera" of North American Crambinae for which immatures are not known for any species (see Table 5). In two of these genera, Catoptria and Pediasia, immatures are known for species extralimital to North America. The following works deal with immatures of North American crambines: Ainslie 1918, 1923 a, b, 1927, 1930; Allyson 1986; Bohart 1947; Deacke 1905; Felt 1894; Forbes 1894, 1905; Matheny & Heinrichs 1972; Mauston 1970; Miller 1940; Muma & Hill 1950; Neunzig 1987; Passoa 1986; Peterson 1948, 1963; Scudder 1894; Sorensen & Thompson 1979; Syme 1961; Tan 1984; Tashiro 1987.

The world fauna of the subfamily was last reviewed by Hampson (1896). It has been subsequently catalogued by Bleszynski & Collins (1962) who recognized 1563 valid species which they placed in 138 genera. Since then, numerous changes in the nomenclature (88 papers here taken into account) have brought the number of world species to 1827 and the number of genera to 151. Faunal lists have been provided for North America (Klots 1983; Munroe 1983) and the Neotropical Region (Bleszynski 1967). Revisions were made for North America (Fernald 1896), the Palearctic region (Bleszynski 1965), New Zealand (Gaskin 1971, 1973, 1975a) and Japan (Okano 1962). Faunal reviews have been published for Great Britain (Goater 1986), Japan (Inoue _et al._ 1982), China (Wang 1980) and the Hawaiian Islands (Zimmerman 1958). There are also lists of the fauna for many countries in Europe.

The subfamily has been divided into tribes only recently (see fig. 2) by Klots for the Chilonini (1970a) and Argyriini (1983); Gaskin for the Crambini (1975a), Chilonini (1973) and Diptychophorini (1971); and Minet (1982) for the Ancylolomiini and Myelobiini. The Ancylolomiini had however been segregated long ago as a subfamily (Ragonot 1891). Gaskin (1988) also used the name Calamotrophini for _Calamotropha_ Zeller. The genus, known from the Palaearctic, Ethiopian and Oriental Regions, was revised by Bleszynski (1961a). Three other Old World genera, were said to be related to _Calamotropha_ Zeller and revised by Bleszynski (1961a).

No fossils of Crambinae are known (Bleszynski 1965). Thus, my analysis relies exclusively on neontological data. The immature stages were not included in the analysis because the information available is limited and it was impossible to obtain the necessary specimens in most taxa.

1.4 Crambini

1.4.1 Monophyly, diversity and bionomics. The Crambini is the largest North American tribe of Crambinae with 16 genera and 117 species recognized by Klots (1983). The tribe was defined as a monophyletic group by Gaskin (1975a) on the basis of the everted ostiolar sclerites of the female genitalia. Gaskin (1975a) included eight of our 16 North American Crambini genera in the tribe (fig. 3). The other North American genera were placed in the Crambini by Klots (1983), presumably on the sole basis of his own findings because he also placed the two Diptychophorini genera under Crambini. The tribe is distributed worldwide (Gaskin 1975a). The species are most common in open habitats. Most Crambini appear to be associated with plants of the family Poaceae although some species have been found to feed on tobacco, sedges and *Sphagnum* mosses (Gaskin 1975b). The Crambini contain pests of turfgrass in the United States and Canada. The genera *Parapediasia*, *Fissicrambus*, *Crambus* (two spp.), *Pediasia* and *Chrysoteuchia* contain six of the most important sod webworms of the temperate regions of the United States (Potter & Braman 1991; Tashiro 1987). Members of the genera *Agriphila*, *Microcrambus* and *Tehama* are also known to infest turfgrass in the United States (Tashiro 1987). Early reports cited by Fernald (1896) also mention the important ravages made by species of *Crambus*, *Pediasia* and *Neodactria* to corn and oat fields in the north-eastern United States.

The world fauna of genus *Euchromius* is probably the best known among Crambini since revisions by Bleszynski (1960, 1961b, 1965), Capps

(1966) and Schouten (1988). Klots (1968) published a revision of the North American species of *Microcrambus*. Bleszynski revised the European species of the *Crambus*-group of genera (Bleszynski 1957), the world species of *Chrysocrambus* (Bleszynski 1958) and the World species of *Culladia* (Bleszynski 1970a). Gaskin (1984) revised *Roxita*.

1.4.2 Historical review of Crambini taxonomy. The first species of Crambini were described by Linnaeus (1758), Scopoli (1763), Denis & Schiffermüller (1775) and Thunberg (1788). All were placed in *Phalaena (Tinea)* Linnaeus.

The genus *Crambus* was first used as a name by Fabricius (1798). Sixty-two species were originally placed in the genus. Subsequently, the name was used by such authors as Latreille (1801) and Duponchel (1836) but Zincken (1817), Treitschke (1832) and Zetterstedt (1840) placed *Crambus* species in the genus *Chilo* Zincken. Haworth (1811) used his genus *Palparia* to include *Crambus* species while Hübner (1825) established eight genera (which were called *coiti*) to place the species of *Crambus*, without recognizing the genus *Crambus* itself. Apart from his genus *Agriphila* Hübner, none of his other generic names was used by subsequent authors until Bleszynski (1952, 1957) revived *Catoptria*, *Pediasia* and *Thisanotia*. Bleszynski did not use tribes in his "system" of Crambinae, but associated some genera into groups, such as the *Crambus*-group, or complexes, such as the *Chilo*-complex or the *Acigona*-complex. These groups of genera were usually listed in an orderly fashion from the more primitive to the more complex in such a way that the tribes of today can be recognized in his classifications (1965, 1967). There were some noticeable exceptions such as Euchromius placed near Diptychophora presumably because of the similarly patterned wings. However, he could not resolve the intergeneric relationships within his groups of genera. This led him to state (1957: 183): "It is very difficult or quite impossible to answer the question how the genera established by me are related to each other".

In North America, Smith (1891) and Fernald (1896) recognized three genera of Crambinae; Crambus Fabricius, Euchromius Guenée and Thaumatopsis Morrison although Arequipa Walker had been described in 1863 and Tehama Hulst in 1888. Raphiptera Hampson 1896 was added to the North American list by Dyar (1903) and Smith (1903). In 1917, Barnes & McDunnough (followed by Forbes 1920, 1923) recognized a fifth genus, Platytes Guenée, described to contain a Palaearctic species in 1845. Basically the same arrangement was followed by McDunnough (1939) with the addition of Loxocrambus Forbes, 1920. The North American classification remained stable until Bleszynski (1959) transfered some North American species from Crambus to Agriphila and Pediasia. Bleszynski (1963a) subsequently described Microcrambus and Fissicrambus which included some North American species. Bleszynski & Collins (1962) resurrected Tehama Hulst 1888 and placed four North American species of "Crambus" in Pediasia Hübner. Bleszynski (1965) resurrected Chrysoteuchia Hübner and associated the North American species (C. topiaria) with that genus. Klots (1968) moved several North American species of Crambus to Microcrambus and described three more species in that genus. Klots (1983) established the classification still in use today; the main changes made consisted in reviving Arequipa Walker, three species were moved from Crambus to Parapediasia Bleszynski 1966, and two other species were moved from Crambus to Fernandocrambus Aurivillius 1922.

1.4.3 Zoogeography of Crambini. Species of Crambini are present on all continents (except Antarctica) and on many remote oceanic islands. They are common at high altitudes where grasslands occur. However, they are virtually absent from wet tropical and equatorial forests. The zoogeography of the North American Crambini has been dealt with by Klots (1961), Bleszynski (1965) and Gaskin (1975a). Because they did not have a sound taxonomic treatment of the whole group as a foundation, their analysis is very weak. Thus, the place and time of origin of the genera, the factors that have affected their past and present distribution, and the influence of humans on these patterns of distribution, can only be usefully discussed when comprehensive revisions of genera become available.

1.5 Problems with the taxonomy of North American Crambinae

At the beginning of my investigations I faced the following situation regarding the taxonomy of North American Crambinae. Firstly, the subfamily was not defined by synapomorphies and its sister-group was unknown. Adult and larval characters needed to be tested on a large scale and with modern methods. Secondly, Gaskin (1975a) defined the Crambini on the basis of a synapomorphy of the female sterigma that is impossible to test in many taxa of the North American fauna because of lack of sclerotization or fusion of the parts involved. Consequently, there were problems concerning the definition of this tribe. In addition, the sister-group of the Crambini had not been recognized.

Thirdly, none of the North American genera were defined by apomorphic characters and their relationships were unknown. Moreover, Klots (1983) pointed out that 15 species belonging to five of his 18 genera of Crambini (with ten spp. in genus Crambus) were misplaced in the classification. Other species in other genera were also believed to be misplaced (e.g. two species in Microcrambus, D. Gaskin, pers. comm.). The North American nomenclature of Crambini genera also needed to be better correlated with available names from the Palaearctic and Neotropical Regions.

The last major problem with our knowledge of the North American crambines was the lack of means of species identification. The most recent revision is that of Fernald (1896). No keys to the genera of any tribe were available.

1.6 Objectives of the thesis

All organisms are somehow related to each other. Nowadays, when possible, the systematist tries to construct classifications that reflect these phylogenetic relationships. The methodology used to study the evolution of a group of organisms had not been formulated clearly until recently. Willi Hennig (1950) provided the conceptual framework of phylogenetic systematics (or cladistics) which allowed the subsequent development of computer programs designed to analyze the evolutionary relationships between groups of organisms. The reasoning of systematics is based on the hypotheticodeductive method. Cladograms are hypotheses of relationships which can be tested by the addition to the analysis of new characters or taxa, or by new hypotheses on the polarity of the characters. Classifications derived from cladograms are preferred because of their information content on the order of nature. Cladistic methodology is based on the recognition of newly acquired (derived) character states. These define monophyletic groups of taxa. The polarity (derived or primitive) of character states is determined by outgroup comparison, i.e. a character state is derived (apomorphic) if it is present only in the group under scrutiny (the ingroup) or a subset of it. A character state is primitive (plesiomorphic) if it is widely distributed in the outgroup (the hypothesized closest relative of the ingroup). Most parsimonious hypotheses of character states changes are preferred because they offer the simplest and most economical solutions (Wiley 1981). In recent taxonomic studies of Pyralidae, the principles and terminology of cladistics are accepted and utilised (for example by Gaskin, Minet and Munroe) but broad scale phylogenetic analyses involving several taxa and characters are not available. Thus, I hypothesized that an evolutionary classification of the North American Crambinae could be developed using cladistic principles and methods. The particular objectives of this study are listed below.

1. To assess the monophyly of the Crambinae and to review its relationships with the other crambiforme subfamilies.

2. a) To redefine the Crambini as a monophyletic entity.
   b) To examine the phylogenetic relationships of all crambine tribes.

3. To analyse the phylogenetic relationships among the major lineages of the North American Crambini.

4. To reevaluate the generic concepts within the tribe, based on the above analysis, so that the genera are putatively monophyletic.

5. To produce a key to the North American genera of Crambini.

6. In summary, to construct a sound classification of the North American genera and species of Crambinae.

A- Synapomorphies of the tympanal organs (i-v) defined by Minet (1983: 204), others as indicated.

i. -conjunctivae each borded by a mostly straight tympanic line
ii. -tympanum originating from a strong thinning of a determined part (external) of the internal lamella of the tympanic drums
iii. -tympanic drums caracteristic, integrating the apodemes (unrecognizable), and made of two partially welded lamellae
iv. -proximal insertion of the scoloparia situated at the level of the internal lamella of the drums
v. -tympanic sacs always paired and largely surrounded by the drums.
vi. -scaled proboscis (Munroe 1972 and Minet 1991).
vii. -hindwing Sc + R and Rs anastomosed or almost so beyond cell (stated as an apomorphy by Minet, 1986).
viii. -forewing with R2 and R3 coincident (Minet 1991).

B- Synapomorphies of the tympanal organs defined by Minet (1982, 1985).

i. -presence of praecinctorium
ii. -tympanal projections present
iii. -spinulae fundamentally present
iv. -scolopal bulgings hypertrophied
v. -some scolopal bodies transformed into squamiform structures.

C- Characters i-iv defined by Minet (1985), character v by Hasenfuss (1960).

i. -forewing R4 stalked or fused with R2 + 3
ii. -bullae tympani closed
iii. -processes spiniformae well fixed in position
iv. -paraspinae fundamentally present.
v. -larval 8th abdominal segment with pinaculum around SD1

D. Four apomorphies (Passoa 1988).

i. -V1 lost on larval thorax
ii. -L2 on larval abdominal segments reduced
iii. -tegumen-vinculum plate developed, transtilla lost
iv. -pupal appendages exarate with metathoracic legs exposed

E. Larva with unisetose L group on A9 (Passoa 1988).

F-J. From Yoshiyasu (1985). Note the contradiction between Yoshiyasu and Passoa.

F. Cheatosemata reduced and tympanic bullae bifurcated at apex.

G. Cochlear of gnathos missing.

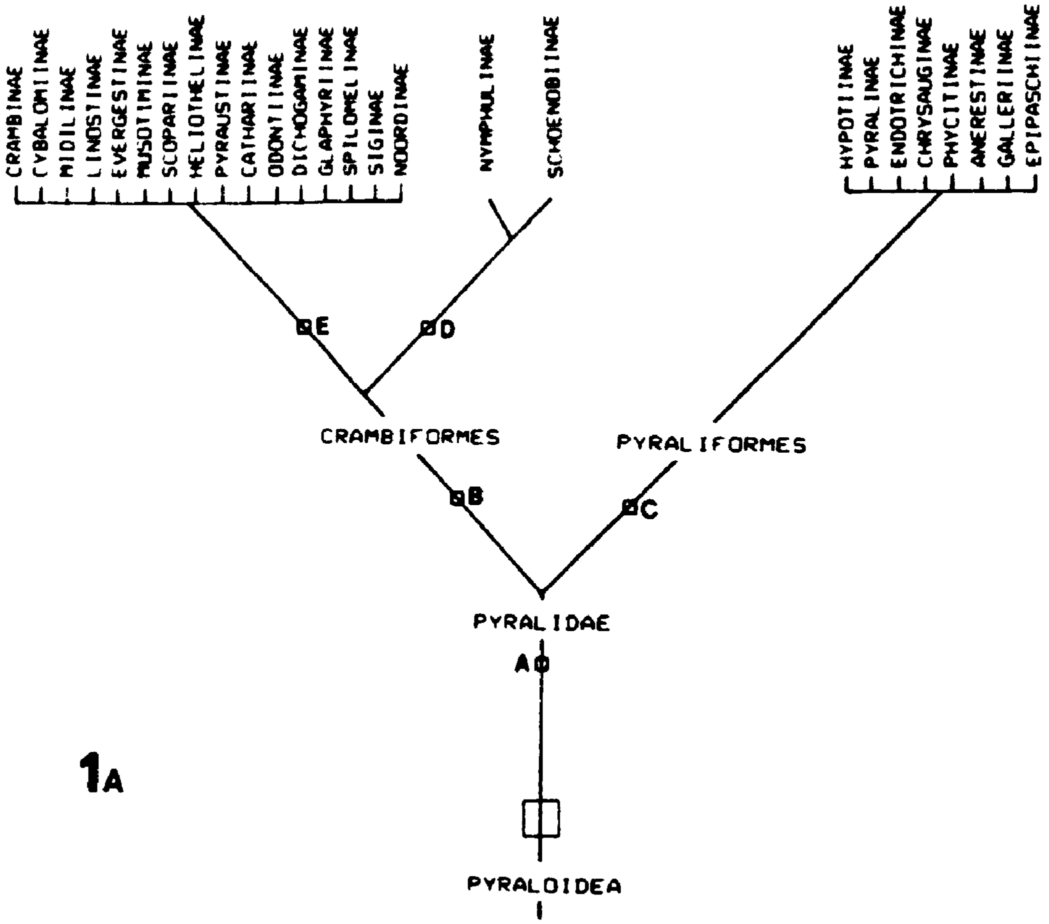
H. Transtilla shortened or reduced.

I. Ductus bursa sclerotized dorsally.

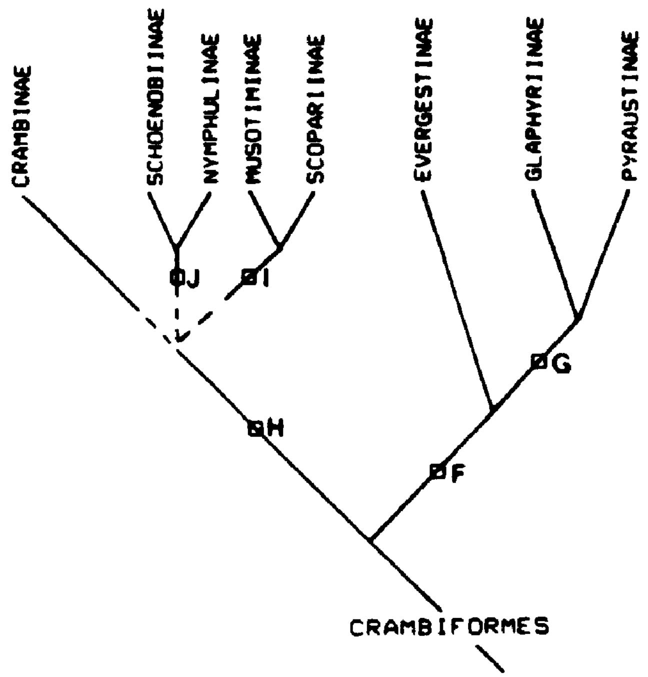
J. Male genitalia tegumen-vinculum plate with muscle 3 and/or 4, and larva without seta V1 on thoracic segments.

Table 1. Character sets used by previous workers to express relationships among Crambiformes subfamilies as illustrated in figure 1.

Fig. 1. Hypothesized relationships among Pyraloid families and Pyralid subfamilies based on a) Hasenfuss (1960), Minet (1982, 1983, 1985, 1986, 1991), Munroe (1972), Passoa (1988) and b) Yoshiyasu (1985). See Table 1 for characters defining nodes A-J.


CRAMBINAE
CYBALOMIINAE
MIDILINAE
LINOSTINAE
EVERGESTINAE
MUSOTIMINAE
SCOPARIINAE
HELIOTHELINAE
PYRAUSTINAE
CATHARIINAE
ODONTIINAE
DICHOGAMINAE
GLAPHYRIINAE
SPILOMELINAE
SIGINAE
NOORDINAE
NYMPHULINAE
SCHOENOBIINAE
HYPOTIINAE
PYRALINAE
ENDOTRICHINAE
CHRYSAUGINAE
PHYCITINAE
ANERESTINAE
GALLERIINAE
EPIPASCHIINAE
E
D
CRAMBIFORMES
PYRALIFORMES
B
C
PYRALIDAE
A
PYRALOIDEA

1A


CRAMBINAE
SCHOENOBIINAE
NYMPHULINAE
MUSOTIMINAE
SCOPARIINAE
EVERGESTINAE
GLAPHYRIINAE
PYRAUSTINAE
J
I
G
H
F
CRAMBIFORMES

1B

A. Two apomorphies defined by Gaskin (1971).

- i. -♀ 8th sternite lost
- ii. -♀ ostiolar sclerites dorsal and ventral, completely invaginated into ostium bursae

B. Tympanum perpendicular to the plane including the free part of the sternite as defined by Minet (1982, 1985).

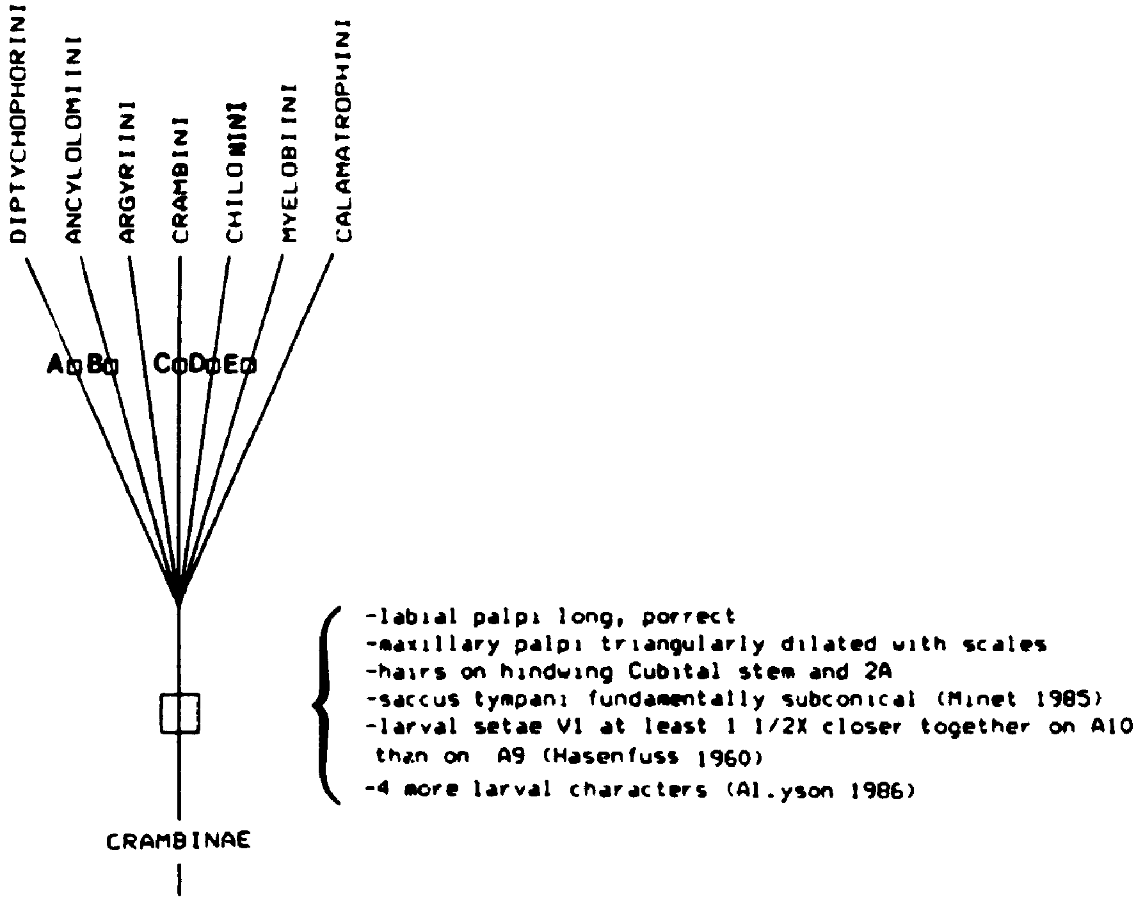
C. Female ostiolar sclerites evaginated and fused in the lateral midlines to form a projecting tube through intersegmental membrane VII-VIII (Gaskin 1975a).

D. Female ostiolar sclerites laterally situated, invaginated or partly so in the ostium bursae (Gaskin 1973).

E. Praecinctorium bilobed (Minet 1982).

Table 2. Synapomorphies used by previous workers to express the monophyly of the tribes of Crambinae (see figure 2).

Fig. 2. Hypothesized characters defining subfamily Crambinae and its tribes. From Gaskin (1971, 1973, 1975a) and Minet (1982, 1985). See Table 2 for characters defining nodes A to E.



-labial palpi long, porrect
-maxillary palpi triangularly dilated with scales
-hairs on hindwing Cubital stem and 2A
-saccus tympani fundamentally subconical (Minet 1985)
-larval setae V1 at least 1 1/2X closer together on A10 than on A9 (Hasenfuss 1960)
-4 more larval characters (Allyson 1986)

2

A. i. -common stalk of forewing veins R4 and R5
ii. -♂ genitalia with pseudosaccus.

B. i. -coalescence of ♀ anal papillae
ii. -laminate extension of ♂ saccus floor present.

C. i. -complex female ostiolar region
ii. -strongly differentiated ♂ sacculus.

D. i. -unspecialized ♀ ostiolar region
ii. -♂ sacculus little differentiated.

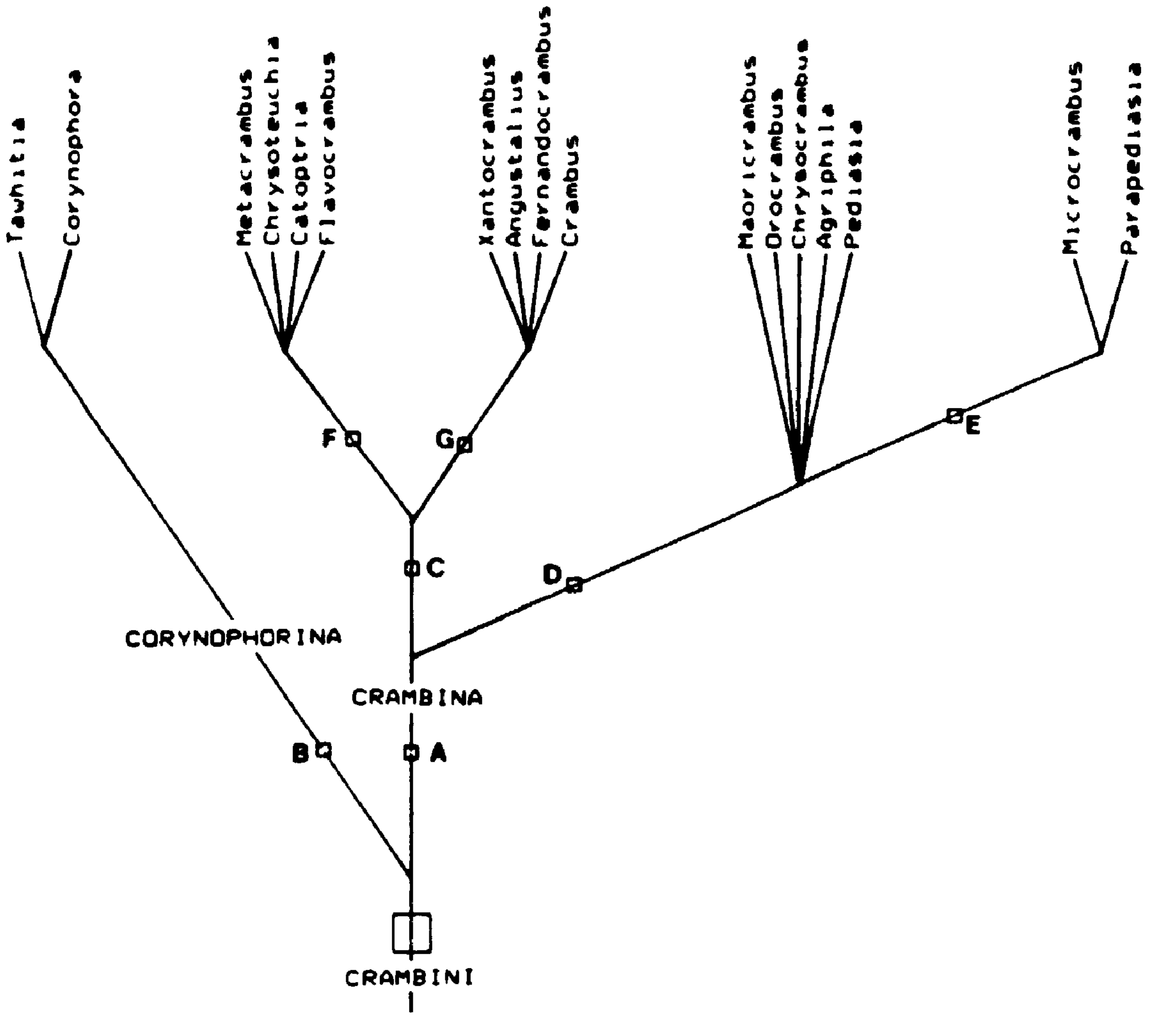
E. -strong brush of scales on caudal margin of ♀ abdominal sternite VII.

F. -male sacculus spinose.

G. -male sacculus lobate.

Table 3. Characters expressing relationships of the genera of Crambini based on Gaskin (1975a). The characters were not said to be apomorphic. Several are in fact plesiomorphies.

Fig. 3. Hypothesized relationships among some Crambini genera. Redrawn from Gaskin (1975a). See Table 3 for characters defining nodes A to G.


Tawhitia
Corynophora
Metacrambus
Chrysoteuchia
Catoptria
Flavocrambus
Xantocrambus
Angustalius
Fernandocrambus
Crambus
Maoricrambus
Orocrambus
Chrysocrambus
Agriphila
Pediasia
Microcrambus
Parapediasia
F
G
C
D
E
CORYNOPHORINA
CRAMBINA
B
A
CRAMBINI

3

2. MATERIAL AND METHODS

2.1 Material

The bulk of my research material was from the Canadian National Collection of insects in the care of the Biosystematics Research Division staff (P.T. Dang, Chief Curator; J.D. Lafontaine, Head Curator of Lepidoptera; J.-F. Landry, Curator of Pyralidae), Centre for Land and Biological Resources Research, Agriculture Canada, Ottawa. This material was supplemented by my own collections (roughly 500 specimens mostly deposited in the CNC) and by about 1800 pinned specimens and 123 genitalia slides borrowed from the following institutions and private collectors. I take this opportunity to thank the private collectors and museum curators for the loan of the material in their care. I have also photographed the crambine types in the collections of the Philadelphia Academy of Sciences (Philadelphia, PA), and I thank Mr. Donald Azuma for giving me this opportunity. The important collection of North American Crambinae types in the British Museum of Natural History (London) was also examined (see Appendix V). This collection is under the very good care of Mr. Michael Shaffer who is deeply acknowledged for his help during my visit to London in May and June 1991.

AMNH	American Museum of Natural History, New York, NY (Dr. F.H. Rindge)
CGC	Cornelius Gielis' private collection, Lexmond, Netherlands

CMP	Carnegie Museum, Pittsburgh, PA (Dr. J.E. Rawlins)
CUC	Cornell University Collection, Ithaca, NY (Dr. J.K. Liebherr)
LACM	Natural History Museum of Los Angeles County, Los Angeles, CA (Mr. J.P. Donahue)
LEM	Lyman Entomological Museum and Research Laboratory, Ste-Anne-de-Bellevue, PQ (Drs. V.R. Vickery & P.M. Sanborne)
NSMH	Nova Scotia Museum, Halifax, NS (Mr. B. Wright)
PJC	Peter M. Jump's private collection, Douglas, AZ
RSC	Rob Schouten's private collection, The Hague, Netherlands
TDC	Terhune S. Dickel's private Collection, Homestead, FL
TMC	Tim L. McCabe's private collection, Albany, NY
UCB	University of California at Berkeley, CA (Dr. J.A. Powell)
USNM	United States National Museum of Natural History, Washington, DC (Drs. D.C. Ferguson and A. M. Solis)

2.2 Collecting and mounting imagos and immatures stages

Collecting. Adults were mostly collected at night by means of both mercury-vapor and ultra-violet lights and sometimes during the day, by sweeping or by netting individuals that flew in front of my steps. This latter technique gave the best result in grassy areas in the White Mountains in Arizona, in various fields around Ottawa, Ontario, in the pampas of three Galápagos islands and in a marginal saline habitat in the Florida Keys.

Usually, collecting was performed on a vertically-set white sheet in front of which the lamp was hung. A long rope attached to two trees normally provided the support for the lamp and the sheet. In Arizona, in areas where trees were scarce, I used tent poles to support the sheet and lamp. In Florida, with T.S. Dickel, the white sheet was laid on the ground and the lamp set in the middle of it at about two feet from the ground because of the windy conditions. The mercury-vapor lamp was powered by a small portable generator while I generally used a 12 volt battery to power the ultra-violet lamp.

Specimens were collected individually in small plastic or glass vials and kept alive in dark, and, if possible, cool conditions, to reduce the moths' activity, until they were ready to be mounted.

Mounting imagos. The specimens to be mounted were killed individually with ammonia vapors; which keeps them relaxed, a most advantageous characteristic over other killing agents such as ethyl acetate and cyanide. Efficient killing chambers can be made with Pyrex tubes of which the cork tops are perforated partly for the insertion of a small glass tube (about half the diameter of the cork) which is filled with cotton wool. Ten to fifteen moths at a time were killed while the previous series was mounted.

For pinning, the specimens were placed on a folded cotton cloth which allows pinning completely through the specimen with minimal damage. Using two curved forceps, the specimens were positioned with the left hand while the minuten pin (size 0.20) was introduced through the mesothorax with the right hand. It was found preferable to use high quality stainless steel minutens because dark coated ones are more fragile and frequently bend at the tip. Minutens had to be cut to 2/3rds of their length when smaller specimens had to be mounted. This reduces the risk of damage by handling when the specimens are double-mounted.

To spread the wings, I used "spreading boxes" made of a layer of plastazote glued to the bottom of small (11 cm^2) plastic boxes, the sides of which, when open, are lower than the plastazote surface, thus allowing maximum maneuverability. Grooves were cut on the plastazote to place the moth's body. This was achieved with a lead ruler and a razor blade. Static electricity was created before the specimen was positioned in the groove to help spreading the wings. This was performed by rubbing the plastazote surface with the curved forceps at the anticipated point of contact with the wings. The wings were positioned and held in place by small triangles of labeling paper which had each been previously perforated by a no. 0 pin cut to 1 cm in length.

The specimens were left to dry for 2-3 days in their spreading boxes before they were removed and stacked in other plastic boxes of which the plastazote bottom was not grooved.

Upon my return from the field, the specimens were double- mounted on polyporus strips set on no. 2 pins. This method can be used for most North American crambines.

However, some species of Thaumatopsis, Epina and Chilo tend to be too large to be pinned with minuten. These larger specimens should be papered in the field. They can then be relaxed in a moist chamber, easily made with a plastic container in which moist tissue or sterilized sand and an anti-bacterial agent is placed to prevent growth of molds. Spreading is then performed on spreading boards made of wood. The wings are held in place by minuten pins mounted on thinned toothpicks. Several specimens can thus be spread before a partly transparent vellum paper band, which had previously been folded longitudinally, is placed on the wings and pinned to the board with round-top pins. The fold on the paper band is made at about 1/5th its width. It is placed alongside to the moth's body, and ensures a better grasp on the pin while it helps prevent scale losses to the sharp paper edge. Antennae were positioned using saliva which temporarily glues them to the board. All species of Crambinae can be mounted on wooden spreading boards of various sizes whether normal pins or minuten are used. Although it is easier to spread nicer specimens on wooden boards, this method is impractical in the field.

Rearings. My intention to study the immature stages of the Crambinae for the phylogenetic analysis led me to rear three different species of Crambinae in Crambus, Agriphila and Pediasia. Females were collected and kept alive in separate vials until eggs were laid. These were gently placed in small plastic boxes (4-6 cm^2) with blotting paper in the bottom. They were misted with water periodically until caterpillars hatched. Small caterpillars were transfered to other plastic boxes to avoid crowding. They were fed with corn silk cut to small pieces (Allyson 1986). Later larval instars were fed with grass leaves cut to pieces. First and last instar larvae and pupae were killed in boiling water and preserved in 70% ethyl alcohol.

2.3 Preparations for morphological studies and illustrations

Whole body preparations. The whole body of at least one specimen of each species used in the analysis (except in the genus Microcausta) was dissected to study the tympanic organs, thoracic and head structures, antennae, legs and genitalia. To achieve this, dried specimens were softened in KOH after their wings had been removed with forceps. The wings were then mounted separately (see below). It was important to choose specimens with at least one leg of each pair and one complete antenna.

Before boiling, the specimen was slowly wetted in a beaker containing a 10% KOH solution, thus preventing the antennae and legs from breaking. Then, it was placed in a vial containing a few milliliters of 10% KOH solution. The vial was placed in a beaker half filled with water and containing a few boiling chips to reduce agitation. The water was allowed to boil for five to 15 minutes, depending on the size of the specimen, on an electric hot plate. Sometimes, specimens were left in a vial containing the KOH solution for about 12 hours at room temperature to achieve the same results.

After boiling, the specimen was placed in a small, glass specimen-dish containing an aqueous solution of 30 % ethanol. Using No. 5 forceps, the legs and head were separated from the thorax while the genitalia were separated from the abdomen. The prothorax was detached from the mesothorax, as the mesothorax from the metathorax. The latter was left attached to the abdomen until the tympanic organs were studied and drawn in side view. They were eventually separated from each other leaving the praecinctorium attached to the abdomen. The thoracic segments were further dismantled to study the furca of each segment. The scales on the whole body were removed with a snipe alula feather mounted on a wooden handle or with a fine camel-hair brush. After separation of the genitalia, the abdomen was emptied by injecting into it a few milliliters of 30% ethanol with a gauge-30 or -33 canula needle and a 15 milliliters syringe. The remaining soft tissues in the abdomen and those in the thorax and head were removed with the help of a small hooked-tip needle mounted on a pin vise. For easier study of the tympanal organs, it was found that it is better if the abdomen is cut longitudinally along the right (or left) pleura with the help of a microknife.

To obtain a better result in cleaning the specimens and to give a better view of some parts, it was usually necessary to stain them. This was achieved by mixing a few drops of a saturated aqueous solution of chlorazol black with a few milliliters of a 70% ethanol solution. The genitalia and abdomen were placed in the solution for a few minutes (1 to 15 depending on the concentration of the stain). It was inadvisable to leave the parts in the solution for too long because they could become too dark and impossible to clear. However, overstained specimens can be cleared in hydrogen peroxide or sodium hypochloride (Javex).

According to Carayon (1969), chlorazol black fixes remarkably in association with insect cuticle. It stains the endocuticle better than the exocuticle and fixes the cuticular intimae. After a short time in chlorazol black, more cleaning was achieved after immersion in ethanol 70%. It was advisable to use more than one bath of ethanol solution to ensure better cleaning of the parts. It was at this stage that, if necessary, the aedeagus was detached from the rest of the genitalia by gently pulling it out with soft forceps.

All parts were then placed in glycerin on a microscope slide on which I glued a 3 mm thick plexiglass ring matching the width of the slide. This proved to be a good method to study and rapidly compare specimens from all possible angles and long after they had been prepared. Epoxy glue gave better results than euparal to cleanly maintain the plexiglass ring in position.

Genitalia preparations. Prepations of genitalia were made for most North American species of Crambinae. In this case, only the abdomen is detached from the thorax by pulling it up with forceps. The previously mentioned set of steps for whole body preparations was the same with the genitalia. Once treated with KOH and partly cleaned in 30% ethanol, the male genitalia were separated from the abdomen at the VII-IX intersegmental membrane while female abdomens were severed between segments VI and VII. The parts were then either placed in glycerin or permanently mounted.

Wing preparations. The method of wing preparation explained here is based on that of Zimmerman (1978) which has been slightly modified.

The right pairs of wings of the specimens selected for whole mounting were generally chosen but in case of damage, the left pair was chosen. When the whole specimen was put into KOH for study, the other pair of wings was stored in a gelatine capsule which was pinned to the label bearing pin. It was found easier if the wings had been properly spread on the specimen to ensure easier manipulation, better application of chemicals and to facilitate proper positioning on the slide. Manipulations were carried out with featherweight forceps and with a fine camel-hair brush when only water or 30% alcohol were involved. The remainder of the procedure can be divided into the five following steps:

1- The wings were placed in a 30% ethanol solution to wet them. Usually, a few drops of 95% ethanol had to be added on the floating wings to soak them completely.

2- Under the stereo-microscope, the wings were then placed in a solution of sodium hypochlorite (commercial "Javex" taken directly from the bottle) for one to two minutes or until the veins became clearly visible and the membrane transparent.

3- Immediately after the wings were bleached, they had to be washed in four different baths of distilled water to prevent the continued effect of the sodium hypochlorite.

4- The wings were then placed in a bath of 30% ethanol to start the dehydrating process.

5- They were then ready to be stained. The stain solution was prepared by mixing 10 gm of chloral hydrate, 5 ml of glacial acetic acid and 1 gm of fuschine acid with 100 ml of 50% ethanol. The wings were left in the solution for about 15 hours after which permanent mounts were made.

Permanent preparations. *Parts other than wings*. The method used for making permanent mounts of the different parts was mainly based on Hardwick's (1950) method for genitalia preparation with some modifications taken from Carayon (1969), Pitkin (1986) and Robinson (1976). Overall, about 300 slides were made. In most cases, male genitalia were spread with pieces of glass to give a more or less apical view, with the aedeagus and sometimes some other parts detached. Usually, the tegumen was separated from its attachment to the vinculum on the left side. While the valva+vinculum+juxta are dorso-ventrally flattened, the tegumen+uncus+gnathos are shown in side view and remain attached to the rest of the genitalia on the right side (see fig. 248). Female genitalia were mounted to give the ventral or a lateral view of these, depending on the shape of the structures.

The parts to be mounted were taken out of the glycerin bath and thoroughly washed in several baths of 70% ethanol so that all the glycerin was removed. The next step consisted in dehydrating the specimens. This was done by placing them in a bath of 95% ethanol and then in 2-propanol for half an hour. It is in 95% ethanol that those scales that had previously been too difficult to remove were usually easily extracted and that the male genitalia were spread in an appropriate position. When spread, male genitalia were maintained in position by putting one or two pieces of broken microscope-slide glass over them. It was also important, at this stage, to ensure that the abdomen was flattened dorsoventrally and to place the corresponding terga and sterna exactly one over the other. Pressure over the spread genitalia was maintained in 2-propanol.

The final step consisted of placing the stained parts in a dish of xylol to prepare the parts chemically for the mounting medium (Canada balsam). Parts were left in xylol for half an hour, after which they were ready for mounting. In the xylol bath, the last details of cleaning were achieved, though with great care, because, at this point, the membranes had lost their elasticity and were easily broken off or pierced. Furthermore, xylol damages alula feathers and camel-hair brushes.

Almost three years after the beginning of this study, I was convinced by other workers that I should use Euparal as a mounting medium instead of Canada balsam. I had not been convinced previously that Euparal slides would last as long as Canada balsam ones since Euparal has been in use in entomology for only three or four decades. Then, Mr. Cees Gielis, a serious amateur of plume moths (Pterophoridae) from the Netherlands, told me that Euparal has been used for more than 100 years in his profession, medical pathology. Euparal, I was also told gives clearer slides than Canada balsam and furthermore, xylol (which is carcinogenetic) isn't used with Euparal. The parts to be mounted only need to be placed on the slide in a Euparal bed after dehydration.

Mounting was achieved by placing correctly prepared (cleared, cleaned and stained) parts in Canada balsam or Euparal on a microscope slide. It was important to get all similar slides (e.g. all male genitalia in side view) with the different parts in the same position and the cover-glasses also in the same position for sake of consistency. To achieve this, a groove the size of a microscope slide was made in a piece of cardboard and a cross was drawn in the middle of the groove. The slide was then cleaned and placed in the groove and a small amount of Canada balsam or Euparal was spread around the center of the slide. Then, four pieces of 0.25, 0.50 or 1.0 mm thick (depending on the thickness of the parts) vinyl cover-glass supports were placed in the mounting medium at each of the four corners of the future position of the cover-glass. The parts were then placed in the chosen position, and the slide was stored in a suitably protected container to avoid dust. For faster hardening of the mounting medium, the slides were sometimes stored on a covered heating plate at about 30 ^{0}C. This process seemed to establish more rapidly the appearance of a yellowish colour in the Canada balsam, but it did not affect the quality of the slide (J.-F. Landry, personal communication). Heating does not affect the color or clarity of Euparal.

The slides were stored for at least 24 hours before the application of the cover-glasses to allow the parts to take and keep a proper position on the slide. Otherwise, if the cover-glasses were immediately applied, the parts tended to migrate to the edges of the area covered by the cover-glass. The cover-glass was applied after the addition of a sufficient amount of mounting medium over the preparation and after it was wetted with xylol (if Canada balsam was used) on the side of contact in order for it to take its proper position rapidly. With Euparal, this was not necessary.

One self-adhesive microscope slide label was affixed to each side of the preparation and information written with the insect data label on the left side. One label with the same number was affixed to the specimen's pin.

Permanent preparations. Wings. A total of 62 pairs of wings, were mounted. After staining, wings were dehydrated with pieces of microscope-slide glass on them if necessary and mounted on slides in exactly the same way as for the other body parts, except that cover-glass supports were not used.

Musculature studies. Attempts were made to study the musculature of the male genitalia in various tribes of Crambinae (see fig. 234). Very little information is available on the techniques for the preparation of the parts (see De Benedictis & Powell, 1989). Fresh or preserved (in 70% ethanol or Kahle's fluid) specimens are easier to study.

Early in the project, reared specimens had been kept frozen for the purpose of future studies such as these. Those fresh specimens were dissected in water or 30% ethanol after which they were washed in glacial acetic acid to remove the excess fat. Muscles were then stained with orseine in 70% ethanol for five minutes. After having been washed of excess stain in 70% ethanol, the parts were transferred to glycerin for study.

To study the muscles of dried specimens, I used a technique devised by P.T. Dang (pers. comm.).

1.-The whole abdomen is first placed in 30% ammonium hydroxide or 1% KOH for a few hours (about four hours in KOH), until it sinks to the bottom of the vial.

2.-Separation of the genitalia from the abdomen and removal of scales is made in 30% ethanol.

3.-The parts are then washed in glacial acetic acid for half-an-hour.

4.-The remaining of the procedure follows the previously explained one.

Preparations of specimens for SEMs. The antennae of at least one species of each genus were prepared for study with the scanning electron microscope. To ensure better photographs, the antennae, usually taken out of glycerin, had to be carefully washed in soapy water or in water mixed with a little bit of glacial acetic acid to remove all solid undesirable particles and greases. A sonicator was used to help in that endeavour. If the antennae came from a dry specimen, they were placed in a hot 10% KOH solution for 5-10 minutes for a complete maceration of the muscles and tendons that keep the antenna in an often improper position. The antennae were then dehydrated as described above for other body parts and soaked in xylene to remove all possible leftover greasy particles. In the liquids, the antennae were held flat and straight with microscope-glass pieces for easier positioning in the machine. The antennae were mounted in trios as shown in figure 341 and glued to the stud with conductive silver paint. This way of mounting, which I learned from Mr. Klaus Bolte (technician at the Canadian Department of Forestry, Ottawa) allowed positioning of the specimens prior to coating by rotating the L-shaped supports. The latter were made with no. 0 pins cut to one-third of their length. The bases were made of the cardboard of recycled folders. To minimize charging, specimens were coated with carbon and gold, sometimes more than once with gold.

2.4 Specimen examination, measurements and illustrations

In many genera, species can be identified with the wing pattern but a doubtful species' identification could usually be verified by brushing the scales of the last abdominal segments to reveal genitalic structures. Otherwise, dissections were performed.

Examination and description of the specimens were made with the help of a Wild M5A stereo-microscope equipped with 20X occulars. The measurements of the length of the palps and forewing were made with the same stereo-microscope but with 15X occulars and a built-in micrometer. The drawings of the genitalia and wings were made with the help of a Wild 1.25X camera-lucida attachment to the stereo-microscope. Details were added by examining the slides through the lenses of a Zeiss Jena binocular microscope. The first drafts of the drawings were made with pencils using 2H or 4H 0.3 mm leads. Final drawings were done on double-coated Mylar with Rapidograph drawing pens. Scanning electron micrographs were made with an AMRAY 1000 scanning electron microscope using Ilford FP4 film at 10 kv and sometimes 5kv if there was too much charging. The photographs of habiti and some body parts were taken by Bill Lukey of the Biographics Unit of Agriculture Canada. Mr. Lukey used the following set-up: a 35 mm Nikon F3 camera mounted on a Leitz Aristophot base, bellows, a 80 mm Leitz lens and diffused fiber optics light. The 100 ASA Kodak Technical Pan film was developed with Kodak Technodol for 15 minutes.

The illustrations of the antennal flagellomeres (figs. 33-75) show them with the ventral side at the top of the photograph. The position of the apical end of the antennae is variable but can be traced by looking at the direction of the sensillae and scales. The latter are often detached and only the empty antennal sockets are visible.

The line drawings of the head, wings, legs and tympanal organs are all mine. Many illustrations of the genitalia were made by M. Friedman for Dr. A.B. Klots and were lent to me by Dr. F.H. Rindge of the American Museum of Natural History, New York. These drawings have never been published. They were always verified with dissected specimens and modified if necessary.

The tympanal organs are illustrated in lateral and ventral views with only one side fully drawn in the latter case.

2.5 Description format and treatment of taxa

In the descriptions of genera and tribes, all North American species are taken into account except for the discussion on the antennal flagellomeres where I studied only one species for each genus.

In the descriptions of new species, the list of the type material was constructed by transcribing the information written on the labels directly except that: USA was mentioned in square brackets if omitted from the label, the altitude in feet was standardized with the use of the apostrophe, only the initials of the collectors were mentioned, the dates were standardized and the century added between square brackets if missing, county was abbreviated as Co., and US state names were abbreviated according to the list used by U.S. Postal Service. Finally, I did not specify if there was one or more labels on the pin.

Descriptions, keys and diagnoses were partially made with the help of DELTA (DEscription Language for TAxonomy), a standardized format for coding taxonomic descriptions invented in Australia by M.J. Dallwitz.

The procedure to obtain printed keys and natural language descriptions and diagnoses is as follows (briefly summarized).

1.- A matrix with taxa, characters and character states was written on paper.

2.- This information was coded in a characters file and an item (taxon) descriptions file. Word Perfect (version 5.0) was used to enter the data.

3.- A specification file is filled in with information on the maximum number of taxa, characters and states; types of characters; number of states per character; etc.

4.- With the format-conversion program (CONFOR), the data are checked for format errors and inconsistencies.

5.- With CONFOR again, the DELTA-format data were converted into formats required by the Natural Language description program (TONAT), the Key generating program (KEY), the interactive identification program (INTKEY) to produce the diagnoses, and PAUP (Phylogenetic Analysis Using Parsimony) program of D.L. Swofford. The outputs (key, descriptions and diagnoses) were printed using the text editor, in this case Word Perfect, version 5.0.

2.6 Terms

The nomenclature for general adult morphology largely follows Forbes (1923). The wing venation nomenclature follows the system adopted by Comstock (1940). The terminology associated with major areas of the wings and wing pattern was found in Covell (1984).

The terminology used to describe the tympanal organs was largely taken from Minet (1982, 1983, 1985) or derived from his work. The following terms were translated from French and are used here for the first time: transverse ridge, tympanic bridge, tympanic crest, tympanic drum, tympanic frame, tympanic pockets, and tympanic wings. Maes (1985) proposed latin terms for the above-mentioned structures but I found that it was not easy to relate the words to the structures. In the Glossary, these terms are defined and both Minet's (first) and Maes' (second) terms are mentioned in parentheses; if the terms were the same in the different nomenclatures, "idem" was used.

The terms employed for a discussion of the genitalia morphology were taken from Klots (1970b). Information concerning the antennal sensilla come from Schneider (1964) and Cornford et al. (1973). The terminology used to characterize the colours is taken from The Naturalist's Colour Guide (Smithe 1975).

2.7 Taxonomic methods

Sorting of specimens. Types were examined for 259 (86%) of the North American nominal species of Crambinae. The remaining species were identified with the collection and notes of Dr. A.B. Klots (AMNH). A reference collection was developed mainly from the material in the Canadian National Collection and specimens borrowed from various institutions, especially from the American Museum of Natural History, New York (AMNH). Dr. Klots' notes, which contained drawings of the male genitalia of most species of North American Crambinae genera (except

Diptychophora, Microcausta, Prionapteryx, Surattha and Mesolia) were kindly loaned to me by the American Museum of Natural History via Drs. F.H. Rindge and J.S. Miller, curators. On my request, the notes were sent to the American Museum by Dr. Klots (who had kept them at home until then) with the help of Dr. D.E. Wagner of the University of Connecticut, Storrs.

I studied and photographed the types of all North American crambines at the National Museum of Natural History, Washington, D.C.; the Philadelphia Academy of Sciences, Philadelphia; the American Museum of Natural History, New York; and the British Museum (Natural History), London (see Appendix V). Photographs of adults were made on 25 or 64 ASA Kodachrome slide film using a Yashica TTL camera mounted on a tripod and equipped with a ringflash unit and a 90 mm Tamron macro lens.

Species recognition. The aim of this work is to develop a better understanding of the systematic position of the crambine tribes and the relationships of the included genera. I did not try resolving problems such as the proper definition or identity of species in difficult species complexes (such as in Pediasia and Loxocrambus) that form obvious monophyletic groups. The latter were treated as single entities. Four distinctive species that were used in the phylogenetic analysis are here described as new.

Criteria for recognition of supraspecific categories. The genus, tribe and subfamily concepts adopted here follow the principles of phylogenetic systematics and are defined (following Wiley, 1981) as categories of the Linnean classification which contain one species, or monophyletic groups of species. A monophyletic group, in cladistic usage, is a group that includes an ancestor (known or putative) and all of its descendants (Wiley 1981). All supraspecific categories adopted here are believed to be monophyletic. If, however, some of them later prove to be paraphyletic, their limits should be reassessed to comply with the principle of monophyly.

Two new tribes and two new genera are proposed. The first phylogenetic analysis provided support for the erection of the new tribes. The new genera, included within the Crambini for which generic relationships are still obscure, were erected on the basis of the following considerations: 1) distinctness from other monophyletic groups, and 2) degree of intrageneric morphological difference. These considerations amount to an estimate of the morphological gaps and are the subjective part of taxonomic work. The only restriction on the use of gaps in a phylogenetic system is that they not be used to erect paraphyletic taxa (Wiley 1981). In the Crambinae, because many of the genera already in use are well defined, it was not difficult to decide that these two taxa needed to be given a formal status at the generic level.

Species examined. *Ingroup*. I selected 47 crambine species in 41 putative genera for my analysis. They are listed in Table 4. For the North American genera that I believe to be monophyletic, I studied the type species, when it was representative of the other species in the genus.

In genera not confined to North America, if the type species was not available, I chose a closely related North American species (as in *Catoptria*), or one that seemed to represent the "gestalt" of the group (as in *Agriphila*), or the only North American species in some cases (as in *Platytes* and *Chrysoteuchia*). Only the genus *Mesolia* Ragonot is not represented in my analysis because it is believed to form a single monophyletic group with *Prionapteryx* Stephens. In addition to these species, I included the species that Klots (1983) believed to be misplaced in the existing classification, except for a few which I was able to associate with recognized monophyletic genera (*Parapediasia bolterella* (Fernald), here transferred to *Thaumatopsis*; *Crambus quadrinotellus* Zeller and *C. albilineellus* Fernald, here transferred to *Fissicrambus*). Also, I decided to include one species for each of the type genera of the other three previously recognized Crambine tribes which are not found in North America, i.e. the Myelobiini, the Calamatrophini and the Ancylolomiini.

Species examined. *Outgroup.* The eight outgroup taxa (see Table 4) of the first analysis were chosen in the light of the following facts and constraints: 1- The outgroup of the Crambinae is not known and no well-supported sister-group hypothesis has been published; and 2- The Crambiformes form a well-supported monophyletic group (Minet 1985). It follows that one or more of the Crambiformes group(s) will most probably prove to be the sister-group of the Crambinae and that a representation of the diversity of these potential sister-groups is the best possible choice as an outgroup. When available I selected the type species of the eight Crambiformes subfamilies now recognized, other than Crambinae.

2.8 Cladistic methods.

My data set was first analyzed with the Hennig86 parsimony program written by Farris (1988, version 1.5). Of the 43 characters, only two, with three and four states, were multistates (see Appendix I). One is treated as additive and the other as non-additive. The multistate characters were binary coded which gave a matrix with a total of 47 codes (Appendix II). I searched for shortest trees with the mhennig* and bb* options of the program. The first option applies branch-swapping to a set of initial trees, retaining only one tree per initial tree swapped. The second option applies extended branch-swapping to the trees generated by mhennig* and retains all the shortest trees it can find, using all of the tree space available in the program. This resulted in an overflow of the tree space. This problem can be alleviated by increasing the tree space, lumping taxa, or deleting conflicting characters. I was able to try two of these three options. Firstly, I proceeded to remove from the analysis some of the characters that were the most incompatible with the others. This was done with a computer software package designed by Dr. M. Sharkey, Ottawa. After removing 11 and then 18 characters, the Hennig86 options mhennig* and bb* again caused an overflow of the available tree space of the program. There was no point in continuing this exercise. Secondly, since I was convinced of the monophyly of the Crambini, notably by virtue of the distribution of character 41, I decided to separate the analysis into two subsets of taxa.

In the first analysis, to resolve the tribal level relationships, all Crambini (except Thaumatopsis and Ancylolomia) were grouped into one taxon (called Crambus et al. on fig. 4). I ran this matrix with the mhennig* and bb* options of Hennig86. Unfortunately, the program was not able to give the same results one run after another and various irrelevant codes were appearing on the screen. The same data set was then analyzed using PAUP. I used the heuristic method called stepwise addition where taxa are connected one after the other to a developing tree until all have been placed. The addition sequence used is called "simple". This calculates a "distance", the advancement index (Farris 1970), between all taxa and a reference taxon possessing the ancestral state for each character. The taxa are then added to this reference taxon following the advancement index from closest to farthest. The outgroup chosen was the group of eight other crambiforme taxa and characters 6, 12, 25, 31, 32, 38, 43 were deactivated because their apomorphic state was not present in at least two members of the ingroup. This trial could not be completed because of insufficient memory; i.e. too many trees were generated. In the second trial, I deactivated character 14 because its multistate nature was thought to cause this massive number of trees to be generated. I used the same outgroup and the same stepwise addition sequence. The resulting trees were used to generate a consensus tree. The chosen tree is a majority-rule consensus tree on which are shown only the branches that are found in the majority of the trees. The majority limit is set at a chosen percentage. I chose a 75% majority-rule consensus tree (fig. 4).

In the second analysis, I wanted to resolve the relationships amongst the Crambini. Based on preceding trials, the only alternative to avoid an overflow of the memory space was to reduce the number of taxa. I first decided to remove the non-Crambinae taxa from the matrix on the basis that the Crambinae are monophyletic and that the sister-group of the Crambini must be looked for among the other Crambinae lineages. I used Hennig86 mhennig* and bb* options with this reduced matrix. I tried subsequent runs of the program by removing more of the non-Crambini taxa from the matrix. Although the trees obtained became shorter, there were more of them, which still caused an overflow of the memory space. When only three outgroup taxa are left, the resolution in the ingroup, as shown by a Nelson (strict) consensus tree, starts to disappear. I had no choice then but to generate a consensus tree based on a subset of all possible trees. I used the "n" option of Hennig86 to achieve this. In a Nelson tree, only the branches that are supported in 100% of the trees are shown. The outgroup chosen was Prionapteryx + Diptychophora + Argyria + Haimbachia + Diatraea + Chilo + Epina + Myelobia + Calamotropha.

2.9 The classification

The results of the cladistic analysis should ideally be transcribed literally into the classification. However, this usually results in very complex systems with names for each branching point. The classification presented here (Table 4) is based on the compromise devised by Wiley (1981) to overcome these problems. It is called an annotated classification. In this system, all clades of the same rank are similarly sequenced, the taxa of interchangeable position are annotated with "sedis mutabilis" and those of uncertain placement are annotated with "incertae sedis". This system was used in Lepidoptera systematics by Nieukerken (1986) and Scoble (1983).

3. CLADISTIC RESULTS

There is a high level of homoplasy with many characters as shown by several occurences of reversal or convergence in both analyses. Several characters were in conflict with each other (see discussion of placement of Ancylolomia below). I did not make the choice of weighting characters because I did not have a basis for deciding which ones should be given more weight. It is also a different approach because it is subjective. However, I suspect that in character-weighting lies one of the few avenues for a better understanding of the phylogeny of these moths. The details concerning the distribution of the character states are given in the character analysis section.

3.1 First analysis

In the first analysis I obtained 270 equally parsimonious trees of 91 steps. A 75% majority-rule consensus tree of these is presented as figure 4. A strict consensus tree would not have recognized the connection of Eufernaldia and Hemiplatytes to Prionapteryx + Pseudoschoenobius + Surattha because these connections are found in 87% of the trees. Similarly, the Haimbachiini would not have been recognized because 9% of the 270 trees show (an)other branching pattern(s) for this clade. Interestingly, 73% of the trees showed a sister-group relationship between a group including the Argyriini, the Crambini, the

Diptychophorini and Calamotropha to another group including the other Crambinae (Haimbachiini, Prionapterygini, Myelobia, Diatraea, Chilo and Epina). This pattern is generated by the distribution of the states of characters 19 and 20 which could not be polarized with certainty. I decided it was best not to recognize this branching pattern because the characters are too unreliable to demonstrate that the Argyriini and Diptychophorini are more closely related to each other, and to the Crambini, than to the other Crambinae. The morphology of the tympanal organs may not be truly homologous among all taxa in which it looks similar. Thus, even though in theory all lineages in the Crambine polychotomy in the first tree are of interchangeable position, this pattern possibly represents real affinities between taxa.

The first tree (figure 4) is the closest to the currently accepted classification of the Crambinae. I believe that until a better representation of the world fauna and of life stages other than the adults are thoroughly analysed, it is best to remain conservative.

My analysis of the crambine lineages does show some interesting results. The monophyly of the Crambinae is supported by three synapomorphies (characters 18, 21 and 30), of which two are recognized for the first time. The monophyly of the Crambini is also supported by three synapomorphies (characters 15, 27, 41) of which one is recognized for the first time.

The traditional grouping called Chilonini (see Klots 1970a, 1983) was not recognized as being monophyletic. Five genera originally placed in the Chilonini are here placed in the Haimbachiini new tribe (type-genus Haimbachia Dyar) based on the presence of a newly discovered character-state (character 36).

The Ancylolomiini were found to be paraphyletic and Ancylolomia to belong with the Crambini. This is based on the shared presence of the derived character-states of the following characters: 11, 15, 28, 41. On the other hand, Ancylolomia shares the derived states character 16 and 29 with some members of the Prionapterygini. In addition, the orientation of the tympanum at 90° from the sternal plane (another possibly derived character state), is found in Ancylolomia, the Prionapterygini, but also Diatraea and Epina. Rather than being subjective about the relative importance of these conflicting characters, I prefer to rely on the results of the first cladistic analysis which shows the affinity of Ancylolomia with the other Crambini in all 270 trees. Surattha, Prionapteryx, Pseudoschoenobius, Mesolia and Eufernaldia, all placed in the "Ancylolomiinae" by Munroe (1983) are here placed in a new tribe, the Prionapterygini (type-genus Prionapteryx Stephens) along with Hemiplatytes formerly in the Chilonini (Klots 1970a, 1983). The monophyly of the Prionapterygini is supported by two newly discovered apomorphies (characters 4 & 5).

Myelobia (shown here amongst the Crambinae "incertae sedis") was placed with the Oriental genus *Eschata* in the Myelobiini by Minet (1985) on the basis of their shared bilobed praecinctorium, a unique feature among Crambinae. I cannot comment on this decision since I haven't studied *Eschata*. *Myelobia* is here found to be most closely related to *Diatraea* but this is based on the distribution of homoplasious characters.

Concerning *Calamotropha*, Gaskin (1988) might have been right in erecting a monobasic tribe for this genus as shown by its position in my analysis. However, its closest relatives might not be among the taxa analysed here. Also, to erect the genus to tribe level would imply that the same should be done for *Chilo* and *Epina*, which, in my opinion, would be premature.

I have also discovered two possible synapomorphies to unite the Diptychophorini (characters 7, 8). The apomorphic state of character 10 also unites the Diptychophorini but it occurs several times in other Crambinae and is not a very reliable character.

The Argyriini, as shown on the cladogram, is not recognized as monophyletic by the analysis. I have nevertheless decided to leave *Argyria*, *Vaxi* and *Urola* in the Argyriini and to retain this grouping in the classification because the phenetic similarity of these three genera is striking and is, I believe, the result of common ancestry.

3.2 Second analysis

The second analysis was aimed at resolving the relationships among the lineages of Crambini. The number of trees generated by this analysis (more than 2000) was more than the available memory capacity of this version of Hennig86. A consensus tree of all these trees is not a valid consensus since all the trees that the program would generate if there was no limit of memory space are not available. This partial consensus tree recognized neither the monophyly of the Crambini nor that of the genus *Almita*, both based on solid, non-conflicting synapomorphies. Because of these artifacts and computer-software problems, I decided to present a modified version of the Nelson tree (figure 5) which shows the monophyly of the Crambini and that of *Almita*. The tree also recognizes the monophyly of the *Agriphila* assemblage with four genera and the *Raphiptera* assemblage with two genera. I also decided to recognize the association of four species in the genus *Parapediasia* on the basis of the shared presence of the derived character-state of character 32. This contradicts the association of *P. decorella* with the *Agriphila* assemblage in earlier analyses of this data set but it is probably just as good a solution given the plasticity of the characters involved. Again, based on earlier versions of my analysis of this data set, and based on the distribution of character-states of characters 11, 13, 14, 38, and 43, I decided to show that Euchromius and Platytes are probably the sister-lineages of the rest of the Crambini.

4. ANALYSIS OF MORPHOLOGICAL CHARACTERS

The following is a list of all the characters which were considered in the cladistic analysis. These are arranged in the sequence of their tagma and position on the tagma. For each character I discuss the observed variation, list the states recognized and examine character state distributions. A total of 43 characters were judged to be informative for an analysis. Many potential characters were rejected. I discuss the reasons for these decisions to contribute to an overview of the morphology of the moths. A list of the characters used in the analysis is given in Appendix I. The data matrix is given in Appendix II.

4.1 FEATURES OF THE HEAD

Some features of the head have traditionally been prominent in the diagnosis and classification of the Crambinae; for example, the length of the labial palpus or the shape of the maxillary palpus. Another character, the produced fronto-clypeus (figs. 7, 10, 11, 17, 20-23), is sometimes diagnostic for an entire genus (eg. Prionapteryx, fig. 21 and Forbes 1923) but most often is present only in some of the included species of a genus (eg. Haimbachia, Capps 1965; Agriphila, fig. 27 and Bleszynski 1965; and Chilo, fig. 23 and Bleszynski 1970b). The produced fronto-clypeus is believed to be an adaptation for dry habitats with hard soil. It is thought to assist the adult to break through the surface upon emergence from its subterranean pupal retreat in the soil (see Miller 1991 for a review). The antennae of all Crambinae are sexually dimorphic but this is not the case for the labial palps (five taxa examined) or the shape of the fronto-clypeus. The eyes of all Crambinae are rather large and little variation in size or shape was observed. With scanning electron microscopy, it can be shown that the eye surface of Crambus and Agriphila (fig. 29) contains interfacetal microsetae. These are present in many Ditrysian families (Davis 1986) and are sometimes greatly enlarged and of some taxonomic value (see Miller 1991). I suspect that they are present in all Crambinae as shown in Crambus and Agriphila. All species examined have chaetosemata (fig. 28). The haustellum of most Crambinae is long and apparently functional. It is however slightly reduced in Thopeutis (fig. 22) and Occidentalia (fig. 11). This probably represents a synapomorphy for these two taxa since these are shown to be sister-genera by the shared presence of state 1 of character 39. The haustellum is very much reduced in Eufernaldia (fig. 7). It would be interesting to perform more SEM work on the proboscis of the Crambinae because there could be some characters of surface sculpturing or different types of sensillae to be found, as have been discovered in the Notodontidae (Miller 1991). I was not able to do this myself because of time constraints.

Labial palpus. The long labial palpus of the Crambinae has traditionally been a character of choice for the diagnosis of this subfamily. Forbes (1923) mentions that it is two times as long as the head and Holloway et al. (1987) state that it is typically very long and porrected straight forward often extending three times eye width. This study is the first attempt to measure this variation. The vestiture of the labial palpus is variable as shown in figures 25, 27 and 31. The dishevelled condition exhibited by Agriphila vulgivagella (Clemens) (fig. 27) is not typical of that genus. This is also found in Chilo erianthalis Capps.

Length of labial palp segment III. The length of this segment was compared to that of the first because the length of the latter remains rather proportionally constant throughout all Crambinae. This character was studied for potential cladistic value. The ratios between the two measurements are given in Appendix IV (character 47). It was divided into two states. The first included taxa with the third segment shorter or equal to 80% the length of the first, while the second included taxa with the third segment equal in length or longer than the first. The first condition is expressed in Prionapteryx (fig. 21), Diptychophora (fig. 16), Urola (fig. 12), Argyria (fig. 15), Myelobia (fig. 9), Haimbachia, Epina and in six of the eight outgroup taxa. The second condition occurs in the remaining two outgroup taxa (Donacaula and Pyrausta) and in all other Crambinae. If plotted on a diagram, the data show a normal distribution. This is why the character was removed from the analysis. It is to be noted that I found the third labial palp segment to be 11.7% longer on one side in a specimen of "Crambus" dimidiatellus Grote (dissection no. BL 115).

Length of the labial palp segment II. The length of the second labial palp segment was also compared to that of the first. The distribution of the ratios (Appendix IV, character 48) prompted me to divide this character into two states. The second labial palp segment is shorter than two times the length of the first (state 0) or equal or longer than 2X the length of the first (state 1). Most Crambinae have their second labial palp segment at least two times the length of the first with the exception of Argyria (fig. 15), Urola (fig. 12), Myelobia (fig. 9), Microcrambus, Almita and Catoptria. Six of the eight outgroup taxa also fall into the first category (state 0). Following the analysis of these data, I was inclined to treat this state as a synapomorphy for the Crambinae with a few reversals and two parallel occurences but again the data cannot be divided into discrete classes and the character was removed from the analysis. Several Crambinae have the second labial palp segment more than four times the length of the first which results in extremely long palpi; examples are Calamatropha (fig. 20), Eufernaldia (fig. 7), Chilo (fig. 23) and Neodactria (fig. 24).

Overall length of the labial palpus. The distribution of the states of this character follows that of the preceeding character very closely. Again I divided the character into two states which expressed short and long palpi. The total length was compared to that of the vertical diameter of the head where it reaches a maximum, i.e. usually on the vertex posteriorly. The palpi were estimated to be short if they were less than 1.5 times the length of the vertical diameter of the head. They were considered to be long if they reached a length of 1.5 times or more that of the vertical diameter of the head. The ratios obtained are given in Appendix IV (character 49). As for the preceeding character, the long labial palpus was considered a synapomorphy for the Crambinae with a reversal once in *Argyria* (fig. 15) and *Urola* (fig. 12), in *Euchromius* (fig. 17) and also in *Myelobia* (fig. 9). The character also shows convergent evolution with regards to two outgroup taxa, *Donacaula* and *Scoparia*, because, as opposed to the six other outgroup taxa, these fell into the second category. However, the values did not fall into discrete classes and the character was removed from the cladistic analysis.

The adaptive significance of the presence of elongate palpi in these groups is probably similar. Crambine moths in repose usually sit along grass blades or stems. Grasses (Poaceae) are the foodplant and grasslands the habitat of most Crambines. Their elongate shape (enhanced by the long labial palpi) presumably contributes to give them a good camouflage and hence an advantage over potential predators. Nothing is known of the natural history of the Argyriini except that *Urola nivalis* (Drury) occurs in grasslands (Forbes 1923). I have collected that species and species of *Vaxi* and *Argyria* at light where more-or-less open grassy areas were present. The species of *Myelobia* have been associated with bamboos (Forbes 1926). The large size of these moths and the presence of long palps may not be evolutionarily compatible but only natural history observations will help to solve this problem.

Maxillary palpus. The Crambinae have elongate and apically tufted maxillary palps which are diagnostic for the subfamily; see for example Bleszynski (1965), de Joannis (1932), Forbes (1923), Hampson (1896) and Okano (1962). This study is the first attempt to document their variation in shape and length and to compare actual measurements with that of other Crambiformes. Two characters were recognized; the shape, and the length of the palpus. The adaptive significance of having long and tufted maxillary palpi is here believed to be associated with camouflage. The apical scales on the maxillary palps of Crambinae perfectly fill the space between the fronto-clypeal scales and the labial palp scales (figs. 25, 27, 31), hence contributing to their perfect elongate shape in their grassy habitat.

Character 1. Shape of the maxillary palpus. Taxa without an apical scale-tuft on their maxillary palpus received a score of 0 while those with such a scale-tuft were attributed a score of 1. The presence of a scale-tuft is found in all Crambinae (see for example figs. 25, 27 & 31) and in Cybalomia, Donacaula and Scoparia. The five remaining outgroup taxa do not have an apical tuft of scales on the maxillary palpus; these are simply covered with one layer of small scales. In the first analysis, the apomorphic state of this character occurs only once to combine Cybalomia, Donacaula and Scoparia with the Crambinae. However, it is possible that the presence of an apically tufted maxillary palpus is a synapomorphy for the Crambinae and that its presence in the other three genera is the result of convergent evolution.

Character 2. Length of the maxillary palpus. The length of the maxillary palpus was compared to the vertical diameter of the head "d". After all measurements were made, I found that the distribution of the ratios (shown in Appendix IV, character 51) perfectly followed the distribution of the two states of the shape of the maxillary palpus (character no. 1) if the limits between the two sets of data were set at less than 2.5 and more than 2.7. Characters 1 and 2 were not combined because the length could not be measured in a few species due to a lack of specimens available for dissection, whereas the shape could be seen in all species. The moths were considered to have a long palpus and given a score of 1 if "d" was less than 2.5X the length of the palpus. They were considered short and given a score of 0 if "d" was more than 2.7X the length of the palpus. The distribution of the states of this character in the first analysis match perfectly that of the preceeding. Consequently, the same conclusion as mentioned above is applicable here.

Ocellus. The presence in the adult of a pair of lateral ocelli belongs to the lepidopteran groundplan (Kristensen 1984). The authors (Forbes 1923; Okano 1962) who have written about Crambine ocelli stated that they are most often present, which is corroborated here. The ocelli of moths are important in detecting ambient light levels to finely tune the timing of flight at the onset of night (Eaton et al. 1983).

Character 3. Ocellus present or absent. As shown by the distribution of the two states of this character in the combined outgroup of the first analysis, the presence of well-formed ocelli is plesiomorphic in the Crambinae; this trait was given a score of 0. The absence of ocelli received a score of 1. This condition is observed in five Crambinae taxa; Myelobia (fig. 9), Diptychophora (fig. 16), Occidentalia (fig. 11), Calamotropha (fig. 20) and Diatraea. It is believed to be constant in Diatraea (Bleszynski 1970b) but rot in Calamotropha (Bleszynski 1961a). This character is highly homoplastic in the Crambinae and is used by the first analysis to partly support the monophyly of Myelobia + Diatraea. It is to be noted that some species of Crambinae have the ocellus reduced in comparison to other species (figs. 22 & 23).

Antennae. The antenna of Crambinae has never been investigated for potential taxonomic characters. The antennae of 41 species of Crambinae were examined with the scanning electron microscope. I was interested to see if there were consistent variation in the shape and size of the segments, in the sensilla types and numbers, and in the microsculpture of the flagellomeres' surface. The results of these investigations are shown in Appendix III and some antennal segments are illustrated in figures 33 to 75. For the sake of consistency, only male antennae were compared and I tried to always photograph the side view of the 15th flagellomere. The crambine antennae were compared to those of Ostrinia nubilalis (Hübner) (Pyraustinae) based on the results obtained by Cornford et al. (1973); this species was considered to be similar to my outgroup species Pyrausta unifascialis (Packard) and replaced it for antennal characters on the matrix. The antennae of the other outgroup taxa were not examined with the scanning electron microscope due to time constraints.

The female antennae are simple (fig. 56) and their flagellomeres longer than those of the males. The male antennae are usually laminate but are bipectinate in some species of Thaumatopsis (fig. 52), in most Prionapteryx species (fig. 67) and in Surattha. They are simply pectinate in some Thaumatopsis (fig. 50) and Ancylolomia species and more-or-less strongly serrate in some other Thaumatopsis, Parapediasia torquatella n.sp. (fig. 43), Pseudoschoenobius (fig. 66), Myelobia (fig. 71) and some Ancylolomia. Apart from other variation in the size and shape of the flagellomeres, which can be seen on figures 33 to 75, there is variation in the numbers of sensilla of different types. No conclusions were drawn from this variation because my method of investigation was not rigorous enough. To have a good estimate of the true variability in sensilla types, numbers and positions, the antennae of many specimens must be examined to determine the degree of variation between segments on the same antenna and between specimens for the same segments. In the following discussion of the types of sensilla found in Crambinae, the numbers refer to the sensilla seen on the side of the flagellomere photographed.

The sensilla coeloconica (fig. 59) are peg-like and recessed in a cuticular pit which may or may not be fringed with pegs. Usually they are few in number (one to five) but in some species like Parapediasia decorella (fig. 45) they are high in number and widely dispersed while other species seem to have none (see Character 4 below). Interestingly, the simply pectinate Thaumatopsis floridella (fig. 50) has no sensilla coeloconica on its pectinations while the bipectinate T. pexella (fig. 52) has many on each pectination. Also interesting is the illustration, albeit incomplete, of these sensilla, then called sense pits, by Fernald (1896).

The sensilla trichodea (fig. 58) are hairs without any specialized basal cuticular ring serving as an articulating membrane. They are the most abundant sensilla in all species of Crambinae examined, with numbers generally around 30 to 50. Urola nivalis (fig. 63), however, has at least 200.

The sensilla chaetica (fig. 57) are similar to the preceeding type of sensillum but do have a cuticular ring at their base. They are usually very few in number (one to three) but one species, Raphiptera argillaceella (fig. 41) has 15 to 20.

Most species also have a sensillum styloconicum (fig. 46) at the apex ventrally. These are sensory cones situated at the apex of an elevation of the cuticle. Sensilla auricillica (fig. 33) are also present in some species. These are similar to sensilla chaetica but are typically more blade-like and with a concave surface. Some structures, which I believe have not previously been documented, were found in Microcrambus elegans (fig. 44). They look like deflated round sacs. Finally, a large sensory pit (possibly a modified sensillum coeloconicum) was discovered in some Crambini taxa (see character 6), an aschoid sensillum was observed on the pectination of Prionapteryx serpentella (fig. 69) and variation was found in the structure of the cuticle (see character 5).

Character 4. Sensilla coeloconica present or absent. Most Crambinae examined, as well as Ostrinia nubilalis (see Cornford et al. 1973), have at least one sensillum coeloconicum on each flagellomere (state 0). Three taxa seem to have lost this type of sensillum (state 1). They are Hemiplatytes prosenes (fig. 65), Prionapteryx serpentella (fig. 67) and Pseudoschoenobius opalescalis (fig. 66). The loss of this type of sensillum in these three taxa is considered apomorphic. The consensus tree based on the first analysis (fig. 4) indicates that the apomorphic condition evolved in the ancestor of the Prionapterygini and that a reversal occurred in Eufernaldia. It would be interesting to verify if this condition occurs in Surattha for which the antennae were not examined due to a scarcity of specimens.

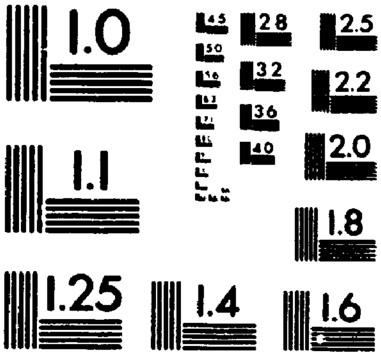
Character 5. Mosaic pattern on flagellomeres present or absent. Most Crambinae and Ostrinia nubilalis (see Cornford et al. 1973) have a mosaic or honeycomb-like pattern on the surface of the flagellomeres' cuticle (state 0). This cuticular pattern was first noted by Fernald (1896) on Crambus laquaetellus Clemens. It is absent at various degrees in the following species: Hemiplatytes prosenes (fig. 65), Prionapteryx serpentella (fig. 67), Eufernaldia cadarella (fig. 68), Thaumatopsis pexella (fig. 52), T. floridella (fig. 50) and Pseudoschoenobius opalescalis (fig. 66). In the first analysis, this character supports the monophyly of the Prionapterygini. A parallel occurence is shown in Thaumatopsis. It is with caution that this character state is used as a synapomorphy for the Prionapterygini since Surattha was not examined and Thaumatopsis species have also lost the mosaic pattern, which may mean that the devel^pment of pectinations causes that pattern to disappear.

Character 6. Large sensory pit on flagellomeres present or absent. This structure, which is probably a magnified version of the smaller peg-fringed sensillum coeloconicum of the other species, is present (state 1) only in some species of Fissicrambus (for example F. fissiradiellus fig. 61) and in Parapediasia teterella (fig. 57), all of which are members of the Crambini. It is usually visible with a good dissecting scope at 25X. All other Crambiformes examined lack this structure (state 0). This character was deactivated in the first analysis. I interpret the presence of this structure as a synapomorphy for Fissicrambus, although three species do not have it as shown by F. minuellus (fig. 60), with a parallel occurence in P. teterella.

Character 7. Apical scales on flagellomeres appressed or erect. The majority of the Crambiformes examined, including the outgroup taxa, have the scales on the antennal flagellomeres appressed on the segments (see

2

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT



figs. 40, 41, 47, 49, 55) (state 0). In some cases however, the tips of the scales are slightly upturned. In Prionapteryx and Thaumatopsis, because of the presence of pectinations, some lateral scales are erect. In Diptychophora (fig. 72) and Microcausta (fig. 73), the second row of scales on each flagellomere, starting with the 12th, is directed at about 45^0 upwards from the horizontal plane (state 1). Basal to the 12th flagellomere, the scales are appressed. This synapomorphy, recognized here for the first time, unites the members of the Diptychophorini.

4.2 FEATURES OF THE THORAX

The only thoracic structures used by previous workers to diagnose and classify Crambinae are the wings (see for example Fernald 1896, Hampson 1896, Forbes 1923, Zimmerman 1958, Okano 1962, and Bleszyski 1952 et seq.). The use of wing venation variation was prominent in the classification established by Hampson (1896). Because of these previous studies, I have made the wing venation a priority in my studies of the thorax. I also looked for possible taxonomical characters in the exoskeleton, the endoskeleton and the legs (figs. 131-134) of most species analyzed but I found little information of taxonomic value.

One interesting leg feature is the presence of an exocrine coxal gland associated with thin long scales in the foreleg of Chilo phragmitellus (Hübner) (fig. 131). This gland was not found in other Chilo species but I did not dissect their legs. So the presence of the gland in other species of Chilo should not be ruled out as the gland may be less visible than in C. phragmitellus. It is possible that this gland bears some importance to the reproductive biology of other species of

Chilo, which are serious pests of sugar cane.

I did not investigate the structure of the post-tarsus nor the wing base sclerites of Crambinae but these two character sets could have valuable taxonomical information.

Wings. For comparisons' sake, the wing venation of the eight outgroup taxa is illustrated on figures 123 to 130. The forewings of the Crambinae are generally characterized as being long and narrow, while the hindwings are broad but there are notable exceptions, especially in forewing shape. The forewing outer margin is variable in shape; it may be straight (figs. 97, 98), convex (figs. 87, 91, 103, 106), or slightly to markedly concave (figs. 115, 119, 121). In the latter case, the apex is often produced, as in Fernandocrambus (fig. 86). The long winged species fold their wings around the body in repose so as to look almost cylindrical. The larger winged species, at least the Argyriini, hold their forewings in a triangular fashion over their body like many other moths.

The crambine wing venation is the same as in many Ditrysian Macrolepidoptera and comprise 12 veins in the forewing and ten in the hindwing. Some species have lost a number of veins, presumably associated with a loss in wing surface area (see characters 10, 12, 17). The forewing subcostal vein is sometimes connected with R1 but no pattern of character distribution was discovered. The end of the forewing discal cell is always closed by the presence of a complete or incomplete cross-vein. The hindwing cell varies in this respect (see character 15). I hypothesize that the adaptive significance of these losses of veins is related to the narrowing of the forewings and ensures better folding of the wings for camouflage purposes.

The fore- and hindwings are coupled with a frenulum located at the base of the hindwing and a retinaculum at the base of the forewing ventrally (figs. 126, 172). The frenulum is always simple in Crambine males but often multiple in the females (see Character 14). The retinaculum is often a double structure. A series of short hairs located at the base of the fold line between M+CU stem and the Anal vein always support the frenulum. A hook of scales also holds the frenulum from above in some species (see Character 13).

Character 8. Forewing less than 2.0X longer than wide or more than 2.1X longer than wide. The Crambinae are generally known for their elongate forewings. To assess this variable, I measured the length of the forewing and compared it with its width at the widest point (between the end of the cell and the apex). This gave a series of ratios presented in Appendix IV (character 50).

I had originally intended to use this character to demonstrate the monophyly of the Crambinae by setting a limit between the two categories of values at 2.4. This shows that most Crambinae (except the Diptychophorini, Argyriini and <u>Microcrambus</u>) have more elongate wings than most other crambiforme taxa (five of the eight outgroup genera) but the ratios could not be separated into discrete categories.

It was found that the Diptychophorini (figs. 90, 91) have their forewing less than 2.0X longer than wide (state 1) while all other Crambiformes (except <u>Glaphyria</u>, fig. 127) have theirs longer than 2.1X its width (state 0). This gap is not very large but the examination of more taxa will hopefully prove that it is useful to isolate the Diptychophorini together. This character state is believed to represent a synapomorphy for this tribe.

Character 9. Forewing outer margin produced at M1-M2 or not produced in that sector. In some Crambini the forewing apex is slightly produced and there is also a slight hump on the outer margin at M3 (figs. 85, 114, 115). In Prionapteryx (fig. 100) and Pseudoschoenobius (fig. 122), the forewing outer margin at M1-M2 is more or less produced (state 1). The apomorphic state is believed to be a synapomorphy for these two taxa.

Character 10. Forewing radius with five veins, or missing one or two veins. All outgroup taxa examined have a full complement of five radial veins in the forewing (state 0). Various Crambinae have lost one (or rarely two) veins in that sector (state 1). The apomorphic state is found in Raphiptera (fig. 119) + Almita (figs. 92, 96), Platytes (fig. 94), Loxocrambus (fig. 85) and Diptychophora (fig. 91) + Microcausta (fig. 90). The loss of veins in that sector is considered to be a synapomorphy in those monophyletic groups with caution for two reasons: 1- It is difficult to determine if the vein losses are homologous; 2- The loss sometimes does not occur in all specimens of a given species. In Argyria nummulalis (fig. 77) and E. cadarella (fig. 103), I did not illustrate R3 because it wasn't present on the wings I mounted, but other specimens possessed it although it was very small. I thus gave a score of 0 to these taxa. Intrageneric variation was found in two genera as shown by Platytes vobisne (fig. 94) versus P. alpinella (Hübner) (in Bleszynski 1965: 394) and Microcrambus elegans (fig. 95) versus M. biguttellus (fig. 93). Only Raphiptera argillaceella (fig. 119) has lost two forewing radial veins. I believe the missing veins in this species are R3 and either R2 or R4 but it is not impossible that other veins are involved. In Almita, Loxocrambus and Microcrambus biguttellus it seems to be clear that R3 is the missing vein. The same is probably true for the Diptychophorini for which this character is a synapomorphy for the tribe.

The tendency to loose one of the radial veins is probably linked with one of these three factors: 1- the reduction in size of the moths (Almita, Raphiptera, Platytes, Diptychophorini), 2-the lenghtening of the wing (Eufernaldia) or, 3- the truncation of the wing apex (Loxocrambus).

Character 11. Forewing R5 free or stalked with R4. The fifth radial vein in the forewing was found to be free from the other radial veins, i.e. connected directly with the end of the cell, in all out-group taxa. The Crambinae which possess that state of the character were thus attributed a score of 0. A score of 1 was given to the taxa with vein R5 forming a common stem with the next radial vein, usually R3+R4. This condition occurs in all Crambini except in Euchromius (fig. 89), and Platytes (fig. 94). It has occurred independently in Eufernaldia (fig. 103), Vaxi (fig. 79) and Calamotropha (fig. 82). In the first analysis (fig. 4), the apomorphic state occurs four times. It contributes to support the monophyly of the Crambini except Euchromius and Platytes (see fig. 5).

The apomorphic state of this character was used by Gaskin (1975a) to separate the Crambini into two subtribes (see fig. 3) and to define the subtribe Crambina. The other subtribe, the Corynophorina, was partly defined by the dorsally coalesced female papillae anales, which is here found to be plesiomorphic in the Crambinae (see character 41).

Character 12. Forewing Cubitus with one or two veins. In most Crambinae, as well as in the outgroup species examined, the forewing Cubitus has two veins CuA1 and CuA2 (state 0). The loss of one of these two cubital veins (state 1) occurs twice in the Crambinae, once in Eufernaldia (fig. 103) and again in Almita (figs. 92, 96) + Raphiptera (fig. 119). As shown by the second analysis (fig. 5), the loss of one cubital vein is considered to be a synapomorphy for Almita + Raphiptera with a parallel occurence in Eufernaldia. This character was deactivated in the first analysis because it occured in only one terminal taxon.

Character 13. Male frenulum hook present or absent. The frenulum hook (figs. 126, 172) is the most common form of subcostal retinaculum in the Lepidoptera and is present in numerous families (Braun 1924). It is a chitinous double-walled outgrowth from the forewing which in the Crambinae arises from the Subcostal vein. The frenulum hook is rare in moth females in general (Braun 1924) and apparently entirely absent in female Crambinae.

In the Crambiformes analyzed here, the structure is present in five of the eight non-crambine taxa and several Crambinae (state 0). It is absent (state 1) in Cybalomia, Donacaula, Scoparia, Surattha, Diptychophora, some Hemiplatytes (scored ?), Diatraea, Epina and all Crambini except Euchromius, some Agriphila and some Catoptria. In the second analysis, the absence of the frenulum hook contributes to isolate Euchromius from the rest of the Crambini. The adaptive significance of the loss of the frenulum hook is unknown but may be related to the way the wings are folded in repose.

Character 14. Female frenulum bristle number 1, or 2, or 3, or 4 and more. This character was treated as unordered (non-additive) because state changes sometimes occur in the same genus (e.g. Eoreuma) and so are likely to occur many times from one genus to another towards a reduction or an increase in bristle number. Once binary coded, it is represented by four codes (1000, 0100, 0010, 0001). The plesiomorphic condition of this character is unknown because the outgroup taxa examined here exhibit all four states without significant importance of one state over the other (see matrix, Appendix II). The presence of one frenular bristle (code 1000) was used by Ragonot (1890) to segregate the Ancylolomiinae. This condition is present in Eufernaldia, Surattha, Prionapteryx, Pseudoschoenobius and Ancylolomia, all formerly placed in the Ancylolomiinae. It also occurs in Cybalomia (Cybalomiinae), Donacaula (Schoenobiinae), some Eoreuma and 17 genera of Crambini. The other three states of this character are even more homoplastic than this so their value for inferring phylogenetic relationships are limited. The character was deactivated in the first analysis because it was creating too many conflicts. It was interesting to find one specimen of Crambus saltuellus Zeller with two frenular bristles on one side and three on the other. This phenomenon had also been reported by Bleszynski (1965).

Character 15. Hindwing cell closed or open. The hindwing cell was found to be closed by cross-veins in all members of the outgroup (figs. 123-130). Thus, Crambinae taxa which possess this condition were given a score of 0. Crambinae with the open cell character state were attributed a score of 1. The cell is open in Epina (fig. 109), the Argyriini (figs. 77, 79, 108), the Haimbachiini (83, 97-99, 102) and in the Crambini

(76, 78, 80, 81, 84-89, 92-96, 110-121). The first analysis shows that the apomorphic condition appeared independently in these four taxa and contributes to support their monophyly independently. It should be noted that Munroe (1972), in his key to the subfamilies of Pyralidae, mentioned incorrectly that all Crambinae (excluding Prionapterygini) had an open hindwing cell.

Character 16. Base of hindwing M1 closer to middle of cell or closer to Sc. In the crambiforme hindwing, the first medial vein (M1) is often connected basally with the fused stem of the Radius and the Subcosta or it is separated from this by a small cross-vein (state 0). In a few Crambinae, the point of origin of the first medial vein is closer to the middle of the cell than it is to the Sc + R stem (state 1). This condition occurs in Prionapteryx (fig. 100), Pseudoschoenobius (fig. 122), Eufernaldia (fig. 103), Ancylolomia (see Bleszynski 1965: 401), Surattha (see Bleszynski 1965: 437) and Microcausta (fig. 90). This condition is not found in the other crambiforme taxa examined which indicates its probable apomorphic nature. The apomorphic state here partly supports the monophyly of the Prionapterygini without Hemiplatytes. It should be noted that the base of the hindwing M1 in Diptychophora (fig. 91) is also well separated from the Sc + R stem but not enough however to be coded as apomorphic here. Since the Diptychophorini wing vein data were taken from Bleszynski (1966), who may not have made his drawings from wings mounted on slides, I remain uncertain about the variation of this character in these taxa.

Character 17. Hindwing M2-M3-CuA1-CuA2 all present or missing one vein.

The outgroup taxa all have the full complement of veins M2-M3-CuA1-CuA2 (state 0). Most Crambinae also have these four veins. The loss of one of these veins in that sector (state 1) is believed to be a synapomorphy for the Prionapterygini (tigs. 100, 122) without *Eufernaldia* (fig. 103) and *Hemiplatytes* (fig. 101), and for *Almita* (figs. 92, 96) + *Raphiptera* (fig. 119). It also occurs in *Microcausta* (fig. 90 and Gaskin 1987). In the latter genus, Gaskin (1987) mentioned that the lost vein is M2. Bleszynski (1965) arrived to the same conclusion regarding *Surattha* and *Prionapteryx*.

Character 18. Hair tuft on hindwing Cu stem present or absent. Long hairs are always found on the dorsal surface of the Crambiforme hindwing (fig. 122). These are found on the veins and on the membrane between the veins except in most Crambinae which have hairs only on the veins. Crambinae with hairs between the veins are *Myelobia*, *Ancylolomia*, *Pseudoschoenobius*, *Surattha*, *Epina*, *Chilo*, *Thopeutis* and some species of both *Prionapteryx* and *Diatraea*. The Crambinae, with the exception of *Microcausta*, all have a series of long hairs on the hindwing Cubital stem below the cell (state 1). This condition was found to be less obvious in *Myelobia* and *Epina* because they have long hairs over all of the wing base, and in *Platytes vobisne* and *Almita texana* presumably because it was more difficult to see in those smaller moths. This could be the same situation for *Microcausta* for which I had no specimens in good enough condition to examine. State 1 is also present in the Phycitinae and Anerastiinae (Pyraliformes) (de Joannis 1932), which presumably represent a convergence given the well established monophyly ot the Pyraliformes and the Crambiformes. State 0, the absence of the Cubital hair tuft is found in all Crambiformes other than Crambinae. Several authors have used the presence of these hairs as one of the main criteria to recognize the Crambinae (Fernald 1896, Hampson 1896, Forbes 1923, de Joannis 1932, Zimmerman 1958, Okano 1962, Bleszynski 1965, Munroe 1972 and Holloway _et al_. 1987). The character was apparently discovered by Lederer according to Ragonot (1890). The presence of these hairs is here considered to be a synapomorphy for the Crambinae. Bleszynski (1965) referred to these hairs as a "basalwärts gerichteten Haarkamm" which literally means "basal stopper directed hair comb". Whether the structure actually functions has a stopper, presumably to the forewing, is unknown.

4.3 FEATURES OF THE ABDOMEN

The abdomen of the Crambinae has eight visible tergal plates and seven sternal plates due to the fusion of segments I and II ventrally. The main features discussed below are the tympanal organs ventrally on segments I-II and the genitalia.

Tympanal organs. It is now widely accepted that the tympanal organs of moths probably evolved originally to warn them of impending bat attacks (Fenton & Fullard 1981). It has also been demonstrated that various species of Odontiinae (Crambiformes) and Galleriinae (Pyraliformes) have secondarily evolved intraspecific communication systems that use sound signals to which the ears are sensitive for mating purposes (Spangler 1988). To my knowledge, evidence of defensive behaviour using sounds or intraspecific sound communication in Crambinae has not been published. However, studies conducted at York University, North York, Ontario, by

Dr. Brock Fenton and Miss Lella Dal Ferro have shown that moths of *Chrysoteuchia topiaria* (Zeller), when submitted to ultrasonic pulses of the same frequency as the one used by a local bat species respond by using four types of evasive flight behaviours (L. Dal Ferro, pers. comm.).

Detailed morphological studies of the pyralid tympanal organs have been documented by Maes (1985) and Minet (1982, 1983, 1985). In summary, the crambine ears (figs. 180-232) are paired structures formed on each side by a sternal invagination (the tympanic drum) closed ventrally by the tympanum and a conjunctivum which connects to the thoraco-abdominal intersegmental membrane. This membrane expands medially to form the praecinctorium which protects the tympanum. The sensory organ, called scoloparium, is anchored on a small sclerite (the spinula) on the tympanum and connects with the tympanic nerves at the tympanic crest, an evagination of the internal lamella of the tympanic drum. The definition of tympanic bridge, tympanic ridge, tympanic pocket, tympanic frame and other terms can be found in the Glossary (see also figs. 180-181).

The tympanal organs of the Pyralidae have been demonstrated to be useful to separate this family into two groups of subfamilies: the Crambiformes and the Pyraliformes (see Table 1 and fig. 1). The tympanal organs have not been shown to exhibit any synapomorphy for the Crambinae although Minet (1985 and pers. comm.) pointed out that the tympanic pockets are typically subconical. The orientation of the tympanum and the shape of the praecinctorium have been used to separate tribes. The tympanum in most Crambinae is more or less oriented at a 45^0 angle to the sternal plane. However, the presence of a tympanum oriented at a right angle from the sternal plane in *Ancylolomia* (fig. 180) and *Talis* (a genus closely related to Prionapteryx) prompted Minet (1982) to write that this condition was a synapomorphy for the Ancylolomiinae *sensu* Ragonot (1890), Forbes (1923) and Munroe (1983), a taxon which is not recognized here. In a phylogenetic analysis, a character like this one, which involves the measurement of the angle of the tympanum to the sternal plane, represents a problem because it is difficult to obtain discrete categories of measurements. I did not try to resolve this problem because I found that the tympanum was oriented at a right angle (or close to it) to the sternal plane in the Prionapterygini, Diatraea (fig. 194) and Epina (fig. 196), a situation which shows the unreliability of this character. Moreover, many other characters show that Ancylolomia doesn't belong with the other genera originally placed with it in the "Ancylolomiinae".

The Crambiformes generally have a simple praecinctorium but there a few exceptions. A bilobed praecinctorium is present in the Pyraustinae (Munroe 1972, Minet 1982, 1985), one genus of Schoenobiinae (Minet 1985), some Evergestinae (Minet 1982) and the Myelobiini (Crambinae). The Myelobiini were defined by Minet (1982) who later (1985) stated that the bilobed praecinctorium was a synapomorphy for the tribe. It includes Myelobia Herrich-Schäffer, known from Central and South America, and the Oriental genus Eschata Walker. I cannot comment on the validity of Minet's decision to unite these two genera into a monophyletic taxon because only Myelobia was examined. In my studies, a bilobed praecinctorium was found only in Myelobia and Pyrausta unifascialis Packard. This similarity undoubtedly evolved independently. Since the character does not contribute to define groupings in the Crambinae, it was rejected from the analysis. The adaptive significance of a bilobed praecinctorium is unknown but it is possible that it provides a better protection to the tympanum.

Character 19. Tympanic frame not distinctly projected beyond venula prima, or distinctly projected beyond venula prima. This character was not polarized by an outgroup comparison because I could not homologize the Crambinae variation in the position of the tympanic frame with that of the other Crambiformes examined so the outgroup is scored as ?. State 1 is attributed to the Crambinae with the tympanic frame strongly projected beyond the venula prima in side view. I believe that this condition is more likely to be derived than the reverse. State 1 occurs in Myelobia (figs. 188, 189) + Diatraea (fig. 194), Calamotropha (fig. 191), the Haimbachiini except Xubida (figs. 192, 197-199), Eufernaldia (fig. 185), Pseudoschoenobius (fig. 184), Chilo (fig. 193), Epina (fig. 196) and Surattha (fig. 182). State 0 is exhibited by Xubida (fig. 195), Prionapteryx (fig. 187), the Argyriini (figs. 201, 202, 206), the Crambini (figs. 203-205, 207-232) and the Diptychophorini (figs. 186, 190). The apomorphic state occurs six times with two secondary reversals in the branches recognized in the consensus tree of the first analysis (fig. 4). It supports the monophyly of the Haimbachiini, the Prionapterygini and Myelobia + Diatraea.

Character 20. Tympanic pockets present or absent. The homology of the structures which can be called tympanic pockets in the different subfamilies of Crambiformes is not entirely certain. These structures are present (state 0) in all non-Crambinae species analysed [except Donacaula longirostrella (fig. 173) and Nymphula ekthlipsis (fig. 176)] and in the following Crambinae: Calamotropha (fig. 191), Pseudoschoenobius (fig.

184), some Prionapteryx spp., the Argyriini except some Argyria spp. (fig. 202), Microcausta (fig. 190) and most of the Crambini (figs. 203-205, 207, 209-217, 219-232). The absence of pockets in Donacaula and Nymphula is scored as ? because of the fundamentally different structure of their tympanic organs in comparison to that of the other crambiforme groups (see next character). The pockets are absent (state 1) in Eufernaldia (fig. 185), some Prionapteryx spp. (fig. 187), Surattha (fig. 182), Myelobia (figs. 188, 189), Argyria lacteella, Diptychophora (fig. 186), Hemiplatytes (fig. 200), the Haimbachiini (figs. 192, 195, 197-199), Diatraea (fig. 194), Chilo (fig. 193) and Epina (fig. 196). The distribution of the states of this character is similar to that of the preceeding, occuring six times independently in the same clades of the consensus tree (fig. 4) and contributing to the monophyly of the same taxa. The adaptive significance or the function of these pockets is unknown. The pockets are secondarily lost in two species of Crambini: Catoptria trichostoma (Christoph) (fig. 208) and Thaumatopsis pectinifer (Zeller) (fig. 218). A possible explanation for this is the loss of evolutionary pressure to maintain these organs as functional. This would be quite possible for C. trichostoma which is an arctic or semi-arctic species, occuring in areas of almost constant daylight in the summer and possibly where bats are absent. I do not know of the habitat requirements of T. pectinifer, which occurs in the southern United States.

Character 21. Tympanal organs of the "crambine type" or "not of the crambine type". This character cannot be polarized. State 1 is attributed to all Crambinae and state 0 to other Crambiformes. I believe that the following combination of characters is unique to the crambine tympanal organs (figs. 180-182, 184-232). The tympanic frame is close to the margin of the cavity (venula prima), usually slightly or strongly protruding ventrally when seen in side view. There usually is a tympanic ridge connecting both venulae primae medio-ventrally. This ridge is most often situated well posterad of the elbow of the tympanic frame. There is often a pair of small, subconical tympanic pockets behind the ridge and these are never approximated along the sternal mid-line. The tympanic bridge is usually moderately long and the tympanic wings moderately large when seen in ventral view. The praecinctorium is well developed and usually simple.

In Donacaula longirostrella (fig. 173) (Schoenobiinae) and Nymphula ekthlipsis (fig. 176) (Nymphulinae), the cephalic end of the tympanic drum is not concealed in the segment as in other Crambiformes. This similarity is interesting because Passoa (1988) hypothesized that the two subfamilies are sister-groups based on larval characters (see table 1 and fig. 1).

The structure of the tympanum in Cybalomia extorris (fig. 175) (Cybalomiinae) has the frame completely enclosed inside the segment when seen in side view and the second sternite is indented on each side (a synapomorphy also occurring in other groups according to Minet (1985)).

The peculiar shape of the bridge in Glaphyria sesquistrialis (fig. 178) (Glaphyriinae) separates this species from the Crambinae on the basis of tympanal organ structure. Also, both sides of the ridge are not connected medially and end near the middle of the bridge.

In Pyrausta unifascialis (fig. 183) (Pyraustinae), the pockets are extremely large, the frame is enclosed in the segment's cavity and the praecinctorium is slightly bilobed apically. The bilobed praecinctorium is typical of that subfamily (Munroe 1972; Minet 1982).

In Mimoschinia rufofascialis (fig. 174) (Odontiinae) the pockets are hypertrophied, largely contiguous and posteriorly rounded. The structure of these pockets is diagnostic of the subfamily, they are never conical (Minet 1982).

In the Scopariinae, represented here by Scoparia basalis (fig. 179), the dorsal part of the drum is reduced (Minet 1982). This species also has a peculiarly shaped ridge medially, unlike that of any Crambinae.

The tympanic wings are larger and the bridge longer in Evergestis simulatilis (fig. 177) (Evergestinae) than in any Crambinae examined. According to Minet (1982), the spinulae are spinose and inserted anteriorly on the tympanum. It was not possible for me see this structure with the techniques used for the preparation of the specimens.

Male genitalia. The male genitalia of the Crambinae are relatively unmodified within the Lepidoptera and the different parts are easily recognized. Klots (1970b) illustrated the genitalia of Fernandocrambus sp. in his comprehensive treatment of the genitalia in the Lepidoptera. In the following discussion, most genitalic features of the crambine males will be dealt with but more information is available in Klots (1970b).

Gnathos fused to tegumen. I exluded this character from the analysis because it is not present in the Crambinae. It is also difficult to homologize because the degree and areas of fusion vary. The gnathos is fused to the tegumen in Mimoschinia, Evergestis and Pyrausta. To my knowledge, these three taxa have never been associated by this character. A close relationship of Evergestis and Pyrausta was, however, mentioned by Munroe (1976).

Coremata on intersegmental membrane VIII-IX. Late in the study, I believed that I had found a very interesting character when I realized that the males of many Crambinae have a coremata (a crown of long hairs) on the abdominal intersegmental membrane VIII-IX. When the genitalia are inside the abdomen, these hairs are directed apically and surround the genitalia. When the genitalia protrude, the hairs are everted. These hairs are believed to be associated with pheromone glands. There is a coremata of very long hairs (usually longer than the genitalia themselves) around the whole membrane in most Crambini, Chilo, Eoreuma and Xubida. The coremata are restricted to a pair of tufts of long hairs dorso-laterally in Parapediasia decorella (Zincken) and Microcrambus biguttellus (Forbes). There are fewer shorter hairs located ventro-laterally in Calamotropha, Hemiplatytes, Myelobia, and Pyrausta. Shorter hairs are also present on Prionapteryx but they are concentrated to a pair of tufts latero-ventrally. No coremata were seen in Scoparia, Nymphula, Glaphyria, Evergestis, Donacaula, Mimoschinia, Diatraea, Ancylolomia, Diptychophora, Urola, Argyria and Occidentalia. Only about half (34/61) of the genera included in this study were investigated for this character so it is not included in the analysis. The coremata should be left intact when a dissection is made and should be visible on the final mount or a note decribing them should be made if the structure is removed. This had not been recognized at the beginning of my studies when a lot of dissections were made.

Character 22. Dorsal connection of tegumen long or very short. The arms of the tegumen of most Crambiformes usually connect dorsally to form a hood over the genitalia. The length of this hood taken in mid-line is usually long, longer than the width of the lateral arms (state 0). However, in some taxa, the dorsal connection of the tegumen arms is only shown by a very narrow sclerotized band situated apically where the uncus and gnathos connect (state 1). This condition is characteristic of Glaphyria, the Argyriini (figs. 250-252), the Diptychophorini (figs. 248, 249) and Calamotropha (fig. 254). Some species of Chilo (fig. 253) and Hemiplatytes (fig. 235) also have a short dorsal connection; these genera were scored as 1. The apomorphic state of this character occurs six times independently in the clades recognized on the consensus tree of the first analysis. It supports the monophyly of the Diptychophorini. Being also present in all Argyriini, it also potentially supports the monophyly of this group.

The short dorsal connection is invariably coupled with long slender tegumen arms (pedunculi) but the arms are also slender in some Crambus species and in Loxocrambus (fig. 266); in these taxa however, the dorsal connection is always longer than the width of the arms.

Character 23. Uncus dorso-ventrally flattened or laterally compressed. In most Crambiformes examined the uncus is more or less dorso-ventrally flattened or tubular (state 0). In some taxa however, the uncus is laterally compressed (state 1). This condition occurs in Occidentalia (fig. 240), Haimbachia (fig. 244), Eoreuma (fig. 243) and Myelobia (fig. 245). The most parsimonious solution according to the results of the first analysis is that the apomorphic state evolved once in the ancestors of the Haimbachiini (with secondary reversals in Xubida and Thopeutis) and in Myelobia independently. The bilobed uncus of Crambus pascuellus (L.) (fig. 233) and Crambus lyonsellus Haimbach is very atypical of the other species in the genus where the uncus corresponds to the above description for state 0. Arequipa turbatella Walker (fig. 284) also has an atypical, trilobed uncus; this taxon was scored ? for this character and the following.

Character 24. Uncus apex pointed (or rounded) or notched. In most male Crambiformes examined the apex of the uncus was found to be most often pointed but it can also be flat and broadly rounded or simply rounded (state 0). In a rather few instances, it is notched. This condition is present in Surattha (fig. 237), Pseudoschoenobius (fig. 239), Myelobia (fig. 245) and Epina (fig. 247). The most parsimonious solution, according to the consensus tree of the first analysis, is that the apomorphic state evolved once independently in Myelobia, Epina and in the ancestor of Surattha, Prionapteryx and Pseudoschoenobius with a reversal in Prionapteryx.

Character 25. Gnathos strongly sclerotized, or reduced or lost. The gnathos is a structure derived from the tenth sternite (Klots 1970b) which attaches on the tegumen ventrad to the uncus. Its function is possibly to support the tuba analis. In the Crambinae groundplan, the structure is well developed (state 0), it is also well developed in most other Crambiformes except Pyrausta and Glaphyria where it is reduced or lost (state 1). In the Crambinae, the derived state occurs in Neodactria (fig. 283), Almita (figs. 278, 279) + Raphiptera (fig. 281), Tehama (fig.

267) and Surattha (fig. 237) and has most probably evolved independently in these four groups. The character was deactivated in the first analysis because of its occurence in a single terminal taxon. In the second analysis it helps to support the monophyly of Almita + Raphiptera.

Character 26. Gnathos directed posterad or directed ventrally. In most Crambiformes the gnathos' arms join ventrad from their point of attachment to the tegumen and then extend apically (state 0). In the Prionapterygini (figs. 237-239) except Eufernaldia and Hemiplatytes, the arms join directly ventrad from the points of attachment to the tegumen to form a ring and there is no apical extension (state 1). This ring is thick laterally in Prionapteryx (fig. 238) and Pseudoschoenobius (fig. 239) but it is rather thin in Surattha (fig. 237). The restricted distribution of the apomorphic state of this character strongly supports the monophyly of these three taxa in the Prionapterygini.

Character 27. Apex of gnathos directed upward or directed downward or posterad. This character is difficult to polarize since I do not know the sister-group of the Crambinae and the outgroup taxa I examined exhibit both states. I chose to attribute the plesiomorphic state to the taxa with the gnathos' apex upturned because three outgroup taxa had this condition while two had the gnathos apex downturned. Also, judging from the greater abundance of derived traits in the Crambini (which have the gnathos' apex downturned or straight), I believe that this trait is more likely to be the derived condition. The taxa in which the gnathos is reduced or lost were scored ?. Cybalomia extorris (Cybalomiinae) was also scored with a question mark because the only available male had been damaged. The Prionapterygini were scored in the same manner because neither state occurs in this group.

In the Crambinae, state 1 occurs in the Crambini (except Ancylolomia), and in Calamotropha (fig. 254). State 0 is present in the Argyriini (figs. 250-252), Diptychophorini (fig. 248, 249), Haimbachiini (figs. 240-244), Chilo (fig. 253), Diatraea (fig. 246), Eufernaldia (fig. 236), Myelobia (fig. 245), Ancylolomia (fig. 265) and Epina (fig. 247) even though in that genus there is also a small downward apical point. As shown by the consensus tree of the first analysis, the most parsimonious solution regarding character-state changes in this character is that the apomorphic state occurs once in the Crambini except Ancylolomia and independently in Calamotropha, Evergestis and Scoparia. It is one of the important traits for the recognition of the Crambini as a monophyletic group and it is utilised here for the first time.

I do not know if the gnathos is used during copulation but if it is, there could be two (possibly three considering the Prionapterygini) basic strategies recognized with regards to the use of the gnathos.

Character 28. Male pseudosaccus present or absent. According to Klots (1970b), the pseudosaccus is "a more or less tubular structure extending cephalad midventrally from the cephalo-ventral angles of the valvae". It remains unclear to me whether this sclerite is actually part of the valvae because it is distinctly separated by a suture from the valvae and it is simple whereas the valvae are paired. As shown by Kuznetsov & Stekolnikov (1979), the pseudosaccus is the ventral point of attachment of the sternal extensor of the valves (muscle M3) in Crambini. This muscle is attached on the juxta dorsally. These authors *(op. cit.)*

referred to the pseudosaccus as a "special sclerite" and wrote that in all Crambiformes except Crambinae (their Pyraustidae) M3 attaches on the saccus. It is possible that the function of the pseudosaccus is to help the opening of the valves by pushing apically on their cephalo-ventral angles during the contraction of M3.

The pseudosaccus is absent (state 0) in all non-crambine Crambiformes analyzed and also in the following Crambinae: the Haimbachiini (figs. 240-244), part of the Prionapterygini (figs. 237-239), the Argyriini (figs. 250-252) and the Diptychophorini (figs. 248, 249). It is present (state 1) in all Crambini (figs. 233, 255-289), *Diatraea* (fig. 246), *Hemiplatytes* (fig. 235), *Eufernaldia* (fig. 236), *Myelobia* (fig. 245), *Chilo* (fig. 253), *Epina* (fig. 247), *Calamotropha* (fig. 254). The most parsimonious solution with regards to character-state changes in this character, according to the consensus tree of the first analysis (fig. 4), is that the pseudosaccus was present in the ancestor of the Crambinae and was lost four times independently in the Argyriini, Diptychophorini, Haimbachiini and the apical clade of the Prionapterygini. Even if the Argyriini were not considered to be monophyletic, this solution would have the same number of steps as its alternative. This involves the independent occurence of the apomorphic state in six clades.

Bleszynski (1966, 1969, 1970b) mentioned that the "*Chilo*-complex" (here not recognized as a monophyletic group) could be separated from the "*Acigona*-complex" (here recognized as the Haimbachiini) in part by the presence of the pseudosaccus in the former group. This is obviously only partly true because the "*Crambus*-group" (Crambini), *Calamotropha* and *Ancylolomia* also have this structure.

Character 29. Aedeagus coecum penis present or absent. In most Crambiformes, the aedeagus is extended antero-ventrally by a short and apically rounded structure called coecum penis (state 0). The structure is present in all outgroup taxa examined, in all Crambini (figs. 233, 255-289), the Haimbachiini (figs. 240-244), the Argyriini (figs. 250-252), Calamotropha (fig. 254), the Diptychophorini (figs. 248, 249), Epina (fig. 247) and some species of Chilo (fig. 253). It is absent (state 1) in the Prionapterygini (figs. 235-239), Diatraea (fig. 246), Myelobia (fig. 245) and Ancylolomia (fig. 265). The most parsimonious distribution of character-state changes of this character is expressed in the consensus tree of the first analysis (fig. 4). It indicates that the coecum penis is lost independently in the Prionapterygini, Ancylolomia, Diatraea + Myelobia, and some species of Chilo. The apomorphic state of this character thus contributes to the monophyly of the Prionapterygini and that of Diatraea + Myelobia.

This character has not been used before in a phylogenetic analysis of any pyralid group. The function of the coecum penis is unknown. However, a pair of muscles (M5), the protractors of the aedeagus, are attached on each side of the coecum penis and on the tegumen as shown in three species of Crambini by Kuznetsov & Stekolnikov (1979). I was able to see that this muscle in Diatraea saccharalis (which has no coecum) is present and attached at the cephalic end of the aedeagus on each side slightly before the end of the sclerotized area (fig. 234).

Character 30. Attachment of the aedeagus from apex or not from apex. In the Lepidoptera, the diaphragma is the membrane which closes the posterior end of the abdomen and which the aedeagus pierces in its middle. Where this membrane is wrapped around the aedeagus it is called the manica (Klots 1970b). Presumably for support and to guide the movements of the aedeagus, the diaphragma is often sclerotized ventrad from the aedeagus to form the juxta. This is usually a V-shaped sclerotized plate in the Crambinae. In the outgroup of the Crambinae, the aedeagus is connected to the membrane (and juxta) at its apex (state 0). This is also found in the crambine genera Ancylolomia (fig. 265) and Surattha (fig. 237). In all other Crambinae, the point of attachment is more or less near the middle of the long axis of the aedeagus. State 1 is treated here as a synapomorphy for the Crambinae with reversals in the above-mentioned two genera.

Character 31. Manica detached from the aedeagus or wrapped around and connected to the aedeagus to the connection with the juxta. In most Crambiformes examined the diaphragma is tightly wrapped around the aedeagus until, near its middle, it is attached to the juxta ventrally (state 0). At this point, the membrane (or manica) is sometimes more sclerotized and forms a small extension as in Chilo (fig. 253) or Argyria lacteella. This extension may be longer, as in most members of Fissicrambus (fig. 268). In the genus Almita (figs. 278, 279), the manica is not wrapped around the aedeagus but is disconnected from it from the base of its main shaft (state 1). The membrane is more sclerotized ventrally at the apex where it connects with the juxta. This character was only activated in the second analysis where its apomorphic state only occurs once to establish the monophyly of genus Almita n. gen.

Character 32. Aedeagus with strongly developed sclerotized extension apico-dorsally or without this structure. The aedeagus of four species of Crambini is apico-dorsally ornate and heavily sclerotized (state 1). In addition, the vesica everts ventrally. The four species in question are *Parapediasia decorella* (fig. 271), *P. teterella* (fig. 270), *P. torquatella* (fig. 272) and *P. hulstella* (fig. 273). Generally, the crambiforme aedeagus is less sclerotized dorsally at apex and is not adorned with complex ornamentations (state 0). The aedeagus of some species of *Crambus* (fig. 288), *Fernandocrambus* (fig. 287), *Chrysoteuchia* (fig. 286) and *Haimbachia* (fig. 244) bears a narrow longitudinal sclerotized band which is spined in some of those species. This is believed to be homologous with the *Parapediasia* ornamentations. This character was activated in the second analysis where the monophyly of genus *Parapediasia* was not recognized because of a conflict with characters 38 and 43. Nevertheless, I contend, as shown by figure 5, that these four species form a monophyletic group and should all be placed in genus *Parapediasia*.

Female genitalia. Variation in the morphology of many crambine female genitalia structures is reviewed here and below under characters 33 to 43. The different parts studied are labeled on figs. 291 to 294. More information will be found in Klots (1970b).

Anterior apophyses. The anterior apophyses of female Crambiformes are variable in length and shape.

Members of *Glaphyria*, *Evergestis*, *Scoparia*, *Mimoschinia* and *Cybalomia* have subbasally enlarged anterior apophyses. In other Crambiformes, however, they are narrow subbasally.

To quantify the variation in length of these structures, I compared their length to those of the papillae anales. The anterior apophyses are longer than the papillae anales in: the entire outgroup (except Evergestis), some of the genera of Prionapterygini (figs. 291, 293-295), the Diptychophorini (figs. 307, 308), Myelobia (fig. 306), Occidentalia (fig. 297), Thopeutis (fig. 298), Chilo (fig. 299) and Diatraea (fig. 305). Reduced anterior apophyses are found in Evergestis, Calamotropha (fig. 310), Eufernaldia (fig. 290), the Haimbachia-assemblage (figs. 292, 296, 300), Epina (fig. 304), and the Crambini (figs. 309, 311-338). I decided to remove this character from the analysis because it was sometimes difficult to decide if a taxon fell into one category or the other. In other words, the two categories created were not discrete nor would be any other possible categories. Also, the information provided by this character was limited in terms of defining natural groups. However, a reduction of the length of the anterior apophyses is seemingly apomorphic in the Crambiformes.

Length of abdominal segment VIII. I had originally included in the analysis a character which dealt with the length of the sclerotized part of the female abdominal segment VIII. I had divided it into six arbitrary classes from long to absent. I later tried to make discrete classes of these data by comparing the length of the segment's sclerotized part dorsally with that of the papillae anales. Although these two categories were less subjective, the data themselves became useless: one half of the outgroup taxa falling into one category and the other half in the other category. The character was originally considered because most female Crambini show a marked reduction of the length of the sclerotized part of the eighth tergite. Tergite VIII is completely membranous in the genus Loxocrambus (fig. 321).

The sterigma. Gaskin (1971, 1973, 1975a) placed a great deal of emphasis on the sterigma (or ostiolar sclerites) to define the crambine tribes. He claimed that the interpretation of the fate of these sclerites "is essential to proper understanding of Crambine phylogeny". In my introductory chapter (Table 2 and fig. 2), I summarized Gaskin's interpretation of the evolution of these sclerites. It is simplistic to believe that only one character-set can unravel the whole phylogeny in a group as diverse and disparate as the Crambinae. I found four major problems associated with the use of this character in a phylogenetic analysis and with Dr. Gaskin's conclusions.

1.- It is in most taxa impossible to tell the origin of the "sclerites" involved in the sterigma because they are often completely fused.

2.- The sclerotization of the antrum or the ductus bursa may have nothing to do with the ostiolar sclerites and it is sometimes hard to recognize the different parts in that area.

3.- The four different states recognized by Gaskin (fusion of dorsal and ventral sclerites [evaginated or invaginated], fusion of the lateral sclerites [evaginated or invaginated]) cannot be homologized. Thus it is erroneous to believe that all four conditions are apomorphic for one tribe or another. Surely one of these states is plesiomorphic.

4.- Dr. Gaskin's interpretations are almost entirely based on a study of the depauperate New Zealand fauna.

In conclusion, I decided to reject this character from my analysis. The various shapes of the sterigma will be described in the diagnosis of each taxon.

Papillae anales sclerotized support. A longitudinal sclerotized band of support is present on the papillae anales of the Argyriini (figs. 301-303), Calamotropha (fig. 310), Myelobia (fig. 306), Chilo (fig. 299), Diatraea (fig. 305), Haimbachia (fig. 300), Epina (fig. 304), Hemiplatytes (fig. 295), Xubida (fig. 292), Glaphyria, Cybalomia, Evergestis and Scoparia. This distribution indicates the plesiomorphic nature of this condition. In most Crambini (including Ancylolomia), the narrow band of support has been transformed almost beyond recognition (presumably because of the lack of coalescence of the papillae), except in the genus Euchromius, which is believed to be the most primitive genus of the Crambini. In the Prionapterygini, the band of support may have followed a transformation series leading to the complete fusion and sclerotization of the whole papillae in Prionapteryx.

Character 33. Ostium bursa at or anterior to base of segment VIII, or in middle of segment VIII which is elongate and well sclerotized. The eighth segment in some Prionapterygini is the longest in all Crambiformes, is heavily sclerotized, tubular, and almost closing back on itself ventrally. The ventral margin is thus protected and the membrane is invaginated, forming an elongate funnel. The ostium is very small, completely protected in the funnel and situated at about midlength (state 1). This condition is only found in Prionapteryx (fig. 294) and Pseudoschoenobius (fig. 291) and so is an exclusive synapomorphy for these two Prionapterygini taxa. The abdominal segment VIII is also elongate in Diptychophora, Microcausta, Pyrausta and Occidentalia but it is not heavily sclerotized or of the form of Prionapteryx.

The ostium in Surattha (fig. 293) is situated at the base of the sclerotized part of segment VIII (state 0) as in many other Crambiformes. The information provided by this character agrees with that of character 9 (state 1) with regards to the affinities of the three terminal taxa in the Prionapterygini.

The polarity attributed to the states of this character is uncertain due to the strongly derived shape of segment VIII in this group but all other Crambiformes with a more-or-less elongate segment VIII have their ostium at its base, not in its middle.

Character 34. Segment VIII and sterigma connected by a simple narrow bridge, or not connected or connected by a double bridge. In the outgroup species examined, there is never an external sterigma. In the Crambinae, the sterigma is usually present but it is absent in Surattha (fig. 293), Hemiplatytes (fig. 295) and Loxocrambus (fig. 321). When it is present, it is usually intimately connected with the eighth tergite (state 0). In Eoreuma (fig. 296) and Haimbachia (fig. 300), the sterigma is only connected to the eighth tergite by a simple and narrow sclerotized bridge (state 1). A similar narrow bridge is present but distinctly double in Thopeutis (fig. 298). The presence of this simple narrow bridge in Eoreuma and Haimbachia is a synapomorphy uniting these two genera.

Character 35. Segment VIII circular in cross section or laterally compressed. In most Crambiformes examined, the female segment VIII is more or less circular in cross section (state 0). However, in Eoreuma (fig. 296), Haimbachia (fig. 300) and Hemiplatytes (fig. 295), the eighth segment is distinctly compressed laterally (state 1). The papillae anales in these three genera are also very narrow. In the consensus tree of the first analysis, the derived condition occurs twice, once at the stem leading to Eoreuma + Haimbachia and once in Hemiplatytes. These two occurences are therefore believed to be convergent. Any other solution would be considerably less parsimonious.

Character 36. Setation on segment VIII variable in position or concentrated apico-dorsally. The presence of long setae on the female tergite VIII in the Crambiformes is a plesiomorphy as shown by its occurence in all outgroup taxa examined except Cybalomia. In the Crambinae these long setae are present in abundance only in Myelobia (fig. 306), the Diptychophorini (figs. 307, 308) and Hemiplatytes (fig. 295). In these groups, the setae are situated on the apical margin, laterally and dorsally on the apical half (state 0) except in Hemiplatytes where they are all found ventrally. In most other Crambinae, these setae have apparently been lost. I found a few of them (2-10) in some species of Thaumatopsis, Agriphila, Neodactria and in Arequipa turbatella. In the Haimbachiini, the setae are always reduced in size and restricted in location to the dorso-apical margin (state 1). The taxa concerned here are Eoreuma (fig. 296), Haimbachia (fig. 300), Xubida (fig. 292), Occidentalia (fig. 297) and Thopeutis (fig. 298). This condition represents a synapomorphy for the Haimbachiini and is used here for the first time.

Character 37. Female intersegmental membrane smooth or with slender spines. The papillae anales of all Crambiformes and the VIII-IX intersegmental membrane of many of them is covered with very tiny spicules (state 0). These are also sometimes present near the ostium.

In Eoreuma (fig. 296) and Haimbachia (fig. 300), the intersegmental membrane VIII-IX is covered with short slender spines (state 1). This is a unique synapomorphy for these two genera.

Character 38. Corpus bursa signa number 0-1, or 2. The number of signa on the female corpus bursa varies from the absence of a signum to the presence of two signa. Most Crambiformes do not have any signa or have only one (state 0). It is only in Crambus (fig. 338), Fernandocrambus (fig. 333), Parapediasia decorella (fig. 328), some Euchromius spp. (fig. 309), Chrysoteuchia (fig. 335), some Microcrambus species, some Haimbachia species and the outgroup genera Nymphula, Evergestis, and Scoparia that two signa are present (state 1). This character was deactivated in the first analysis because its apomorphic state was not found in the ingroup except for some Haimbachia (scored ?) and some Crambini (scored 0). In the consensus tree generated by the second analysis, the apomorphic state of this character contributed to the monophyly of a clade made of Fernandocrambus, Crambus, Chrysoteuchia and Parapediasia decorella. However, I believe that the latter taxon should be placed with the three other species of Parapediasia on the basis of the shared presence of the unique apomorphic state of character 32 (see also fig. 5) in this group. It should be noted that one Euchromius species in Africa was mentioned to have three signa by Schouten (1988) but one of these three structures is not a true signum but a ring of sclerotization at the entrance of the corpus bursa.

Character 39. Posterior apophyses shorter than the length of the first three abdominal segments or as long or longer than the length of the first four abdominal segments. The posterior apophyses of *Thopeutis* (fig. 298) and *Occidentalia* (fig. 297) were found to be very long in comparison to those of other Crambiformes (except *Pyrausta*). I calculated that they were at least as long or longer than the first four abdominal segments (state 1) in those three taxa while in other crambiforme taxa they are shorter than the length of the first three abdominal segments (state 0).

By virtue of the presence of this apomorphic state, *Thopeutis* and *Occidentalia* are considered to be most closely related to each other than to any other crambiforme taxon.

The extreme length of the posterior apophyses in these insects suggests that the eggs are laid in a difficult to reach position. Frohne (1939) studied the biology of *Thopeutis forbesellus* and found that the eggs are laid into the gallery entrance holes of the larvae of the same species.

Character 40. Posterior apophyses subbasally narrow or subbasally enlarged. The posterior apophyses of most Crambiformes are generally narrow subbasally (state 0) but they may be enlarged slightly at the apex. The posterior apophyses of *Xubida* (fig. 292), *Eoreuma* (fig. 296) and *Haimbachia* (fig. 300) are however distinctly enlarged subbasally (state 1). This is a unique synapomorphy for this group of three genera; one that has never been documented before.

Character 41. Papillae anales coalesced dorsally or not coalesced dorsally. The papillae anales of all Crambini (figs. 309, 311-338) are not coalesced dorsally (state 1). In these species there is a membranous area which separates both papillae. This membranous area is devoid of the characteristic setae found on the papillae themselves. This condition is also found in Mimoschinia. In the other Crambiformes analyzed (figs. 288-308, 310), the papillae anales are always connected dorsally in the middle (state 0). At the point of connection the cuticle is not different and is just as setose as on the papillae. I consider that the uncoalesced papillae anales is a synapomorphy for the Crambini and that the condition evolved in parallel in Mimoschinia.

The absence of coalesced papillae anales may mean that these are not used as a true ovipositor and that the eggs when laid just fall on the ground in the appropriate habitat. This hypothesis was also mentioned by Felt (1894) and Bleszynski (1965). Gaskin (1975a) mentioned that the coalescence of the papillae anales also occurs in his subtribe Corynophorina of the Crambini and that this condition was an apomorphy for this subtribe! These assertions are contradicted by the present analysis.

Character 42. Dorsally coalesced papillae anales poorly sclerotized and generally elongate or strongly sclerotized and triangular in shape (with or without an apical lobe). The peculiar triangular shape and high degree of sclerotization of the papillae anales (state 1) in the three apical clades of the Prionapterygini is considered to be a unique synapomorphy for the group composed of Surattha (fig. 293), Prionapteryx (fig. 294) and Pseudoschoenobius (fig. 291). In the other Crambiformes, the papillae anales are generally poorly sclerotized and elongate (state 0). The uncoalesced Crambini were scored ?. The papillae anales of Eufernaldia cadarella (fig. 290) look triangular in side view but they are only sclerotized dorsally and anteriorly and they are also distinctly compressed laterally while those of the the more derived Prionapterygini are not.

The shape and degree of sclerotization of the papillae anales in the Prionapterygini strongly suggest that the females of these moths insert their eggs in plant tissue. This is even more strongly suggested in Surattha and Pseudoschoenobius which possess a thin laterally compressed and apically rounded extension to their papillae located apico-dorsally in the middle. This structure is believed to have been present in the ancestors of Surattha, Pseudoschoenobius and Prionapteryx but lost in the latter genus. This scheme would agree with the evolution of characters 9 and 33.

Character 43. Uncoalesced papillae anales simple, only slightly divided, or strongly divided into two distinct lobes. This character is scored as additive because I believe that the strongly divided papillae must have arisen from the non-distinctly divided ones. The character was deactivated in the first analysis because it brought no input to the resolution of the tree.

The uncoalesced papillae anales of the Crambini are variable in shape when seen in side view. The plesiomorphic state (00) is believed to be represented in taxa where the apical margin of the papillae is straight as in many other Crambiformes. In the Crambini, this is present in Ancylolomia (fig. 313), Thaumatopsis (figs. 314, 315, 318, 319), "Crambus" angulatus (fig. 312) and Euchromius (fig. 309). The second state (10) occurs in genera with the apical margin of the papillae anales not straight but not clearly divided into two lobes. This condition is present in *Parapediasia teterella* (fig. 329), *Tehama* (fig. 323), *Fissicrambus* (fig. 320), *Microcrambus* (fig. 316), *Loxocrambus* (fig. 321), *Pediasia* (fig. 326), *Almita portalia* (fig. 332), *La* (fig. 322), *Catoptria* (fig. 317) and *Platytes* (fig. 311). The third state represents genera for which the apical margin of the papillae anales is distinctly separated into a basal broadly rounded hump and a narrower apical hump. This condition occurs in *Parapediasia decorella* (fig. 328), *Almita texana* (fig. 331), *Fernandocrambus* (fig. 333), *Agriphila* (fig. 324), *Arequipa* (fig. 325), *Chrysoteuchia* (fig. 335), *Crambus* (figs. 337, 338) and *Raphiptera* (fig. 334).

The assigment of one taxon to one of the three categories can be difficult and this leads to some subjectivity but this character is one of the few to bring any resolution in the Crambini. The presence of state 11 supports the monophyly of the *Crambus*-assemblage, a clade including *Agriphila* and its sister-group composed of *Crambus*, *Fernandocrambus* and *Chrysoteuchia*. It also supports the monophyly of the *Raphiptera*-assemblage composed of *Raphiptera* and *Almita*. The presence of state 00 on the other hand contributes to isolate *Euchromius* as the most primitive genus in the Crambini.

5. SYNOPSIS OF THE MAJOR LINEAGES OF CRAMBINAE AND OF THE GENERA OF CRAMBINI OF NORTH AMERICA

The following are descriptions of the major lineages recognized by the cladistic analysis and of all genera of North American Crambini. When variation is mentioned (with terms such as usually with, often without, etc.), it refers to intergeneric (in tribe descriptions) or interspecific (in generic description) variation. The full names of the species mentioned can be found in Table 4.

5.1 SUBFAMILY CRAMBINAE

Diagnosis. The Crambinae are believed to form a monophyletic group on the basis of the following synapomorphies: the hindwing dorsally is adorned with a comb of hairs on the base of the Cubital-stem (character 18); the structure of the tympanal organs is typical (character 21); and the aedeagus is attached medially to the juxta (character 30). The moths usually also have elongate wings and palpi and are often brown in colour (except the Diptychophorini and Argyriini).

Redescription.

Head (figs. 6-32). Fronto-clypeus usually rounded but sometimes produced anterad, with or without one or more points. Ocellus usually present, sometimes reduced or lost. Chaetosema well developed. Labial palpus variably elongate; about as wide as head to 4X width of head. Haustellum usually long and functional, sometimes reduced, rarely lost. Vestiture (figs. 25, 27, 31) with a tuft of scales directed medially on each side of occiput; fronto-clypeal and vertexal scales appressed or produced; maxillary palpus scales produced or more-or-less forming a triangle; labial palpus scales often produced, sometimes dishevelled. Male antennal flagellomeres (figs. 33-55, 57-75) usually serrate, sometimes strongly serrate, pectinate or bipectinate; usually with 35-60 sensilla trichodea on each side, one to three sensilla cheatica, three sensilla coeloconica, one sensillum coeloconicum and sometimes with one sensillum auricillicum (Appendix III). Female antennal flagellomeres (fig. 56) usually simple.

Wings (figs. 76-122). Female frenulum from simple to multiple (more than three bristles). Male frenulum hook (fig. 172) present or absent. Forewing Sc always present; R1 present and free (although sometimes connecting with Sc), stalked with R2 or connected with Sc, or absent; R2 usually free (sometimes connected with R3+4); R3 present and connected to R4 (sometimes very faint or lost); R4 present; R5 present and free or connected to R3+4, or absent; M1 present; M2 & M3 shortly stalked or not stalked; Cubitus with CuA1 & CuA2 (sometimes with CuA2 lost) or with CuA1 but without CuA2; Anal sector with usually one, but sometimes two veins. Hindwing Rs connected to Sc+R1 at about 2/3 of its length; M1 fused to Sc+R1 or connected to it by a very short cross-vein at anywhere between 1/4 to 1/2 of its length, or distinctly separated from Sc+R1 but connected to it by a cross-vein at about 1/2 of its length; cell open or closed; M2, M3, CuA1 & CuA2 all present and connected below cell, or with one vein missing; Cu2 and anal veins 2 and 3 always present. Forewing pattern (figs. 135, 136, 138-170) most often brown or straw-coloured with paler longitudinal markings.

Legs (figs. 131-134). Typical of most Lepidoptera, i.e. with coxa, trochanter, femur, tibia (equipped with an epiphysis on the foreleg, a pair of apical spurs on the midleg and two pairs of median and apical spurs on the hindleg), five tarsomeres, and a post-tarsus formed of a pair of ungues and pulvilli, a median pseudempodial seta and a large arolium. Not variable except for the presence of an exocrine coxal gland in the foreleg of Chilo phragmitellus (fig. 131) and a large tuft of hairs on the hind tibia in some species of Diatraea.

Tympanal organs (figs. 171, 180-182, 184-232). Anterior tergo-sternal sclerite present, simple. Venulae primae often joined in the middle ventrally to form a complete ring, otherwise blending into sternite. If connected ventrally, usually forming a transverse ridge behind which tympanic pockets may be present or absent. Posterad to the tympanal structures on the sternite, venulae secundae may be present. Tubercula usually seen only in the most heavily stained specimens. Venulae secundae variable in degree of sclerotization and length, connected to venulae primae or not connected, convergent, parallel, or divergent. Tympanic bridge present, more or less projected ventrally, connected or not medially, with wings long, or small. Praecinctorium usually simple and scaled but double and hairy in Myelobia. Tympanic frame more or less projected ventrally beyond venulae primae. Tympanum positioned obliquely or at right angle from sternal (horizontal) plane. Tympanic drum variable in size even in same species between sexes and probably between individuals of same sex, hemispherical and rather unvariable in that matter. Tympanic crest variable in shape, size, position and orientation, sometimes apparently lost. Spinula sometimes visible, spine-shaped. Scoloparium never seen due to the method of preparation.

Male genitalia (figs. 233-289). Uncus usually simple, sometimes bilobed or trilobed. Gnathos sometimes reduced, apically upturned, straight or downturned. Tegumen variable in shape, dorsally usually largely sclerotized, often ventrally sclerotized to form a bridge between two pedunculi. Valva often with costa heavily sclerotized at base and with a projection; cucullus variable in shape, always upturned apically; sacullus sclerotized in a few genera. Vinculum with or without saccus, sometimes with lateral margins produced anteriorly. Juxta usually small, flat and trough-shaped, sometimes with elongate arms, rarely modified into long simple narrow projection. Pseudosaccus present or absent. Aedeagus usually attached to juxta near middle; manica sometimes sclerotized but usually appressed on aedeagus; coecum penis sometimes absent; vesica with or without cornuti.

Female genitalia (figs. 290-338). Anal papillae connected dorsally or not (Crambini); if connected, sometimes triangular in shape and strongly sclerotized (Prionapterygini); if not connected, sometimes divided into two lobes. Posterior apophyses variable in length, usually narrow, sometimes basally enlarged (Haimbachiini). Anterior apophyses variable in length, usually short and sometimes lost in Crambini. Segment VIII most often strongly sclerotized and connected with sterigma ventrally, reduced in length dorsally (especially in Crambini). Sterigma usually present, variable in shape. Ductus bursae sclerotized or not. Corpus bursae usually without but sometimes with one to three signa.

Relationships. The sister-group of the subfamily is unknown. Yoshiyasu (1985) illustrated the relationships among eight crambiforme subfamilies with a cladogram on which he showed that the Crambinae were forming a monophyletic group with the Scopariinae, Musotiminae, Nymphulinae and Schoenobiinae on the basis of the reduced transtilla in the male genitalia (fig. 1). Passoa (1988) on the other hand used a character of the larval setation to unite most crambiforme subfamilies as the sister-group of the Nymphulinae + Schoenobiinae, hence contradicting the results of Yoshiyasu (see fig. 1). Within the Crambinae, five tribes are recognized in North America and three partly North American taxa (Chilo, Epina and Diatraea) are unassigned to any of the recognized tribes (see below for diagnoses of tribes and figure 4). Three more genera treated here (Ancylolomia, Myelobia and Calamotropha) are extralimital to North America. Within the subfamily, the relationships between the suprageneric lineages are unresolved.

Diversity and distribution. The Crambinae are distributed almost everywhere where there is land except for Antarctica. They are most abundant in diversity in areas rich in grasses. There are approximately 150 genera world wide. Based on the results of this study, the North American fauna contains 35 genera distributed in five tribes and three more genera unassigned to any tribe. The most diverse tribe is the Crambini with 19 genera and two species una signed to a genus.

Natural history and immature stages. The larvae of Crambinae are generally grass (Poaceae) feeders but many have been reported on sedges (Cyperaceae), some Crambini and Diptychophorini are known to feed on mosses, and a few Australian species are known to feed on Iridaceae and Xanthorrhoeaceae (Iridales) (Common 1990). The subfamily contains several pests of economic importance which feed on graminaceous crops such as corn, millet, sugar cane and rice (genera Chilo, Diatraea and Eoreuma). Many other genera in the Crambini are also pests of sod in North America.

5.1.1 PRIONAPTERYGINI new tribe

Type genus: Prionapteryx Stephens, 1834: 316; type species: Prionapteryx nebulifera Stephens, by monotypy.

Diagnosis. The members of this tribe can be characterized by two synapomorphies of their male antennal flagellomeres: the sensilla coeloconica are absent (character 4) and the mosaic pattern of the cuticle is lost (character 5). However, the plesiomorphic state of character 4 is retained in Eufernaldia and there is a parallel occurence of the derived state of character 5 in Thaumatopsis (Crambini). The position of the tympanum at 90^0 to the sternal plane in this tribe might represent another synapomorphy but this character is also found in other groups.

Description.

Head (figs. 7, 10, 21). Fronto-clypeus usually produced, with one or more points, except in Hemiplatytes where it is rounded and not produced. Ocellus strongly developed, except in Surattha. Chaetosema well developed. Labial palpus short (1.75X width of head in one specimen of Pseudoschoenobius opalescalis) to very long (3.25X width of head in one specimen of Hemiplatytes prosenes). Vestiture variable, maxillary palpus triangularly scaled in Prionapteryx, Surattha and Pseudoschoenobius. Male antennal flagellomeres (figs. 65-69) serrate in Hemiplatytes and Eufernaldia, with paired basal humps in Pseudoschoenobius, bipectinate in *Prionapteryx* and *Surattha*; cuticular pattern not in a mosaic except on pectinations; without sensilla coeloconica except in *Eufernaldia*; without sensilla other than trichodea in *Prionapteryx* and *Pseudoschoenobius*.

Wings (figs. 100, 101, 103, 122). Female frenulum simple except in *Hemiplatytes*, triple. Male frenulum hook present, except in some *Hemiplatytes*. Forewing R1 present and free or connected with Sc. R2 free. R3 present and connected to R4 (sometimes very faint). R5 present and free or shortly stalked with M1 or connected to R3+4. M2 & M3 never stalked. Cubitus usually with CuA1 & CuA2 (CuA2 sometimes lost in some *Prionapteryx* and *Eufernaldia*). Anal sector with 2A and traces of 3A. Hindwing M1 distinctly separated from Sc+R1 but connected to it by a cross-vein at about 1/2 of its length or before. Cell closed. M2, M3, CuA1 & CuA2 all present; or with one vein missing (*Prionapteryx*, *Pseudoschoenobius*). Forewing variably elongate (2.52X its width in one mounted specimen of *Surattha indentella* to 3.58X its width in one mounted specimen of *Eufernaldia cadarella*). Forewing (fig. 141) outer margin with a very pronounced notch at M3 in *Prionapteryx* and a less pronounced one in *Pseudoschoenobius* and *Surattha*.

Tympanal organs (figs. 181, 182, 184, 185, 187, 200). Venulae primae joined to form a complete ring. Tympanic pockets usually present but absent in one *Prionapteryx* sp., some *Hemiplatytes* spp. and in *Eufernaldia*. Venulae secundae absent in *Surattha*, *Pseudoschoenobius*, *Eufernaldia* and some *Prionapteryx* spp. Tympanic bridge projected ventrally or not projected (*Surattha*), more or less connected medially (*Surattha*, *Pseudoschoenobius*, *Eufernaldia*) to clearly disconnected (*Prionapteryx*), with wings of medium length. Praecinctorium simple, with short scales. Tympanic frame always strongly projected ventrally beyond venulae primae. Tympanum usually at right angle to sternal plane except in one observed specimen of *Prionapteryx* which had tympanum at about half right angle to sternal plane. Tympanic drum more circular in *Surattha*, more elongate otherwise. Tympanic crest near middle of long axis of the drum, sometimes part of frame (*Surattha*), variable in shape. Spinula not visible.

Male genitalia (figs. 235-239). Uncus well developed, strongly down-curved in *Hemiplatytes* and *Eufernaldia*, otherwise straight and apically down-curved, sometimes subapically enlarged and basally with short lateral extensions setose ventrally. Gnathos variable, with apical upturned points in *Eufernaldia* and *Hemiplatytes*, directed ventrally in other three genera, reduced in *Surattha*. Tegumen unsclerotized ventrally, short with large dorsal connection except in *Hemiplatytes* (with narrow pedunculi and short dorsal connection). Valval cucullus very large, with a costal process basally in *Surattha*, *Prionapteryx* and *Pseudoschoenobius*, also with a projected sacculus in *Prionapteryx* and *Pseudoschoenobius*. Vinculum very narrow laterally, usually with a long saccus. Pseudosaccus distinct only in *Eufernaldia* and *Hemiplatytes*. Juxta well-sclerotized. Aedeagus without coecum penis, usually long, straight and very narrow, less narrow and slightly down-curved in Eufernaldia.

Female genitalia (figs. 290, 291, 293-295). Anal papillae coalesced dorsally, with longitudinal sclerotized band of support in Hemiplatytes, L-shaped support in Eufernaldia, completely sclerotized in Surattha, Pseudoschoenobius and Prionapteryx, with an additional apical and laterally compressed rounded extension medially in Surattha and Pseudoschoenobius. Posterior apophyses about as long as papillae in Eufernaldia and Hemiplatytes, many times longer in other three genera. Anterior apophyses about as long as posteriors. Segment VIII short and somewhat laterally compressed (Hemiplatytes and Eufernaldia) or elongate and tubular. Ostium situated at midlength of segment VIII and protected in ventral funnel in Prionapteryx and Pseudoschoenobius, situated at base of segment VIII in Surattha, otherwise at apex of segment VII. Without sclerotized connection between segment VIII and sterigma. Sterigma sometimes forming an internal tube (some Prionapteryx spp., Eufernaldia) sometimes with a sclerotized external plate surrounding ostium (some Prionapteryx spp.). Ductus bursae distinct from corpus only in Hemiplatytes. Corpus bursae very fragile except in Hemiplatytes; without signum.

Relationships. My analysis did not reveal any well defined hypothesis for relationship between the Prionapterygini and other lineages of Crambinae.

However, the group may be close to the Haimbachiini as shown by the similar shape of the female genitalia of Hemiplatytes and those of some Haimbachiini.

Within the tribe, the relationships between the genera are well defined. Prionapteryx and Pseudoschoenobius are sister-genera on the basis of their notched forewing outer margin at M2 (character 9) and the median position of their female ostium bursae (character 33). These two genera are most closely related to Surattha because of the peculiar shape and orientation of their male gnathos (character 26) and because of the high degree of sclerotization and shape of their female anal papillae (character 42). This clade is the sister-group of Eufernaldia on the basis of the position of their hindwing vein M1 (character 16) and genus Hemiplatytes is believed to be the sister-group of these four genera on the basis of two antennal characters as mentioned in the diagnosis. In addition to the synapomorphies mentioned, it is also possible to see the transformation in the shape of the female genitalia from Hemiplatytes to Prionapteryx (see Chapter 4, character 42 and figures).

Diversity and distribution. In North America, Munroe (1983) recognized five genera in the Ancylolomiinae (now Prionapterygini, see below). This includes Mesolia Ragonot which was not taken into account in my study because too few specimens were available, species identifications were not reliable and Mesolia is obviously very closely related to Prionapteryx if not a synonym of that genus. My analysis has shown that Hemiplatytes also belongs with the Prionapterygini. There are at present 16 recorded North American species of Prionapterygini (Munroe 1983).

Fourteen more species in *Eufernaldia*, *Mesolia* and *Prionapteryx* (with *Surattha* as a synonym) were listed in the Neotropical checklist of Bleszynski (1967). In distribution, the New World species extend from Massachussetts in the North (*Prionapteryx achatina*) to Argentina in the South. The highest diversity in North America is in Arizona with nine species present.

Genera *Surattha* and *Prionapteryx* are also present in the Palaearctic Region with ten and one species respectively (Bleszynski 1965). From the information provided by Bleszynski (1965), it seems that the following Palaearctic genera are probably also members of the Prionapterygini: *Talis* Guenée (14 species), *Elethyia* Ragonot (3 species), *Prionapteron* Bleszynski (1 species), *Drasa* Kapur (1 species) and *Burmannia* Bleszynski (1 species). Thirty-four species of *Surattha* were listed from the Ethiopian, Oriental and Australian regions by Bleszynski & Collins (1962). Three species of *Talis* were listed by the same authors from Africa.

Natural history and immature stages. The bionomics and the immatures of *Surattha indentella*, the "Buffalograss webworm" were studied by Sorensen & Thompson (1969, 1971, 1979). The larva feeds on different species of grasses. It constructs tunnels of silk in which it retreats in the daytime. The natural history of *Prionapteryx nebulifera* was investigated by Daecke (1905). The larva feeds on huckleberry (probably *Gaylussacia baccata* (Wang) K. Koch) (Ericaceae) and sand myrtle (*Leiophyllum buxifolium* (Berg.) Ell.) (Ericaceae) in New Jersey. The larva spins tunnels on all stems of the plants under attack. I observed the same phenomenon in the Florida Keys one night at the emergence of *Prionapteryx serpentella* moths. Tunnels were along stems of *Ernodea littoralis* Sw. (Rubiaceae). The immatures and natural history of the other North American genera are unknown.

Comments. The Prionapterygini as defined here is close in concept to the Ancylolomiini (ae) of Ragonot (1891), Forbes (1923), Minet (1982) and Munroe (1983) except for the exclusion of the genus *Ancylolomia* which was moved to the Crambini based on the results of my cladistics analysis and for the inclusion of *Hemiplatytes* placed with the "Chilonini" by Klots (1983). For more details see Chapter 3.1.

5.1.2 HAIMBACHIINI new tribe

Type genus: Haimbachia Dyar 1909: 28; type species: Crambus placidellus Haimbach, by original designation.

Diagnosis. The tribe can be distinguished by a synapomorphy of the female genitalia: the setation on the female segment VIII is concentrated apico-dorsally. The female sterigma and segment VIII are sometimes linked by a narrow sclerotized bridge which may be simple or double.

Description. Based on my observations on the North American species.

Head (figs. 11, 18, 22). Fronto-clypeus produced or not, rounded or with one or several points or ridges. Ocellus well developed, reduced or absent. Chaetosema well developed. Labial palpus generally long, or very long (2.2X-2.45X width of head in dissected specimens of Eoreuma, Xubida and Haimbachia) or short (1.59X width of head in dissected specimens of Thopeutis and Occidentalia). Haustellum usually much reduced. Vestiture of vertex and fronto-clypeus usually with short appressed scales; palps variable, sometimes dishevelled. Male antennal flagellomeres (figs. 53, 74, 75) serrate, with full complement of sensilla in Thopeutis, Occidentalia and Eoreuma but with generally more than average sensilla trichodea and also more than average sensilla coeloconica (15) and sensilla auricillica (2-4) in Thopeutis. Female antennal flagellomeres simple.

Wings (figs. 83, 97-99, 102). Female frenulum varying from simple to triple. Male frenulum hook present. R1 present and free or connected with Sc (Haimbachia). R2 free (but sometimes connected with R3+4 in Occidentalia and Eoreuma). R3 present and connected to R4 (sometimes faint). R5 present and free (but sometimes connected to R3+4 in Xubida). M2 & M3 not stalked. Cubitus with CuA1 & CuA2. Anal sector with 2A and traces of 3A. Hindwing M1 fused to Sc+R1 or connected to it by a very short cross-vein at anywhere between 1/4 to 1/2 of its length. Cell usually open but closed in Occidentalia. M2, M3, CuA1 & CuA2 all present and connected. Forewing elongate (2.44-3.26X its width); usually brown with thin longitudinal lines along venation (fig. 136), transverse lines vestigial or absent (except in Haimbachia).

Tympanal organs (figs. 192, 195, 197-199). Venulae primae sometimes joined to form a complete ring in Eoreuma, otherwise only partially visible posterad to the tympanic sac. Transverse ridge present in Eoreuma, otherwise ill-defined or completely absent. Tympanic bridge absent. Venulae secundae usually present, sometimes rather large (Occidentalia). Tympanic bridge more (Occidentalia, Eoreuma, Haimbachia) or less (Thopeutis) projected ventrally. Praecinctorium simple, with a dorsal sclerotized support in Thopeutis and Occidentalia. Tympanic frame typically very strongly projected ventrally beyond venulae primae. Tympanic crest usually present, not seen in Haimbachia floridalis and three other species of Haimbachia, situated anteriorly in the tympanic sac. Tympanum in line with the sternal plane. Tympanic drum semi-circular, reduced in *Haimbachia*. Spinula not visible.

Male genitalia (figs. 240-244). Uncus variable, broadly downcurved, apically rounded, with a ventral subapical spine in *Occidentalia*, *Haimbachia* and *Eoreuma*. Gnathos short or long, strongly elbowed, apically upturned. Tegumen generally with narrow pedunculi, medium-sized to broad connection dorsally, ventrally unsclerotized. Valval costa always with strongly sclerotized process, sometimes double, sometimes assymetrical (some *Eoreuma*); cucullus generally long and narrow; sacculus without projection but usually strongly sclerotized. Vinculum usually produced anteriorly and with cephalo-ventral margin convex, with a saccus only in *Occidentalia*. Pseudosaccus absent. Juxta well developed. Aedeagus usually medium-sized with well developed coecum penis; vesica rarely with cornuti.

Female genitalia (figs. 292, 296-298, 300). Anal papillae connected dorsally, narrow with complete or incomplete narrow longitudinal band of sclerotization in *Eoreuma*, *Xubida* and *Haimbachia*, short with apophyses ending dorsally and strongly sclerotized in *Occidentalia* and *Thopeutis*. Posterior apophyses about as long as papillae in *Xubida*, otherwise longer to extremely long in *Occidentalia* and *Thopeutis*, subbasally enlarged in *Haimbachia*, *Xubida* and *Eoreuma*. Anterior apophyses short in *Xubida* to very long in *Occidentalia* and *Thopeutis*. Segment VIII shortened dorsally or very long in *Occidentalia* and *Thopeutis*, often with a narrow sclerotized bridge connecting to sterigma (except in *Xubida* and *Occidentalia*). Sterigma a strongly sclerotized protruding tube (*Occidentalia*, *Thopeutis*, *Haimbachia*), only a ventral plate (some *Xubida*) or poorly sclerotized (*Xubida* and *Eoreuma*). Ductus bursae variable in size and length, usually unsclerotized. Corpus bursae variable in shape, with or without signum.

Relationships. The phylogenetic relationships of this tribe with the other crambine major lineages were not resolved. However, Bleszynski (1966, 1970) mentioned that the "*Acigona*-complex" (now the Haimbachiini) were close to the "*Chilo*-complex" (see Discussion under *Chilo*).

Within the Haimbachiini, I have discovered strong hypotheses of sister-group relationships. *Occidentalia* and *Thopeutis* are obvious sister-genera on the basis of their extremely long female apophyses (character 39) and many other features of their female genitalia. *Haimbachia* and *Eoreuma* seem to be most closely related on the basis of the spinose female intersegmental membrane VIII-IX (character 37) and the simple narrow sclerotized bridge between the sterigma and segment VIII (character 34). The hypothesized sister-group of the latter two genera is *Xubida* on the basis of the subbasally enlarged posterior apophyses in these three genera (character 40). The five genera are united by the common dorso-apical localization of setae on the female segment VIII (character 36). The absence of a male pseudosaccus also suggests the common ancestry of the Haimbachiini.

Diversity and distribution. There has been a great deal of confusion with regards to the generic placement of the species in the "*Acigona*"-complex of genera (which corresponds to the Haimbachiini) because a second (Pyralidae, Crambinae) type-species (*Acigona cicatricella* Hübner) was improperly designated by Bleszynski & Collins (1962). The other species originally included in *Acigona* Hübner is a Noctuidae and was designated type of the genus by Hampson (1926). Agnew (1987) proposed *Friedlanderia* with type-species *Acigona cicatricella* Hübner as a replacement name. However, Agnew (*op. cit.*) was not able to reassign to their proper genera the numerous species of *Coniesta* Hampson, *Eoreuma* Ely, *Haimbachia* Dyar, *Achilo* Amsel, *Donacoscaptes* Zeller, *Girdharia* Kapur and *Xubida* Schaus that Bleszynski (1965, 1967) synonymized with *Acigona*. Undoubtedly, *Friedlanderia* and *Coniesta*, each with one known Palaearctic species, *Pseudobissetia* with three Near East and African species (Bleszynski & Collins 1962) and *Bissetia* Kapur with two species in the Oriental and Ethiopian Regions (Bleszynski 1969) belong to the Haimbachiini. Three species from the Oriental, Palaearctic, Neotropical and Ethiopian Regions were listed in *Girdharia* by Bleszynski & Collins (1962). The same authors listed one species of *Achilo* from Venezuela. In North America, according to Klots (1983), *Haimbachia* includes ten species, *Eoreuma* seven, *Xubida* eight, *Thopeutis* one, and *Occidentalia* one. The latter genus had been incorrectly synonymized by Klots (1983). Genus *Thopeutis* also includes one Palaearctic species. *Haimbachia* also includes five species in Mexico and southward (Capps 1965). Except for the species of *Haimbachia*, the remaining 49 Neotropical species listed under *Acigona* by Bleszynski (1967) are yet unassigned to *Eoreuma*, *Xubida*, *Achilo*, *Occidentalia* or *Donacoscaptes*. All these species most probably are Haimbachiini.

Natural history and immature stages. The biology of several species is known. All larvae seem to be stem borers in Cyperaceae and Poaceae, often in aquatic or semi-aquatic habitats. For example, *Thopeutis forbesellus* thrives on *Scirpus* spp. (Frohne 1939) in North America, *Friedlanderia cicatricella* is associated with *Scirpus lacustris* in Europe (Bleszynski 1965), *Haimbachia quiriguella* Schaus has been reared on rice in Guatemala (Capps 1965), *Pseudobissetia terrestrella* (Christoph) infests corn in northern Africa and the Middle East (Bleszynski 1965), *Bissetia steniella* (Hampson) is a pest of sugar-cane in India (Rahman & Tandon 1940), *Friedlanderia* ? *ignefusalis* (Hampson) is a pest known as the Millet stem borer in West Africa (Ajayi 1990), *Xubida rutubella* (Schaus) as well as *Eoreuma loftini* (Dyar) and *Eoreuma morbidella* (Dyar) are well known pests of sugar cane in Mexico (Agnew *et al*. 1988) (*E. loftini* also infests corn and rice (Rodriguez-del-Bosque *et al*. 1990)), and the larva of *Thopeutis forbesellus* bores in stems of *Juncus* (Dyar & Heinrich 1927). Some information on the morphology of the immatures of some of the above-mentioned species can be found in the references cited and in Hasenfuss (1960), Bleszynski (1969, 1970) and references therein.

5.1.3 MYELOBIINI

Type genus: Myelobia Herrich-Schäffer, [1854] 1850-1858: wrapper, pl. 32, figs. 150-153; type species: Myelobia pustulata Herrich-Schäffer, by subsequent designation by Kirby (1892).

Diagnosis. The two included genera are believed to form a monophyletic group in the Crambinae on the basis of their bilobed praecinctorium. They are the largest of Crambinae with wingspans reaching 12.5 cm.

Description. Based on my observations on one species of Myelobia from Brazil.

Head (fig. 9). Fronto-clypeus rounded, not produced. Ocellus absent. Chaetosema present. Labial palpus with shortest third segment of all Crambinae examined; overall length 2.58X head width in one specimen examined. Vestiture with thin medium-sized projected scales on whole head; maxillary palpus triangularly scaled; labial palpus scales not strongly projected. Male antennal flagellomeres (fig. 71) strongly serrate (female's less strongly serrate); with slightly more sensilla coeloconica (4-7) than in most Crambini and without sensillum auricillicum in species examined.

Wings (fig. 106). Female frenulum triple. Male frenulum hook rudimentary. Forewing R1 present and connected with Sc; R2 free;

R3 present and connected to R4; R5 present and free; M2 & M3 not stalked; Cubitus with CuA1 & CuA2; Anal sector with 2A and traces of 3A. Hindwing M1 distinctly separated from Sc+R1 but connected to it by a cross-vein at about 1/2 of its length; cell closed; M2, M3, CuA1 & CuA2 all present. Forewing elongate (2.58X its width), usually pale brown in colour (fig. 135b) with shades of darker brown on transverse lines and in between, often with a dark brown dot at apex of cell.

Tympanal organs (figs. 188, 189). Tympanal organs compact. Venulae primae almost joined to form a complete ring, partially desclerotized on each side of transverse ridge. Tympanic pockets absent. Venulae secundae present, strongly sclerotized, parallel. Tympanic bridge projected ventrally, almost connected medially, wings medium-sized. Praecinctorium double and hairy. Tympanic frame very strongly projected ventrally beyond venulae primae and concave laterally to form the tympanic crest which is anteriorly situated in the tympanic sac. Tympanum oblique to sternal plane. Tympanic drum short and almost circular. Spinula visible.

Male genitalia (fig. 245). Uncus laterally flattened, apically bilobed. Gnathos short, denticulate at apex dorsally. Tegumen pedunculi narrow, connected near base of uncus, ventrally sclerotized. Valva without projections on costa and sacculus. Vinculum laterally narrow, with a bulbous saccus. Juxta with thin lateral arms projected posterad. Pseudosaccus present. Aedeagus opened apico-dorsally, without a complete coecum penis; vesica armed with a single cornutus.

Female genitalia (fig. 306). Anal papillae connected dorsally, narrow. Posterior apophyses thin, slightly shorter than papillae. Anterior apophyses very long, subbasally slightly enlarged. Segment VIII narrowing down ventrally, not forming a complete ring and not connected to sterigma. Sterigma internal, short, cup-shaped. Ductus and corpus bursae not differentiated, very long, without signum.

Relationships. Minet (1982) erected the tribe Myelobiini on the basis of the bilobed praecinctorium of two genera: the Neotropical Myelobia and Eschata Walker from the Oriental region. My analysis shows that genus Myelobia is most closely related to Diatraea but this is not supported by any exclusive synapomorphy.

Diversity and distribution. Genus Myelobia is found in the Neotropical region from Mexico to Argentina. It includes 17 species (Bleszynski 1967). The ten species of genus Eschata are mostly distributed in India (Bleszynski & Collins 1962).

Natural history and immature stages. Dyar (1917) and Forbes (1926) mentioned that the larva of Myelobia is a borer in bamboo. Dyar (op. cit.) added a short description of the larva of M. smerintha Hübner. Passoa (1986) gave a diagnosis of the larva of M. decolorata (H.-S.) but since the determination was doubtful, he did not give a full description.

The bionomics and immature stages of _Eschata_ are apparently unknown.

Comments. I did not study the genus _Eschata_ and I cannot comment on its hypothesized relationship with _Myelobia_. The above description being based on only one species, it certainly is not the best representation of the tribe or even of the genus _Myelobia_.

5.1.4 ARGYRIINI

Type genus: *Argyria* Hübner, 1818: 28; type-species: *Argyria nummulalis* Hübner, by subsequent designation by Fernald (1896).

Diagnosis. I have not found any character-state which would qualify as a synapomorphy for the three North American genera associated here. Nevertheless, I believe this group to be monophyletic. The moths can be distinguished by the generally short labial palpus and forewing, by their very short dorsal connection of the vinculum, dorsally shortened female segment VIII, short anterior apophyses and by their mostly satiny-white colour with sometimes orange or dark-brown markings.

Description. Based on my observations on the North American species.

Head (figs. 12, 13, 15, 30-32). Fronto-clypeus rounded, somewhat produced in *Vaxi auratella*. Ocellus and chaetosema present. Labial palpus generally short, especially in *Argyria* and *Urola* (1.35X and 1.4X width of head respectively in dissected specimens of *A. nummulalis* and *U. nivalis*). Haustellum well developed. Vestiture variable, fronto-clypeal scales usually appressed, never long; vertexal scales sometimes produced anterad between antennae; labial palpus scales apically produced in *Vaxi* only; maxillary palpus more or less triangularly scaled. Male antennal flagellomeres (figs. 62-64) serrate, with higher number of sensilla trichodea in *Urola nivalis* but apparently without other types of sensilla, with higher number of sensilla coeloconica in *Argyria nummulalis* and apparently without sensillum styloconicum and auricillicum, with slightly more than average sensilla trichodea in *Vaxi auratella* and possibly without sensillum auricillicum.

Wings (figs. 77, 79, 108). Female frenulum at least triple. Male frenulum hook present. Forewing R1 present and free (*Argyria*, *Urola*) or connected with Sc (*Vaxi*); R2 free; R3 present and connected to R4 (sometimes very faint or lost in some *Argyria*); R5 present and free (*Argyria*, *Urola*) or connected to R3+4 (*Vaxi*); M2 & M3 not stalked; Cubitus with CuA1 & CuA2; Anal sector with only 2A (*Argyria*) or with 2A and traces of 3A (*Vaxi*, *Urola*). Hindwing M1 fused to Sc+R1 or connected to it by a very short cross-vein at anywhere between 1/4 to 1/2 of its length; cell open; M2, M3, CuA1 & CuA2 all present and connected below cell. Forewing generally shorter than in most Crambini (2.12X-2.31X its width in mounted specimens of *Vaxi auratella* and *Urola nivalis* respectively). Forewing (fig. 140) mostly satiny white, sometimes with orange or dark-brown markings at median line, outer margin or along inner margin; never with median longitudinal markings.

Tympanal organs (figs. 201, 202, 206). Tergo-sternal sclerite sharply bent at base in *U. nivalis* and *A. nummulalis*. Venulae primae joined to form a complete sclerotized ring. Tympanic pockets not very strongly developed (*U. nivalis*, *V. auratella*) and sometimes absent (*A. nummulalis*). Venulae secundae present (*U.*

nivalis, *A. nummulalis*) or absent (*V. auratella*). Tympanic bridge strongly produced ventrally. Praecinctorium simple, with free dorsal margin sclerotized to apex in *Argyria nummulalis*. Tympanic frame slightly (*A. nummulalis*) or relatively strongly projected ventrally. Tympanic crest well developed, situated near middle in tympanic sac. Tympanum slightly oblique to the sternal plane. Tympanic drum more or less globular, sometimes partially closed anteriorly (*A. nummulalis*). Spinula visible only in *Urola nivalis*.

Male genitalia (figs. 250-252). Uncus rounded in *Urola*, otherwise simple and narrow. Gnathos apically upturned, conspicuously elbowed (*Urola*, *Argyria lacteella*) or elongate. Tegumen peduncull narrow, generally connected close to base of uncus; unsclerotized ventrally. Valval costa with free arm; cucullus well developed; sacculus with basal weakly sclerotized but strongly setose lobe in *Urola* and *Argyria lacteella*. Vinculum without saccus, basally up-turned, convex (*Argyria*, *Urola*) or concave (*Vaxi*), projected posteriorly in a long thin arm in *Urola*. Intersegmental membane with conspicuous lateral coremata in *Urola* and *Argyria*. Pseudosaccus absent. Juxta well sclerotized, conspicuously developed into a simple long arm in *Urola*. Aedeagus variously shaped; vesica usually with cornuti.

Female genitalia (figs. 301-303). Anal papillae connected dorsally, narrow. Posterior apophyses about as long as papillae, subapically enlarged in *Vaxi*. Apophyses anteriores very short. Segment VIII shortened dorsally, strongly fused to sterigma. Sterigma with an externally sclerotized ventral extension (*Urola*, *Vaxi*) or internal and cup-shaped (some *Argyria*). Ductus bursae long or short (*Urola*), sclerotized or not. Corpus bursae variously shaped, without signum.

Relationships. The phylogenetic affinities of this tribe to other Crambinae is unknown. However, a possible affinity of the Argyriini with the Crambini is possible (see Relationships of Crambini below). Within the group it seems that *Vaxi* is the less derived genus because of its generally longer (compared with other Argyriini) labial palpus and forewing, and less derived male genitalia. Genus *Urola* seems to be directly derived from *Argyria lacteella* (or a related species) with which it shares various derived character-states in the male genitalia.

Diversity and distribution. At present, the North American fauna contains three genera of Argyriini: *Argyria* (four species), *Vaxi* (three species) and *Urola* (one species) (Klots 1983). Thirty-four more species in these three genera are known from the Neotropical Region (Bleszynski 1967). I do not know if other genera elsewhere in the world should be associated with the North American Argyriini. The North American species of *Vaxi* are distributed in the East from Québec to Florida and Texas. The other two genera are also mostly restricted to eastern North America with an extension in the Southwest to Arizona for *Urola*.

Natural history and immature stages. I am not aware of any report on the morphology of the immature stages of Argyriini. The bionomics of the species is also unknown except for some information on the seasonal abundance of _Urola nivalis_ in Virginia (Tolley & Robinson 1986).

Comments. Bleszynski (1967) synonymized _Urola_ under _Argyria_.

5.1.5 DIPTYCHOPHORINI

Type genus: Diptychophora Zeller, 1866: 153; type-species: Diptychophora kuhlweini Zeller, by monotypy.

Diagnosis. This tribe is believed to form a monophyletic group (at least in North America) on the basis of the following two synapomorphies: the forewing length compared to its width is extremely reduced (character 8) and the terminal scales on the flagellomeres are erect (character 7). The moths are usually small (less than 15 mm in wingspan) and often brightly coloured.

Redescription. Based on Gaskin (1971, 1974, 1975c, 1985, 1986, 1987) and my own observations on the North American species and some others such as Pareromene exsectella (Christoph) from Japan.

Head (fig. 16). Fronto-clypeus rounded, not produced. Ocellus and cheatosema reduced or absent. Labial palpus variably elongate (1.61X width of head in P. exsectella, but not longer than head width in D. harlequinalis). Haustellum fully developed. Vestiture with appressed scales on fronto-clypeus, sometimes with produced vertexal scales; maxillary palpus triangularly scaled; labial palpus scales often produced. Male antennal flagellomeres (figs. 73, 73) with erect apical scales, with average numbers of sensilla except for absence of sensillum auricillicum.

Wings (figs. 90-91). Female frenulum simple, double or triple. Male frenulum hook present or absent. Forewing R1 present and free or connected with Sc; R2 free; R3 present and connected to R4 or missing; R5 present and free; M2 & M3 not stalked; Cubitus with CuA1 & CuA2; Anal sector with only 2A. Hindwing M1 distinctly separated from Sc+R1 but connected to it by a cross-vein at about 1/2 of its length; cell usually closed; M2, M3, CuA1 & CuA2 present and connected below cell; or with one vein missing (*Microcausta*). Forewing often brightly coloured (fig. 140d) with median and subterminal lines, a short white diagonal mark at apex and black dots apically in Cubital sector; outer margin often notched near M1 and M3.

Tympanal organs (figs. 186, 190). Based on *Microcausta flavipunctalis.* *Diptychophora* *harlequinalis*, *D.* *powelli* B. Landry, and *P.* *exsectella*. Venulae primae usually not joined to form a complete ring but almost so in *D.* *powelli*. Transverse ridge may be present or absent (*D.* *harlequinalis*). Tympanic pockets usually absent, except in *M.* *flavipunctalis*. Venulae secundae sometimes present, poorly sclerotized, convergent. Tympanic bridge slightly projected ventrally in *D.* *harlequinalis* (condition unknown in *Microcausta*), sometimes very short with tympanic frame and tympanum connected very close to ventral margin of venulae primae (*Microcausta*) in which case tympanic wings very short. Praecinctorium simple. Tympanic frame only slightly projected ventrally beyond venulae primae. Tympanum oblique but close to being in line with sternal plane. Tympanum slightly variable in shape, sometimes partially closed medially (D. harlequinalis). Tympanic crest anteriorly situated in tympanic sac. Spinula not visible.

Male genitalia (figs. 248, 249). Uncus simple. Gnathos most often apically up-turned. Tegumen peduncull narrow and connected dorsally very close to base of uncus, not sclerotized ventrally. Valval costa and sacculus sometimes sclerotized and projected. Vinculum usually narrow, with a saccus, with fenestrae in Microcausta. Juxta well developed. Pseudosaccus absent. Aedeagus usually slender, sometimes ornate apically; vesica with or without cornuti.

Female genitalia (figs. 307, 308). Anal papillae connected dorsally. Posterior apophyses always much longer than papillae. Anterior apophyses usually slightly shorter than posterior ones, rarely very short. Segment VIII variable in length, not connected to sterigma. Sterigma usually not sclerotized. Antrum of ductus bursae usually sclerotized. Ductus bursae usually long, sometimes partly sclerotized beyond antrum, usually with a secondary pouch before connection with ductus seminalis. Corpus bursae often small and circular, usually simple, double in one species, usually without or with one, rarely two, signa.

Relationships. The phylogenetic affinities of the Diptychophorini with other crambine tribes are unknown. In North America, the two genera present, *Microcausta* and *Diptychophora*, are quite distinct from each other but undoubtedly related (see Diagnosis).

Diversity and distribution. The tribe is pantropical in distribution (Gaskin 1971). It contains nine genera and 192 species. The New World fauna includes six genera, many of which were recently described (Gaskin 1986, 1987) to accomodate very few species with highly derived male genitalic features. I described a new species from Mexico (Landry 1990) which would have required a new genus if this trend had been followed. However, I decided to describe it in *Diptychophora*, the oldest generic name available in this fauna. I believe that we have only seen a small fraction of the diversity in this group and that it is wiser to wait for a more complete data set before starting to change the nomenclature of this group to any extent. Since the publication of my paper, I have seen four more undescribed Diptychophorines from South America. In North America, two species of *Diptychophora* and two of *Microcausta* have been reported; three of those are in Arizona and one species of *Microcausta* occurs in Florida.

Natural history and immature stages. Some information on the morphology of the immature stages is known from three New Zealand species of *Glauchocaris* (Gaskin 1971). All were reported to feed on mosses.

5.1.6 UNASSIGNED GENERA OF CRAMBINAE

DIATRAEA Guilding, 1828

Iesta Dyar, 1909

Diatraerupa Schaus, 1913

Trinidadia Dyar & Heinrich, 1927

Eodiatraea Box, 1953

Crambidiatraea Box & Capps, 1955

Zeadiatraea Box, 1955

Diagnosis. There is no single synapomorphy to define *Diatraea* but the lack of ocellus in all species, the presence of pockets of specialized scales on the males' second abdominal segment laterally in most species, the basal extensions of the tegumen in most species, and the hair tufts on the male hind tibia in several species form a unique combination of characters; the last three character-states being present only in this genus. It is possible also that the shape of the female sterigma is unique to *Diatraea*.

Description. Based on Dyar & Heinrich (1927), Box (1931, 1953, 1955), Bleszynski (1969) and my observations on the North American species.

Head. Fronto-clypeus slightly convex, not produced to strongly produced, truncated or with a point. Ocellus absent. Chaetosema well developed. Labial palpus at least 2X width of head (2.26X its width in prepared specimen of *D. evanescens*). Haustellum usually short, slightly shorter than labial palpi in D. evanescens. Vestiture with vertexal scales medium-sized, slightly produced anteriorly; fronto-clypeal scales appressed; maxillary palpus scales produced, not triangular. Male antennal flagellomeres serrate, female's filiform (sensilla not studied).

Wings (fig. 104). Female frenulum double or triple. Male frenulum hook present. Forewing R1 present and connected with Sc. R2 usually free but sometimes connected with R3+4. R3 present and connected to R4. R5 present and free. M2 & M3 rarely stalked. Cubitus with CuA1 & CuA2. Anal sector with 2A and traces of 3A. Hindwing M1 fused to Sc+R1 or connected to it by a very short cross-vein near the middle of the wing. Cell closed. M2, M3, CuA1 & CuA2 present. Forewing elongate (2.66X its width in mounted specimen of D. evanescens). Forewing straw-coloured; pattern (fig. 135e) often with darker or paler lines along venation, often with a small dark-brown discal spot, sometimes with variably distinct median and subterminal transverse lines.

Tympanal organs (fig. 194). Venulae primae sometimes joined to form a complete ring, otherwise only partially visible posteriorly to tympanic sac. Transverse ridge present, or ill-defined or completely absent. Tympanic pockets absent. Venulae secundae usually present. Tympanic bridge distinctly projected ventrally, shortened longitudinally. Praecinctorium simple, with a dorsal sclerotized support. Tympanic frame typically very strongly projected ventrally beyond venulae primae. Tympanic crest situated anteriorly in tympanic sac. Tympanum at right angle to sternal plane. Tympanic drum semi-circular. Spinula not visible.

Male genitalia (figs. 234, 246). Uncus usually narrow and apically hooked, sometimes flattened, broad and lobed. Gnathos usually narrow, apically upturned and with denticles dorsally towards apex, sometimes shorter with thick spines or flattened and with lateral extensions. Tegumen with a broad dorsal connection, arms usually narrow, usually with a pair of extensions extended posterad from base of ventral margin. Vinculum laterally narrow, with short bulbous saccus. Valval costal process usually present at base, short, simple or double; cucullus long and narrow; sacculus not strongly sclerotized or projected. Pseudosaccus present. Juxta prominent, usually elongate with paired lateral arms or short with very long lateral arms. Aedeagus usually without coecum penis, often short and straight, usually dorso-apically opened; vesica with or without cornuti.

Female genitalia (fig. 305). Anal papillae elongate, connected dorsally, without distinct sclerotized longitudinal band of support. Posterior apophyses about as long as papillae. Anterior apophyses 2-3X length of posterior ones. Segment VIII larger dorsally, not connected to sterigma. Sterigma with shallow sclerotized, often spinose, depressions on each side of median ostium. Ductus bursae short, wide, often sclerotized. Corpus bursae variable in shape and length, without signum.

Relationships. In my analysis of the major lineages of Crambinae (fig. 4), Diatraea is shown as the sister-group of Myelobia but this is not supported by any exclusive synapomorphy. Diatraea was believed to be a derivative of Chilo (Bleszynski 1966), which is probably a valuable suggestion.

Diversity and distribution. Bleszynski (1967) listed 55 species in Diatraea which occurs from New Jersey southward to Argentina. In North America, seven species occur mostly in the Gulf Coast states.

Natural history and immature stages. Diatraea saccharalis, D. grandiosella, D. crambidoides and D. lineolata, are among the most economically important pests of graminaceous crops such as corn, sugar cane and sorghum in the warmer parts of the New World. These species of Diatraea, and probably all others, also feed on various other Poaceae. The larval morphology of the first three species mentioned above was illustrated by Neunzig (1987). Comprehensive treatments of the genus were provided by Dyar & Heinrich (1927), Box (1931, 1960) and Bleszynski (1969). Several recent reports demonstrate important research efforts made on these pest insects (Agnew et al. 1988, Pashley et al. 1990, Rodriguez-del-Bosque et al. 1988a, 1988b, 1990, Tiwari et al. 1991).

Comments. In addition to the features mentioned in the description, it should be noted that the males of many species of Diatraea have a pair of pockets containing short specialized scales laterally on the second abdominal segment (see fig. 194) and that some also have a tuft of hairs on the inner side of the hind tibia.

CHILO Zincken, 1817

Chilona Sodoffsky, 1837

Proceras. auct. (not Bojer, et al., 1856)

Borer Guenée, 1862

Diphryx Grote, 1881

Nephalia Turner, 1911

Hypiesta Hampson, 1919

Silveria Dyar, 1925

Chilotraea Kapur, 1950

Diagnosis. The moths of this genus can be distinguished by a synapomorphy of their wing pattern: the presence of shining golden scales.

Description. Based on Bleszynski (1970b) and my own observations.

Head (fig. 23). Fronto-clypeus rounded, produced or not, with or without one or two points. Ocellus and chaetosema well developed. Labial palpus at least 3X as long as head width (3.69X in one dissected specimen of C. phragmitellus). Vestiture variable, sometimes with dishevelled palpi (C. erianthalis), maxillary palpus scaling usually produced (not triangular). Male antennal flagellomeres (fig. 70) serrate, with full complement and average numbers of sensilla except for more than average sensilla coeloconica (7) and no sensillum auricillicum.

Wings (figs. 105, 107). Female frenulum triple or quadruple. Male frenulum hook present. Forewing R1 present and free (although sometimes connecting with Sc); R2 free; R3 present and connected to R4; R5 present and free (sometimes shortly stalked with M1 or connected to R3+4); M2 & M3 not stalked; Cubitus with CuA1 & CuA2; Anal sector with 2A and traces of 3A. Hindwing M1 fused to Sc+R1 or connected to it by a very short cross-vein at anywhere between 1/4 to 1/2 of its length; cell closed; M2, M3, CuA1 & CuA2 present. Forewing of average length (2.54X its width in one specimen of C. phragmitellus). Forewing pale brown, pattern (fig. 135c) sometimes with transverse lines and with shining golden scales. Sexually dimorphic; females with more elongate wings (fig. 105).

Tympanal organs (fig. 193). Venulae primae joined to form a complete ring. Transverse ridge present. Tympanic pockets absent. Venulae secundae usually present, sometimes rather large. Tympanic bridge only slightly projected ventrally. Praecinctorium simple, without dorsal sclerotized support. Tympanic frame typically very strongly projected ventrally beyond venulae primae. Tympanic crest usually present, situated anteriorly in tympanic sac. Tympanum oblique at about 45^0 to sternal plane. Tympanic drum semi-circular. Spinula visible.

Male genitalia (fig. 253). Uncus simple, short and stout. Gnathos also short and stout, elbowed, apically upturned. Tegumen usually with narrow pedunculi often with a short connection dorsally, unsclerotized ventrally. Valva usually with a broad cucullus; often with a short process at base of costa; without process on sacculus. Vinculum very narrow with a short saccus, often produced anterad. Pseudosaccus present. Juxta well developed with two lateral arms of variable length, often asymetrical, extended posterad. Aedeagus usually long and slender, with or without coecum penis, sometimes divided into dorsal and ventral flaps; manica often sclerotized ventrally and elongate; vesica with or without cornuti.

Female genitalia (fig. 299). Anal papillae connected dorsally and ventrally, with an incomplete narrow sclerotized band of support in middle. Posterior apophyses about as long as papillae. Anterior apophyses about 2X length of posterior ones. Segment VIII wide dorsally, narrower ventrally, never connected to a sterigma. Latter absent. Antrum of ductus bursae evenly sclerotized for short distance. Ductus bursae variable in length and width, often with long sclerotized internal ridges. Corpus bursae variable in shape, with one, two or no signum.

Relationships. The phylogenetic relationships of Chilo to the other Crambinae remain unresolved. In his revision of the genus, Bleszynski (1970) mentioned that the following genera, along with Chilo, formed the "Chilo-complex": Diatraea Guilding, Leonardo Bleszynski, Zacatecas Bleszynski, Chilandrus Bleszynski, Myelobia Herrich-Schaeffer, Chiqua Bleszynski, Malgasochilo Bleszynski, Epina Walker and Japonichilo Okano. All these genera were grouped on the basis of their similar male and female genitalia, the presence of a saccus and pseudosaccus in the male genitalia and a triple frenulum in the female. This complex of genera was believed to be closely related to the "Acigona-complex" (here placed in the Haimbachiini, new tribe). However, no mention of the rationale behind this assertion was made. Both groups of genera in North America share a similarly projected tympanic frame.

Diversity and distribution. Genus Chilo includes 41 species which are mostly distributed in the Ethiopian and Oriental Regions. Several species also occur in the Palearctic Region while the Nearctic fauna includes only four species. Only Chilo chiriquitensis (Zeller) extends south into the Neotropical Region to Panama.

Natural history and immature stages. Several species of Chilo are notorious pests of graminaceous crops such as sugar cane, rice and maize. The extensive literature published on the pest species has been listed by Katiyar (1964). Bleszynski (1969) also treated the pest species of Chilo. The larvae are borers in the stalks of their hostplant. The larva of C. phragmitellus which feeds on Phragmites communis Trin. (Poaceae), was described by Hasenfuss (1960).

Comments. An exocrine gland with associate narrow and elongate scales (fig. 131) was discovered in the foreleg coxa of Chilo phragmitellus.

EPINA Walker, 1866

Diatraenopsis Dyar & Heinrich, 1927

Diagnosis. Two synapomorphies, the peculiar shape of the male gnathos and that of the female sterigma, can be used to diagnose the genus.

Description. Based on my own observations.

Head. Fronto-clypeus rounded, not produced. Ocellus vestigial. Chaetosema present. Labial palpus of medium length (2.1X head width in one specimen of E. alleni). Haustellum about as long as labial palpus. Vestiture with short scales produced anteriorly on fronto-clypeus and vertex; maxillary palpus with dorsal scales longer, not distinctly triangular. Male antennal flagellomeres serrate (not studied with scanning electron microscope); female flagellomeres filiform.

Wings (fig. 109). Female frenulum double. Male frenulum hook absent. Forewing R1 present and free. R2 free. R3 present and connected to R4. R5 present and free. M2 & M3 not stalked. Cubitus with CuA1 & CuA2. Anal sector with 2A and traces of 3A. Hindwing M1 connected to Sc+R1 by a very short cross-vein slightly beyon middle. Cell open. M2, M3, CuA1 & CuA2 all present. Forewing elongate (2.41X its width in one mounted specimen of E. alleni). Forewing pattern (fig. 135a) pale to dark brown with small discal spot and thin lines along and between venation. Distinctly dimorphic in size and colouration: the males being smaller and darker. Wingspan reaching 5.0 cm in females of E. dichromella.

Tympanal organs (fig. 196). Venulae primae joined to form a complete ring. Transverse ridge present. Tympanic pockets absent. Venulae secundae absent. Tympanic bridge strongly projected ventrally. Praecinctorium simple, with a dorsal sclerotized support. Tympanic frame strongly projected ventrally beyond venulae primae. Tympanic crest present, situated anteriorly in tympanic sac. Tympanum at right angle to sternal plane. Tympanic drum semicircular. Spinula not visible.

Male genitalia (fig. 247). Uncus thickly sclerotized, somewhat laterally compressed, shortly bilobed apically. Gnathos straight, with arms connected beyond middle, apically truncated. Tegumen dorsal connection large, pedunculi medium-sized, unsclerotized ventrally. Vinculum broadly rounded, extended anteriorly, about as long as valva. Valval costal process very large, with large curved arm; cucullus narrow, slightly longer than costal process; sacculus unsclerotized. Pseudosaccus present. Juxta short, thickly sclerotized. Aedeagus narrow, long, slightly downcurved, apically with free thin ventral flap; vesica without cornutus.

Female genitalia (fig. 304). Anal papillae long, narrow, connected dorsally and ventrally, without complete narrow sclerotized band of support. Posterior apophyses shorter than papillae, straight.

Anterior apophyses about as long as posterior ones. Segment VIII equally long dorsally and ventrally, intimately connected to sterigma. Sterigma strongly sclerotized, with two elongate, rounded and ridged lateral depressions dorsally, and short protruding tube. Ductus bursae narrow, as long as segment VII. Corpus bursae rounded, without signum.

Relationships. My cladistic analysis did not provide a clear hypothesis of relationship between *Epina* and the other crambine lineages.

Diversity and distribution. The genus at present contains two species. One of them, *E. alleni*, is found from Nova Scotia to New Jersey. The other, *E. dichromella*, occurs in Florida and Cuba.

Natural history and immature stages. Unknown although I suspect that the larva is a borer in a large riparian grass or sedge species.

CALAMATROPHA Zeller, 1863

Myeza Walker, 1863

Diagnosis. No single character can be used to distinguish this genus from other crambine genera but the closed hindwing cell coupled with the connected vein R5 in the forewing is a unique combination of features. In addition, the reduced ocellus, the dorsally connected female anal papillae, the triple female frenulum, the presence of a pseudosaccus and the Crambini-like tympanal organs is a unique combination of apomorphic and plesiomorphic traits.

Description. Based on Bleszynski (1961a) and on my observations on Calamotropha paludella (Hübner).

Head (fig. 20). Fronto-clypeus usually rounded and somewhat projected. Ocellus usually or strongly reduced. Chaetosema present. Labial palpus 2-4X head width (2.43X in one dissected specimen of C. paludella). Vestiture with projected vertexal scales between antennae, appressed on fronto-clypeus, only shortly produced on maxillary palpus; labial palpus triangularly dilated with scales. Male antennal flagellomere (fig. 54) serrate, with full complement and average number of sensilla except for high number of sensilla trichodea (100-120) and no sensillum auricillicum.

Wings (fig. 82). Female frenulum usually triple, sometimes double. Male frenulum hook present. Forewing R1 present and sometimes connected with Sc; R2 free; R3 present and connected to R4; R5 present and connected to R3+4; M2 & M3 not stalked; Cubitus with CuA1 & CuA2; Anal sector with 2A and traces of 3A. Hindwing M1 fused to Sc+R1 or connected to it by a very short cross-vein at anywhere between 1/4 to 1/2 of its length; cell closed; M2, M3, CuA1 & CuA2 all present. Forewing of average length (2.46X its width in one prepared specimen of C. paludella). Forewing brown (fig. 135d), generally with faint transverse lines and a dark-brown spot in cell, rarely (two species) with large longitudinal dark-brown and white bars from base to apex.

Tympanal organs (fig. 191). Venulae primae not entirely joined to form a complete ring, anterior (lateral) part curved towards middle before transverse ridge. Latter medially convex. Tympanic pockets present. Venulae secundae present, thin, parallel. Tympanic bridge projected ventrally, with a better sclerotized ventral bar, connected medially, tympanic wings medium-sized. Praecinctorium simple, not extended beyond transverse ridge. Tympanic frame rather strongly projected ventrally beyond venulae primae. Tympanum oblique to sternal plan. Tympanic drum medium-sized, hemicircular. Tympanic crest anteriorly situated in tympanic sac. Spinula visible.

Male genitalia (fig. 254). Uncus usually long and slender with basal hairs, rarely bifurcated. Gnathos often long and slender, variably shaped, apically down-turned, straight or upturned.

Tegumen pedunculi medium-sized or narrow laterally, usually with a very short dorsal connection, unsclerotized ventrally. Valva variously shaped, often without free membranous cucullus; sclerotized costa often with spines or projections; sacculus more rarely sclerotized. Vinculum often wide laterally, ventro-cephalic margin convex or concave; without saccus. Pseudosaccus present. Juxta very narrow and V-shaped in *C. paludella*. Aedeagus usually medium-sized, coecum penis well developed; vesica usually with cornuti.

Female genitalia (fig. 310). Anal papillae connected dorsally and ventrally, narrow. Posterior apophyses about as long as papillae. Anterior apophyses absent to about as long as posterior ones. Segment VIII narrower dorsally but not as reduced as in most Crambini, with or without sclerotized connection with sterigma. Sterigma usually a short internal or external variable tube. Ductus bursae usually long and unsclerotized. Corpus bursae variably shaped, usually without but sometimes with one large signum.

Relationships. As explained below under the same heading concerning the Crambini, genus *Calamotropha* shares a number of derived features with the Crambini. However, it also has various plesiomorphic features such as the presence of the male frenulum hook and the coalesced papillae anales of the females. This may mean that the genus is an intermediate between the Crambini and their ancestor. This is probably why Gaskin (1988) erected a tribe for the genus.

Diversity and distribution. In his revision of 1961, Bleszynski dealt with the 81 then known species of the genus on a worldwide basis. The most speciose geographical regions are the Ethiopian and the Oriental regions with 32 and 37 species respectively. Fourteen species are known from the Palaearctic Region while five are found in the Australian Region.

Natural history and immature stages. The larvae of only two species are known. That of *C. paludella* is a borer in *Typha latifolia* L. (Typhaceae). A description was provided by Hasenfuss (1960). The immatures of *C. shichito* Marumo (1931) from Japan were described and figured. A short description of the latter was given by Bleszynski (1965) but the foodplant was not mentioned. I was not able to see the original description.

5.1.7 CRAMBINI, status revised

Type genus: Crambus Fabricius, 1798.

Diagnosis. The tribe is believed to be monophyletic on the basis of the shared presence of the following derived character-states: the apex of the gnathos is directed downward or straight behind (character 27) and the female anal papillae are disconnected dorsally (character 41). In addition, the open hindwing cell (character 15) and the shape of the tympanal organs are diagnostic but not exclusive to the Crambini.

Redescription.

Head (figs. 6, 8, 14, 17, 19, 24-29). Fronto-clypeus usually rounded but sometimes produced anterad, with or without one or more points (Agriphila, Catoptria). Ocellus present. Chaetosema well developed. Labial palpus variably elongate; about 1.3-4X longer than head width. Haustellum usually long and functional, sometimes reduced, rarely lost ("Crambus" angulatus). Vestiture (figs. 25, 27): fronto-clypeal and vertexal scales appressed or produced; maxillary palpus scales more produced rather than forming a triangle; labial palpus scales often produced, sometimes dishevelled (Agriphila). Male antennal flagellomeres (figs. 33-52, 55, 57-61) usually serrate, sometimes strongly serrate, pectinate or bipectinate (Thaumatopsis, some Parapediasia and some Palaearctic Pediasia); variability in sensilla number expressed under each genus. Female antennal flagellomeres (fig. 56) usually simple.

Wings (figs. 76, 78, 80, 81, 84-89, 92-96, 110-121). Female frenulum with one, two, three or more bristles. Male frenulum hook usually absent, present in Euchromius and some Catoptria and Agriphila. Forewing R1 present and free (although sometimes connecting with Sc in some species of Pediasia, Agriphila and Thaumatopsis), or connected with Sc (Loxocrambus, "Crambus" angulatus, Chrysoteuchia, "Crambus" dimidiatellus, Fernandocrambus and Neodactria except in one species); or absent (Platytes, Raphiptera, one species of Fissicrambus). R2 free (sometimes connected with R3+4 in Agriphila). R3 present and connected to R4 (sometimes very faint or lost as in some Euchromius, Microcrambus and Crambus) or missing (Almita, Loxocrambus). R5 present and sometimes free (Euchromius, Platytes) but usually connected to R3+4; or absent (Raphiptera). M2 & M3 sometimes shortly stalked (Almita, La, Tehama) but usually not stalked (except in some species of Thaumatopsis, Loxocrambus, Microcrambus, Agriphila and Fernandocrambus). Cubitus with CuA1 & CuA2 (most genera) or with CuA1 but without CuA2 (Almita, Raphiptera). Anal sector with 2A and traces of 3A. Hindwing M1 fused to Sc+R1 or connected to it by a very short cross-vein at anywhere between 1/4 to 1/2 of its length. Cell open. M2, M3, CuA1 & CuA2 all present and connected below cell in most genera; with one vein missing in Raphiptera and Almita.

Tympanal organs (figs. 171, 180, 203-205, 207-232). Note that most of the features discussed in descriptions may vary between sexes and between individuals of the same sex in same species as shown in two ventral views of Crambus pascuellus (fig. 223). Venulae primae usually joined to form a complete sclerotized ring, except in T. pectinifer, T. solutella and T. actuella. Transverse ridge usually present except in the above-mentioned trio of species and in C. trichostoma. Tympanic pockets usually present, except in the above-mentioned four species and in L. awemensis; also reduced in Arequipa turbatella and Almita texana. Venulae secundae present or absent. Tympanic bridge more or less produced ventrally; normally connected medially except in species with reduced organs (T. pectinifer and C. trichostoma) and in R. argillaceella; tympanic wings reduced in T. pectinifer and C. trichostoma. Praecinctorium simple, variable in length; sometimes with free dorsal margin sclerotized for support. Tympanic frame only very slightly projected ventrally beyond venulae primae. Tympanic crest usually present but not visible in L. canellus; normally anteriorly situated but sometimes more central (P. trisecta), variable in size, usually crescent-shaped but sometimes more elongate (Euchromius). Tympanum slightly oblique to sternal plane or at 90° to that plane in Ancylolomia. Tympanic drum sometimes reduced (T. pectinifer, C. trichostoma), generally rather elongate, sometimes more circular (L. canellus). Spinula normally visible.

Male genitalia (figs. 233, 255-289). Uncus usually simple, sometimes bilobed or trilobed (Arequipa, many Ancylolomia). Gnathos sometimes reduced (Almita, Raphiptera), apically upturned in Ancylolomia but otherwise downturned or straight. Tegumen variable in shape, dorsally usually largely sclerotized, often ventrally sclerotized to form a bridge between two pedunculi. Valval costa often heavily sclerotized at base and with a projection; cucullus variable in shape, sacullus sclerotized in a few genera (Crambus, Fernandocrambus, Fissicrambus, Tehama, Thaumatopsis). Vinculum with or without a saccus, sometimes the lateral margins produced anterad. Juxta usually small, flat and trough-shaped, sometimes extended posterad, rarely with two lateral arms (one species of Microcrambus). Pseudosaccus present. Aedeagus usually attached to juxta near middle but attached apically in Ancylolomia; manica sometimes sclerotized ventrally (Fissicrambus); usually appressed on aedeagus but disconnected on most of length in Almita; coecum penis present except in Ancylolomia; vesica with or without cornuti.

Female genitalia (figs. 309, 311-338). Anal papillae not connected dorsally, sometimes distinctly divided into two lobes (Crambus, Fernandocrambus, Chrysoteuchia). Posterior apophyses variable in length, usually narrow, never much longer than papillae, rarely lost (Raphiptera). Anterior apophyses usually short and sometimes lost. Segment VIII most often strongly sclerotized and connected with sterigma ventrally, often reduced in length dorsally to lost (Loxocrambus). Sterigma usually present, absent in Loxocrambus. Ductus bursae sclerotized or not. Corpus bursae with 0-3 signa.

Relationships. The relationships of the tribe among the other Crambinae are presently considered unresolved. However, it is possible that the Crambini are more closely related to the Argyriini on the basis of the open hindwing cell (character 15), the shape of the female segment VIII with very short anterior apophyses and the similar shape of the tympanal organs (characters 19 and 20). Calamotropha also seems to be close to the Crambini on the basis of the shape of the gnathos apically (character 27), the stalked forewing vein R5, the open hindwing cell and the presence of tympanic pockets (character 20).

Diversity and distribution. Nineteen North American genera are here believed to belong to the Crambini. Based on the definition of the Crambini given in the above diagnosis, Gaskin's (1975a) subtribe Corynophorina cannot be considered a member of the Crambini because it is plesiomorphic for characters 15 and 27. However, he added seven more Palaearctic, Oriental and New Zealand genera to the Crambini list (Metacrambus, Flavocrambus, Xanthocrambus, Angustalius, Maoricrambus and Orocrambus). Twelve more genera of Crambini are found in the Neotropical fauna (Munroe, in press). Thus, in total, the World fauna of Crambini includes at least 39 genera. The tribe has the most widespread distribution of all recognized tribes; it is the same as the distribution given for the subfamily.

Natural history and immature stages. The Crambini include several pests of sod in North America but few species are injurious to graminaceous crops. Most species feed above ground on the leaves and stems of grasses or sedges, or on mosses (Catoptria). The larvae are known to web galleries with silk, frass and debris in which they retreat in the daytime. Chrysoteuchia is known to have a more varied diet and to feed below ground on roots of grasses. The immature stages were described for several species in various genera (see below under the same heading in the discussion of the genera).

Comments. The status of the tribe is revised here to include Ancylolomia (see discussion in chapter 4) and to exclude the Corynophorina of Gaskin (1975a).

5.1.7.1 A KEY TO THE GENERA AND UNASSIGNED SPECIES OF CRAMBINI OF NORTH AMERICA

Based on external features and male genitalia.

1. Hindwing venation lacking one vein among M2-M3-CuA1-CuA2..2
1'. Hindwing with M2-M3-CuA1-CuA2 present....................3

2(1). Forewing apex produced; median line incomplete; with large longitudinal white streak from base to median line...*Raphiptera*
2'. Forewing apex not produced; median line complete; pattern with only thin paler lines along venation...........*Almita*

3(1'). Forewing R5 free...4
3'. Forewing R5 connected to R3+4...........................5

4(3). Forewing pattern with straight yellowish median line and a series of terminal dots followed by silver dots on basal half of outer margin................................*Euchromius*
4'. Forewing pattern with zigzaged terminal and <-shaped median dark brown lines................................*Platytes*

5(3'). Haustellum absent......................"*Crambus*" *angulatus*
5'. Haustellum present.......................................6

6(5'). Male antennal flagellomeres strongly serrate, pectinate or bipectinate...........*Thaumatopsis*, *Parapediasia* (part)..7
6'. Male antennal flagellomeres slighty serrate...............8

7(6). Aedeagus without apico-dorsal projections, vesica with cornuti.....................................*Thaumatopsis*
7'. Aedeagus with variously shaped apico-dorsal projections, vesica without cornuti...*Parapediasia* *hulstella* and *P.* *torquatella*

8(6'). Aedeagus with a typical short point apico-ventrally; frons sometimes produced with a point..................*Agriphila*
8'. Aedeagus variably shaped but never with a short point apico-ventrally as above; frons never produced with a point.....9

9(8'). Male antennal flagellomeres with a large sensory "pit" on each side...10
9'. Male antennal flagellomeres without sensory "pit"........11

10(9). Aedeagus with cornuti (except *F. minuellus* and *F. intermedius*), without apico-dorsal projection; manica strongly sclerotized ventrally (except *F. quadrinotellus* and *F. albilineellus* .... *Fissicrambus*

10'. Aedeagus without cornuti, with a pair of lateral flaps apico-dorsally; manica not better sclerotized ventrally .... *Parapediasia teterrella*

11(9'). Forewing apex produced and hooked, with a large white longitudinal band as in *Crambus* .... *Fernandocrambus*

11' Forewing apex not produced and hooked 12

12(11'). Forewing pattern usually with large satiny-white longitudinal band from base to at least end of cell, sometimes to outer margin; also with small brown patch at apex with white on both sides or at least ventrally (this pattern sometimes faint in *C. lyonsellus*, *C. albellus*, *C. girardellus*, *C. gausapalis* and *C. alienellus labradoriensis*) .... *Crambus*

12'. Forewing large white band absent, present in *Catoptria latiradiella* but not as above and apex uniformely brown...13

13(12''). Forewing mostly white, with or without markings 14

13'. Forewing colouration not mostly white 18

14(13). Uncus trilobed; forewing subterminal line made of separate brown spots .... *Arequipa*

14'. Uncus simple; forewing subterminal line absent or if present, continuous 15

15(14'). Forewing completely satiny white .... *Crambus perlellus*

15'. Forewing with at least some subterminal or terminal markings 16

16(15'). Forewing with black dots in middle of outer margin and some indication of *Crambus*-like subterminal line; juxta without long arms 17

16'. Forewing without black dots in outer margin; subterminal line double and curved inwards before reaching inner margin; juxta with pair of long lateral arms .... *Microcrambus copelandi*

17(16). Forewing median line indicated at least with brown spots on inner margin and below cell; aedeagus produced ventrally .... *Microcrambus biguttellus*

17'. Forewing median line if present not reaching inner margin, outlining end of cell, <-shaped; aedeagus apico-dorsally p[illegible] or not produced.... *Crambus lyonsellus* & *C. albellus*

18(13'). Forewing with subterminal and sometimes median lines (sometimes very faint) 19

18'. Forewing without transverse lines; with large dark-brown band on costa from base to apex outlined with white line on inner side and remaining wing surface uniformly pale brown .... "*Crambus*" *dimidiatellus*

19(18). Subterminal line simple 20

19'. Subterminal line double 25

20(19). Gnathos reduced, very thin, shorter than uncus 21

20'. Gnathos not reduced, as long as or slightly longer than uncus 22

21(20). Uncus dorsally carinate; valve costa without projection; sacculus with two long narrow projections .... *Tehama*

21'. Uncus dorsally convex; valve costa with large projection; sacculus without projection .... *Neodactria*

22(20'). Tegumen fused to vinculum; forewing R3 often missing, with apex often truncated or outer margin produced medially; sacculus without projection .... *Loxocrambus*

22'. Tegumen not fused to vinculum; forewing always with R3, apex not truncated, outer margin not produced; sacculus with or without a projection 23

23(22'). Forewing subterminal line orange and narrow; costal process of valva bilobed; aedeagus straight, dorso-apically opened with pair of pointed lateral projections .... *La*

23'. Forewing subterminal line if present, not orange, diffuse or narrow; costal process of valve simple; aedeagus not as above 24

24(23'). Forewing subterminal line darker than ground colour of wing, sometimes faint; aedeagus short and down-curved from middle, apically twisted on itself, with 1 cornutus; juxta remaining attached to aedeagus when latter is pulled .... *Pediasia*

24'. Forewing subterminal line continuous or not, white; aedeagus variously shaped (if down-curved then long and narrow), not apically twisted on itself; cornuti if present numerous; juxta not remaining attached to aedeagus when latter is pulled .... *Catoptria*

25(18'). Forewing interspace of subterminal line silver, contrasting with ground colour of wing; without median line; with shorter diagonal silver line across apex; vinculum cephalic margins laterally produced anteriorly .... *Chrysoteuchia* *topiaria*

25'. Forewing interspace of subterminal line not silver, of same colour as ground colour; with a least some indication of a median line; without diagonal bar across apex; cephalic margins of vinculum not produced anteriorly 26

26(25'). Forewing with complete narrow contrasting median line; forewing ground colour greyish with orange or brown markings; aedeagus apico-dorsally produced..*Parapediasia decorella* & *P. ligonella*

26'. Forewing median line poorly indicated, diffuse, usually most visible as a big spot on inner margin; forewing ground colour beige with dark brown markings; aedeagus never with apico-dorsal projection, often with narrow apico-ventral projection ....*Microcrambus* (except *M. copelandi* & *M. biguttellus*)

5.1.7.2 SYNOPSIS OF THE GENERA OF CRAMBINI OF NORTH AMERICA

Euchromius Guenée

(Figs. 17, 49, 89, 149, 204, 256, 309)

Euchromius Guenée, 1845: 324.

Type species: Tinea bella Hübner, 1796, by subsequent designation by Hampson (1896). Type material lost (Bleszynski 1965).

Eromene Hübner, 1825: 366, preoccupied by Hübner, 1821.

Type species: Tinea bella Hübner, 1796, by monotypy. Type material lost (Bleszynski 1965).

Ommatopteryx Kirby, 1897: 274. Unnecessary replacement name for Euchromius Guenée.

Diagnosis. This genus can be diagnosed by a possible synapomorphy of the male genitalia: the gnathos bears a dorsal hump (dorsal thorns of Schouten 1988) on which the tip of the uncus rests. The forewing pattern is also diagnostic of the genus. There is always: 1- a simple or double yellow medial fascia; 2- a subterminal line from the inner margin to the middle of the wing; 3- a row of large black terminal dots; and 4- a row of silver spots aside the black dots on the outer side. Euchromius is also one of the four Crambini taxa with the female anal papillae completely undivided (see character 43 in chapter 4).

Redescription. Based on Bleszynski (1965), Capps (1966), Schouten (1988) and my own observations.

Head (fig. 17). Fronto-clypeus often produced, rounded or with one or more points. Ocellus and chaetosema well developed. Haustellum long. Labial palp variable in length (short in *E. ocelleus*, 1.3X diameter of head in one dissected specimen). Vestiture as in *C. pascuellus* (fig. 25) except for shorter apical scales on labial palp of *E. ocelleus*. Antennal flagellomeres (fig. 49) very similar to those of *Crambus pascuellus* except for the apparent absence of sensilla auricillica.

Wings (fig. 89). Female frenulum double. Male frenulum hook present. Forewing R1 present, free; R2 free; R3 present, connected to R4 (lost in some species); R5 present, free; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing elongate (2.83X its width in mounted specimen of *E. ocelleus*). Forewing pattern characteristic, see Diagnosis above and fig. 149.

Tympanal organs (fig. 204). Transverse ridge distinct, rather large; anterior margin straight; posterior margin slightly concave. Tympanic pockets rather large, extended beyond posterior margin of transverse ridge. Venulae secundae present; heavily sclerotized; parallel. Tympanic bridge very short, slightly produced ventrally, with long arms connected medially; wings expanded laterally. Praecinctorium rather long, with long thin dorsal sclerotized support. Tympanic crest conspicuous and bell-shaped, about 1 1/2 times longer than high; situated medially. Tympanic drum distinctly larger posteriorly, extended to posterior margin of pockets. Spinula not seen.

Male genitalia (fig. 256). Uncus apically bilobed in some species, with dorso-basal hump in some species. Gnathos most often with mid-dorsal hump on which the uncus apex rests; sometimes with paired basal extensions. Tegumen with large pedunculi. Valva usually very complex with well sclerotized and differentiated sacculus and costal process and a narrow membranous cucullus. Vinculum broad to slender. Saccus present in some species. Juxta well sclerotized, variable in shape. Aedeagus short and swollen or long and slender, with cornuti in most species.

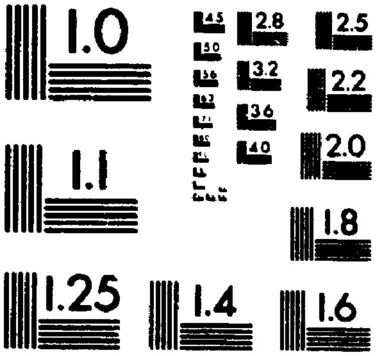
Female genitalia (fig. 309). Papillae anales variable in degree of sclerotization and setation, not divided into two lobes. Posterior apophyses longer than papillae. Anterior apophyses short or virtually absent. Segment VIII long in comparison with other Crambini, connected laterally to sterigma. Sterigma always strongly sclerotized, variable in shape, generally protruding. Ductus bursae variable in length and degree of sclerotization. Ductus seminalis sometimes sclerotized at base. Corpus bursae variable in size and shape, with none to three signa but most often with two signa.

Relationships. My analysis shows that this genus is probably the most primitive of all Crambini by virtue of the presence of the following plesiomorphies: undivided female papillae anales (character 43), absence of connection of the forewing R5 to R3+4 (character 11), presence of a frenulum hook in the male (character 13), and a rather elongate segment VIII.

Diversity and distribution. In their catalogue of the Crambinae of the world, Bleszynski and Collins (1962) listed 30 species in this genus distributed throughout the world except the Australian biogeographic region and South America. Most of those species are Palaearctic. Since the publication of this catalogue, species have been found in Australia (R. Schouten, pers. comm) and South America (Capps 1966). The genus now contains 51 species. It is absent from New Zealand (Dugdale 1988) and most Pacific islands except Hawaii and the Galápagos. It is also absent from northern North America (occuring in Canada only in southernmost British Columbia).

Natural history and immature stages. The species in this genus mostly occur in warm arid and semi-arid conditions into subtropical woodland and monsoon areas (Schouten 1988). Only the larva of E. ocelleus is known. It feeds on the roots of corn and sorghum (Capps 1966). Euchromius ocelleus is believed to have a typically mixed pattern of geo-orientation at rest (Crawford 1971a).

3



Platytes Guenée

(Figs. 14, 48, 94, 150, 205, 255, 311)

Platytes Guenée, 1845: 324.

Type species: *Tinea cerussella* Denis & Schiffermüller, 1775, by monotypy. Type material lost (Bleszynski 1965).

Nagahama Marumo, 1933: 46.

Type species: *Crambus ornatellus* Leech, 1889, by monotypy. Type material: holotype ♂ in BM(NH) studied.

Diagnosis. Genus *Platytes* can be recognized by a plesiomorphic condition of its forewing venation: Radial vein R5 is not connected to R3+4. This is also present in *Euchromius* but the two genera have very different wing patterns (see figs. 149 and 150). I know of no synapomorphy for the species of *Platytes*.

Redescription. Based on Bleszynski (1965) and my study of *P. vobisne*.

Head (fig. 14). Ocellus and chaetosema well developed. Fronto-clypeus rounded, not projected. Haustellum barely longer than labial palpus. Labial palpus 1.91X width of head in *P. vobisne*. Vestiture with appressed scales on fronto-clypeus; occipital scales projecting anterad between antennae; labial palp sometimes laterally dilated; maxillary palpus dishevelled. Male antennal flagellomere (fig. 48) with average number of sensilla coeloconica, chaetica and trichodea but apparently without sensillum auricillicum and styloconicum.

Wings (fig. 94). Female frenulum double. Male frenulum hook absent. Forewing R1 absent in P. vobisne, not in P. alpinella (Hübner) (Bleszynski 1965: 394); R2 free; R3 present, connected to R4; R5 present, free; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing M2 sometimes reduced or lost; M3, CuA1 & CuA2 present. Forewing elongate (2.63X its width in prepared specimen of P. vobisne). Forewing apex sometimes slightly produced in Palaearctic species. Forewing pattern (fig. 150) with Z-shaped subterminal line, similar but less pronounced median line, and dark and pale longitudinal bands.

Tympanal organs (fig. 205). Transverse ridge present, narrow; anterior margin medially blending into tympanic bridge; posterior margin convex. Tympanic pockets present, conical. Venulae secundae present, divergent. Tympanic bridge medium-sized, wings spread laterally. Praecinctorium short, without dorsal sclerotized support. Tympanic crest about three times longer than high, anteriorly situated. Tympanic drum elongate, extended to middle of transverse ridge. Spinula not visible.

Male genitalia (fig. 255). Uncus medium-sized, pointed, poorly setose. Gnathos narrow and elbowed in P. vobisne. Tegumen variable in shape, without ventral connection; apical margins of pedunculi with short setae. Valva always with well sclerotized medium-sized projection on costa; cucullus generally narrow, long, apically rounded; sacculus not sclerotized. Vinculum small, with convex cephalo-ventral margin but no saccus. Juxta slightly extended posterad, not surrounding the aedeagus, closely attached to it subapically (remaining attached to aedeagus when latter is pulled). Pseudosaccus globular. Aedeagus very short with subapical area of stronger sclerotization, dorsally in P. vobisne; vesica without cornutus.

Female genitalia (fig. 311). Anal papillae not divided into two lobes; setation rather long. Posterior apophyses about as long as papillae. Anterior apophyses absent. Segment VIII rather wide dorsally. Sterigma with ventral bilobed concave plate and dorsally with a pair of small lobes at base of membranous area in large sclerotized segment. Ductus bursae generally wide and short. Corpus bursae more or less well demarcated from ductus, more or less circular; with one or two signa.

Relationships. This genus is believed to be one of the most primitive in the Crambini, along with Euchromius, because it retains the plesiotypic condition of the free R5 in the forewing. It is interesting to note also that the female corpus bursae has sometimes two signa, as in Euchromius.

Diversity and distribution. Genus Platytes is believed to be exclusively Holarctic in distribution (Bleszynski 1965). It contains only six species, one of which is found in North America. Our only species is known from western Ontario, eastward to Connecticut, southward to Oklahoma and westward to central Colorado. This species is however very poorly represented in collections and its distribution consequently poorly known.

Natural history and immature stages. The bionomics and immature stages of our North American species are unknown but some information on two species in Europe is available. Platytes alpinella is stated to feed on moss (Bleszynski 1965) while P. cerussella (D. & S.) was reported to feed on "roots of small, stiff grasses growing on sand and shingle, perhaps also on sand sedge" (Goater 1986). The immature stages of P. cerussella were described by Schwarz (1964), Hasenfuss (1960) and others cited in Bleszynski (1965).

Comments. Some of the variation in the male genitalia could not be expressed because the North American fauna contains only one species and I was using Bleszynski's (1965) sometimes poor illustrations to document variability in the Palaearctic fauna. Klots (1983) stated that the only North American species of Platytes was misplaced in this genus. This was found to be erroneous based on several morphological features shared by our species and the Palaearctic elements.

Catoptria Hübner

(Figs. 38, 120, 167, 168, 207, 208, 257-260, 317)

Catoptria Hübner 1825: 365.

Type species: Catoptria speculalis Hübner, 1825, by subsequent designation by Bleszynski (1956). Type-material lost (Bleszynski 1965).

Exoria Hübner, 1825: 367.

Type species: Tinea combinella (Denis & Schiffermüller), 1775, by subsequent designation by Shibuya (1928: 45). Type-material lost (Bleszynski 1965).

Diagnosis. This genus cannot be characterized with any synapomorphy and a lot of variability in wing pattern and genitalia structure is expressed in the North American species. Nevertheless, the following combination of characters should separate Catoptria from other North American Crambini: female frenulum double; female corpus bursae without signum; if forewing with large median longitudinal stripe, this interrupted twice by large median and subterminal transverse bands; gnathos dorsally with subterminal hump depressed in middle to accomodate tip of uncus; and, wingspan 18 mm or longer.

Redescription. Based on Bleszynski (1965) and my own observations on the Nearctic species.

Head. Shape variable; fronto-clypeus rounded and not protruding or protruding with or without a point. Ocellus and chaetosema well developed. Labial palpus variably elongate (2.3X width of head in *C. latiradiella*) but conspicuously shorter in *C. maculalis*. Vestiture usually with appressed scales on fronto-clypeus; vertexal scales sometimes porrect between antennae; with thin hair-like scales on palpi and occiput in *C. trichostomus*. Male antennal flagellomeres (fig. 38) about as long as wide, with full complement and average number of sensilla except for the possible lack of a sensillum auricillicum.

Wings (fig. 120). Female frenulum double. Male frenulum hook present or absent. Forewing R1 present, free; R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing variably elongate (2.64X its width in one mounted specimen of *C. latiradiella*). Forewing pattern (figs. 167, 168) variable, with a wide white longitudinal stripe and/or with median and/or subterminal lines in some species; with only paler lines on venation in other species. Forewing colour of various shades of brown, sometimes with yellow or appearing grey or black.

Tympanal organs (figs. 207, 208). Transverse ridge present and rather large in *C. latiradiella* and *C. oregonica*, missing in *C. trichostoma* and *C. maculalis*. Tympanic pockets rather large in *C. latiradiella* and *C. oregonica*, missing in *C. trichostoma*, very small in *C. maculalis*. Venulae secundae usually absent but very faint in *C. trichostoma*. Tympanic bridge short and projected ventrally in *C. trichostoma* and *C. maculalis*, longer and not distinctly projected in *C. latiradiella* and *C. oregonica*; wings spread laterally in all species. Praecinctorium extended to posterior margin of transverse ridge and with long thin dorsal sclerotized support in *C. latiradiella*, very short and without support in *C. trichostoma* and *C. maculalis*. Tympanic crest absent in *C. trichostoma*, otherwise about two to three times longer than high and anteriorly situated. Tympanic drum bean-shaped (*C. latiradiella*), with posterior end larger (*C. oregonica*), oval (*C. maculalis*) or very shallow and elongate (*C. trichostoma*); drum extended to end of pockets (*C. oregonica*), to middle of pockets (*C. latiradiella*), to middle of tympanic bridge (*C. maculalis*) or to anterior edge of wings (*C. trichostoma*). Spinula visible in all species.

Male genitalia (figs. 257-260). Uncus long and narrow to short and bulky, sometimes subapically larger. Gnathos usually long and narrow, usually with subapical hump with median depression in which uncus tip rests, apically pointed or remaining enlarged. Tegumen short, bulky and dorsally convex, to elongate and linear (*C. latiradiella*). Valva with strongly sclerotized projection on costa; cucullus variable in shape, usually bent upward at apex; sacculus with or without one or two projections on inner side near base of free part of costal projection, without projection in *C.*

trichostoma and C. oregonica. Vinculum variable in shape; saccus sometimes well developed (C. oregonica). Pseudosaccus usually strongly carinate. Juxta more or less elongate. Aedeagus quite variable in shape; often variously sclerotized apically, sometimes with projections; vesica armed with cornuti in many species.

Female genitalia (fig. 317). Anal papillae not strongly divided into two lobes. Posterior apophyses shorter than papillae. Anterior apophyses absent or very short. Segment VIII generally wider dorsally than in most Crambini, sometimes very long. Sterigma variously shaped, often elaborate, sometimes with shortly protruding tube. Ductus bursae usually sclerotized, most often long and narrow, sometimes wide and short. Corpus bursae usually small and circular, usually with one signum but without signum in the four North American species.

Relationships. Catoptria is most closely related to Agriphila according to Bleszynski (1965) based on the double female frenulum, the single signum on the corpus bursae and the produced forehead. My analysis did not clearly show this relationship but this is not surprising. The four North American species seem to belong to four different lineages within the genus and each closest relative is found in the Palaearctic region. The sister-species of C. latiradiellus is probably C. specularis Hübner from the Alps; that of C. oregonica is probably C. zermattensis (Frey) also from the Alps; that of C. maculalis is possibly C. permiaca (Petersen) from the Eastern USSR, China and Japan; and that of *C. trichostoma* is possibly *C. margaritella* (Denis & Schiffermüller) from boreal Europe.

Diversity and distribution. *Catoptria* is primarily a Palaearctic genus. Most of the species actually occur in the mountains of Central Europe. Only three species are endemic to North America. The fourth North American species (*C. speculalis*) is Holarctic. *Catoptria* now includes approximately 80 species.

Natural history and immature stages. The larvae of some species of *Catoptria* are known to feed on mosses. In North America, the bionomics of the species have not been worked out. However, that of the Holarctic species *C. maculalis* is known (Bleszynski 1965); the larva feeds on ground mosses in silken tunnels. The immatures of *C. maculalis* were described by Schwarz (1964). A well illustrated description of the larva and pupa of the European species *C. lithargyrella* was provided by Schwarz (1964) and partly reproduced by Bleszynski (1965). Another interesting aspect of the bionomics of these moths is that they mostly occur in boreo-montane habitats in Europe. In North America, three species occur at high latitudes, two of them exclusively, and the fourth, *C. oregonica*, is in the Rocky Mountains.

Thaumatopsis Morrison, status revised

(Figs. 19, 50, 52, 87, 113, 117, 146, 147, 203, 218, 219,
261-264, 314, 315, 318, 319)

Thaumatopsis Morrison, 1874: 161.

Type species: Thaumatopsis longipalpus Morrison, 1874, by monotypy.

Type repository: USNM [examined].

Propexus Grote, 1880a: 19.

Type species: Crambus edonis Grote, by subsequent designation by Fernald (1896). A male in the BM(NH) was designated lectotype. Three paralectotypes (1♂; 2♀♀) were also designated (see Appendix V).

Diagnosis. Genus Thaumatopsis is not easy to diagnose because its members are quite variable in wing pattern and shape. Nevertheless, the following combination of characters should separate the species of Thaumatopsis from those of other genera (except possibly Parapediasia hulstella and P. torquatella): all species have either bipectinate, pectinate or strongly serrate male antennae; all females have only one bristle in the frenulum; all females have no signum on the corpus bursae; most females have their papillae anales undivided; and all males have a strongly developed costal process on their valva and have no sclerotized projection on their sacculus.

Redescription.

Head (fig. 19). Frons rounded. Ocellus and chaetosema present. Labial palpus usually very long (3.2X width of head in one dissected specimen of *T. pexella*) but shorter (2.18X width of head) in one dissected specimen of *T. bolterella* (fig. 19). Vestiture usually with vertexal and fronto-clypeal scales short and appressed, with longer scales projecting forward betweeen antennae in *T. pexella*-group; palpi mostly as in *C. pascuellus* (fig. 25). Antennae bipectinate (fig. 52), pectinate (fig. 50) or strongly serrate. Antennal flagellomeres in two species with higher than average number of sensilla trichodea (more than 100), without sensillum auricillicum, with unusually high number of sensilla coeloconica, no sensilla chaetica in *T. pexella* (fig. 52), with slightly more than usual number of sensilla coeloconica in *T. floridella* (fig. 50).

Wings (figs. 87, 113, 117). Female frenulum simple. Male frenulum hook absent. Forewing R1 present, free (except for a few species in which it is fused with Sc); R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked (except in a few species with a short stalk); Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing elongate (2.8X-2.84X its width in prepared specimens of *T. pexella* and *T. bolterella*). Forewing pattern (figs. 146, 147) sometimes with subterminal and\or median lines present; often with a white and\or a dark-brown longitudinal streak; sometimes with paler longitudinal lines superimposed on venation.

Tympanal organs (figs. 203, 218, 219). Transverse ridge absent in *T. pectinifer*-group, otherwise usually narrow or very narrow (as in *T. floridella*); anterior margin slightly produced anterad in most species, rarely more thickly sclerotized medially (as in *T. atomosella*). Tympanic pockets sometimes very small (as in *T. floridella*), mostly larger, more or less conical. Venulae secundae present or absent, variously shaped. Tympanic bridge usually long and distinctly produced ventrally; wings usually rather well extended laterally but reduced in *T. pectinifer*-group. Praecinctorium reduced in length in *T. pectinifer*-group, otherwise rather large and with a dorsal sclerotized support variable in size. Tympanic crest absent in *T. pectinifer*-group, otherwise rather large, situated slightly anteriorly to middle but more so in *T. bolterella*. Tympanic drum reduced and not extended posterad inside body in *T. pectinifer*-group, otherwise extended to transverse ridge or shorter. Spinula not visible in *T. pectinifer*-group, otherwise visible.

Male genitalia (figs. 261-264). Uncus usually thick and sharply pointed apically, with a more or less pronounced dorsal hump at base in *T. pectinifer*-group. Gnathos usually medium-sized, reduced in *T. pectinifer*-group, with a larger apex and a ventrally directed tooth in *T. pexella*-group. Tegumen variable in shape, pedunculi large or narrow, sclerotized ventrally. Valval costal process strongly sclerotized, often spoon-shaped but long and pointed in T. fernaldella-group; sacculus sometimes sclerotized, without process; cucullus moderately long and narrow. Vinculum with a long saccus in T. bolterella and T. pectinifer groups, with the ventro-cephalic margin emarginate in T. pexella-group or only slightly concave in T. fernaldella-group. Juxta forming a complete sclerotized ring around the aedeagus in T. bolterella-group. Pseudosaccus variable. Aedeagus more or less apically divided into two sclerotized lobes and with one big cornutus in T. pexella-group; narrow and elongate with the ventral wall apically flat, with one or two subapico-dorsal processes and without cornuti in T. bolterella-group; apically bilobed, although not strongly sclerotized, and with large or small cornuti in T. pectinifer-group but also with a bulbous projection of the manica dorsally near exit of ductus ejaculatorius; usually short and with vesica opening apically like a mushroom and bearing numerous tiny cornuti in T. fernaldella-group.

Female genitalia (figs. 314, 315, 318, 319). Anal papillae usually not divided into two lobes, setation variable. Posterior apophyses usually longer than papillae. Anterior apophyses usually distinct, rather long in T. bolterella-group. Segment VIII more or less narrow dorsally. Sterigma usually large and protruding, complex and variable in shape. Ductus usually short and wide but long in some species in various groups. Corpus bursae circular in T.

fernaldella-group, variously elongate in other groups, never with a signum.

Relationships. This genus may represent a primitive lineage in the Crambini because of the absence of division of the papillae anales in most species and because the anterior apophyses are usually distinct. It seems to be most closely related to some members of genus *Parapediasia* (namely *P. torquatella* and *P. hulstella*) due to the similar shape of their flagellomeres and male genitalia. *Thaumatopsis* is also very close to "*Crambus*" *dimidiatellus* (see p. 263). Within the genus I recognize four groups of species on the basis of various features of the male genitalia. The *T. fernaldella*-group has the vesica everted like a mushroom with many tiny cornuti, most species also have a long, narrow projection on the costa of the valve; the antenna is either pectinate or strongly serrate. The *T. pectinifer*-group has pectinate antennae and share a peculiar dorsal bulbous projection of the manica; these also are smaller species with narrow pointed wings and reduced tympanal organs. The *T. pexella*-group has bipectinate antennae and the aedeagus is apically divided into two sclerotized lobes characteristic for this group of species (fig. 262). The species in the *T. bolterella*-group all share an apically flat and rounded aedeagus with two (only one in *T. bolterella*) large spine-like projections subapico-dorsally; these species have the antennae serrate or pectinate.

Diversity and distribution. So far as is known, this genus contains 20 species and is restricted to the Nearctic Region. Most species are found in the southern United-States from Texas to California. Klots (1983) included 12 species. Six new species are known to me. *Thaumatopsis bolterella* and *T. digrammella* (Hampson) are transferred from *Parapediasia*. *Thaumatopsis digrammella* is reported here from North America (Arizona) for the first time. As far as is known, only *T. digrammella*, *T. fernaldella* and *T. pexella* ssp. *strictalis* extend in range to Mexico but little collecting has been done in the mountains and deserts of northern Mexico where this genus should be sought.

Natural history and immature stages. The immatures of only one species are known. Muma and Hill (1950) described and illustrated the immature stages and gave an account of the biology of *T. pectinifer* (Zeller) which was found to have been injurious to corn in Nebraska. Mature larvae were feeding on corn, various species of native sedges (*Cyperus* spp., Cyperaceae) and sand paspalum (*Paspalum stramineum* Nash., Poaceae). Larvae feed just below the soil surface from silken tubes. The egg of *T. edonis* (Grote) was described by Matheny & Heinrichs (1982).

Comments. The status of *Thaumatopsis* is revised to include *T. bolterella* (Fernald) formerly placed with *Parapediasia* (Klots 1983).

Tehama Hulst

(Figs. 34, 88, 142, 220, 267, 323)

Tehama Hulst, 1888: 115.

Type species: Spermatophtora bonifatella Hulst, 1887, by original designation. Type repository: USNM [examined].

Diagnosis. The genus can be diagnosed by the shape of the valva, the most prominent feature of which is the strongly sclerotized and bilobed sacculus. The strongly carinate uncus of the male is also diagnostic. The only species in this genus is sometimes confused with Parapediasia teterrella because of their similar brown colour and their similar, albeit poorly pronounced forewing pattern.

Redescription.

Head. Very similar in shape to that of Crambus pascuellus (fig. 8) except for slightly shorter labial palpi. Vestiture as in C. pascuellus (fig. 25). Male antennal flagellomeres (fig. 34) with average numbers of sensilla except for possible absence of a sensillum styloconicum.

Wings (figs. 88). Female frenulum simple. Male frenulum hook absent. Forewing R1 present, free; R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 on short stalk; Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing elongate (almost 3X longer than wide). Forewing (fig. 142) pale brown with darker brown markings; pattern often very faint, usually with a short oblique apical bar and a spot mesally below cell, sometimes with a complete subterminal line, sometimes also with a distinct longitudinal bar in middle basally.

Tympanal organs (fig. 220). Transverse ridge distinct, rather narrow, posterior margin strongly sclerotized. Tympanic pockets rather large, slightly extended beyond transverse ridge. Venulae secundae present, heavily sclerotized, divergent. Tympanic bridge not produced ventrally, elongate on the long axis; tympanic wings only slightly expanded laterally. Praecinctorium rather long with a long thin dorsal sclerotized support. Tympanic crest large and conspicuous, anteriorly situated. Tympanic drum bean-shaped, partly closed laterally, extended to anterior margin of transverse ridge. Spinula visible.

Male genitalia (fig. 267). Uncus rather wide, strongly carinate. Gnathos reduced, very slender arms connected ventrally at their apices. Tegumen with rather large pedunculi. Valva with strongly developed and bilobed sacculus; laterally compressed membranous cucullus; costal process poorly developed. Vinculum short; ventro-cephalic margin slightly emarginate. Juxta membranous. Aedeagus slender, as long as valva, with short coecum; vesica without cornuti.

Female genitalia (fig. 323). Anal papillae with long setae, only slightly divided into two humps. Posterior apophyses longer than papillae. Anterior apophyses absent. Segment VIII narrow dorsally, long ventrally. Sterigma strongly sclerotized with long protruding tube almost reaching apex of papillae. Ductus bursae short, not differentiated from long corpus bursae. Latter without signa.

Relationships. This autapomorphic taxon could have been derived from one of several possible ancestors in the higher Crambini (fig. 5). Its closest relative is unknown.

Diversity and distribution. The only species in this genus is distributed from Greenland to Alaska, southward in the West to all states and provinces west of the Prairies. I have not seen specimens from the United States east of the Prairies or from the Prairies themselves, but from eastern Canada, I have seen specimens from Manitoba, Québec and Nova Scotia.

Natural history and immature stages. The immatures and the biology of Tehama bonifatella (also called the Western Lawn Moth and the Fawn-coloured lawn moth) were described in detail by Bohart (1947). The larva and pupa were figured again by Bleszynski (1965). The caterpillar is polyphagous on Poaceae and is one of the two most serious turfgrass pests in California (Tashiro 1987). It was also found to be able to complete its development on White clover (Trifolium repens L., Fabaceae) (Bohart 1947). McDonough et al. (1982) reported their success in synthetizing the sex pheromone of this species. Crawford (1971a) concluded that the moth had a typically mixed geo-orientation response in its choice of resting position.

Fissicrambus Bleszynski, status revised

(Figs. 60, 61, 78, 143, 227-229, 268, 269, 320)

Fissicrambus Bleszynski, 1963a: 153.

Type species: *Crambus fissiradiellus* Walker, by original designation. Lectotype designated by Bleszynski (1963a): BM(NH) [examined].

Diagnosis. In North America, the members of this genus can be recognized by two synapomorphies. The first (character 6) is the presence of large sensory pits laterally on the antennal flagellomeres. These, however, are lost in an apparently monophyletic subgroup of three species (*F. minuellus*, *F. hemiochrellus*, *F. mutabilis*). The other synapomorphy is the ventrally sclerotized manica in the middle of the aedeagus. This is the point of attachment to the juxta. It is lost in the sister-species pair *F. quadrinotellus* + *F. albilineellus*. The moths can often be recognized by their fawn-coloured forewing with a longitudinal streak from base to beyond middle and poorly marked median and subterminal lines.

Redescription. Based on Bleszynski (1963a, 1967) and my own observations on the North American species.

Head. Shaped as in *Crambus pascuellus* (fig. 8) with slightly shorter labial palpus (1.85X width of head in one specimen of *F. fissiradiellus*). Vestiture with fronto-clypeal and vertexal scales short and appressed, maxillary palpi more triangularly scaled than in *Crambus pascuellus* (fig. 25). Male antennal flagellomeres (figs. 60, 61) usually with a large sensory pit on each side laterally (fig. 61), this structure missing in *F. minuellus* (fig. 60), *F. hemiochrellus* (Ainslie 1918) and *F. mutabilis* (Ainslie 1923a). Numbers of sensilla trichodea usually above normal in three species (see Appendix III); number of sensilla coeloconica high (± 20) in *F. minuellus*; other types of sensilla usually present in average numbers.

Wings (fig. 78). Female frenulum usually simple, almost double in *F. minuellus*. Male frenulum hook absent. Forewing R1 present, free (except for *F. haytiellus* for which it is lost); R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing with M2, M3, CuA1 & CuA2 present. Forewing elongate (2.52 to 2.78X its width in prepared specimens of *F. quadrinotellus* and *F. fissiradiellus* respectively). Forewing usually fawn-coloured; pattern (fig. 143) usually with a white longitudinal streak from base to beyond middle; sometimes with paler lines following venation; median and subterminal lines poorly marked.

Tympanal organs (figs. 227-229). Transverse ridge distinct, usually medium-sized, narrower in *F. quadrinotellus*, anterior margin usually smooth. Tympanic pockets usually rather large, small in *F. quadrinotellus*, not extended much beyond posterior margin of ridge, more or less conical. Venulae secundae present or absent, weakly sclerotized. Tympanic bridge usually rather long and not projected ventrally; tympanic wings usually spreading laterally except in *F. albilineellus* where pockets and drums are close to one another. Praecinctorium variable in size, with corresponding long or short dorsal sclerotized support. Tympanic crest semicircular, sometimes situated near middle (*F. albilineellus*) but usually anterad to middle, very strongly so in *F. mutabilis*. Tympanic drum elongate (*F. minuellus*, *F. albilineellus*) or more circular (*F. fissiradiellus*), extended to middle of transverse ridge. Spinula always visible.

Male genitalia (figs. 268, 269). Uncus usually long, narrow and apically downcurved, very short in *F. fissiradiellus*. Gnathos usually long, narrow and apically downcurved, sometimes with denticles ventrally at apex, sometimes with a subapical hump dorsally in the *F. quadrinotellus* species-pair, shorter and thicker in *F. fissiradiellus*. Tegumen short and bulky with wide pedunculi or more elongate with narrow pedunculi, sclerotized ventrally. Valva with a strongly sclerotized costa, with or without variable projections; cucullus usually free, variable in shape, fused to sclerotized costa in *F. minuellus*; sacculus sclerotized or not, with or without projection. Vinculum short, without a saccus. Juxta and pseudosaccus variable, juxta not forming a complete sclerotized ring. Aedeagus with manica sclerotized ventrally in most species except *F. quadrinotellus* species-pair, sometimes with ventral or dorsal projections at apex; vesica usually with few, sometimes very long cornuti, as in the F. quadrinotellus species-pair.

Female genitalia (figs. 320). Anal papillae poorly, if at all divided into two lobes. Posterior apophyses longer than papillae. Anterior apophyses varying from virtually absent to long and wide in F. minuellus. Segment VIII mostly very narrow dorsally. Sterigma usually sclerotized, typically protruding, short and rounded. Ductus bursae generally wide, long or short, sometimes thickly sclerotized. Corpus bursae most often elongate, without signum.

Relationships. My analysis (fig. 5) has not shown any evidence of relationships between Fissicrambus and other genera of Crambini. The genus is however shown not to be closely related to Crambus and allied genera. It is possible that Loxocrambus is closely related to Fissicrambus, especially F. albilineellus, on the basis of the shape of the genitalia and the forewing pattern. Bleszynski (1963a) mentioned that Fissicrambus belongs to the Pediasia-group of genera without further explanation. Within the genus, I recognized two groups of species: the F. quadrinotellus species-pair (also including F. albilineellus) lacks the sclerotized manica but shares an extremely long cornutus on the vesica; the F. mutabilis-group (also including F. hemiochrellus and F. minuellus) shares the loss of the antennal sensory pits and the presence of stiff setae on the inner side at the base of the cucullus of the valve. These groups provide only a partial and tentative reconstruction of the intra-generic affinities in Fissicrambus. Many of our North

American species have their closest relatives in the Neotropical Region. For example, *F. fissiradiellus* is most closely related to *F. adonis* Bleszynski described from the Yucatan Peninsula, Mexico.

Diversity and distribution. The distribution of *Fissicrambus* seems to cover a wide range of the Neotropical realm. Six of our nine North American species also occur in at least the northern portion of the Neotropical Region. The other three species are mostly restricted to the southern United States. Only *F. mutabilis* ranges over most of the U.S., reaching southern Canada in the East. The genus now contains a total of 17 species, including *F. albilineellus* which is here transferred from *Crambus*, but excluding *F. hospition* Bleszynski here transferred to *Loxocrambus*. Following Bleszynski (1963a, 1967) and opposed to Klots (1983), *F. quadrinotellus* is considered to be a member of *Fissicrambus*.

Natural history and immature stages. Contrary to Bleszynski's statement (1963a), the immatures and biology of two species of *Fissicrambus* were known when his paper was published. Indeed, Ainslie had described the biology and immatures of *F. hemiochrellus* in 1918 and those of *F. mutabilis* in 1923(a). Subsequently, Wylie (1944) reported the feeding damage of *F. haytiellus* to lawns and Carpet grass (latin name not mentioned but probably *Axonopus affinis* Chase) pastures in Florida. Tan (1984) redescribed the immatures of *F. mutabilis* and described those of *F. haytiellus*, *F. minuellus* and *F. profanellus* in Florida. The larvae feed above-ground on the leaves of a more or less restricted range of grasses, including several graminaceous crops such as corn for *F.*

mutabilis (Ainslie 1923a). The latter species is considered to be one of the six most important sod webworms in the temperate regions of the United States (Tashiro 1987). Its common name is the striped webworm. The moth was reported to exhibit a strong geopositive response in its choice of resting position (Crawford 1971a).

Comments. The status of this genus in North America is revised to include *F. albilineellus* (Fernald) which was formerly placed with *Crambus* (Klots 1983), and to exclude *L. hospition* Bleszynski which is here transferred to *Loxocrambus*.

Microcrambus Bleszynski

(Figs. 44, 46, 93, 95, 170, 231, 274, 275, 316)

Microcrambus Bleszynski, 1963a: 167.

Type species. *Microcrambus discobolus* Bleszynski, 1963a, by original designation. Type-repository: BM(NH) [not examined].

Diagnosis. Klots (1968) recognized that this genus is "embarrassingly difficult to recognize". Notwithstanding this fact, I think that the following will prove useful. The aedeagus apically produced ventrally may represent a synapomorphy for this genus with a loss in *M. copelandi*. The shape of the vinculum may also represent a uniquely derived character-set for this taxon (see below). Most species also have a similar forewing pattern and colour except for *M. copelandi* and *M. biguttellus* which are satiny-white. All species are small, usually around 12 mm in wingspan (up to 20 mm in *M. polingi*), and have their wings comparatively less elongate than those of most other Crambini. The presence of a large ventral plate to the female sterigma (including in *M. copelandi*) is also possibly a synapomorphy that links *M. copelandi* with most other species of *Microcrambus*.

Description. Based on Bleszynski (1963a), Klots (1968) and my own observations.

Head. Similar in shape to that of *Crambus pascuellus* (fig. 8) but with a slightly shorter labial palpus (1.92X width of head in one specimen of *M. elegans*). Vestiture mostly as in *C. pascuellus* (fig. 25) except for fronto-clypeal scales slightly wider and appressed; vertexal scales sometimes protruding anterad between the antennae. Male antennal flagellomeres of *M. biguttellus* (not illustrated) and *M. elegans* (figs. 44, 46) similar in shape to those of *Neodactria luteolella* (fig. 58); both species with full complement of sensilla, with fewer sensilla trichodea in *M. biguttellus*; *M. elegans* with sac-like structures apico-dorsally (fig. 44).

Wings (figs. 93, 95). Female frenulum usually double, sometimes triple. Male frenulum hook absent. Forewing R1 present, free; R2 free; R3 present, connected to R4 (but sometimes lost); R5 present, connected to R3+4; M1 present; M2 & M3 not stalked (except in *M. kimballi* in which they are stalked from 2/3); Cubitus with CuA1 & CuA2. Hindwing with M2, M3, CuA1 & CuA2 present. Forewing shorter than in most Crambini (2.19X its width in one mounted specimen of *M. elegans*). Forewing pattern (fig. 170) with a double subterminal line, usually appearing dirty beige spotted with brown but sometimes mostly pure white with chesnut-brown transverse lines (*M. copelandi* and *M. biguttellus*), usually with some indication of the median line.

Tympanal organs (fig. 231). Transverse ridge medium-sized, usually with a straight anterior margin medially. Tympanic pockets usually as figured, sometimes compressed laterally as in *M. copelandi*.

Venulae secundae absent. Tympanic bridge of medium size (about twice the width of the transverse ridge), generally not as produced ventrally as in M. elegans; tympanic wings generally produced laterally, except in M. copelandi. Praecinctorium short, with dorsal sclerotized support. Tympanic crest usually about twice as long as high, situated anteriorly. Tympanic drum bean-shaped, generally extended to posterior edge of transverse ridge. Spinula unusually strongly sclerotized, sometimes with associated structures (for example the scoloparium) also visible.

Male genitalia (figs. 274, 275). Uncus long or short, narrow, thick or flat. Gnathos usually long and narrow but sometimes much reduced, usually apically down-curved. Tegumen elongate or short, with wide or narrow pedunculi. Valva with a strongly sclerotized costa with variable projections; sacculus usually weakly sclerotized and without projections, sometimes with an apical knob or spine; cucullus free, wide or narrow, projecting upward. Vinculum most often with both lobes more or less oval and with the margin conspicuously more strongly sclerotized, also usually with a spine-like processus at the point of connection with the tegumen pedunculi, very small in M. biguttellus and M. copelandi. M. biguttellus with a pair of lateral depressions with long hairs on membrane VIII-IX. Saccus present or absent. Pseudosaccus variable, sometimes weakly sclerotized (M. copelandi). Juxta variable, unusual with a pair of long free arms in M. copelandi. Most species, except M. copelandi, with floor of aedeagus better sclerotized and usually produced apically; vesica with or without cornuti of variable size and number.

Female genitalia (fig. 316). Anal papillae not clearly divided into two lobes. Posterior apophyses shorter than papillae. Anterior apophyses absent. Segment VIII medium-sized dorsally. Sterigma often with large ventral and sometimes also dorsal plates associated or not with a long protruding tube. Ductus bursae usually long and narrow. Corpus bursae usually fairly small and circular; with 0-2 signa.

Relationships. My analysis (fig. 5) has not shown that Microcrambus is more or less related to any other genus in the Crambini. The genus belongs to the more derived Crambini with a reduced segment VIII in the female and R5 connected to R3+R4 in the forewing. However, it is not included in the higher Crambini which have the papillae anales strongly divided into two lobes. Based on Bleszynski's illustrations (1963a, 1967), it seems possible that Microcrambus is related to Tortriculladia Bleszynski, a Neotropical genus. Within Microcrambus, all of the North American species have very distinctive genitalia which makes the grouping of species difficult. Microcrambus biguttellus and M. copelandi are divergent in various features from the other species of the genus, of which the most obvious is the satiny-white colour of the wings. However, M. biguttellus is clearly closely related to the other species of Microcrambus examined because: a) the aedeagus is apico-ventrally better sclerotized and produced; b) the shape of the vinculum is the same as in the other species, and c) so is the wing pattern. I also think that *M. copelandi* belongs with *Microcrambus* because of the shape of the female sterigma (very similar to that of *M. polingi* for example), that of the tympanal organs and that of the male genitalia in general.

Diversity and distribution. The genus at present includes 47 species mostly restricted in distribution to various parts of the Neotropical region (Bleszynski 1967, Klots 1968). Five of the nine North American species also occur in Mexico or the West Indies. Two mostly occur in the southeastern United States. Four are present in southern Canada.

Natural history and immature stages. The members of this genus are not known to be of economic pest status on turfgrasses or graminaceous crops in North or South America. However, Robinson and Tolley (1982) associated *M. elegans* (Clemens), the Pretty crambus, with turfgrass in Virginia. I do not know of the kind of association the authors were referring to because I have not seen the reference. The same authors (Tolley & Robinson 1986) found the moth very commonly from June to October in Virginia. The egg and first instar larva of *M. elegans* were described by Fernald (1896). This was transcribed by Mauston (1970). Matheny and Heinrichs (1972) gave a description and showed scanning electron micrographs of the egg. Allyson (1986) provided a description of the last instar larva of this species which she reared on corn silk.

Loxocrambus Forbes, status revised

(Figs. 36, 85, 114, 145, 164, 166, 215, 216, 225, 266, 321)

Loxocrambus Forbes, 1920: 225.

Type species: Loxocrambus canellus Forbes, 1920, by original designation. Type material: Cornell University, Ithaca, New York [examined].

Diagnosis. The members of this genus share a peculiar attachment (or fusion) of the pedunculi of the tegumen to the vinculum so that it is extremely difficult to disconnect them without considerable damage. This is believed to be a synapomorphy for this compact group of species. In addition, the female sterigma is always membranous and the anterior apophyses are very long in comparison to most Crambini. Moreover, in two species the forewing apex is truncated and\or the outer margin is produced in the median sector.

Redescription.

Head. Similar to Crambus pascuellus (fig. 8) in shape except for a shorter haustellum (not much longer than labial palpus) and a shorter labial palpus (1.61-2.08X width of head in mounted specimens of L. canellus and L. coloradellus respectively). Vestiture mostly as in C. pascuellus (fig. 25) except for shorter appressed vertexal and fronto-clypeal scales. Male antennal flagellomeres (fig. 36) with average number of all sensilla except for the absence of a sensillum auricillicum in L. canellus.

Wings (figs. 85, 114). Female frenulum simple (3 spp. examined). Male frenulum hook absent. Forewing venation with R1 present, connected with Sc; R2 free; R3 missing or present and connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 usually not stalked, except in occasional specimens; Cubitus with CuA1 & CuA2. Hindwing with M2, M3, CuA1 & CuA2 present. Forewing apex often truncated or outer margin produced in median sector. Forewing elongate (2.79-2.95X its width in mounted specimens of L. coloradellus and L. canellus respectively). Forewing pattern (figs. 145, 164, 166) usually with subterminal line present and with dark brown dots in subterminal sector at apex of median veins, usually with paler lines following venation and with a thicker white line from base to beyond cell in middle, median line present or absent.

Tympanal organs (figs. 215, 216, 225). Transverse ridge with anterior margin medially produced anteriorly or fused to the tympanic bridge. Tympanic pockets virtually absent to rather large, more or less conical. Venulae secundae present, strongly sclerotized, divergent, parallel or convergent. Tympanic bridge medium-sized and produced ventrally. Praecinctorium rather long, with dorsal sclerotized support. Tympanic crest usually not visible but 5X longer than high in L. coloradellus and anteriorly situated. Tympanic drum circular in L. canellus, otherwise more elongate, extended to transverse ridge or shorter. Spinula visible. One specimen of Loxocrambus sp. (fig. 225) from California had no tympanal organs!

Male genitalia (fig. 266). Uncus medium-sized, concave dorsally at base, with a down-curved apical tooth. Gnathos rather flat and narrow, weakly sclerotized and down-curved apically. Tegumen elongate with narrow pedunculi strongly fused to vinculum, sclerotized ventrally. Valva with free costal process variable in length; cucullus slightly longer, narrow or wide; sacculus only slightly sclerotized at base. Vinculum medium-sized or narrow, ventro-cephalic margin usually broadly convex, with a true saccus only in L. awemensis. Pseudosaccus variable. Juxta large and partially forming a ring around the aedeagus. Aedeagus narrow, variable in length, apically better sclerotized ventrally; vesica with one large cornutus (very long in L. coloradellus).

Female genitalia (fig. 321). Anal papillae weakly (if at all) divided into two lobes. Posterior apophyses long, longer than length of papillae. Anterior apophyses also long, similar in length to posterior ones. Segment VIII either completely membranous dorsally or very narrowly sclerotized. Sterigma absent; membrane with one long seta on each side of ostium in L. canellus. Ductus wide or narrow, unsclerotized. Corpus elongate or circular, without signum.

Relationships. This genus seems to be closer to *Fissicrambus* and is especially similar to *F. albilineellus* (Fernald) in wing pattern and general shape of the male genitalia. *Loxocrambus* does not have the antennal sensory pits of *Fissicrambus* and its tegumen arms are fused to the vinculum. Within *Loxocrambus* most species are very similar to *L. canellus* in male genitalia (except for *L. coloradellus* which has a very long cornutus on the vesica).

Diversity and distribution. The five named species in *Loxocrambus* are restricted in their distribution to North America, occuring in the South from Florida and Texas to Arizona and California to Manitoba and Michigan in the North. One possibly undescribed species from southern California was discovered by Klots (manuscript notes). The exact taxonomic status of four species (all species other than *L. coloradellus*) is unclear at present due to their extreme similarity in wing pattern and in male and female genitalia.

Natural history and immature stages. Unknown.

Comments. *Fissicrambus hospition* Bleszynski and *Crambus coloradellus* Fernald are here transfered to *Loxocrambus*. The previous concept of the genus included only the species with the forewing apex truncated. The genitalia of *L. coloradellus* are described here for the first time.

Neodactria new genus

(Figs. 24, 58, 121, 156, 230, 283, 330)

Type species. *Crambus luteolellus* Clemens, 1860.

Type presumed lost. Clemens types are in the collections of the Philadelpia Academy of Sciences but an investigation of these did not the reveal the presence of the type of *N. luteolella*. A neotype will have to be designated.

Derivation of name. I have used a manuscript name of Klots. I do not know its origin. I have not been able to find "Neodactria", "Dactria", or anything similar in indexes of zoological nomenclature, atlases, or dictionaries. *Neodactria* is probably a neologism. However, it could have been made from the combination of the greek word *neos* (new), the contraction "dac" from the greek word *dactylos*, a finger, and from the latin word *tres* meaning "three". This would presumably relate to the presence of three digit-like structures on the moth but I was not able to make any reasonable connection with the morphology of the moths.

Diagnosis. This genus is believed to be characterized by the following apotypic condition: the aedeagus is dorsally opened apically. In addition, the gnathos is reduced in all species. The similar forewing pattern in all members of this genus is also noteworthy (see below and fig. 156).

Description.

Head (fig. 24). Fronto-clypeus not produced, rounded. Ocellus and chaetosema well-developed. Labial palpus of average length (3.03X head width in one dissected specimen of N. luteolella). Vestiture mostly as in C. pascuellus (fig. 25) except for more dishevelled labial palpus and appressed scales on fronto-clypeus; sometimes with vertexal scales slightly produced anterad. Male antennal flagellomeres serrate (fig. 58) with fewer than average (± 30 versus 35-55) long sensilla trichodea; other sensilla all present in average numbers but sensillum auricillicum absent.

Wings (fig. 121). Female frenulum simple. Male frenulum hook absent. Forewing with R1 present, connected with Sc (except in N. murella in which it is free); R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing with M2, M3, CuA1 & CuA2 present. Forewing elongate (2.79X its width in one mounted specimen of N. luteolella). Forewing pattern (fig. 156) without longitudinal lines, usually with waved subterminal and median lines. Forewing colour of various shades of brown.

Tympanal organs (fig. 230). Transverse ridge medium-sized in N. luteolella but narrower in other species, anterior margin usually straight or widely convex, posterior margin straight, convex or concave. Tympanic pockets small, not extended much beyond transverse ridge, more or less conical. Venulae secundae present but usually weakly sclerotized, divergent. Tympanic bridge medium-sized or longer, not distinctly projected ventrally in one species, usually with arms connected medially. Praecinctorium extended to transverse ridge or beyond, with dorsal sclerotized support variable in length. Tympanic crest 2-4X longer than high, situated anterior to middle. Tympanic drum more or less bean-shaped, extended from slightly before to slightly beyond transverse ridge. Spinula usually well sclerotized.

Male genitalia (fig. 283). Uncus varying from long and narrow to short and thick, to thick and sinuate. Gnathos reduced to a poorly sclerotized narrow flap. Tegumen varying from short and bulky to elongate, connected ventrally. Costal process of valva strongly sclerotized, variable in shape; cucullus narrow, pointed dorsally; sacculus sclerotized, with a distinct ridge near base of cucullus in one undescribed species. Vinculum produced anterad laterally, with a short saccus. Juxta strongly sclerotized, medium-sized. Pseudosaccus usually large. Aedeagus long and narrow with short coecum penis; dorsally opened (trough-shaped) apically; vesica without cornutus.

Female genitalia (fig. 330). Anal papillae not divided into two lobes. Posterior apophyses longer than papillae. Anterior apophyses about as long as papillae. Segment VIII dorsally narrow. Sterigma usually with a short sclerotized protruding tube with ostium in middle. Ductus bursae wide, unsclerotized, not distinctly differentiated from elongate corpus bursae. Latter without signum.

Relationships. My analysis (fig. 5) shows that *Neodactria* does not belong to the *Crambus*-assemblage but its relationships with other genera of Crambini are unknown. Based on the general shape of the genitalia of both sexes, this genus is associated with *Pediasia*, *La*, *Fissicrambus* and *Thaumatopsis*.

Diversity and distribution. Klots (1983) listed five names in *Crambus*, with the annotation "mispl." (for misplaced) which were included in his manuscript genus *Neodactria*. Three other species were recognized by Klots (manuscript notes) as undescribed. Two of these are undoubtedly undescribed. I also discovered another potentially undescribed species of *Neodactria* in Arizona. At present, a preliminary estimate indicates that there are at least six species in this Nearctic genus. The *N. luteolella*-group (including also *N. zeella* and *N. caliginosella)*. was believed by Klots (manuscript notes) to be a single species of variable colouration. All have very similar male genitalia. As far as known, the three forms occur sympatrically from Newfoundland to British Columbia, to California in the southwest and Florida and Texas in the southeast. This group also reaches the Antilles (Bleszynski 1967; Jaume 1967). Further research is required to determine the status of these three taxa. The other species of *Neodactria* are very localized in various parts of North America.

Natural history and immature stages. The immatures of the three "species" in the N. luteolella-group have been described by Felt (1894), Peterson (1948) and Neunzig (1987) for N. caliginosella, by Fernald for N. zeella, and by Mauston (1970) for N. luteolella. The egg chorion ultrastructure of N. caliginosella and N. luteolella was documented by Matheny and Heinrichs (1972). Neodactria caliginosella, the Sooty crambus or Corn root webworm, was reported to be a pest of lawns in Michigan (Kennedy 1980) and to seedling corn in Virginia (Dominick 1964). The last author mentioned however that the larva prefered the leaves of narrow leaf plantain (Plantago lanceolata L., Plantaginaceae) to those of corn. The seasonal abundance of this species in Virginia was studied by Tolley & Robinson (1986). Tashiro (1987) indicated that this species is one of the six most important sod webworms in the temperate regions of the United States. Neodactria luteolella, the Yellow crambus, was reported to be associated with turfgrass in Virginia (Robinson & Tolley 1982). This species was reported to orient geopositively at rest (Crawford 1971a).

Comments. Neodactria luteolella was placed in Pediasia by various workers (Bleszynski 1967; Mauston 1970) but this species and its relatives clearly lack the distinctive synapomorphy of the aedeagus of Pediasia and therefore do not belong to this genus.

Arequipa Walker

(Figs. 35, 112, 163, 211, 284, 325)

Arequipa Walker, 1863: 195.

Type species. Arequipa turbatella Walker, 1863, by monotypy. Type material in BM(NH); lectotype male and one paralectotype here designated (see Appendix V).

Diagnosis. This genus contains a single species which can be distinguished from other Crambinae by the trilobed uncus and the wing pattern which consists of a more-or-less prominent series of brown dots along the median and subterminal transverse lines over a pure white background.

Redescription.

Head. Similar in shape to that of Crambus pascuellus (fig. 8) but labial palpus longer (2.6X width of head in one dissected specimen) and haustellum only slightly longer than labial palpus. Vestiture as in C. pascuellus (fig. 25). Male antennal flagellomeres (fig. 35) longer than wide, with full complement and average number of sensilla except for the absence of a sensillum auricillicum.

Wings (fig. 112). Female frenulum simple. Male frenulum hook absent. Forewing R1 present, free; R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing of average length (2.52X as long as wide in one mounted specimen). Forewing pattern (fig. 163) most often with median and subterminal lines with a series of dots, also with seven dots at outer margin. Forewing pure white except for brown dots.

Tympanal organs (fig. 211). Transverse ridge distinct with anterior margin convex medially and posterior margin straight. Tympanic pockets virtually absent. Venulae secundae absent. Tympanic bridge long and large, very distinctly projected ventrally with arms connected in middle. Praecinctorium long, extended beyond transverse ridge. Tympanic crest large, slightly more than 2X as long as high, situated medially. Tympanic drum oval, extended to a little beyond middle of pons tympani. Spinula distinct. Sternite III with a pair of oblique sclerotized bars anteriorly.

Male genitalia (fig. 284). Uncus with two long, apically enlarged projections and a short mid-ventral spine projected posterad; long projections with short, thick spines on apical half ventrally. Gnathos long and narrow, only slightly elbowed, apically bent with ventral point. Tegumen narrow, ventrally unsclerotized, peduncull produced posterad. Valval base of costa well sclerotized, not armed; cucullus short, quadrate, laterally compressed; sacculus well sclerotized, longer than cucullus, forming floor of valva, apically twisted towards inner side and dorsally. Vinculum globular, without saccus, rather with ventro-cephalic margin convex. Pseudosaccus strongly sclerotized, elongate. Juxta heart-shaped, not produced cephalad. Aedeagus long, narrow, mostly straight; vesica with one single narrow moderately long cornutus.

Female genitalia (fig. 325). Anal papillae strongly divided into two lobes. Posterior apophyses very thin, shorter than papillae. Anterior apophyses absent. Segment VIII dorsally narrow. Sterigma forming a dorsal plate with lateral pockets, protruding to base of papilla ; ostium at margin of segment VII, at base of plate. Ductus bursae long, narrow, sclerotized basally. Corpus bursae circular, with one signum.

Relationships. Some characters, such as the strongly divided papillae anales of the female, suggest a close association of this species to Crambus. Others, like the simple signum on the bursae and the simple frenulum of the female, tend to refute this hypothesis. This species at present stands apart from any known group of Crambini species.

Diversity and distribution. The only species of Arequipa is distributed in Eastern North America from Nova Scotia to Ontario, westward to Iowa and southward to Virginia.

Natural history and immature stages. Unknown. This species is never common in collections.

Comments. The internal genitalia of the female are shown here for the first time. Felt (1894) illustrated the female sterigma and the male genitalia.

Pediasia Hübner

(Figs. 59, 110, 162, 212, 276, 326)

Pediasia Hübner, 1825: 365.

Type species: *Tinea fascelinella* Hübner, 1813, by subsequent designation by Bleszynski (1954). Type-material lost (Bleszynski 1965).

Carvanca Walker, 1856: 119.

Type species: *Carvanca trisecta* Walker, 1856, by monotypy. Holotype in BM(NH), examined.

Pseudopediasia Ganev, 1987: 36.

Type species: *Pseudopediasia mikkolai* Ganev, 1987, by original designation. Holotype ♀ in the Finnish Museum of Natural History, Helsinki, not examined.

Oseriates Fazekas, 1991: 308. **New synonym.**

Type species: *Tinea aridella* Thunberg, lectotype ♀ in Uppsala Museum (Bleszynski 1965), not examined.

Diagnosis. This very distinct genus can be recognized by the following synapomorphy of the male genitalia: the aedeagus is always strongly down-curved from the middle and the apex is only partially sclerotized longitudinally but twisted to form a complete tube.

Redescription. Based on Bleszynski (1965) and my own observations on the Nearctic species.

Head. As in Crambus pascuellus (fig. 8) in shape except for longer labial palpus (2.75X width of head in one dissected specimen of P. trisecta), distinctly shorter in P. browerella. Vestiture similar to that of C. pascuellus (fig. 25) except for fronto-clypeal scales appressed; vertexal scales slightly projecting anterad at base of antennae. Male antennal flagellomeres (fig. 59) serrate, sometimes more strongly serrate or shortly pectinate in a few Palaearctic species, with a full complement of sensilla except for absence of sensillum auricillicum in P. trisecta.

Wings (fig. 110). Female frenulum simple. Male frenulum hook absent. Forewing R1 present, free (in half of species, otherwise fused with Sc, sometimes this varies in a same species); R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing with M2, M3, CuA1 & CuA2 present. Forewing elongate (2.75X its width in one specimen of P. trisecta). Forewing (fig. 162) often paler along venation, never with a larger white stripe, sometimes with faint indications of median and subterminal lines, mostly uniformly coloured, of various shades of brown.

Tympanal organs (fig. 212). Transverse ridge large to very narrow, anterior margin sometimes slightly convex or concave, posterior margin convex in some species. Tympanic pockets always longer than posterior margin of transverse ridge, usually only slightly so but sometimes 2X as long as width of ridge, more or less conical.

Venulae secundae present or absent, divergent if present. Tympanic bridge medium-sized, shorter in P. browerella. Praecinctorium extended to apex of pockets in P. trisecta (not observed in other spp.), with a long thin dorsal sclerotized support. Tympanic crest about 1 1/2-2X longer than high, anteriorly situated. Tympanic drum generally bean-shaped, more circular in P. browerella, extended to middle of pockets or to anterior margin of ridge. Spinula usually visible.

Male genitalia (fig. 276). Uncus medium-sized, gently narrowing towards apex, apically hooked, rarely reduced. Gnathos usually narrow, more or less strongly elbowed, usually hooked at apex, sometimes with denticles dorsally at apex, sometimes thick and shoe-shaped as in P. trisecta. Tegumen variable, often short with wide pedunculi in North American species. Valva always with strong costal arm; cucullus variable in shape; sacculus not always with a short spine on inner side at base of cucullus as in all North American species. Vinculum strongly produced posterad, never with a saccus but rather with broadly convex ventro-cephalic margin. Pseudosaccus always strongly sclerotized. Juxta generally large, trough-shaped. Aedeagus strongly downcurved, twisted apically beyond attachment of manica; vesica usually with one medium-sized cornutus, but sometimes more, or with several minute cornuti.

Female genitalia (fig. 326). Anal papillae not divided into two lobes, or very slightly so. Posterior apophyses usually about as long as papillae. Anterior apophyses similar in length to posterior ones. Segment VIII dorsally medium-sized to narrow. Sterigma most often membranous. Ductus bursae long to very long, narrow or wide, often sclerotized. Corpus bursae usually small and circular, without signum.

Relationships. The cladistic affinities of Pediasia to the other genera of Crambini in North America are still obscure (see fig. 5). The relatively long female anterior apophyses and the undivided papillae anales suggest that Pediasia is more ancient than the Crambus assemblage. No attempt was made to understand the intrageneric relationships because the genus is very well defined and most of the species are very similar to each other.

Diversity and distribution. Bleszynski and Collins (1962) listed 51 species in the genus Pediasia but several of them, including five North American taxa, were subsequently moved to other genera by various workers. Because the Palaearctic Region is the center of highest diversity and probably the center of origin of Pediasia, a better estimate of overall diversity is based on the revision of this fauna by Bleszynski (1965). This included 41 species. Two of these are holarctic. Six species are apparently restricted to North America. Probably less than 20 species have been described from the Oriental and Ethiopian Regions together. The four species listed for the Neotropical Region by Bleszynski (1967) belong to other genera. Pediasia trisecta is one of the most widespead crambine species in North America. Its range extends from coast to coast in Canada, southward to New Mexico in the West and to South Carolina in the East. The other species are more localized in distribution. Pediasia browerella reaches Baffin Island in the North.

Natural history and immature stages. Bleszynski (1965) mentions that the larvae of Pediasia feed on grasses and make a silken tunnel. In North America, Mauston (1970) described the immatures of P. dorsipunctella and P. trisecta which he reared on grass cuttings. A more complete report on the bionomics of P. trisecta, with descriptions of all stages, was published by Ainslie (1927). This species, which is also called the Larger sod webworm, is believed to be one of the six most important sod webworms in the temperate regions of the United States (Tashiro 1987). Its bionomics was also studied by Mailloux and Streu (1982) and its seasonal abundance was recorded in Virginia (Tolley & Robinson 1986). Crawford (1971a) reported that the species of Pediasia exhibit a typical geopositive response in their choice of resting posture.

Comments. Pediasia is here defined for the first time by the presence of a synapomorphy (see Diagnosis above). One genus is synonymized here. Oseriates Fazekas (1991) was described to accomodate five species which have their forewing first Radial vein connected to the subcosta. This condition occurs several times in various genera of Crambini and, at least in Pediasia, both states of this character sometimes occur in the same species! The structure of the genitalia of the included species demonstrate that this genus is a synonym of Pediasia.

La Bleszynski

(Figs. 51, 84, 161, 217, 280, 322)

La Bleszynski, 1966: 488.

Type species. Neerupa benepunctalis Hampson, 1919. Fixed by original designation by Bleszynski (1966: 488). Type repository: BM(NH) [not examined].

Diagnosis. Members of La are medium-sized brown moths. The males have the valva with a strongly sclerotized bilobed pars basalis and the aedeagus with apical or subapical extensions laterally. The latter is believed to represent a synapomorphy for this genus.

Redescription. Based on specimens of the species described below as new and Bleszynski (1966).

Head. As in Crambus pascuellus (fig. 8) except for less strongly developed ocellus, better developed chaetosema and shorter haustellum (about as long as second segment of labial palpus). Labial palpus 2X diameter of head. Vestiture as in Crambus pascuellus (fig. 25) except that scales on fronto-clypeus are appressed. Antennal flagellomeres (fig. 51) more elongate than those of Crambus pascuellus (fig. 33), cuticular pattern with fewer larger cells, with fewer sensilla trichodea and apparently no sensilla auricillica.

Wings (fig. 84). Female frenulum multiple. Male without frenulum hook. Forewing with R1 present, free; R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 shortly stalked; Cubitus with CuA1 & CuA2. Hindwing with M2, M3, CuA1 & CuA2 present. Forewing pattern (fig. 161) with median and subterminal lines.

Tympanal organs (fig. 217). Transverse ridge distinct, of medium width, anterior margin with triangular dent mesally prolonged by a short thin extension posteriorly inside body, posterior margin slightly concave. Tympanic pockets rather large, rounded, extended to posterior margin of ridge. Venulae secundae present but weakly developed. Tympanic bridge medium-sized, with arms connected mesally, slightly produced ventrally, narrow in ventral view. Praecinctorium short, with thin elongate sclerotized dorsal support. Tympanic crest small, anteriorly situated. Tympanic drum bean-shaped, extended to anterior edge of transverse ridge. Spinula visible.

Male genitalia (fig. 280). Uncus more or less cylindrical, downcurved. Gnathos longer than uncus, trough-shaped. Tegumen broadly convex, with rather large pedunculi. Valva with strongly sclerotized, large bilobed costal process; membranous cucullus; often with small rounded projection on inner side of sacculus near dorsal margin. Vinculum rather large laterally, sometimes extended cephalad. Pseudosaccus present. Saccus absent. Juxta weakly sclerotized. Aedeagus about as long as valva, slender, apically trough-shaped, with apical or subapical extensions laterally; coecum penis short and slender; vesica without cornuti.

Female genitalia (fig. 322). Papillae anales not distinctly divided into two lobes. Posterior apophyses about as long as papillae. Anterior apophyses very short. Sternite and tergite VIII joined to form a ring, connected on each side of sterigma; the latter pouch-like. Ductus bursae short. Corpus bursae of equal medium-sized diameter for whole length, without signum.

Relationships. The relationships of La to most other genera of Crambini are unknown, as shown by the results of my cladistic analysis (fig. 5). Bleszynski (1966) mentioned that the genus is "rather close to the Pediasia complex".

Diversity and distribution. The genus was previously known to contain only three species distributed in Bolivia and Peru (Bleszynski 1966). Another species, probably new to science, was discovered on the Galápagos Islands (unpublished) and the following new species from the southwestern United States, discovered by Klots (unpublished notes), represents the first record of the genus north of the equator. Bleszynski (loc. cit.) mentioned that the genus has "several undescribed species".

Natural history and immature stages. I collected specimens of this genus in the pampa zone, 1000 m elevation, on Isla Isabela in the Galápagos

Islands and in the White Mountains of Arizona at approximately 7500' (2286 m) of elevation. The vegetation of the Galápagos pampa is mostly grasses interspersed with patches of *Lycopodium* sp. and Bracken Fern (*Pteridium aquilinum* (L.) Kuhn.). The immature stages are unknown.

Comments. My description of this genus differs slightly from that of Bleszynski (1966) since it is mostly based on the new species described below. In the forewing venation, R1 is not always coincident with Sc, R2 is not always stalked with R3+4+5, and M2 is sometimes stalked with M3; in the female genitalia, the anterior apophyses are not lacking but are very short; and, the female frenulum has more than two bristles in the new species. The apical shape of the aedeagus, here considered as a synapomorphy for the genus, defines it in evolutionary terms for the first time.

La cerveza sp. nov.

(Figs. 51, 84, 161, 217, 280, 322, 340)

Type material. HOLOTYPE. ♂: [USA] NM, Sta Fe Co., 6 mi. NE Santa Fe, 8000', 31.vii.1964, F., P., & M. Rindge (AMNH). PARATYPES (22 ♂♂, 2 ♀♀). 11 ♂♂: [USA] TX, Big Bend Nat. Park, Green Gulch, A. & M.E. Blanchard, dates as follows; one 3.v.[19]72, four 12.v.[19]72, six 2.vi.[19]72; two with male genitalia on slide nos. AB 3517 and AB 5156; one with wings on slide no. AB 3832 (USNM). 6 ♂♂: [USA] TX, Brewster Co., Chisos Mountains, Green Gulch, 5500', 6.vi.1973, D.C. Ferguson; one with genitalia on slide no. BL 245 (USNM). 2 ♂♂: [USA] TX, Brewster Co., Big Bend Natl. Park, Green Gulch, 5400', 8.v. & 10.v.1972, J.G. Franclemont (USNM). 1 ♀: [USA] AZ, Apache Co., South Fork Cmpgd., 12 km W Springerville, 20.vii.1989, MVL, B. & J.-F. Landry; genitalia on slide no. BL 262 (CNC). 1 ♂: [USA] CO, Colorado Spgs., Rock Creek Canyon, 10.vii.1959, Margot May coll.; genitalia on slide no. 24.vi.1969 # 2, A.B. Klots (AMNH). 1 ♂: [USA] CO, Chaffee Co., Castles, 8 mi E Buena Vista, 8800', 11.vii.1982, R.W. Hodges, pinyon-juniper-oak-cottonwood-willow-*Rhus* (USNM). 1 ♀: [USA] NM, Grant Co., Cherry Cr. Camp., 16.vi.[19]74, P.M. Jump coll. (PJC). 1 ♂: same data as holotype, whole body on slide no. BL. 128 and Wing on slide no. BL 27 (CNC).

Diagnosis. The species can be distinguished from similar looking specimens of *Neodactria* spp. and from *Thaumatopsis* *bolterella* by various characters of the male and female genitalia; noticeably, the shape of the aedeagus, that of the process on the valve costa and that of the gnathos of the male.

Derivation of name. Dr. Stanislas Bleszynski was a good taxonomist of the old school who nevertheless thought that a little humour in a classification did not hurt (M. Shaffer, pers. comm.). Thus, among several nomenclatural acts of his, he christened two species in the genus *La* with the following names: *La* *paloma* and *La* *cucaracha*. I tend to agree with this philosophy. The name of this new species is derived from the Spanish noun for beer, my favorite beverage. The forewing ground colour of this species reminds me of the colour of a good dark ale brewed in Québec.

Description. Wingspan 20-29 mm (holotype 24 mm); males (n=19) 20-24 mm; females (n=2) 27-29 mm. Colour mostly brown.

Head mostly whitish brown, ventrally white. Maxillary and labial palpi with scales brown basally and whitish brown apically. Antennae uniformly whitish brown. Thorax mostly whitish brown, some scales with a darker brown band in middle. Legs mostly whitish brown except for darker brown inner side of foreleg and of midleg coxa. Forewing costa dark brown at base, at connections with median and subterminal lines and at apex; paler between these areas, more conspicuously so before apex. Middle of wing with an indistinct longitudinal white streak from base to outer margin, also with a dark greyish-brown diagonal streak above white streak from middle of wing to apex. Mostly greyish brown below white streak, more cinereous in terminal area. Both median and subterminal lines tawny; median line usually indistinct above middle, internally lined with whitish-brown scaling, connecting slightly before middle on inner margin and beyond middle on costa, strongly projected towards outer margin at radial sector and less so in fold; subterminal line darker brown near costa, externally lined with white, white scaling lined with greyish-brown scales near inner margin, slightly flexed towards outer margin at radial sector and in fold. Basal fringe alternatively white and greyish brown in patches of various lenghts; apical fringe uniformly whitish brown. Hindwing uniformly greyish brown. Abdomen uniformly whitish brown.

Male genitalia (fig. 280). Uncus wider and setose on basal half, apical half narrowing with apex not sharply pointed. Gnathos apically downcurved, desclerotized, rounded. Costal process of valva with two projections similar in length; base of costal process broad and sparsely setose dorsally; inner projection directed meso-dorsally, with short setae on most of length; outer projection 3/4 cucullus length, laterally flattened but inclined towards inner side, directed upward at 30^0; sacculus with short rounded projection dorsally on inner side. Vinculum short (i.e. not projected cephalad), dorsally about 2X basal width in lateral view, ventrally a narrow ring. Pseudosaccus diamond-shaped in ventral view, almost reaching anterior margin of vinculum, reaching 1/3 height of vinculum in lateral view. Aedeagus slightly inclined ventrally, straight, with two pairs of subapical projections laterally, most apical pair larger and spine-like.

Female genitalia (fig. 322). Posterior apophyses about as long as papillae, straight, apically rounded. Sterigma ventrally a heart-shaped flap, dorsally a short rectangular plate, prolonged cephalad in body cavity by a T-shaped extension. Ostium on left side. Ductus bursae membranous and very short. Corpus bursae extended to middle of segment VI, subapically with a dorsal rounded bulge.

Variation. Colour variation in the forewing includes differences in the conspicuousness of the median and subterminal lines, differences in contrast between pale and darker areas and slight differences in shades of brown. No variation in the genitalia was noted.

Geographical distribution (fig. 340). Known from the Chisos Mountains in southwestern Texas and various mountains of the Rocky Mountain system in Colorado, New Mexico and Arizona.

Natural history. Unknown apart from the fact that specimens were collected in mountains at elevations varying between 5400' and 8800' (1646-2682 m). One of the paratypes was collected in a "pinyon-juniper-oak-cottonwood-willow-Rhus" habitat. The only specimen I have collected was taken at light in a coniferous forest at about 2300 meters altitude. The mercury-vapor lamp was located by a small meadow in which the vegetation was completely dry except for the presence of a few flowers.

Comments. This species was recognized as undescribed by A.B. Klots.

Parapediasia Bleszynski, status revised

(Figs. 43, 45, 47, 57, 80, 151-153, 159, 209,
210, 270-273, 327-329)

Parapediasia Bleszynski, 1966: 485.

Type species: Crambus tenuistrigatus Zeller, 1881, by original designation. The genus was diagnosed by Bleszynski in 1963 (a) but he designated the type species only later (Bleszynski 1966). The male lectotype designated by Bleszynski (1963a) is in the BM(NH) and was examined.

Diagnosis. The genus is believed to be monophyletic on the basis of the shared presence of various sclerotized ornamentations at the dorsal apex of the aedeagus (character 32). The forewing pattern is similar in the five North American species of this genus (see Wings below).

Description. Based on Bleszynski (1963a) and my own observations.

Head. In P. teterrella very similar in shape to that of Crambus pascuellus (fig. 8) except for shorter labial palpus (1.64X head diameter). Labial palpus also shorter in P. decorella and P. ligonella but longer in the other two species. Vestiture of short, wide, appressed scales; maxillary palpus also more conspicuously triangularly scaled than in C. pascuellus (fig. 25). Antennal flagellomeres (figs. 43, 45, 47, 57) variable: in P. decorella (fig. 45) with high number of sensilla coeloconica (≈35-40) and very few sensilla trichodea (3); in P. torquatella (fig. 43) strongly serrate with somewhat reduced cuticular pattern and possibly no sensillum styloconicum; in P. teterrella (figs. 47, 57) similar to those of most other Crambini except for presence of large sensory pit.

Wings (figs. 80). Female frenulum with one (P. teterrella), two (P. decorella) or three (P. ligonella) bristles. Male frenulum hook absent. Forewing elongate (from 2.59-2.93X longer than wide in four mounted specimens, see Appendix IV). Forewing R1 present, free; R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing pattern (fig. 151-153, 159) usually with paler veins, median and subterminal lines well marked and fringe on outer margin shining.

Tympanal organs (figs. 209, 210). Transverse ridge medium-sized in length and width. Tympanic pockets rather large. Venulae secundae absent. Tympanic bridge medium-sized, shorter in P. teterrella. Praecinctorium medium-sized, with a dorsal sclerotized support. Tympanic crest generally narrow but very large in P. decorella, situated anteriorly. Tympanic drum bean-shaped, generally short, extended to apex of pockets only in P. teterrella. Spinula visible at 50X.

Male genitalia (figs. 270-273). Uncus sharply pointed, down-curved only apically. Gnathos usually narrow and apically straight, strongly trough-shaped in P. decorella. Tegumen large and dorsally convex or thinner, strongly sclerotized ventrally. Valva with strongly developed costa; cucullus long, narrow, membranous; sacculus sclerotized, without projection in P. hulstella and P. torquatella. Vinculum narrow usually with distinct saccus. Juxta strongly sclerotized. Pseudosaccus dorso-ventrally flattened and directed ventrally except in P. teterrella. Aedeagus long and narrow or short and bulky, with strongly sclerotized ornaments apico-dorsally; vesica scobinate, without cornuti.

Female genitalia (figs. 327-329). Anal papillae strongly divided into two humps (P. decorella) to undivided (P. teterrella). Posterior apophyses very short. Anterior apophyses absent or reduced to tiny knobs. Segment VIII dorsally narrow. Sterigma strongly sclerotized, generally invaginate, cup-shaped or with one or two large plates dorsally and ventrally. Ductus bursae usually long and narrow, sometimes basally enlarged. Corpus bursae circular with 0-2 signa.

Relationships. Parapediasia belongs to the higher Crambini that share the following: the forewing R5 free, reduced female segment VIII, and reduced apophyses. It is possibly closely related to genus Fissicrambus with which P. teterrella shares the presence of large sensory pits on the antennal flagellomeres. Within Parapediasia in North America, P.

ligonella and *P. decorella* are most closely related to each other in wing pattern and female genitalia features; *P. hulstella* and *P. torquatella* n.sp. are undoubtedly sister-species based on their very similar aedeagus as well as on other characters; *P. teterrella* seems to stand apart from the others and may be closer to the ancestral stem of the genus.

Diversity and distribution. Nine species of *Parapediasia* were listed from South and Central America and the Antilles for the Neotropical fauna by Bleszynski (1967). One of them (*P. ligonella*) is reported here from North America (Florida) for the first time. Four more species also occur in North America ranging from southern Canada to the southern United States. *Parapediasia teterrella* is everywhere in the lowlands in this range; *P. decorella* is restricted to east of the Prairies from Maine to Florida and Texas; *P. hulstella* is only known from California, Colorado and Texas; and *P. torquatella* occurs in Arizona, Colorado and New Mexico; the latter species is described as new below.

Natural history and immature stages. *Parapediasia teterrella* (the Bluegrass Webworm) is the single most important webworm species infesting turfgrass in North America (Tashiro 1987). Ainslie (1930) published a very thorough report on the biology and morphology of this species. Additions to this can be found in Tashiro (1987), Crawford (1971a), Clark & Haynes (1990) and Marshall (1990). Its larva was most recently described by Tan (1984) and Neunzig (1987) although it has been known since Murtfeldt (1893). *Parapediasia decorella* was successfully reared on St. Augustine grass (*Stenotaphrum secundatum* (Walt.)) in Florida and its larva described by Tan (1984). This species was reported on turfgrass in Virginia (Robinson & Tolley 1982). The egg chorion characteristics of P. teterrella and P. bolterella were published by Matheny and Heinrichs (1972). The immature stages and the natural history of the other species are unknown.

Comments. The status of Parapediasia is revised to exclude Thaumatopsis bolterella (Fernald) and to include P. hulstella (Fernald) formerly classified with Crambus (Klots 1983). The monophyly of the genus is established for the first time.

Parapediasia torquatella sp. nov.

(Figs. 43, 159, 272, 340)

Type material. HOLOTYPE. ♂: [USA] AZ, Coconino Co., State Mtn. Loop Rd., 6900', 20 mi NW Flagstaff, 19.vii.1965, J.G. Franclemont (USNM). PARATYPES (44 ♂♂). One ♂, same data as holotype except for date: 14.vii.1965. 18 ♂♂: AZ, Coconino Co., Fort Valley, 7350', 7.5 mi NW Flagstaff, J.G. Franclemont, dates as follows: one 29.vi.1961, one 5.vii.1964, one 7.vii.1964, four 8.vii.1964, two 9.vii.1964, six 10.vii.1964, one 12.vii.1964, one 13.vii.1964, one 5.vii.1965 (USNM). 6 ♂♂, same locality, R.W. Hodges, dates as follows: one 28.vi.1961, one 30.vi.1961, three 3.vii.1961, one 6.vii.1961 (USNM). 3 ♂♂: AZ, Coconino Co., Hart Praire, 8500', 10 mi NNW Flagstaff, 8.vii.1964, J.G. Franclemont (1 USNM, 2 CNC). 1 ♂: AZ, Coconino Co., Walnut Canyon, 6500', 6-1/3 mi EESE Flagstaff, 18.vii.1965, J.G. Franclemont (USNM). 2 ♂♂: AZ, Coconino Co., West Fork, 6500', 16 mi SW Flagstaff, 21.vii.1965, J.G. Franclemont (USNM). 6 ♂♂: AZ, [Apache Co.], Greer Rd., White Mts., 27.vi.1935, J.A. Comstock (LACM). 1 ♂: AZ, Apache Co., Alpine Divide Camp, 4 mi N Alpine, 8500', 17.vii.1965, F., P. & M. Rindge (AMNH). 3 ♂♂: [USA], NM, Catron Co., 8 mi S Quemado, UV Lite, 27.vi.1987, P.M. Jump, Acc. # 1117 (PJC). 1 ♂ (genitalia on slide BL 170, SEM antennal preparation # 33): [USA] CO, Park Co., S Platte Riv. nr Lake George, 8000', T.C. Emmel (LACM). 1 ♂: CO, Teller Co., Florissant, Big Spring Ranch, 8640', 8.vii.1962, T.C. Emmel (LACM).

Diagnosis. This species is unlike any other North American Crambine. Its pale brown forewing colour with paler veins and distinct median and subterminal lines are diagnostic. The aedeagus is also very peculiar; it is adorned with a collar-like sclerotized structure apically. This is similarly developed in P. hulstella but the two species differ in wing pattern.

Derivation of name. The name is derived from the latin torquatus which means "adorned with a necklace or collar" in reference of the shape of the apical portion of the aedeagus.

Description. Wingspan 27-30 mm (n=45 males), holotype: 27 mm. Females unknown. Colour pale greyish brown.

Head mostly dark brown, paler on occiput between antennae, on lower fronto-clypeus, on inner side of labial palpi and on haustellum; antennal flagellomeres strongly serrate (fig. 43) with average numbers of sensilla coeloconica, chaetica and trichodea but apparently without sensillum styloconicum and sensillum auricillicum. Thorax mostly dark brown with paler brown scales in middle; scales on tegulae reaching apex of thorax. Leg coxa and femur with contrasting white and chesnut-coloured longitudinal bands; other leg segments almost uniformly pale brown, slightly darker towards apical tarsi. Forewing ground colour pale brown; white or pale yellowish brown on costa and on veins; median and subterminal lines dark brown, not indented, broadly curved; median line not reaching inner margin; outer margin with wide band of beige scales and with seven evenly spaced dark brown dots on margin; basal fringe dark brown with few paler scales at apex of R5, M1 and at anal angle; apical fringe paler brown and shining. Hindwing pale brown with concolorous basal fringe, apical fringe slightly paler. Abdomen with whitish and yellowish-brown scales.

Male genitalia (fig. 272). Uncus wide for most of length, apically narrower. Gnathos shallowly trough-shaped. Tegumen rather wide and broadly convex with narrower pedunculi, ventrally with a median flap projecting cephalad between pedunculi. Pars basalis with a dorsal rounded hump followed by a large upwardly directed projection which is apically flattened and triangular. Cucullus narrow, directed dorsally at 45^0. Sacullus sclerotized but not forming a projection. Juxta V-shaped with rather narrow arms.

Pseudosaccus short, rounded, flattened, directed at 45^0 ventrally, only narrowly carinate. Vinculum with a distinct protruding saccus. Aedeagus short and bulky; apical projection flat and surrounding the opening like a large collar.

Female genitalia. Unknown.

Variation. Some specimens have the forewing transverse lines more yellowish brown than dark brown. Others have their subterminal line bordered with white on the outer side. No variation in the structure of the male genitalia was observed because only one dissection was made.

Geographical distribution (fig. 340). This species is known from various mountain ranges of the Rocky Mountain system: the Coconino Plateau and the White Mountains in Arizona, the San Francisco Mountains in New Mexico and in Colorado near Florissant.

Natural history. Specimens of Parapediasia tcrquatella were collected with an ultra violet light. Catches were made at high altitude between 6500 and 8640 feet [1981-2633 m].

Comments. This species was discovered by A.B. Klots but a description was never published.

Almita new genus

(Figs. 39, 40, 92, 96, 157, 158, 213, 214, 278, 279, 331, 332, 339)

Type species. *Almita* *texana* new species, described below. Type repository: USNM.

Derivation of name. This name is the diminutive of the Spanish term *alma*, meaning "soul". Alma is also the first name of my friend and colleague Dr. M. Alma Solis, Curator of the Pyralidae collection at the (U.S.) National Museum of Natural History, Washington, D.C. The gender of the name is feminine.

Diagnosis. The genus is diagnosed by a synapomorphy (character 31) of the male genitalia, the manica is disconnected from the aedeagus from its base. The combination of the following homoplasies also help to diagnose this genus: forewing Radius missing one vein (character 10), forewing Cubitus missing one vein (character 12), hindwing M2-M3-CulA-CuA2 missing one vein (character 17) and, gnathos reduced or lost (character 25). The pale brown forewing (appearing mouse grey) with a median and a subterminal line and with two to four darker spots between the subterminal line and the outer margin is also diagnostic of this genus.

Description.

Head. Not dissected, but similar to that of Crambus pascuellus (fig. 8). Labial palp 2X diameter of head in length. Vestiture with appressed wide, short scales between antennae on frontoclypeus; vertex laterally with longer scales directed medially, these longer and larger in A. texana; maxillary palpus triangularly scaled; labial palpus with straight long scales. Male antennal flagellomeres as in most Crambini (further details provided under each species).

Wings (figs. 92, 96). Female frenulum simple. Male frenulum hook absent. Forewing with R1 present, free; R2 free; R3 missing; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 but without CuA2. Hindwing M2, M3, CuA1 & CuA2 with one vein missing. Forewing elongate. Forewing pattern (figs. 157, 158) with a median and a subterminal line and with two to four darker spots between subterminal line and outer margin. Forewing colour pale brown.

Tympanal organs (figs. 213, 214). Transverse ridge present, rather wide, anterior and posterior margins slightly convex. Tympanic pockets small. Venulae secundae absent. Tympanic bridge medium-sized, slightly projected ventrally, with arms connected medially, wings expanded laterally. Praecinctorium short, with short triangular dorsal sclerotized support. Tympanic crest small, anteriorly situated. Tympanic drum bean-shaped and extended to posterior edge of transverse ridge or reduced (A. texana). Spinula visible.

Male genitalia (figs. 278, 279). Uncus long, strongly sclerotized, variable in shape. Gnathos weakly sclerotized. Tegumen short, with large pedunculi. Valva with simple or bilobed costal process; cucullus membranous; sacculus variable. Vinculum rather large, without saccus. Pseudosaccus present. Juxta weakly sclerotized. Aedeagus well sclerotized, with short coecum penis, with the manica disconnected from the aedeagus from its base.

Female genitalia (fig. 331, 332). Papilla analis moderately to strongly sclerotized, divided in a small dorsal hump and a larger ventral hump. Both pairs of apophyses very short. Segment VIII dorsally narrow. Sterigma strongly sclerotized. Ostium opening centrally. Ductus and corpus bursae undifferentiated. Corpus bursae without signa.

Relationships. The genus is most closely related to Raphiptera based on the presence of the derived traits of characters 10, 12, 17 and 25 (see Diagnosis above).

Diversity and distribution. The genus at present includes two species described as new below. These are known from the southern United States, namely Arizona, New Mexico and Texas.

Natural history. Unknown.

Comments. I suspect that the relatives of the species included in this genus should be looked for in mountainous and arid regions of northern Mexico. Two other small species from Puerto Rico and Dominica with a similar wing pattern have been found in the USNM collections, but their genitalia proved to not be congeneric with *Almita*.

Almita texana new species

(Figs. 40, 96, 157, 214, 278, 331, 339)

Type material. HOLOTYPE. ♂: [USA] TX, Brownsville (USNM). PARATYPES (27 ♂♂, 3 ♀♀). 12 ♂♂, 1 ♀: same data as holotype; one male with genitalia on slide no. BL 246, the female with genitalia on slide no. BL 251, one male with wing on slide no. BL 62 (USNM). 13 ♂♂, 2 ♀♀: [USA] TX, San Benito; dates as follows; 4 ♂♂ 1-7.iv. one with genitalia on slide no. BL 274, 9 ♂♂ and 1 ♀ 24-30.iii. one male with antenna prepared for SEM no. 32, 1 ♀ 24-30.vi. (USNM). 2 ♂♂: [USA] TX, Cameron Co., Laguna Atascosa, 28.ii.[19]73 with genitalia on slide USNM no. 99484, 6.iii.[19]78, A. & M.E. Blanchard (USNM).

Diagnosis. The forewing pattern is similar to that of *A. portalia* but *Almita texana* usually has at least four spots distinct at the outer margin while *A. portalia* normally has only two distinct spots. *A. texana* is also smaller than *Almita portalia* by one to 6 mm. In male genitalia, the shape of the uncus, the virtual absence of a gnathos in *A. texana* and the development of the saccullus are conspicuous differences between the species. In the female genitalia, the shape of the sterigma will differentiate both taxa.

Derivation of name. The name is derived from the name of the only state of the United States where the species is known.

Description. Wingspan 9.5-12 mm (holotype 9.5 mm); males (n=4) 9.5-12 mm; females (unavailable for measuring because the wings were not spread). Colour pale brown.

Head whitish brown. Maxillary and labial palpi mostly whitish brown, slightly darker on outer side. Antennae whitish brown. Antennal flagellomeres (fig. 40) with average number and full complement of sensilla except for absence of a sensillum auricillicum. Thorax whitish brown. Legs mostly whitish brown, darker brown on inner side of foreleg and on mid- and hindleg tarsi mostly at base of segments. Forewing (fig. 157) pale greyish brown with scales greyish brown on basal half, whitish brown at tip; veins with uniformly colored whitish-brown scales before subterminal line, white beyond that line on Median and Cubital veins only. Median and subterminal lines distinct, simple, brown; median line with some tawny scales in middle of wing, connecting slightly before middle on costa and on inner margin, strongly projected towards outer margin beyond cell and less so in Cubital sector, larger in latter mentioned areas; subterminal line thin, mostly following outer margin in Cubital and Median sectors, broadly flexed anteriorly before reaching costa, slightly flexed anteriorly before reaching inner margin, less distinct at both ends. Terminal area without grey tint of anterior areas, with scales more contrasting brown and whitish brown, generally darker brown around dots; with two distinct dark-brown dots between veins and between subterminal line and outer margin in Cubital sector; with two similarly coloured and distinct dots above and below the two main dots, closer to outer margin; also with a distinct dark-brown dot near outer margin at apex and another indistinct one below, close to outer margin. Fringe with two rows of short and long scales uniformly pale whitish brown. Hindwing uniformly pale whitish brown. Abdomen uniformly whitish brown.

Male genitalia (fig. 278). Uncus longer than whole valva + pseudosaccus, slender, mostly straight, subapically downcurved, apically blunt, with few short and fat setae only on lateral edges dorsally, also with very small setae dorsally at base. Gnathos very small. Tegumen not extended dorso-apically, height shorter than 1/2 length of uncus. Costal process of valva bilobed with large, glabrous, pointed projection curved inwards, situated on outer side, and directed apico-dorsally, also with short, rounded, compressed setose lobe on inner side dorsally; cucullus directed dorsally at 45^0, laterally flattened, twisting towards inner side apically, with small sclerotized hump at base on inner side;

sacculus with inner side of ventral edge slightly projected apically into a point. Vinculum short and rounded, with ventrocephalic margin slightly concave. Pseudosaccus about half vinculum length, directed dorsally at 45^0, laterally flattened, broad based, tapering apically. Juxta indistinct. Aedeagus circular in cross-section, slender, about as long as valva + pseudosaccus, medially upturned, apically downcurved and separated into two distinct lateral parts between which is the opening; ventral extension almost as long as aedeagus, in line with horizontal plane, apically downcurved and more strongly sclerotized.

Female genitalia (fig. 331). Posterior apophyses slightly shorter than length of papillae. Anterior apophyses very short, apically curved. Sternite VIII with small protuberances (modified setae?) at base of apophyses. Sterigma protruding ventrally, dorsally forming a large invaginated sclerotized pocket. Membrane of sternite VIII with small pocket medially. Protruding part of sterigma with one ventral and two lateral lobes with ostium in between; internal part laterally flattened with a heavily sclerotized external layer and a surrounding membranous layer. Corpus bursae extending anteriorly to segment V.

Variation. In colour pattern there is variation in the distinctness of the median and subterminal lines and in that of the dots of the terminal sector, especially with respect to the two most apical dots. The contrast between the dark and pale areas of the scales also varies. In the male genitalia, a specimen other than the one illustrated had the setae on the uncus generally longer. In the female genitalia no variation was observed as only one dissection was prepared.

Geographical distribution (fig. 339). This species is known only from Cameron County, in southernmost Texas, U.S.A.

Natural history. Unknown.

Comments. Three additional specimens of this species are known. They were not included in the type series because they lack an abdomen. They were collected in Brownsville and San Benito, Texas. They are deposited in the USNM.

__Almita__ __portalia__ new species

(**Figs**. 39, 92, 158, 213, 279, 332, 339)

Type material. HOLOTYPE. ♂: [USA] AZ, S.W.R.S., 5 mi. W Portal, 30.iv.1961, M.A. Cazier (AMNH). PARATYPES. (3 ♂♂, 6 ♀♀). 2 ♂♂: [USA] AZ, Cochise Co., Chiricahua Mt's, Southwestern Research Station, 18.iv.1961 (genitalia on slide no. 8 jan. 1968 # 1, A.B. Klots), 27.iv.1962 (antenna prepared for SEM no. BL 31 and genitalia on slide no. BL 273), C.W. Kirkwood (AMNH). 1 ♂: [USA] AZ, Cochise Co., SW.R.S. vic. Portal, 14.iv.1969, at light in house, 5400', V. Roth & A.B. Klots (genitalia on slide no. 6 July 1969 # 5, A.B. Klots) (AMNH). 1 ♀: USA, AZ, Cochise Co., Chiricahua Mts., Cave Creek, 27.vii.1989, MVL, B. & J.-F. Landry (CNC). 2 ♀♀: USA, AZ, Cochise Co., Chiricahua Mts., Sunny Flat Cmpg., 28.vii.1989, MVL, B. & J.-F. Landry (CNC) (one with whole body on slide no. BL 153 and wings on wing slide no. BL 28). 1 ♀: [USA], AZ, Coconino Co., Vail Lake Rd., 9 1/2 mi SE Flagstaff, 6500', 18.vii.1961, R.W. Hodges (USNM). 1 ♀: [USA], NM, Las Vegas, [E.] Oslar (USNM). 1 ♀: [USA] AZ, Redington (USNM).

Diagnosis. The forewing pattern is similar to that of _A. texana_ but _Almita portalia_ usually has only two distinct spots between the subterminal line and the outer margin while _A. texana_ normally has at least four. _A. portalia_ is also larger than _Almita texana_ by one to six mm. In male genitalia, the shape of the uncus, the presence of a gnathos and the development of the saccullus are conspicuous differences between the species. In female genitalia, the taxa can be differentiated by the shape of the sterigma.

Derivation of name. The name is derived from the locality of Portal, Cochise Co., Arizona, where the holotype of the species was collected.

Description. Wingspan 13-19 mm (holotype 18 mm); males (n=4) 17-18 mm; females (n=4) 13-19 mm. Colour grey although scales are brown and white.

Head mostly whitish brown, white ventrally. Maxillary and labial palpi pale brown. Antennae whitish brown at base, darker brown beyond first third of flagellum. Antennal flagellomeres (fig. 39) apparently without sensilla styloconica (Appendix III) and with fewer than average sensilla trichodea. Legs generally whitish brown; darker brown on inner side of prolegs, inner side of coxa and femur of midleg and last three tarsal segments of mid- and hindleg. Forewing (fig. 158) mostly pale brown with most scales brown on basal half and white apically. Veins in Radial, Median and Cubital sectors with paler scales, completely white on M-stem and beyond subterminal line. With a thin longitudinal stripe of pale yellowish-brown scales from base to median line in the fold. Both median and subterminal lines with yellowish-brown and dark-brown scales; median line simple, connecting slightly before middle on costa and on inner margin, strongly projected towards outer margin beyond cell and slightly so in fold, usually more distinct in middle of wing; postmedian line equally distinct on whole length, simple, mostly straight but flexed anterad and darker brown at both extremities. Terminal area generally with scales more contrasting brown and white, especially so around the two distinct dark brown dots; latter located between postmedian line and outer margin in cubital sector; with indistinct dark brown spots closer to outer margin above and below cubital dots and at apex. Fringe with row of short scales brown on basal half and whitish brown apically; row of elongate scales of various lengths, whitish brown banded with brown at 2/3rds of length. Hindwing uniformly pale brown. Abdomen usually uniformly whitish brown but sometimes with dark-brown scales mid-dorsally on various segments without recognizable pattern.

Male genitalia (fig. 279). Uncus slightly longer than tegumen, down-curved, convex dorsally and slightly concave ventrally in basal cross-section, with a short crest on whole length, larger at base, tapering to a moderately pointed apex. Gnathos very thin (flattened dorso-ventrally), about as long as uncus. Costal process of valva half length of valva, curved inward, large for most of length but flattened at apex; cucullus laterally flattened, directed dorsally at about 45°; projection of saccullus short, rounded and laterally flattened. Vinculum slightly shorter than valva, cephalic margin dorso-ventrally flattened, large and straight. Pseudosaccus small (about 1/4th length and 1/5th height of vinculum), semicircular in cross-section, with a small subapical hump dorsally. Juxta V-shaped in apical view. Aedeagus slender, slightly concave from middle to apex dorsally, as long as valva plus pseudosaccus, ventral extension directed apico-ventrally at about 30°, about half length of aedeagus; subapical tooth-like extensions shaped like shark teeth, pointed dorsally on one side, ventrally on other.

Female genitalia (fig. 332). Posterior apophyses slightly shorter than papillae, straight, apically rounded. Anterior apophyses slightly shorter than posterior ones, similar in shape. Sterigma crescentic in apical view, with dorsal edge longer and convex and ventrally concave, vase-shaped in ventral view.

Variation. In forewing colour pattern, I have noted that some specimens have a thin longitudinal yellowish-brown stripe in the middle of the cell. Also, the distinctness of the lines and dots varies; some specimens for example do not show the accessory spots at apex and above and below the two cubital dots. As mentioned in the description, there is also some variation in the colour pattern of the abdomen. In male genitalia, a second specimen did not show any variation. The female genitalia variation was not assessed because only one female was dissected.

Geographical distribution (fig. 339). Known from the Chiricahua Mountains, the Galiuro Mountains and the Mogollon Plateau in Arizona and the Rocky Mountains in New Mexico.

Natural history. Unknown apart for the fact that this species occurs in montane habitats from 5400 to 6500 feet (1646 to 1981 meters) in altitude.

Comments. The female genitalia and wing drawing and description are based on a paratype (slides genitalia BL 153 and wings BL 28) from Cave Creek, Cochise Co. AZ, which was completely macerated for study. The description of the colouration of the abdomen was based on the paratypes since the holotype had been dissected prior to my studies. This new species had been recognized by Klots.

Raphiptera Hampson

(Figs. 6, 41, 119, 148, 232, 281, 334)

Raphiptera Hampson, 1896: 962.

Type species: Crambus minimellus Robinson, 1870, by original designation. Type in the Philadelphia Academy of Sciences [examined].

Diagnosis. This genus can be recognized by the apomorphic loss of three veins in the forewing and one in the hindwing. This combination of losses is also present in the genus Almita but the latter is well defined by another synapomorphy, and the wing pattern of the two genera is quite different. That of Raphiptera is similar to Crambus except that the forewing ground colour is almost dark grey. In addition, Raphiptera is the only genus of Crambini in North America in which the female genitalia lack the posterior apophyses.

Redescription.

Head (fig. 6). Ocellus and chaetosema well developed. Frontoclypeus not produced, rounded. Labial palpus 3X width of head in length. Haustellum barely longer than labial palpus. Vestiture as in C. pascuellus (fig. 25). Male antennal flagellomere (fig. 41) with fewer than average sensilla trichodea, more than average sensilla chaetica and apparently without sensillum coeloconicum.

Wings (fig. 119). Female frenulum simple. Male frenulum hook absent. Forewing R1 absent; R2 free; R3 present, connected to R4; R5 absent; M1 present; M2 & M3 not stalked; Cubitus with CuA1 but without CuA2. Hindwing M2, M3, CuA1 & CuA2 with one vein missing. Forewing 3.26X its width in length in mounted specimen. Forewing apex produced. Forewing pattern (fig. 148) with large white longitudinal stripe from base to apex interrupted by the subterminal line. Similar to Crambus species. Forewing ground-colour dark greyish brown.

Tympanal organs (fig. 232). Transverse ridge distinct, with anterior margin convex and posterior margin straight. Tympanic pockets present, conical. Venulae secundae present, slightly divergent. Tympanic bridge medium-sized with arms not connected medially. Praecinctorium short, extended to before middle of tympanic bridge, with short dorsal sclerotized support. Tympanic crest very small, at least 2X longer than high, situated anteriorly. Tympanic drum elongate, extended to middle of transverse ridge. Spinula not visible.

Male genitalia (fig. 281). Uncus medium-sized, gently bent ventrad, setose only ventrally. Uncus reduced to two thin arms bent ventrally. Tegumen medium-sized, with pedunculi progressively narrower towards apex, unsclerotized ventrally. Strongly sclerotized costa of valve with pointed projection apically curved inwards; cucullus short and narrow, pointed dorsally; sacculus unsclerotized. Vinculum broad and crescent-shaped in anterior view, without saccus. Pseudosaccus rather long, laterally compressed, separated from floor of vinculum. Juxta surrounding the aedeagus, arms not connected dorsally. Aedeagus short, narrow, apically with dorsal sclerotized projecting bar; vesica without cornutus.

Female genitalia (fig. 334). Anal papillae strongly divided into two lobes as in Crambus. Posterior and anterior apophyses absent. Segment VIII rather large but without sclerotized connection dorsally. Sterigma with a large quadrangular plate with ostium at apex medially. Ductus bursae long, narrow, unsclerotized. Corpus bursae ovoid, with one signum.

Relationships. Based on the loss of two veins in the forewing and one in the hindwing, this genus is believed to be the sister-genus of Almita. Both genera also share a weakly developed gnathos.

Diversity and distribution. The only species of this genus is distributed in Eastern North America from Labrador south to Florida, Louisiana and Texas and west to Nebraska.

Natural history and immature stages. The only species of Raphiptera can only be collected in bogs. Its bionomics and immature stages are unknown.

Comments. The female genitalia of this species are figured and described here for the first time. The skewed numbers of sensilla chaetica and sensilla trichodea and the apparent absence of a sensillum coeloconicum may be an artefact because the picture taken was that of a subapical segment.

Agriphila Hübner

(Figs. 27-29, 37, 111, 155, 172, 222, 285, 324)

Agriphila Hübner, 1825: 365.

Type species: Tinea deliella Hübner, by subsequent designation by L'Homme (1935). Type material lost (Bleszynski 1965).

Diagnosis. All species in this genus can be characterized by the following synapomorphy: the apex of the aedeagus is terminated ventrally with a short spine. Moreover, the females all share a similar invaginated cup-shaped sterigma.

Redescription. Based on Bleszynski (1965) and my own observations on the Nearctic species.

Head. (figs. 27-29) Ocellus and chaetosema well developed. Labial palpus variably long (3.24X width of head in one dissected specimen of A. ruricolella). Fronto-clypeus often produced with a point. Vestiture of labial palpus sometimes strongly dishevelled (fig. 27), otherwise more like that of C. pascuellus (fig. 25) or intermediate; head scaling variable in length of scales and degree of projection. Male antennal flagellomeres (fig. 37) medium-sized with full complement and average numbers of sensilla, sensilla trichodea long.

Wings (fig. 111). Female frenulum double. Male frenulum hook (fig. 172) present or absent. Forewing R1 present, free (but sometimes connected in some specimens of *A. straminella*); R2 free (except for some species in which it is connected with R3+4+5); R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked (except for a few species in which they are partly stalked); Cubitus with CuA1 & CuA2. Hindwing with M2, M3, CuA1 & CuA2 present. Forewing variably elongate (2.41X its width in one mounted specimen of *A. ruricolella*). Forewing pattern (fig. 155) often with paler longitudinal lines along venation, sometimes with a thicker line in middle; median and subterminal lines often present, waved or not. Forewing colour of various shades of brown, fringe with a golden shine.

Tympanal organs (fig. 222). Transverse ridge generally rather narrow anterior margin medially concave, convex, straight or blending into the tympanic bridge (one specimen of *A. anceps*), posterior margin generally slightly convex, more rarely concave. Tympanic pockets as shown, or more conical and extended beyond transverse ridge, or almost inexistant. Venulae secundae absent or indistinct. Tympanic bridge medium-sized as shown. Praecinctorium rather long with long thin dorsal sclerotized support. Tympanic crest about 1 1/2-2X longer than high, anteriorly situated. Tympanic drum generally bean-shaped, sometimes more circular, extended to anterior margin of tympanic bridge to apex of pockets. Spinula generally visible.

Male genitalia (fig. 285). Uncus medium-sized, apically bent. Gnathos medium-sized, rounded and thickened apically. Tegumen variable, mostly elongate in the North American species. Valval short costal process usually rounded apically; cucculus wide in side view, strongly compressed, bent upward; sacullus without projection. Vinculum narrow in side view, with ventro-cephalic margin convex but without a saccus. Pseudosaccus usually short, not strongly carinate. Juxta more or less V-shaped. Aedeagus rather short, with short rounded coecum penis, apically rounded with a ventral point; vesica sometimes with many (5-100) small cornuti but without cornuti in North American species.

Female genitalia (fig. 324). Anal papillae usually well divided into two lobes, setation of medium length. Posterior apophyses shorter than papillae. Anterior apophyses very small, usually knob-like. Segment VIII medium-sized dorsally. Sterigma well sclerotized, invaginated and cup-shaped. Ductus bursae variable in length and width, sometimes sclerotized. Corpus bursae usually circular, with one signum.

Relationships. My analysis shows the affinity of genus Agriphila to Crambus-Fernandocrambus-Chrysoteuchia on the basis of the shape of the female papillae anales. Bleszynski (1965) wrote that Agriphila was close to Catoptria on the basis of the produced forehead, the double frenulum of the female and the single signum on the bursae.

Diversity and distribution. Agriphila is a Holarctic genus with its highest diversity, 26 species, in the Palaearctic Region (Bleszynski 1965). Two of those are also in North America. Our fauna contains nine more species (Klots 1983). With the addition of one species described since (Ganev 1985), the total of known species of Agriphila is 36. In North America, most species are associated with localities in the Rocky Mountains system and the Sierra Nevada from Alaska to California. Only two species, A. ruricolella and A. vulgivagella, are widespread over much of the United States and Southern Canada.

Natural history and immature stages. Bleszynski (1957) reported that the bionomics of most species are unknown. The larvae are generally polyphagous on grasses and thrive in silken galleries amongst grass stems. In North America, the immatures of A. vulgivagella were described by Felt (1894), Mauston (1970) and Neunzig (1987); those of A. ruricolella were described by Mauston (1970). The egg chorion characteristics of these two species were described and figured by Matheny and Heinrichs (1972). The reproductive biology of A. plumbifimbriella was treated by Crawford (1971b). A. ruricolella and A. vulgivagella were reported to be associated with turfgrasses in Viginia (Robinson & Tolley 1982; Tolley & Robinson 1986). Lintner (1882) reported that the depredations of A. vulgivagella, the Vagabond crambus, were sometimes conspicuously noticeable. However, the species of Agriphila generally seem to have a minor impact on turfgrass in North America.

Comments. Crambus angulatus Barnes & McDunnough was placed in Agriphila by Klots (1983) with the annotation that it was misplaced in that genus. It is treated here as incerta sedis (see 5.1.7.3 below). The monophyly of Agriphila is clearly established for the first time on the basis of a synapomorphy (see Diagnosis above).

Fernandocrambus Aurivillius

(Figs. 42, 86, 144, 224, 287, 333)

Fernandocrambus Aurivillius, 1922: 263.

Type species: Fernandocrambus backstromi Aurivillius, 1922, by subsequent designation by Bleszynski (1963b). Type material in the Naturhistoriska Riksmuseum, Stockholm [not examined].

Juania Aurivillius, 1922: 264.

Type species: Juania annulata Aurivillius, 1922, by monotypy. Lectotype ♀ designated by Clarke (1965) deposited in the Naturhistoriska Riksmuseum, Stockholm [not examined].

Diagnosis. The genus can be recognized by the shape of the male genitalia, comprising a strongly sclerotized sacculus, a well sclerotized costa, usually with projections, and an aedeagus usually with a narrow band of sclerotization adorned with one (rarely more) thorn apically. The forewing pattern of the two North American species is like that of Crambus except that the forewing apex is pointed and produced.

Redescription. Based on Clarke (1965) and Bleszynski (1967) and my analysis of Fernandocrambus harpipterus (Dyar).

Head. Similar to that of Crambus pascuellus (fig. 8) but more strongly sclerotized, with longer haustellum and longer labial palpus (2.6X width of head in dissected specimen of F.

harpipterus). Vestiture as in Crambus pascuellus (fig. 25). Male antennal flagellomeres (fig. 42) with full complement and average numbers of sensilla.

Wings (fig. 86). Female frenulum double. Male frenulum hook absent. Forewing R1 present, connected with Sc; R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 free, connected with M3 or sometimes lost; Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing apex produced in a hooked point in many species. Forewing variably elongate (3.55X its width in one mounted specimen of F. harpipterus). Forewing pattern (fig. 144) very variable, Crambus-like in some species.

Tympanal organs (fig. 224). Transverse ridge present, narrow, with anterior and posterior margins slightly convex. Tympanic pockets extended beyond transverse ridge, conical. Venulae secundae present, moderately sclerotized, strongly divergent. Tympanic bridge rather long and distinctly projected ventrally, with arms connected medially and with a median longitudinal sclerotized bar ventrally. Praecinctorium extended to transverse ridge, with long thin sclerotized support. Tympanic crest three times longer than high, situated anteriorly near middle. Tympanic drum elongate, partially closed laterally, extended to transverse ridge. Spinula barely visible.

Male genitalia (fig. 287). Uncus medium-sized, variable in length. Gnathos with narrow arms connected near base, tubular on most of length sometimes with short apical point, variable in length. Tegumen rather short and bulky, with wide pedunculi, sclerotized ventrally. Valval costa sclerotized at base, with or without a projection; cucullus variable in length and width; saccullus strongly sclerotized, with or without a projection. Vinculum medium-sized, without saccus, lateral margins sometimes strongly extended anterad. Juxta short and dorso-ventrally flattened in F. harpipterus. Pseudosaccus variable, narrow and laterally compressed in F. harpipterus. Aedeagus medium-sized, with a narrow sclerotized band towards apex usually armed with one (sometimes more) hook(s) at apex; vesica usually without cornutus, with one in the North American species.

Female genitalia (fig. 333). Anal papillae divided into two lobes. Posterior apophyses from about as long as papillae to very short. Anterior apophyses short or absent. Segment VIII variable in length. Sterigma variable, often with a projecting tube. Ductus bursae variable in length and width, sclerotized or not. Corpus bursae distinct from ductus bursae, more or less circular, with two signa.

Relationships. Genus Fernandocrambus is undoubtedly very closely related to Crambus as shown by the shared double papillae anales of the females, the two signa on their corpus bursae and the overall similarity of the male genitalia of Fernandocrambus to that of some Crambus species.

Bleszynski (1967) suggested that Fernandocrambus was a Neotropical derivative of Crambus. This is probably a reasonable assumption which is supplemented by the little variation attained in the morphology of the genitalia of Fernandocrambus compared with the high degree of variability exhibited by the species of Crambus in that respect.

Diversity and distribution. Genus Fernandocrambus contains 50 species (Bleszynski 1967) and is distributed from Patagonia to the Southern United States (Arizona, New Mexico, Texas). It is interesting to note that the Juan Fernandez Islands alone have 29 apparently endemic species (Bleszynski 1967).

Natural history and immature stages. The bionomics of F. harpipterus were studied by Crawford (1971b). The same author (1971a) mentioned the typical geonegative orientation of the moths of this species in their choice of resting position. Nothing is known of the morphology of the immature stages.

Comments. The internal male and female genitalia of F. harpipterus were illustrated by Crawford (1971b).

Chrysoteuchia Hübner

(Figs. 55, 56, 116, 169, 226, 286, 335)

Chrysoteuchia Hübner, 1825: 366.

Type species: Tinea hortuella Hübner, 1796, by subsequent designation by Shibuya (1928). Type material lost (Bleszynski 1965).

Amphibolia Snellen, 1884.

Type species: Catastia pyraustoides Erschoff, 1877, by monotypy. Female lectotype in Leningrad (Bleszynski 1965), not examined.

Veronese Bleszynski, 1962.

Type species: Crambus distinctellus Leech, 1889, by monotypy. Male lectotype in BM(NH) (Bleszynski 1965), not examined.

Diagnosis. I know of no synapomorphy uniting all members of this genus. However, most (including our only species) can generally be recognized by their wing pattern, which shows at least one (sometimes two) broadly curved subterminal line and contrasting paler longitudinal lines along the veins. The male genitalia have a thin gnathos, well developed costal process and cucullus on the valve, and, in many species, one or more large thorns at the end of the aedeagus. In addition, only Crambus, Agriphila and Fernandocrambus also have bilobed female anal papillae.

Redescription. Based on Bleszynski (1965) and my own observations on Chrysoteuchia topiaria.

Head. In Chrysoteuchia topiaria very similar in shape to that of Crambus pascuellus (fig. 8) with labial palpus of almost same length. Vestiture with scales on fronto-clypeus wider and appressed, and second labial palpus segment slightly tufted dorsally, otherwise similar to Crambus pascuellus (fig. 25). Antennal flagellomeres (figs. 55, 56) with higher than average number of sensilla trichodea, no sensillum chaeticum on male observed (fig. 55) but three present on female (fig. 56), apparently no sensillum styloconicum and sensillum auricillicum in observed male.

Wings (fig. 116). Female frenulum double. Male frenulum hook absent. Forewing R1 present, connected with Sc; R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing elongate (2.56X longer than wide in one mounted specimen of C. topiaria). Forewing pattern (fig. 169) often distinctive with at least one subterminal line, sometimes with a secondary one which may be restricted to apical region; with paler longitudinal markings following venation, pattern absent in some mostly black or mostly white species.

Tympanal organs (fig. 226). Transverse ridge distinct, rather large, with both margins slightly convex. Tympanic pockets rather large, extended slightly further than ridge, rounded. Venulae secundae absent. Tympanic bridge medium-sized, strongly projected ventrally, with arms connected medially; tympanic wings not spread laterally. Praecinctorium rather long, with long thin dorsal sclerotized support. Tympanic crest slightly more than twice longer than high, anteriorly situated. Tympanic drum elongate, closed laterally, extended to apex of pockets. Spinula distinctly visible.

Male genitalia (fig. 286). Uncus down-curved, variable in shape but usually long and rather narrow. Uncus usually thin, apically straight or down-curved. Tegumen variable in shape, sometimes long and narrow, otherwise medium-sized, dorsally convex or not, usually ventrally sclerotized. Valva usually with a well sclerotized costal process which may or may not be produced; sacculus also well sclerotized and usually with a horn-like projection towards apex; cucullus short, apically broad or narrow, sometimes with a distinct patch of hairs on inner side basally. Vinculum medium-sized, ventro-cephalic margin emarginate, sometimes strongly so. Juxta narrow in C. topiaria. Aedeagus often with one (sometimes two) apical thorns; vesica usually with cornuti.

Female genitalia (fig. 335). Papillae anales often divided into two distinct lobes. Posterior apophyses longer than papillae. Anterior apophyses virtually absent. Segment VIII dorsally narrow. Sterigma strongly sclerotized and complex, usually with a protruding tube. Ductus bursae long, narrow and distinct from corpus bursae, sometimes basally enlarged and sclerotized. Corpus bursae usually circular, with one or two signa, sometimes without signum.

Relationships. My analysis (fig. 5) shows that Chrysoteuchia is very close to Crambus on the basis of the presence of two signa on the female corpus bursae in many species of both taxa. The bilobed papillae anales also contributes to associate these two taxa. The only North American species (C. topiaria) is most similar in wing pattern to the European C. culmella. These two species are however distinct in male genitalia. C. topiaria seems to be more closely related to C. mandschurica (Christoph) with regards to the features of the male genitalia.

Diversity and distribution. Most of the 23 species in this genus are distributed in the Far East of the Palaearctic Region with one species reaching Europe and another endemic to North America. The latter is one of the most common North American species and is distributed from Alaska to Newfoundland, throughout the Rocky Mountains States and the North-central and Northeastern States.

Natural history and immature stages. The bionomics and immature stages of only two species are known. The European species (C. culmella) feeds on various species of grasses and is sometimes considered a pest in England on upland pastures where the soils are acidic. As opposed to Crambus spp , it does not web its tunnels. The immatures of the North American C. topiaria were described first by Scudder (1894) who christened the species "the Cranberry Girdler" because of its pest status on cranberry (Vaccinium Oxycoccos L., Ericaceae). The immatures were redescribed by Mauston (1970). This species is also known as the subterranean webworm (Tashiro 1987). It is believed to be the most diverse of the destructive sod webworms in feeding habits. It is an economic pest of turfgrasses of which it destroys the roots; it is also known to feed on coniferous seedling plants in nurseries as well as *Rumex* sp. (Polygonaceae) (Scudder 1894; Tashiro 1987). Because of its pest status, the bionomics of the species was studied in detail and its female sex pheromone discovered (McDonough & Kamm 1979; Kamm *et al.* 1989). Scanning electron micrographs and a description of the egg of *C. topiaria* were provided by Matheny & Heinrichs (1972). The moth was reported to have a typical geopositive orientation in its choice of resting postures (Crawford 1971a).

Crambus Fabricius, status revised

(Figs. 8, 25, 26, 33, 115, 132-134, 138, 171, 223,
233, 288, 289, 337, 338)

Crambus Fabricius, 1798: 420.

Type species: Phalaena (Tinea) pascuella Linnaeus, 1758. Holotype in the collection of the Linnean Society, London [not examined]. Designated by Curtis (1826).

Palparia Haworth, 1811.

Type species: Phalaena (Tinea) pascuella Linnaeus, 1758. Designated by Bleszynski (1963b).

Chilus Billberg, 1820.

Type species: Phalaena (Tinea) pascuella Linnaeus, 1758. Designated by Whalley (1966).

Argyroteuchia Hübner, 1822.

Type species: Phalaena (Tinea) pascuella Linnaeus, 1758. Designated by Bleszynski (1963b).

Tetrachila Hübner, 1822.

Type species: Phalaena (Tinea) pascuella Linnaeus, 1758. Designated by Nye (1964).

Diagnosis. The species of Crambus, as defined here, can be recognized by the satiny-white longitudinal band in the middle of the forewing which runs from the base to at least the end of the disco-cellular area. In the North American species, this pattern may be less apparent in C.

lyonsellus, C. allienellus, C. girardellus and C. albellus. It has been completely lost in C. perlellus in which the wings are pure satiny-white without markings. All North American Crambus species, except C. perlellus, also have a complete subterminal transverse line, no distinct median transverse line, a series of at least four dark brown dots on the outer margin and a brown diagonal bar at the apex. The white forewing band is also present in the Fernandocrambus species that reach North America but in these, the apex of the forewing is conspicuously produced and hooked. Raphiptera also has a similar forewing pattern but its venation lacks two veins in the forewing and one in the hindwing.

Redescription. Based on Bleszynski (1965) and my own analysis of the Nearctic species.

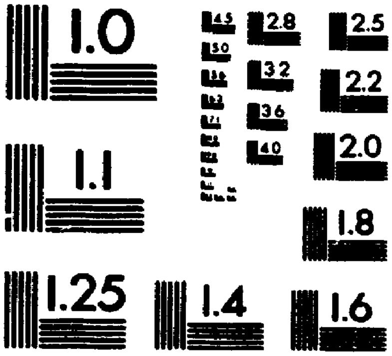
Head (fig. 8). Ocellus and chaetosema well developed; fronto-clypeus always rounded, never projected. Labial palpus variable in length (2.14X width of head in one dissected specimen of C. pascuellus). Haustellum long. Vestiture often as in C. pascuellus (fig. 25), sometimes fronto-clypeal scales appressed and labial palpus more triangular. Male antennal flagellomeres (fig. 33) with full complement and average numbers of sensilla in C. pascuellus.

Wings (fig. 115). Female frenulum double in 31 species checked, two species had three frenular bristles, one specimen of a double frenulum species had two bristles on one side and three on the other. Male frenulum hook absent. Forewing R1 present, free; R2 free, R3 present, connected to R4 (sometimes apparently missing); R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing elongate (3.09X its width in one mounted specimen of _C. pascuellus_). Forewing pattern (fig. 138) usually with a satiny-white longitudinal band in middle from base to at least end of disco-cellular area, frequently ending on outer margin; also with a complete subterminal transverse line, no distinct median transverse line, a series of at least four dark-brown dots on outer margin and a brown diagonal bar at apex. Wings however completely satiny-white in _C. perlellus_.

Tympanal organs (figs. 171, 223). Transverse ridge present, variable in width, with anterior margin sometimes anteriorly projected medially, convex, or straight, rarely concave, posterior margin usually straight or convex, rarely concave. Tympanic pockets present, variable in size and more or less conical, sometimes incompletely defined as a true pocket. Venulae secundae generally absent; if present, weakly sclerotized. Tympanic bridge usually medium-sized, not distinctly projected ventrally and with arms connected medially, rarely with a median longitudinal sclerotized bar ventrally as in _Fernandocrambus_. Praecinctorium variable in length, usually with a dorsal sclerotized support. Tympanic crest usually about 3X longer than high, situated more or less anteriorly. Tympanic drum usually elongate, more or less bean-shaped, variable in length, usually at least reaching transverse

4

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT



PRECISION℠ RESOLUTION TARGETS

PIONEERS IN METHYLENE BLUE TESTING SINCE 1974
MICRO-D
[illegible] COUNTY ROAD 5, BURNSVILLE, MN [illegible], USA
TEL. 612 [illegible] FAX 612 [illegible] TLX [illegible]

ridge. Spinula usually visible.

Male genitalia (figs. 233, 288, 289). Uncus usually simple, divided into two medium-sized, profusely setose lobes in *C. pascuellus* and *C. lyonsellus*, with short spines dorsally in one group of species, variable in shape, apparently trilobed in two Palaearctic species. Gnathos usually long and narrow, more or less elbowed, often curved ventrad, rarely reduced (*C. awemellus*). Tegumen variable in shape, sometimes not elbowed (*C. leachellus*), sometimes with pedunculi produced posterad ventrally (*C. dissectus*), ventrally with or without sclerotized connection. Valva with well sclerotized costa, with or without projection; cucullus variable in shape, rarely sclerotized (*C. awemellus*); sacculus always well sclerotized, usually with a projection or a series of spines or folds. Vinculum usually quadrangular, rarely with a saccus (*C. satrapellus*), sometimes with lateral margins strongly extended anterad (*C. braunellus*). Pseudosaccus variable in shape and size, sometimes very long and separated from floor of vinculum. Juxta not extended posterad, usually flat, V-shaped or heart-shaped. Aedeagus variable in shape, with or without spines or areas of stronger sclerotization apically; coecum penis sometimes elongate and convoluted; vesica with 0-7 cornuti, most often with a single medium-sized cornutus.

Female genitalia (figs. 337, 338). Anal papillae usually divided into a narrow dorsal lobe and a shorter, broader ventral lobe.

Posterior apophyses about as long as papillae. Anterior apophyses very short or absent. Segment VIII usually narrow dorsally. Sterigma very complex, strongly sclerotized, usually with a variable projecting "tube". Ductus bursae usually long, narrow and sclerotized. Corpus bursae more or less circular, medium-sized, with two signa.

Relationships. Crambus seems to be more closely related to Chrysoteuchia and Fernandocrambus on the basis, in the female, of two signa on the corpus bursae and strongly divided papillae anales (fig. 5, characters 38 and 43 respectively). Within the North American fauna, various groups of species can be recognized. The most diverse of these (with probably 14 species) can be defined by the presence of spines, instead of hairs, on the uncus. Eight other groups of four or less species can also be recognized on the basis of various features of the male genitalia.

Diversity and distribution. The genus as recognized here apparently reaches its highest diversity in the Nearctic Region with 40 species being recorded (Klots 1983). Of these, three are also present in the Palaearctic Region and at least one (C. satrapellus) is in the Neotropical Region. Fourteen more species have been recorded from South and Central America (Bleszynski 1967) and 24 more are known from the Palaearctic Region (Bleszynski 1965). At least 14 undescribed species were recognized by Klots (personnal notes). The genus is not present in Australia or New Zealand (Gaskin 1975a). Several species have been described from the Ethiopian and the Oriental Regions (Bleszynski &

Collins 1962) but their affinities to the New World and Palaearctic species-groups are unknown. These might in fact belong to other genera. Thus, I can only say that Crambus contains at least 92 species in the New World and the Palaearctic Region. In North America, the spiny uncus group has only one of its members also in the Palaearctic Region (C. hamellus). Most of the Palaearctic species seem to form a monophyletic group characterized by an elongate and spiny sacculus. In North America, this group is represented only by the Holarctic species C. perlellus and three more species. In North America, five or six species reach subarctic localities but none seems to be truly arctic. All States and Provinces have each a good diversity of species of Crambus.

Natural history and immature stages. The egg chorion characteristics were described by Matheny & Heinrichs (1972) for C. alboclavellus, C. laquaetellus, C. praefectellus and C. pascuellus. More or less complete descriptions of the larva were given for C. pascuellus (Hasenfuss 1960; Mauston 1970), C. perlellus (Hasenfuss 1960 and several others listed by Bleszynski 1965), C. leachellus and C. unistriatellus (Mauston 1970), C. quinquareatus (Tan 1984) and C. praefectellus (Ainslie 1923b; Tan 1984). The larvae are known to feed on grasses or sedges (Cyperaceae) blades and stems and to make silken galleries at the base of the stems. The silver-striped webworm, C. praefectellus, is believed to be one of the six most destructive webworm species in the temperate parts of the United States (Tashiro 1987). Ainslie (1923b) provides details on the bionomics of this species. Crambus agitatellus, C. perlellus and Leach's crambus, C. leachellus, were associated with turfgrass in Virginia (Robinson & Tolley

1982). The seasonal abundance of three species in Virginia was reported by Tolley & Robinson (1986). Six species of *Crambus* displayed a typical geonegative response in their choice of resting posture (Crawford 1971a). Kamm (1971) studied the biology of *Crambus tutillus*.

Comments. All ten species stated as misplaced by Klots (1983) are reassigned here to other genera except for two which are left unplaced in this classification. The genus *Crambus* as redefined here is believed to be monophyletic, but there is no single synapomorphy to support this hypothesis.

5.1.7.3 UNASSIGNED SPECIES OF NORTH AMERICAN CRAMBINI

"Crambus" dimidiatellus Grote

(Figs. 76, 160, 221, 277, 336)

Crambus dimidiatellus Grote, 1883: 57. Holotype ♂ in Snow Museum, University of Kansas, Lawrence [examined].

Crambus leucorhabdon Hampson 1919: 440. Holotype ♀ in British Museum (Natural History), London [examined].

Diagnosis. This species can be diagnosed by the forewing pattern with a wide dark brown band on the costa from base to apex and the rest of the wing mostly uniformly coloured, pale brown. The widely opened aedeagus apically and the protruding vesica are also diagnostic.

Redescription.

Head. Similar in shape to that of Neodactria luteolella (fig. 24) except for longer labial palpus (4.0X width of head in one dissected specimen). Vestiture with short, thin and appressed scales on fronto-clypeus; with tufts of long scales projecting anterad from base of antennae. Male antennal flagellomeres serrate (not studied with scanning electron microscope).

Wings (fig. 76). Female frenulum simple. Male frenulum hook absent. Forewing R1 present, connected with Sc; R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing 2.83X as long as width in one mounted specimen. Forewing pattern (fig. 160) with large dark brown band on costa from base to apex bordered by narrow white band along cell; remaining wing surface pale brown.

Tympanal organs (fig. 221). Transverse ridge large with anterior margin convex and posterior margin straight. Tympanic pockets large and rounded, extended to posterior margin of ridge. Venulae secundae present but weakly sclerotized. Tympanic bridge long, not projected ventrally, with arms connected medially. Praecinctorium long, extended beyond pockets, with long thin dorsal sclerotized support. Tympanic crest 2X wider than high, situated anteriorly near middle. Tympanic drum bean-shaped, partially closed anteriorly, extended to posterior margin of transverse ridge. Spinula small but distinct.

Male genitalia (fig. 277). Uncus long, rather narrow, mostly straight, apically hooked. Gnathos about as long as uncus, flat, rather broad. Tegumen unsclerotized ventrally, strongly convex dorsally, with rather wide pedunculi. Valva with medium-sized strongly sclerotized process on costa; cucullus long and narrow; sacculus with a short recurved projection at base of free part of cucullus. Vinculum with rather wide saccus about as long as valva. Juxta strongly sclerotized, arms extended dorsally but not surrounding aedeagus, slightly extended posterad, V-shaped with broad arms in cephalic view. Pseudosaccus flattened. Aedeagus rather narrow, slightly down-curved from middle, apically wide open with sterigma protruding; sterigma without cornuti; coecum penis short with flat extension.

Female genitalia (fig. 336). Anal papillae not divided into two lobes. Posterior apophyses about as long as papillae. Anterior apophyses about half as long as papillae. Segment VIII medium-sized dorsally, membranous ventrally. Sterigma a rather large crescent-shaped plate surrounding ostium ventrally. Ductus bursae short and wide, not clearly differentiated from elongate corpus bursae. Latter without signum.

Relationships. "Crambus" dimidiatellus is the sister-species of "Crambus" melchiellus Druce described from Mexico. Both are verv similar in wing pattern and male genitalia except for the presence of a pair of large cornuti on the vesica of C. melchiellus. This presence of cornuti on the vesica brings this pair of species close to the Thaumatopsis bolterella-group of species. The absence of any sign of pectination or stronger serration on the male antennae of the two species prevented me from including them in Thaumatopsis. It is to be noted that Bleszynski (1967) considered "C." melchiellus to belong to Thaumatopsis.

Distribution. "Crambus" dimidiatellus is distributed throughout the Rocky Mountains from Washington to New Mexico.

Natural history and immature stages. Unknown.

"Crambus" angulatus Barnes & McDunnough

(Figs. 81, 154, 282, 312)

Crambus angulatus Barnes & McDunnough, 1918: 171. A lectotype among the seven male syntypes in the USNM needs to be designated.

Diagnosis. Similar in habitus to Platytes except that the forewing venation is complete, the haustellum is lacking entirely and the aedeagus differs morphologically.

Redescription.

Head. Similar to that of Crambus pascuellus (fig. 8). Labial palpus 2.1X width of head in one dissected specimen. Haustellum represented by two lobes smaller than pilifers. Vestiture with a pair of tufts of scales projecting anterad from base of antennae; maxillary palpus with erect scales. Male antennal flagellomeres serrate (not studied with scanning electron microscope).

Wings (fig. 81). Female frenulum simple. Male frenulum hook absent. Forewing R1 present, connected with Sc; R2 free; R3 present, connected to R4; R5 present, connected to R3+4; M1 present; M2 & M3 not stalked; Cubitus with CuA1 & CuA2. Hindwing M2, M3, CuA1 & CuA2 present. Forewing elongate (2.83X as long as width in one mounted specimen). Forewing pattern (fig. 154) similar to that of Platytes except that the subterminal line is not as zigzaged and the median line is continuous as there are no longitudinal bands.

Tympanal organs (not illustrated). Transverse ridge very narrow and convex, anterior margin fused with pons tympani. Tympanic pockets very small. Venulae secundae absent. Tympanic bridge medium-sized with median arms 2X length of tympanic wings. Praecinctorium short, extended to middle of bridge, with thin dorsal sclerotized support. Tympanic crest at least 2X as long as wide, situated near middle. Tympanic drum oval, extended to before middle of tympanic bridge. Spinula visible.

Male genitalia (fig. 282). Similar to those of Platytes except for the aedeagus, which is also short but apically divided into two lateral lobes and its vesica is armed with a rather long cornutus.

Female genitalia (fig. 312). Anal papillae not divided into two lobes. Posterior apophyses thick, shorter than papillae. Anterior apophyses absent. Segment VIII dorsally medium-sized. Sterigma very small, cup-shaped. Ductus bursae very short, wide. Corpus bursae wide, elongate, without signum.

Relationships. This species appears, based on wing pattern and general shape of the male genitalia, to be close to Platytes. However, it differs from it in very important characters of the venation, aedeagus and female sterigma (see Diagnosis above). The species really seems to be isolated among the North American Crambini. In addition, based on Bleszynski's revision (1965), I could not find any Palaearctic taxon which seemed to be closely related to this species.

Distribution. "Crambus" angulatus is only known from Southern California.

Natural history and immature stages. Unknown.

Comments. This species was classified under Agriphila by Klots (1983) who, however, noted that it was misplaced there. This is corroborated here because the species does not have the conspicuous apomorphy of the male aedeagus of Agriphila, nor a number of other characteristics of that genus, such as the divided female papillae anales, the presence of one signum on the female corpus bursae, etc.).

Fig. 4. Relationships between the major lineages of Crambinae. Results of the first analysis on 35 unweighted characters for 31 taxa (all Crambini exept *Ancylolomia* and *Thaumatopsis* combined). 75% majority rule consensus tree obtained with PAUP from 270 trees of length-91 steps. Black round dots indicate synapomorphies. Apostrophes indicate number of parallelisms in the Crambiformes. Open dots indicate reversals. For species names see Table 4.

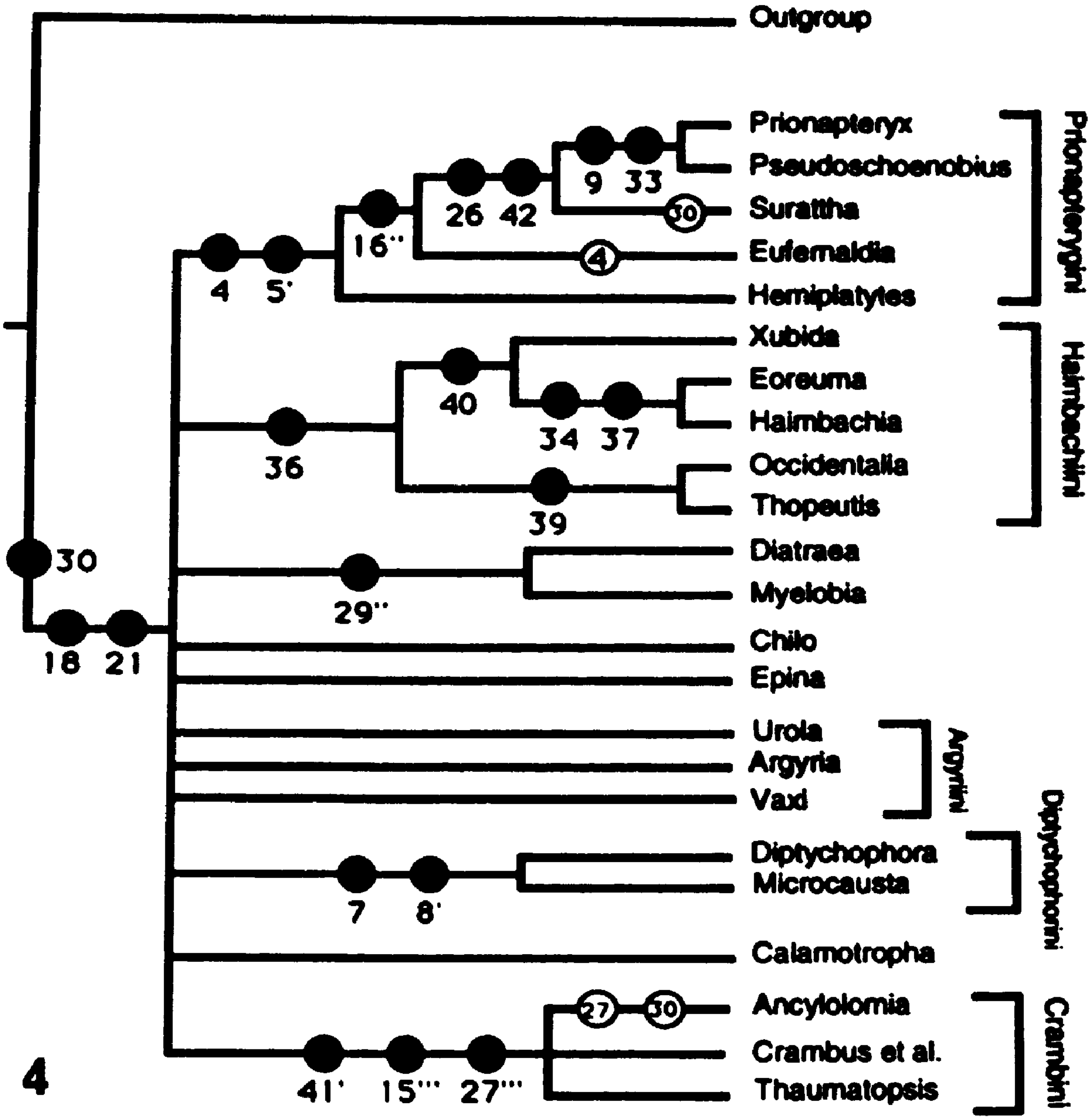

Outgroup
Prionapteryx
Pseudoschoenobius
Surattha
Eufernaldia
Hemiplatytes
Xubida
Eoreuma
Haimbachia
Occidentalia
Thopeutis
Diatraea
Myelobia
Chilo
Epina
Urola
Argyria
Vaxi
Diptychophora
Microcausta
Calamotropha
Ancylolomia
Crambus et al.
Thaumatopsis
Prionapterygini
Haimbachiini
Argyriini
Diptychophorini
Crambini
30
18
21
4
5'
16''
26
42
9
33
30
4
36
40
34
37
39
29''
7
8'
41'
15'''
27'''
27
30

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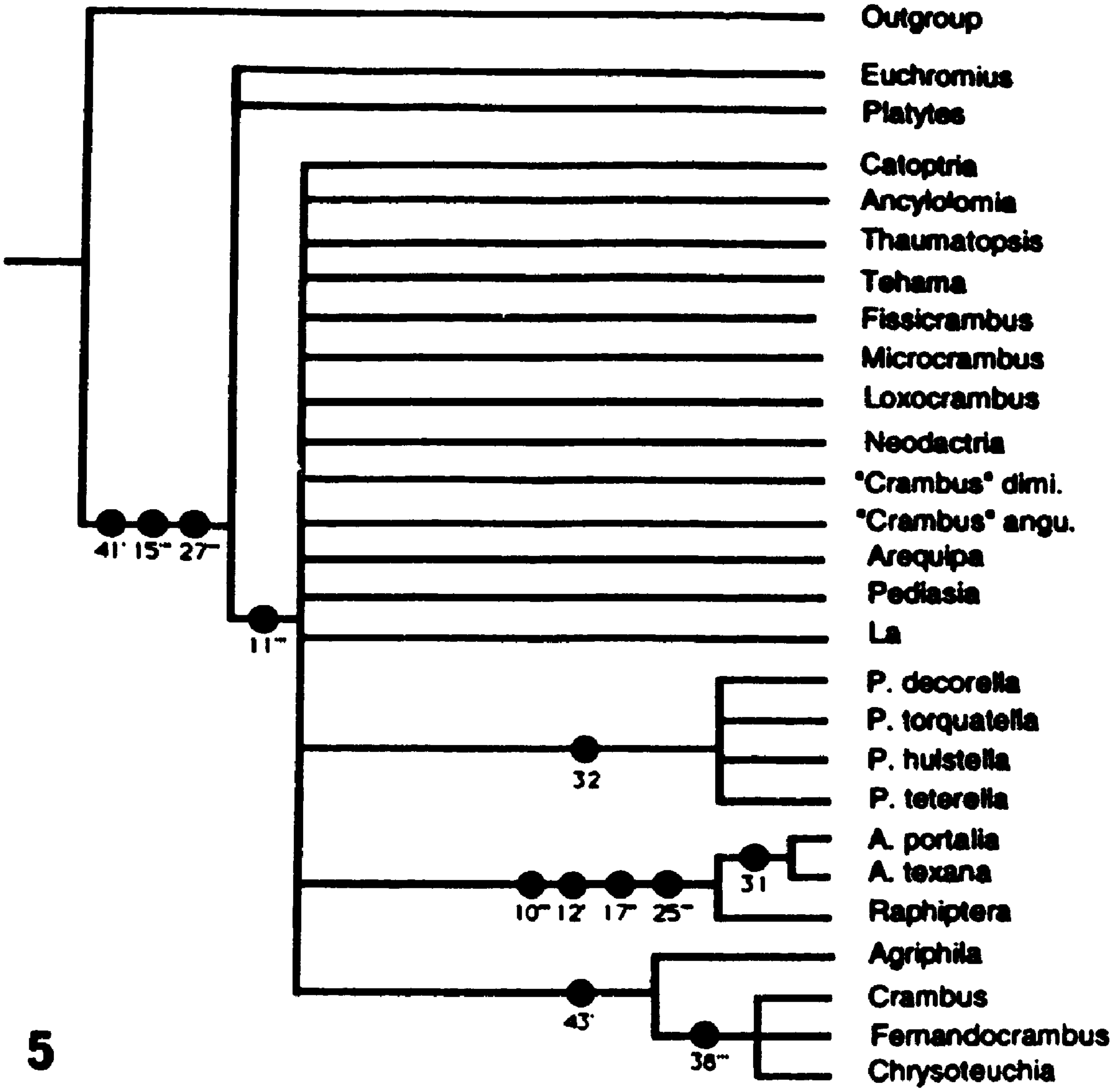
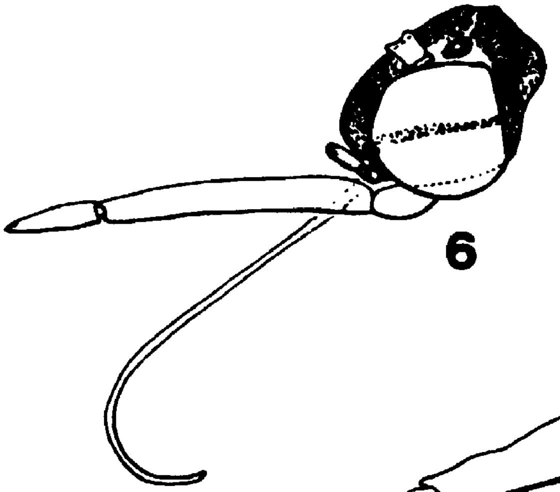
Fig. 5. Relationships between the major lineages of Crambini. Results of the second analysis on 43 unweighted characters for 36 taxa. Modified strict consensus tree obtained with hennig86. For species names see Table 4.


Outgroup
Euchromius
Platytes
Catoptria
Ancylolomia
Thaumatopsis
Tehama
Fissicrambus
Microcrambus
Loxocrambus
Neodactria
"Crambus" dimi.
"Crambus" angu.
Arequipa
Pediasia
La
P. decorella
P. torquatella
P. hulstella
P. teterella
A. portalia
A. texana
Raphiptera
Agriphila
Crambus
Fernandocrambus
Chrysoteuchia
41' 15" 27"
11'''
32
10" 12' 17' 25"
31
43'
38'''

5

Figs. 6-11. Side views of descaled heads of Crambinae: 6, *Raphiptera argillaceella* (Packard); 7, *Eufernaldia cadarella* (Druce); 8, *Crambus pascuellus* (L.); 9, *Myelobia* sp.; 10, *Pseudoschoenobius opalescalis* (Hulst); 11, *Occidentalia comptulatalis* (Hulst).



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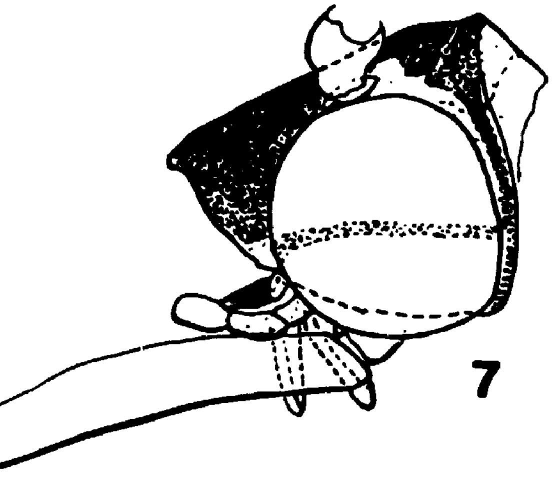

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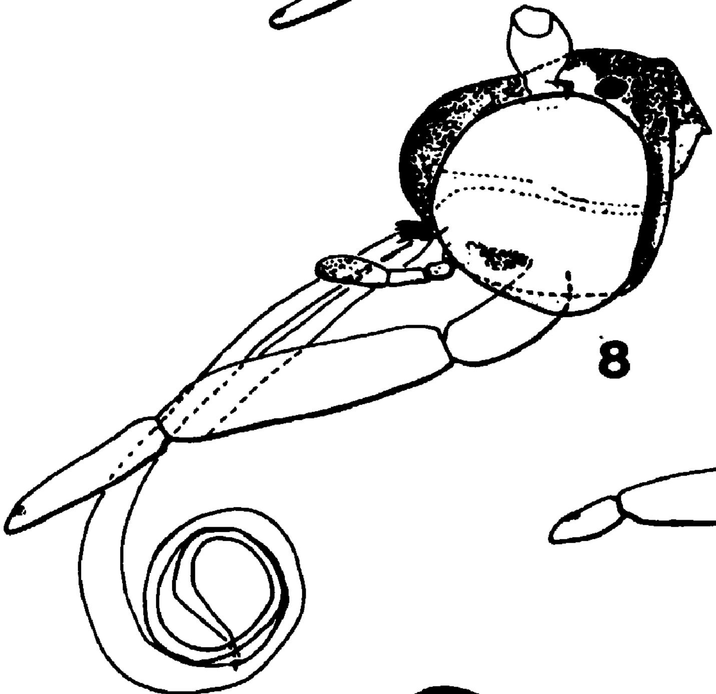

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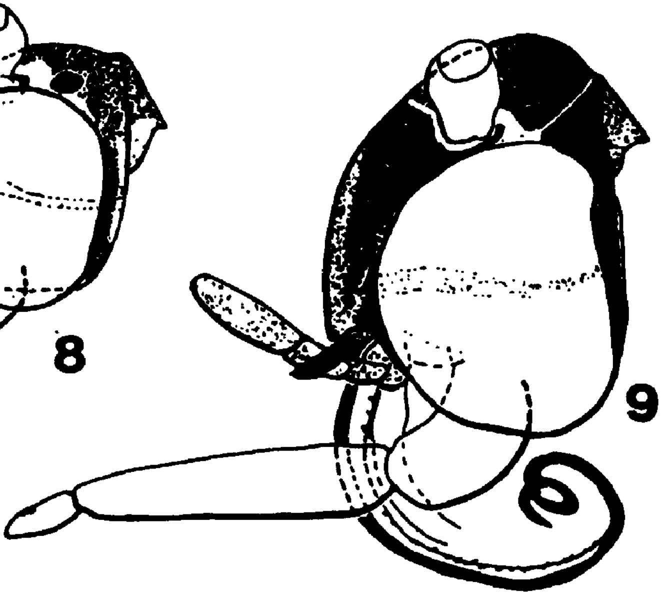

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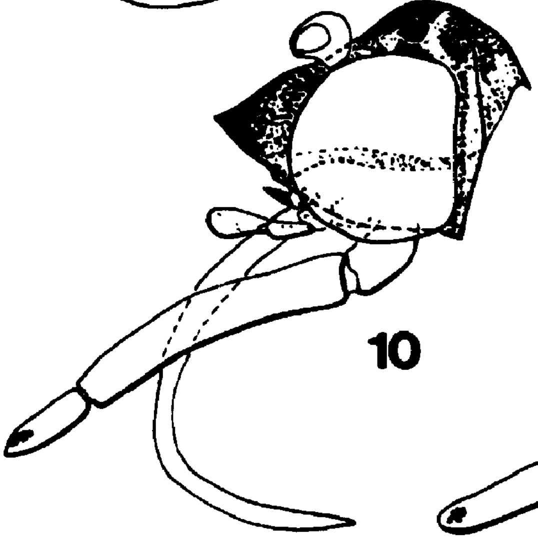

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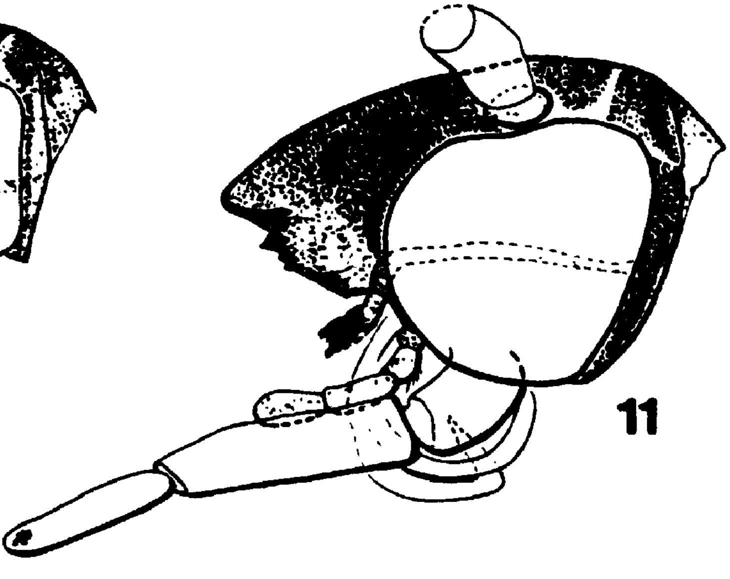

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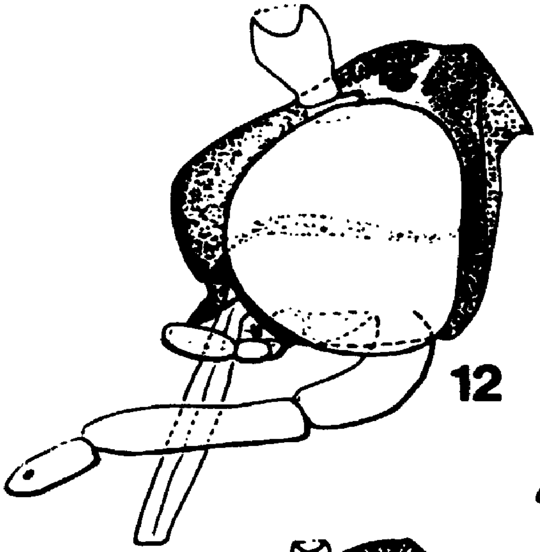
Figs. 12-17. Side views of descaled heads of Crambinae: 12, *Urola nivalis* (Dru 13, *Vaxi auratella* (Clemens); 14, *Platytes vobisne* Dyar; 15, *Argyria nummulalis* Hübner; 16, *Pareromene exsectella* (Christoph); 17, *Euchromius ocelleus* (Haworth).



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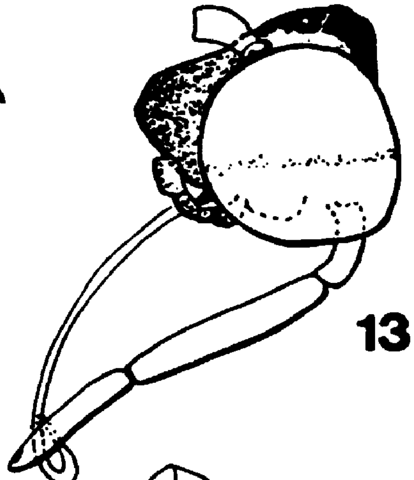

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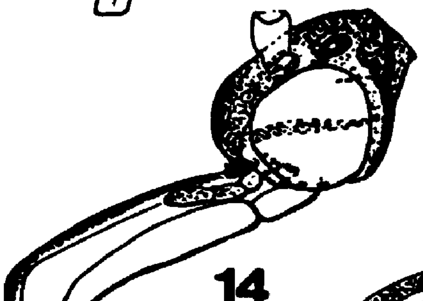

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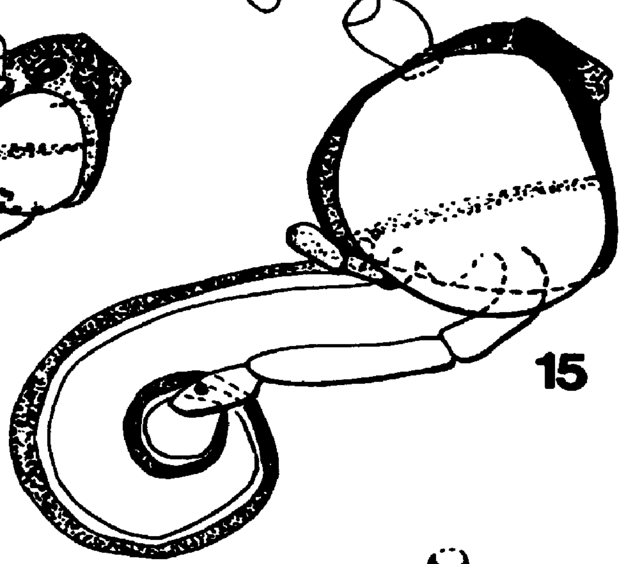

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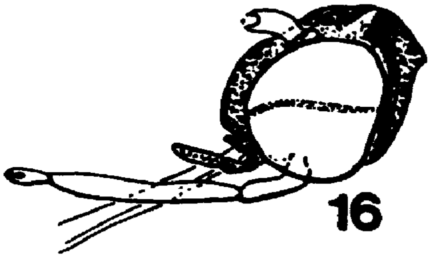

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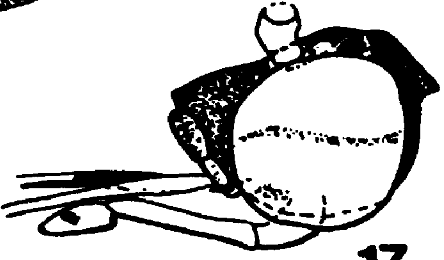

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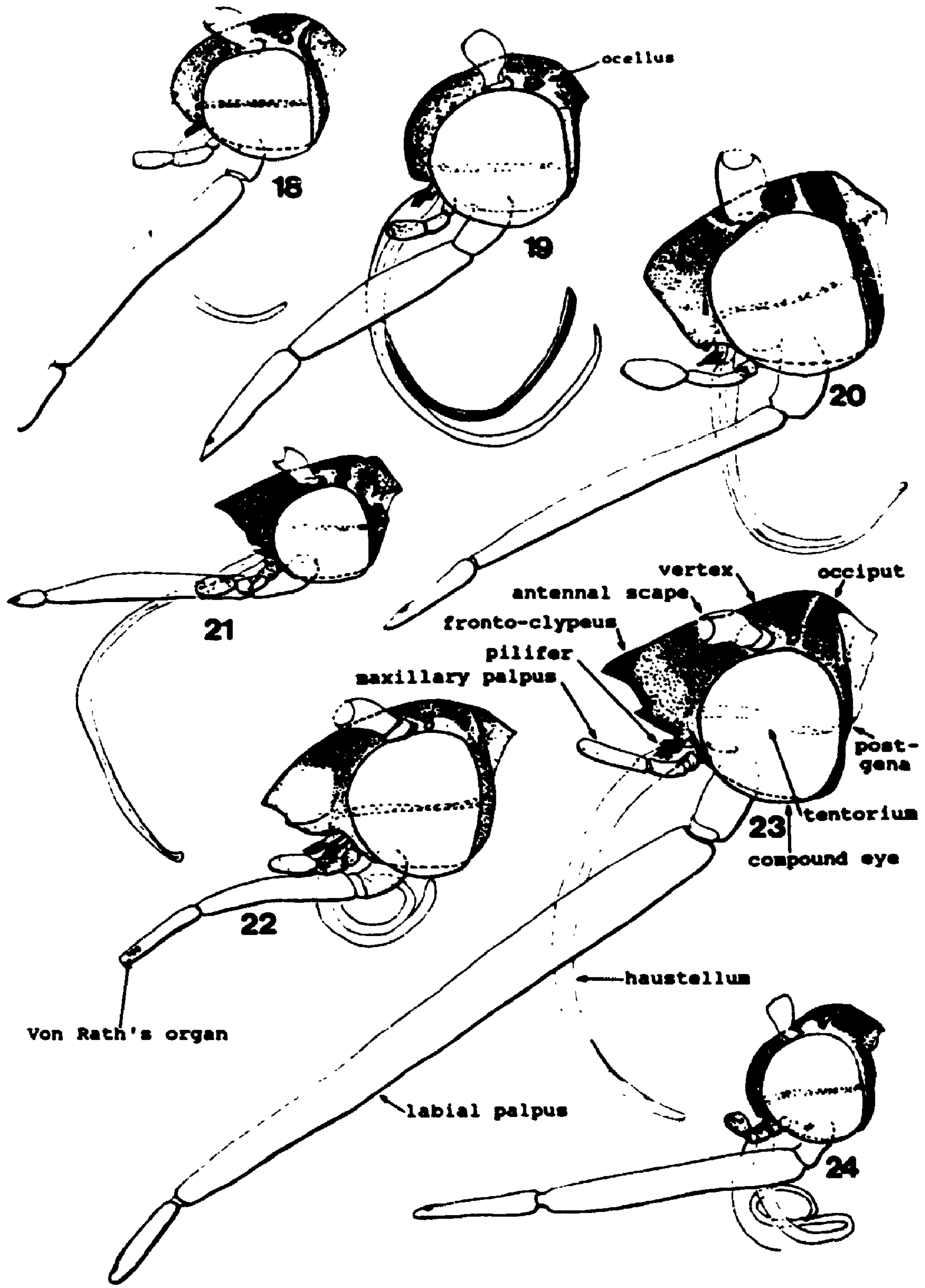
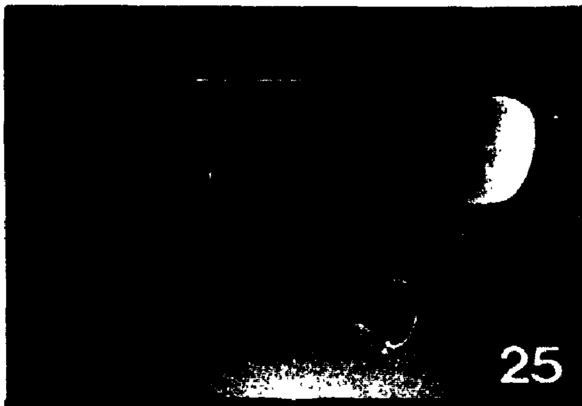
Figs. 18-24. Side views of descaled heads of Crambinae: 18, *Eoreuma densella* (Zeller); 19, *Thaumatopsis bolterella* (Fernald); 20, *Calamatropha paludella* (Hübner); 21, *Prionapteryx serpentella* Kearfott; 22, *Thopeutis forbesellus* (Fernald); 23, *Chilo phragmitellus* (Hübner); 24, *Neodactria luteolella* (Clemens).


18
ocellus
19
20
21
vertex
occiput
antennal scape
fronto-clypeus
pilifer
maxillary palpus
post-gena
tentorium
23
compound eye
22
Von Rath's organ
haustellum
labial palpus
24

Figs. 25-32. Scanning electron micrographs of head features of Crambinae: 25, lateral view of head of *Crambus pascuellus* (L.) (1 mm); 26, proboscis of *C. pascuellus* (100 µm); 27, lateral view of head of *Agriphila vulgivagella* (Clemens) (1 mm); 28, ocellus and chaetosema of *A. vulgivagella* (100 µm); 29, facets and interfacetal seta of *A. vulgivagella* (10 µm); 30, proboscis of *Urola nivalis* (Drury) (100 µm); 31, lateral view of head of *U. nivalis* (0.5 mm); 32, ocellus, microsculpture of head and part of chaetosema of *U. nivalis* (20 µm).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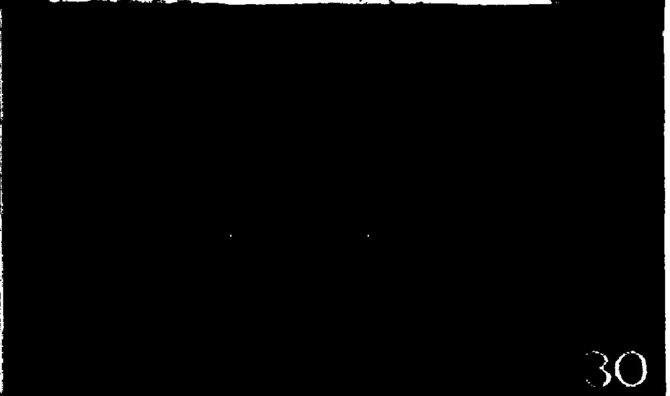
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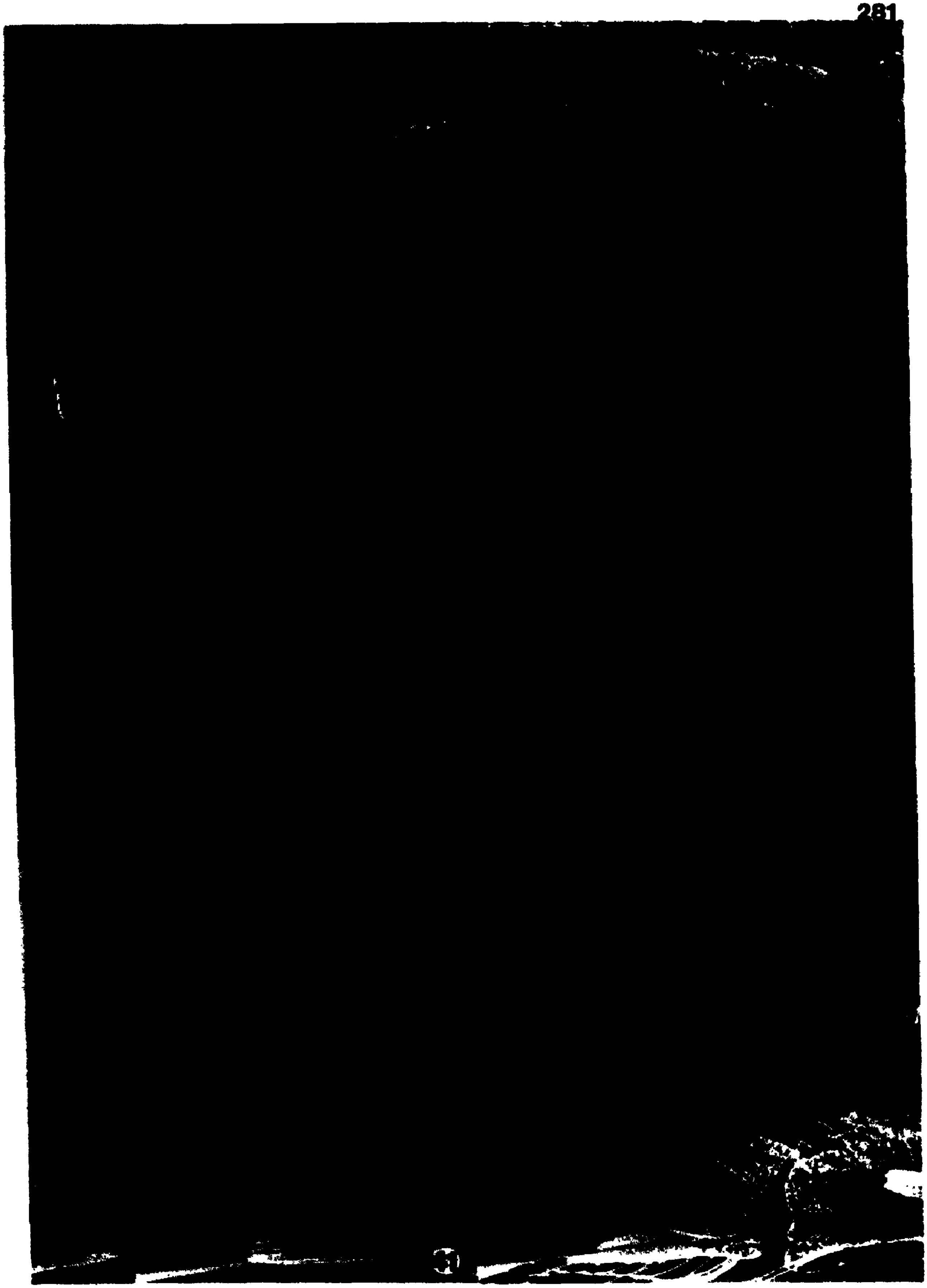
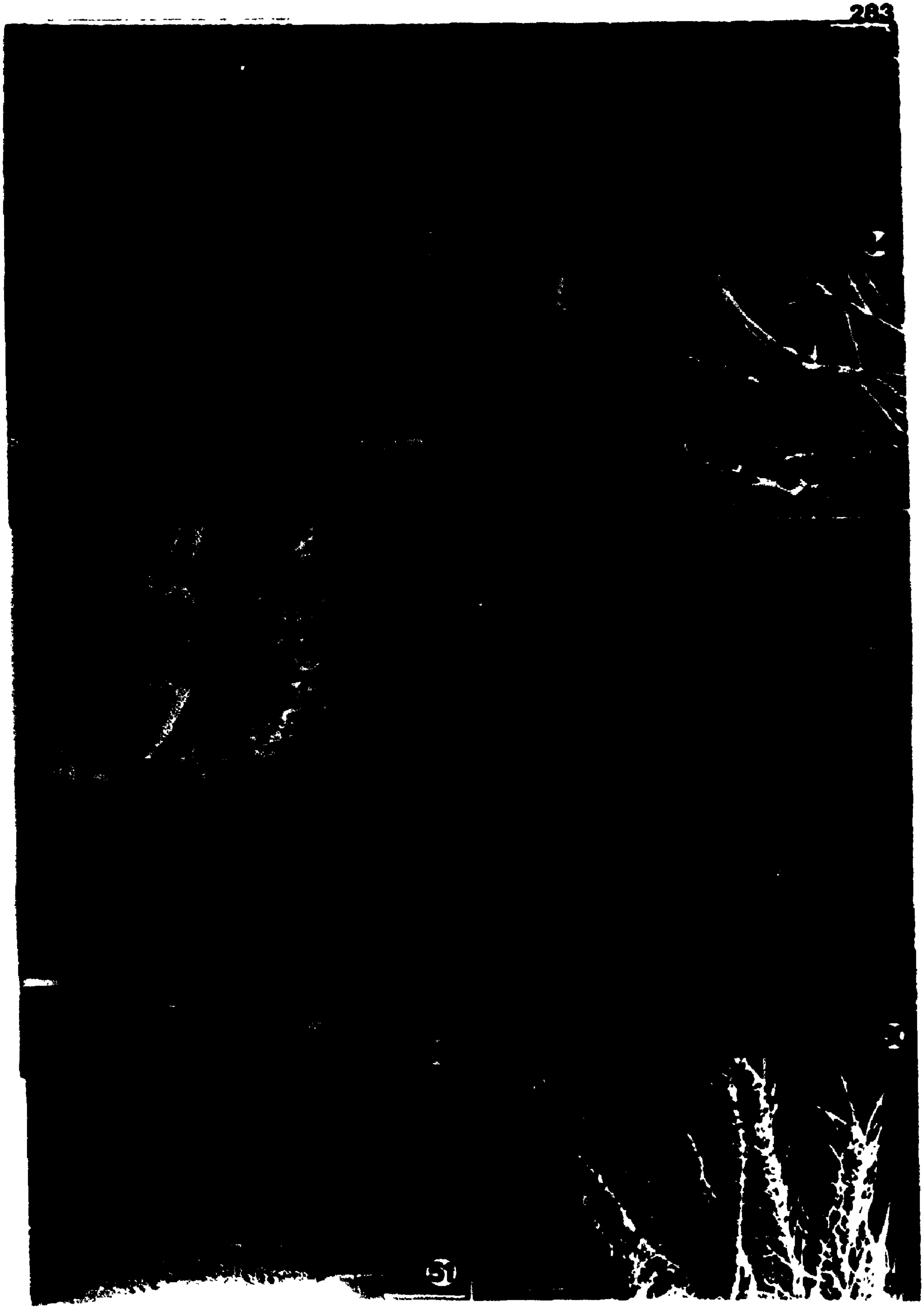
Figs. 33-42. Side views of antennal flagellomeres (usually near the 15th segment) of Crambinae: 33, *Crambus pascuellus* (L.), arrow points to sensillum auricillicum (50 µm); 34, *Tehama bonifatella* (Hulst) (50 µm); 35, *Arequipa turbatella* Walker (100 µm); 36, *Loxocrambus* sp. (50 µm); 37, *Agriphila ruricolella* (Zeller) (50 µm); 38, *Catoptria latiradiella* (Walker) (50 µm); 39, *Almita portalis* n. sp. (25 µm); 40, *Almita texana* n. sp. (50 µm); 41, *Raphiptera argillaceella* (Packard) (20 µm); 42, *Fernandocrambus harpipterus* (Dyar) (50 µm).



Figs. 43-52. Side views of antennal flagellomeres (usually near the 15th segment) of Crambinae: 43, *Parapediasia torquatella* n.sp. (50 μm); 44, *Microcrambus elegans* (Clemens) (10 μm) arrow points to unidentified sac-like structure; 45, *Parapediasia decorella* (Zincken) (100 μm); 46, *M. elegans* (10 μm) arrow points to sensillum styloconicum; 47, *Parapediasia teterrella* (Zincken) (50 μm); 48, *Platytes vobisne Dyar* (50 μm); 49, *Euchromius ocelleus* (Haworth) (50 μm); 50, *Thaumatopsis floridella* Barnes & McDunnough (50 μm); 51, *La cerveza* n. sp. (50 μm); 52, *Thaumatopsis pexella* (Zeller) (100 μm).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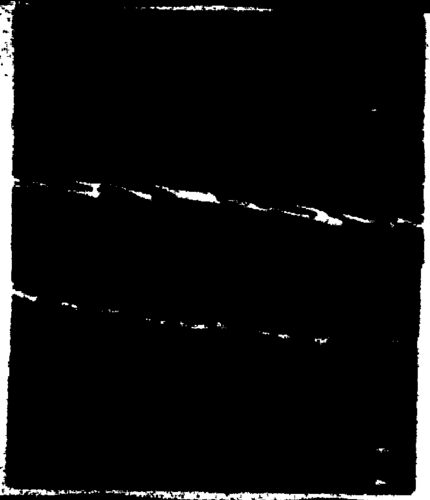
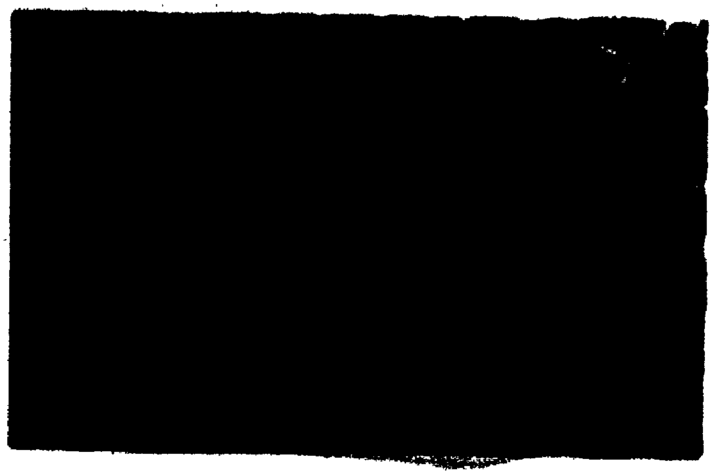
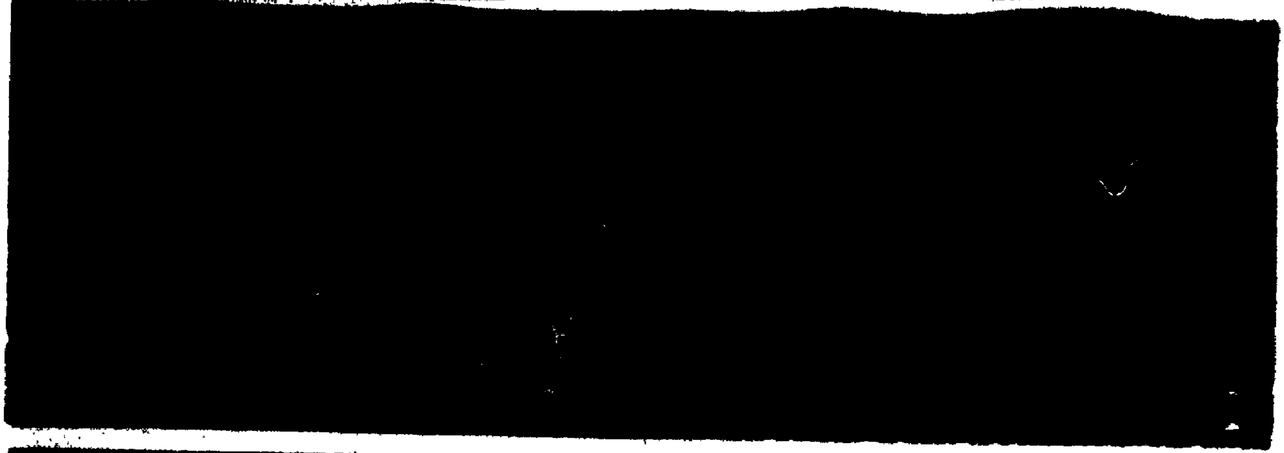
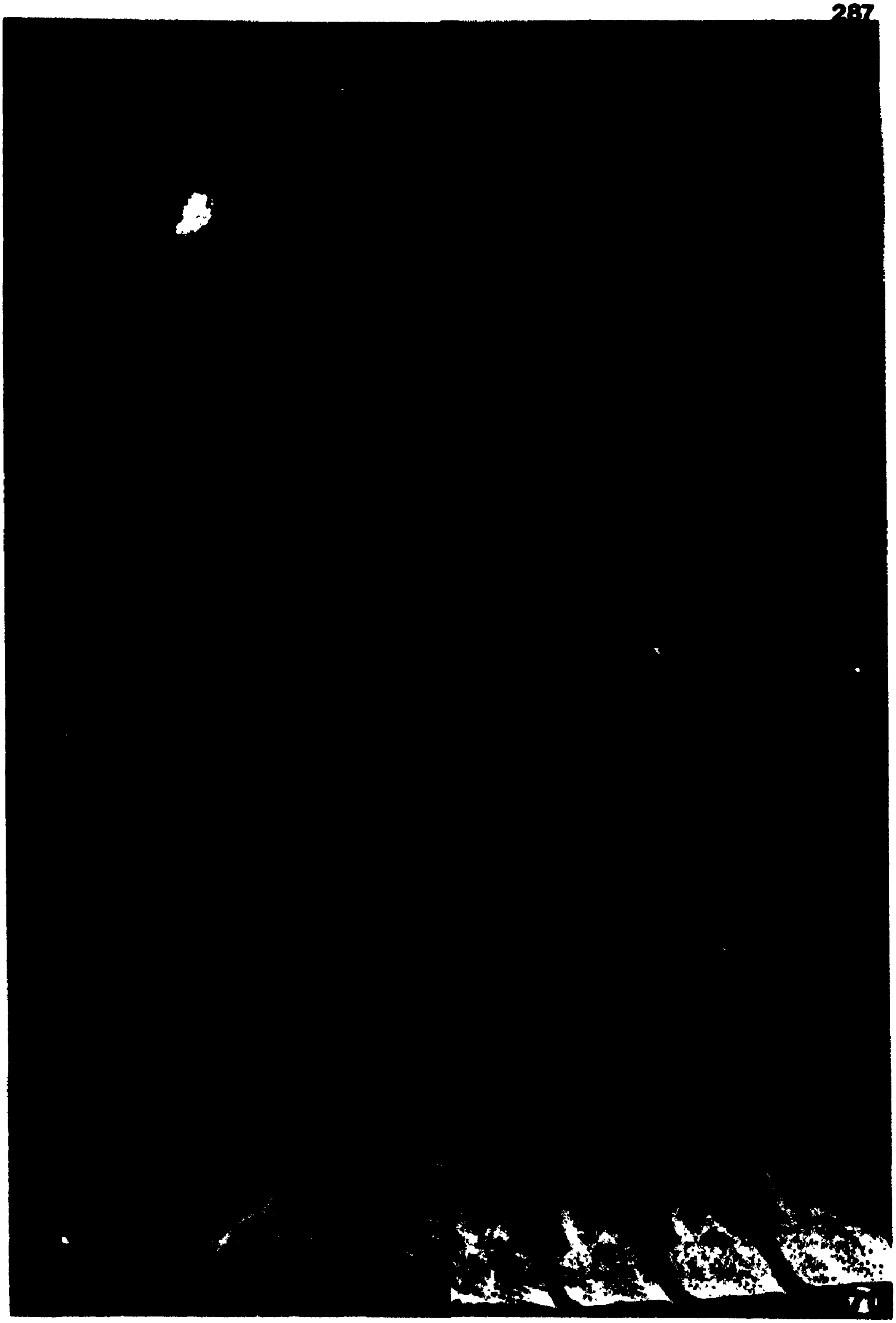
Figs. 53-61. Side views of antennal flagellomeres (usually near the 15th segment) of Crambinae: 53, *Occidentalia comptulatalis* (Hulst) (50 µm); 54, *Calamatropha paludella* (Hübner) (50 µm); 55, *Chrysoteuchia topiaria* (Zeller) ♂ (100 µm); 56, *Chrysoteuchia topiaria* (Zeller) ♀ (100 µm); 57, *Parapediasia teterrella* (Zincken) (10 µm) arrow points to sensillum chaeticum; 58, *Neodactria luteolella* (Clemens) (50 µm) arrows point to sensilla trichodea; 59, *Pediasia trisecta* (Walker) (50 µm) arrows point to sensilla coeloconica; 60, *Fissicrambus minuellus* (Walker) (50 µm); 61, *F. fissiradiellus* (Walker) (50 µm).







Figs. 62-71. Side views of antennal flagellomeres (usually near the 15th segment) of Crambinae: 62, *Argyria nummulalis* Hübner (100 μm); 63, *Urola nivalis* (Drury) (50 μm); 64, *Vaxi auratella* (Clemens) (50 μm); 65, *Hemiplatytes prosenes* (Dyar) (50 μm); 66, *Pseudoschoenobius opalescalis* (Hulst) (50 μm); 67, *Prionapteryx serpentella* Kearfott (100 μm); 68, *Eufernaldia cadarella* (Druce) (50 μm); 69, *P. serpentella* (10 μm); 70, *Chilo phragmitellus* (Hübner) (50 μm); 71, *Myelobia* sp. (100 μm).



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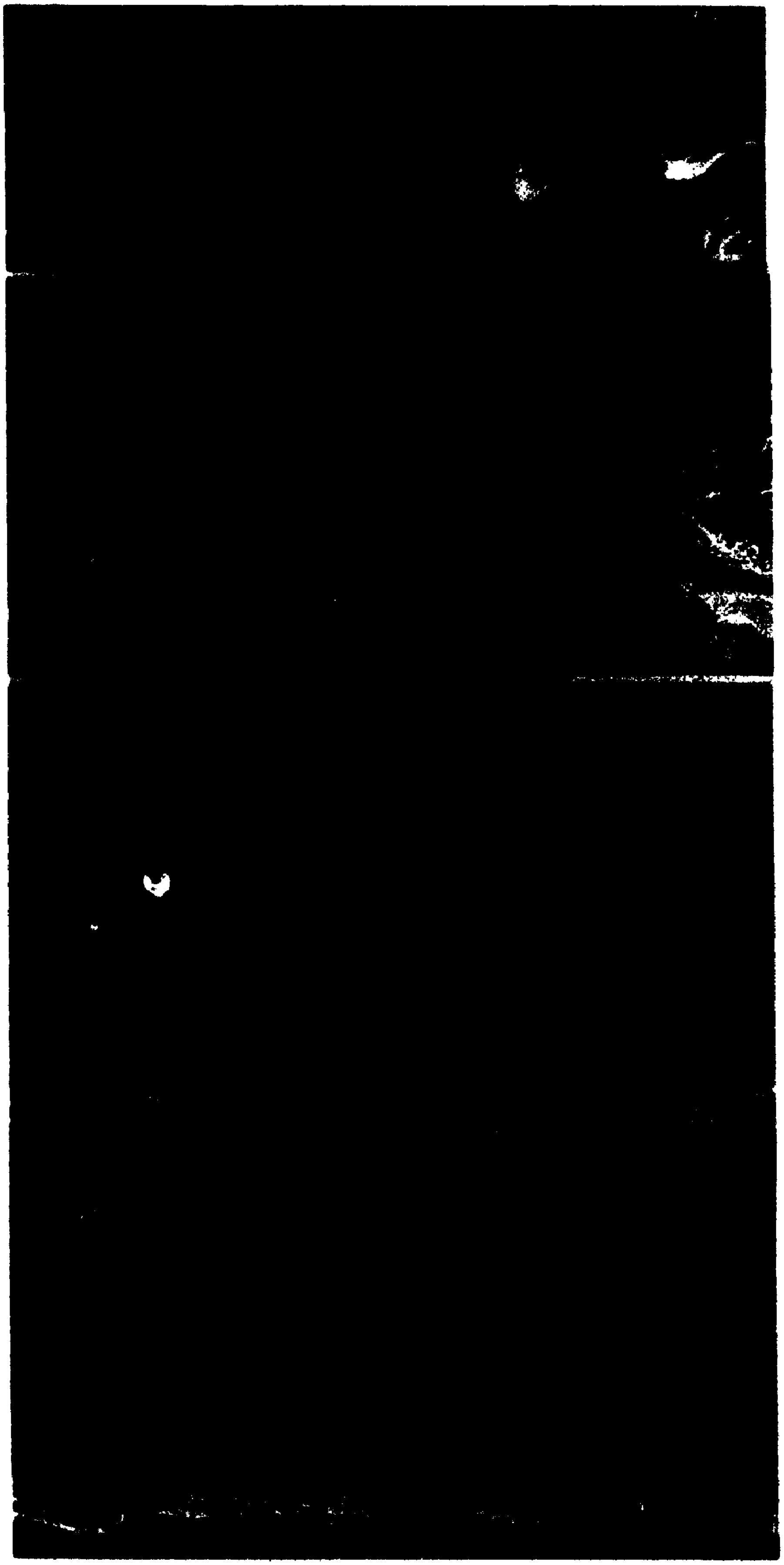
Figs. 72-75. Side views of antennal flagellomeres (usually near the 15th segment) of Crambinae: 72, *Diptychophora harlequinalis* (Barnes & McDunnough) (100 μm); 73, *Microcausta flavipunctalis* Barnes & McDunnough (50 μm); 74, *Thopeutis forbesellus* (Fernald) (50 μm); 75, *Eoreuma densella* (Zeller) (50 μm).



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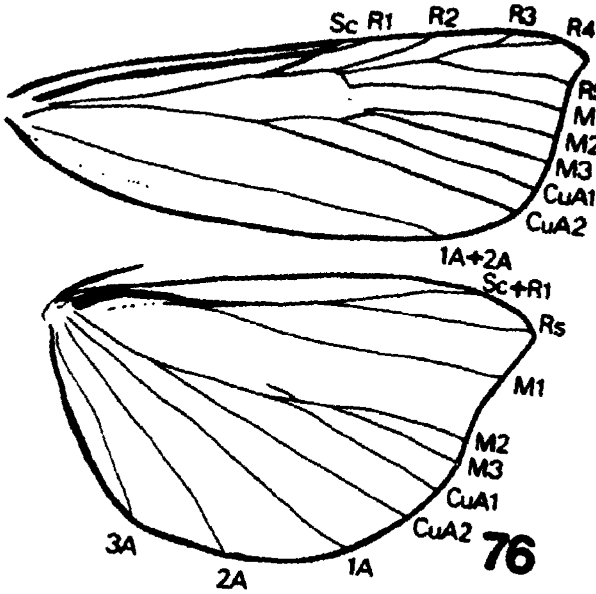
Figs. 76-81. Wing venation of Crambinae: 76, "Crambus" dimidiatellus Grote; 77, Argyria nummulalis Hübner; 78, Fissicrambus fissiradiellus (Walker); 79, Vaxi auratella (Clemens); 80, Parapediasia teterrella (Zincken); 81, "Crambus" angulatus Barnes & McDunnough.



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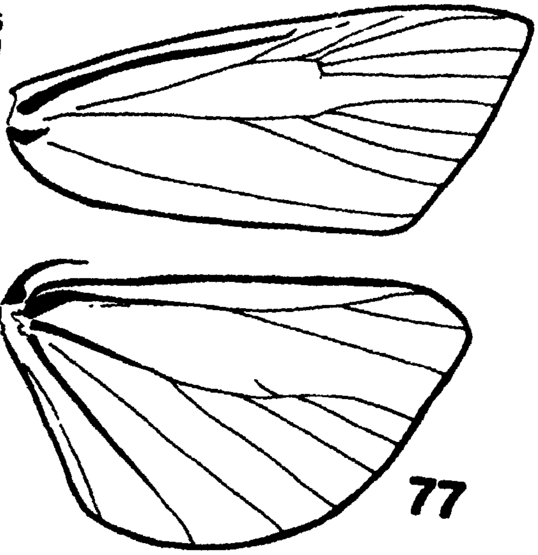

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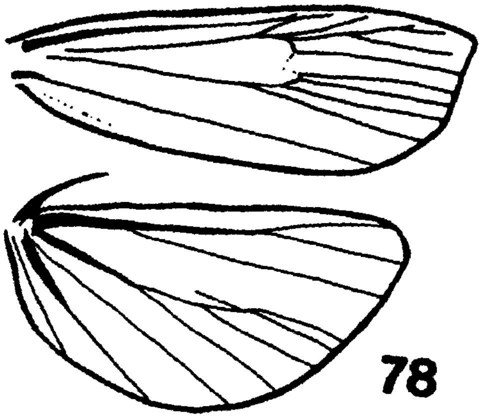

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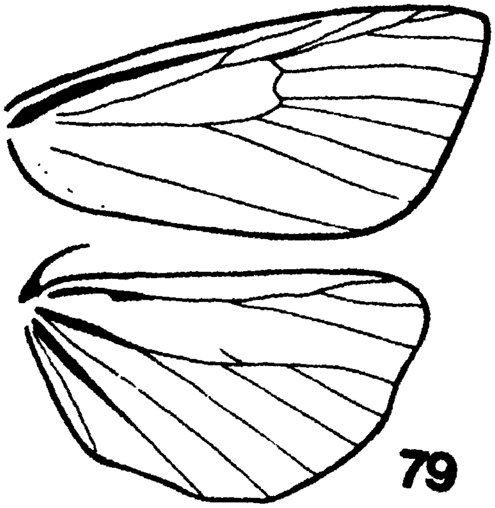

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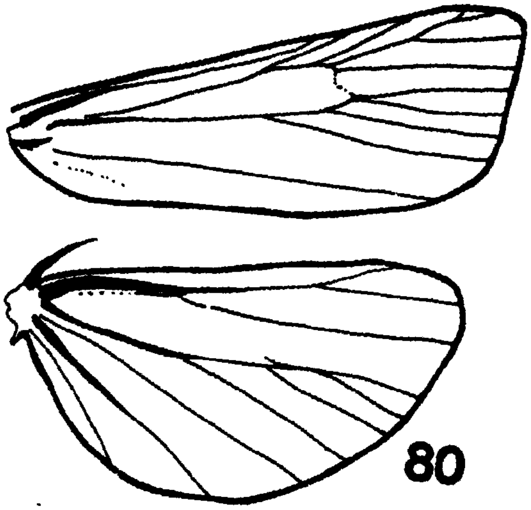

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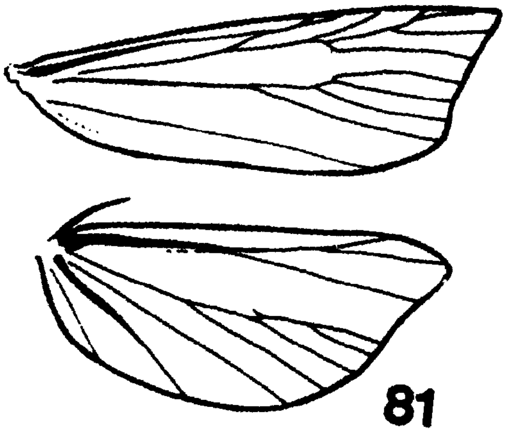

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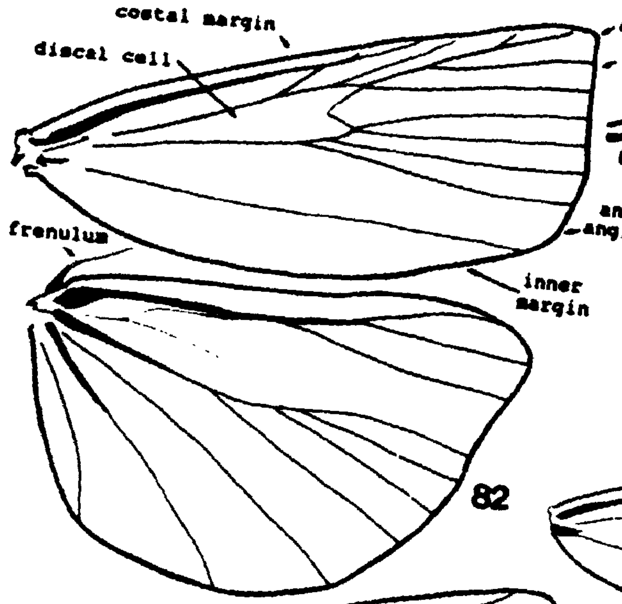
Figs. 82-88. Wing venation of Crambinae: 82, *Calamatropha paludella* (Hübner); 83, *Thopeutis forbesellus* (Fernald); 84, *La cerveza* n. sp.; 85, *Loxocrambus* sp.; 86, *Fernandocrambus harpipterus* (Dyar); 87, *Thaumatopsis pexella* (Zeller); 88, *Tehama bonifatella* (Hulst).



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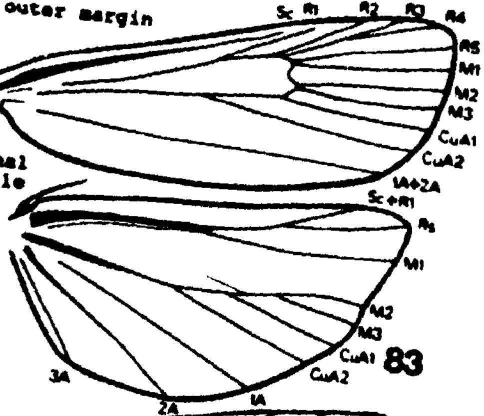

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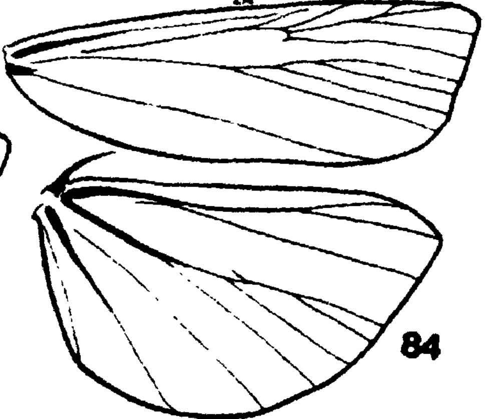

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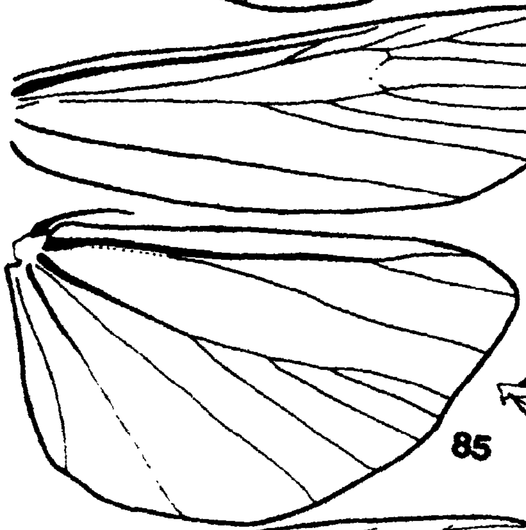

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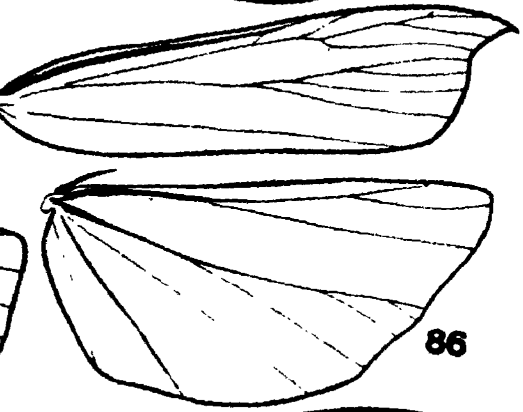

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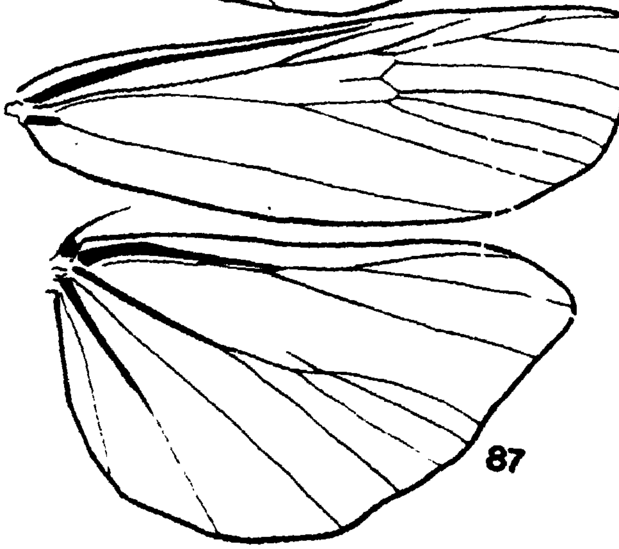

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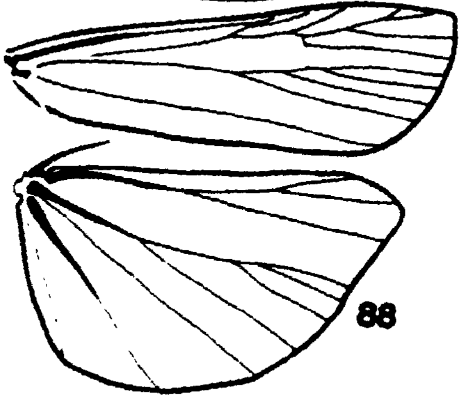

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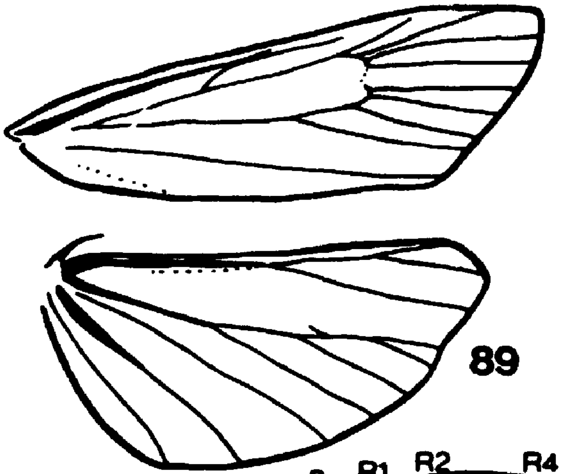
Figs. 89-95. Wing venation of Crambinae: 89, *Euchromius ocelleus* (Haworth); 90, *Microcausta flavipunctalis* Barnes & McDunnough (from Bleszynski 1966); 91, *Diptychophora harlequinalis* (Barnes & McDunnough) (from Bleszynski 1966); 92, *Almita portalia* n. sp.; 93, *Microcrambus biguttellus* (Forbes); 94, *Platytes vobisne* Dyar; 95, *Microcrambus elegans* (Clemens).



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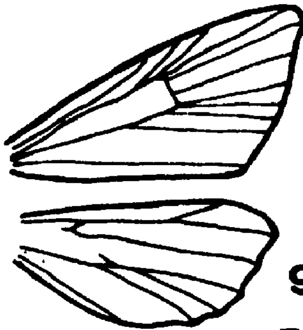

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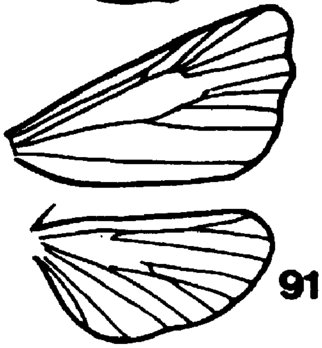

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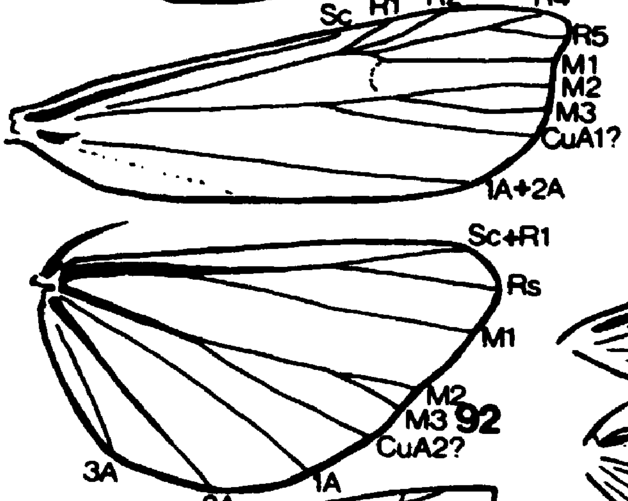

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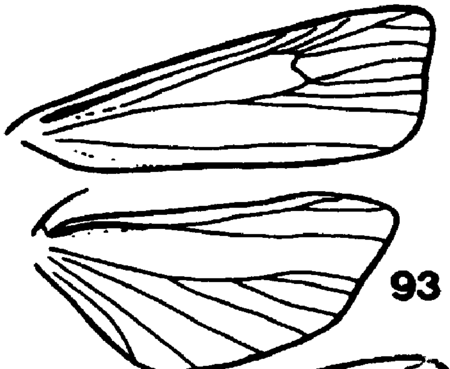

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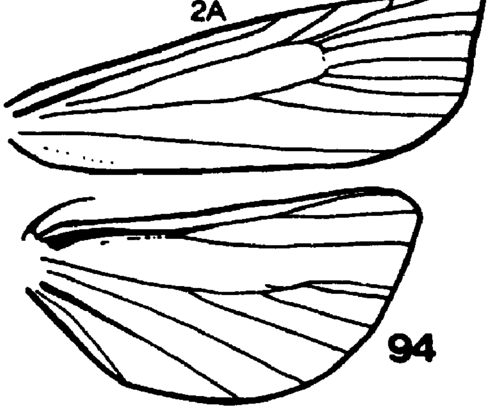

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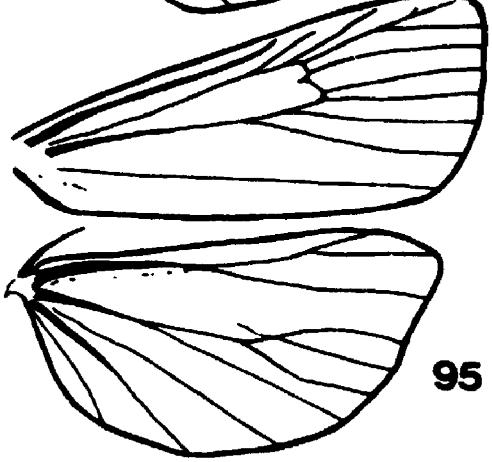

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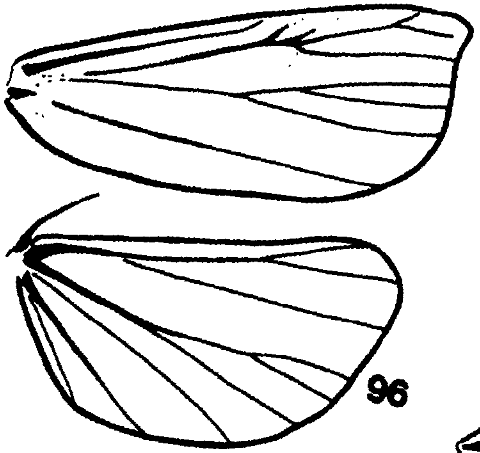
Figs. 96-102. Wing venation of Crambinae: 96, *Almita texana* n. sp.; 97, *Eoreuma densella* (Zeller); 98, *Xubida panalope* (Dyar); 99, *Occidentalia comptulatalis* (Hulst); 100, *Prionapteryx serpentella* Kearfott; 101, *Hemiplatytes prosenes* (Dyar); 102, *Haimbachia floridella* Capps.



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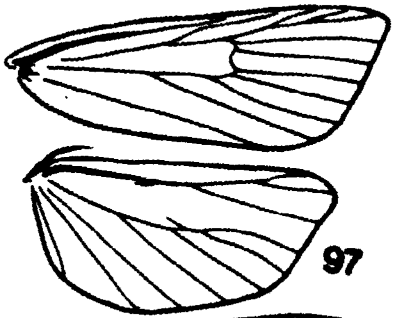

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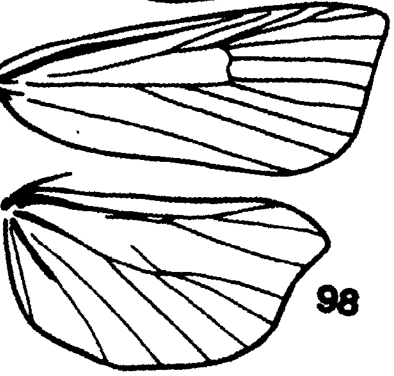

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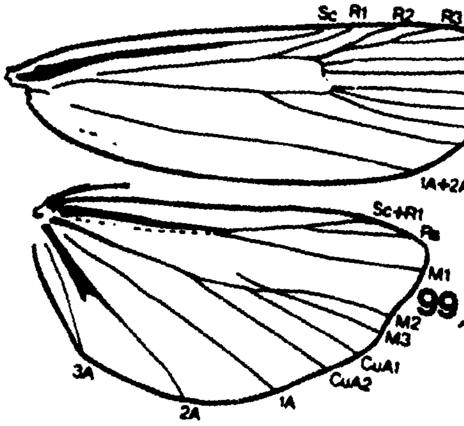

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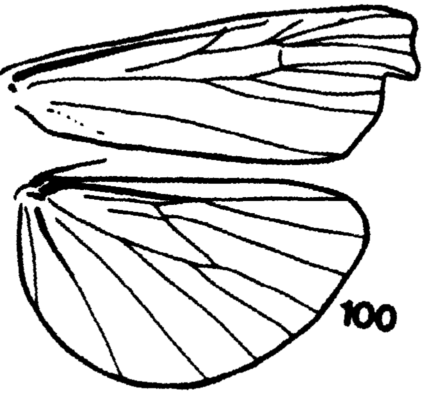

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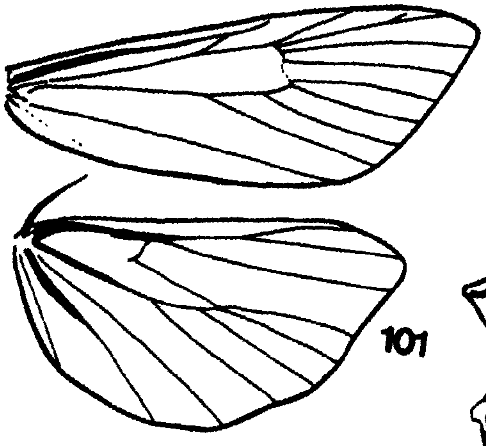

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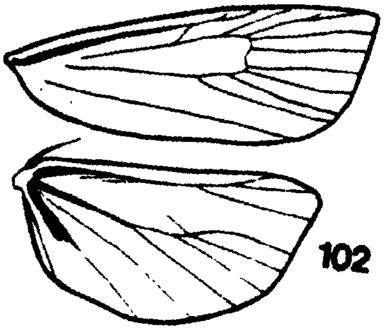

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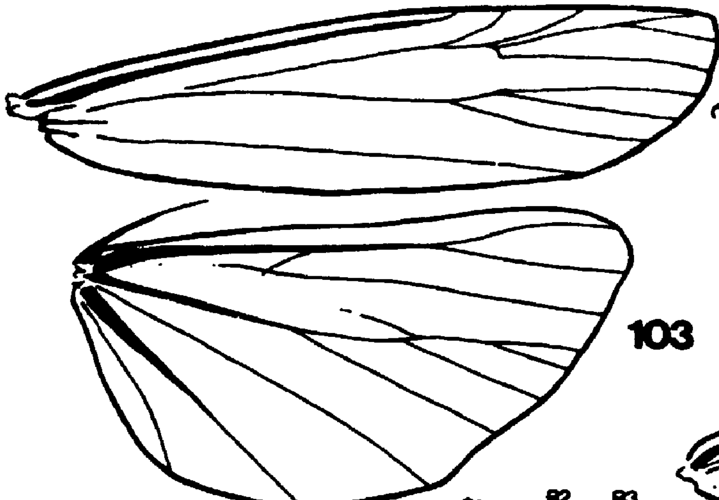
Figs. 103-109. Wing venation of Crambinae: 103, *Eufernaldia cadarella* (Druce); 104, *Diatraea evanescens* Dyar; 105, *Chilo phragmitellus* (Hübner) ♀; 106, *Myelobia* sp.; 107, *Chilo phragmitellus* (Hübner) ♂; 108, *Urola nivalis* (Drury); 109, *Epina dichromella* (Walker).



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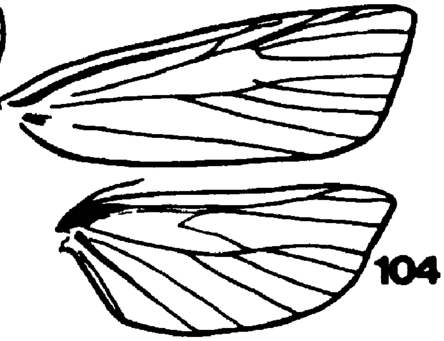

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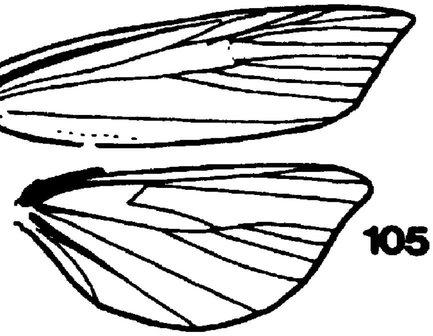

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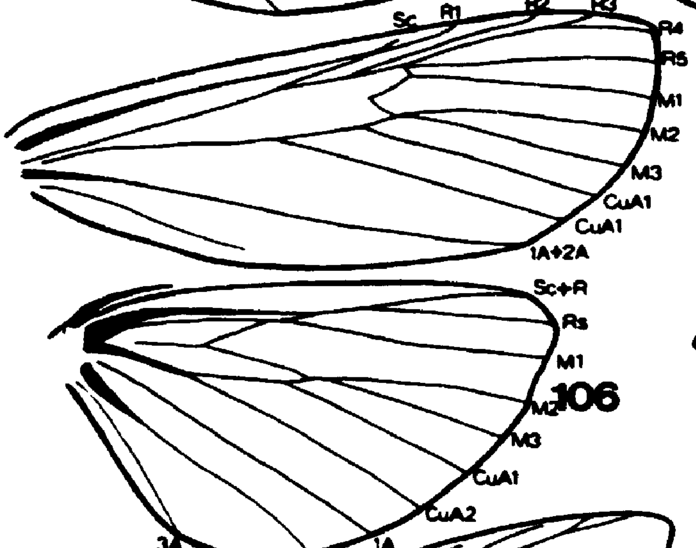

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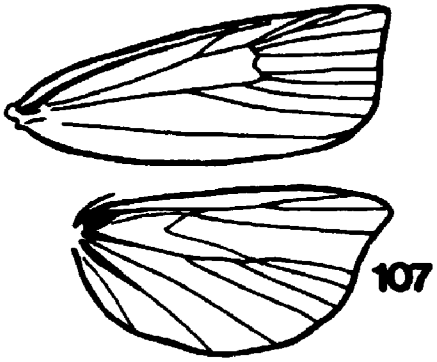

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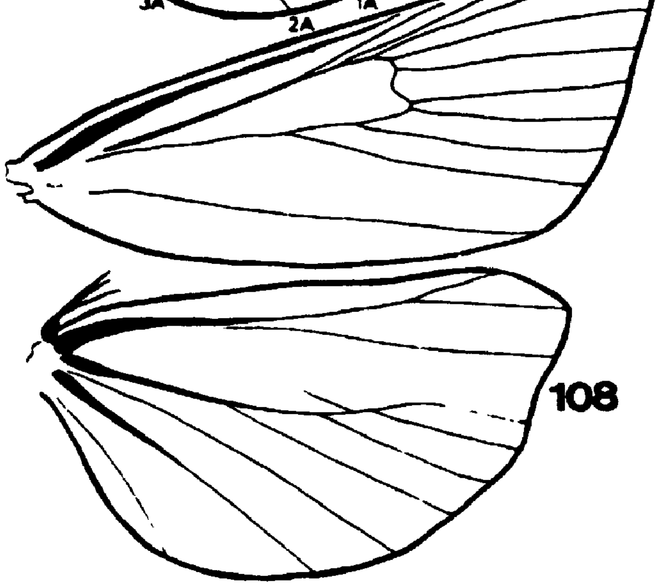

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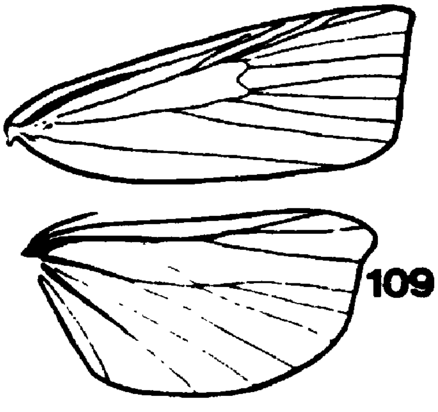

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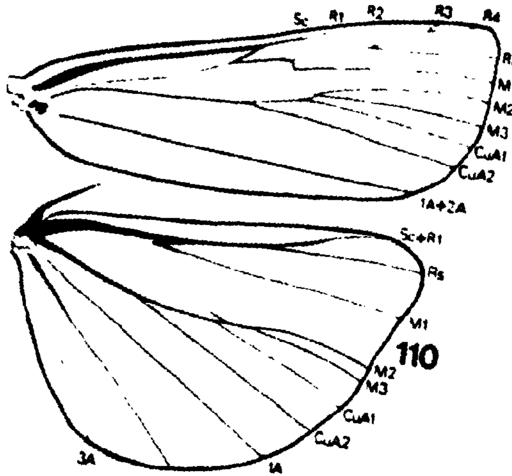
Figs. 110-117. Wing venation of Crambinae: 110, *Pediasia trisecta* (Walker); 111, *Agriphila ruricolella* (Zeller); 112, *Arequipa turbatella* Walker; 113, *Thaumatopsis pectinifer* (Zeller); 114, *Loxocrambus coloradellus* Fernald; 115, *Crambus pascuellus* (L.); 116, *Chrysoteuchia topiaria* (Zeller); 117, *Thaumatopsis bolterella* (Fernald).



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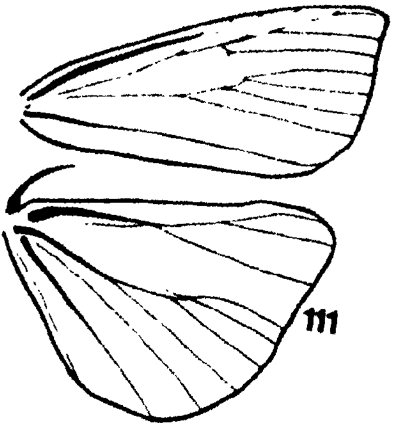

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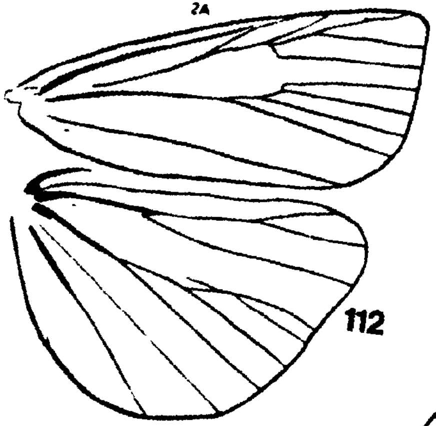

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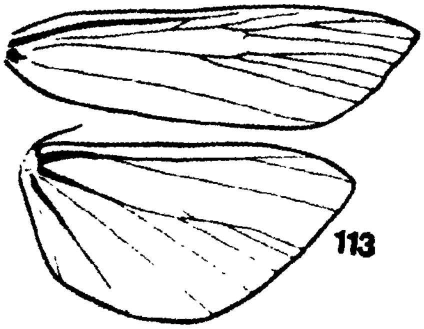

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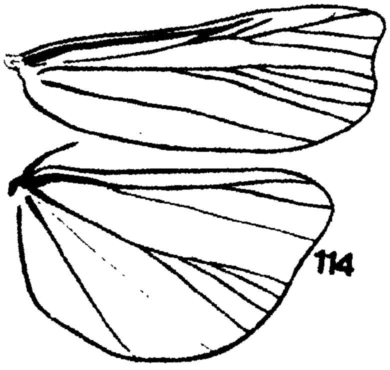

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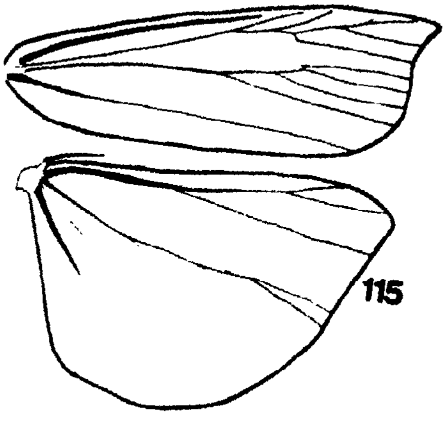

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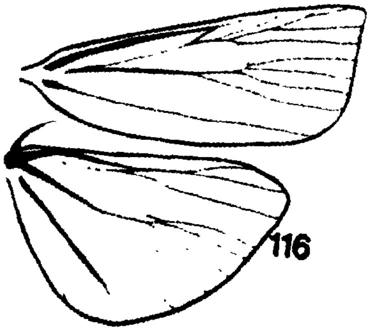

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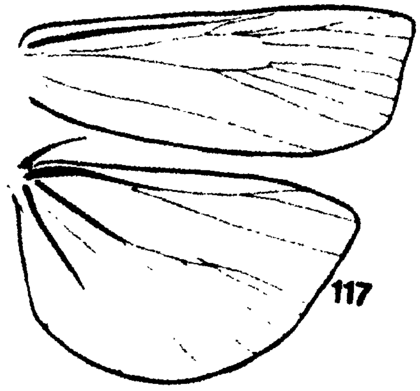
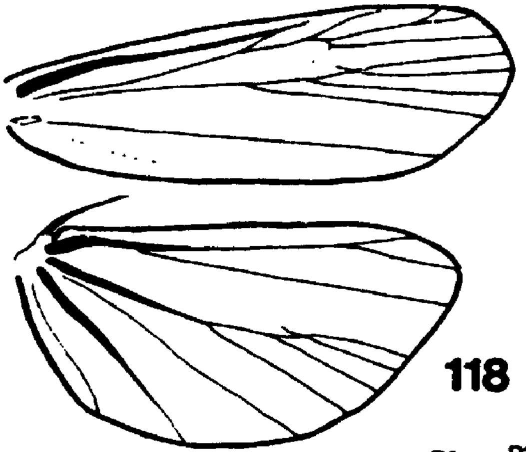


117

Figs. 118-123. Wing venation of Crambinae and Evergestinae: 118, *Loxocrambus canellus* Forbes; 119, *Raphiptera argillaceella* (Packard); 120, *Catoptria latiradiella* (Walker); 121, *Neodactria luteolella* (Clemens); 122, *Pseudoschoenobius opalescalis* (Hulst) showing pecten of hairs on Cubital stem; 123, *Evergestis simulatilis* (Grote).



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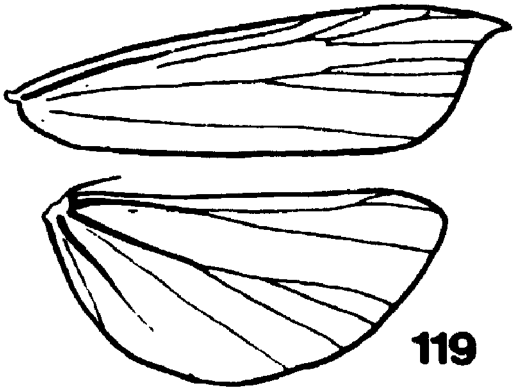

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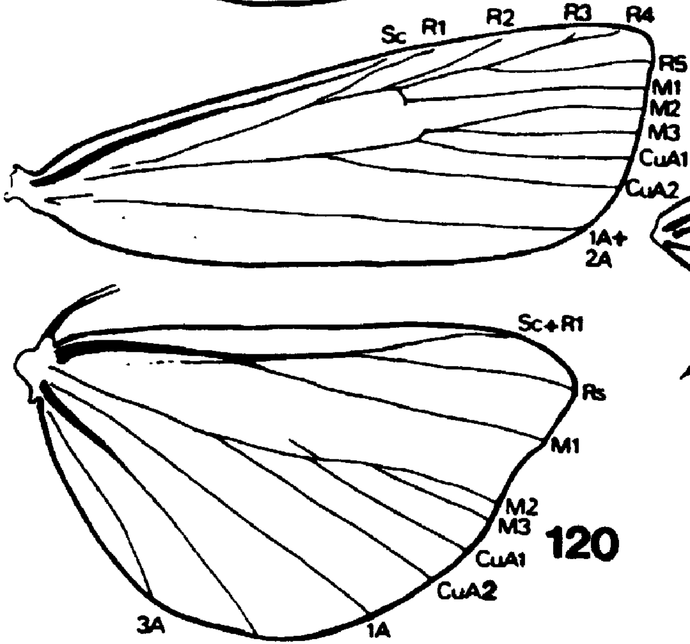

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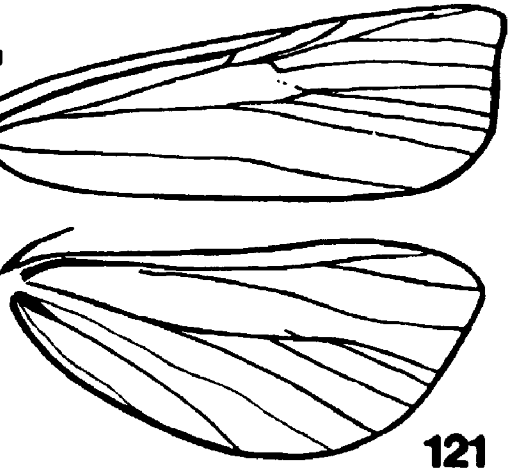

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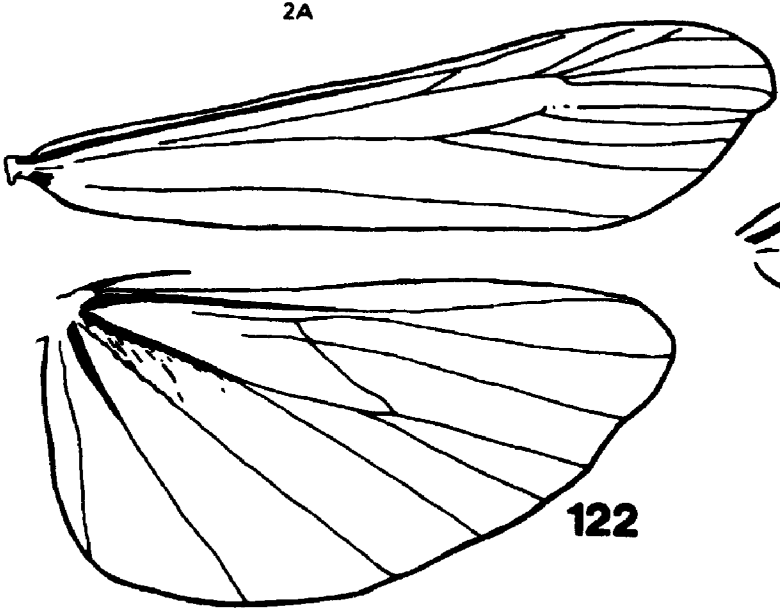

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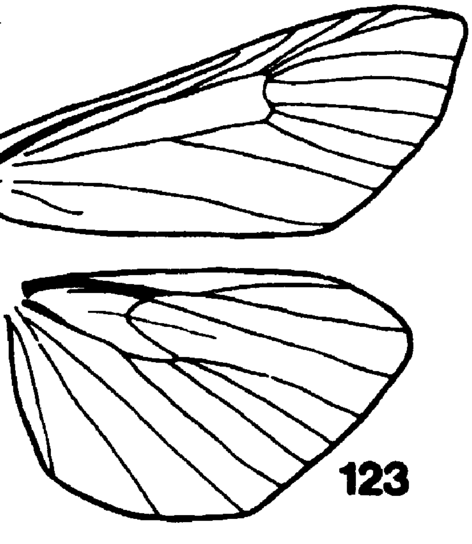

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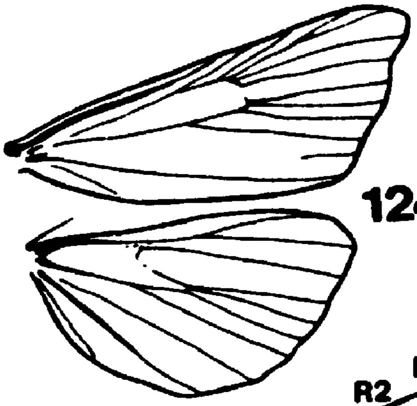
Figs. 124-130. Wing venation of Crambiformes: 124, *Cybalomia extorris* Warren; 125, *Scoparia basalis* Walker; 126, *Pyrausta unifascialis* (Packard); 127, *Glaphyria sequistrialis* Hübner; 128, *Donacaula longirostrella* (Clemens); 129, *Nymphula ekthlipsis* (Grote); 130, *Mimoschimia rufofascialis* (Stephens).



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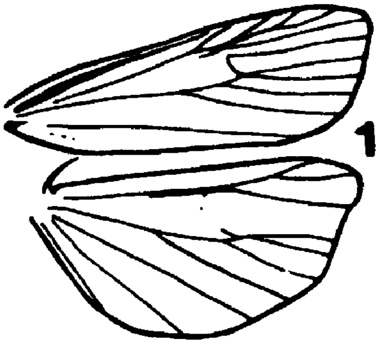

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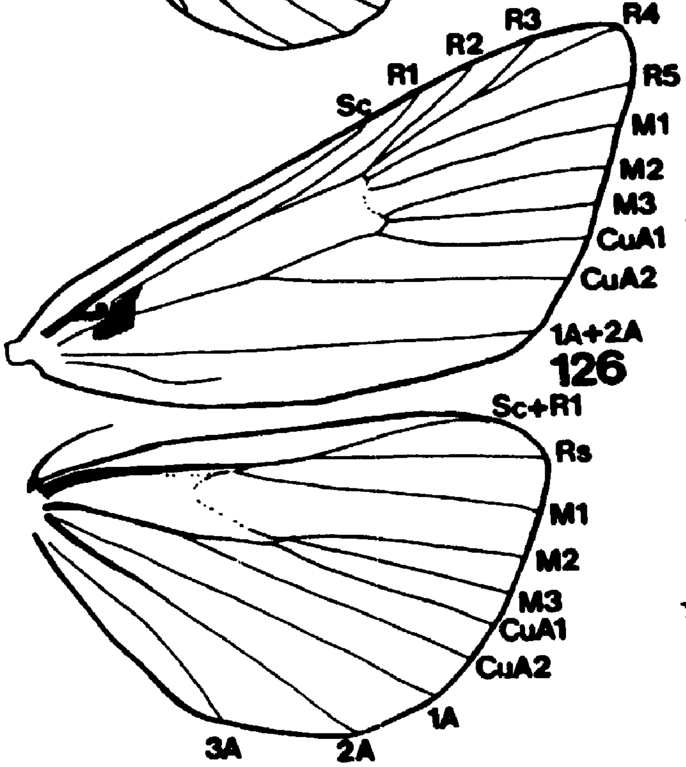

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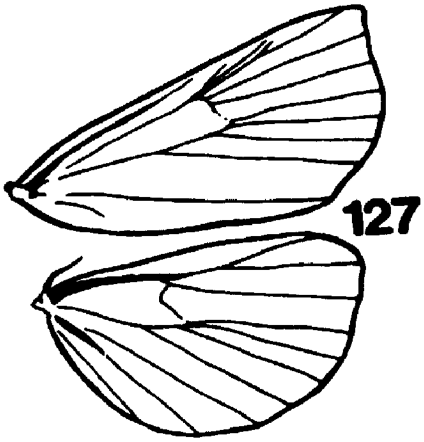

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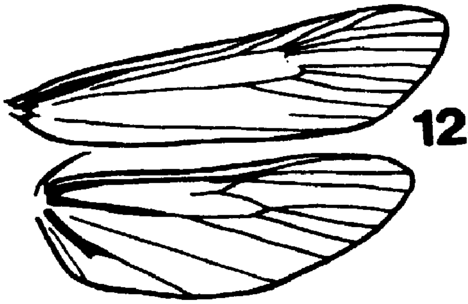

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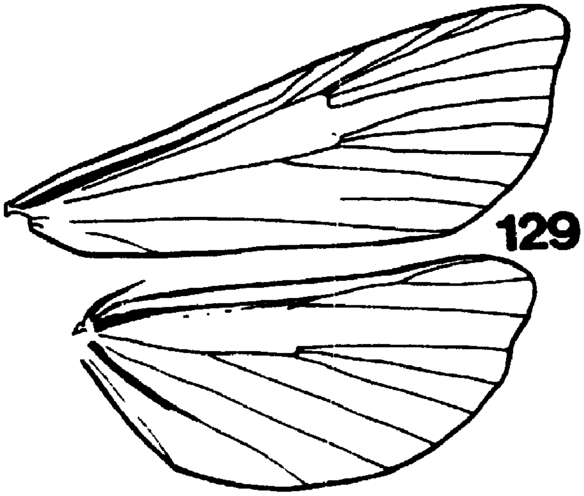

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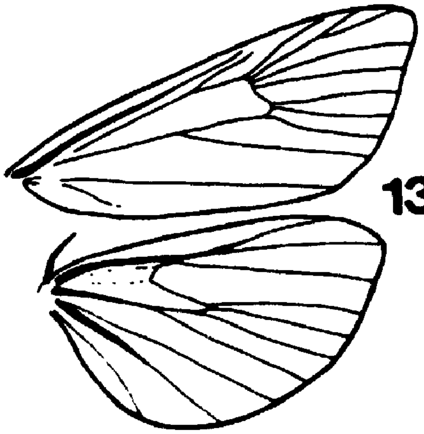

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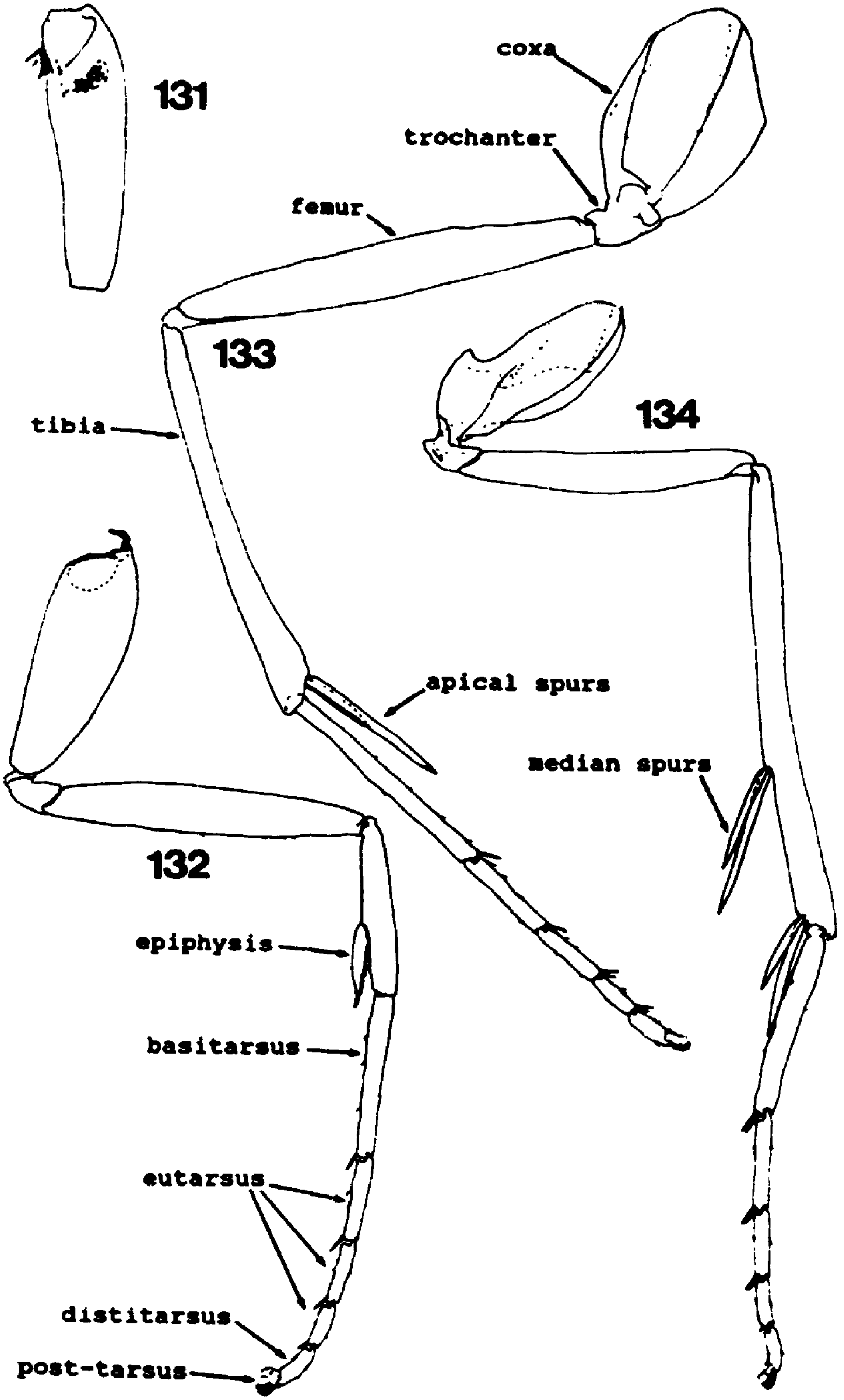
Figs. 131-134. Legs of Crambinae: 131, forecoxa of *Chilo phragmitella* (Hübner) showing exocrine gland; 132, Foreleg of *Crembus pascuellus* (L.); 133, Midleg of *Crambus pascuellus*, 134, Hindleg of *Crambus pascuellus*.


131
coxa
trochanter
femur
133
tibia
134
apical spurs
median spurs
132
epiphysis
basitarsus
eutarsus
distitarsus
post-tarsus

Figs. 135-137. Dorsal views of adult crambiforme moths. 135: a) *Epina dichromella* (Walker) ♂ (Florida, USNM, wingspan=37 mm); b) *Myelobia* sp. ♂ (Brazil, CNC, wingspan=59 mm); c) *Chilo phragmitella* (HÜbner) ♀ (locality unknown, CNC, wingspan=37 mm); d) *Calamotropha paludella* (Hübner) ♂ (France, CNC, wingspan=25 mm); e) *Diatraea saccharalis* (F.) ♂ (Texas, CNC, wingspan=26 mm). 136: a) *Xubida panalope* (Dyar) ♂ (Florida, TDC, wingspan=25 mm); b) *Haimbachia floridalis* Capps ♂ (Florida, CNC, wingspan=15 mm); c) *Eoreuma densella* (Zeller) ♂ (Florida, TDC, wingspan=20 mm); d) *Occidentalia comptulatalis* (Hulst) ♂ (Nova-Scotia, CNC, wingspan=21 mm); e) *Thopeutis forbesellus* (Fernald) ♂ (Québec, CNC, wingspan=24 mm). 137: a) *Cybalomia extorris* Warren ♂ (Utah, CNC, wingspan=18 mm); b) *Glaphyria sequistrialis* HÜbner ♂ (Texas, CNC, wingspan=17 mm); c) *Scoparia basalis* Walker ♀ (Ontario, CNC, wingspan=16 mm); d) *Nymphula ekthlipsis* (Grote) ♀ (Ontario, CNC, wingspan=23 mm); e) *Mimoschinia rufofascialis* (Stephens) ♀ (California, CNC, wingspan=15 mm); f) *Donacaula longirostrella* (Clemens) ♂ (Nova-Scotia, CNC, wingspan=24 mm); g) *Pyrausta unifascialis* (Packard) ♀ (Québec, CNC, wingspan=22 mm); h) *Evergestis simulatilis* (Grote) ♂ (British Columbia, CNC, wingspan=27 mm).

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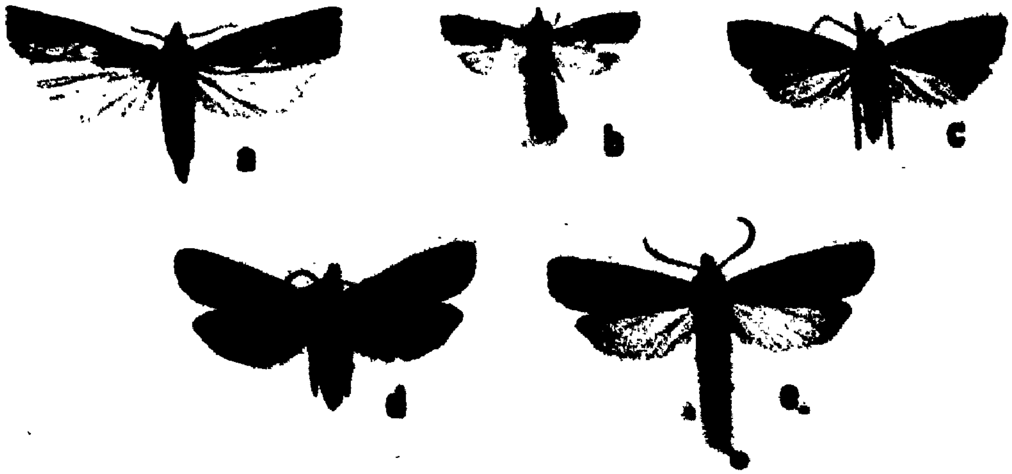

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Figs. 138-141. Dorsal views of adult crambine moths. 138, *Crambus pascuellus* (L.) ♂ (British Columbia, CNC, wingspan=24 mm); 139, *Ancylolomia japonica* Zeller ♂ (Japan, CNC, wingspan=24 mm); 140: a) *Argyria nummulalis* Hübner ♂ (Florida, CNC, wingspan=20 mm); b) *Urola nivalis* (Drury) ♂ (Ontario, CNC, wingspan=23 mm); c) *Vaxi auratella* (Clemens) ♂ (Ontario, CNC, wingspan=17 mm); d) *Diptychophora harlequinalis* (Barnes & McDunnough) ♀ (Arizona, PJC, wingspan=14 mm). 141: a) *Surattha indentella* Kearfott ♂ (Texas, USNM, wingspan=25 mm); b) *Pseudoschoenobius opalescalis* (Hulst) ♂ (Arizona, PJC, wingspan=25 mm); c) *Prionapteryx serpentella* Kearfott (Florida, CNC, wingspan=20 mm); d) *Eufernaldia cadarella* (Druce) ♂ (Arizona, PJC, wingspan=29 mm); e) *Hemiplatytes prosenes* (Dyar) ♂ (California, CNC, wingspan=22 mm).

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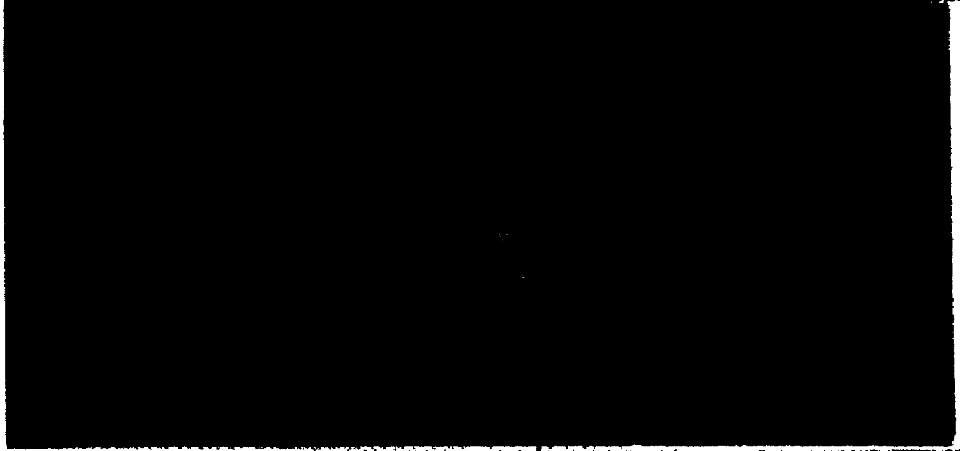

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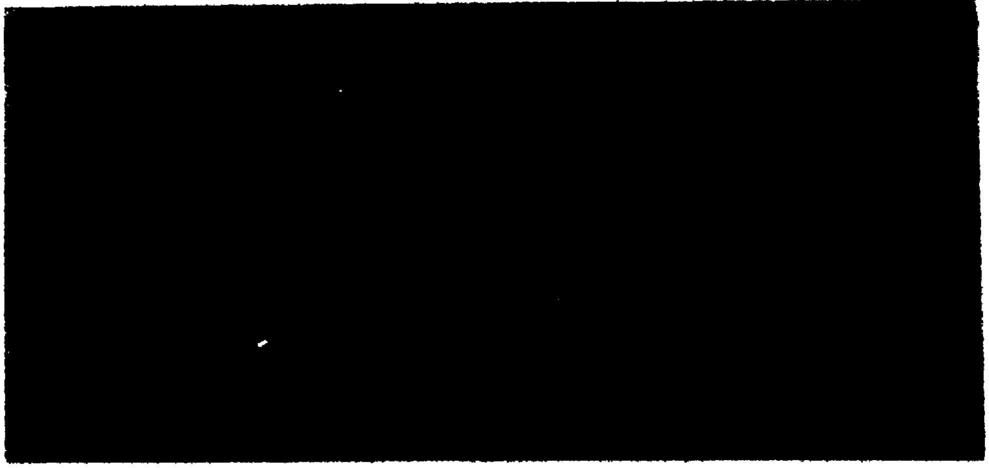

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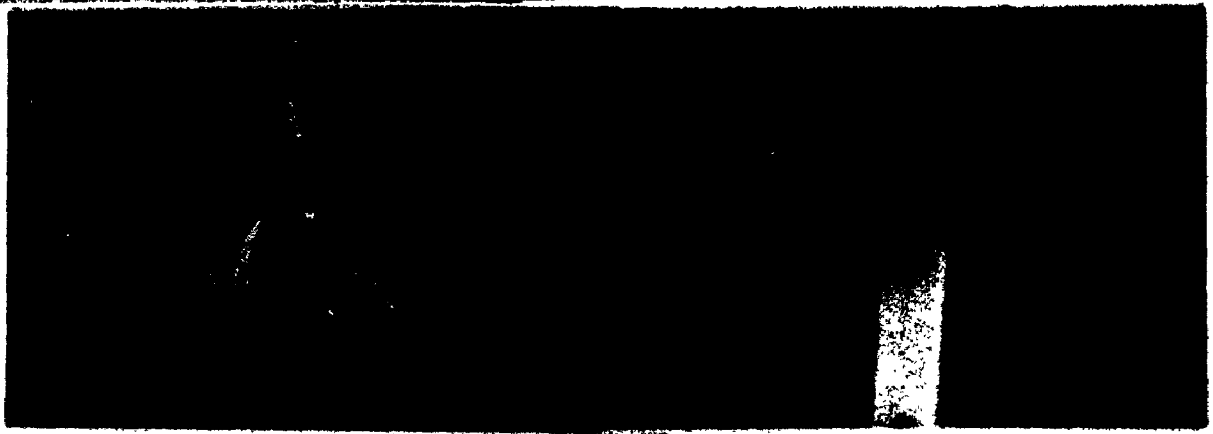
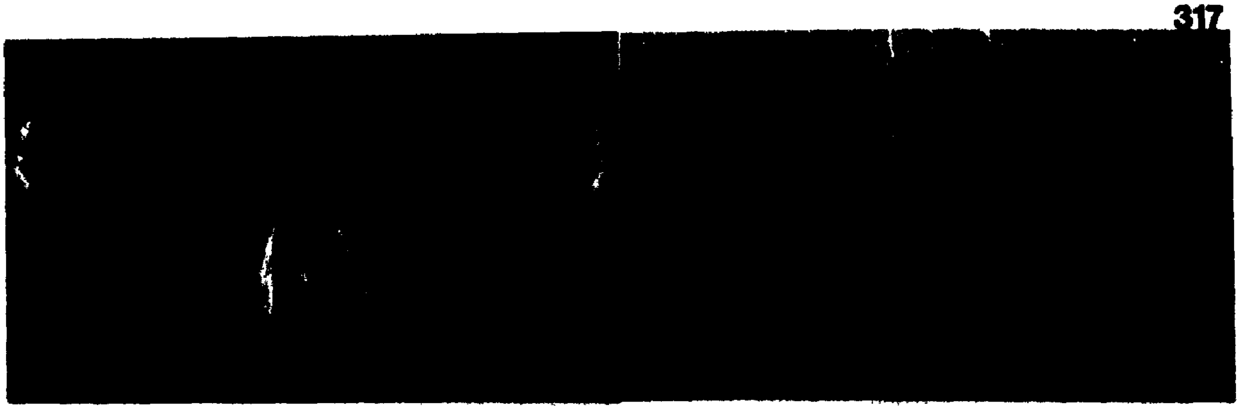
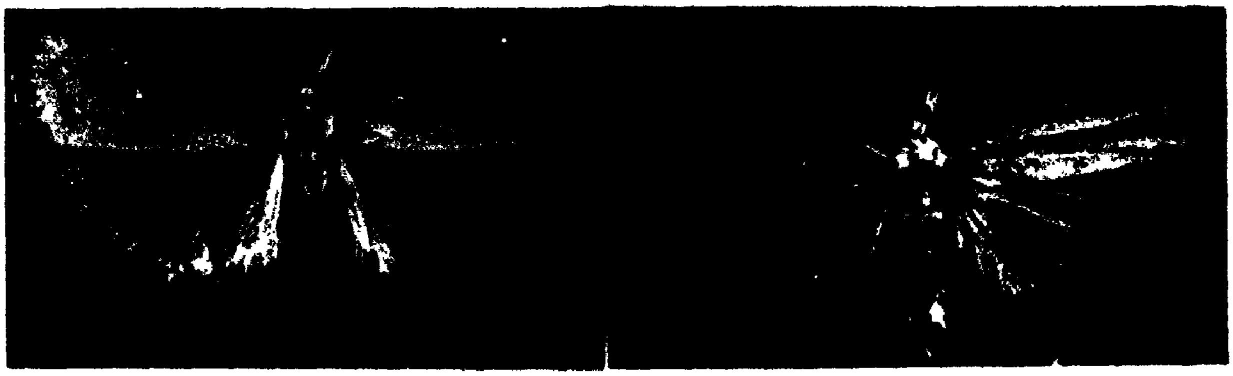
Figs. 142-148. Dorsal views of adult crambine moths. 142, *Tehama bonifatella* (Hulst) ♀ (Oregon, CNC, wingspan=24 mm); 143, *Fissicrambus fissiradiellus* (Walker) ♂ (Texas, NSMH, wingspan=17 mm); 144, *Fernandocrambus harpipterus* (Dyar) ♂ (Arizona, CNC, wingspan=25 mm); 145, *Loxocrambus* sp. ♂ (Arizona, PJC, wingspan=18 mm); 146, *Thaumatopsis bolterella* (Fernald) ♀ (Texas, USNM, wingspan=24 mm); 147, *Thaumatopsis pexella* (Zeller) ♂ (Arizona, LACM, wingspan=30 mm); 148, *Raphiptera argillaceella* (Packard) ♂ (Ontario, CNC, wingspan=18 mm).

Figs. 149-156. Dorsal views of adult crambine moths. 149, *Euchromius ocelleus* (Haworth) ♀ (Texas, CNC, wingspan-21 mm); 150, *Platytes vobisne* Dyar ♂ (Connecticut, AMNH, wingspan-13 mm); 151, *Parapediasia decorella* (Zincken) ♂ (Florida, USNM, wingspan-20 mm); 152 *Parapediasia hulstella* (Fernald) ♀ (Texas, USNM, wingspan-25 mm); 153, *Parapediasia teterrella* (Zincken) ♀ (Arizona, PJC, wingspan-19 mm); 154, "*Crambus*" *angulatus* Barnes & McDunnough ♂ (California, LACM, wingspan-17 mm); 155, *Agriphila ruricolella* (Zeller) ♀ (Québec, CNC, wingspan-21 mm); 156, *Neodactria luteolella* (Clemens) ♂ (Québec, CNC, wingspan-20 mm).



Figs. 157-164. Dorsal views of adult crambine moths. 157, *Almita texana* n.sp. ♂ holotype (Texas, USNM, wingspan=9 mm); 158, *Almita portalia* n.sp. ♀ paratype (Arizona, CNC, wingspan=15 mm); 159, *Parapediasia torquatella* n.sp. ♂ holotype (Arizona, USNM, wingspan=27 mm); 160, "*Crambus*" *dimidiatellus* Grote ♂ (Arizona, USNM, wingspan=35 mm); 161, *La cerveza* n.sp. ♂ paratype (Texas, USNM, wingspan=23 mm); 162, *Pediasia trisecta* (Walker) ♂ (Québec, CNC, wingspan=27 mm); 163, *Arequipa turbatella* Walker ♂ (Ontario, CNC, wingspan=20 mm); 164, *Loxocrambus hospition* (Bleszynski) ♀ (Arizona, PJC, wingspan=20 mm).





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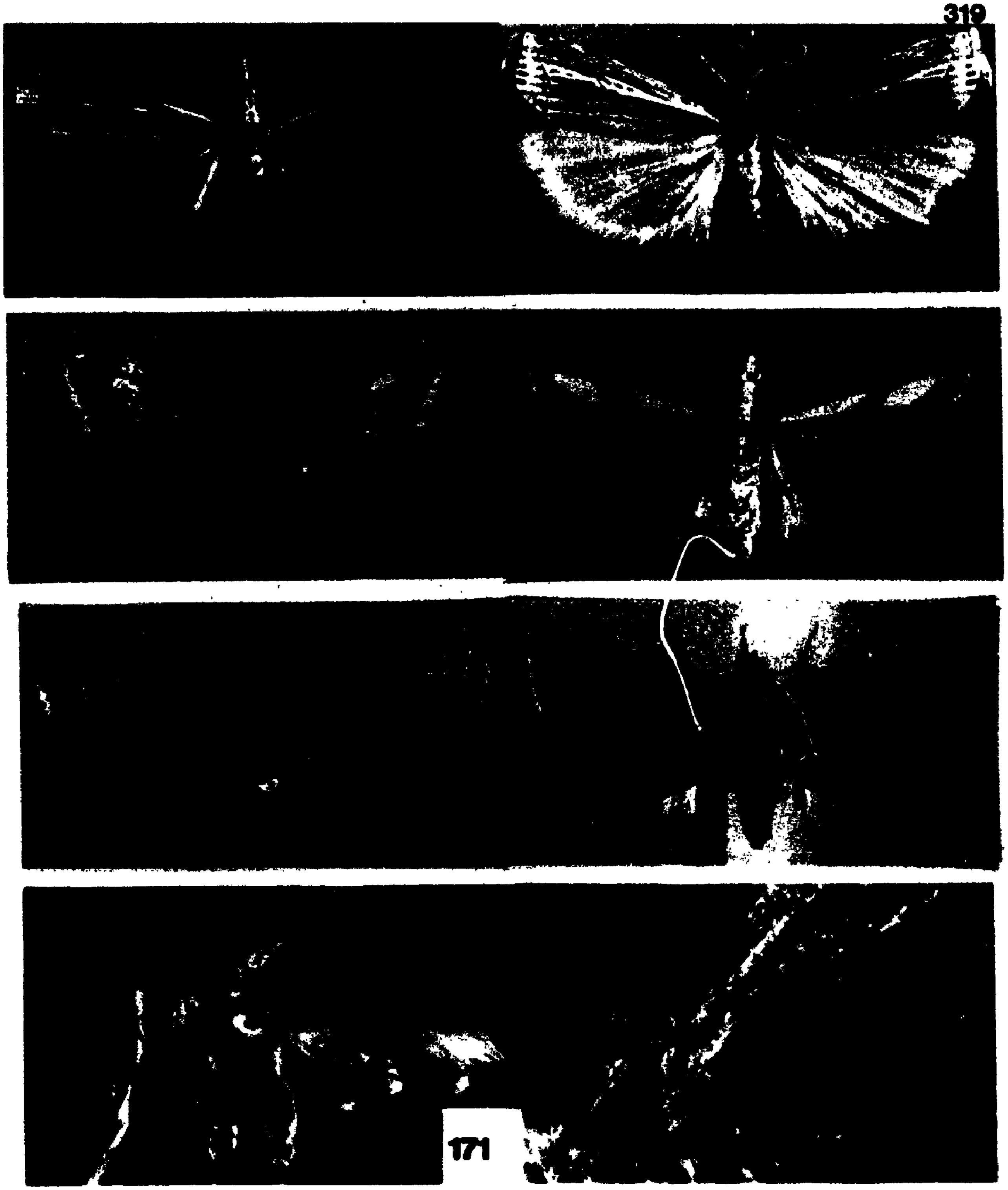
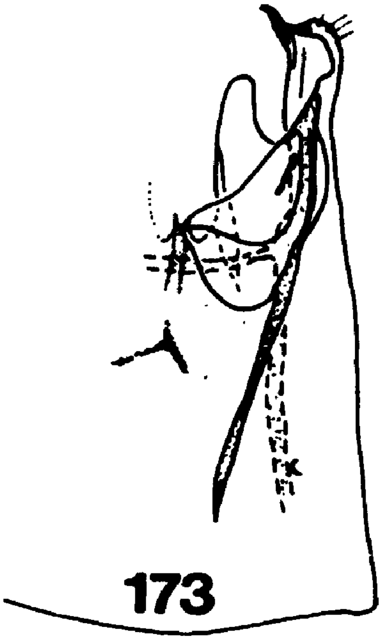
Figs. 165-172. Dorsal and lateral views of adult crambine moths. 165, *Fissicrambus profanellus* (Walker) ♂ (Florida, TDC, wingspan=22 mm); 166, *Loxocrambus coloradellus* (Fernald) ♂ (Texas, CNC, wingspan=18 mm); 167, *Catoptria trichostoma* (Christoph) ♂ (Northwest Territories, CNC, wingspan=18 mm); 168, *Catoptria latiradiella* (Walker) ♂ (Manitoba, CNC, wingspan=21 mm); 169, *Chrysoteuchia topiaria* (Zeller) ♂ (Colorado, TDC, wingspan=18 mm); 170, *Microcrambus elegans* (Clemens) ♀ (Québec, CNC, wingspan=17 mm); 171, lateral view of thorax and base of wings of *Crambus leachellus* (Zincken) showing praecinctorium. 172, lateral view of thorax and base of wings of *Agriphila vulgivagella* (Clemens) showing frenulum hook.



171

Figs. 173-179. Tympanal organs of Crambiformes. 173, *Donacaula longirostrella* (Clemens), ventral view; 174, *Mimoschinia rufofascialis* (Stephens): a) lateral view, b) ventral view; 175, *Cybalomia extorris* Warren: a) lateral view, b) ventral view; 176, *Nymphula ekthlipsis* (Grote), ventral view; 177, *Evergestis simulatilis* (Grote), ventral view; 178, *Glaphyria sesquistrialis* Hübner, ventral view; 179, *Scoparia basalis* Walker, ventral view.



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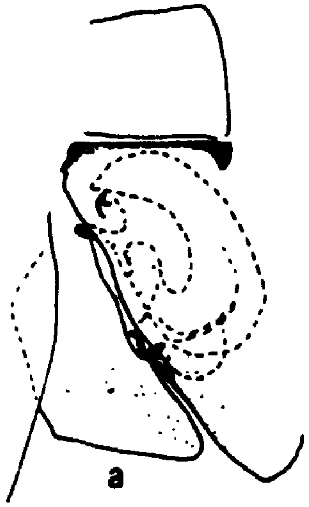

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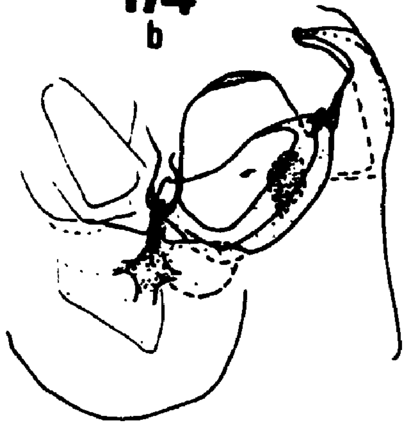
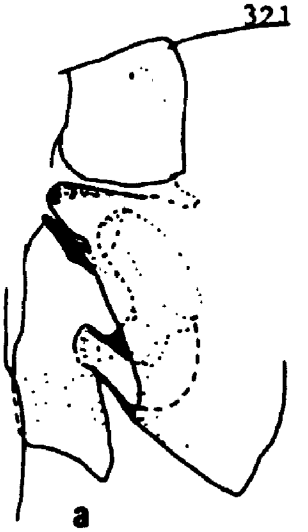
b





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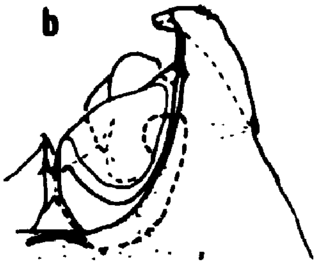
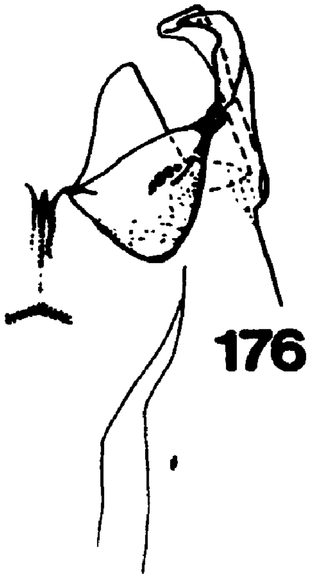
b





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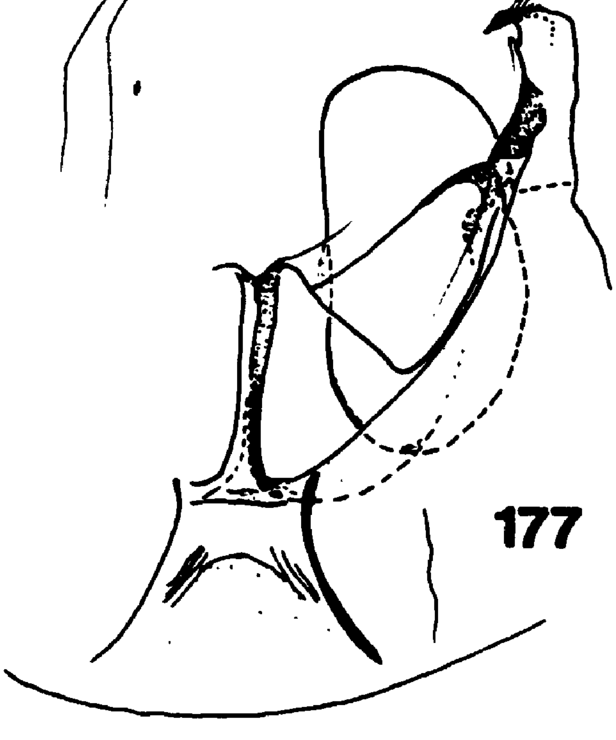

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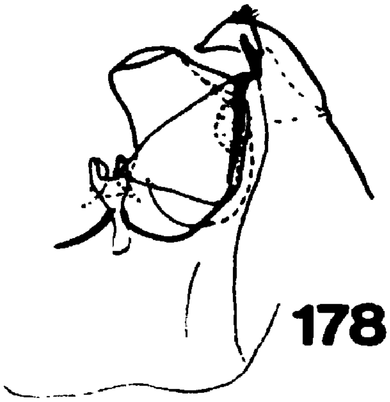

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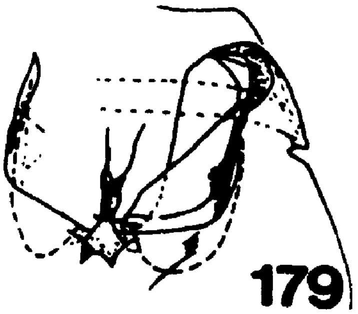

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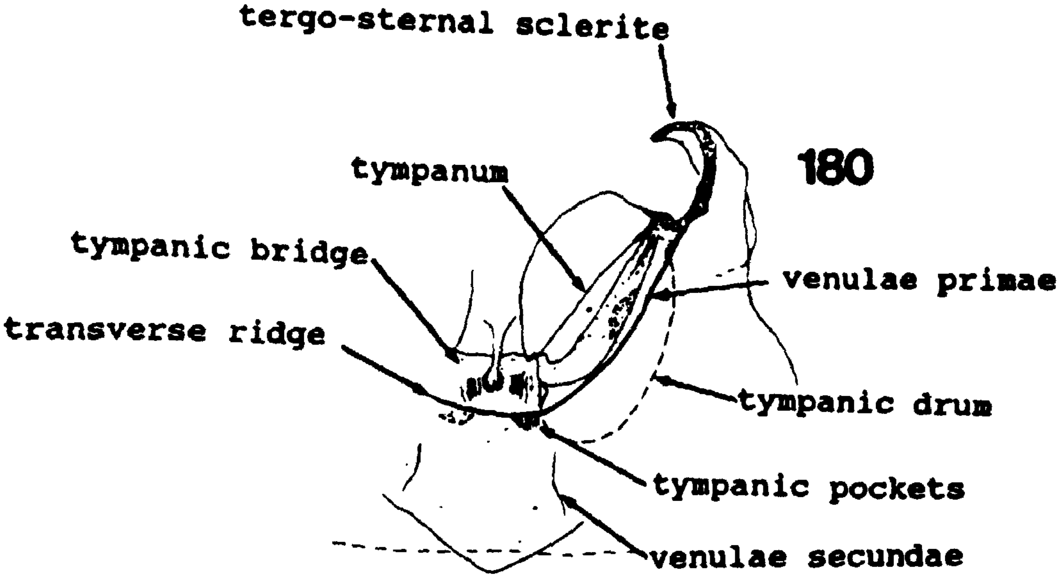
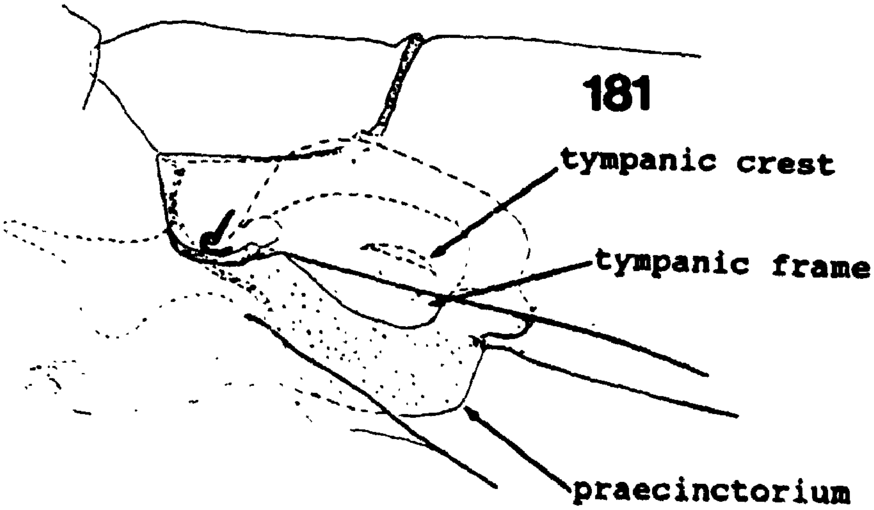
Figs. 180-181. Tympanal organs of Crambinae. 180, *Ancylolomia* sp., ventral view; 181, *Eufernaldia cadarella* (Druce), lateral view.


tergo-sternal sclerite
tympanum
tympanic bridge
transverse ridge
venulae primae
tympanic drum
tympanic pockets
venulae secundae

180


tympanic crest
tympanic frame
praecinctorium

181

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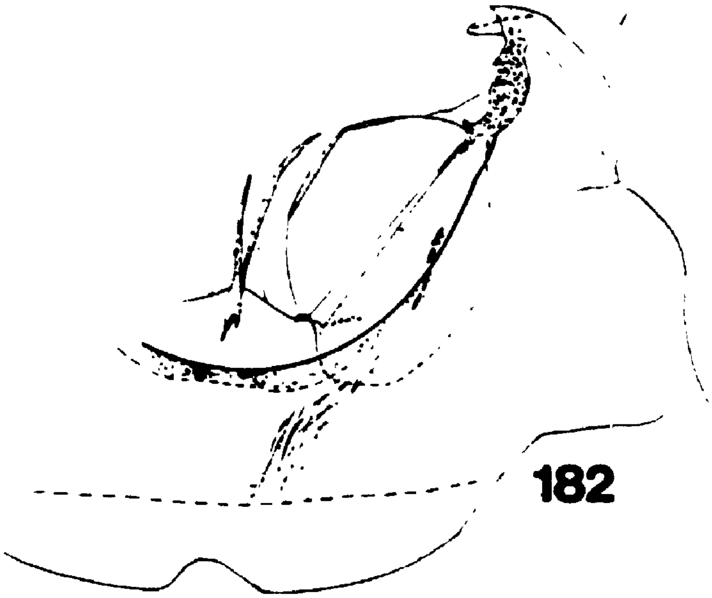
Figs. 182-187. Ventral views of tympanal organs of Crambinae and Pyraustinae. 182, *Surattha indentella* Kearfott; 183, *Pyrausta unifascialis* (Packard); 184, *Pseudoschoenobius opalescalis* (Hulst); 185, *Eufernaldia cadarella* (Druce); 186, *Diptychophora harlequinalis* (Barnes & McDunnough); 187, *Prionapteryx serpentella* Kearfott.



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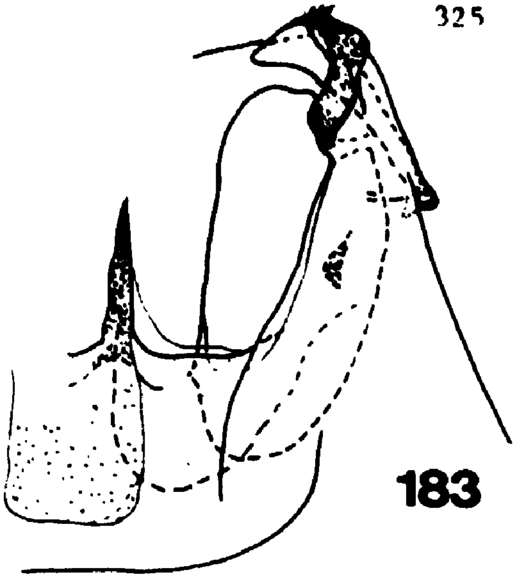

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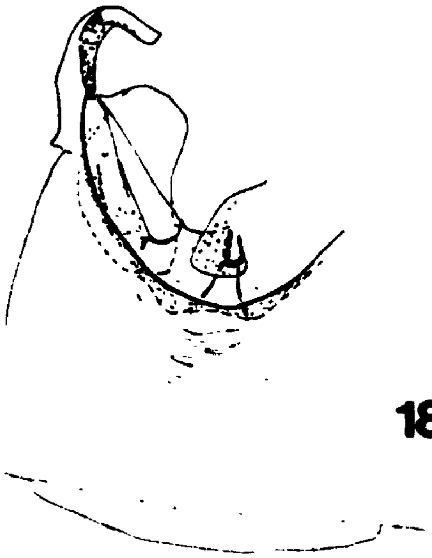

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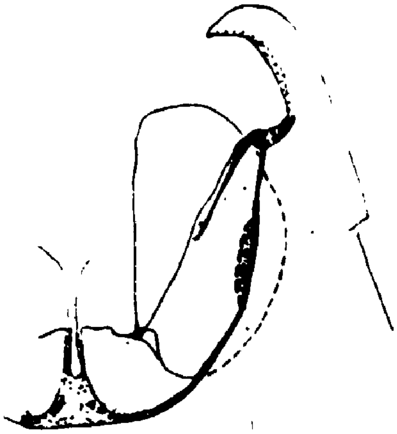

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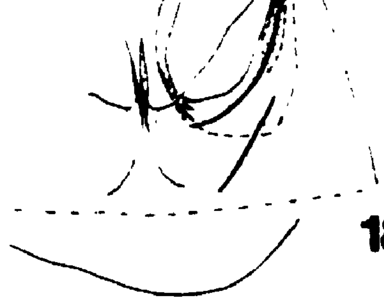

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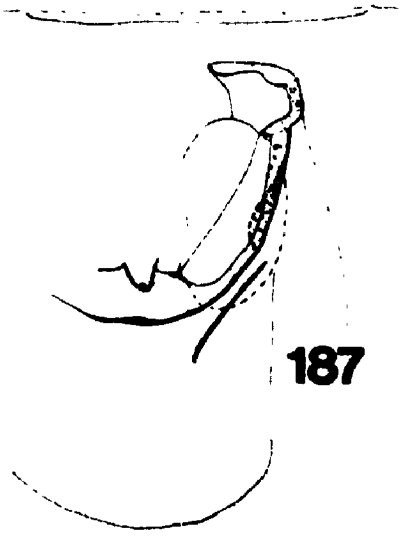

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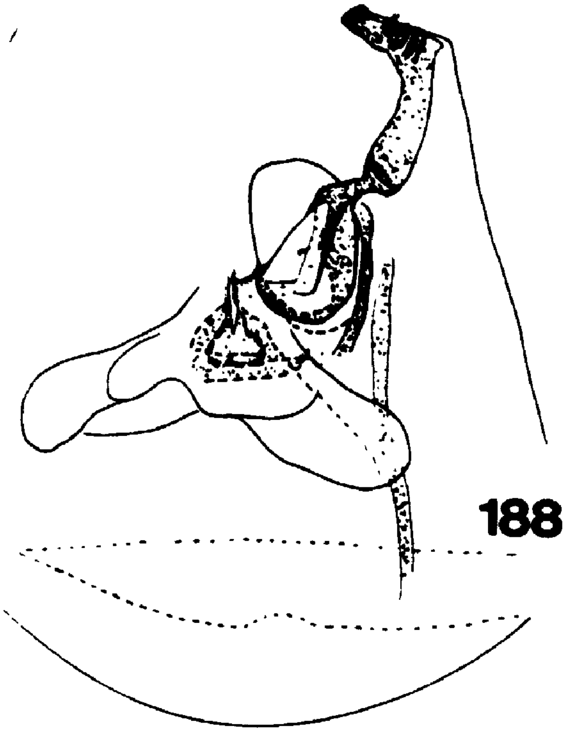
Figs. 188-191. Tympanal organs of Crambinae. 188-189, *Myelobia* sp.: 188, ventral view; 189, lateral view. 190, *Microcausta flavipunctalis* Barnes & McDunnough: a) enlargment of mid-ventral region, b) ventral view; 191, *Calamotropha paludella* (Hübner), ventral view.



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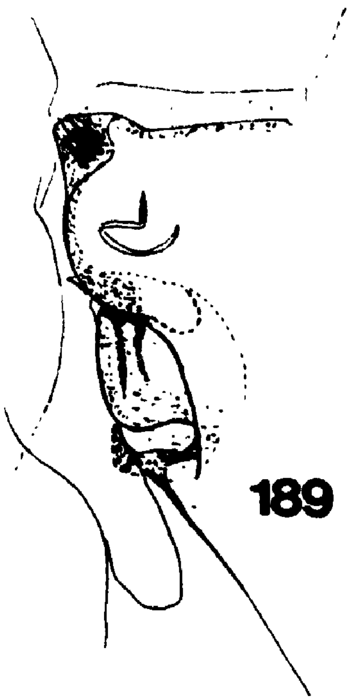

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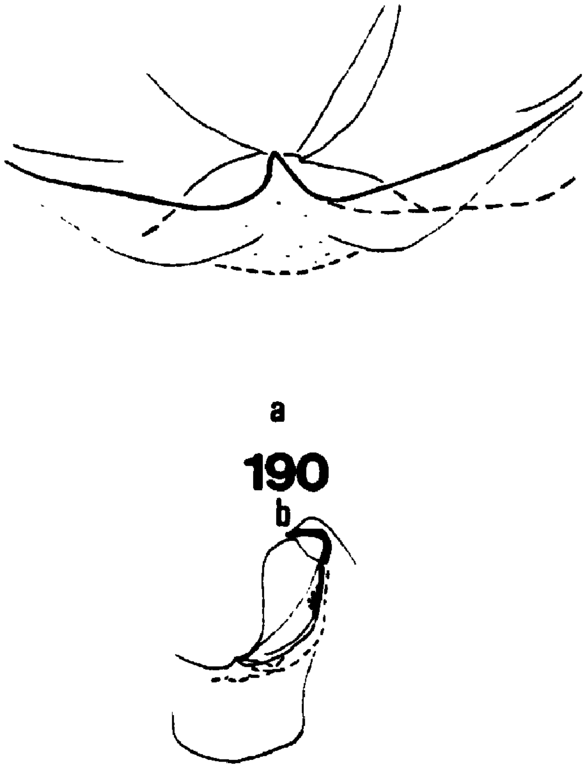

a

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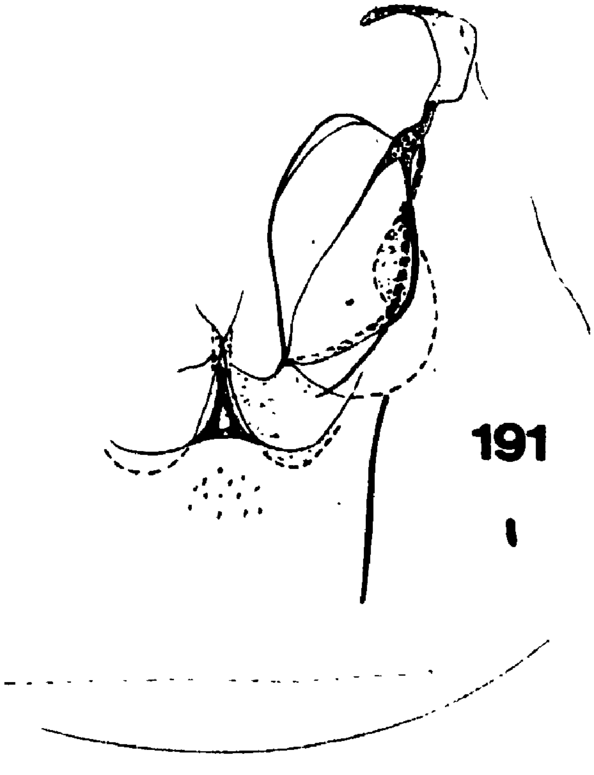
b



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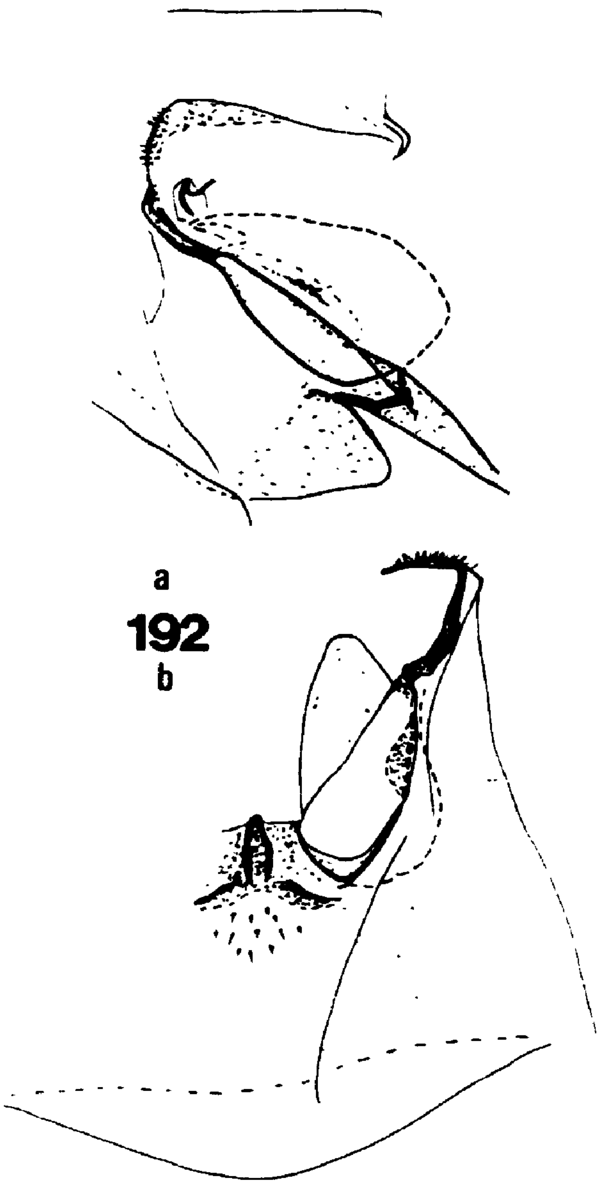
Figs. 192-194. Tympanal organs of Crambinae, a) lateral views, b) ventral views. 192, *Thopeutis forbesellus* (Fernald); 193, *Chilo phragmitellus* (Hübner); 194, *Diatraea evanescens* Dyar.



a
192
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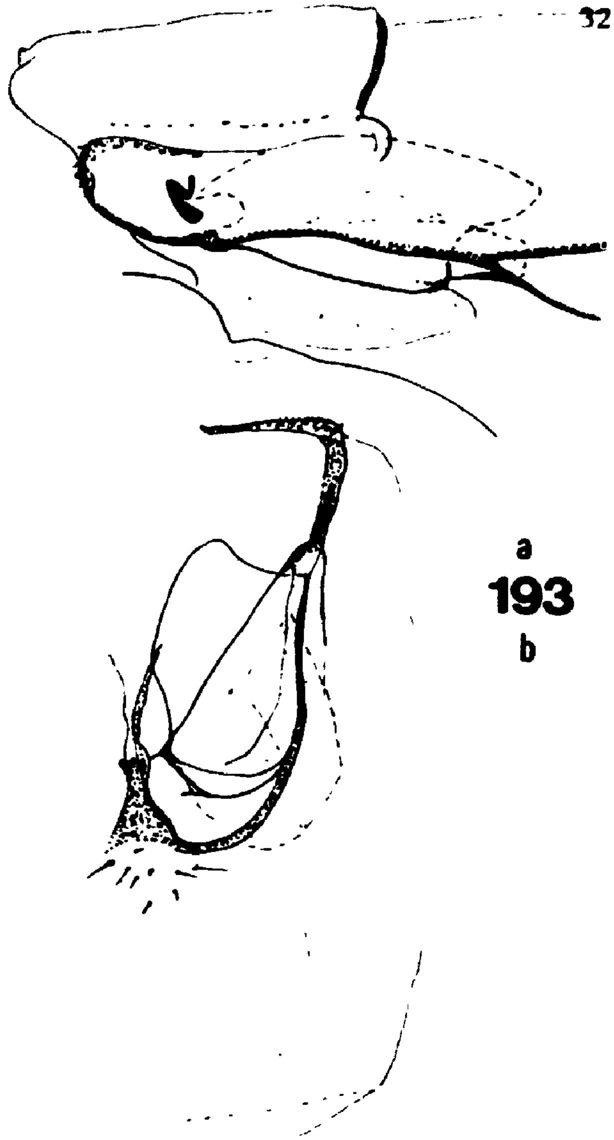

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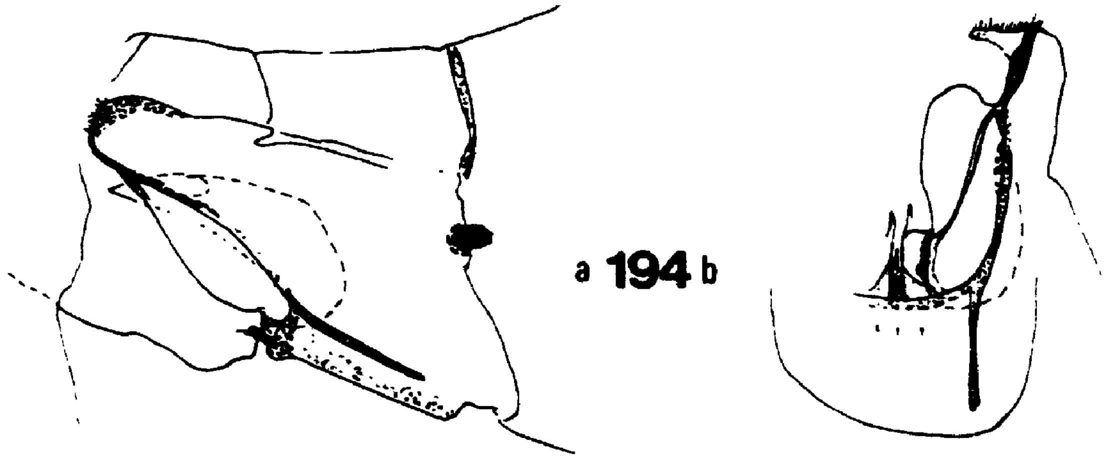
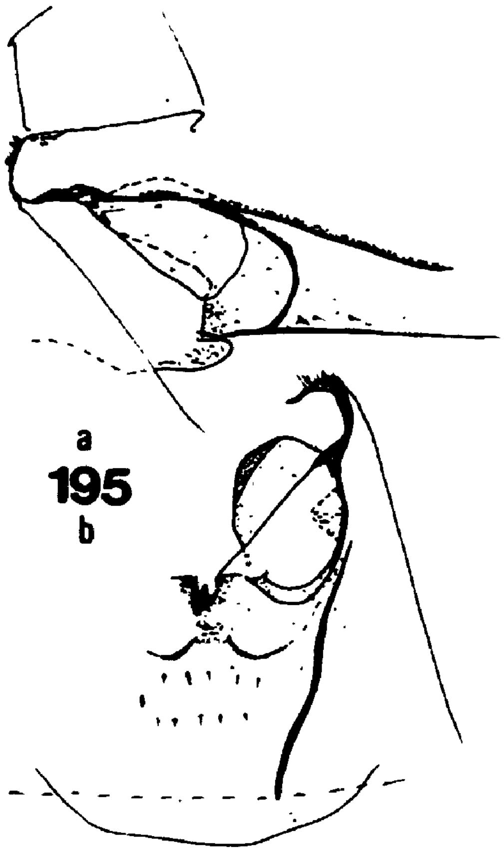


a 194 b

Figs. 195-197. Tympanal organs of Crambinae, a) lateral views, b) ventral views. 195, *Xubida panalope* (Dyar); 196, *Epina alleni* (Fernald); 197, *Occidentalia comptulatalis* (Hulst).



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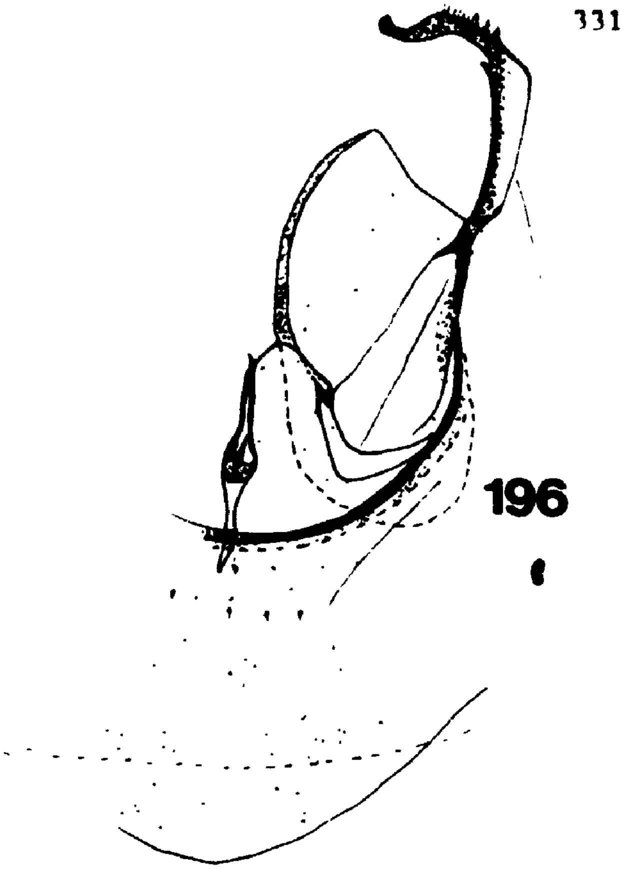

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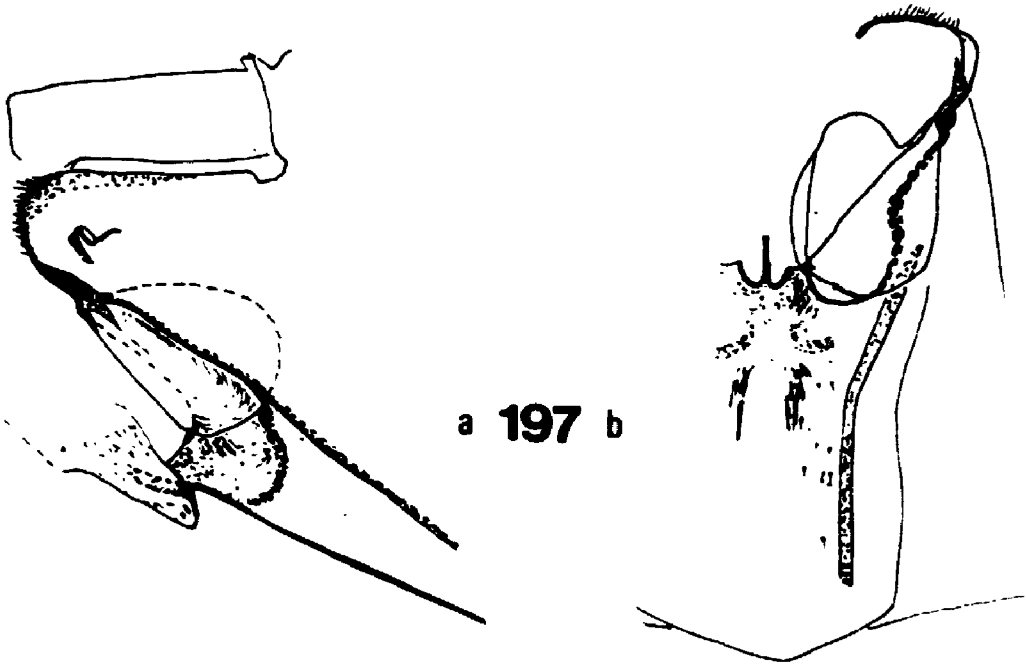
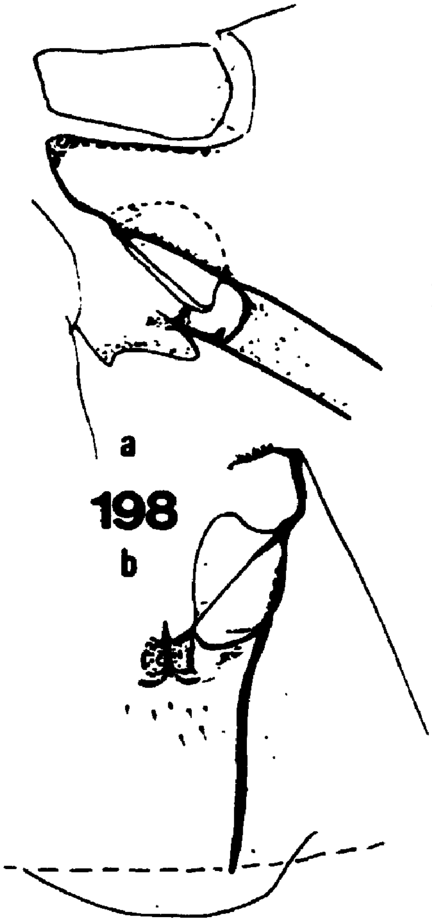


a **197** b

Figs. 198-201. Tympanal organs of Crambinae: a) lateral views, b) ventral views. 198, *Haimbachia floridalis* Capps; 199, *Eoreuma densella* (Zeller); 200, *Hemiplatytes prosenes* (Dyar); 201, *Urola nivalis* (Drury).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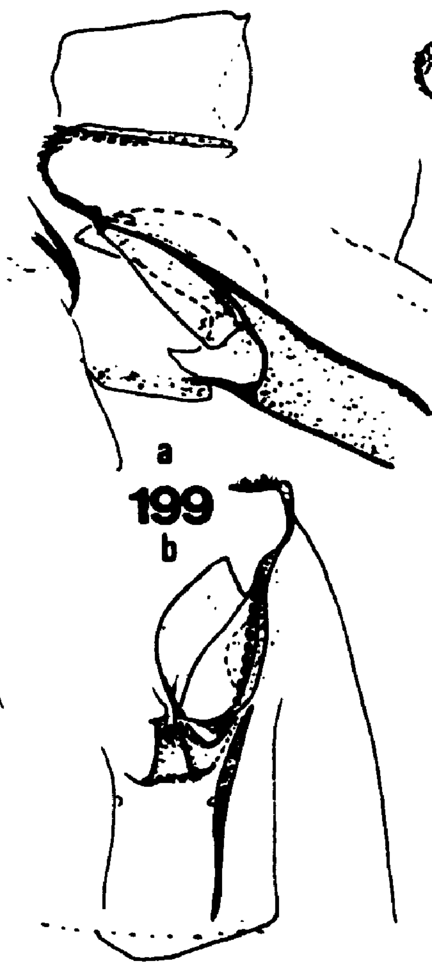
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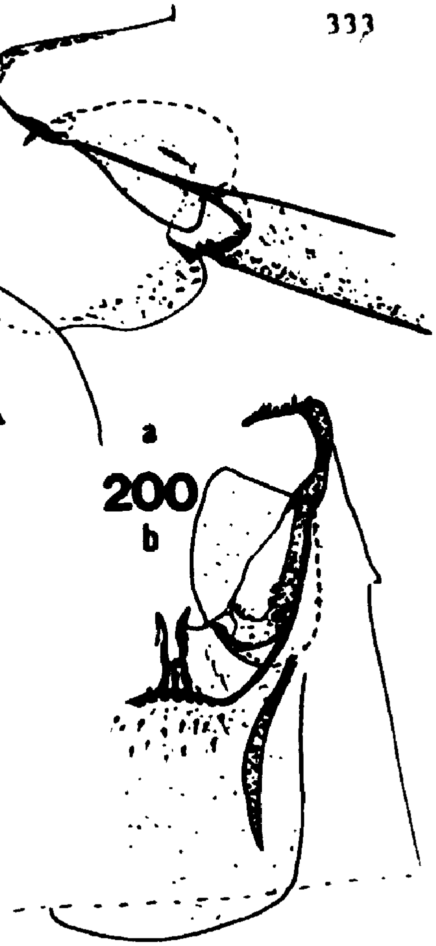
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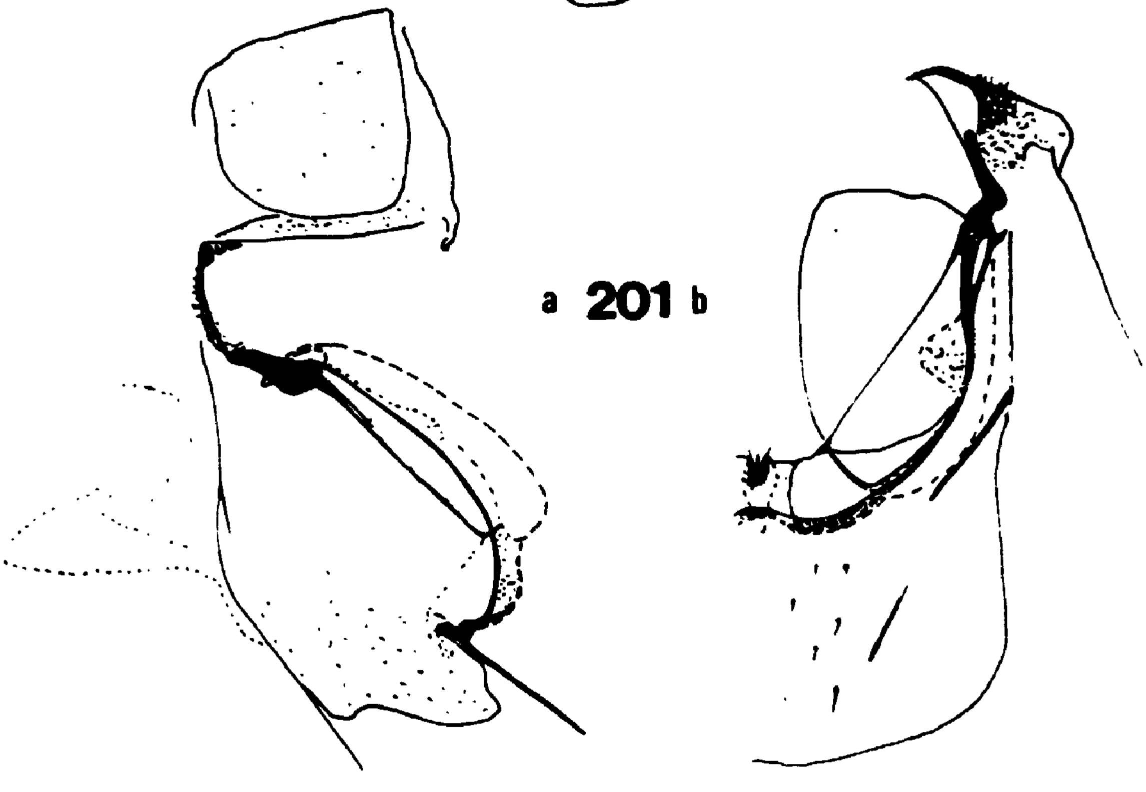
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Figs. 202-206. Tympanal organs of Crambinae. 202, *Argyria nummulalis* Hübner: a) lateral view, b) ventral view; 203, *Thaumatopsis pexella* (Zeller): a) lateral view; b) ventral view; 204, *Euchromius ocelleus* (Haworth): a) ventral view, b) lateral view; 205, *Platytes vobisne* Dyar: a) lateral view, b) ventral view; 206, *Vaxi auratella* (Clemens), ventral view.

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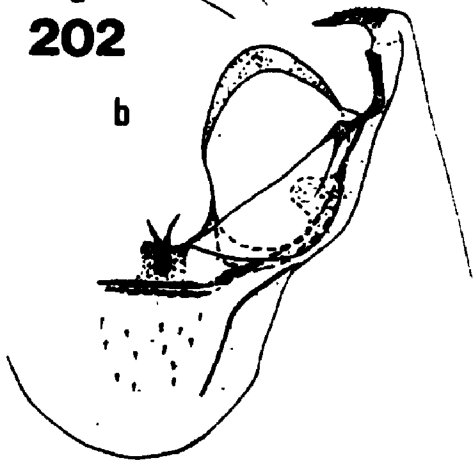

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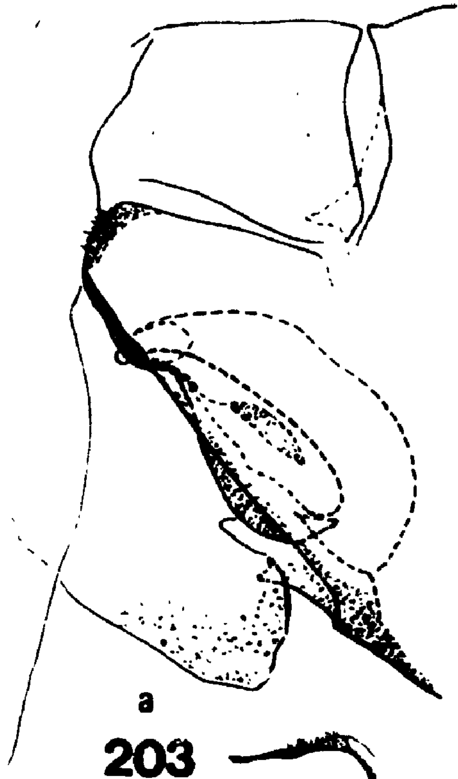

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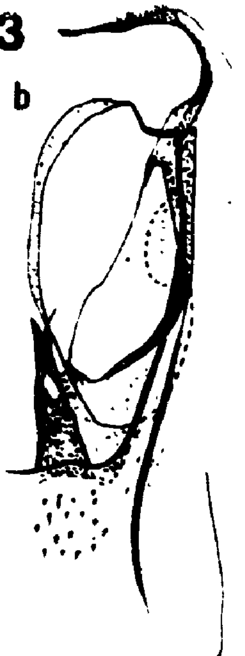

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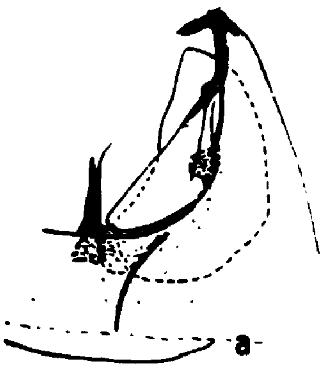

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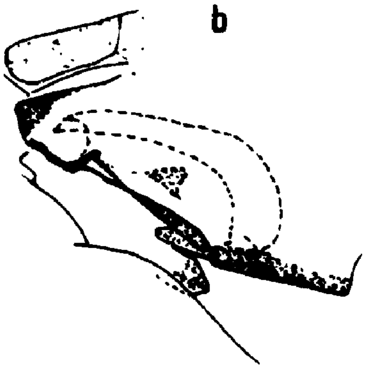

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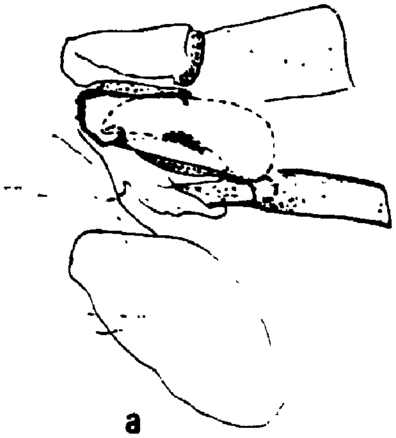

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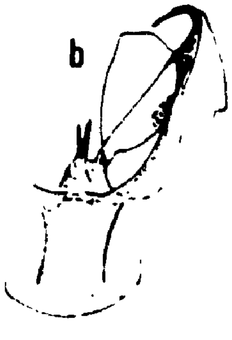

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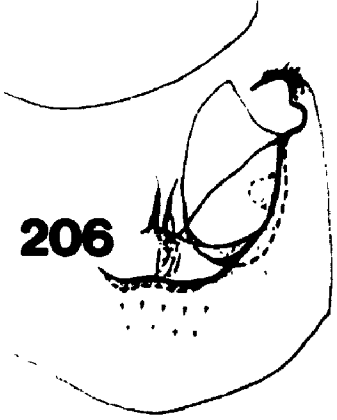
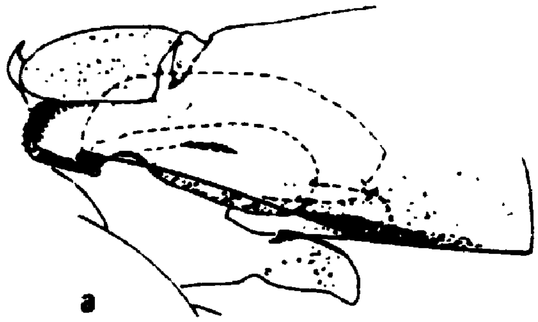


206

Figs. 207-212. Tympanal organs of Crambinae. 207, *Catoptria latiradiella* (Walker): a) lateral view, b) ventral view; 208, *Catoptria trichostoma* (Christoph), ventral view; 209, *Parapediasia hulstella* (Fernald), ventral view; 210, *Parapediasia teterrella* (Zincken): a) lateral view, b) ventral view; 211, *Arequipa turbatella* Walker: a) ventral view, b) lateral view; 212, *Pediasia trisecta* (Walker), ventral view.



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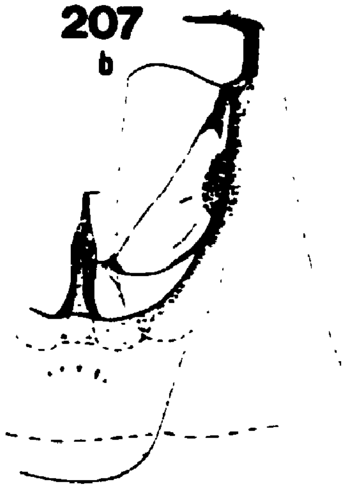

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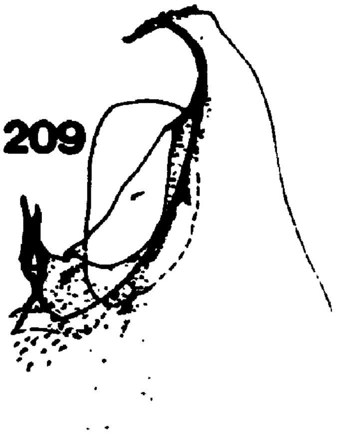

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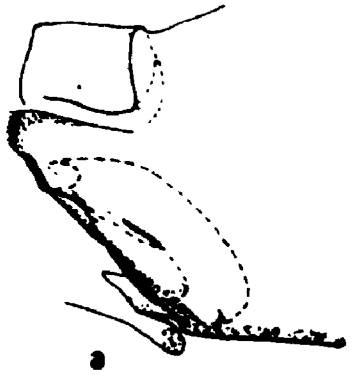

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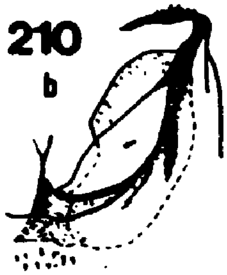

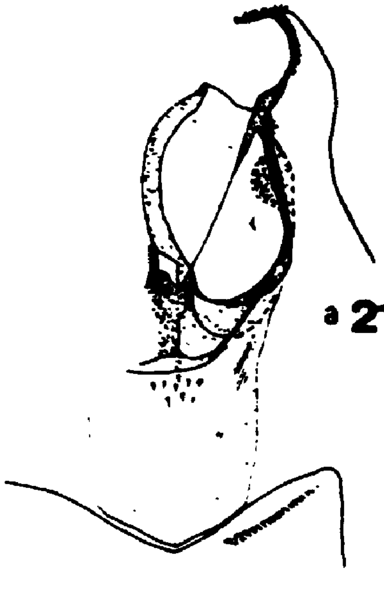

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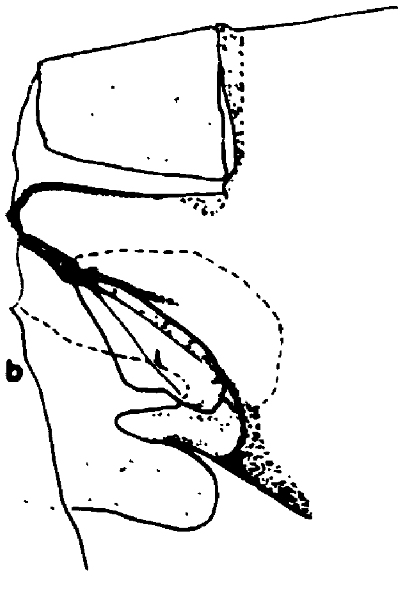
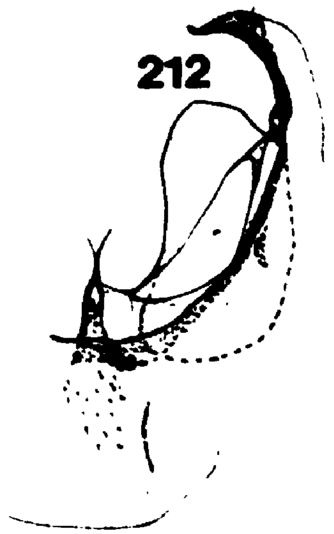
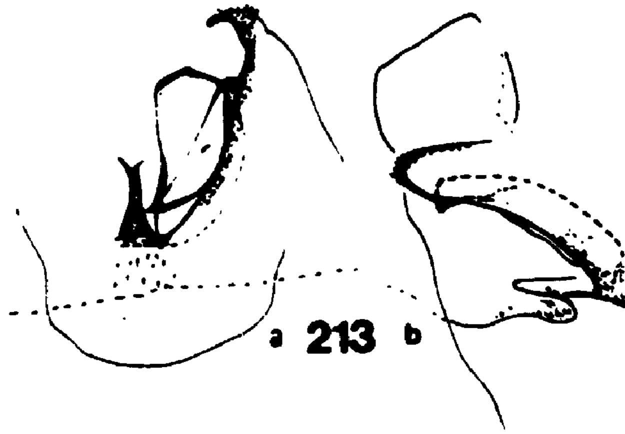




212

Figs. 213-217. Tympanal organs of Crambinae. 213, *Almita portalia* n. sp.: a) ventral view, b) lateral view; 214, *Almita texana* n. sp., ventral view; 215, *Loxocrambus canellus* Forbes: a) lateral view, b) ventral view; 216, *Loxocrambus coloradellus* (Fernald), a) lateral view, b) ventral view; 217, *La cerveza* n. sp., ventral view.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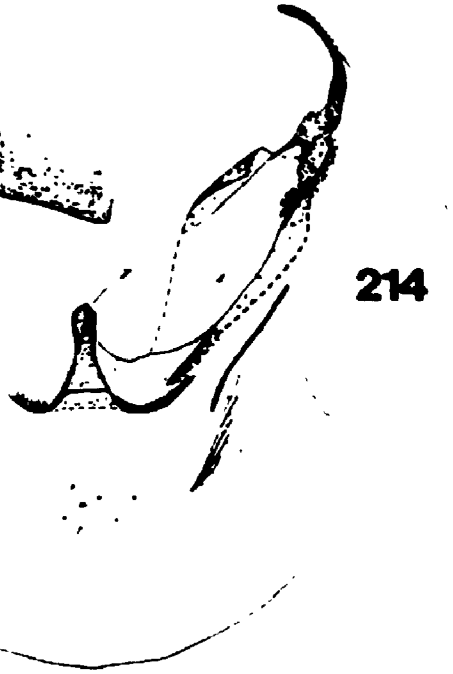
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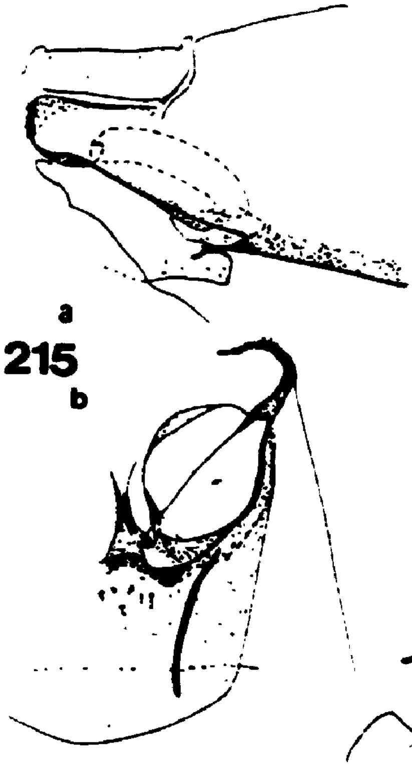
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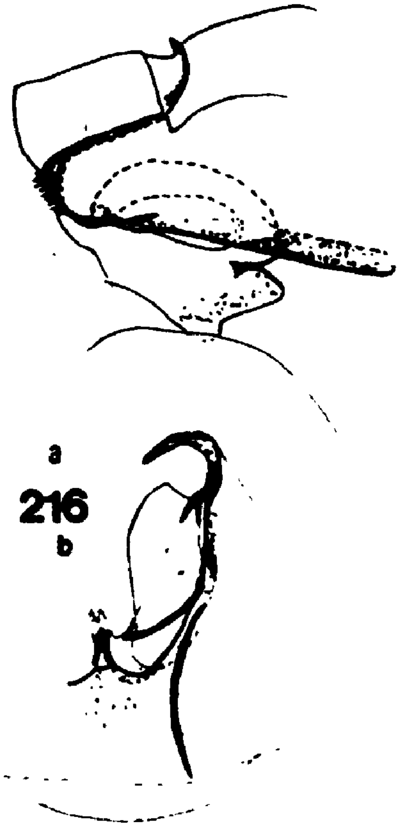
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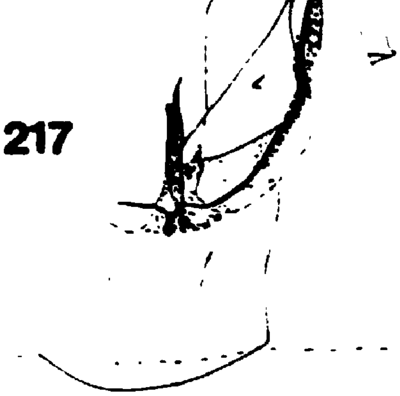
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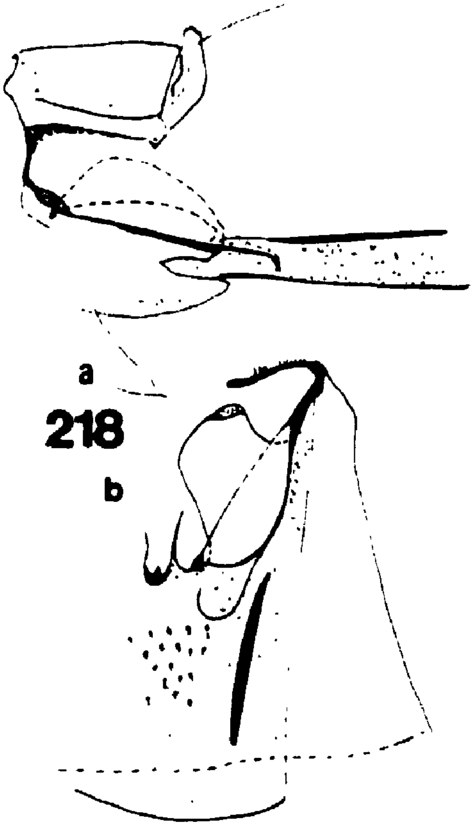
Figs. 218-221. Tympanal organs of Crambinae: a) lateral views, b) ventral views. 218, _Thaumatopsis pectinifer_ (Zeller); 219, _T. bolterella_ (Fernald), ventral view; 220, _Tehama bonifatella_ (Hulst); 221, "_Crambus_" _dimidiatellus_ Grote.



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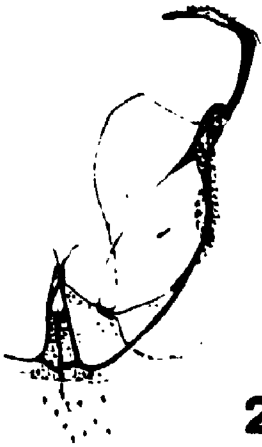

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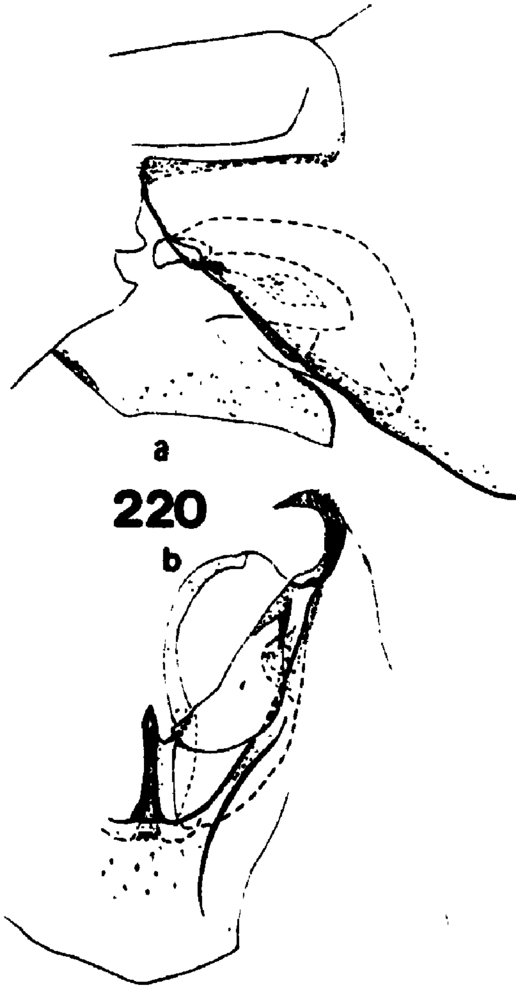

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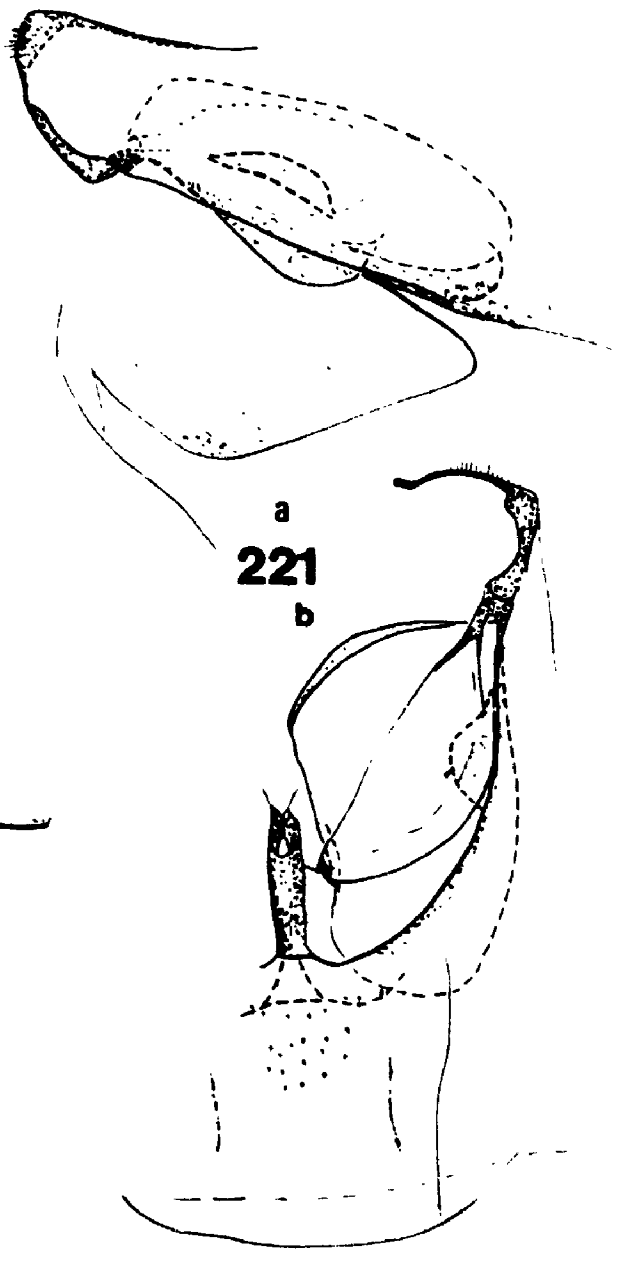

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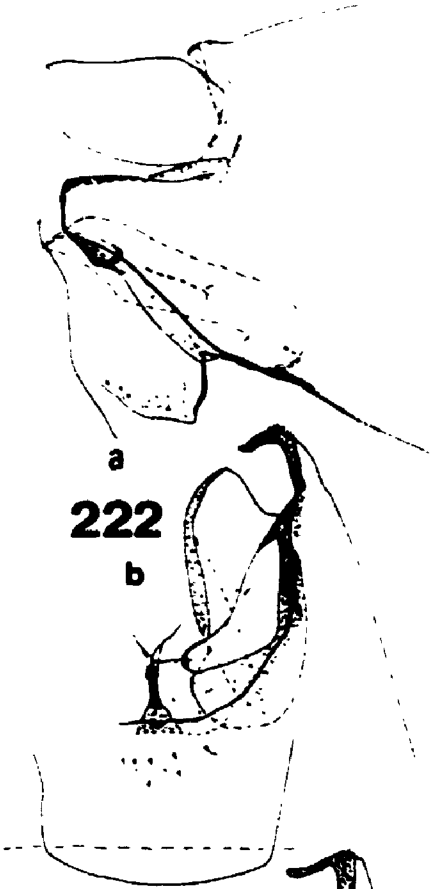
Figs. 222-225. Tympanal organs of Crambinae. 222, *Agriphila ruricolella* (Zeller): a) lateral view, b) ventral view; 223, *Crambus pascuellus* (L.); a) lateral view of male, b) ventral view of female, c) ventral view of male; 224, *Fernandocrambus harpipterus* (Dyar): a) ventral view, b) lateral view; 225, unusual specimen of *Loxocrambus* sp. without tympanal organs, ventral view.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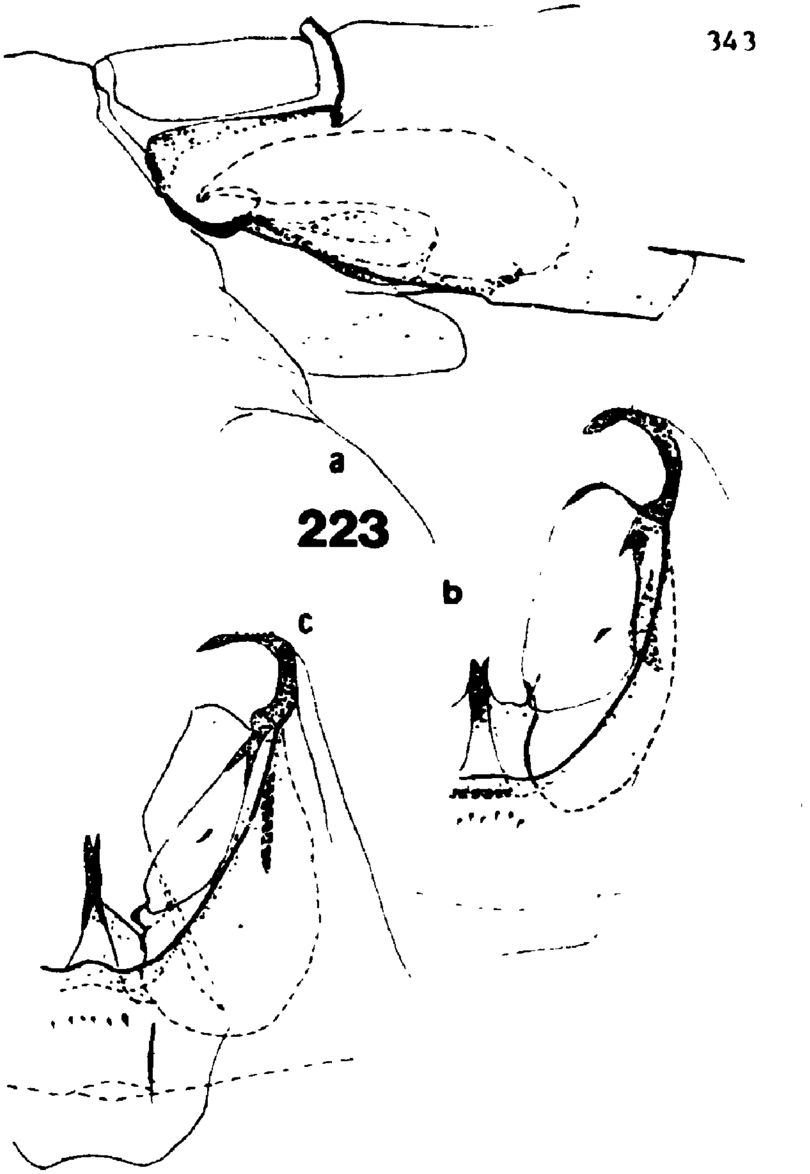
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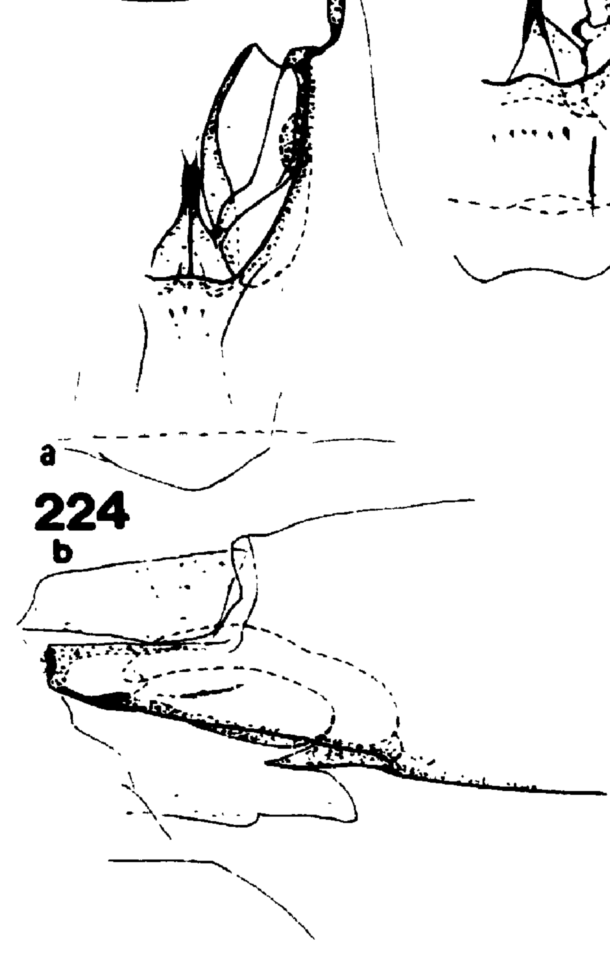
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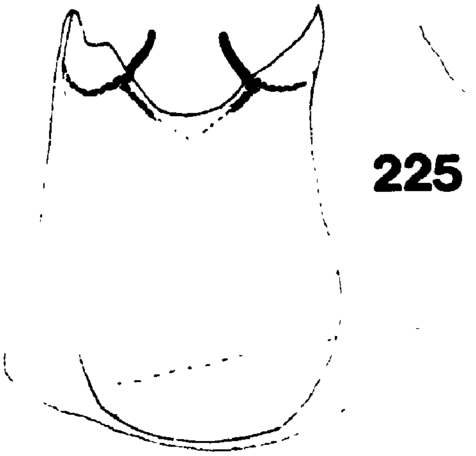
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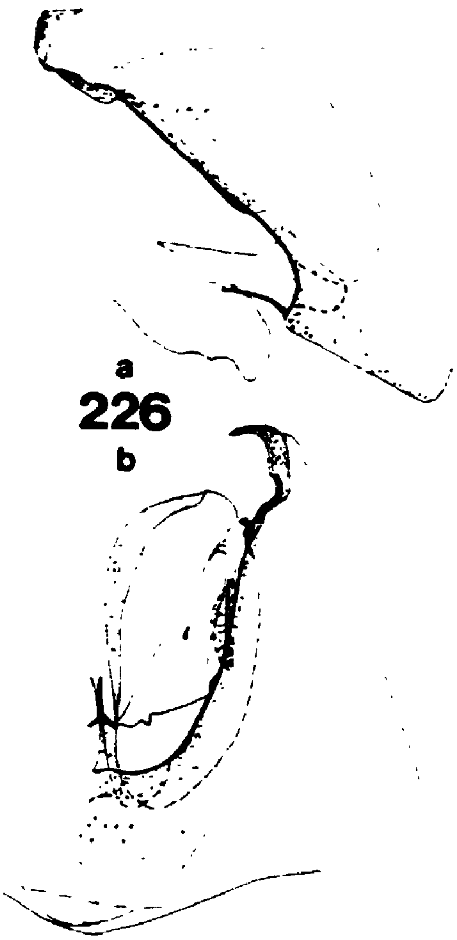
Figs. 226-229. Tympanal organs of Crambinae. 226, _Chrysoteuchia topiaria_ (Zeller): a) lateral view, b) ventral view; 227, _Fissicrambus minuellus_ (Walker): a) lateral view, b) ventral view; 228, _F. fissiradiellus_ (Walker), ventral view; 229, _F. albilineellus_ (Fernald): a) ventral view, b) lateral view.



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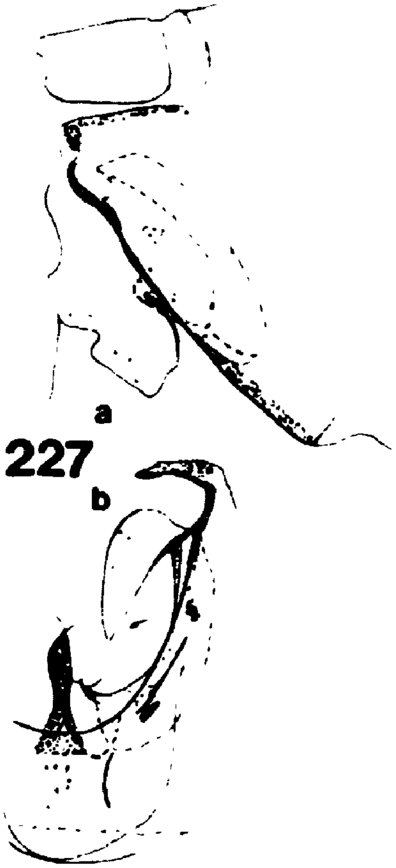

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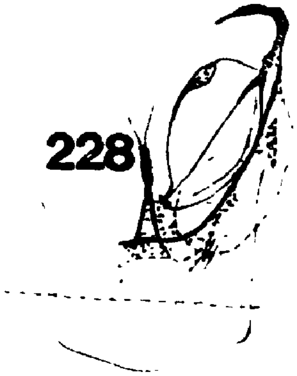

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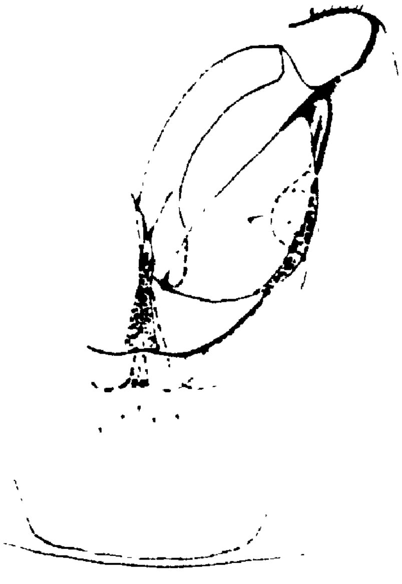
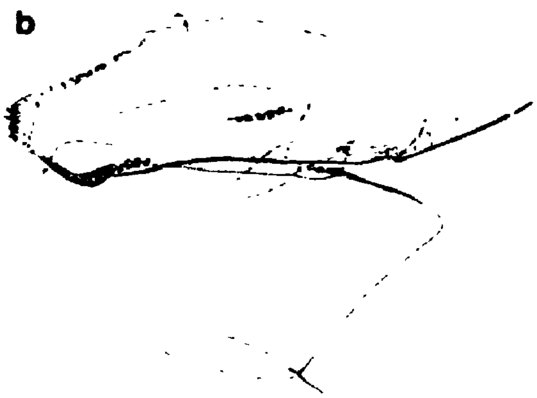
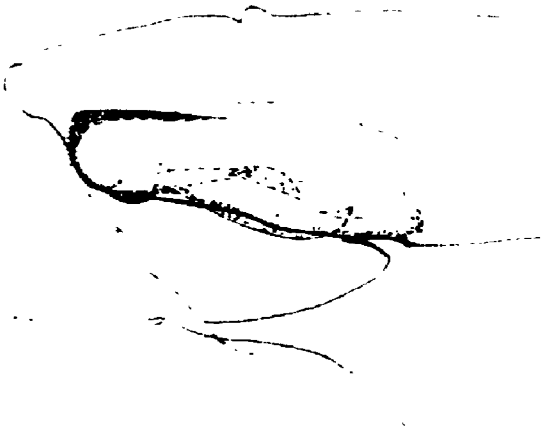




a 229 b

Figs. 230-232. Tympanal organs of Crambinae: a) lateral views, b) ventral views. 230, *Neodactria luteolella* (Clemens); 231, *Microcrambus elegans* (Clemens); 232, *Raphiptera argillaceella* (Packard).



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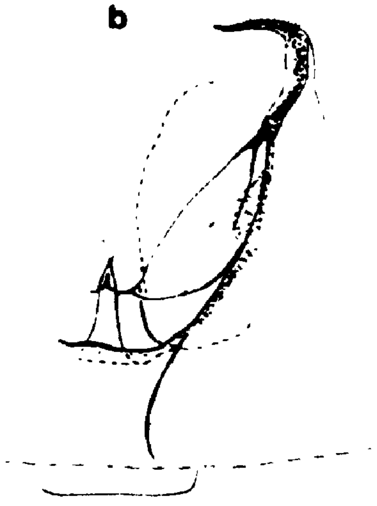

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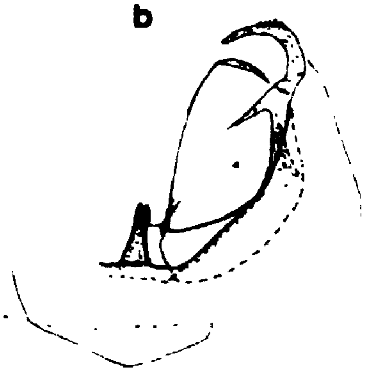
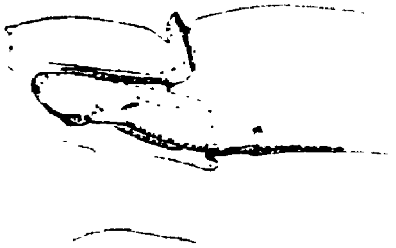
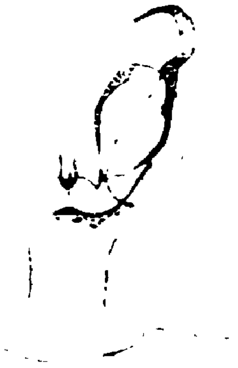


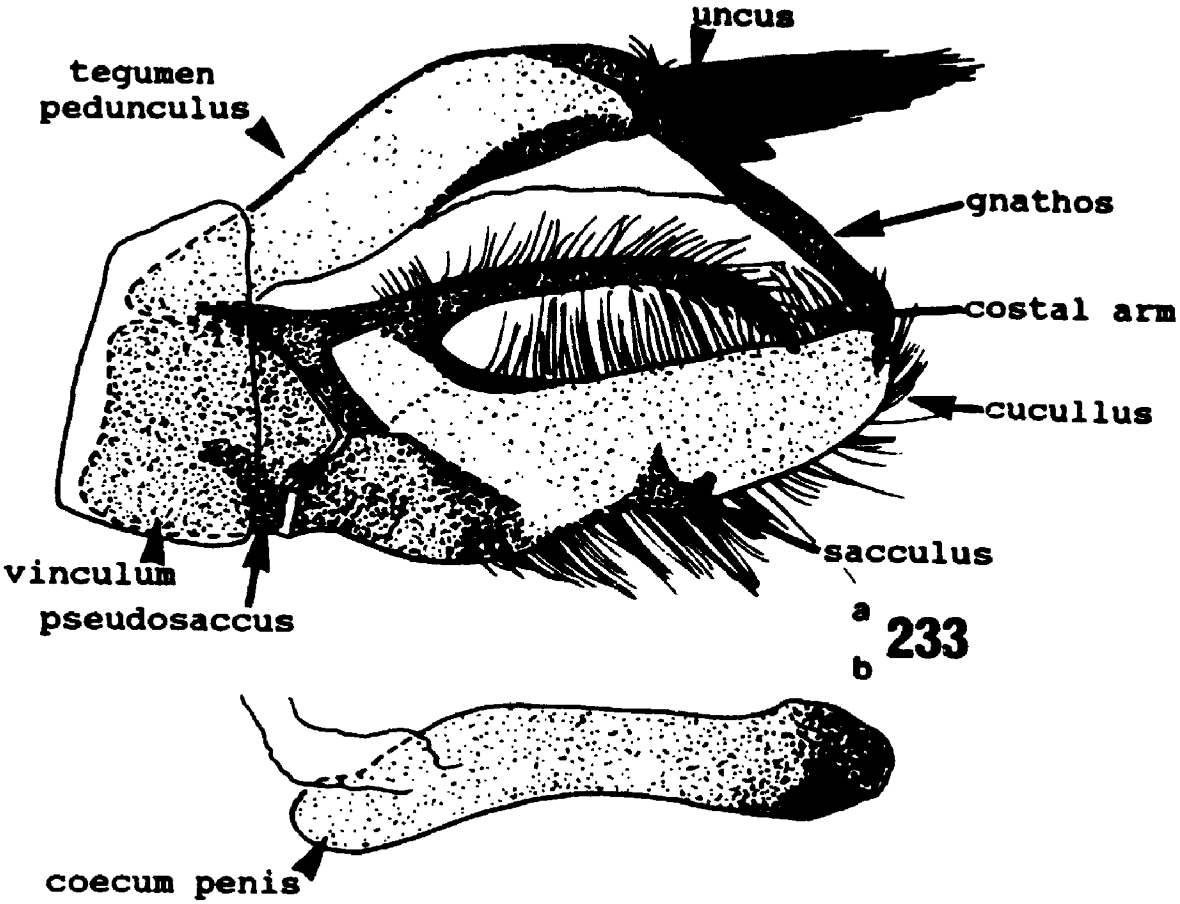


a **232** b

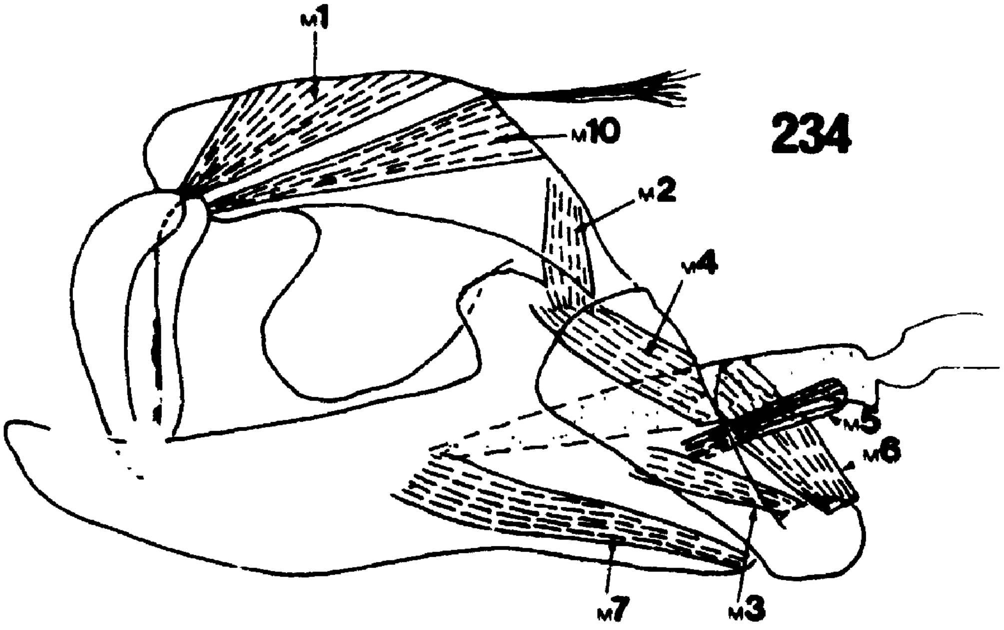


Figs. 233-234. Male genitalia of Crambinae. 233 a-b, *Crambus pascuellus* (L.); 234, *Diatraea saccharalis* (F.) showing musculature. M1-depressor of uncus, M2-tergal extensor of valva, M3-sternal extensor of valva, M4-tergal flexor of valva, M5-protractor of aedeagus, M6-retractor of aedeagus, M7-intravalvular muscle, M10-depressor of gnathos.

Note on the figures of the male genitalia. A few figures are taken from the literature (figs. 249, 254, 265). Eighteen are mine (figs. 233, 234, 236-239, 244, 245, 248, 250-253, 262, 267, 278, 280, 284, 287, 288). These are in most cases lateral views with the aedaegus removed or not, except for fig. 248 which shows the tegumen still attached to the vinculum and only the left valva. The other figures were made by M. Friedman for Dr. A.B. Klots and were courteously lent to me by Dr. F.H. Rindge, American Museum of Natural History, New York. These drawings are lateral views with the proximal valva and the aedeagus removed (e.g. fig. 235), or dorsal views of the vinculum+valvae with the aedeagus and the tegumen+uncus+gnathos detached and shown in lateral view (e.g. fig. 240). They were verified with mounted specimens and modified if necessary.

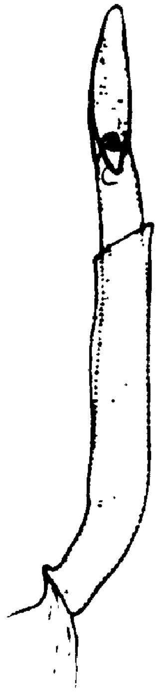

uncus
tegumen
peduncululus
gnathos
costal arm
cucullus
sacculus
vinculum
pseudosaccus
a
b
coecum penis

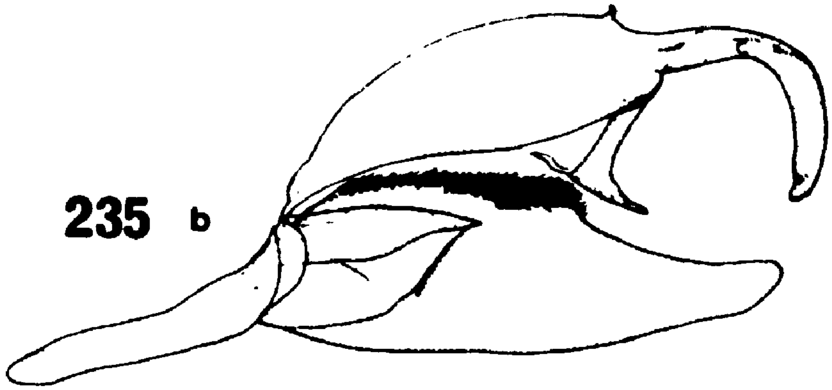
233


м1
м10
м2
м4
м5
м6
м7
м3

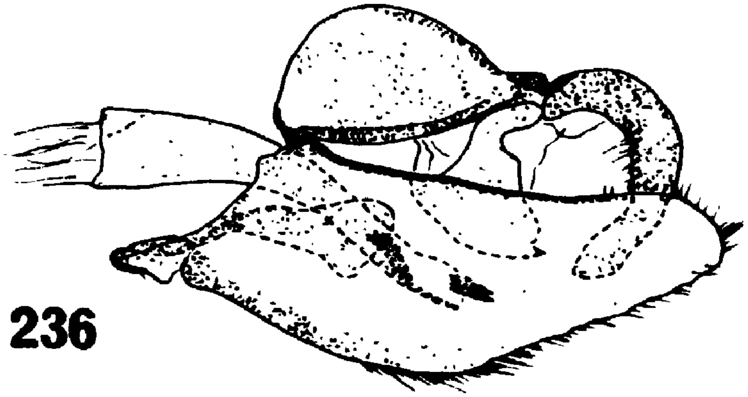
234

Figs. 235-237. Male genitalia of Crambinae. 235 a-b, _Hemiplatytes prosenes_ (Dyar); 236, _Eufernaldia cadarella_ (Druce); 237 a-b, _Surattha indentella_ Kearfott.





a **235** b



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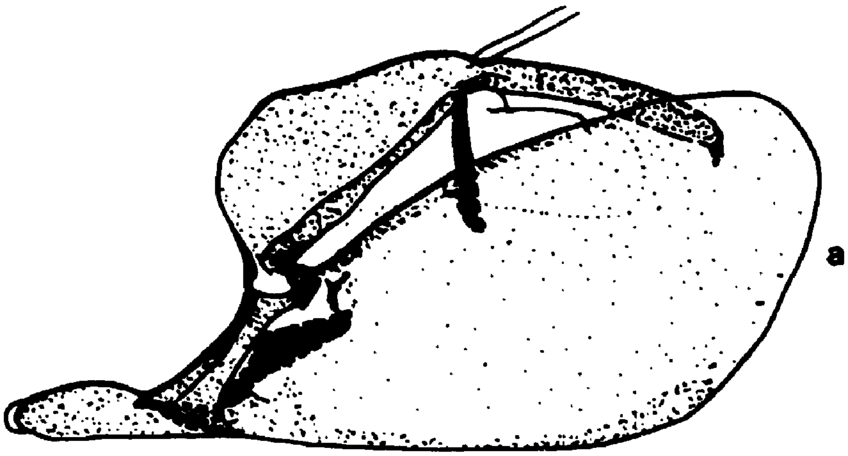
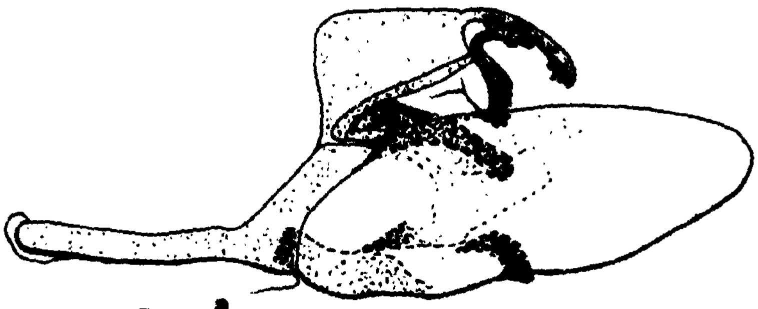


a **237** b

Figs. 238-240. Male genitalia of Crambinae. 238 a-b, *Prionapteryx serpentella* Kearfott; 239, *Pseudoschoenobius opalescalis* (Hulst); 240 a-c, *Occidentalia comptulatalis* (Hulst).



238 a

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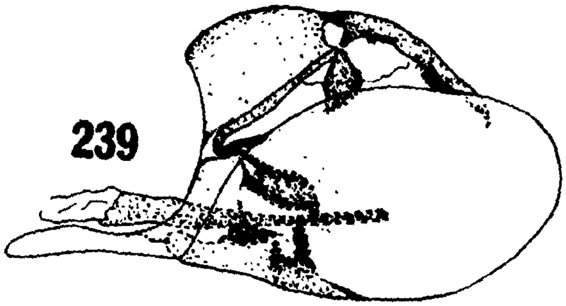
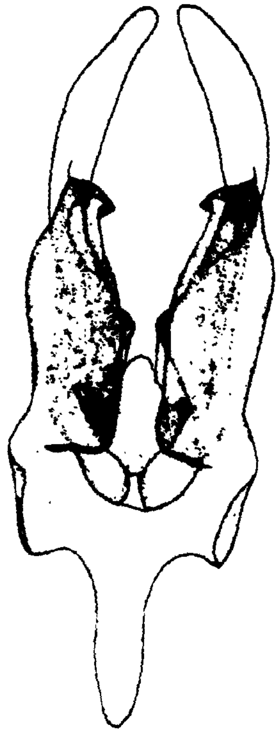
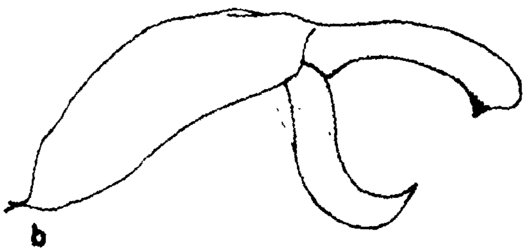




a **240**



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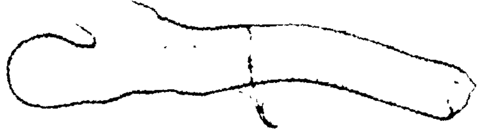
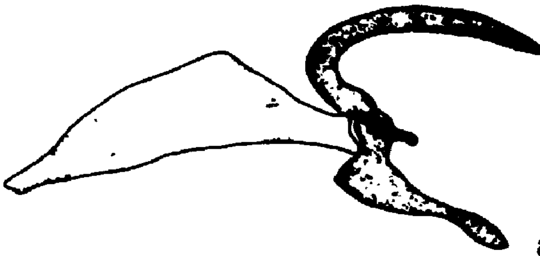


Figs. 241-243. Male genitalia of Crambinae. 241 a-c, *Thopeutis forbesellus* (Fernald); 242 a-c, *Xubida panalope* (Dyar); 243 a-c, *Eoreuma densella* (Zeller).



a

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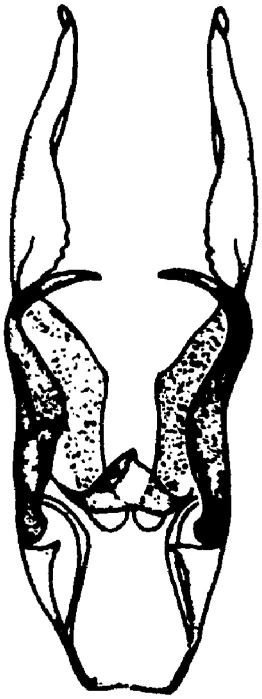
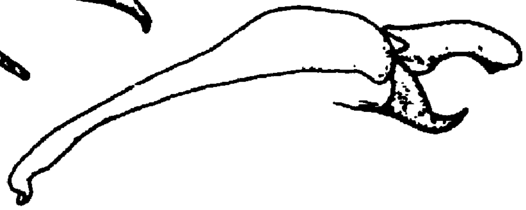
b



c

a



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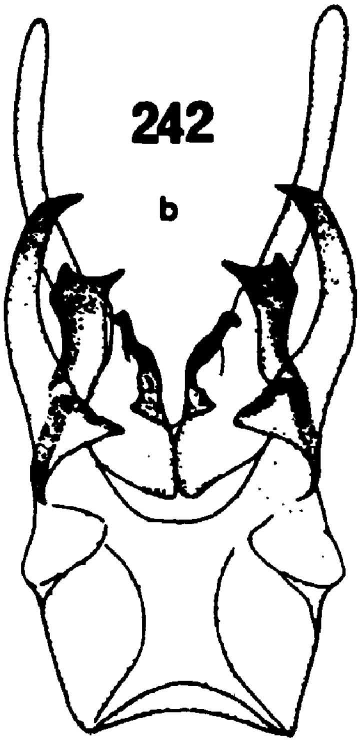
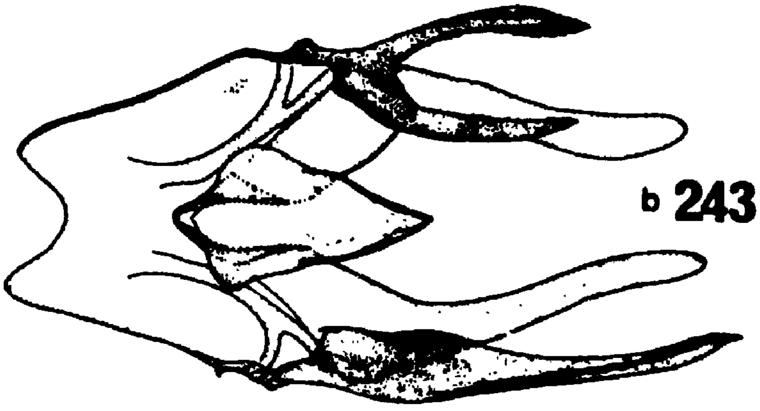
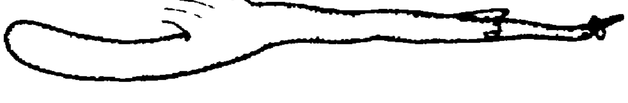




b 243

c



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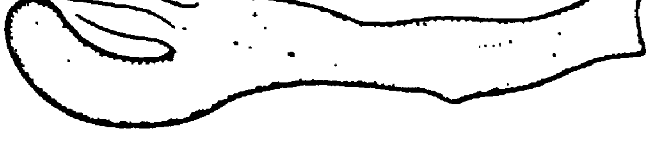

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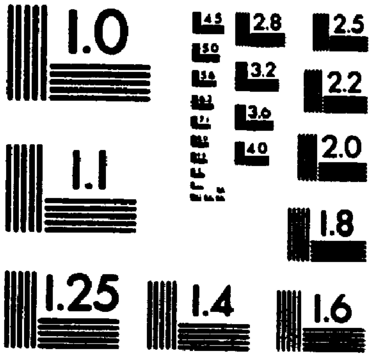
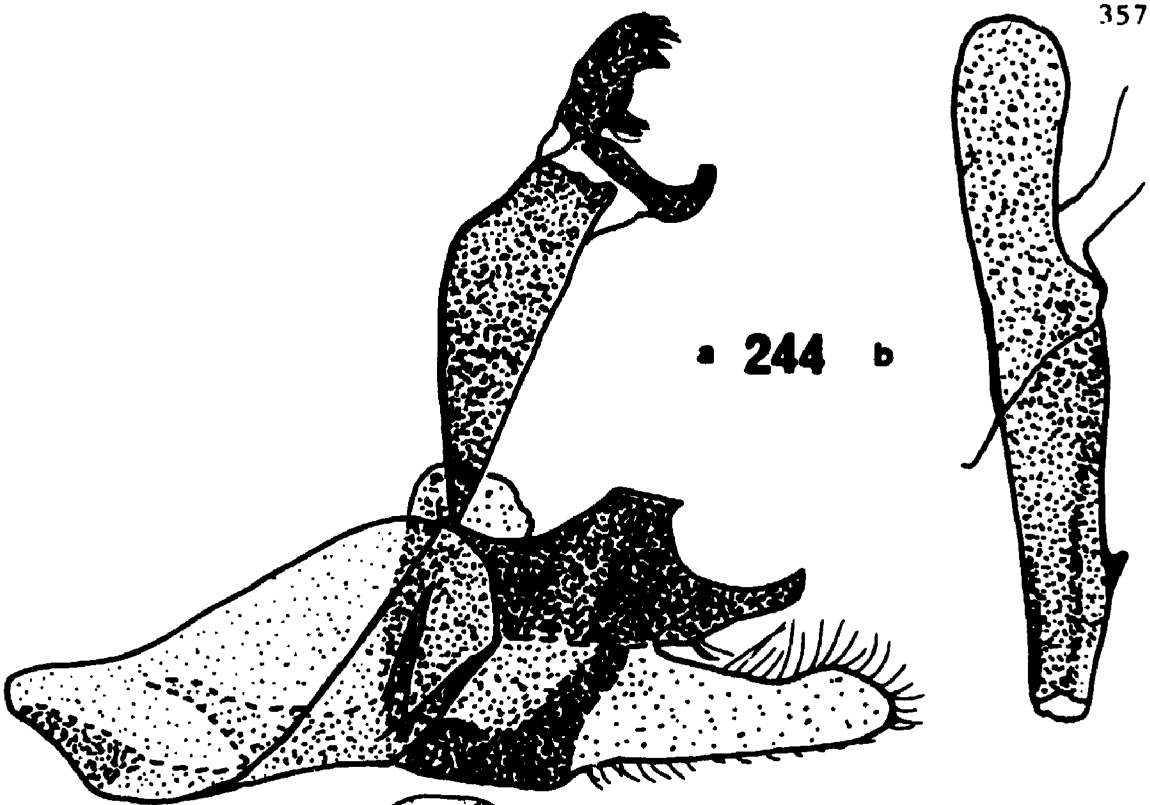


Figs. 244-246. Male genitalia of Crambinae. 244 a-b, *Haimbachia floridalis* Capps; 245, *Myelobia* sp.; 246 a-c, *Diatraea evanescens* Dyar.



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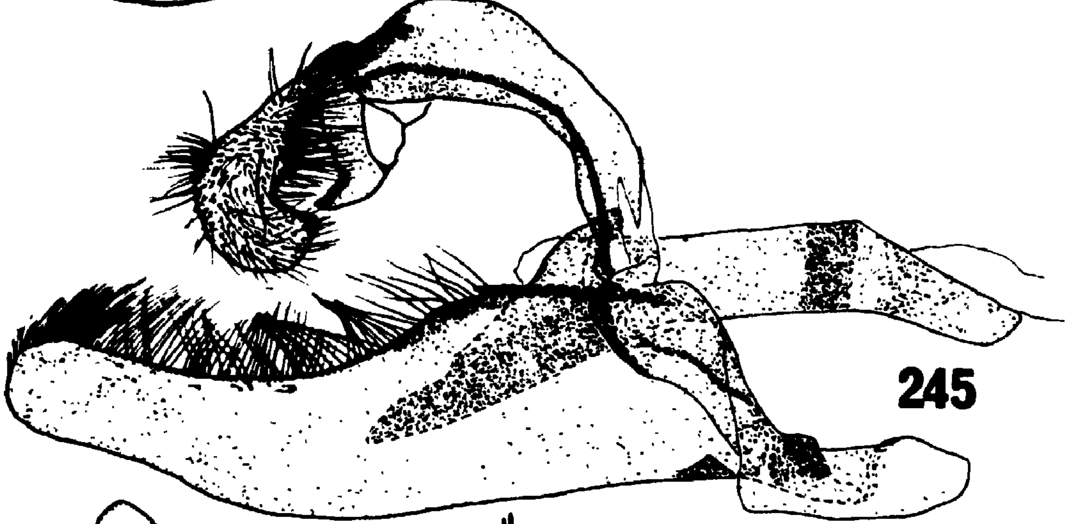

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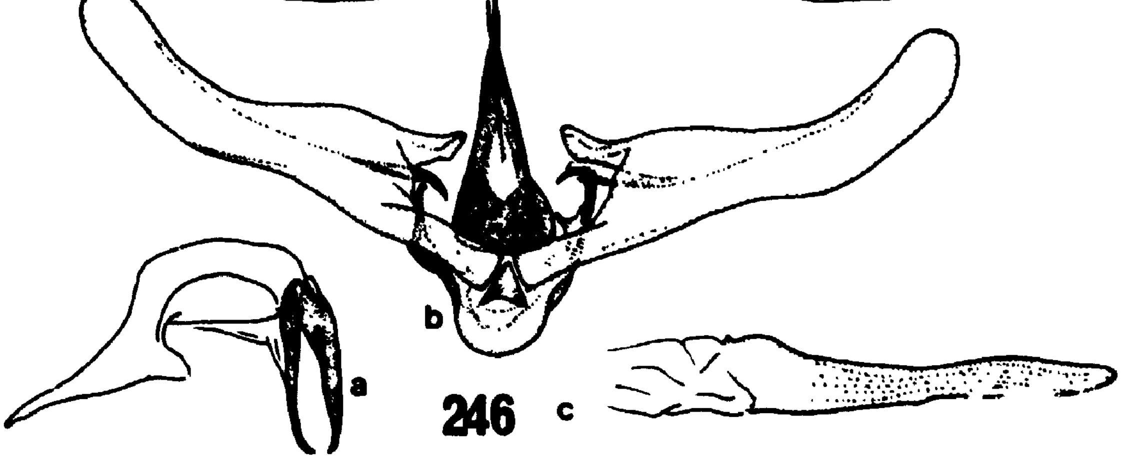

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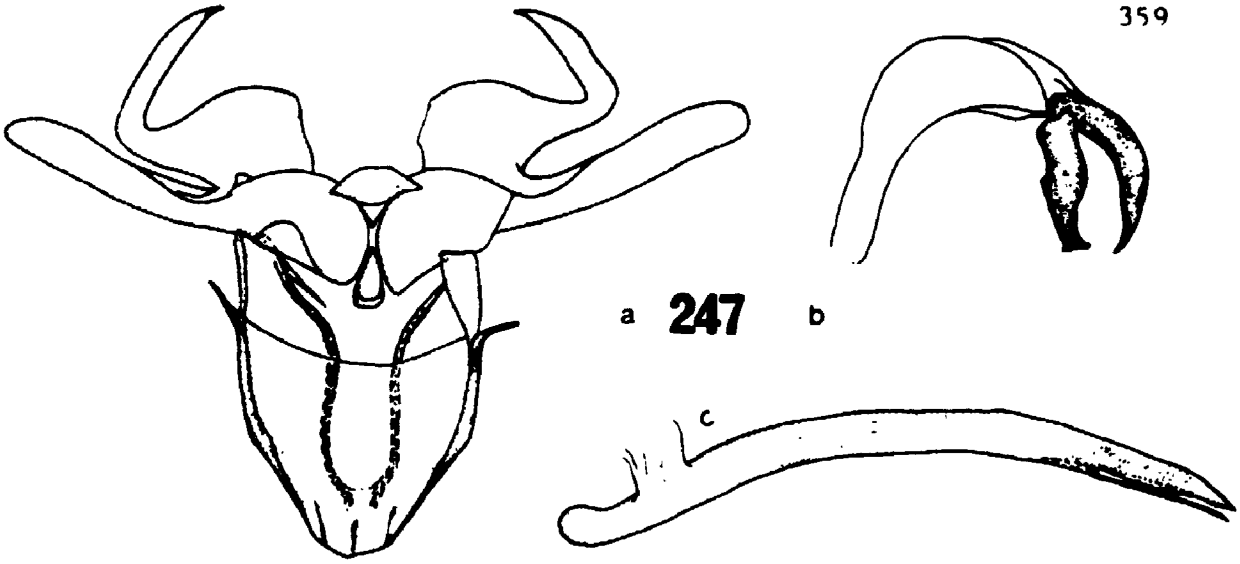
Figs. 247-249. Male genitalia of Crambinae. 247 a-c, *Epina alleni* (Fernald); 248 a-b, *Microcausta flavipunctalis* Barnes & McDunnough; 249 (from Gaskin 1986), *Diptychophora harlequinalis* (Barnes & McDunnough).



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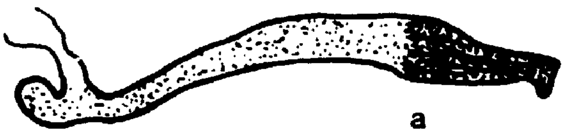

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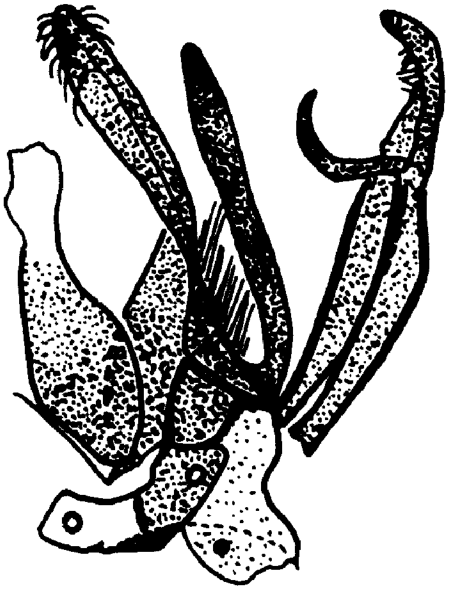

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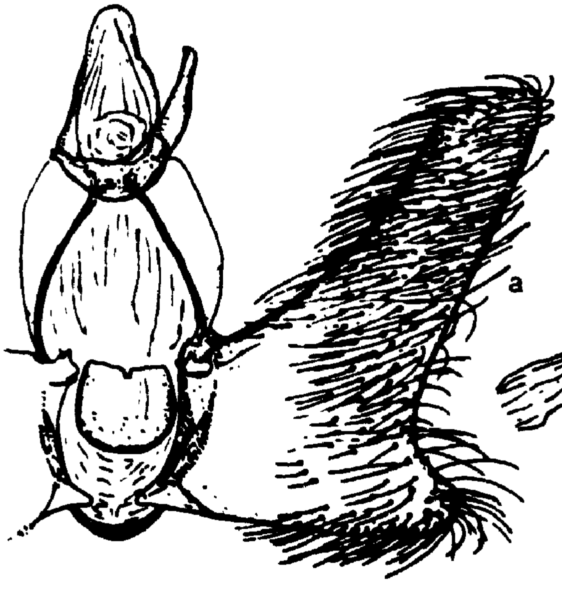

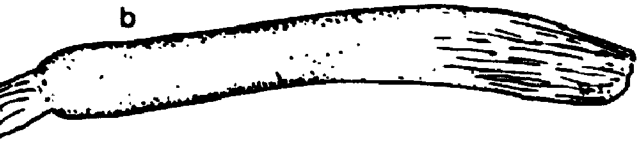

Figs. 250-252. Male genitalia of Crambinae. 250, *Urola nivalis* (Drury); 251, *Argyria nummulalis* Hübner; 252 a-b, *Vaxi auratella* (Clemens).

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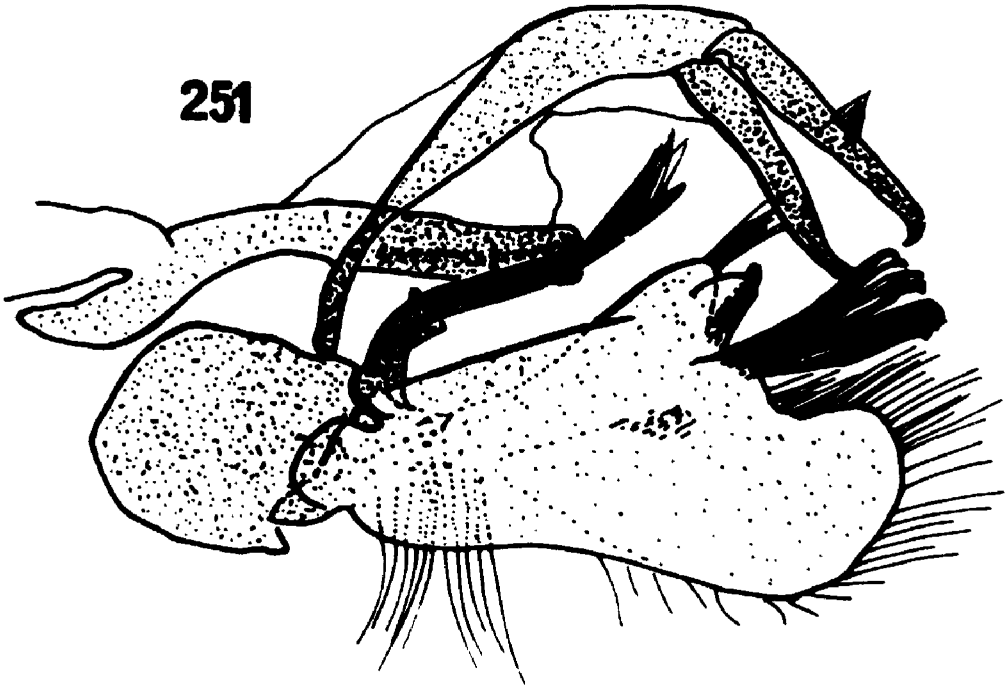
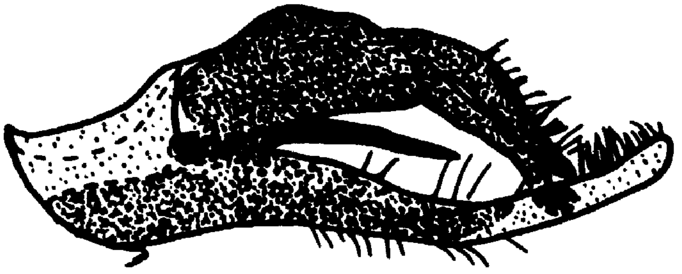
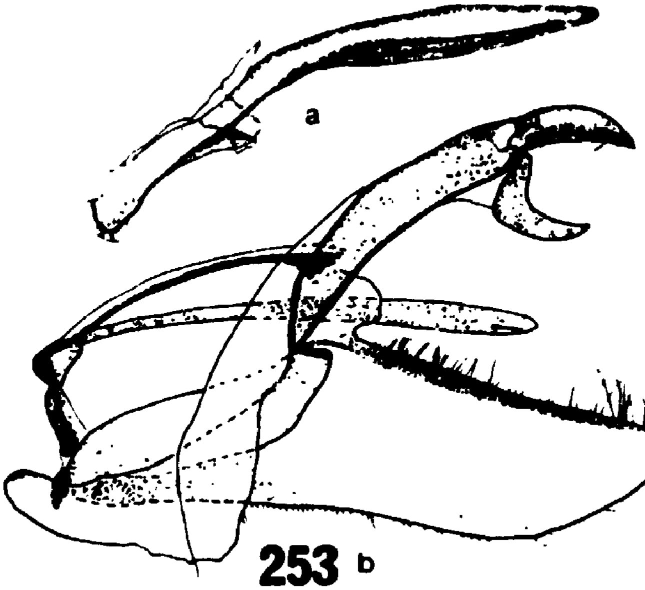
251





a **252** b

Figs. 253-256. Male genitalia of Crambinae. 253 a-b, *Chilo phragmitellus* (Hübner); 254 a-b (from Bleszynski 1965), *Calamotropha paludella* (Hübner); 255 a-c, *Platytes vobisne* Dyar; 256 a-b, *Euchromius ocelleus* (Haworth).



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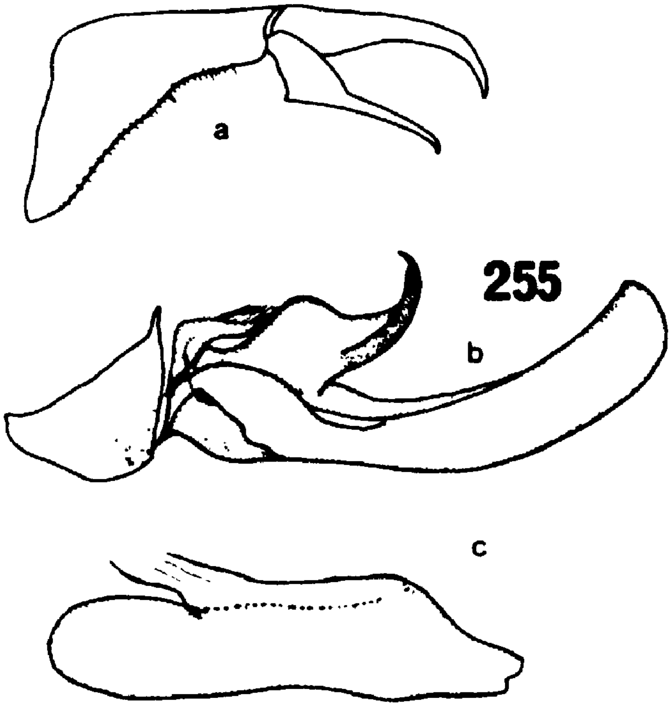

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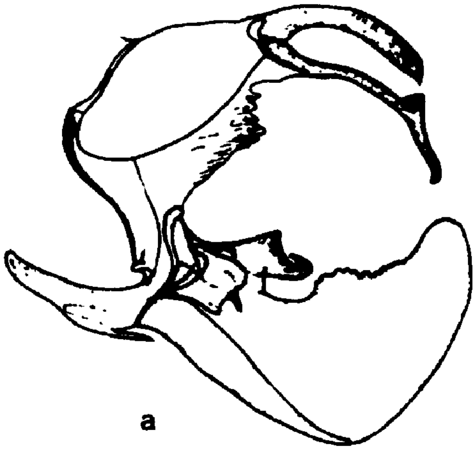

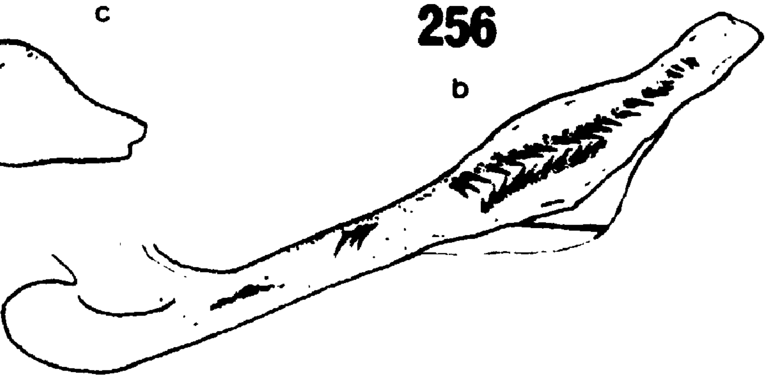

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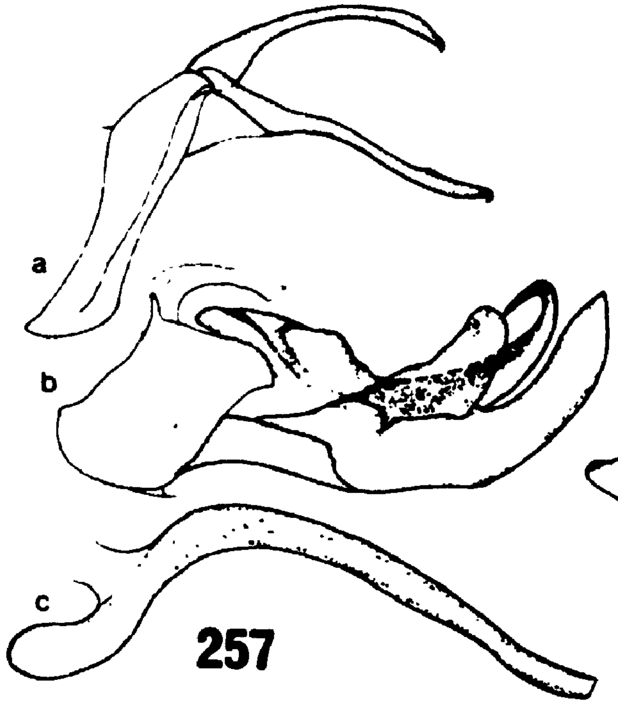
Figs. 257-260. Male genitalia of Crambinae. 257 a-c, *Catoptria latiradiella* (Walker); 258 a-b, *Catoptria trichostoma* (Christoph); 259 a-c, *Catoptria oregonica* (Grote); 260 a-b, *Catoptria maculalis* (Zetterstedt).



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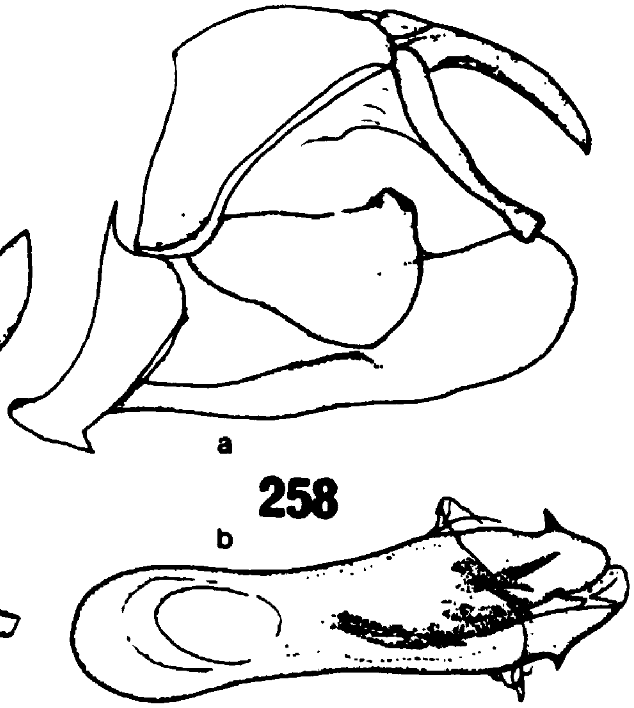

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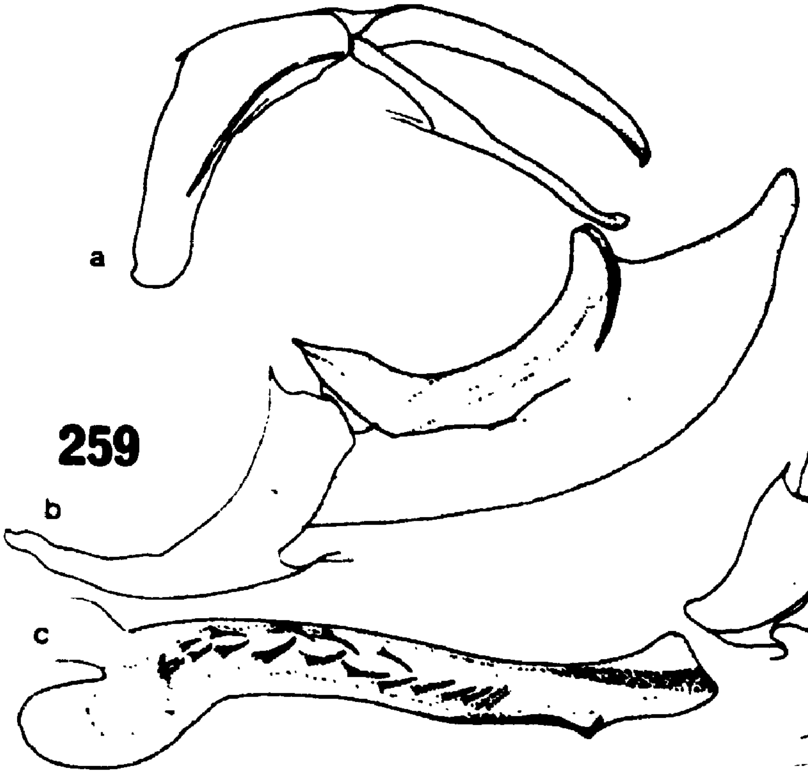

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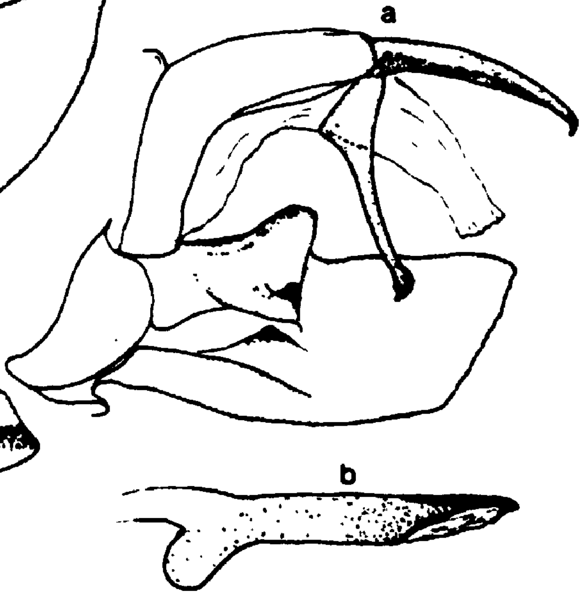
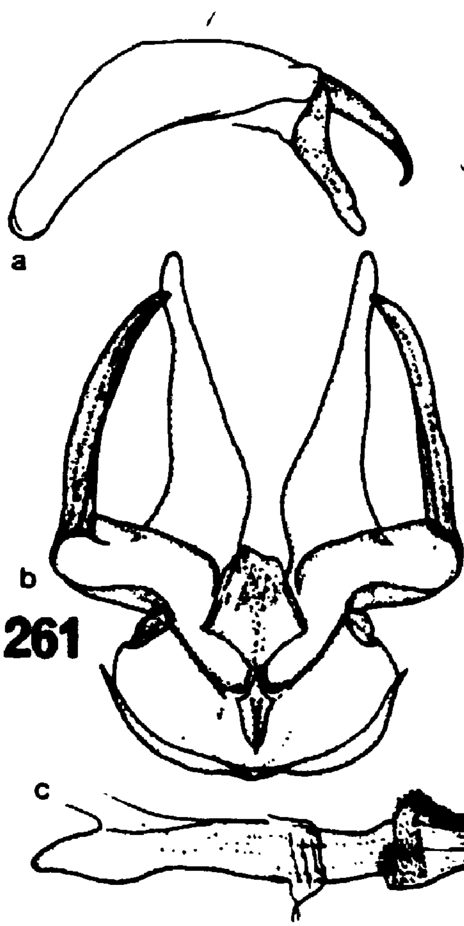


Figs. 261-264. Male genitalia of Crambinae. 261 a-c, *Thaumatopsis fernaldella* Kearfott; 262, *Thaumatopsis pexella* (Zeller); 263 a-c, *Thaumatopsis bolterella* (Fernald); 264 a-c, *Thaumatopsis pectinifer* (Zeller).



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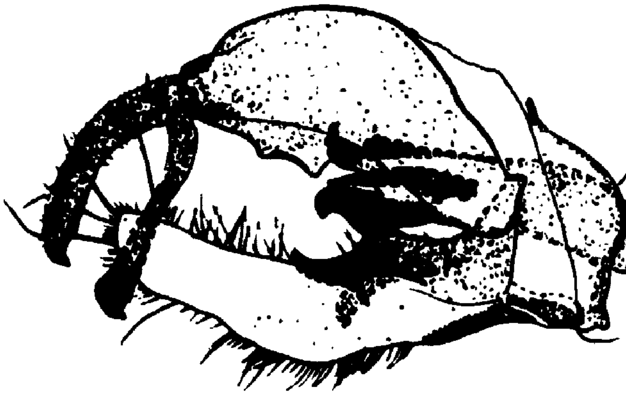

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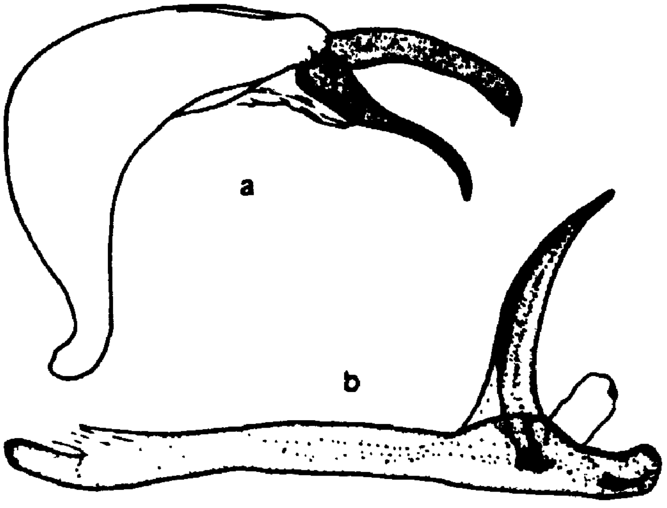

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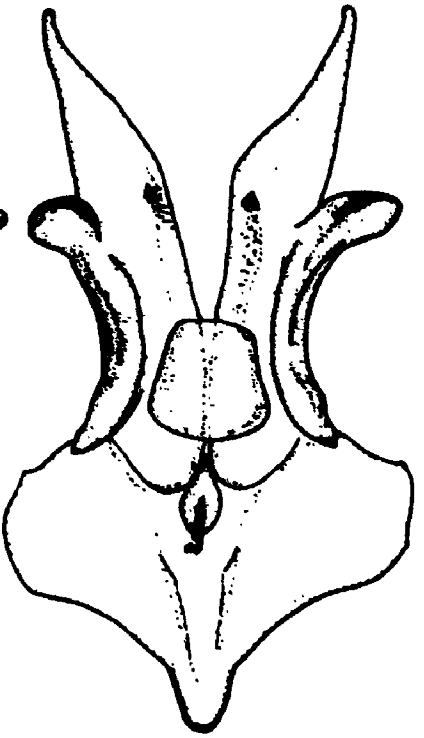

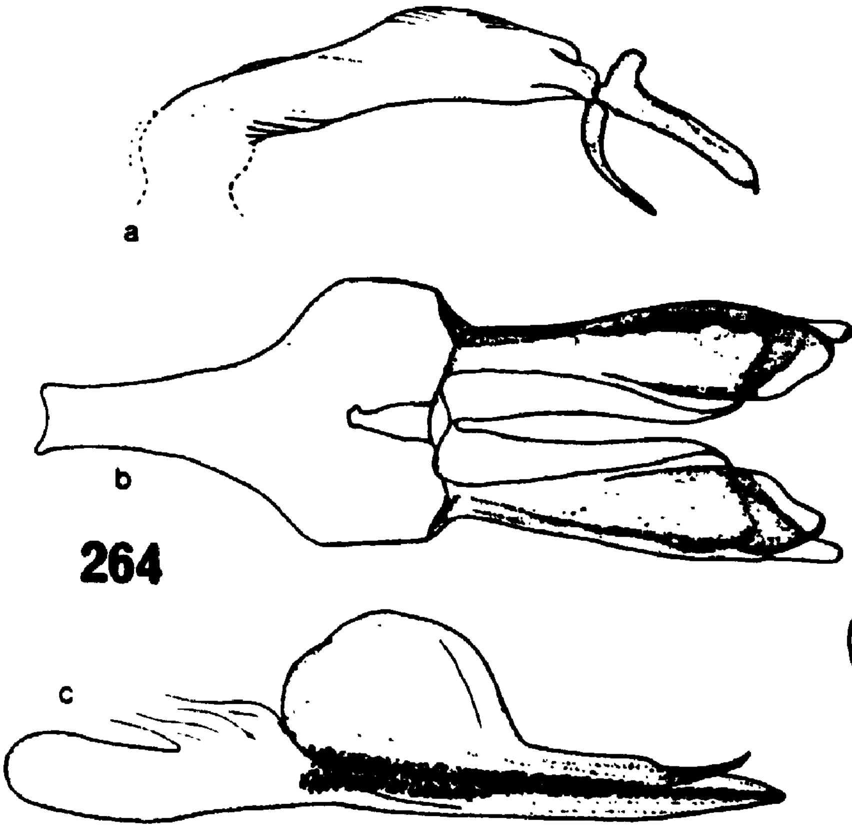

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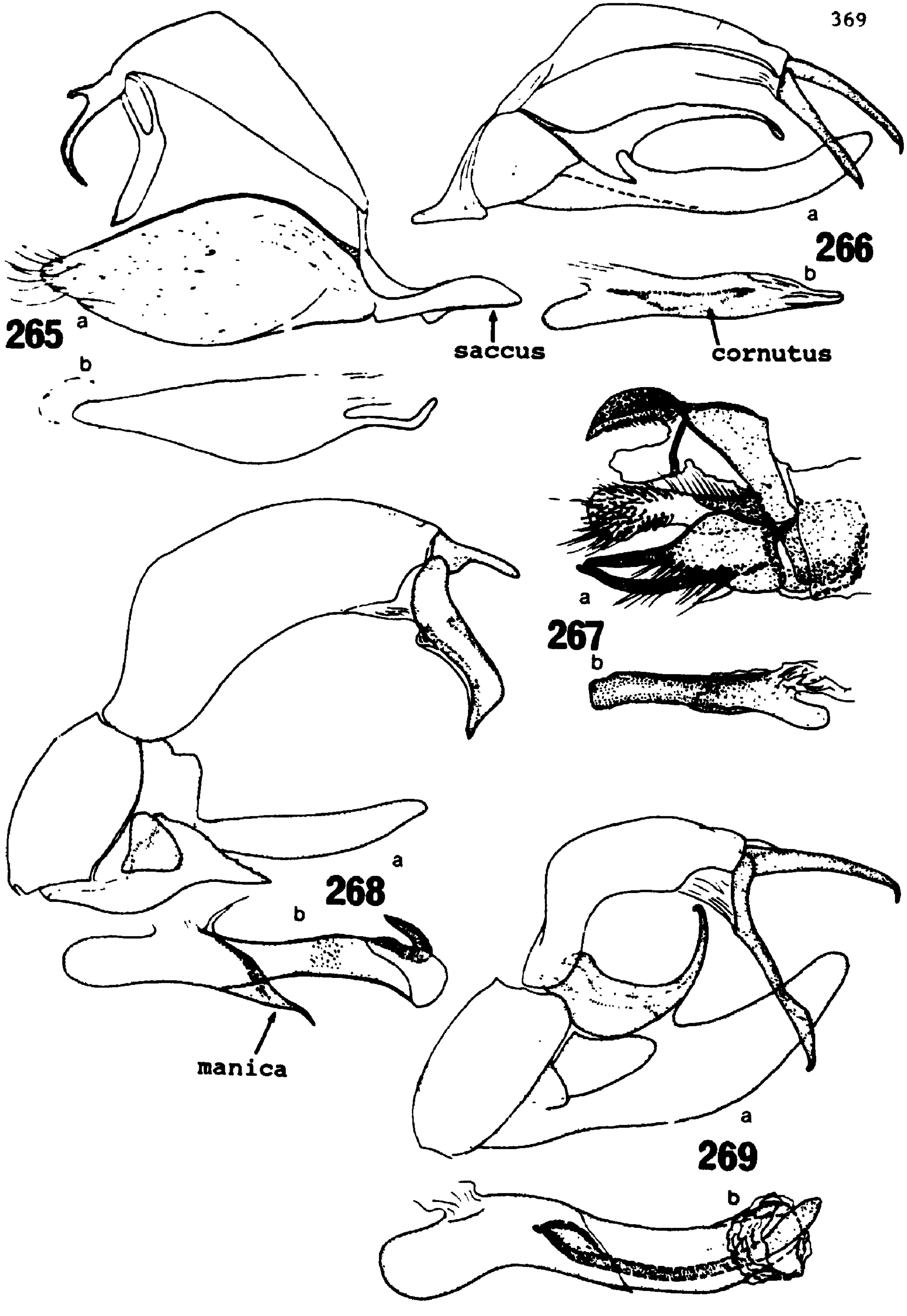
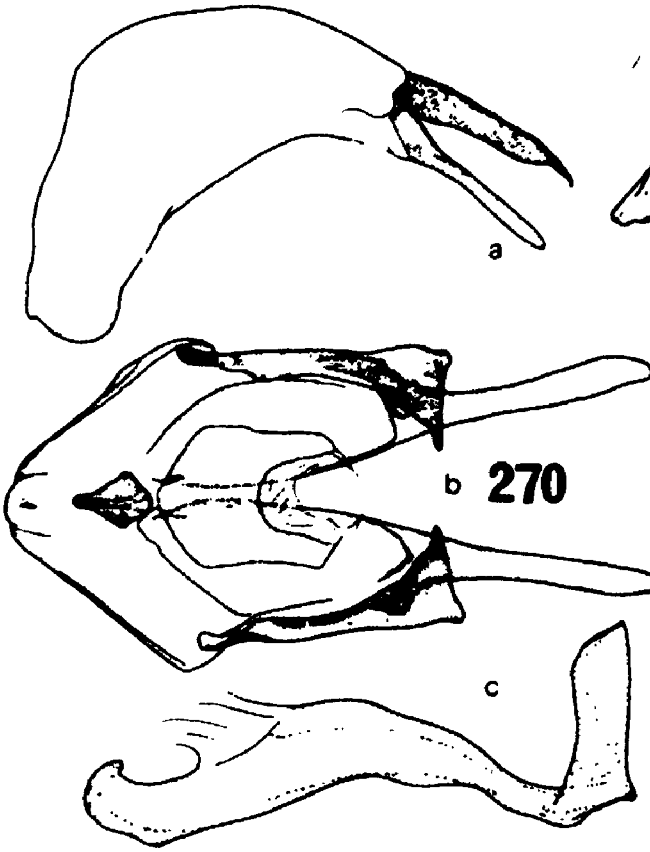
Figs. 265-269. Male genitalia of Crambinae. 265 a-b (from Bleszynski 1965), *Ancylolomia japonica* Zeller; 266 a-b, *Loxocrambus canellus* Forbes; 267 a-b, *Tehama bonifatella* (Hulst); 268 a-b, *Fissicrambus fissiradiellus* (Walker); 269 a-b, *Fissicrambus quadrinotellus* (Zeller).


a
266
b
265
a
saccus
cornutus
b
a
267
b
268
a
b
manica
a
269
b

Figs. 270-273. Male genitalia of Crambinae. 270 a-c, *Parapediasia teterrella* (Zincken); 271 a-c, *Parapediasia decorella* (Zincken); 272 a-c, *Parapediasia torquatella* n.sp.; 273 a-b, *Parapediasia hulstella* (Fernald).



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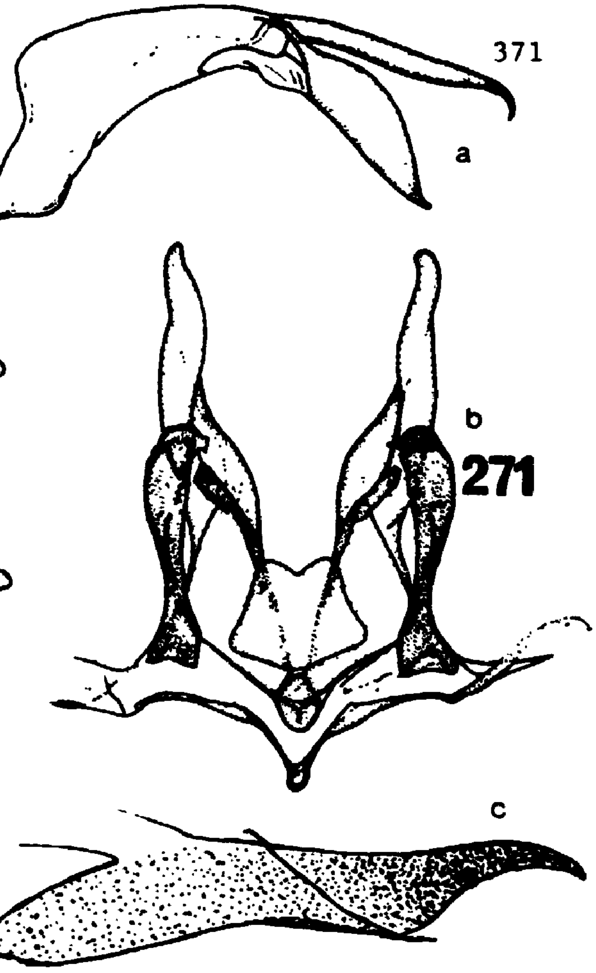

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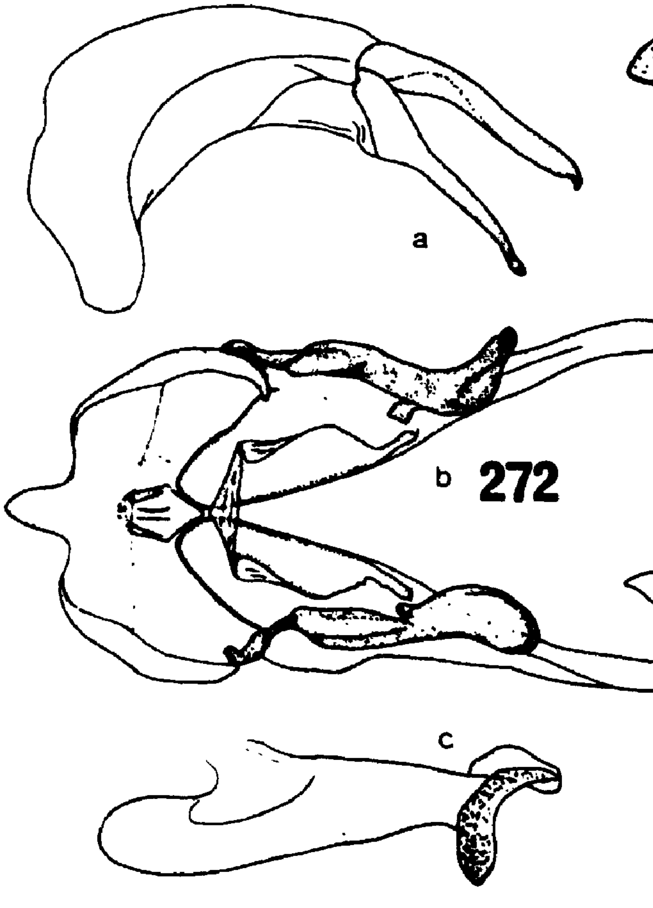

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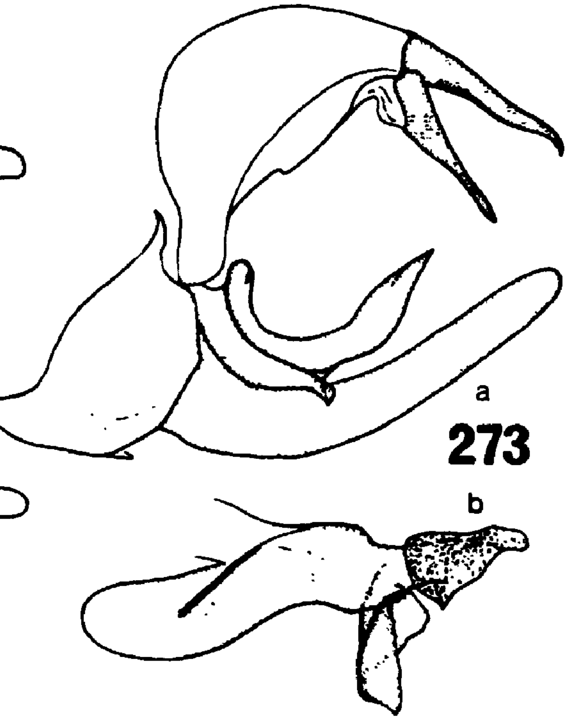

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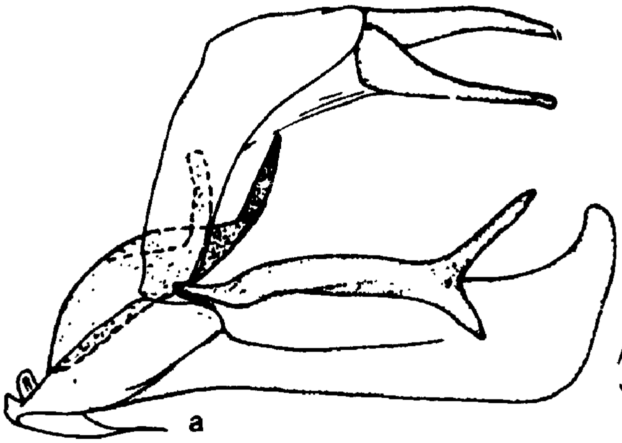
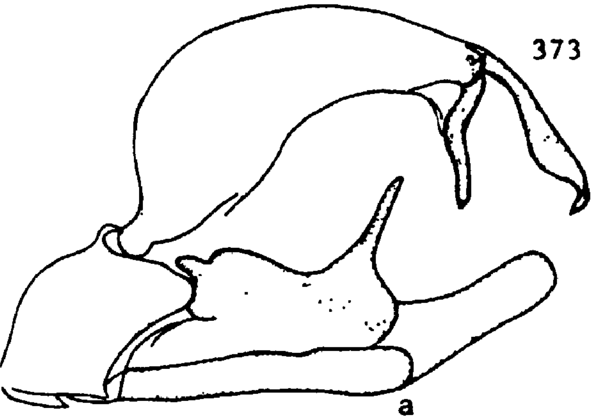
Figs. 274-277. Male genitalia of Crambinae. 274 a-b, *Microcrambus copelandi* Klots; 275 a-b, *Microcrambus elegans* (Clemens); 276 a-c, *Pediasia trisecta* (Walker); 277 a-c, "*Crambus*" *dimidiatellus* Grote.





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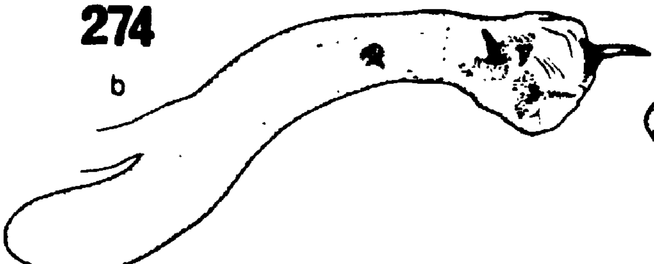

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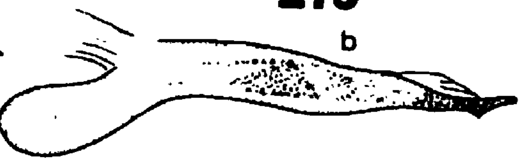

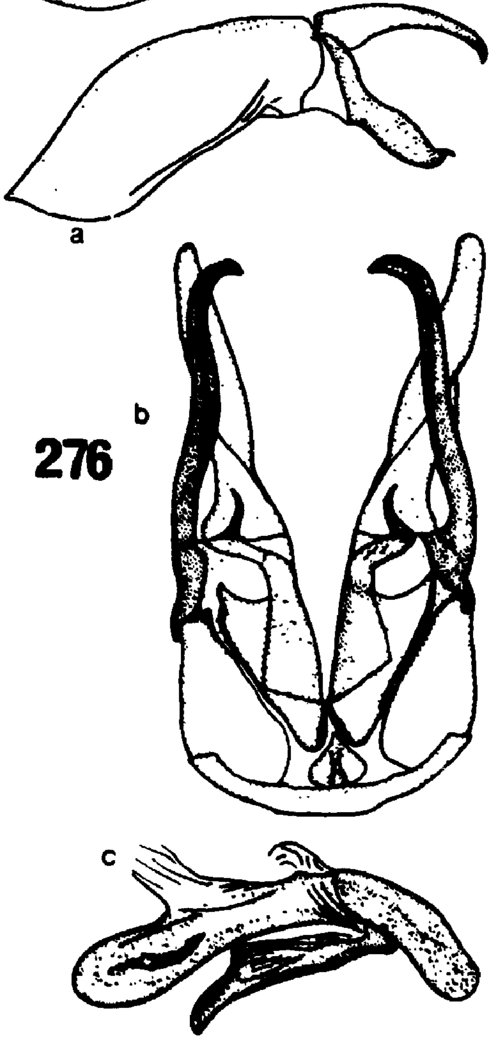

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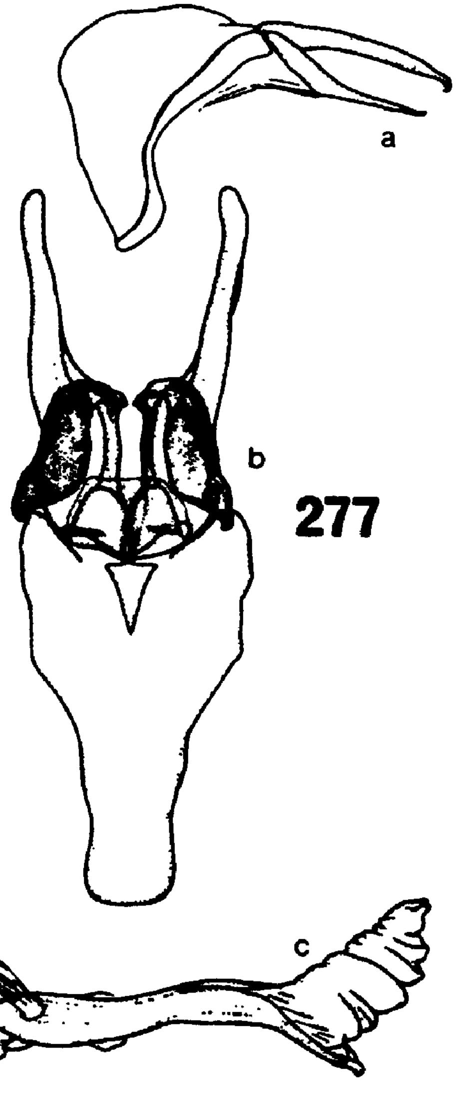

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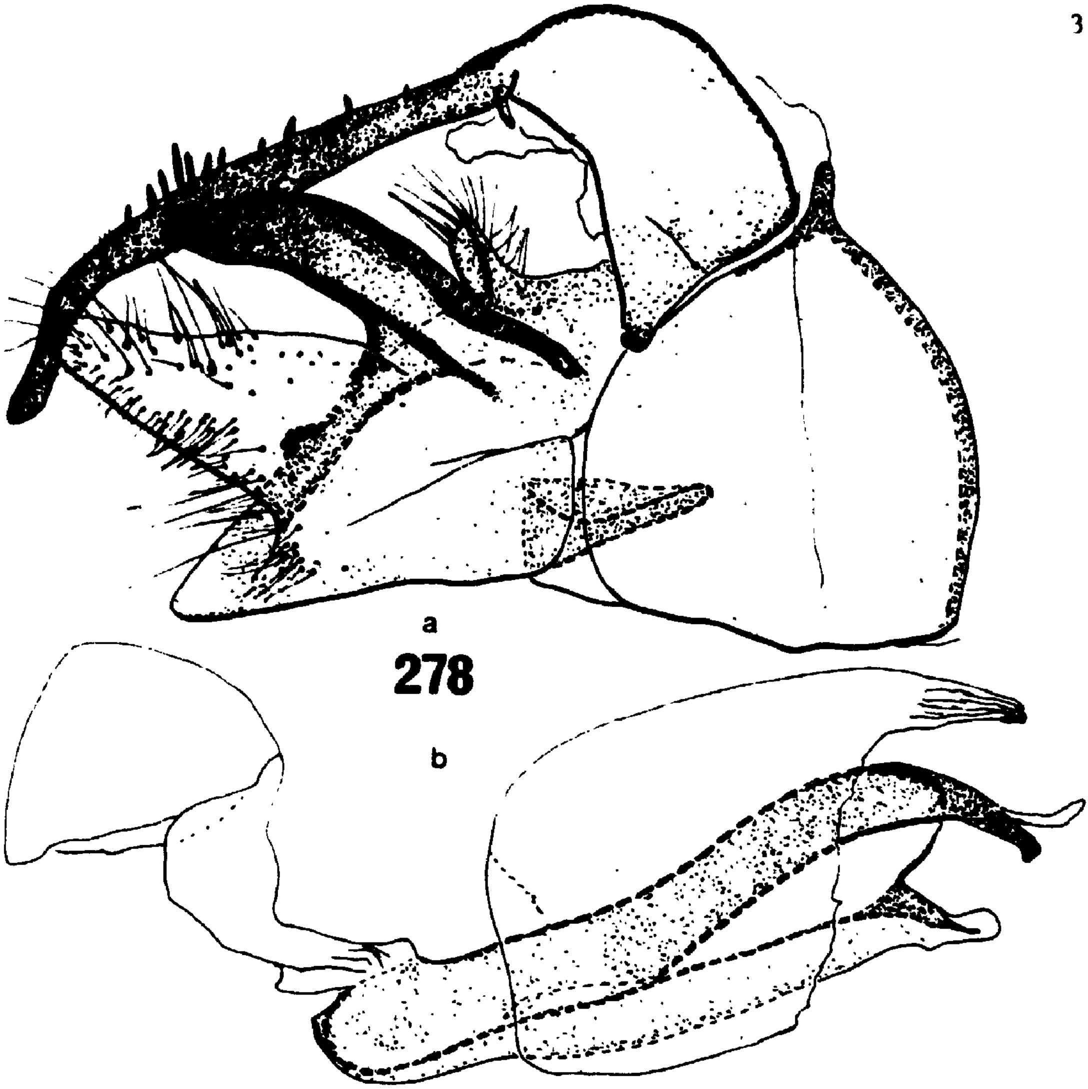
Figs. 278-279. Male genitalia of Crambinae. 278 a-b, *Almita texana* n.sp.; 279 a-c, *Almita portalia* n.sp.



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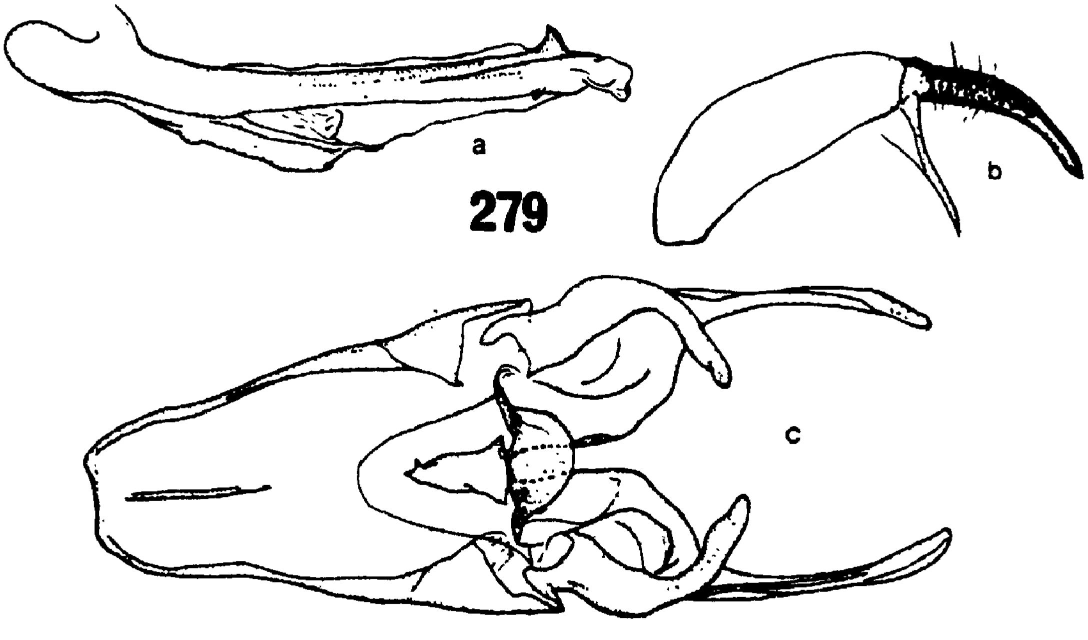

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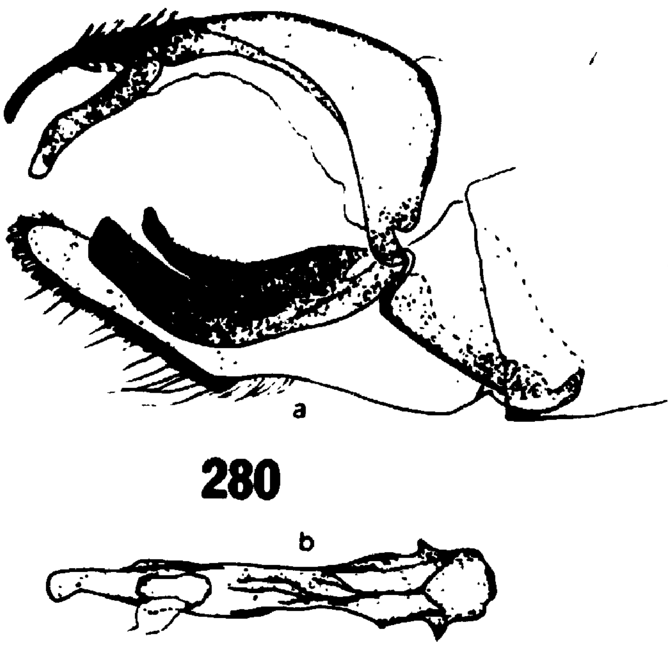
Figs. 280-283. Male genitalia of Crambinae. 280 a-b, *La cerveza* n.sp.; 281 a-c, *Raphiptera argillaceella* (Packard); 282 a-b, "*Crambus*" *angulatus* (Barnes & McDunnough); 283 a-c, *Neodactria luteolella* (Clemens).



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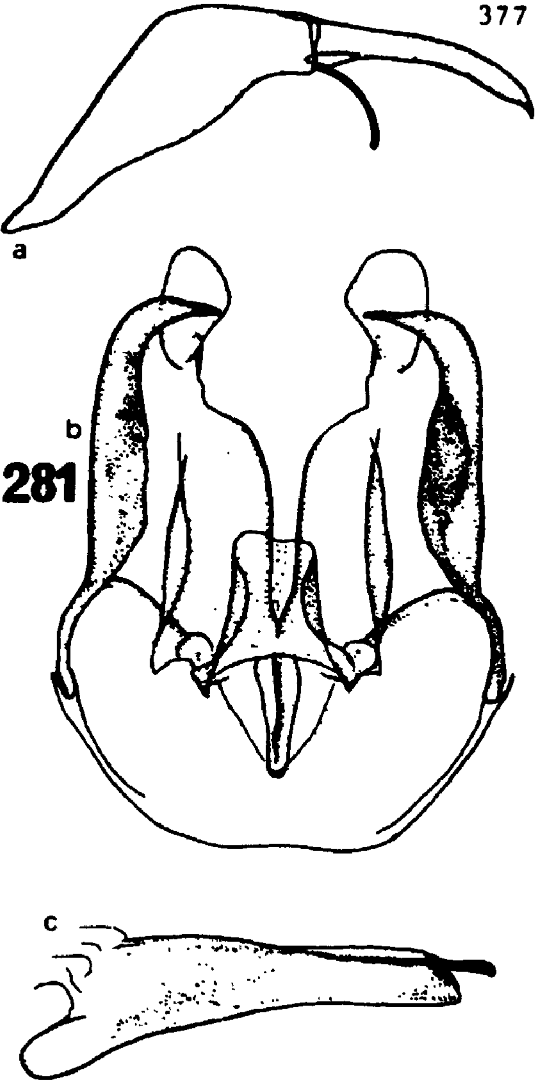

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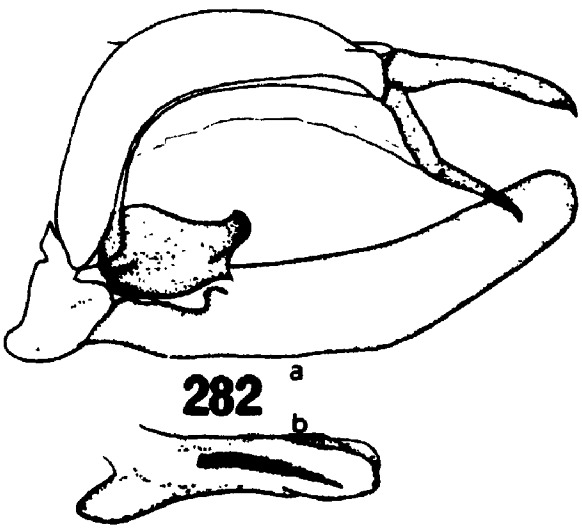

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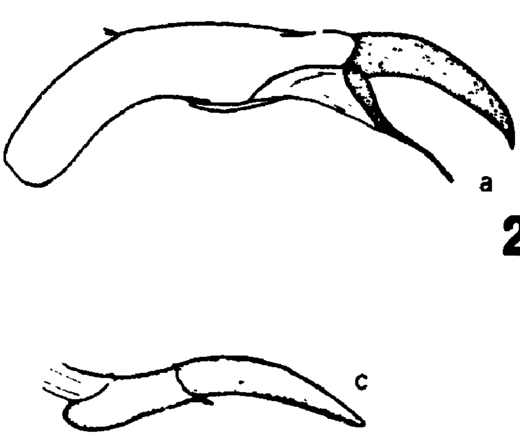

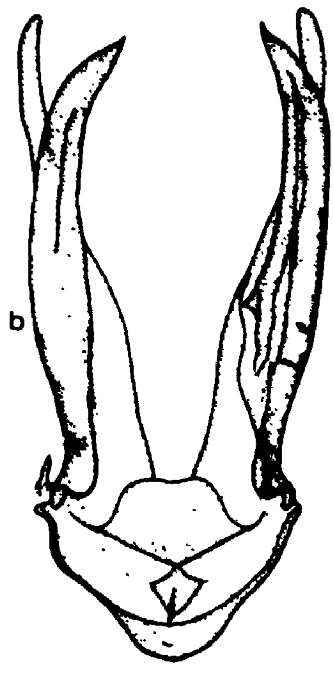

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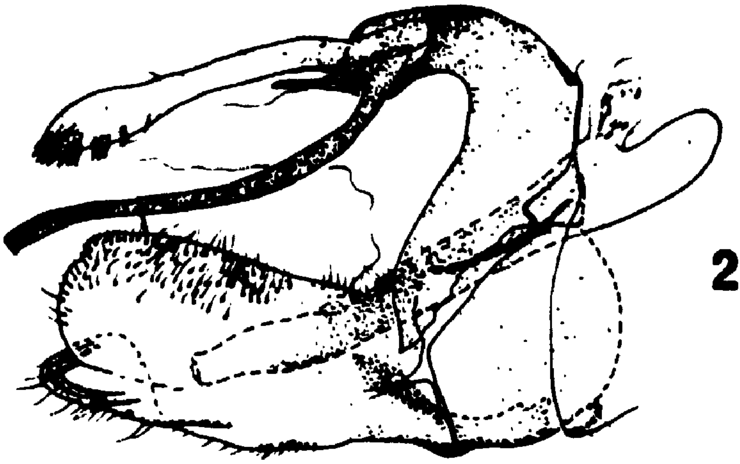
Figs. 284-286. Male genitalia of Crambinae. 284, *Arequipa turbatella* Walker; 285 a-b, *Agriphila ruricolella* (Zeller); 286 a-b, *Chrysoteuchia topiaria* (Zeller).



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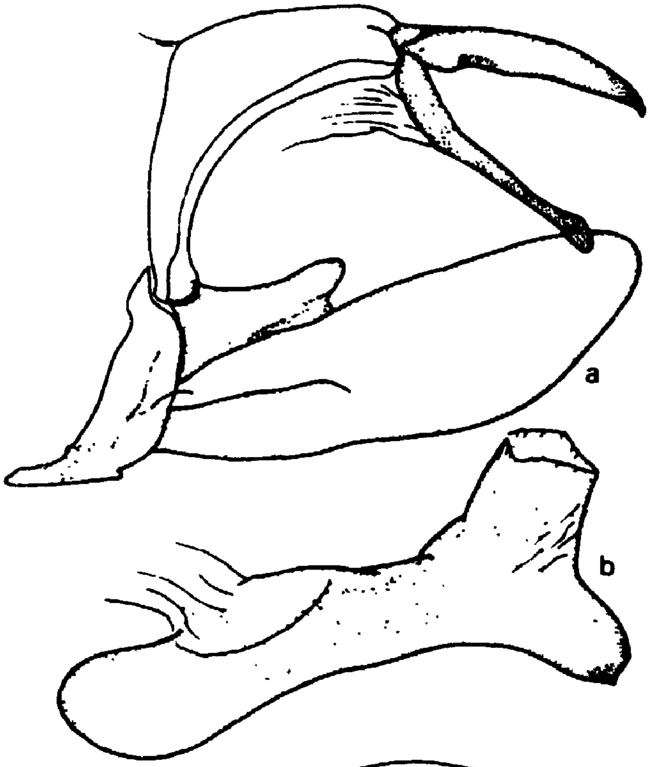

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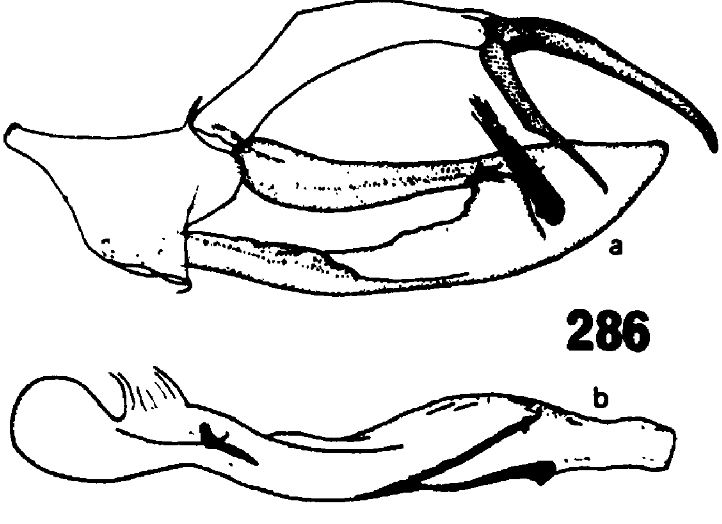

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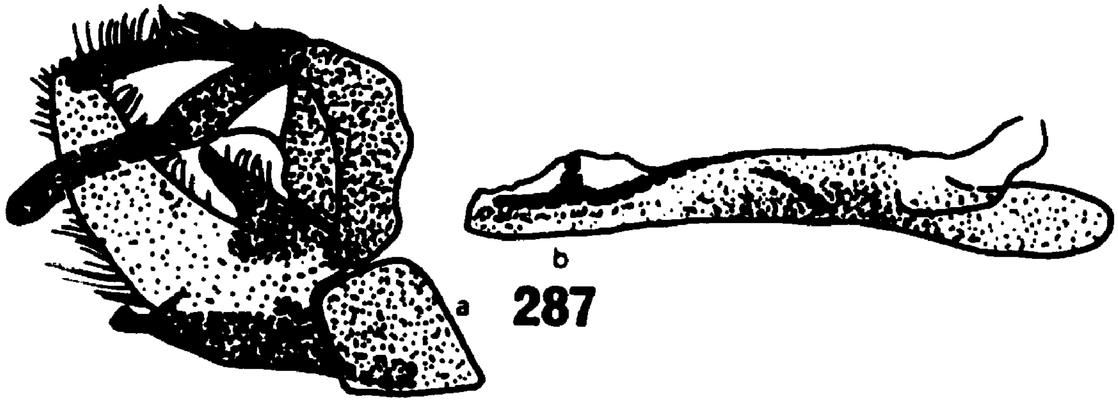
Figs. 287-289. Male genitalia of Crambinae. 287 a-b, *Fernandocrambus harpipterus* (Dyar); 288 a-b, *Crambus awemellus* McDunnough; 289 a-b, *Crambus leachellus* (Zincken).



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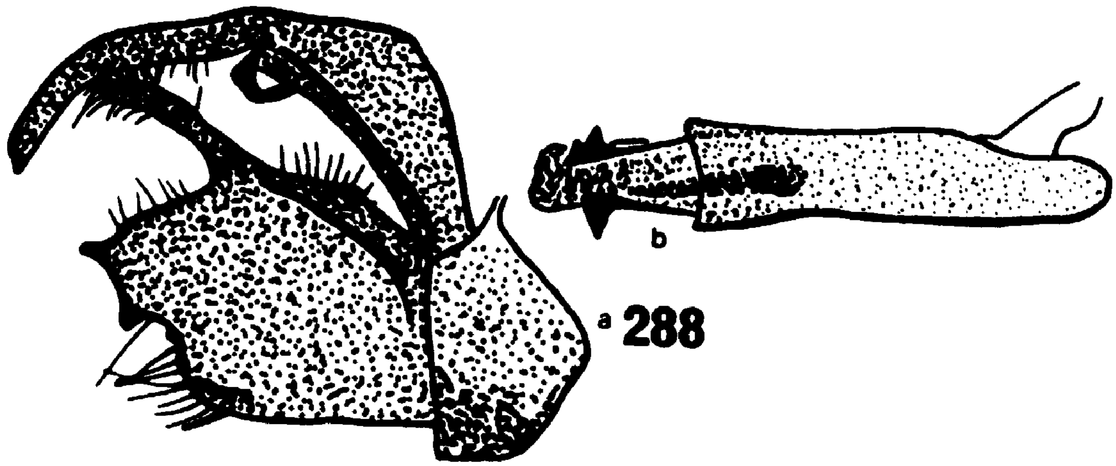

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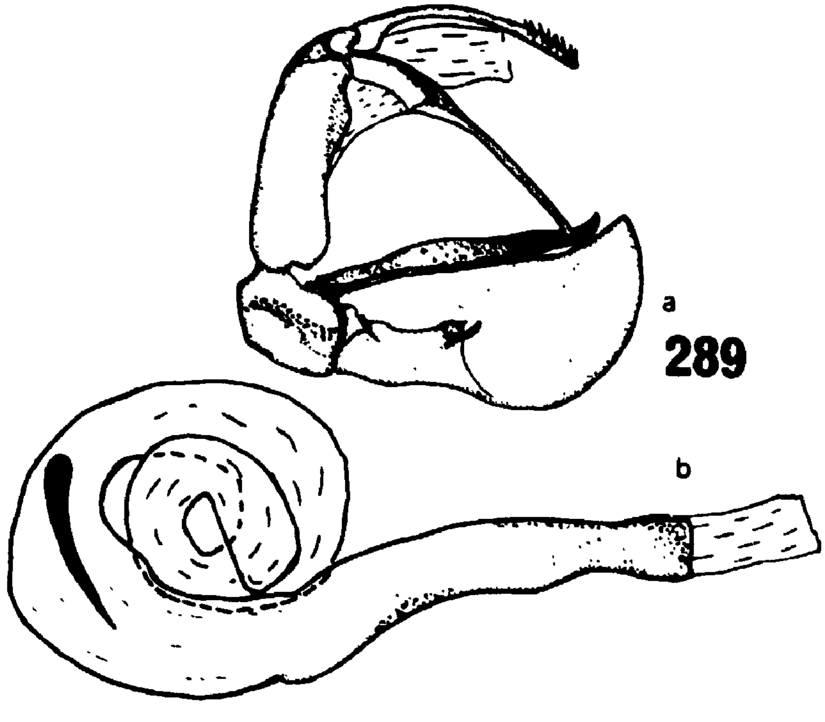

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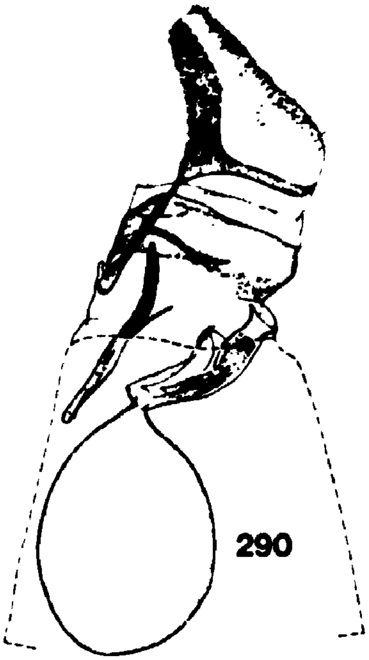
Figs. 290-295. Female genitalia of Crambinae. 290, Eufernaldia cadarella (Druce); 291, Pseudoschoenobius opalescalis (Hulst); 292, Xubida panalope (Dyar); 293, Surattha indentella Kearfott; 294, Prionapteryx serpentella Kearfott; 295, Hemiplatytes prosenes (Dyar).

Note on the figures of the female genitalia. Except for figures 299, 305, 308, 313, 316, 322, 323, 326,328, 329, 332, 334, 335, 337, which are ventral views, all other drawings show the genitalia in lateral view. A few figures were taken from the literature (307-309, 320, 338). The following are mine (figs. 291, 293, 294, 299, 300, 306, 310-313, 316, 322, 323, 325, 326, 328, 330-333). The others were made for Dr. A.B. Klots by M. Friedman and were lent to me by Dr. F.H. Rindge of the American Museum of Natural History, New York. These were all checked with mounted specimens and modified if necessary.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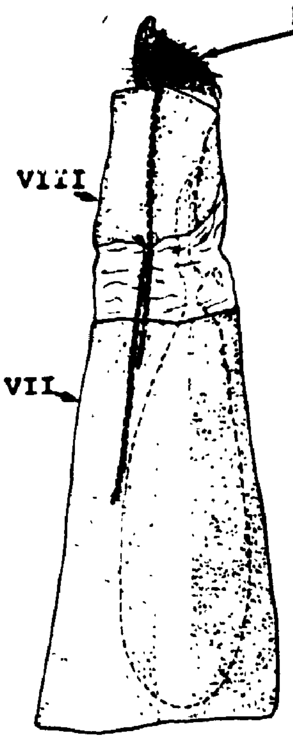

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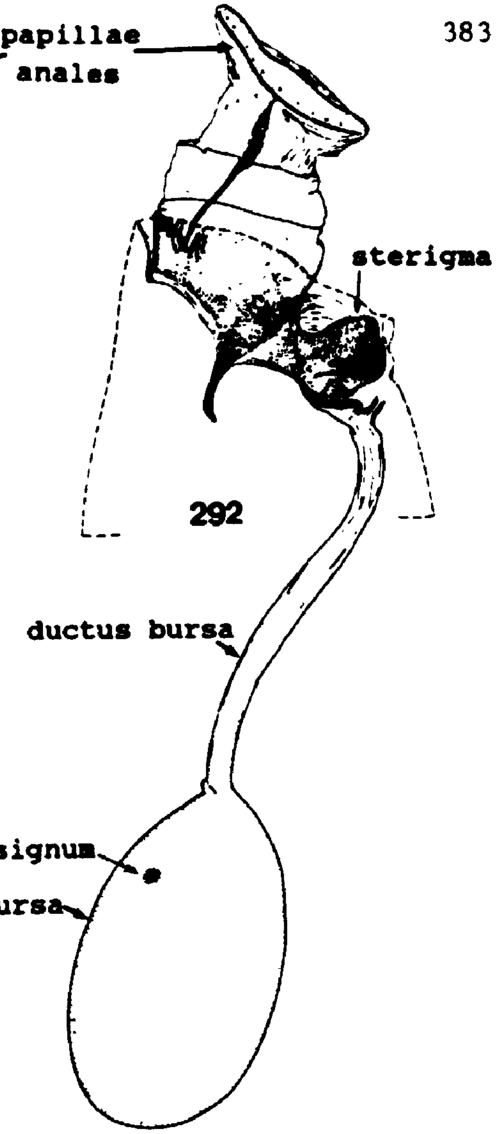

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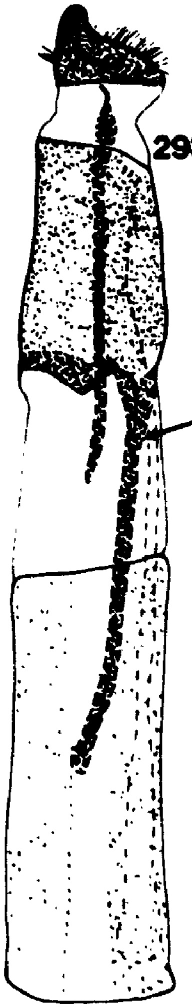
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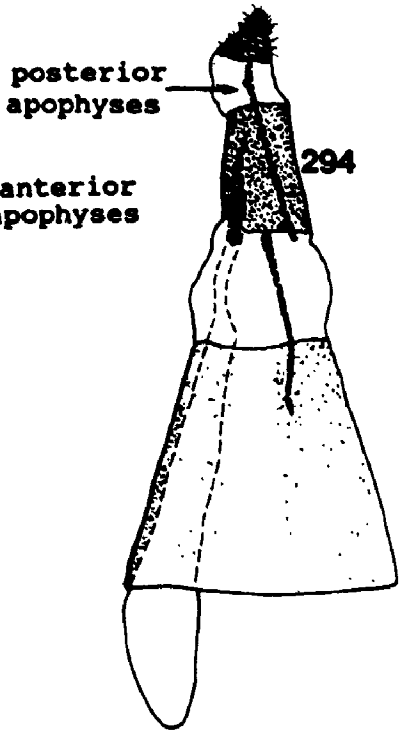

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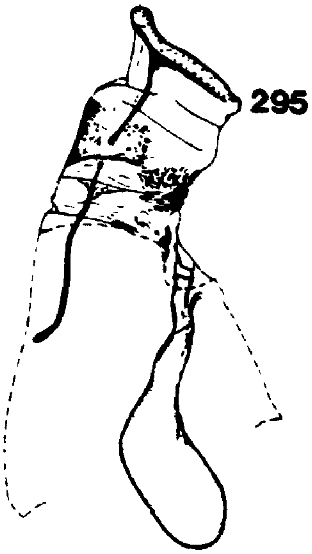
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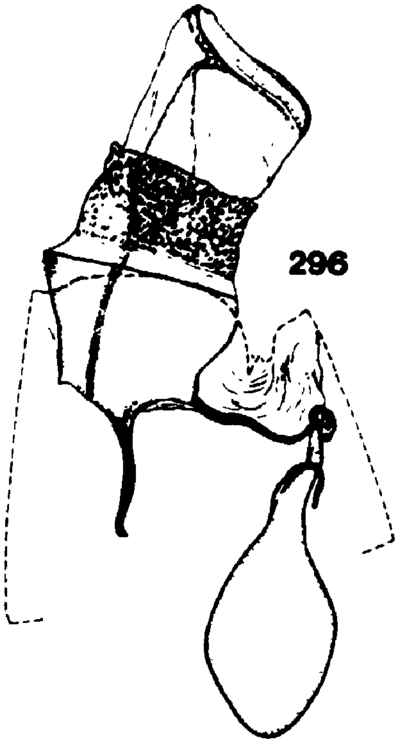
Figs. 296-300. Female genitalia of Crambinae. 296, *Eoreuma densella* (Zeller); 297, *Occidentalia comptulatalis* (Hulst); 298, *Thopeutis forbesellus* (Fernald); 299, *Chilo phragmitellus* (Hübner); 300, *Haimbachia pallescens* Capps.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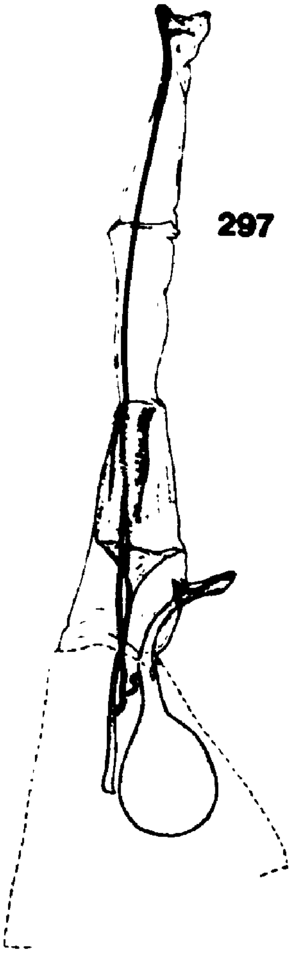
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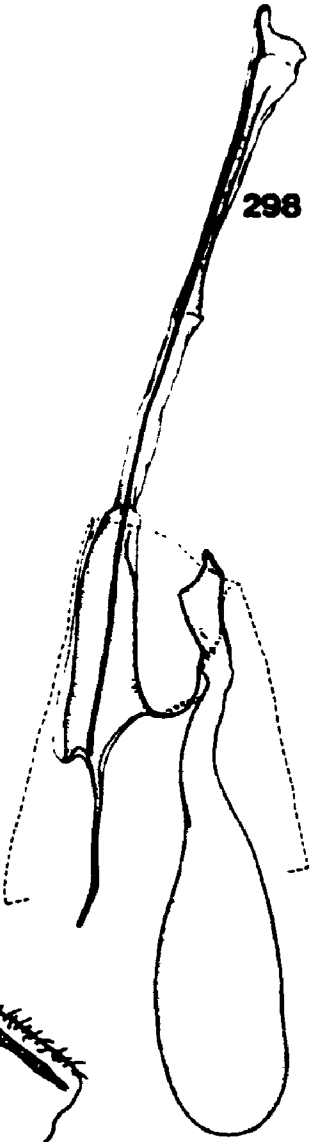
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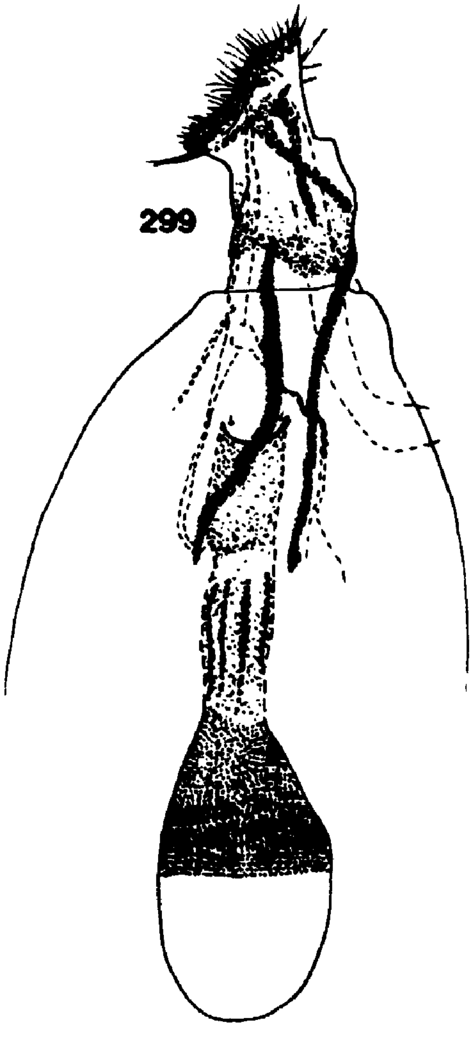
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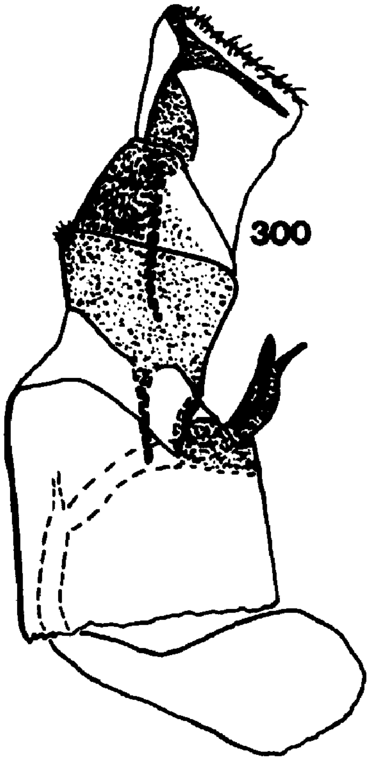
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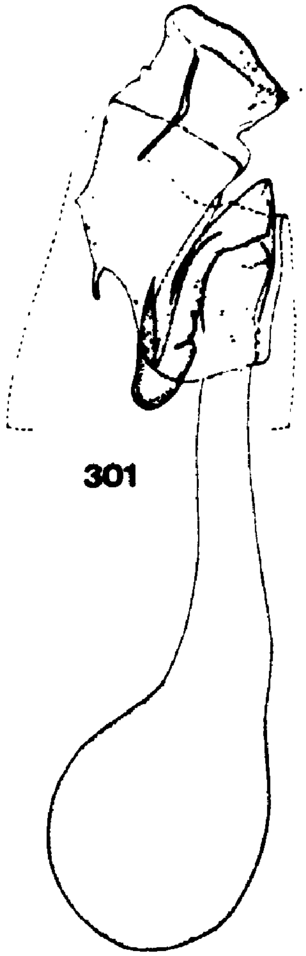
Figs. 301-306. Female genitalia of Crambinae. 301, *Vaxi auratella* (Clemens); 302, *Argyria nummulalis* Hübner; 303, *Urola nivalis* (Drury); 304, *Epina alleni* (Fernald); 305, *Diatraea evanescens* Dyar; 306, *Myelobia* sp.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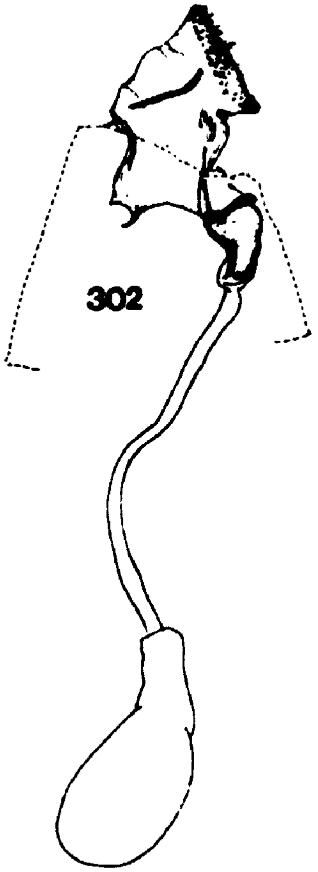
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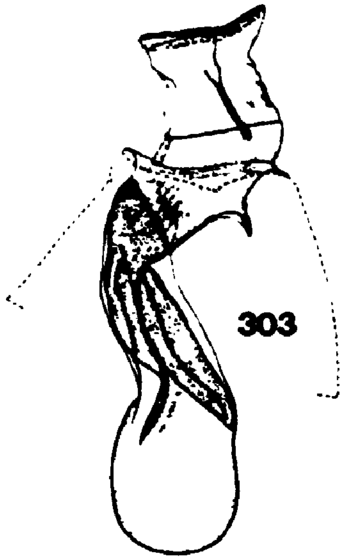
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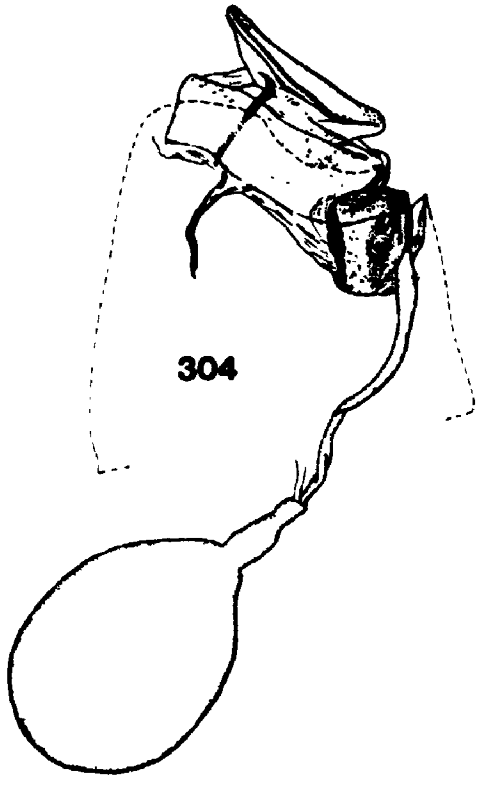
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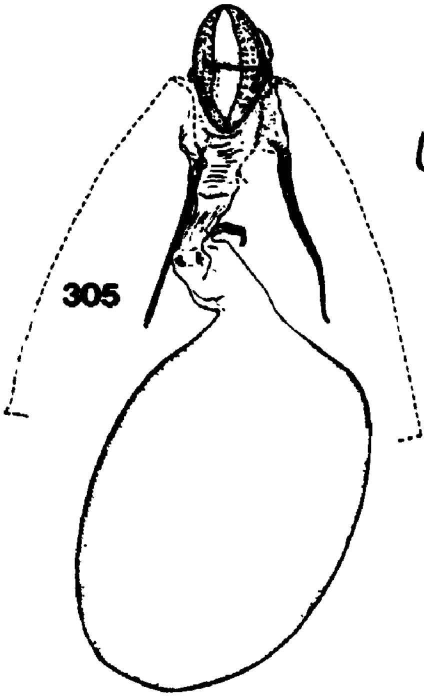
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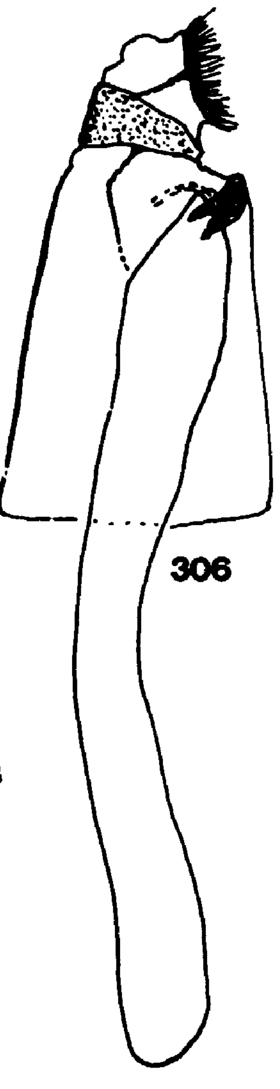
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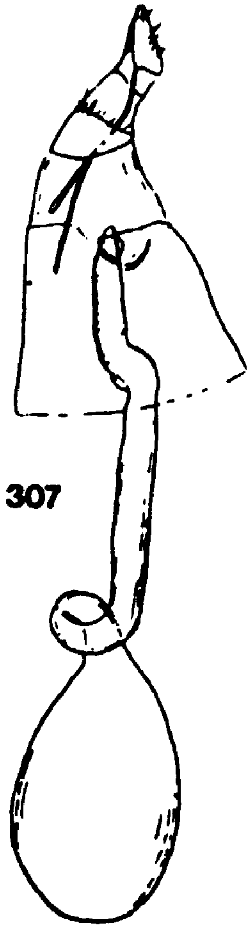
Figs. 307-312. Female genitalia of Crambinae. 307 (from Bleszynski 1966), *Microcausta flavipunctalis* Barnes & McDunnough; 308 (from Bleszynski 1966), *Diptychophora harlequinalis* (Barnes & McDunnough); 309 (from Schouten 1988), *Euchromius ocelleus* (Haworth); 310, *Calamotropha paludella* (Hübner); 311, *Platytes vobisne* Dyar; 312, "*Crambus*" *angulatus* Barnes & McDunnough.



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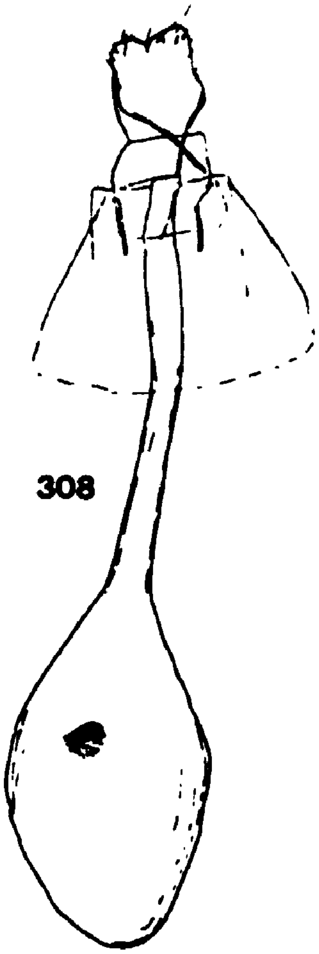

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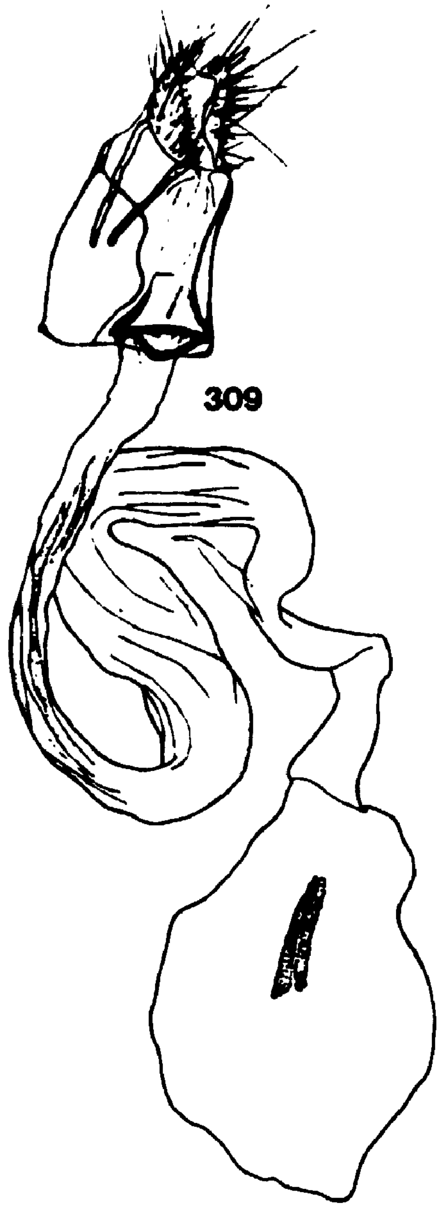

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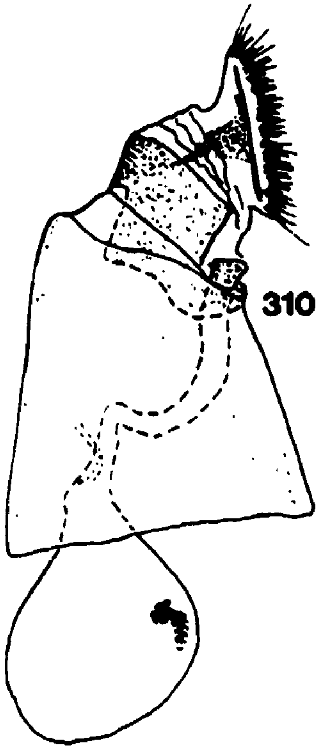

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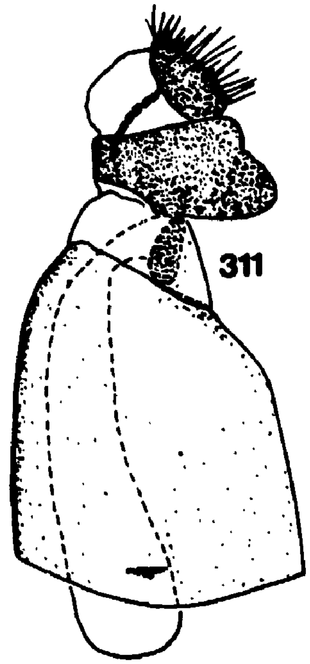

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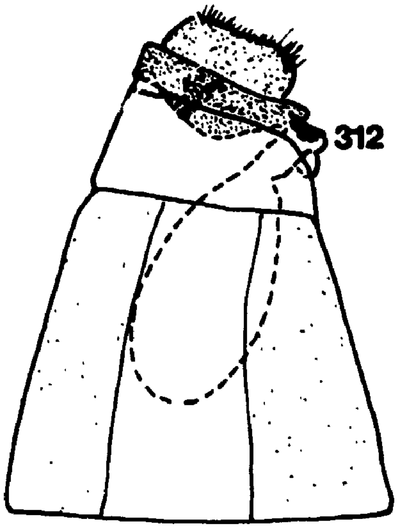

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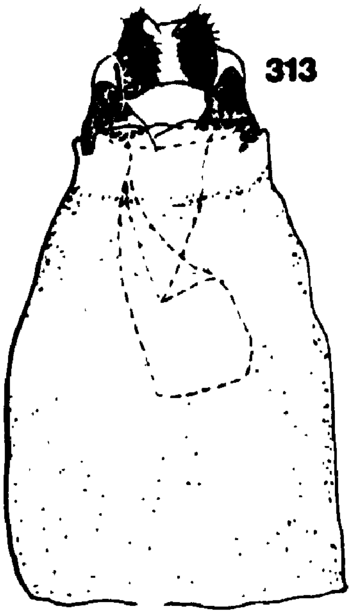
Figs. 313-319. Female genitalia of Crambinae. 313, *Ancylolomia japonica* Zeller; 314, *Thaumatopsis fernaldella* Kearfott; 315, *Thaumatopsis pectinifer* (Zeller); 316, *Microcrambus elegans* (Clemens); 317, *Catoptria latiradiella* (Walker); 318, *Thaumatopsis pexella* (Zeller); 319, *Thaumatopsis bolterella* (Fernald).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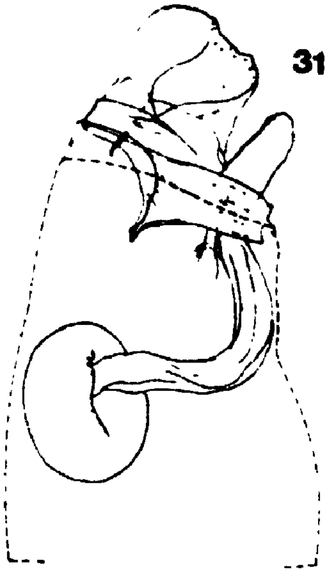
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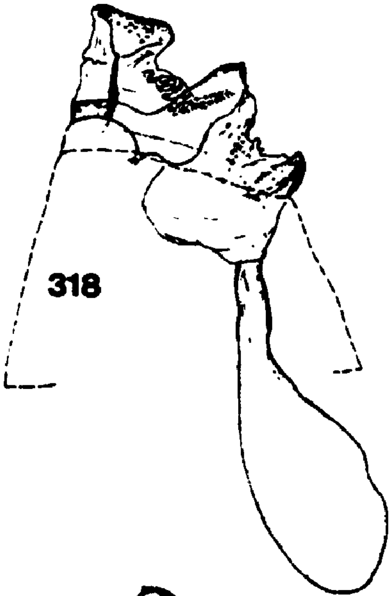
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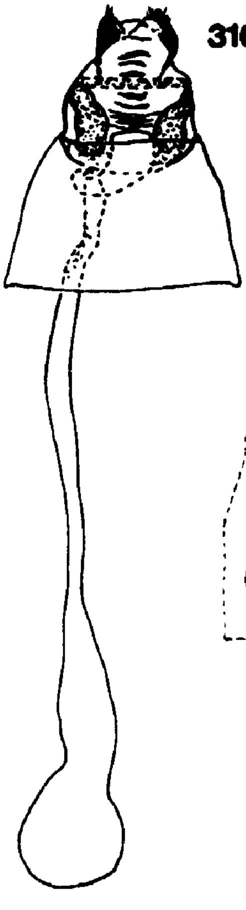
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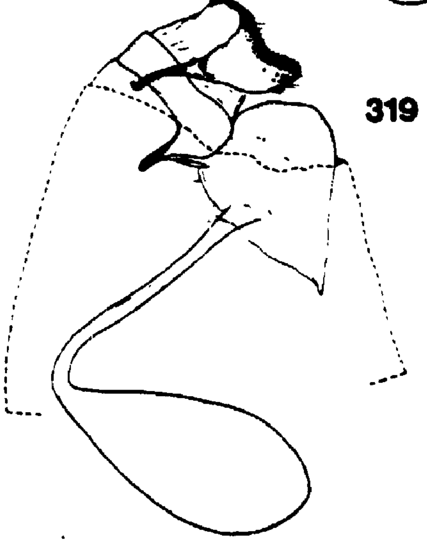
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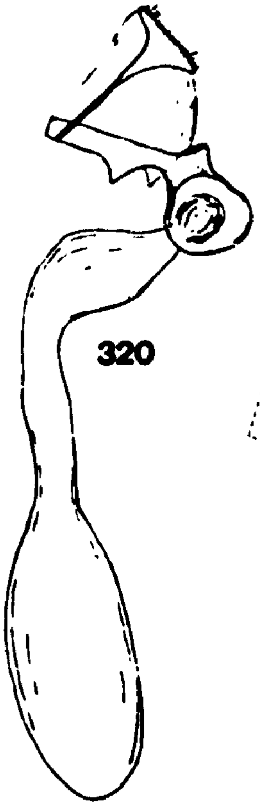
Figs. 320-326. Female genitalia of Crambinae. 320 (from Bleszynski 1963a), *Fissicrambus fissiradiellus* (Walker); 321, *Loxocrambus coloradellus* (Fernald); 322, *La cerveza* n.sp.; 323, *Tehama bonifatella* (Hulst); 324, *Agriphila ruricolella* (Zeller); 325 a-lateral view, b-ventral view of sterigma, *Arequipa turbatella* Walker; 326, *Pediasia trisecta* (Walker).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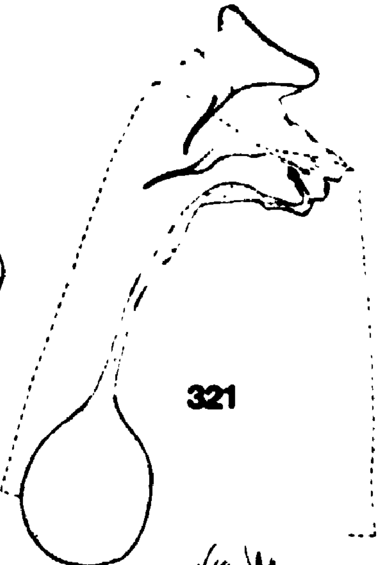
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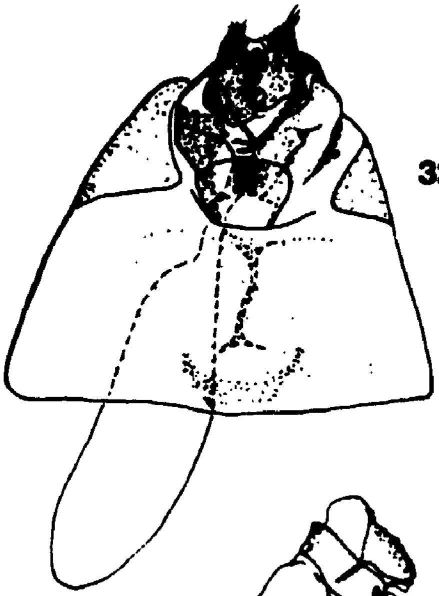
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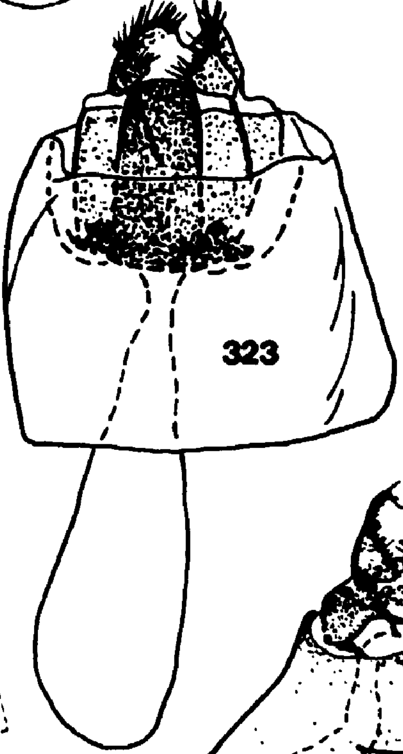
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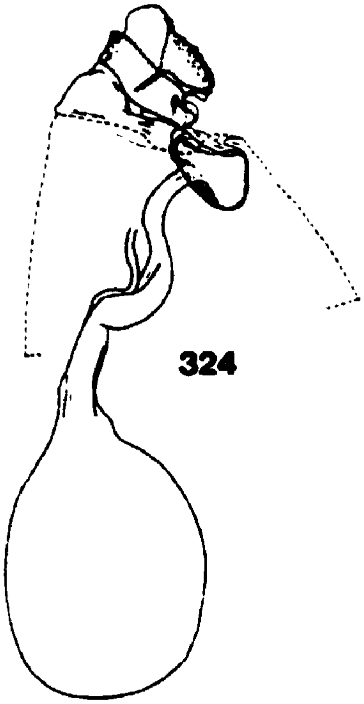
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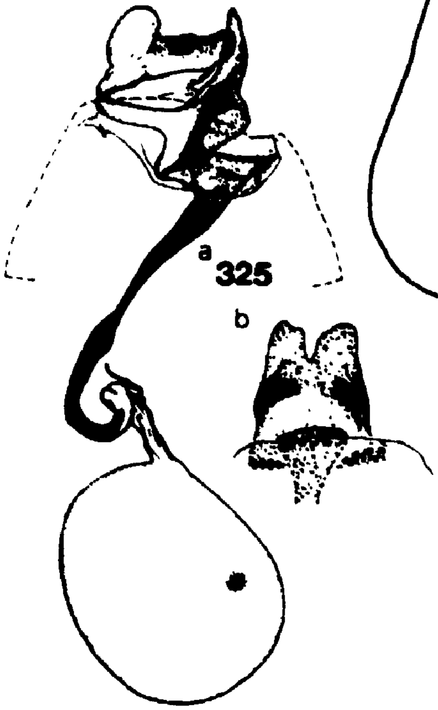

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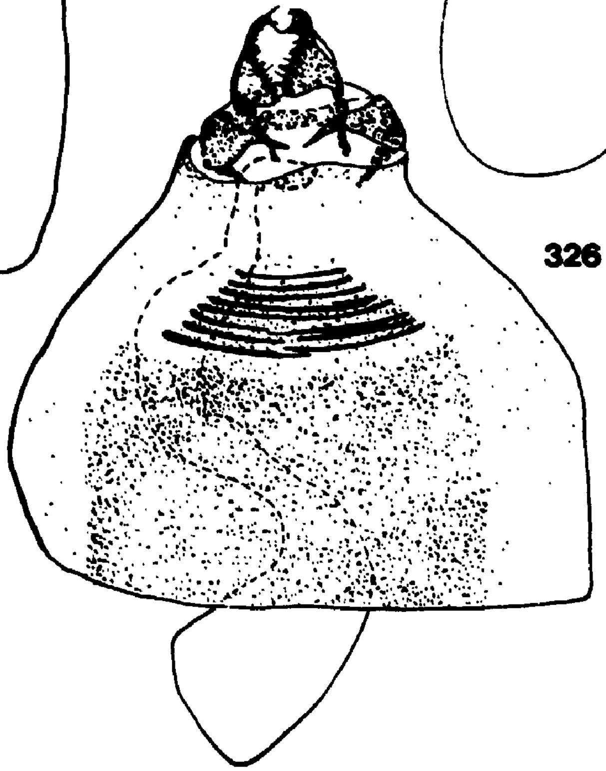
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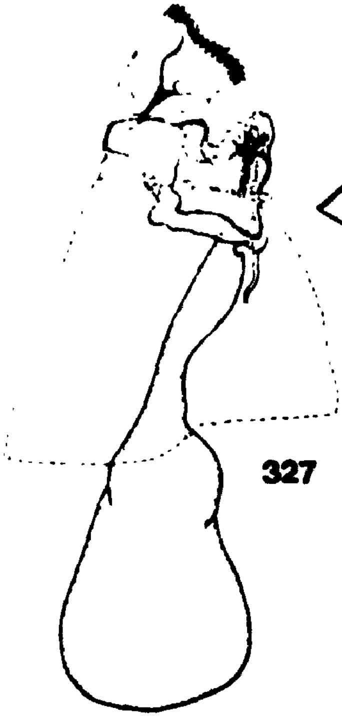
Figs. 327-332. Female genitalia of Crambinae. 327, *Parapediasia hulstella* (Fernald); 328, *Parapediasia decorella* (Zincken); 329, *Parapediasia teterrella* (Zincken); 330, *Neodactria luteolella* (Clemens); 331, *Almita texana* n.sp.; 332, *Almita portalia* n.sp.



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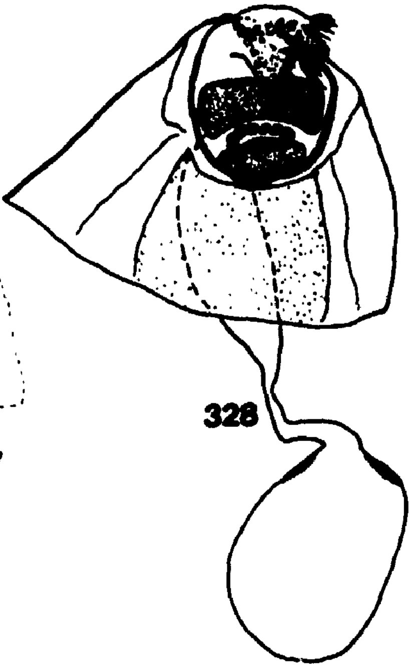

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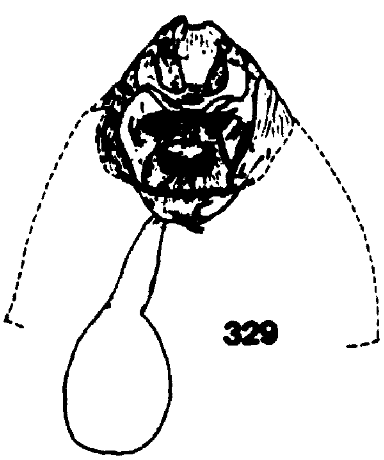

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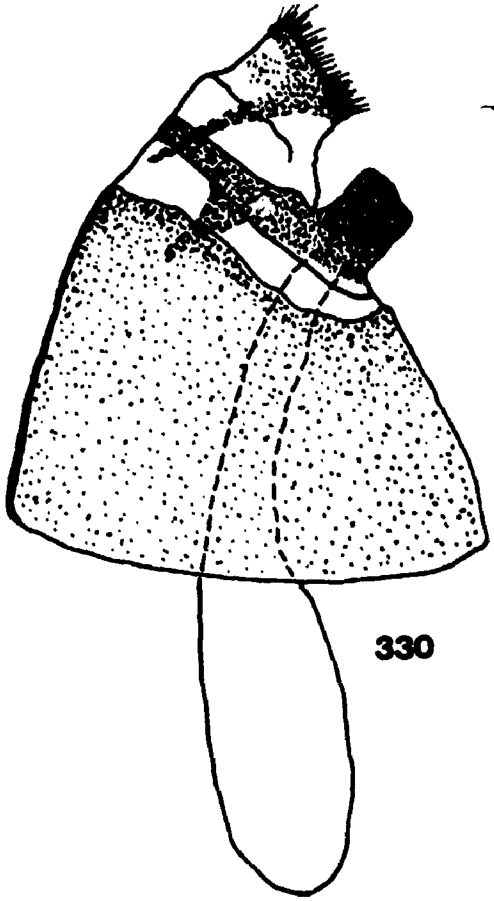

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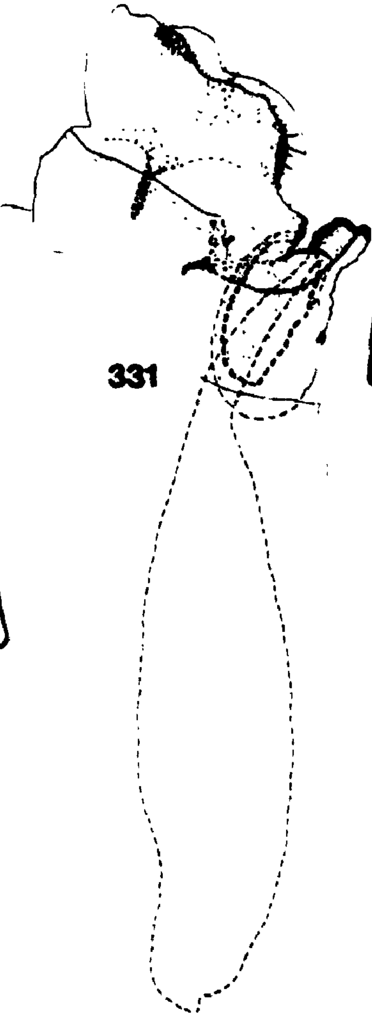

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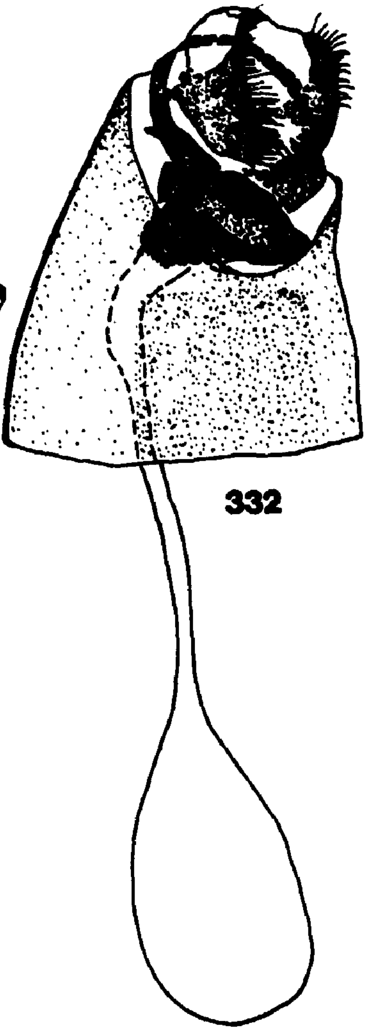

332

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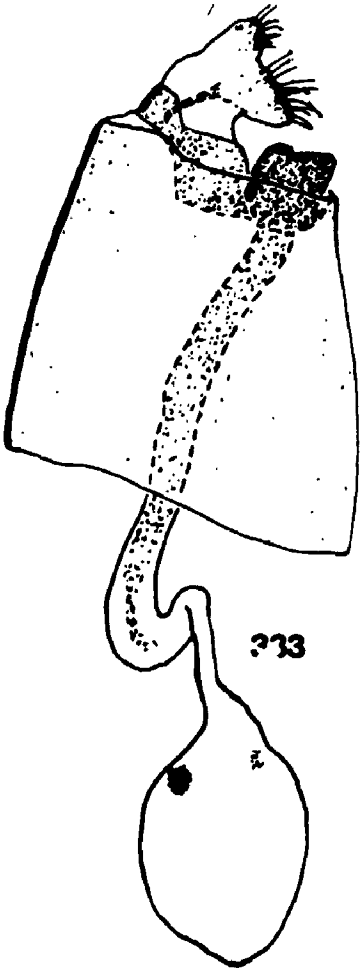
Figs. 333-338. Female genitalia of Crambinae. 333, *Fernandocrambus harpipterus* (Dyar); 334, *Raphiptera argillaceella* (Packard); 335, *Chrysoteuchia topiaria* (Zeller); 336, "*Crambus*" *dimidiatellus* Grote; 337, *Crambus leachellus* (Zincken); 338 (from Klots 1940), *Crambus pascuellus* (Linnaeus).



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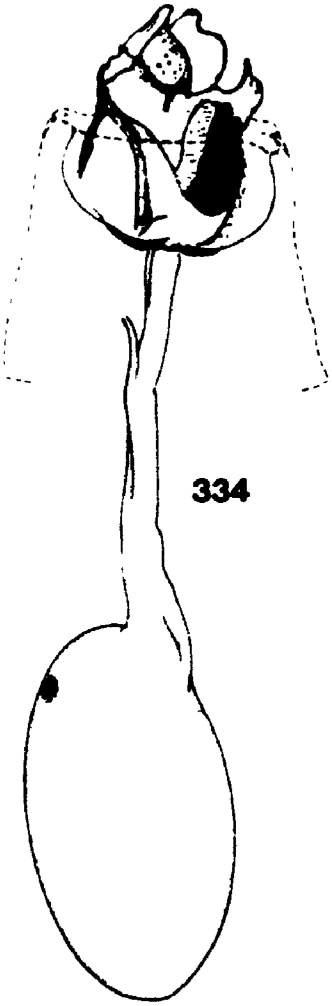

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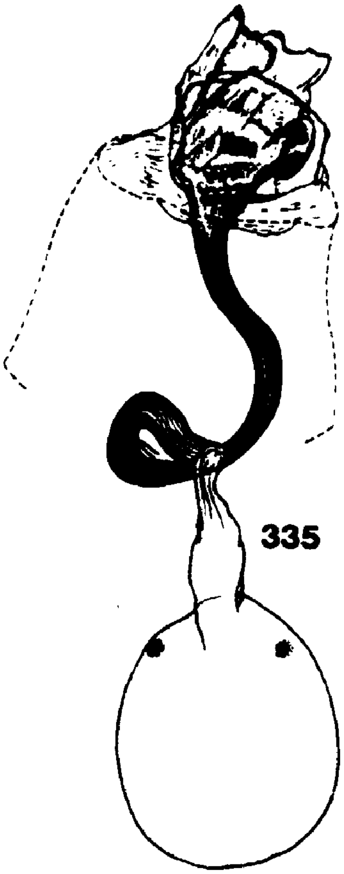

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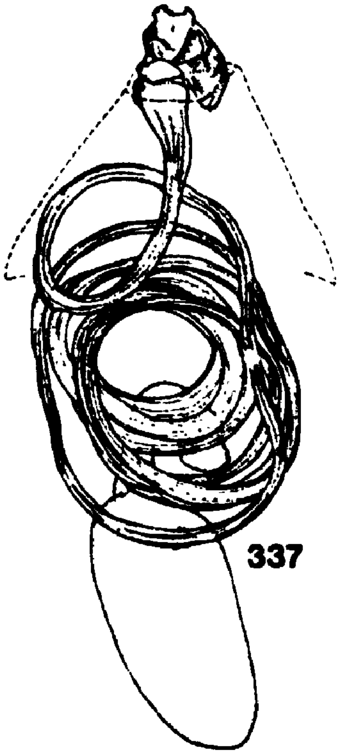

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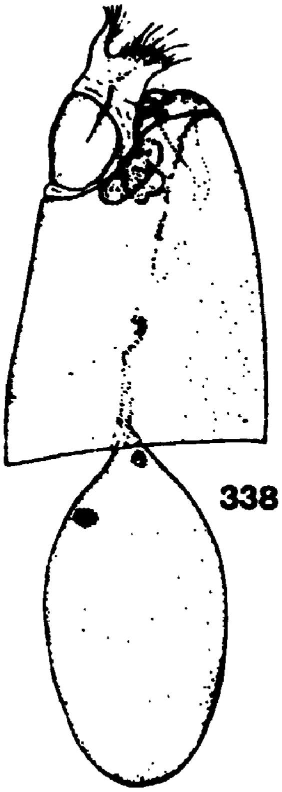

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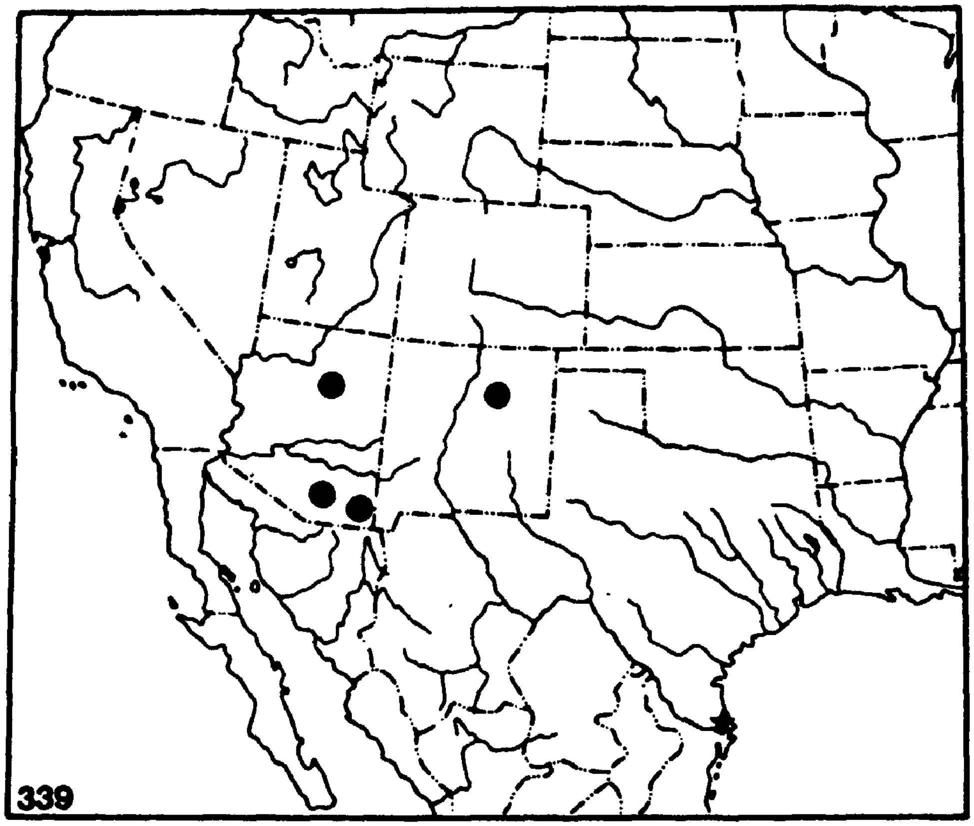
Figs. 339-340. Known distribution of new crambine species. 339, *Almita texana* n.sp. (stars), *Almita portalia* n.sp. (dots); 340, *La cerveza* n.sp. (stars), *Parapediasia torquatella* n.sp. (dots).



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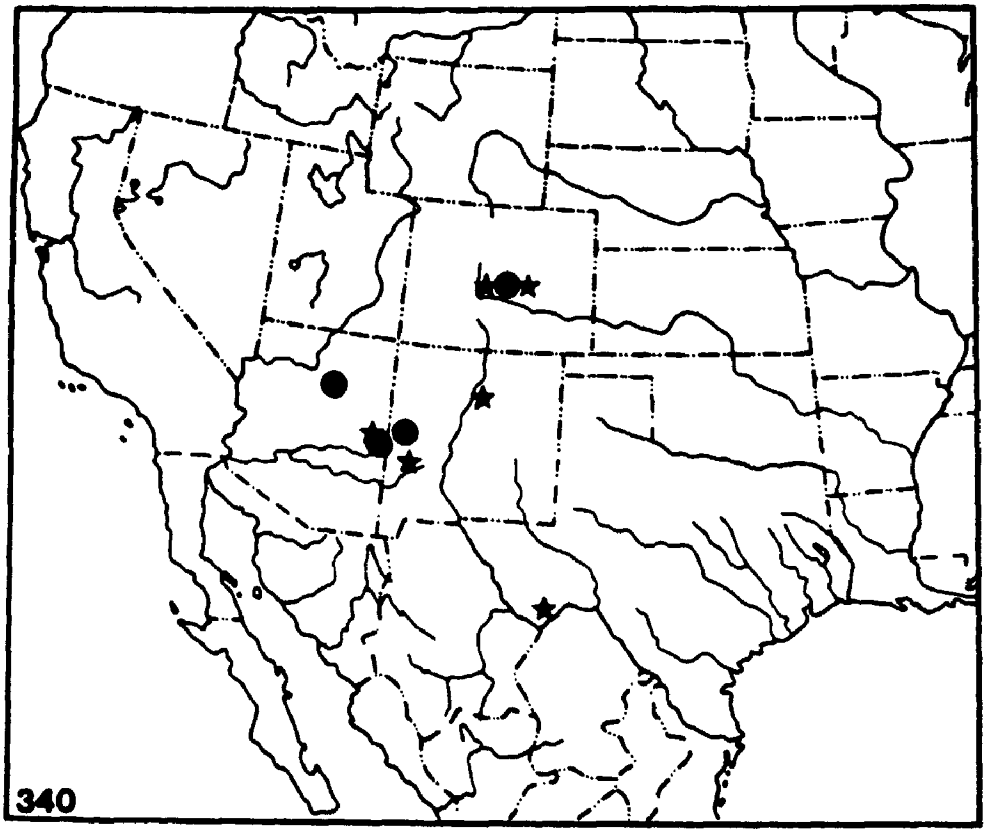

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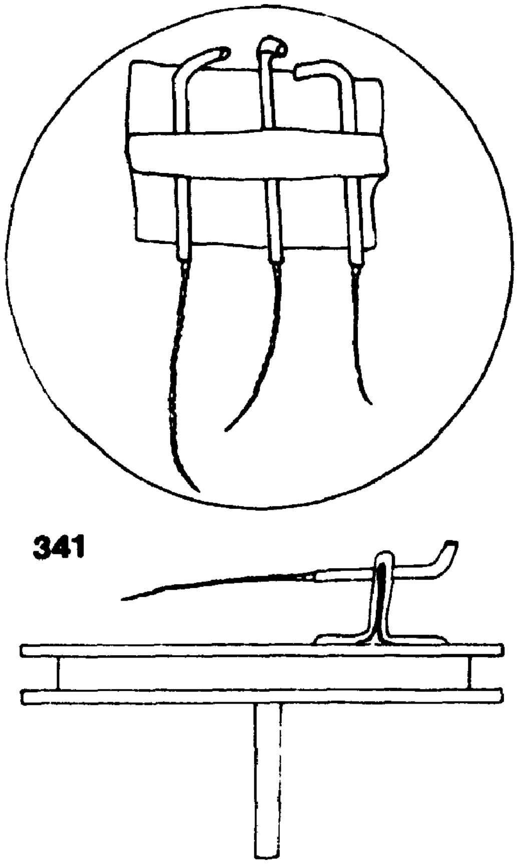
Fig. 341. Device used to mount antennae for analysis with the scanning electron microscope.



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APPENDIX I

Characters and alternate states used in the cladistic analysis. Multistate characters were treated as additive (+) or nonadditive (-).

1. Maxillary palpus without scale-tuft at apex (0); with a scale-tuft apically (1).

2. Maxillary palpus more than 2.5X shorter than the vertical diameter of the head (0); less than 2.7X shorter than this measure (1).

3. Ocellus present (0); absent (1).

4. Antennal sensilla coeloconica present (0); absent (1).

5. Mosaic pattern on flagellomeres' cuticle present (0); absent (1).

6. Flagellomeres' large sensory pits absent (0); present (1).

7. Apical scales on flagellomeres appressed (0); erect (1).

8. Forewing less than 2.0X longer than wide (1); more than 2.1X longer than wide (0).

9. Forewing outer margin produced at M1-M2 (1); not produced in that sector (0).

10. Forewing Radius with 5 veins (0); missing 1 or 2 veins (1).

11. Forewing R4 and R5 free (0); stalked (1).

12. Forewing Cubitus with 2 veins (0); with 1 vein (1).

13. Male frenulum hook present (0); absent (1).

14. (-) Female frenulum bristle number 1 (1000); 2 (0100); 3 (0010); 4 or more (0001).

15. Hindwing cell closed (0); hindwing cell open (1).

16. Base of hindwing M1 closer to middle of cell (1); closer to Sc + R (0).

17. Hindwing M2-M3-CuA1-CuA2 all present (0); missing one vein (1).

18. Hair tuft on hindwing Cubital stem dorsally present (0); absent (1).

19. Tympanic frame not distinctly projected beyond venula prima (0); distinctly projected beyond venula prima (1).

20. Tympanic pockets present (0); absent (1).

21. Tympanic organ of the "crambine type" (1); "not of the Crambine type" (0).

22. Tegumen dorsal connection long (0); very short (1).

23. Uncus dorso-ventrally flattened (0); laterally compressed (1).

24. Uncus apex pointed or rounded (0); W-shaped (1).

25. Gnathos strongly sclerotized (0); reduced or lost (1).

26. Gnathos directed posteriorly (0); directed ventrally (1).

27. Apex of gnathos directed upward (0); directed downward or posteriorly (1).

28. Male pseudosaccus absent (0); present (1).

29. Aedeagus coecum penis present (0); absent (1).

30. Attachment of aedeagus from apex (0); not from apex (1).

31. Aedeagus ventral extension absent (0); present (1).

32. Aedeagus with strongly developped sclerotized extension apico-dorsally (1); without this structure (0).

33. Ostium bursae at apical margin or in segment VII (0); in middle of segment VIII (1).

34. Female segment VIII & sterigma connected by a simple narrow sclerotized bridge (1); if connection present, bridge not simple and narrow (0).

35. Female segment VIII circular in cross section (0); laterally compressed (1).

36. Setation on female segment VIII variable in position (0); concentrated apico-dorsally (1).

37. Female intersegmental membrane VIII-IX smooth (0); with slender spines (1).

38.(-) Corpus bursa signa number 0 and 1 (0); 2 (1).

39. Posterior apophyses shorter than length of 1st three abdominal segments (0); longer than length of 1st four abdominal segments (1).

40. Posterior apophyses subbasally narrow (0); subbasally enlarged (1).

41. Female papillae anales coalesced dorsally (0); not coalesced dorsally (1).

42. Dorsally coalesced papillae anales poorly sclerotized and generally elongate (0); strongly sclerotized and triangular in shape (1).

43.(+) Uncoalesced papillae anales simple (00); more or less divided (10); strongly divided (11).

APPENDIX II

Data matrix for 47 species of Crambinae and 8 outgroup taxa. For complete taxonomic names see Table 4. For character state descriptions, see Appendix I and character analysis (chapter 4). A question mark was used when a) the state of the character was unknown in the taxon, b) the character was not found in the taxon, or c) all states of the character were found in the taxon.

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      123456789 0123444456789 0123456789 0123456789 01233

Outgroup
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Mimos 000??0000 000001000000? 0000000000 0000000000 01000
Donac 110??0000 000110000000? ?000000000 0000000000 00000
Everg 000??0000 000000100000? 0000000100 0000000010 00000
Glaph 000??0010 000000010000? 0010010?00 00000000?0 00000
Nymph 000??0000 000000100000? ?000000000 0000000010 00000
Scopa 110??0000 000100100000? 0000000100 0000000010 00000
Cybal 110??0000 000110000000? 0000000?00 0000000000 00000

Crambinae except Crambini
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Surat 1?0???000 0001100001111 1100111?01 0000000000 00100
Urola 110000000 0000????10010 0110000000 1000000000 00000
Argyr 110000000 0000000110010 ?110000000 1000000000 00000
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Crambini
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All Crambini combined; =*Crambus et al.* on fig. 4

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Tribe 110000000 0101????10010 0100000110 1000000?00 01???;
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APPENDIX III

Types and numbers of sensilla on one side of one flagellomere (generally the fifteenth) in 41 species of Crambinae.

Taxon	sensilla coeloconica	sensilla chaetica	sensilla trichodea	sensilla styloconica	sensilla auricillica
Hemip	0	1	25-30	0	1?
Eufer	3-4	0?	≈100	1	0
Prion	0	0	≈70	0	0
Pseud	0	0	≈50	0	0
Thope	15	1	90-100	1	2-4
Occid	5	1	80-90	1	1
Eoreu	4	2	80-90	1	1
Urola	7	0	≈200	?	0
Argyr	≈20	2	50-60	?	0
Vaxi	3	1	75-80	1	?
Dipty	1	1	≈40	1	0
Micst	3	2	40-50	1	0
Myelo	4-7	1	≈40	1	0
Chilo	7	3	50-60	1	0
Calam	2-3+	2+	100-120	1	0
Euchr	2	1	60-70	1	0
Platy	1	1	≈50	?	0
Catop	3-4	3	35-50	1	0
Thaum	100+	0	100-120	2	0
Tflor	8	2	≈100	1	0
Teham	2	2	50-70	?	1-2
Fissi	1	1	≈60	1	2

Fminu	≈20	3	≈100	1	0
Finter	1	0	80-100	1	2
Micro	3	1	50-60	1	2
Mbigu	3	2	≈35	1	2
Loxoc	4-5	1	50-60	1	0
Neoda	3	1	≈30	1	0
Arequ	3	1	≈40	1	0
Pedia	5	1	90-100	1	0
Lansp	1	1	≈30	1	0
Ptete	2	2+	70-100	1	2-3
Pdeco	≈35-40	2	3	1	0
Ptorq	3	2-3	50-55	?	0
Almit	2	2	50-60	1	0
Porta	2	1	30-35	?	2
Raphi	0?	15-20	20-25	1	1?
Agrip	2	1	35-40	1	2-3
Ferna	2	2-3	35-40	1	1
Chrys	3	0*	≈80	?	0
Cramb	2	2	≈50	1	2-3

Note that "Fminu" is *Fissicrambus minuellus* (Walker), "Finter" is *Fissicrambus intermedius* (Kearfott), "Tflor" is *Thaumatopsis floridella* Barnes & McDunnough and "Mbigu" is *Microcrambus biguttellus* (Forbes). The other abbreviations are the same as the ones used elsewhere. The names follow the order used in Table 4.

*3 were seen on a female specimen.

APPENDIX IV

Measurements for characters 47-51. Unless otherwise indicated, the measurements were made on male specimens. The full names of the taxa are given in Table 4.

Character	47	48	49	50	51
Taxon					
Mimos	0.8	1.8	1.33	2.34	2.89
Cybal♀	0.8	1.6	1.47	2.35	1.87
Donac	1.44	4.2	2.4	3.54	1.74
Everg	0.25	0.6	1.03	2.24	3.46
Pyrau	1.3	3.2	1.72	2.21	2.77
Glaph	0.53	0.86	1.38	2.00	3.0
Nymph	0.58	1.0	1.03	2.55	3.55
Scopa	0.6	1.6	1.36	2.63	1.65
Ancyl	---	---	---	3.13	---
Calam	1.27	3.94	2.43	2.46	1.44
Pseud	1.2	3.4	1.75	3.45	2.06
Eufer	3.0	6.6	3.02	3.58	1.61
Prion	0.57	3.0	2.21	2.83	1.2
Surat	---	---	---	2.42	---
Myelo	0.45	1.95	0.98	2.58	1.56
Vaxi	1.8	2.6	1.8	2.12	2.0
Urola♀	0.58	1.36	1.4	2.31	2.21
Argyr	0.62	1.5	1.35	2.28	2.0
Micst	---	---	---	1.9	---
Dipty♀	0.5	2.2	1.61	1.9	2.33
Hemip	1.8	6.3	3.25	2.77	1.75
Xubid	---	---	---	2.44	1.35
Eoreu	1.6	5.5	2.45	2.72	1.38
Haimb	0.75	3.25	2.2	2.75	1.46
Occid	1.46	2.0	1.59	3.26	1.79
Thope	2.0	3.2	1.59	2.75	1.61
Diatr	1.0	4.1	2.26	2.66	1.84
Chilo	1.1	6.65	3.69	2.54	1.53
Epina	0.7	2.3	2.1	2.41	1.71
Thaum	2.64	4.64	3.2	2.8	1.77
Tbolt	2.14	2.9	2.18	2.84	1.67
Ptero	1.6	2.0	1.64	2.59	---
Pdeco	---	---	---	2.83	---
Ptorq	---	---	---	2.61	---
Almit	---	---	---	2.46	---
Teham	1.4	2.9	1.83	2.94	1.89
Fissi	1.9	2.1	1.85	2.78	1.94
F.qua	---	---	---	2.52	---
Micro	1.0	1.83	1.92	2.19	2.4
Loxoc	1.4	2.56	1.61	2.95	1.67
P.hul	---	---	---	2.93	---

Character	47	48	49	50	51
Taxon					
L.col	1.9	2.3	2.08	2.79	---
Ferna	1.4	2.9	2.6	3.55	1.71
Neoda	2.6	5.5	3.03	2.79	1.78
C.dim	3.0	4.0	4.0	2.68	1.72
C.ang	2.16	3.83	2.1	2.83	1.92
Agr‘	2.15	3.08	3.24	2.41	1.81
Arequ	1.79	2.86	2.6	2.52	1.95
Chrys	1.27	2.27	2.0	2.56	1.81
Pedia	1.83	3.58	2.75	2.78	1.56
Cramb	1.44	2.25	2.14	3.09	1.94
Porta♀	2.12	1.87	1.66	2.79	1.75
Lansp	1.83	2.83	2.72	3.17	1.33
Catop♀	1.15	1.92	2.3	2.64	1.5
Euchr	1.0	2.25	1.31	2.83	1.72
Raphi	1.57	4.57	3.0	3.26	1.68
Platy	1.37	3.12	1.91	2.63	1.5

Character 47: length of the 3rd labial palpus segment compared to the 1st.

Character 48: length of the 2nd labial palpus segment compared to the 1st.

Character 49: length of the labial palpus compared to the width of the head.

Character 50: length of the forewing compared to its width.

Character 51: length of the maxillary palpus compared to the width of the head.

APPENDIX V

THE TYPES OF NORTH AMERICAN CRAMBINAE (LEPIDOPTERA; PYRALIDAE) IN THE BRITISH MUSEUM (NATURAL HISTORY)

The species mentioned herein were described by Zeller, Walker, Grote, Hampson, Bleszynski, Christoph, Stephens, Drury, Leech, Haworth and Turati in order of importance. Most of the specimens described by Zeller have a green label with Zeller's handwriting; green was his code for North America. The specimens described by Walker from Nova Scotia all have a small pale blue round label with "N. Scotia Redman" and a tiny lozenge-shaped pale green label with "R", probably for Redman.

Throughout the text, the information in square brackets was added by myself. The question marks reflect my incapacity to understand clearly information on a label or are unsolved problems for which I have asked the help of the Curator of the Pyralidae at the British Museum, Mr. Michael Shaffer.

The species are presented in alphabetical order of the species name. For each species, the name is followed by the name of the describer and reference, the number of original specimens and type locality, the data on all labels for all lectotype designations, the BM genitalia slide number for the unique holotypes or previously designated lectotypes and finally, the currently accepted name. In addition to the labels listed for each lectotype, two more labels were affixed to these specimens; a

BM lectotype label was placed in first position and a label with "Lectotype species name by B. Landry 1991" was affixed last on the pin.

Unless otherwise indicated, the syntype, lectotype, paratype, paralectotype and holotype labels are small, white, circular with a pale blue, navy blue, yellow, pale blue and red border respectively.

List of names.

Crambus abtrusellus Walker 1863: 158. The description is based on one female from St. Martin's Falls, Albany River [Ontario]. Its BM genitalia slide no. is 1051. *Pediasia truncatella* (Zetterstedt).

Prionopteryx [sic] *achatina* Zeller 1863: 13. Apparently described from only one specimen of sex unspecified from North America. Type not located. *Prionapteryx achatina* Zeller.

Crambus aculeilellus Walker 1863: 158. Described from a single male from Georgia. Its BM genitalia slide No. is 18732. *Crambus satrapellus* (Zincken).

CALARINA Walker 1866b: 1769-1770 (-*Surattha*)

Type species *C. albirenella* Walker 1866b: 1770. By monotypy. Described from one male and one female from South Hindostan and Java. Lectotype designated by Bleszynski (1965). The syntype from Java was not located. The BM Slide No. is 7454. *Surattha nigrifascialis* (Walker).

Crambus alboclavellus Zeller 1863: 19. Described from one male specimen from Ohio. Its BM genitalia Slide label is No. 18735. *Crambus agitatellus* Clemens.

Crambus anceps Grote 1880a: 18. The description was based on 2 specimens of unspecified sex. One of these was located and made lectotype, with the following complement of labels. 1. Sauzalito Oct. 6; 2. Crambus anceps Grote Type; 3. Crambus anceps Grote; 4. Pyralidae Brit. Mus. Slide No. 4645 sex?. *Agriphila anceps* (Grote).

Crambus argentictus Hampson 1919: 290. Described from 3 ♂ and 6♀ from Mexico (Jalapa and Misantla) and 1♂ from Bahamas (Andros). One lectotype, with the following labels, and 10(??) paralectotypes were designated. 1. Syntype; 2. Type; 3. Jalapa Mexico M. Trujillo; 4. Crambus argentictus Hmpsn Type ♂; 5. Godman-Salvin Coll. 1904.-1. B.C.A. Lep. Het. Crambus quinquareatus, Zell.; 6. 117 Bleszynski 195; 7. Pyralidae Brit. Mus. Slide No. 2248 ♀. *Crambus quinquareatus* Zeller.

Crambus attenuatus Grote 1880a: 18-19. The original number of specimens from Vancouver Island was not specified in the description but 2 in the collection match it. One of those, with the following set of labels, was made lectotype. 1. Vancouver Island; 2. 5927; 3. Type; 4. Zell. Coll. 1884; 5. Crambus attenuatus Grote ♂ type; 6. Crambus attenuatus Grote. This specimen has no abdomen. The other syntype, made paralectotype, has no abdomen either??. *Agriphila attenuata* (Grote).

Crambus aureorufus Hampson 1919: 291. Described from 3 males from Brazil (São Paulo). Two of these were located. The lectotype, here designated, bears the following labels. 1. Syntype; 2. Type H.T.; 3. Sao Paulo. 88.-169; 4. Crambus aureorufus Hmpsn ♂ type; 5. 110 Bleszynski 195; 6. Pyralidae Brit. Mus. Slide No. 5592 ♀. The paralectotype has no abdomen. *Crambus satrapellus* (Zincken).

Crambus aurifimbrialis Walker 1863: 157. The description is based on 10 specimens of both sexes from Nova Scotia. One of these, with the following set of labels, is designated lectotype. 1. R; 2. N. Scotia Redman [upside down]; 3. Type [with a green contour]; 4. 86. Crambus aurifimbrialis.; 5. GAB 1938 71; 6. Pyralidae Brit. Mus. Slide No. ♂ 18729. None of the other syntypes were found??. *Agriphila vulgivagella* (Clemens).

Crambus bidens Zeller 1872: 535-536. Described from both sexes but without indication that there were more than 1♂ and 1♀ syntypes. One of these was located and designated lectotype. It bears the following labels. 1. Cr. bidens Z. Pack. Mass. [a Zeller green label]; 2. Zell. Coll. 1884; 3. Pyralidae Brit. Mus. Slide No. 18733 ♀. *Crambus bidens* Zeller.

Crambus biliturellus Zeller 1874: 429. The description is based on a single male from Vancouver Island. Its BM genitalia slide number is 5682. *Pediasia trisecta* (Walker).

Crambus bipunctellus Zeller 1863: 23. The description was based on at least a pair from Ohio and Illinois. A female with the following set of labels was made lectotype. 1. Type; 2. Illinois; 3. Crambus bipunctellus Mon. 23; 4. 2 punctellus Z.; 5. Zell. Coll. 1884; 6. GAB 1938 87; 7. 204 Bleszynski 195; 8. Pyralidae Brit. Mus. Slide No. 18738. Paralectos ??. *Arequipa turbatella* Walker.

Crambus cacuminellus Zeller 1850: 35-36. Three specimens are mentioned in the original description of this species although Bleszynski (1965: 297) referred to a ♀ holotype only. This female "type" is here made lectotype. It bears the following labels. 1. Lectotype; 2. Type [upside down]; 3. Cacuminellus Z., Vereinghl. p. 35., Graubundt. Hopff. lit 23/5 49 original; 4. Zell. Coll. 1884. This specimen is not dissected. No other syntypes were located. *Catoptria maculalis* (Zetterstedt).

STENOCHILO Hampson 1896: 922 (=*Thopeutis*)

typus *S. canicostalis* Hampson 1896: 950. By monotypy. Described from 1 female from Hillaya, Sind. [Pakistan?]. Its BM genitalia slide no. is 605. *Thopeutis galleriella* (Ragonot).

Crambus chalybirostris Zeller 1863: 40-41. The description is based on at least a pair from Ohio and Illinois. One of these was located and made lectotype, with the following set of labels. 1. Type; 2. Chalybirostris barbipalpellus Koll. Ohio Schl. lit. 400; 3. 8 [?]; 4. Zell. Coll. 1884; 5. GAB 1938 72; 6. Bisset tube not located B. Landry 1991. No other syntype was found??. *Agriphila vulgivagella* (Clemens).

Chilo crambidoides Grote 1880a: 15. Described from an unspecified number of species of unspecified sex from Kansas. A specimen in the collection is presumed to be the unique holotype. Its BM genitalia slide number is 100. *Diatraea crambidoides* (Grote).

Chilo culmicolellus Zeller 1863: 7. The description mentions a female from Columbia. This female specimen is not dissected. *Diatraea lineolata* (Walker).

Crambus curtellus Walker 1863: 160-161. The description is based on a male from St. Domingo. The specimen is in fact a female with genitalia slide no. 2221. *Fissicrambus fissiradiellus* (Walker).

Chilo demotella Walker 1866b: 1749-1750. The description is based on one male from unknown locality. The specimen has no abdomen. *Chilo demotellus* Walker.

EOREUMA Ely 1910: 204
Type species *Chilo densellus* Zeller 1881: 158. The description of this species mentions two males and three females from Texas. A male with the following complement of labels is here made lectotype. 1. Lectotype [small round label with red circle in middle]; 2. Bosque Co. Texas; 3. Densellus Z. ♂ Texas Stt. 68; 4. Zell. Coll. 1884 5 24/5; 6. 7125 Pyralidae Brit. Mus. Slide No. ♂. Four paralectotypes are also designated. *Eoreuma densella* (Zeller).

EPINA Walker 1866b: 1707

typus *E. dichromella* Walker 1866b: 1707. By monotypy. The description is based on one female from unknown locality. The type is in fact a male with BM genitalia slide no. 7133. *Epina dichromella* Walker.

Crambus dissectus Grote 1880a: 16. Described from one specimen of unspecified sex from New York. The specimen is a ♀ with BM Slide No. 18740. *Crambus alienellus dissectus* Grote.

Crambus duplicatus Grote 1880b: 79. Described from one female (in fact a male) from New York. Its male genitalia BM slide no. is 4616. *Neodactria luteolella* (Clemens).

PROPEXUS Grote 1880a: 19 (=*Thaumatopsis*)

typus *Crambus (Propexus) edonis* Grote 1880a: 19. By monotypy. This species was described from 2 males and 2 females from Kansas. A male was selected as the lectotype. It bears the following labels. 1. Type; 2. Propexus edonis Grote ♂ Type; 3. GAB 1938 39; 4. Pyralidae Brit. Mus. Slide No. ♂ 18722. The 3 other syntypes were made paralectotypes. *Thaumatopsis edonis* (Grote).

Note: three specimens, including one labelled Type, are under *P. displosus* MS in the BM collection. This name has not been published and is consequently not valid. It probably refers to a series of 3 specimens from Texas that Grote (1880a: 19) believed to be probably the same as *P. edonis*. This is verified by the examination of the male genitalia of one of those (Pyralidae Brit. Mus. Slide No. 18723).

Crambus elegantellus Walker 1863: 179. Described from 4 specimens of both sexes from unknown type locality. The lectotype, here designated, bears the following labels. 1. Syntype; 2. Type [with green contour]; 3. 140. Crambus elegantellus.; 4. GAB 1938 81. 5. Pyralidae Brit. Mus. Slide No. 18731 ♀. No paralectotypes are designated. Possible candidates are probably in the collection but they have no labels attached to them. *Crambus satrapellus* (Zincken).

NUARACE Walker 1863: 188 (-*Prionapteryx*)

typus *N. eugraphis* Walker 1863: 188. By monotypy. Described from 1♀ from Sto. Domingo. The abdomen on this specimen is missing. *Prionapteryx eugraphis* (Walker).

Crambus exesus Grote 1880a: 16-17. Presumably described from 2 specimens although the number of syntypes is not specified. The lectotype, here designated, bears the following labels. 1. Type; 2. Crambus exesus Grote Type [82-54 on the back]; 3. 4; 4. Abdomen missing. The paralectotype is presumed to be the specimen that Grote sent to Zeller for identification in 1878 (re: correspondance of Zeller and Grote in BM entomology library) and for which Zeller had no name but placed it between *latistrius* and *halterellus* (see Grote 1880a: 17). It bears the following labels. 1. 4; 2. Grote 4/78 [a green Zeller label]; 3. Zell. Coll. 1884; 4. Abdomen missing. *Crambus unistriatellus* Packard.

Crambus exsiccatus Zeller 1863: 37-38. The description was based on 3 males and 7 females from Illinois. A lectotype male with the following set of labels is here designated. 1. Holotype; 2. Exsiccatus Z. fuscisquamellus Koll. Illinois Jgchbg.; 3. Zell. Coll. 1884; 4. GAB 1938 50; 5. 240 Bleszynski 195; 6. Pyralidae Brit. Mus. Slide No. ♂ 5683. No other syntypes were found. Pediasia trisecta (Walker).

Crambus fissiradiellus Walker 1863: 160. The description is based on two females from Jamaica and St. Domingo. The specimen from Jamaica was made lectotype by Bleszynski (1967: 154) with the note that the genitalia slide 1952 86 was lost. This slide is still considered lost. The specimen from St. Domingo was not located. Fissicrambus fissiradiellus (Walker).

Crambus floridus Zeller 1872: 537. Described from 4 specimens of both sexes from Massachusetts. A lectotype (but no paralectotypes) was designated by Klots 1940: 56-57. The BM Slide No. is 18730. Crambus pascuellus floridus Zeller. Any other syntype?

Crambus fuscicostellus Zeller 1863: 44. Described from several specimens of both sexes from Illinois and Ohio. A specimen from Ohio with the following complement of labels was made lectotype. 1. Type; 2. Crambus a Schlig. lit 427; 3. Fuscicostellus Ohio Scldg.[?]; 4. GAB 1938 55. The Bisset tube containing the genitalia was not located. Fissicrambus mutabilis (Clemens).

Catharylla fuscipes Zeller 1863: 51-52. Described from at least a male and a female from Illinois. A specimen with the following complement of labels is here made lectotype. 1. Type; 2. Catharylla fuscipes Z. Mon.

51 Am. Sept.; 3. Zell. Coll. 1884; 4. 1939/236 [upside down]; 5. ♂ Pyralidae Brit. Mus. Slide No. 13030. No other syntypes were located??. Argyria subaenescens (Walker).

Crambus fuscisquamellus. This is a MS name of Kollar mentioned as such in Zeller (1863: 37). Hence it is not a valid name.

Crambus geminatellus Zeller 1863: 48. Described from one male taken in North America. This specimen was not located in the collections of the BM. Pediasia dorsipunctella (Kearfott).

Eromene gigantea Turati 1924: 129. The original description is based on 5 specimens of unspecified sex from Berca [Libya]. A lectotype female and 4 paralectotypes (2 males, 2 females) were designated by Schouten (1988). The lectotype genitalia slide no. is 17540. Euchromius ocelleus (Haworth).

Crambus goodellianus Grote 1880a: 17. Described from an unspecified number of specimens of unspecified sex from Massachusetts and Pennsylvania. A specimen, with the following set of labels, was made lectotype. 1. Type; 2. Crambus goodellianus Grote Type; 3. Crambus goodellianus Grote; 4. GAB 1938 70; 5. 126 Bleszynski 195. Unfortunately, the tube in which the genitalia had been stored in by Bisset was not located. No other syntypes were found. Parapediasia decorella (Zincken). Prionopteryx [sic] griseosparsa Hampson 1896: 964. Described from 1♀ from Colorado. The specimen is in fact a male. Dissected? my photo too dark.

Pseudoschoenobius opalescalis (Hulst).

Crambus hastiferellus Walker 1863: 155-156. Described from 8 specimens of both sexes from Nova Scotia. One male was designated lectotype by Klots (1940: 59), the 4 other males of the series were designated "cotypes" and the females were believed to belong to C. pascuellus (L.). The BM Slide No. of the lectotype is 18742.In the collection, there are 4 male paralectotypes under C. leachellus and 3 female paralectotypes under C. hamellus (Thunberg). Crambus leachellus (Zincken).

Crambus hemiochrellus Zeller 1877: 49-51. The description is based on several specimens of both sexes from Texas. Bleszynski (1963a :158) designated a male lectotype and 1 male, 2 females paralectotypes. The lectotype BM genitalia slide no. is 18724.
Fissicrambus hemiochrellus (Zeller).

Fissicrambus hospition Bleszynski 1963a: 159-160. The description mentions a male holotype and a female paratype in the BM from Tucson, Arizona, and another female paratype from the same locality in the author's collection. The holotype genitalia slide no. is 1550.
Loxocrambus hospition Bleszynski.

MICROCAUSTA Hampson 1895: 340

typus M. ignifimbrialis Hampson 1895: 340. By monotypy. Described from an unspecified number of males from Grenada and St. Vincent. A male with the following set of labels is here made lectotype. 1. Lectotype; 2. St.

Vincent, W.I. H.H., Smith; 3. W. Indies 94-247; 4. ♂ Pyralidae Brit. Mus. Slide No. 15356; 5. Microcausta ignifimbrialis Hmpsn type ♂; 6. Lectotype Microcausta ignifimbrialis Hampson det. M. Shaffer 1979. The other syntype(s) was (were) not located??. *Microcausta ignifimbrialis* Hampson.

Crambus indotatellus Walker 1866b: 1752-1753. Described from 1♂ from St. Martin's Falls, Albany River [Ontario]. The specimen is in fact a female, BM Slide No. 1071. *Crambus alienellus labradoriensis* Christoph.

Crambus innotatellus Walker 1863: 156. Described from 4 specimens of both sexes from Nova Scotia. All 4 specimens were located. The lectotype, here designated, bears the following labels. 1. Syntype; 2. N. Scotia Redman; 3. R; 4. Pyralidae Brit. Mus. Slide No. 18743 ♀. Two paralectotypes have no abdomen, the other was dissected by Bisset (GAB 1938-90) but it was not located. *Crambus perlellus innotatellus* Walker.

Crambus inornatellus Walker 1863: 157. The description is based on a pair from Nova Scotia. A female lectotype was designated by Bleszynski (1965: 392), its BM genitalia slide label is 4611. The other syntype was not located. *Tehama bonifatella* (Hulst).

Crambus interminellus Walker 1863: 157-158. The description is based on 6 specimens of both sexes from Nova Scotia. A lectotype with the following set of labels is here designated. 1. R; 2. N. Scotia Redmond; 3. Type [with green contour]; 4. Crambus inteiminellus; 5. GAB 1938 48; 6. Pyralidae Brit. Mus. Slide No. 5681 sex?. No other syntypes were found??. I didn't make a genitalia drawing or noted the sex of the lectotype *Pediasia trisecta* (Walker).

Crambus interruptus Grote 1877: 101-102. The description is based on a series of specimens of unspecified sex from Grimsby, Ontario and at least one other locality in Canada. A lectotype with the following labels was designated. 1. Type; 2. Crambus interruptus Grote Type; 3. Crambus interruptus Grote -myellus?; 4. Pyralidae Brit. Mus. Slide No. 5639 ♀; 5. 93 gren; 6. GAB 1938 60. Three other specimens were made paralectotypes. *Catoptria latiradiella* (Walker).

SURATTHA Walker 1863: 75

typus *S. invectalis* Walker 1863: 76. By monotypy. Described from 1 ♀ from unknown locality. The BM slide No. is 2945. *Surattha invectalis* Walker.

DIPTYCHOPHORA Zeller 1866: 153-154

typus *D. kuhlweini* Zeller 1866: 154-155. By monotypy. The description is based on 1 female from Rio de Janeiro, Brasil. The type has not been located as noted by Gaskin (1986: 110). *Diptychophora kuhlweini* Zeller.

Crambus labradoriensis Christoph 1858: 314. Described from an unspecified number of specimens. One specimen with the following labels was designated lectotype. 1. Zell. Coll. 1884; 2. Cramb. labradoriensis Z. Mon. 21 Labr. Christoph [a Zeller green label]; 3. G.A.B. 1938 62; 4. Pyralidae Brit. Mus. Slide No. 18741 ♂. No other syntypes were located. *Crambus alienellus labradoriensis* Christoph.

Crambus laciniellus Grote 1880a: 18. The description is based on a large series of both sexes from Maine. A lectotype, with the following set of labels is here designated. 1. ♂; 2. Crambus laciniellus ♂ Type Mt. Desert; 3. GAB 1938 61; 4. Pyralidae Brit. Mus. Slide No. 4610 ♂. Is it my designation of lectotype? Are there any paralectotypes? *Pediasia laciniella* (Grote).

Crambus latiradiellus Walker 1863: 157-158. Description based on 2 males from Nova Scotia. These were both located and one, with the following set of labels, was made lectotype. 1. Syntype; 2. Type [with green contour]; 3. R; 4. N. Scotia Redman; 5. GAB 1938 59; 6. Pyralidae Brit. Mus. Slide No. 18727 ♀. The other syntype was made paralectotype. *Catoptria latiradiella* (Walker).

Crambus lativittellus Zeller 1863: 18. Described from one female from unknown locality. This specimen was not located. Although this specimen should have been considered a paralectotype of *pulchellus*, it has been used in contemporary literature and consequently is considered valid.?? ask Ales. *Crambus leachellus* (Zincken).

Crambus leuconotus Zeller 1881: 167-168. Described from 20 specimens of both sexes from Guarinó, Columbia. One lectotype with the following labels and 13 paralectotypes were designated. 1. Syntype; 2. Type; 3. Zell. Coll. 1884; 4. Crambus leuconotus Z., Columb. Pet.; 5. 113 Bleszynski 195; 6. Pyralidae Brit. Mus. Slide No. 2247 ♂. The six other syntypes were not in the main collection. *Crambus leuconotus* Zeller.

Crambus leucorhabdon Hampson 1919: 440. Described from 1 female from Florissant, Colorado. The female genitalia slide is BM no. 7911. "*Crambus dimidiatellus* Grote.

Crambus lienigiellus Zeller 1843: 142. The description is based on 2 males from Livonia (Kokenhusen and Morästen) [part of the Baltic USS Republics of Estonia and Latvia]. Bleszynski (1965: 372) mentions that the types are lost. The syntypes could not be located in the BM collections. *Pediasia truncatella* (Zetterstedt).

Leucania lineolata Walker 1856: 100. The description is based on one specimen of unspecified sex from Venezuela. Its BM genitalia slide label is ♀ 7126. *Diatraea lineolata* (Walker).

Crambus macropterellus Zeller 1863: 48. Described from a single female from North America. It was not located in the BM collections. *Thaumatopsis pexella* (Zeller).

UROLA Walker 1863: 181

typus *U. michrochysella* Walker 1863: 181. By subsequent designation by Bleszynski (1963b: 94). Described from 12 specimens of both sexes from North America, Georgia, Honduras and unknown locality. Two of these specimens were found. One with the following set of labels is here designated lectotype. 1. Type [with green contour]; 2. 112/85 [with "N. Amer." on back]; 3. 1957 307; 4. Pyralidae Brit. Mus. Slide No. 13031 ♂. The paralectotype bears the same labels??. *Urola nivalis* (Drury).

Crambus micralis Hampson 1919: 286 The description mentions 1 male type from Colombia (Honda) and 2 males and 2 females from Tanamo, Cuba. The holotype has BM genitalia slide no. 5569. Microcrambus discludellus (Möschler). Are the 4 paratypes there?

Crambus minuellus Walker 1863: 164. Described from a female from Honduras. The type has no abdomen. Fissicrambus minuellus (Walker).

Crambus moestellus Walker 1863: 155. Described from 1♀ from St. Martin's Falls, Albany River [Ontario]. The BM Slide No. is 18745. Crambus alienellus labradoriensis Christoph.

PRIONAPTERYX Stephens 1834: 316

typus P. nebulifera Stephens 1834: 317. By monotypy. Described from one specimen (sex unspecified) from unknown locality. The BM Slide No. is 7105. Prionapteryx nebulifera Stephens.

Chilo neuricellus Zeller 1863: 8. The description mentions a female from Venezuela. The type is presumed lost (Box 1931). One specimen simply labelled Venezuela maybe the type. Diatraea lineolata (Walker).

Phaleana Pyralis nivalis Drury 1773: index. This species was apparently described from only one specimen of unspecified sex. The type was not found in the BM collection. Urola nivalis (Drury).

Crambus nivihumellus Walker 1863: 159-160. Described from 2 females from

North America and another from St Martin's Falls, Albany River [Ontario]. One of these, with the following labels, is designated lectotype. 1. Syntype, 2. Type [green contour]; 3. N.-Amer. [112/85 on back]; 4. 93. Crambus nivihumellus.; 5. GAB 1938 89; 6. Pyralidae Brit. Mus. Slide No. 18737 ♂. The paralectotype from Albany River has two additional labels: 1. 271; 2. 912 [or 913] Crambus striatus. The other paralectotype, from North America, has no abdomen. Crambus girardellus Clemens.

VAXI Bleszynski 1962: 11-12

typus Conocrambus obliqua Hampson 1919: 444. By original designation. This species was described from 1 male from Castro Paraña, Brazil. It is in fact a female with BM genitalia slide no. 7131. Vaxi obliqua (Hampson).

Crambus occidentalis Grote 1880a: 16. Described from 3 specimens of unspecified sex from Sauzalito, California. The lectotype, here designated, bears the following labels. 1. Lectotype; 2. Lectotype [green contour]; 3. Sauzalito Oct. 8.76; 4. Crambus occidentalis Grote Type; 5. Abdomen missing. One of the two paralectotypes was dissected by Bisset (GAB 1938-79) but the dissection was not located. Crambus occidentalis Grote.

Palparia ocellea Haworth 1811: 486. Described from one English specimen??. The BM genitalia slide no. is 17541. Euchromius ocelleus (Haworth).

Prionopteryx [sic] olivella Grote 1881b: 274. Described from 1♂ from Carbondale, Illinois. The BM Slide No. is 7108. Mesolia incertella (Zincken).

Crambus oregonicus Grote 1880a: 17. The description is based on 2 specimens of unspecified sex from Oregon. One of these, a male, was made lectotype by Klots (1942: 421). It is in the collections of the American Museum of Natural History, New York. A paralectotype in the BM collection is here designated. It bears the following labels. 1. Paralectotype; 2. Type [upside down]; 3. Oregon; 4. 5923; 5. Crambus oregonicus Grote ♂ Type; 6. Crambus oregonicus Grote; 7. GAB 1938 73. Genitalia not remounted??. Catoptria oregonica (Grote).

NAGAHAMA Marumo 1933: 46 (=Platytes)

typus Crambus ornatellus Leech 1889: 106. By original designation. The description was based on 1 male specimen taken at Nagahama, Japan. Its BM genitalia Slide no. is 7072. Platytes ornatella (Leech).

Crambus pectinifer Zeller 1877: 51-53. The description was based on a series of specimens of both sexes from Texas. One of those, a male with the following set of labels, was designated lectotype. 1. Type; 2. 29 IX; 3. Crambus pectinifer Z.; 4. Pyralidae Brit. Mus. Slide No. ♂ 5510; 5. 20 Bleszynski 195. Four paralectotypes were designated; 2 with Zeller green labels and 2 with Erschev [or r?] labels and date labels 29.IX and 30.IX as in the description. Thaumatopsis pectinifer (Zeller).

Crambus pexellus Zeller 1863. 48. Described from an unspecified number of males from Georgia. A specimen with BM slide no. 18388 could possibly be made lectotype. Thaumatopsis pexella (Zeller).

Crambus polyactinellus Zeller 1863: 25-26. Described from one female, "probably from America". This type was not located in the BM. Parapediasia decorella (Zincken).

Crambus profanellus Walker 1866b: 1753-1754. The description is based on a male from Jamaica. The type has no abdomen. Fissicrambus profanellus (Walker).

DIPHRYX Grote 1881b: 273 (=Chilo)

typus D. prolatella Grote 1881b: 273. By monotypy. The description is based on 1 female from Wisconsin. This specimen has no abdomen. Chilo plejadellus Zincken.

Urola pulchella Walker 1863: 83. Description based on 1 female from North America. The abdomen of this specimen is missing.
Vaxi auratella (Clemens).

Crambus pulchellus Zeller 1863: 18. Described from one male from North America, Illinois. Its forewings have been glued back to the thorax and the genitalia slide number is 5677. Crambus leachellus (Zincken).

Crambus quadrinotellus Zeller 1877: 53-55. Described from 1 male and 7 females from Chiriqui (Panama). Bleszynski (1963a: 161) designated a lectotype but no paralectotypes. The lectotype genitalia BM slide number is 7219 ♀. *Fissicrambus quadrinotellus* (Zeller). Any paralectotypes or syntypes in the collection?

Crambus quinquareatus Zeller 1877: 38. Described from 3 males and 1 female from Texas. Only one of those 4 syntypes was located. It is here designated lectotype and bears the following labels. 1. Type; 2. Crambus quinquareatus Z. Ex. Lep. p. 40 Texas B 4/75; 3. Zell. Coll. 1884; 4. GAB 1938 75; 5. 125 Bleszynski 195. Unfortunately, the Bisset tube in which the genitalia were stored was not located. *Crambus quinquareatus* Zeller.

Crambus repandus Grote 1880b: 79-80. The description is based on a male from Colorado. This holotype is in fact a female (BM slide no. 18725). *Thaumatopsis repanda* (Grote).

Hypena rufinalis Walker 1866a: 1133. The description is based on 1 female from St. Martin's Falls, Albany River [Ontario]. The specimen is in fact a male with BM genitalia slide no. 5640. *Pediasia truncatella* (Zetterstedt).

Catharylla rufisignella Zeller 1872: 542. The description was based on 1 male from Texas. The abdomen of this specimen is missing. *Argyria rufisignella* (Zeller).

Crambus ruptifascia Hampson 1919: 291. The description was based on 1 female from Mexico (Milpas). The BM genitalia slide no. is 2237. *Fernandocrambus ruptifascia* (Hampson).

Crambus ruricolellus Zeller 1863: 40. Described from at least a pair from Ohio and Illinois. One syntype located and made lectotype, with the following set of labels. 1. Type; 2. Zell. Coll. 1884; 3. Ruricolellus Z. contaminatellus Schl. Ohio Schl. lit. 428; 4. GAB 1938 88; 5. Pyralidae Brit. Mus. Slide No. 18728 ♂. *Agriphila ruricolella* (Zeller).

Jartheza sabulifera Walker 1863: 85. Description based on 1 male from unknown locality. Its BM genitalia slide no. is 7031. *Chilo plejadellus* Zincken.

Crambus saltuellus Zeller 1863: 22. Described from more than one specimen from Illinois and Ohio. The syntypes were not traced. *Crambus saltuellus* Zeller.

Crambus semifusellus Walker 1863: 159. Described from 2 males from North America. The 2 syntypes were found. The designated lectotype bears the following labels. 1. Syntype; 2. Type; 3. N. Amer. [112/8? on back]; 4. GAB 1938 85; 5. Pyralidae Brit. Mus. Slide No. 18736 ♂. The paralectotype has no abdomen. *Crambus laqueatellus* Clemens.

Crambus sericinellus Zeller 1863: 49. Described from 1♀ from North America, Ohio. The specimen singled-out as type in the collection is not the type because it bears a label with date 17/4/78, indicating that it was received at that date It was sent by Grote as noted in the correspondance of Grote to Zeller. A possible holotype was located. It was dissected by Bisset (GAB 1938 91) but this dissection was not located. Crambus perlellus innotatellus Walker.

Chilo squamulella Zeller 1881: 158-159. Described from 2 females from Bosque Co., Texas. A specimen with the following set of labels is here made lectotype. 1. Lectotype [small round label with red circle in middle]; 2. Bosque Co. Texas; 3. Squamulellus Texas Stt. 65; 4. Zell. Coll. 1884; 5. 7126 Pyralidae Brit. Mus. Slide No. ♀. The other female is here made paralectotype. Haimbachia squamulella (Zeller).

Urola subaenescens Walker 1863: 182. Described from 1 male from unknown locality. Its BM genitalia slide no. is 13029. Argyria subaenescens (Walker).

CATHARYLLA Zeller 1863: 50 (=Argyria?)

typus Crambus tenellus Zeller 1839: 174. By subsequent designation by Schaus 1922: 131. The description is based? on 1 female from South America. This specimen has BM slide no. 7094. Catharylla tenella Zeller.

PARAPEDIASIA Bleszynski 1966: 485

typus Crambus tenuistrigatus Zeller 1881: 168-170. By original designation. The description was based on 2 males and one female from Mariquita, Columbia. Bleszynski (1963a: 138) designated a male as the lectotype of this species and stated that no other syntypes could be found, which is unfortunately corroborated here. The lectotype genitalia slide no. is 2219. Parapediasia tenuistrigata (Zeller).

Crambus terminellus Zeller 1863: 27. The description is based on at least a male and a female from Ohio. A male with the following set of labels was made lectotype. 1. Type; 2. terminellus Schl. h lit 427; 3. Zell. Coll. 1884; 4. GAB 1938 64; 5. Pyralidae Brit. Mus. Slide No. 18726 ♂. No other syntypes were found?? Microcrambus elegans (Clemens).

Crambus topiarius Zeller 1866: 155-156. Described from 5 males and 2 females from Maine. A lectotype with the following labels was designated. 1. Lectotype; 2. N. Amer. ???65; 3. Zell. Coll. 1884; 4. Lectotype Crambus topiarius Zeller det. M. Shaffer, 1979. The lectotype is not dissected. One male paralectotype with BM SLide No. 18744, was also designated. Others?? Chrysoteuchia topiaria (Zeller).

Crambus trichostomus Christoph 1858: 313-314. The description of this species was made from an unspecified number of specimens of unspecified sex. A lectotype should be made with a BM specimen. Catoptria trichostoma (Christoph).

CARVANCA Walker 1856: 119 (=Pediasia)

typus C. trisecta Walker 1856: 119-120. By monotypy. Described from one specimen of unspecified sex from Nova Scotia. Its BM genitalia slide no. is ? 4620. I didn't make a drawing or noted the sex. Pediasia trisecta (Walker).

AREQUIPA Walker 1863. 195.

typus *A. turbatella* Walker 1863: 196. By monotypy. The description was based on 2 females from the United States. One, with the following labels, was designated lectotype. 1. Syntype; 2. Type [with a green contour]; 3. U.S. [with 44/1 on back]; 4. 1. Arequipa turbatella; 5. GAB 1938 86; 6. Pyralidae Brit. Mus. Slide No. 18739 ♂. The other syntype was located and made paralectotype. *Arequipa turbatella* Walker.

Crambus undatus Grote 1881a: 35. This species was apparently described from only 1 specimen of unspecified sex. Its dissected genitalia are on BM slide no. ???18746 or 18747. *Agriphila undata* (Grote).

APPENDIX VI

List of the Crambinae of America north of Mexico.

(The species synonyms as well as the subspecies names are omitted). Nomenclatural changes are indicated in bold face.

CRAMBINAE

PRIONAPTERYGINI new tribe

Hemiplatytes Barnes & Benjamin, 1924
Alamogordia Dyar & Heinrich, 1927

epia (Dyar, 1912)
parallela (Kearfott, 1908)
prosenes (Dyar, 1912)

Eufernaldia Hulst, 1900

cadarella (Druce, 1896)

Surattha Walker, 1863
Calarina Walker, 1866
Platytesia Strand, 1919

indentella Kearfott, 1908
santella Kearfott, 1908

Mesolia Ragonot, 1888
Eugrotea Fernald, 1896

baboquivariella (Kearfott, 1907)
huachucaella Kearfott, 1908
incertella (Zincken, 1821)
oraculella Kearfott, 1908

Prionapteryx Stephens, 1834
Nuarace Walker, 1863

achatina Zeller, 1863
cuneolalis (Hulst, 1886)
nebulifera Stephens, 1834
serpentella Kearfott, 1908
yavapai (Kearfottt, 1908)

Pseudoschoenobius Fernald, 1896

opalescalis (Hulst, 1886)

/

HAIMBACHIINI new tribe

Thopeutis Hübner, 1818
Cephis Ragonot, 1892
Stenochilo Hampson, 1896
Hombergia de Joannis, 1910

forbesellus (Fernald, 1896)

Occidentalia Dyar & Heinrich, 1927

comptulatalis (Hulst, 1886)

Xubida Schaus, 1922

chiloidella (Barnes & McDunnough, 1913)
dentilineatella (Barnes & McDunnough, 1913)
linearella (Zeller, 1863)
lipan Klots, 1970
panalope (Dyar, 1917)
puritella (Kearfott, 1908)
punctilineella (Barnes & McDunnough, 1913)
relovae Klots, 1970

Haimbachia Dyar, 1909

albescens Capps, 1965
arizonensis Capps, 1965
cochisensis Capps, 1965
diminutalis Capps, 1965
discalis Dyar & Heinrich, 1927
floridalis Capps, 1965
indistinctalis Capps, 1965
pallescens Capps, 1965
placidella (Haimbach, 1907)
squamulella (Zeller, 1881)

Eoreuma Ely, 1910

arenella Blanchard & Knudson, 1983
callista Klots, 1970
confederata Klots, 1970
crawfordi Klots, 1970
densella (Zeller, 1881)
evae Klots, 1970
loftini (Dyar, 1917)
multipunctella (Kearfott, 1908)

UNASSIGNED GENERA

- *Eoina* Walker, 1866
  - *Diatraenopsis* Dyar & Heinrich, 1927

      - *dichromella* (Walker, 1866)
      - *alleni* (Fernald, 1888)

- *Chilo* Zincken, 1817
  - *Chilona* Sodoffsky, 1837
  - *Proceras* *auct.* (not Bojer *et al.*, 1856)
  - *Borer* Guenée, 1862
  - *Diphryx* Grote, 1881
  - *Nephalia* Turner, 1911
  - *Hypiesta* Hampson, 1919
  - *Silveria* Dyar, 1925
  - *Chilotraea* Kapur, 1950

      - *erianthalis* Capps, 1963
      - *demotellus* Walker, 1866
      - *plejadellus* Zincken, 1821

- *Diatraea* Guilding, 1828
  - *Iesta* Dyar, 1909
  - *Diatraerupa* Schaus, 1913
  - *Trinidadia* Dyar & Heinrich, 1927
  - *Eodiatraea* Box, 1953
  - *Crambidiatraea* Box & Capps, 1955
  - *Zeadiatraea* Box, 1955

      - *crambidoides* (Grote, 1880)
      - *evanescens* Dyar, 1917
      - *grandiosella* Dyar, 1911
      - *lineolata* (Walker, 1856)
      - *lisetta* (Dyar, 1909)
      - *saccharalis* (F., 1794)
      - *venosalis* (Dyar, 1917)

ARGYRIINI

- *Argyria* Hübner, 1818
  - *Catharylla* Zeller, 1863

      - *lacteella* (F., 1794)
      - *nummulalis* Hübner, 1818
      - *rufisignella* (Zeller, 1872)
      - *subaenescens* (Walker, 1863)

- *Urola* Walker, 1863

      - *nivalis* (Drury, 1773)

Vaxi Bleszynski, 1962

auratella (Clemens, 1860)
critica (Forbes, 1820)
tripsacas (Dyar, 1921)

DIPTYCHOPHORINI

Microcausta Hampson, 1895

flavipunctalis Barnes & McDunnough, 1913
bipunctalis Barnes & McDunnough, 1914

Diptychophora Zeller, 1866
Ditomoptera Hampson, 1893
Scissolia Barnes & McDunnough, 1914
Colimea Dyar, 1925

harlequinalis (Barnes & McDunnough, 1914)
incisalis (Dyar, 1925)

CRAMBINI **status revised**

Euchromius Guenée
Ommatopteryx Kirby, 1897
Eromene Hübner, 1825, praeoccupied by Hübner, 1821

ocelleus (Haworth, 1811)
californicalis (Packard, 1873)

Platytes Guenée, 1845
Nagahama Marumo, 1933

vobisne Dyar, 1920

Catoptria Hübner, 1825
Exoria Hübner, 1825

trichostoma (Christoph, 1858)
maculalis (Zetterstedt, 1840)
latiradiella (Walker, 1863)
oregonica (Grote, 1880)

Thaumatopsis Morrison, 1874, **status revised**
Propexus Grote, 1880

pexella-group

edonis (Grote, 1880)
magnifica (Fernald, 1891)
pexella (Zeller, 1863)

fernaldella-group

atomosella Kearfott, 1908
fernaldella Kearfott, 1905
fieldella Barnes & McDunnough, 1912
floridella Barnes & McDunnough, 1913

bolterella-group

bolterella (Fernald, 1887), **new combination**
crenulatella Kearfott, 1908
digramella (Hampson, 1919), **new combination**
repanda (Grote, 1880)

pectinifer-group

actuella Barnes & McDunnough, 1918
pectinifer (Zeller, 1877)
solutella (Zeller, 1863)

Tehama Hulst, 1888

bonifatella (Hulst, 1887)

Fissicrambus Bleszynski, 1963, **status revised**

albilineellus Fernald, 1893, **new combination**
quadrinotellus Zeller, 1877
fissiradiellus (Walker, 1863)
haytiellus (Zincken, 1821)
hemiochrellus (Zeller, 1877)
intermedius (Kearfott, 1908)
minuellus (Walker, 1863)
mutabilis (Clemens, 1860)
profanellus (Walker, 1866)

Microcrambus Bleszyski, 1963

biguttellus (Forbes, 1920)
copelandi Klots, 1968
croesus Bleszynski, 1967
discludellus (Möschler, 1890)
elegans (Clemens, 1860)
kimballi Klots, 1968
matheri Klots, 1968
minor (Forbes, 1920)
polingi (Kearfott, 1908)

Loxocrambus Forbes, 1920, **status revised**

awemensis McDunnough, 1929
canellus Forbes, 1920
mohaviellus Forbes, 1920
coloradellus Fernald, 1893, **new combination**
hospition Bleszynski, 1963

Neodactria B. Landry, **new genus**

caliginosella (Clemens, 1860), **new combination**
luteolella (Clemens, 1860), **new combination**
modestella (Barnes & McDunnough, 1918), **new combination**
murella (Dyar, 1904), **new combination**
zeella (Fernald, 1885), **new combination**

Arequipa Walker, 1863

turbatella Walker, 1863

Pediasia Hübner, 1925
Carvanca Walker, 1856
Pseudopediasia Ganev, 1987
Oseriates Fazekas, 1991, **new synonym**

abnaki (Klots, 1942)
aridella (Thunberg, 1788)
browerella (Klots, 1942)
dorsipunctella (Kearfott, 1908)
ericella (Barnes & McDunnough, 1918)
laciniella (Grote, 1880)
trisecta (Walker, 1856)
truncatella (Zetterstedt, 1840)

La Bleszynski, 1966

cerveza B. Landry, **new species**

Parapediasia Bleszynski, 1966, **status revised**

decorella (Zincken, 1821)
ligonella (Zeller, 1881)
teterrella (Zincken, 1821)
torquatella B. Landry, **new species**
hulstella (Fernald, 1885), **new combination**

Almita B. Landry, **new genus**

portalia B. Landry, **new species**
texana B. Landry, **new species**

Raphiptera Hampson, 1896

argillaceella (Packard, 1867)

Agriphila Hübner, 1825

anceps (Grote, 1880)
attenuata (Grote, 1880)
biarmica (Tengström, 1865)
biothanatalis (Hulst, 1886)
costalipartella (Dyar, 1921)
plumbifimbriella (Dyar, 1904)
ruricolella (Zeller, 1863)
straminella (Denis & Schiffermüller, 1775)
undata (Grote, 1881)
vulgivagella (Clemens, 1860)

Fernandocrambus Aurivillius, 1922
Juania Aurivillius, 1922

harpipterus (Dyar, 1916)
ruptifascia (Hampson, 1919)

Chrysoteuchia Hübner, 1825
Amphibolia Snellen, 1884
Veronese Bleszynski, 1962

topiaria (Zeller, 1866)

Crambus Fabricius, 1798, **status revised**
Palparia Haworth, 1811
Tetrachila Hübner, 1822
Argyroteuchia Hübner, 1825
Chilus Billberg, 1820

agitatellus Clemens, 1860
ainsliellus Klots, 1942
albellus Clemens, 1860
alienellus (Zincken, 1817)
angustexon Bleszynski, 1962
awemellus McDunnough, 1921
bidens Zeller, 1872
bigelovi Klots, 1967
braunellus Klots, 1940
cockleellus Kearfott, 1908
cypridalis Hulst, 1886
cyrilellus Klots, 1942
daeckellus Haimbach, 1907
girardellus Clemens, 1860
gausapalis Hulst, 1886
hamellus (Thunberg, 1794)

<u>harrisi</u> Klots, 1967
<u>johnsoni</u> Klots, 1942
<u>laqueatellus</u> Clemens, 1860
<u>leachellus</u> (Zincken, 1818)
<u>leuconotus</u> Zeller, 1882
<u>lyonsellus</u> Haimbach, 1915
<u>multilinellus</u> Fernald, 1887
<u>occidentalis</u> Grote, 1880
<u>pascuellus</u> (L., 1798)
<u>perlellus</u> (Scopoli, 1763)
<u>praefectellus</u> (Zincken, 1821)
<u>quinquareatus</u> Zeller, 1877
<u>rickseckerellus</u> Klots, 1940
<u>saltuellus</u> Zeller, 1863
<u>sanfordellus</u> Klots, 1942
<u>sargentellus</u> Klots, 1942
<u>satrapellus</u> (Zincken, 1821)
<u>sperryellus</u> Klots, 1940
<u>trichusalis</u> Hulst, 1886
<u>tutillus</u> McDunnough, 1921
<u>unistriatellus</u> Packard, 1867
<u>watsonellus</u> Klots, 1942
<u>whitmerellus</u> Klots, 1942
<u>youngellus</u> Kearfott, 1908

UNASSIGNED SPECIES OF CRAMBINI

"<u>Crambus</u>" <u>dimidiatellus</u> Grote, 1883
"<u>Crambus</u>" <u>angulatus</u> Barnes & McDunnough, 1918

GLOSSARY OF TERMS ON THE TYMPANAL ORGANS

Following each term, in parentheses, is the equivalent term used by Minet (1982 et seq.) and the one used by Maes (1985). Idem means that the same term was used by Minet and Maes respectively.

Praecinctorium (idem, idem): bag-shaped, scaled medio-ventral extension of the thoraco-abdominal membrane.

Scoloparium (idem, idem): nervous structure connecting the tympanum to a fix point on the tympanic drum, usually on the tympanic crest.

Spinula (idem, idem): small, tooth- or spine-shaped sclerite situated in the middle of the tympanum and anchoring the scoloparium; typical of the Crambiformes.

Tergo-sternal sclerite (sclérite tergo-sternal, idem): chitinized band uniting laterally the anterior angles of the first sternite and the first tergite ("tergosternal bars" of Brock, 1971).

Transverse ridge (arête transversale, no name): medio-ventral sclerotized band formed at the fusion of the venulae primae.

Tubercula (idem, no name): small circular sclerotized structures located laterally or latero-ventrally on the first sternite ("tuberculate plate" of Kristensen, 1978 and "tubercular plate" of Nielsen, 1978).

Tympanic bridge (apodème?, pons tympani): median zone of the first sternite usually projected anteriorly and ventrally, it forms the posterior point of attachment of the praecinctorium and its lateral "wings" connect with the tympanum posteriorly.

Tympanic crest (saillie tympanique, processus tympani): invagination of the internal lamella of the drum forming the point of support of the scoloparium.

Tympanic drum (caisse tympanique, bulla tympani): hemispherical antero-lateral invagination of the first sternite which forms the resonnance chamber of the phonoreceptor; it is made of two intimately connected lamellae, one internal, the other external.

Tympanic frame (cadre tympanique, fornix tympani): edge of the internal lamella of the tympanic drum supporting the tympanum.

Tympanic pockets (fossettes tympaniques, saccus tympani): concave zones located right behind the transverse ridge; there are usually one on each side of the middle of the ridge.

Tympanic wings ([illegible], alae tympani): lateral extensions of the tympanic bridge.

Tympanum (idem, idem): thin, subtriangular membrane located antero-ventrally on the first sternite; it is able to sense air vibrations which are transmitted to the sensory nerve system; it is separated from the conjonctive membrane (which connects with the thorax) by a line running from the base of the tergosternal sclerite to the antero-lateral angle of the "wings" of the tympanic bridge.

Venulae (idem , idem): lateral sclerotized lines at the surface of the second sternite.

a) **venulae primae**: situated on each side of the tympanal organs.

b) **venulae secundae**: post-tympanic in location.

Table 4. Annotated classification with species examined in the cladistic analysis. (Ingroup species arranged according to the classification adopted here). Species marked with an asterisk are types of genera.

PYRALIDAE
CRAMBIFORMES
CRAMBINAE (all tribes and unplaced taxa *sedis mutabilis*)

PRIONAPTERYGINI **new tribe**

Hemiplatytes prosenes (Dyar)

Eufernaldia cadarella (Druce)

Surattha indentella Kearfott

Prionapteryx genus-group

Prionapteryx serpentella Kearfott
*Pseudoschoenobius opalescalis (Hulst)

HAIMBACHIINI **new tribe**

Thopeutis genus-group
Thopeutis forbesellus (Fernald)
*Occidentalia comptulatalis (Hulst)

Haimbachia genus-group
Xubida panalope (Dyar)
Haimbachia floridella Capps
*Eoreuma densella (Zeller)

ARGYRIINI, all three genera *sedis mutabilis*

Urola nivalis (Drury)
*Argyria nummulalis Hübner
Vaxi auratella (Clemens)

DIPTYCHOPHORINI

Microcausta flavipunctalis Barnes & McDunnough
Diptychophora harlequinalis (Barnes & McDunnough)

CRAMBINI **status revised**

Euchromius ocelleus (Haworth), *sedis mutabilis*
Platytes vobisne Dyar, *sedis mutabilis*

/

Next 14 lineages *sedis mutabilis*

Catoptria latiradiella (Walker)
Ancylolomia japonica Zeller
Thaumatopsis pexella (Zeller)
*Tehama bonifatella (Hulst)
*Fissicrambus fissiradiellus (Walker)
Microcrambus elegans (Clemens)
*Loxocrambus canellus Forbes
Neodactria new genus
  *N. luteolella (Clemens)
*Arequipa turbatella Walker
Pediasia trisecta (Walker)
La cerveza new species

Parapediasia, four species *sedis mutabilis*
P. decorella (Zincken)
P. torquatella new species
P. teterrella (Zincken)
P. hulstella (Fernald)

Raphiptera assemblage

Raphiptera argillaceella (Packard)
  Almita new genus
  *A. texana new species
  A. portalia new species

Agriphila assemblage
  Agriphila ruricolella (Zeller)

Crambus genus-group, three genera *sedis mutabilis*
*Crambus pascuellus (L.)
Fernandocrambus harpipterus (Dyar)
Chrysoteuchia topiaria (Zeller)

Crambini *incertae sedis*, two species *sedis mutabilis*

"Crambus" dimidiatellus Grote
"Crambus" angulatus Barnes & McDunnough

Crambinae *incertae sedis*, five taxa *sedis mutabilis*

Myelobia sp.
*Epina dichromella (Walker)
*Chilo phragmitellus (Hübner)
Diatraea evanescens Dyar
*Calamatropha paludella (Hübner)

SCOPARIINAE
 Scoparia basalis Walker
NYMPHULINAE
 Nymphula ekthlipsis (Grote)
GLAPHYRIINAE
 *_Glaphyria sesquistrialis_ Hübner
PYRAUSTINAE
 Pyrausta unifascialis (Packard)
EVERGESTIINAE
 Evergestis simulatilis (Grote)
SCHOENOBIINAE
 Donacaula longirostris (Clemens)
ODONTIINAE
 Mimoschinia rufofascialis (Stephens)
CYBALOMIINAE
 Cybalomia extorris Warren

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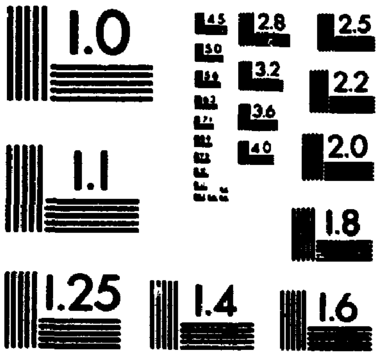
6 of/de 6

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT



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