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A comparative morphological study of the adult Crambidae (Lepidoptera, Pyraloidear

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Abstract

A historic review of the most important authors on the systematics of the Crambidae from LINNAEUS to the present is given. The differences in approach, progress made, and problems encountered are discussed. A comparative study compares the different morphological structures from adult Crambidae (with emphasis on the Spilomelinae-Odontiinae-Pyraustinae) and assesses their intra- and interspecijic variability. The combination of male and female genitalia, and the tympanal organs, are found to be very usefal for identifications at lower taxonomic levels. Although the tympanal organs are not as complex as the genitalia they provide usefal characters together with the genitalia.

Key words: Comparative morphology, Pyraloidea, Crambidae subfamilies, tympanal organs.

Samenvatting

Een historisch overzicht geeft een idee van de systematiek der Crambidae vanaf LINNAEUS tot nu. De verschillen in aanpak, problemen en resultaten van verschillende auteurs worden aangehaald. De vergelijkende morjologische studie is gebaseerd op de morjologie van adulte Crambidae. Vertrekkende van de intra- en interspecifieke variabiliteit worden de verschillende strukturen vergeleken. De nadruk lag op de Spilomelinae-Odontiinae-Pyraustinae. De combinatie van mannelijke en vrouwelijke genitalia samen met de tympanaalorganen bleken zich uitstekend te lenen voor identificaties op de lagere taxonomische niveau's. Alhoewel de tympanaalorganen niet zo complex zijn als de genitalia kunnen ze nuttige bijkomende data verschaffen.

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Introduction

The Pyraloidea (sensu MINET, 1991), one of the largest lepidopteran superfamilies with a number of species probably exceeding 30.000 (MUNROE, 1972) can be divided in two monophyletic groups, the Pyralidae and Crambidae, but the subfamilies and genera remain mostly ill-defined. Before embarking on a full-scale reclassification of the Crambidae on subfamilial, tribal and generic level, I felt it necessary to make a morphological analysis of the different structures that could be taken into account. This paper, examines these structures in adult Crambidae. The analysis is rather descriptive and gives a somewhat "dry" or "uninspired" feel.

Historical review

What authors considered as "Pyraloidea" varied considerably:

COMMON (1970) considered the Hyblaeidae, Thyrididae, Tineodidae, Oxychirotidae and Pyralidae as part of the Pyraloidea, placing the Pterophoridae in a separate superfamily, the Pterophoroidea, and the Alucitidae in the Copromorphoidea.

BROCK (1971) recognized the Thyrididae, Pyralidae, Oxychirotidae, Pterophoridae and Alucitidae (Orneodidae) as belonging to the Pyraloidea but did not include the Hyblaeidae. KUZNETZOV & STEKOLNIKOV (1979) also included the Alucitidae and Carposinidae.

MINET (1981[1982]) recognized only three pyraloid families: Pyralidae, Crambidae and Dudgeoneidae, including the latter on the basis of its tympanal organs. The Dudgeoneidae were separated from the Cossidae by BERGER (1957), were again considered as related to the Cossidae by CLENCH (1959), and transferred to the Aegerioidea [now Sesioidea] by BROCK (1971). This arrangement was also followed by FLETCHER & NYE (1984). They were again transferred to the Cossidae by MINET (1991).

Abdominal tympanal organs are also found in some tineids (MAES, 1985; DAVIS & HEPPNER, 1987) which probably indicates the independent origin of these structures in different groups. KIRIAKOFF (1952) considered that thoracic and abdominal tympanal organs had different origins. But even abdominal tympanal organs of Geometridae and Pyraloidea exhibit many structural differences and are not believed homologous (COOK & SCOBLE, 1992).

FLETCHER & NYE (1984) consider the following families as belonging to the Pyraloidea: Pyralidae, Oxychirotidae, Tineodidae, Thyrididae, Hyblaeidae, Lathrothelidae and Pterophoridae.

In this paper the arrangement of MINET (1991) is followed. He considers the superfamily Pyraloidea with two families: the Pyralidae and Crambidae.

Not only have concepts of the superfamily Pyraloidea differed greatly, the composition of the Pyralidae and Crambidae itself has been unclear.

The first descriptions of Pyraloidea are to be found in the work of LINNAEUS (1758), and most species were described in the 18th and especially the 19th centuries. HERRICH-SHÄFFER (1849) defined the Pyraloidea on the basis of wing venation. As such he removed some unrelated groups such as the Hypeninae (Noctuidae) and Nolidae. His "Pyralidides" contained the genera *Aglossa*, *Hypsopygia*, *Hypotia*, *Asopia* and *Pyralis*, now in the Pyralinae. His "Crambides" contained all the other genera, which are now distributed among different subfamilies.

GUENÉE (1854) considered "le tablier", now known as the praecinctorium (MUNROE, 1959f) as an important character. His arrangement largely followed that of HERRICH-SHAFFER (1849). LEDERER (1863) did not accept the system proposed by GUENÉE and considered the structures now known to be tympanal organs as respiratory organs.

Other authors such as HÜBNER (1793-[1825]); DUPONCHEL (1831); SCHRANK (1802); TREITSCHKE (1829); BOISDUVAL (1832, 1841); ZELLER (1852); WALKER (1858-1865) limited themselves mostly to the description of new species and genera. The consequence of this was that while the number of described species increased greatly, only a few authors had an overall view of the group; HAMPSON (1896, 1898, 1899) and MEYRICK (1884, 1885, 1886, 1890) are examples of this.

At the turn of the 19th century, HAMPSON (1896, 1898, 1899) revised the different subfamilies of the Pyraloidea in a series of extensive papers. This work included all species known at that time (± 10.000), their synonyms, distributions, descriptions and a key to the different genera. Due to their completeness, these papers are still used as a starting point for studies on any group for which no recent study exists.

The number of described species, the increasing size of collections and new research methods resulted in specialization by workers. It also became clear that the old axiom that species could be described and identified adequately using only external morphological characters was untrue. Identifications are based on genitalia.

Recognition of the importance of the genitalia as a tool for identification was slow. Because of their complexity, only the male genitalia were used at first. A few works can be cited in this context.

FORBES (1923) was already using the genitalia in his work, although he limited himself to the conventional characters of wing venation, labial and maxillary palps, and the proboscis to distinguish the different families and subfamilies.

SHIBUYA (1928) followed HAMPSON's (1896, 1898, 1899) system.

MÜLLER-RUTZ (1929) showed the relative importance of characters such as palps and wing venation in differentiating the different genera of the

Pyraustinae. He split the Pyraustinae into two groups according to the presence or absence in the male genitalia of a scaphium, placing those with it into what was later defined as the Evergestinae and those without it into the Pyraustinae along with the Odontiinae and Spilomelinae. His work was limited to the West European region.

BÖRNER (1925) worked using a variety of structures, but not the genitalia, and divided the Pyraloidea into two groups according to the presence or absence of the praecinctorium.

PIERCE & METCALFE (1938) provided detailed plates of male and female genitalia.

SYLVEN (1947) studied the Swedish Pyralinae, Nymphulinae and Pyraustinae, and his work may be thought of as an extension of the work of MÜLLER-RUTZ. He compared characters such as the genitalia, labial and maxillary palps, and wing venation. He showed clearly the weakness of the systems proposed by HAMPSON and MEYRICK.

MARION (1952-1977) revised the Pyraustinae of France on the basis of the male genitalia. His most important contributions were the definition of the Evergestinae and the definition of the tribe Cybalomiini for the genera *Cybalomia* LEDERER and *Hyperlais* MARION. This tribe was considered as a subfamily by MUNROE (1959f).

AMSEL worked on the Microlepidoptera in general. His more important contributions to the study of the Pyraustinae were the establishment of an index (AMSEL, 1957b) for the works of HAMPSON (1898, 1899) and his study of a collection of microlepidoptera from Venezuela (AMSEL, 1956, 1957a). In this work he not only figures the genitalia of new species but also those of previously described species. His results confirmed those of SYLVEN. Furthermore, he showed the importance of the presence or absence of the gnathos. He proposed the subfamily Linosterinae for the genus *Linosta* MÖSCHLER; this name was later changed to Linostinae by MUNROE (1959f) and is now widely accepted. He placed *Dichogama* LEDERER in the tribe Dichogamini and *Heliothela* GUENÉE in the tribe Heliothelini; both tribes were recognized by MINET (1981[1982]) as separate subfamilies. AMSEL also published a series of papers on the microlepidoptera of the Middle East.

HASENFUSS (1960) is mentioned here for his work on the chaetotaxy of the larvae of European Pyraloidea.

HANNEMANN (1964) gave a complete review of the Pyraloidea of western Europe, describing major external characters and providing drawings of the male and female genitalia. The Pyraloidea of western Europe are also covered by the work of MARION (1952-77) and GOATER (1986).

MUNROE has made a major contribution to our knowledge of the Pyraustinae. In 1959 he revised the Linostinae (MUNROE, 1959f). He proposed the Midilinae as a new subfamily (MUNROE, 1970d). His joint studies with MUTUURA on the *Ostrinia* HÜBNER complex (MUTUURA & MUNROE, 1970) and the *Nomophila* HÜBNER complex (MUNROE, 1973a), his notes on the Pyraustinae of the eastern palearctic (MUNROE & MUTUURA, 1968-1971) and his revision of the North American Pyraustinae in the series "Moths of America North of Mexico"(MUNROE, 1972-76) are also major achievements.

Essentially, MUNROE followed the classification proposed by BÖRNER, characterising only some small and geographically restricted subfamilies such as the Linostinae and the Midilinae. He avoided the major "dustbins" within this group, namely the definition and characterization of the different subfamilies of what is called here the "Pyraustinae-Odontiinae-Spilomelinae complex".

Finally, the work of KUZNETZOV & STEKOLNIKOV (1979) should be mentioned here. In contrast to others who have studied the sclerotized parts of the genitalia, these authors studied the muscles and their points of attachment. This approach is very promising since it may explain the form and function of the genitalia and as such may be helpful in elucidating the phylogeny of the group. Only a few species have been studied to date and the results are insufficiently comprehensive to be of general use. Nevertheless, a broad survey of the different types of genitalia might indicate which species would be of interest for such a study.

All authors since HAMPSON have looked for new ways to make correct identifications and to delimit natural groups. A disadvantage has been that they worked on regional faunas so that the global approach HAMPSON obtained is lacking.

MINET (1983, 1991) tried to correct this and his work is based on larval and adult characters of Pyraloidea from all zoogeographical regions. The centerpiece of his work both extends and refines that of KENNEL & EGGERS (1933) on tympanal organs, and that of BROCK (1971) on the importance of the internal structure of the thorax and its attachment to the abdomen. His work deals with the higher classification of the Pyraloidea.

Two monophyletic groups may be recognized, the Pyralidae and Crambidae but there is still confusion among the definition of the different subfamilies when recent checklist are consulted (LERAUT, 1980; INOUE, 1982; MUNROE, 1972-76; VIVES MORENO, 1992; HEPPNER & INOUE, 1992).

Methods

Representatives of 192 genera were examined (usually the type-species of the genus) (see Appendix 1). These taxa were selected among the different subfamilies of the Crambidae (following MINET, 1981[1982]) to cover a substantial amount of the variation within each of the subfamilies. Abdomens were carefully removed from the thorax and mounted for viewing with an electron microscope or dissected and mounted in Euparal (methodology: MAES, 1985).

The study of the thoracic structures was soon abandoned since material would have to be destroyed permanently and this was against the policy of most Musea who put material at my disposal. Emphasis was laid on those structures which could be preserved permanently.

General Morphology

A. Head

1.a. Frons

This is usually flat or slightly rounded, protruding somewhat. Some authors have used the degree of scaling as a character at the generic level, although differences do exist between different species within the same genus. There will also be differences between fresh or worn specimens of the same species. The value of scaling as a character is very limited.

Protrusions are present, for example in some Odontiinae such as *Cornifrons* Lederer (Plate 1: D, c) and *Tegostoma* Zeller.

1.b. Vertex

Behind the frons. The antennae, ocelli and chaetosemata are situated on this sclerite.

1.c. Chaetosema

This organ is present in some groups of Crambidae. It is a paired, sensory organ above the compound eyes and behind the ocelli (if these are present), protruding slightly and covered with stiff bristles.

1.d. Antennae (Plate 1: E-H)

The antennae are filiform; some, for example *Linosta* Möschler, have lamellate segments. The dorsal side of the antennae is densely scaled, the lateral and ventral sides are covered with different sensory organs.

1.e. Proboscis

The proboscis is seldom absent as in, for exemple, *Siga* Cramer or atrophied as in, for example, *Cynaeda* Hübner. The base is always scaled. It consists of two half tubes comprised of a series of sclerotized rings. These tubes fit into each other longitudinally, forming dorsal and ventral sutures. The following structures may be sclerotized (Plate 2: A-H).

Small sensilla: without hexagonal protrusions, only a small extension on the surface of the proboscis bearing a sensory palp.

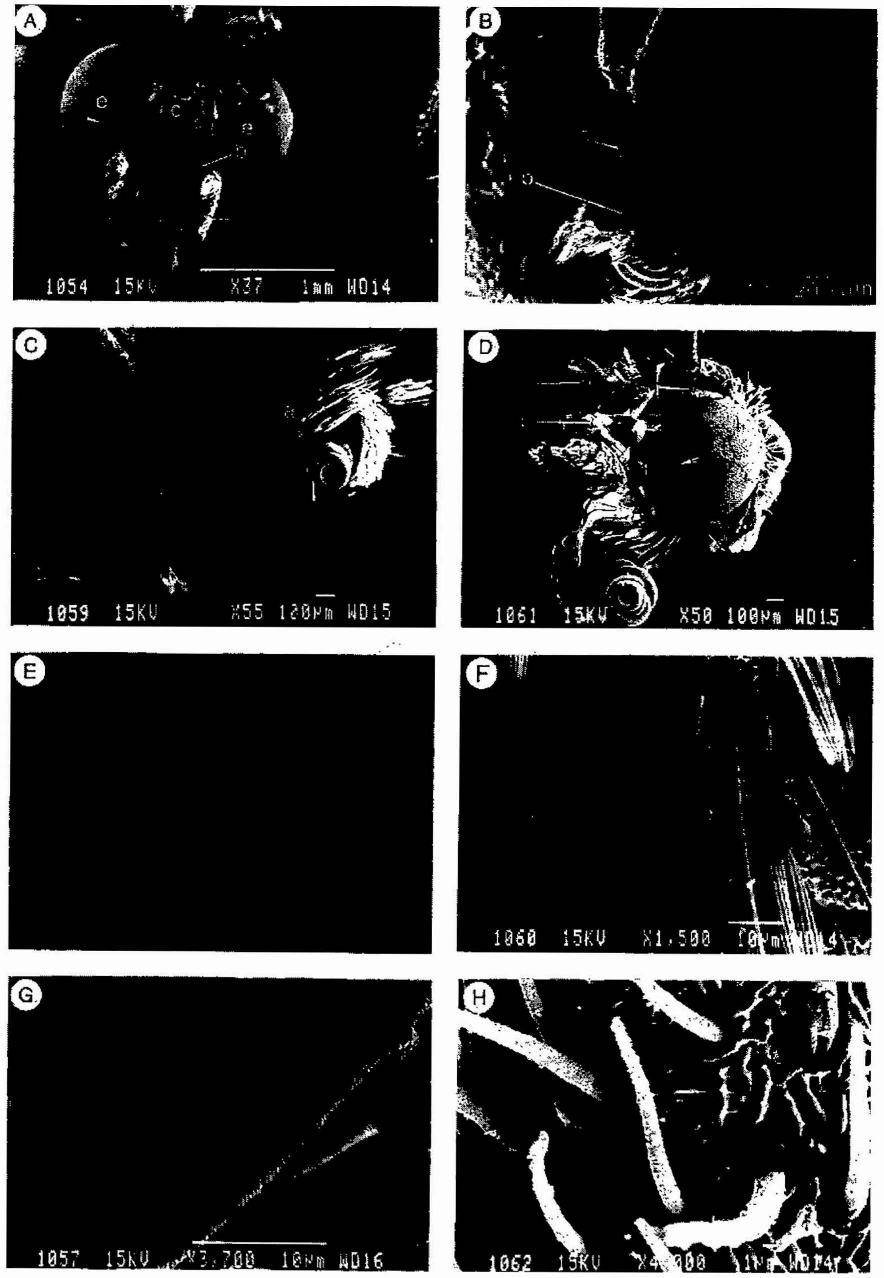


Plate 1. A: *Eurrhypara hortulata*: frontal view head; B: lateral view head: *E. hortulata*; C: idem: *Mutuuraia terrealis;* D: idem: *Cornifrons ulceratalis*; E-G: antenna *E. hortulata*; H: idem: *Cornifrons ulceratalis*. Legend: a: labial palps; b: maxillary palps; c: frons; d: proboscis; e: compound eyes.

1.e.1. Sensilla: Börner (1938) distinguished two types:

Large sensilla: hexagonal protrusions with lateral flanges, and apically a sensory palp.

1.e.2. Sensory hairs:

Setae-like protrusions in slight invaginations on the proboscis. They are disposed randomly on the surface of the proboscis. A few are found on the inside.

1.e.3. Sclerotizations:

Plates: the segmented rings carry a number of triangular plates resembling "sharks' teeth". They are fixed in slit-like openings and are probably movable.

Ventral suture: the ventral suture bears a number of hair-like protrusions which are bent apically.

Most of these structures can only be studied with the aid of the SEM. Considerable variation occurs between the probosces of the same species. No good characters at the specific level have been observed.

1.f. Palps

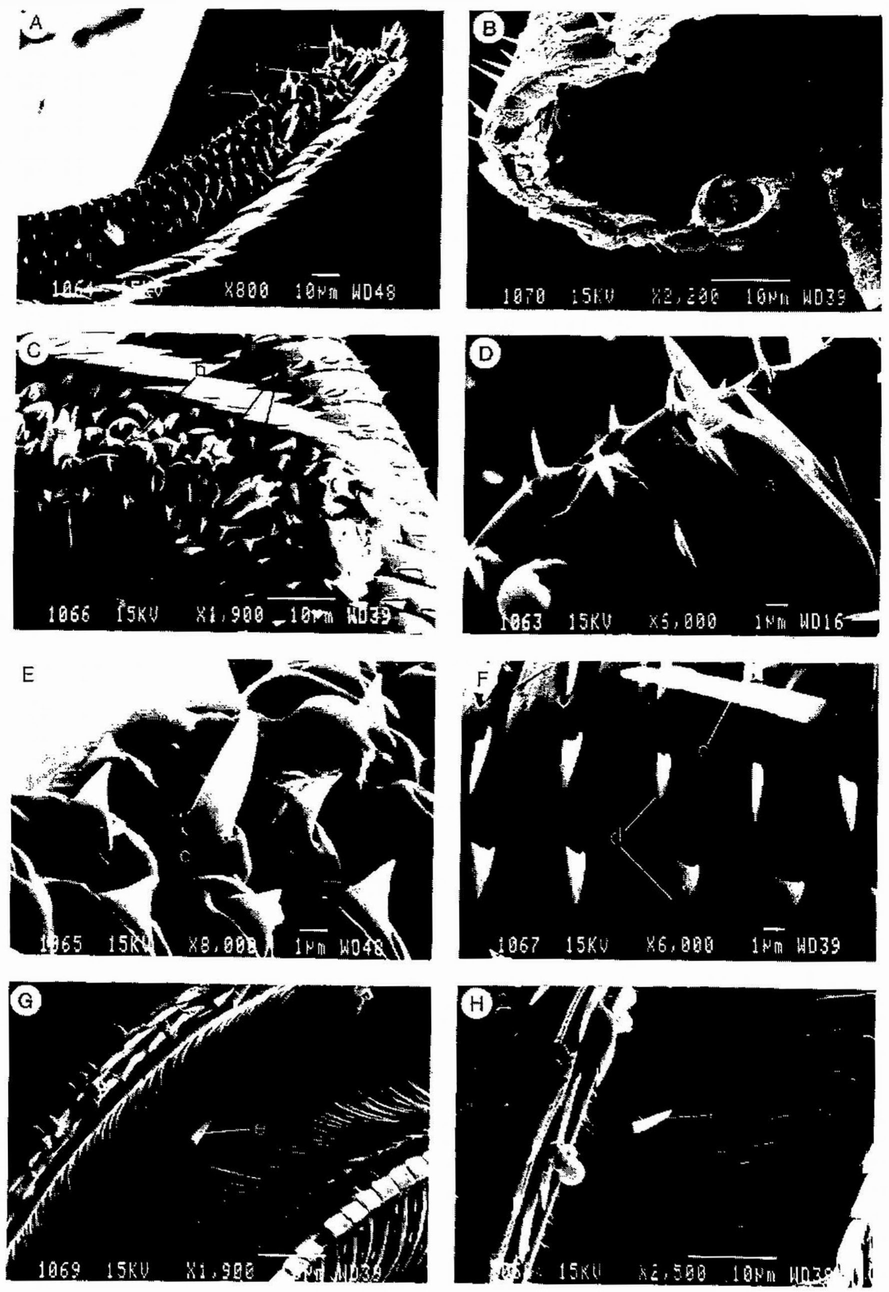
The Crambidae have both labial and maxillary palps (except in the Linostinae). They are usually well developed and densely scaled, concealing the coiled proboscis.

Maxillary palps: situated above the labial palps, approaching each other apically and thus covering the base of the proboscis. They are four segmented. The basal segment bears a number of setae (all material was descaled for study). The form of the basal segment and the number of setae on it may vary on the same specimen between the left and right palps (Plate 3). Small differences in the length and shape of the segments exist between different species (Plate 4).

Labial palps: the labial palps are three segmented and densely scaled. The apical segment bears an internal sensory organ. Intraspecific variation is slight (Plate 5). Sexual dimorphism is rare and is apparent only in the apical segment, for exemple in *Paratalanta pandalis* (Hübner) (Plate 7: J-L).

The length of the palps may differ (Plate 6 & 7); in *Evergestis* Hübner spp., for example, the first segment is longer than the second. In several odontiine species the first and second segment are of different lengths, for example *Metaxmeste* Hübner, *Orenaia* Duponchel, *Cynaeda* Hübner, *Hercyna* Treitschke and *Titanio* Hübner. In *Orenaia* spp. the first segment

Plate 2. Proboscis Pyraustinae (*Eurrhypara hortulata*). A: lateral view: large taste bud (a), small taste bud (b), sensory hair (c); B: transversal view; C: apical part: large taste bud (a), small taste bud (b); D: large taste bud (a); E: small taste bud (c); sensory hair (c), plate (d); E-H: internal sensory hair (e).



is larger than the second. In *Cynaeda* and *Metamexte* spp. the second segment is larger than the first. In the Pyraustinae and Spilomelinae the second segment is the longest (*Agrotera* Schrank, *Diasemia* Hübner, *Diasemiopsis* Munroe, *Dolicharthria* Stephens, *Ebulea* Doubleday, *Nomophila* Hübner, *Opsibotys* Warren, *Paratalanta* Meyrick, *Perinephela* Hübner, *Phlyctaenia* Hübner, *Pyrausta* Schrank, *Sitochroa* Hübner).

The palps of congeneric species are difficult to differentiate and the differences between different genera are difficult to define in descriptions.

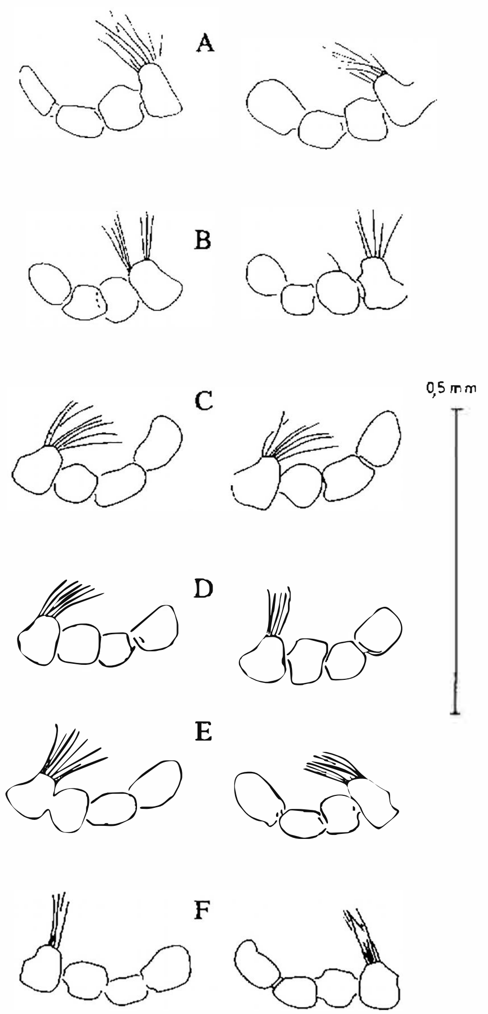


Plate 3. Intraspecific variability maxillary palps of *Eurrhypara hortulata*.

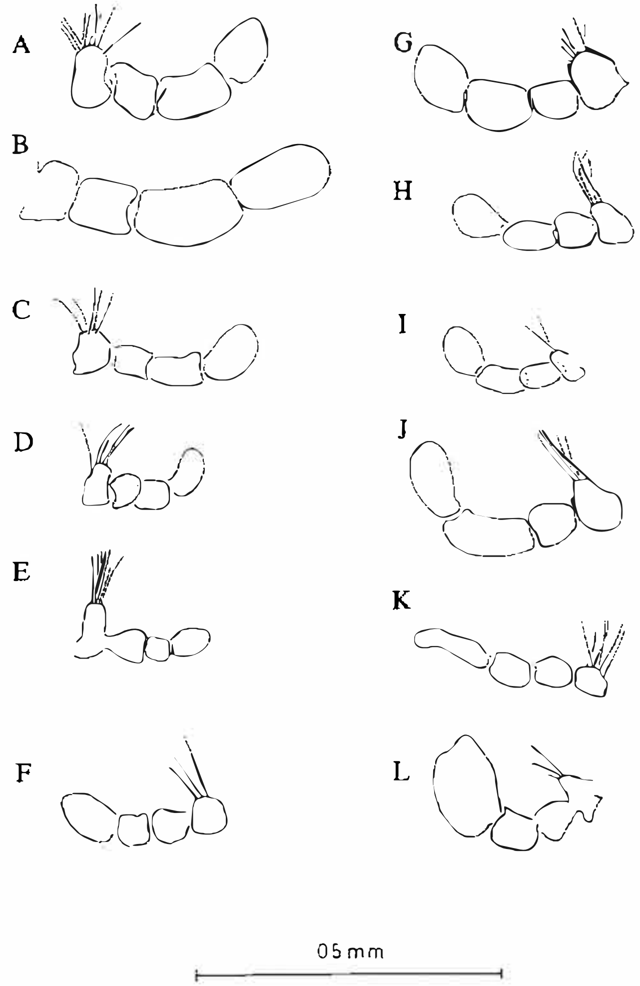


Plate 4. Interspecific variability maxillary palps Crambidae. A: *Metaxmeste phrygialis*; B: *Cynaeda dentalis*; C: *Paratalanta pandalis*; D: *Opsibotys fuscalis*; E: *Nomophila noctuella*; F: *Dolicharthria punctalis*; G: *Orenaia alpestralis*; H: *Perinephela lancealis*; I: *Pyrausta cingulata*; J: *Sitochroa palealis*; K: *Diasemiopsis ramburialis*; L: *Diasemia litterata*.

B. Thorax

As in other Lepidoptera, the thorax consists of three segments (pro-, meso- and metathorax). Each thoracic segment bears a pair of legs and the meso- and metathorax each bear a pair of wings. The patagia are situated in the intersegmental membrane between the head and thorax. The base of the forewings is covered by a triangular sclerite, the tegula. There is evidence that this sclerite is modified into a cymbal organ in some Pyralidae (SPANGLER *et al.*, 1984). The internal structures of the thorax are not included in this study for reasons explained earlier. KENNEL & EGGERS (1933) and MINET (1983) consider the accessory tympanum (akzessorische Trommelfell; tympanum accessoire). It is not known if these structures have an acoustic function, also they are not restricted to those groups with tympanal organs (COOK & SCOBLE, 1992).

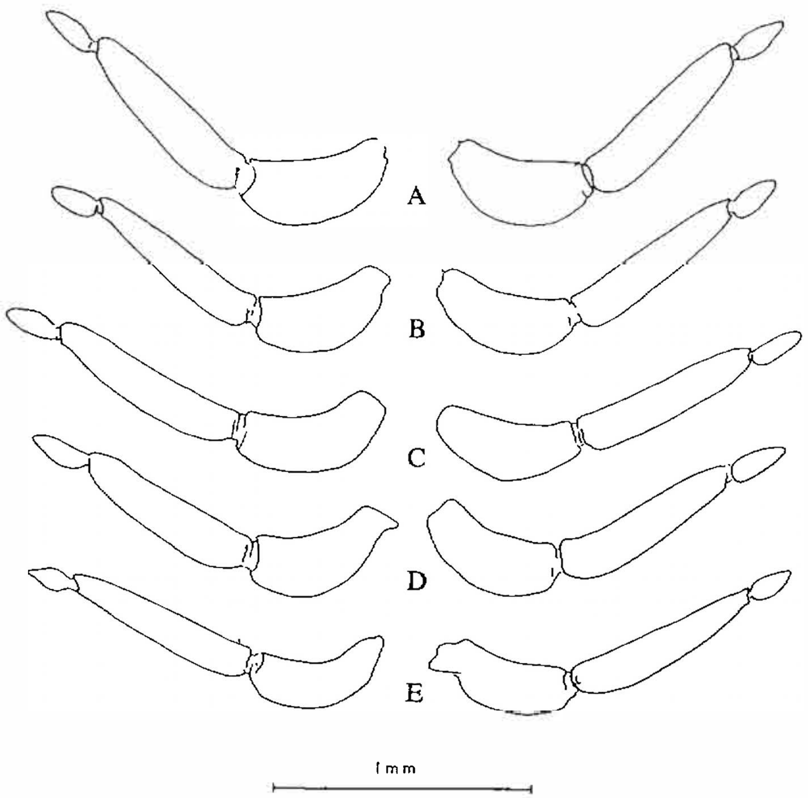


Plate 5. Intraspecific variability labial palps of *Eurrhypara hortulata*. A-D: ♂; E: ♀.

1. Legs

The tibia of the fore-leg bears a flange-like structure, the epiphysis, on its inner side. Some Pyraustinae have the tibia enlarged with a groove containing a hair-pencil (for example: illustrated in *Ostrinia* HÜBNER by MUTUURA & MUNROE (1970)). The fore-legs lack spurs, the mid-legs bear one pair of spurs and the hind-legs bear two pairs of spurs. They are borne on the tibia. The metatarsus ends in two claws and a pulvillus.

2. Wings

2.1. Wing venation

The typical pattern is given in plate 8. In the forewing the subcosta (Sc) is free. The first radial vein (R1) anastomoses with the radial stem but may rarely anastomose with R2. R2 is usually free, for example in the Scopariinae, but may anastomose with R3+4 or originate from a point at the base of the cell. There are always three median veins present. M1 is usually closer to R5 than to M2 and M3. M2 and M3 originate from the hind corner of the cell; they are separated at the base, originating together or anastomosing just beyond the cell. The cubital veins Cu1a and Cu1b are always well-defined. The anal vein may sometimes be forked at its base.

In the hindwing the subcostal vein and the first radial vein anastomose to form Sc+R1. This vein anastomoses for a shorter or a longer distance with the radial stem (Rs) beyond the cell. The median veins (M1, M2 and M3) are always present. Two cubital veins (Cu1 and Cu2) and three anal veins (A1, A2 and A3) are present.

2.2. Variation in the wing venation (Plate 8)

The wing venation of the Crambidae is very uniform. Nevertheless, authors such as HAMPSON and MEYRICK based their keys on venational characters.

In this study a large number of wing preparations of the pyraustine *Eurrhypara hortulata* (LINNAEUS) have been examined. All specimens were from the same locality, collected over a period of two years. Variation was observed in veins R2 and R3+4, M2 and M3 of the forewing. In the hindwing there was some variation of veins M2 and M3.

R2 is always anastomosed with R3+4 forming R2+3+4 from which diverge the other veins. The point where R2 anastomoses with R3+4 varies, as does the length of R3+4. The lengths of the other radial veins differ depending upon the length of R2 or R3+4. Normally R2 anastomoses with R2+3+4 before R3+4, but the reverse was also observed: R4 anastomosing with R2+3+4 to form R2+3 (Plate 8: L).

Variation in M2 and M3 is less obvious. Both veins may approach each other basally remaining separated at the base; they may originate from the same point or be anastomosed for a short length. The same pattern of variation of the Median vein may be observed in the fore- and hind-wings.

2.3. Wing coupling mechanism

The wing coupling mechanism in the Pyraloidea is of the frenate type. The costa of the hind-wing bears a frenulum which hooks into the retinaculum of the fore-wing. The retinaculum consists of a series of hardened bristles at the base of the stem of the Cubital vein, the wing usually slightly folded there. Some subfamilies, for example Scopariinae and most Pyraustinae, have a sclerotized hook emerging from the Sc to form a subcostal retinaculum (Plate 9: 1). Sexual dimorphism of the frenulum may occur: the male frenulum consists of a strong, simple bristle, in the females it consists of two or more bristles (Plate 9: 2). The frenulum in the genus *Pycnarmon* LEDERER is not pointed at the tip (as in other Crambidae) but ends in a rounded sclerotization (Plate 9: 3).

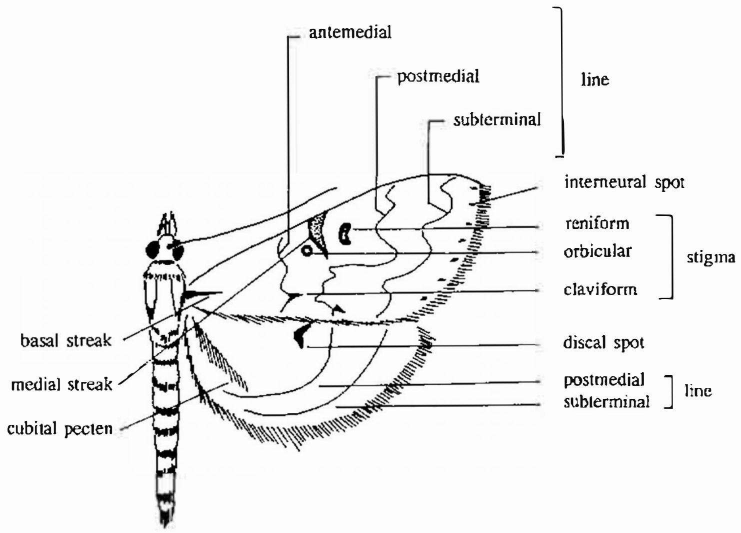


Fig. 1. Wing-pattern Crambidae.

2.4. Wing pattern

The typical wing pattern (fig. 1) is here compared with that of the Noctuidae (MARION, 1954; GOATER, 1986). All gradations between a well defined and a completely absent wing pattern occur. Such variability may even be found within the same genus. *Pyrausta aurata* (SCOPOLI) and *P. purpuralis* (LINNAEUS) have well defined wing patterns. *P. sanguinalis* (LINNAEUS) and *P. castalis* (TREITSCHKE) have ill defined wing patterns, and it is completely absent in *P. cardinalis* (GUENÉE).

A complete wing pattern is present in most Scopariinae. On the forewing, an antemedian and a postmedian line divide the wing into three fields: an antemedian, a median and a postmedian field. The postmedian field may be devided by the subterminal line which is largely parallel with the postmedian line. In the antemedian field a basal streak may occur. The orbicular stigma may be present in the cell before the median fascia. Between the median fascia and the postmedian line the reniform stigma may be present. The claviform stigma or spot is usually present on the stem of Cu in the median field. The interneural spots may be present behind the subterminal line or fascia (if present) and the outer edge of the wing. They are situated in the spaces between the veins.

On the hindwing, the postmedian and subterminal line may occur. A discal spot may be present.

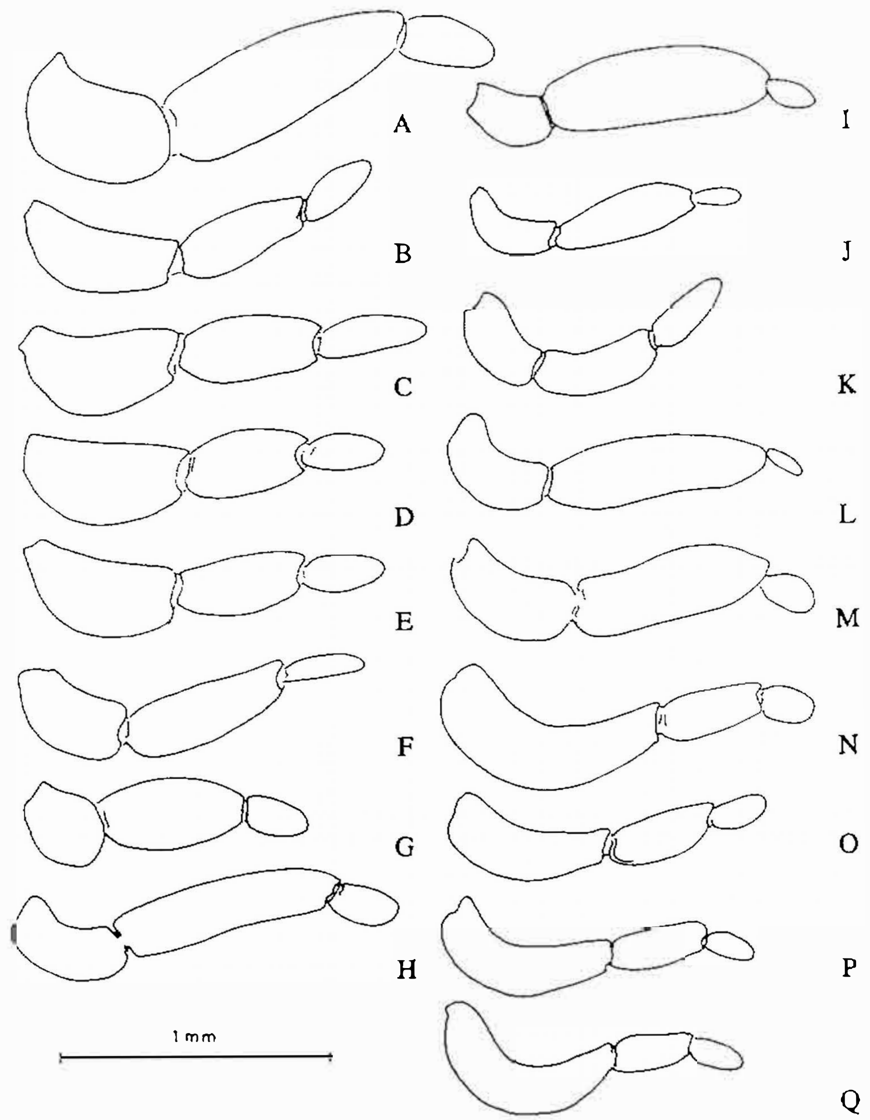


Plate 6. Interspecific variability labial palps Crambidae. A: *Metaxmeste phrygialis*; B: *M. schrankiana*; C: *Orenaia alpestralis*; D: *O. helveticalis*; E: *O. rupestralis*; F: *Titanio pollinalis*; G: *Hercyna normalis*; H: *Cynaeda dentalis*; I: *Diasemia litterata*; J: *Diasemiopsis ramburialis*; K: *Agrotera nemoralis*; L: *Dolicharthria punctalis*; M: *Nomophila noctuella*; N: *Evergestis frumentalis*; O: *E. limbata*; P: *E. pallidata*; Q: *E. extimalis*.

C. Abdomen

The abdomen consists of ten segments. It is generally accepted that the apparent first abdominal sternite of Ditrysian Lepidoptera is in reality the second, which has moved forward to oppose the first tergite (BROCK, 1971). As a consequence, the tympanal organs are situated on the second sternite. The genitalia are situated at the distal end of the abdomen. They are modifications of the 9th and 10th segments. Certain subfamilies, for example the Odontiinae and Schoenobiinae, also have modifications of the 7th and 8th segments; these are usually limited to the sternites of the male. The section below entitled "General morphology" deals with the description of the different stuctures found in the abdomen. The following section deals with the intra- and interspecific variability of these structures in a case study of some species of the genus *Achyra* GUENÉE.

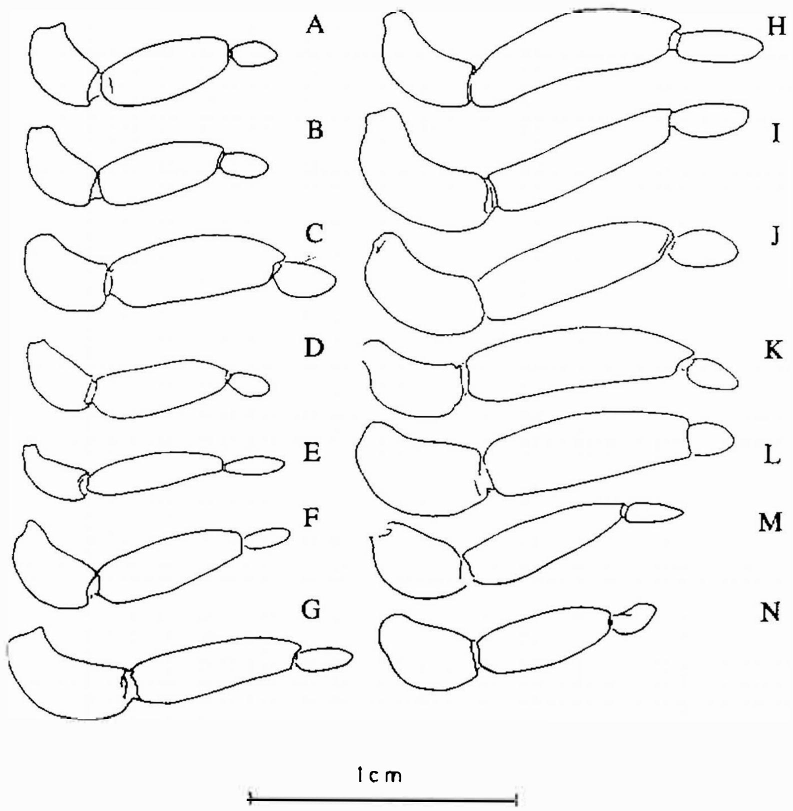


Plate 7. Interspecific varability labial palps Pyraustinae. A: *Pyrausta aurata*; B: *P. cingulata*; C: *P. purpuralis*; D: *P. nigrata*; E: *P. sanguinalis*; F: *Opsibotys fuscalis*; G: *Perinephela lancealis*; H: *Ebulea crocealis*; I: *Sitochroa palealis*; J: *Paratalanta pandalis* ♂; K-L: *P. pandalis* ♀; M: *Phlyctaenia coronata*; N: *P. stachydalis*.

1. General Morphology

1.1. Tympanal organs

These structures were first studied in detail by KENNEL & EGGERS (1933). They may be divided into the sclerotized and non-sclerotized parts. The former are modifications of the sternite and are mostly situated externally. The latter are more delicate parts and are situated internally. The tympanal organs are paired structures located in the anterior part of the first visible sternite (=sternite 2). They consist essentially of a membrane, the tympanum, associated with a bladder and chordotonal sensillae. The latter are connected to the metathoracic ganglion. The paired bladders lie against the median thoracacic air sac which is not innervated.

1.1.1. Non-sclerotized structures

These consist of the epithelial lining of the bladders, the chordotonal sensillae which together form the scoloparia and the median thoraco-abdominal air sac. In pinned specimens the scloparia are dehydrated. The other structures may only be observed after histological staining of specimens preserved in alcohol.

The works of KENNEL & EGGERS (1933), CORO (1972) and MINET (1981 [1982], 1983, 1985) provide detailed descriptions of these structures.

1.1.2. Sclerotized structures (Plates 10 & 11)

These structures are easily studied on pinned specimens. They have the advantage that they maintain their shape, even on material that has long been dry.

The different parts of these structures have already been named by KENNEL & EGGERS (1933) and MINET (1981[1982]) in German and French respectively. In order to develop a uniform nomenclature for universal use, latinized names were proposed by MAES (1985) and this nomenclature is followed here. The latinized names are followed by the German (KENNEL & EGGERS) and French (MINET) alternatives.

ala tympani, plural: alae tympani (- , -): The connection between the fornix tympani and the pons tympani. It is also the apical end of the saccus tympani, if one is present. See also pons tympani.

bulla tympani, plural: bullae tympani (Tymanalkessel, caisse tympanique): These are the sclerotized parts of the tympanal bladders. KENNEL & EGGERS assumed that they are formed by an invagination of the sternite and the pleurite. The histological study of CORO (1972) confirmed that they indeed originate from an invagination but he presented no data as to its origin. They are usually bean-shaped with their longitudinal axis parallel to that of the body. Two forms may be distinguished:

1. open: in which the epithelium is not completely enclosed by the bulla tympani.

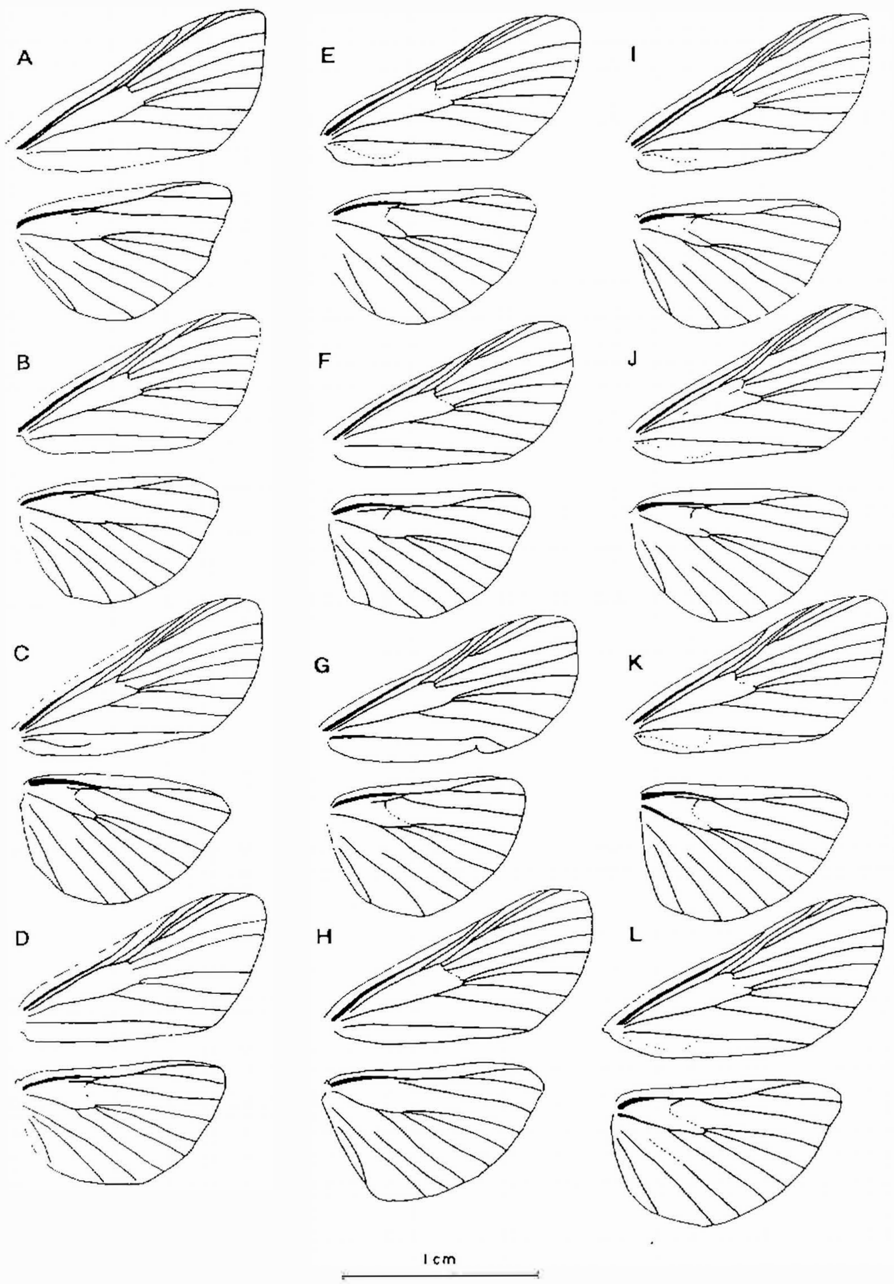


Plate 8. Wing venation *Eurrhypara hortulata*. A-B: ♀; C-L: ♂.

2. closed: in which the epiphelial membrane is completely enclosed by the bulla tympani.

conjunctivum (Conjunctivum, conjonctivum): This membrane is connected directly to the tympanum. It is opaque in both living and dead material and its surface forms many small folds and is not scaled. The inner side is delimited by strongly dispersed nuclei (Coro, 1972).

fornix tympani (-, cadre tympanique): This is the frame over which the tympanum is stretched. It may be either broad or narrow.

intersegmental thoraco-abdominal membrane (-, -): This membrane may be modified ventrally into a torulus tympani or a praecinctorium.

ligna tympani (- , ligne tympanique): This line delimits the conjuctivum and the tympanum. If the fornix tympani is compared to a bow, the ligna tympani is the bow-string.

paraspina (-, paraspina): A needle like sclerotization of the anterior part of the ligna tympani.

pons tympani (mediane Scheidewand, -): This is the median zone of the first sternite. It forms a connection between the praecinctorium or the torulus tympani and this sternite. This definition includes only the sclerotizations parallel to the body-axis. The horizontal arms form the rami tympani (singular: ramus tympani). The alae tympani (singular: ala tympani) connect the pons tympani with the fornix tympani.

praecinctorium (Ventralleiste, praecinctorium): This is a median expansion of the intersegmental thoraco-abdominal membrane. When less developed it is termed the torulus tympani. When strongly developed it forms a simple or bilobed pouch: the praecinctorium. Minet (1983) reported some muscles in the praecinctorium. Both structures are scaled to some degree.

processus spiniforme (- , processus spiniforme): A small protuberance on the anterior part of the bullae tympani. It occurs only on bullae tympani of the closed type.

processus tympani (Insertionsfalte, saillie tympanique): An invagination of the bullae tympani beneath or even in the fornix tympani. When present it is the place of attachment of the scoloparium.

puteolus tympani, plural: puteoli tympani (- , -): These are incavations in the zona glabra tympani. See also zona glabra tympani.

ramus tympani, plural: rami tympani (- , -): These are sclerotized arms that delimit the exterior edge of the saccus tympani, in Pyraustinae they are usually at 90° to the body axis. See also pons tympani.

rugae odontoidae (-, stries odontoïdes): Small wrinkles on the margin of the tympanum-fornix tympani; restricted to the hearing organs of the "Pyralidae" type.

Plate 9. Wing-coupling mechanism Crambidae. 1: frenulum ♀ (double); 2: frenulum ♂ with retinaculum; 3: frenulum male *Pycnarmon* species.

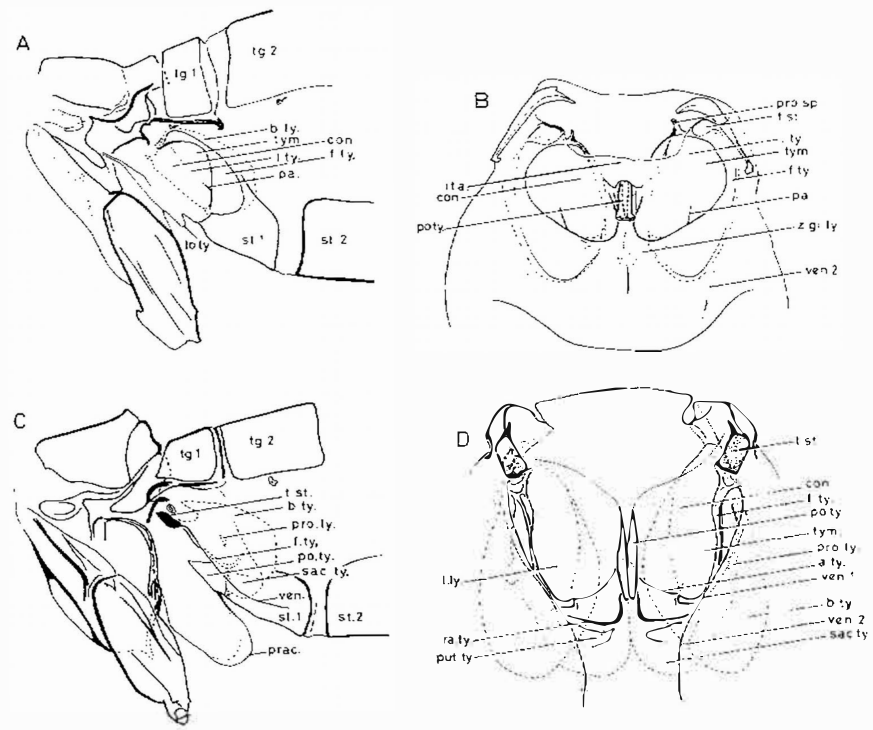


Plate 10. General morphology tympanal organs Pyralidae. A-B: "Pyralidae" type; C-D: "Crambidae" type.

a.ty.: ala tympani; b.ty.: bulla tympani; con.: conjunctivum; f.ty.: fornix tympani; i.t.a.: intersegmental thoraco-abdominal membrane; l.ty.: ligna tympani; pa.: paraspina; po.ty.: pons tympani; prae.: praecinctorium; pro.sp.: processus spiniforme; pro.ty.: processus tympani; put.ty.: puteolus tympani; ra.ty.: ramus tympani; ru.od.: rugae odontoïdae; sac.ty.: saccus tympani; sco.: scoloparium; spi.: spinula; t.st.: tergo-sternal sclerite; to.ty.: torulus tympani; tym.: tympanum; ven.: venula; z.gl.ty.: zona glabra tympani.

saccus tympani (- , poche tympanique, fossette tympanique): In certain cases the fornix tympani is strongly invaginated in the sternite, forming a cavity. This cavity may be strongly developed posterior to the fornix tympani, forming the saccus tympani.

scoloparium (Scoloparium, scoloparium): This is comprised of the chordotonal nerve, consisting of four scolopale cells and connected to the tympanum and the dorsal or dorso-lateral side of the bulla tympani. The scoloparium is of the inverted type (Kennel & Eggers, 1933; Coro, 1972). The scoloparium is thread-like. Near the sensilla the structure is thickened. Minet (1981[1982]) considered the form and the place of this thickening to be of taxonomic importance.

spinula (- , spinula): A small sclerite on the inside of the tympanum marking the attachment of the scoloparium; it is usually conical, sometimes plate-like.

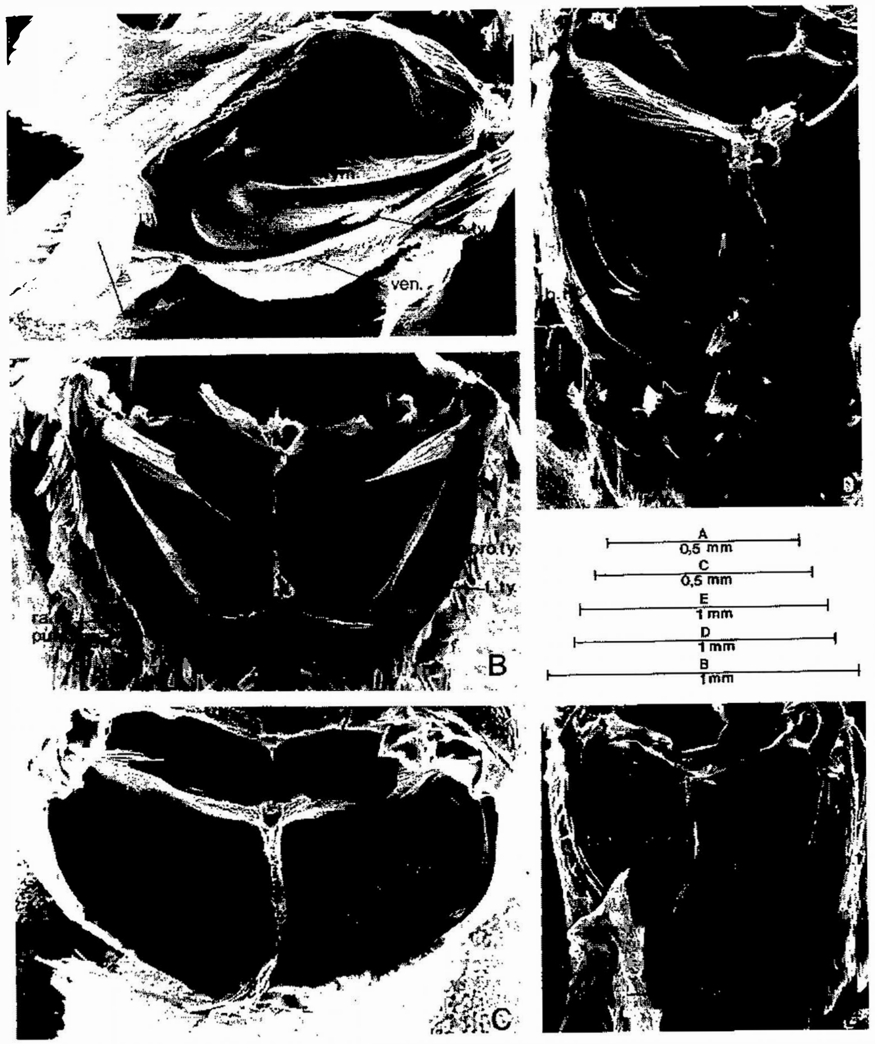


Plate 11. Tympanal organs "Crambidae" type. A: *Dolicharthria punctalis*, ventral view; B: *Titanio normalis*, idem; C: *Pyrausta cingulata*, frontal view; D: *Nomophila noctuella*, ventral view; E: *Pyrausta cingulata*, idem.

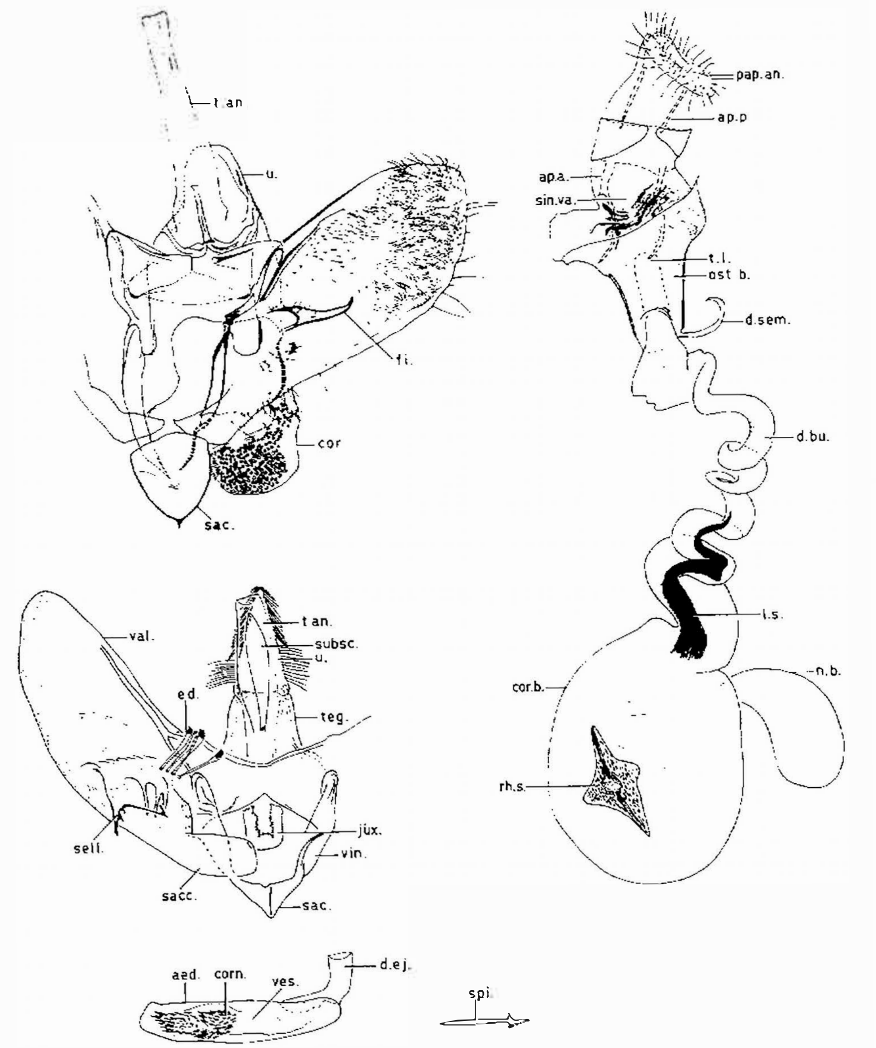


Plate 12. General morphology of the genitalia. A: male genitalia of *Pleuroptya ruralis*: Spilomelinae; B: male genitalia of *Sclerocona acutellus*: Pyraustinae; C: aedoeagus of *Achyra nudalis*: Pyraustinae; D: spicula of *Algedonia luctualis*: Pyraustinae; E: female genitalia of *Algedonia luctualis*: Pyraustinae.

aed.: aedoegus; ap.a.: apophyses anteriores; ap.p.: apophyses posteriores; cor.: coremata; cor.b.: corpus bursae; corn.: cornutus; d.bu.: ductus bursae; d.ej.: ductus ejaculatorius; d.sem.: ductus seminalis; ed.: editum; fi.: fibula; jux.: juxta; l.s.: ribbon-shaped signum; n.b.: appendix bursae; ost.b.: ostium bursae; pap.an.: papillae anales; rh.s.: rhomboid signum; sac.: saccus; sacc.: sacculus; sell.: sella; sin.va.: sinus vaginalis; spi.: spicula; subsc.: subscaphium; t.an.: tuba analis; teg.: tegumen; t.l.: tong-shaped protrusion; u.: uncus; val.: valva; ves.: vesica; vin.: vinculum.

tergo-sternal sclerite (-, tergite tergo-sternal): A small sclerite anterior to the fornix tympani lying between the tergite and sternite. Its form and degree of sclerotization may vary. The origin of this structure is not clear.

torulus tympani, plural: toruli tympani (Ventralleiste, bourrelet ventral): This is a median expansion of the intersegmental thoraco-abdominal membrane; when strongly developed it forms the praecinctorium. See also intersegmental thoraco-abdominal membrane and praecinctorium.

tympanum (Trommelfell, tympanum): This is the very thin membrane, transparent when dry, of the auditory organ. It is thinner than the conjunctivum. Coro & Fernandez (1972) observed some very flattened cell nuclei associated with it. The scoloparium may be either attached to the tympanum directly or indirectly via the spinula.

venula, plural: venulae (- , venula): A medio-lateral sclerotized ridge on the inside of the sternite, of which two forms may be recognized:

1. venula prima, plural: venulae primae: lateral to the fornix tympani, usually only a fold in the sternite.
2. venula secunda, plural: venulae secundae: posterior to the fornix tympani, usually starting as an extension of the venula prima at the end of the ramus tympani. The venula secunda is more strongly sclerotized than the venula prima.

zona glabra tympani (- , dépression tympanique): zone posterior to the pons tympani and the rami tympani, devoid of scales, sometimes sloping to form a puteolus tympani (plural: puteoli tympani).

1.2. Pregenital segments

A pregenital segment in its simpliest form is ring-shaped with a tergite dorsally and a sternite ventrally. Laterally a stigma may be observed. Each segment is connected to the adjacent segments by an intersegmental membrane. The caudal edges of the two sclerites of a segment is usually sclerotized to form a transversal ridge. This ridge is lacking on the distal edge so that the distal margin of the sclerite is less well defined.

There are no modifications up to the 7th segment. The 7th and 8th segments may be modified. Some male Odontiinae possess a slightly modified 7th sternite. In this case, a number of sutures may be present and the sternite has a specific form, for example *Tegostoma* species. Analogous modifications were described in the Noordinae by Minet (1980) and also occur in the Schoenobiinae.

1.3. Genitalia (Plate 12)

The genitalia are modifications of the 9th and 10th segments. The general description of their morphology here follows the nomenclature proposed by Tuxen (1956).

1.3.1. Male genitalia

The sclerites of the 9th and 10th segments form a transverse ring upon which the other sclerotized parts of the genitalia are implanted. The dorsal part of this ring is the tegumen which terminates laterally in the pedunculi. In many Pyraloidea paired extensions of the tegumen occur at its base, more or less at the level of the pedunculi. These extensions are invaginated in the intersegmental membrane between the 8th and 9th segments. They terminate bluntly and carry a number of setae modified into scales or hairs at their ends. These structures were named coremata by Pierce & Metcalfe (1914) and were redefined by Amsel (1956). The coremata are well developed in the Spilomelinae (Plate 12, cor.) and less so in the Pyraustinae. In the Phycitinae an analogous structure, the culcitae, is an unpaired ventral modification of the 8th segment (Amsel, 1956). Marion (1952) uses the term coremata in the sense of Pierce & Metcalfe (1914) but later (Marion, 1961) uses the term culcitae for the same structure.

Distally connected to the tegumen is the uncus. The gnathos, if present, articulates with the base of the uncus. In the Evergestinae the gnathos articulates with the base of the tegumen. The tuba analis is situated between the gnathos and the uncus. When a reduction of the gnathos occurs (for example in the Pyraustinae or Spilomelinae, sensu Minet (1981 [1982]) sclerotization of the tuba analis may occur. A dorsal sclerotization is termed a scaphium, a ventral sclerotization being called a subscaphium.

A number of setae may usually be found on the dorsal side of the uncus. In most subfamilies these setae are simple, sometimes flattened and in most species of Pyraustinae they are modified. They are longitudinally flattened and invaginated distally to some degree, being more or less fork-shaped.

The ventral part of the transversal ridge is termed the vinculum. It is U- or V-shaped. The valvae attach to both arms of the vinculum. They are connected to the tegumen by the pedunculi.

Medio-ventrally an apically directed extension may occur on the vinculum, termed the saccus.

The abdomen is closed posteriorly by a membrane: the diaphragma. This membrane is situated between the arms of the vinculum and at the base of the tegumen. It is perforated medially by the aedoeagus, the sclerotized part of the penis. The tube-like membrane around the aedoeagus is called the anellus. The ductus ejaculatorius originates laterally or terminally from the aedoeagus. The apical part of the aedoeagus is invaginated and forms the vesica. Spine- or plate-like sclerotizations on the vesica are called cornuti.

The ventral part of the diaphragma, the fultura inferior, is often heavily sclerotized to form a shield supporting the aedoeagus. This shield-like structure is called the juxta. The dorsal part of the diaphragma, the fultura superior, may form a transtilla. In the Pyraloidea this name refers to the medially directed extensions of the dorso-proximal part of the valvae, for example in *Loxostege* Hübner and *Achyra* Guenée species.

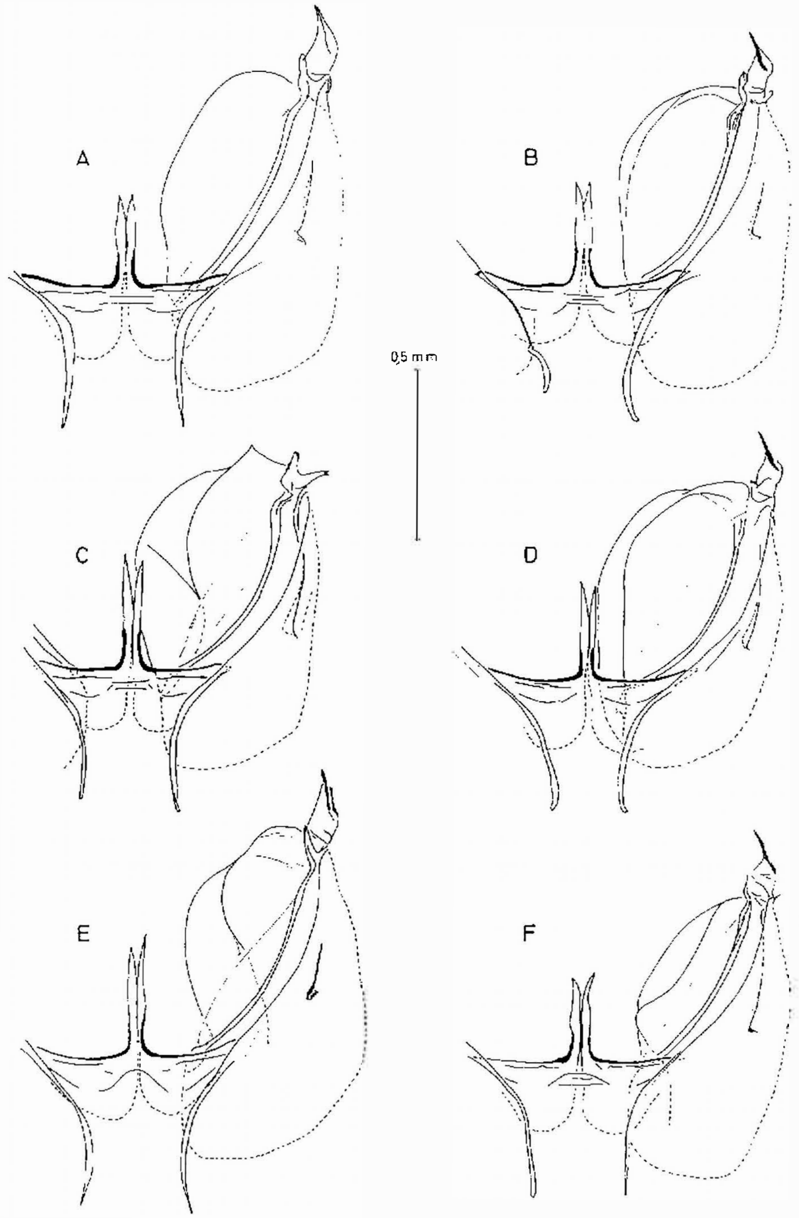


Plate 13-1. Intraspecific variability of the tympanal organs of *Achyra coelatalis*. Rwanda: A, B, C, D, E, F (♂♂).

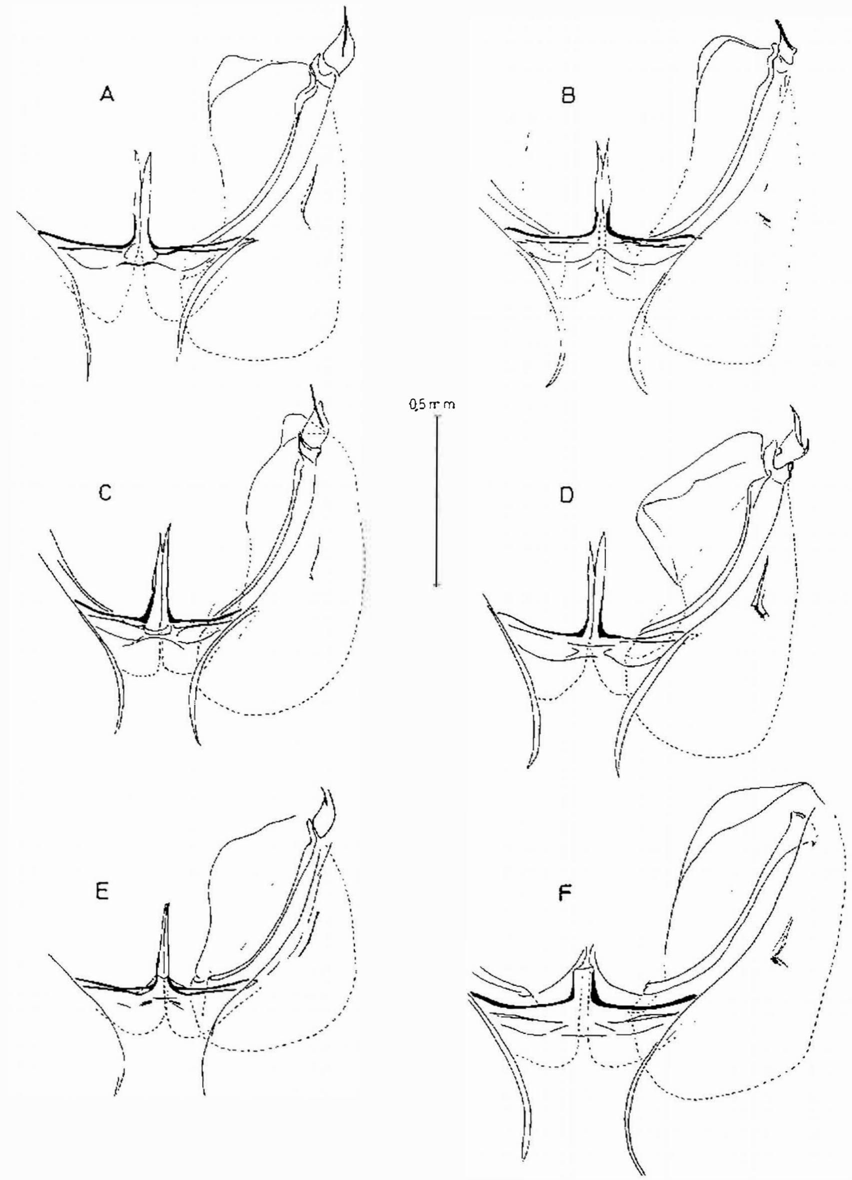


Plate 13-2. Intraspecific variability of the tympanal organs of *Achyra coelatalis*. Cameroon: A, B, D, E; Seychelles: F; Rwanda: C.

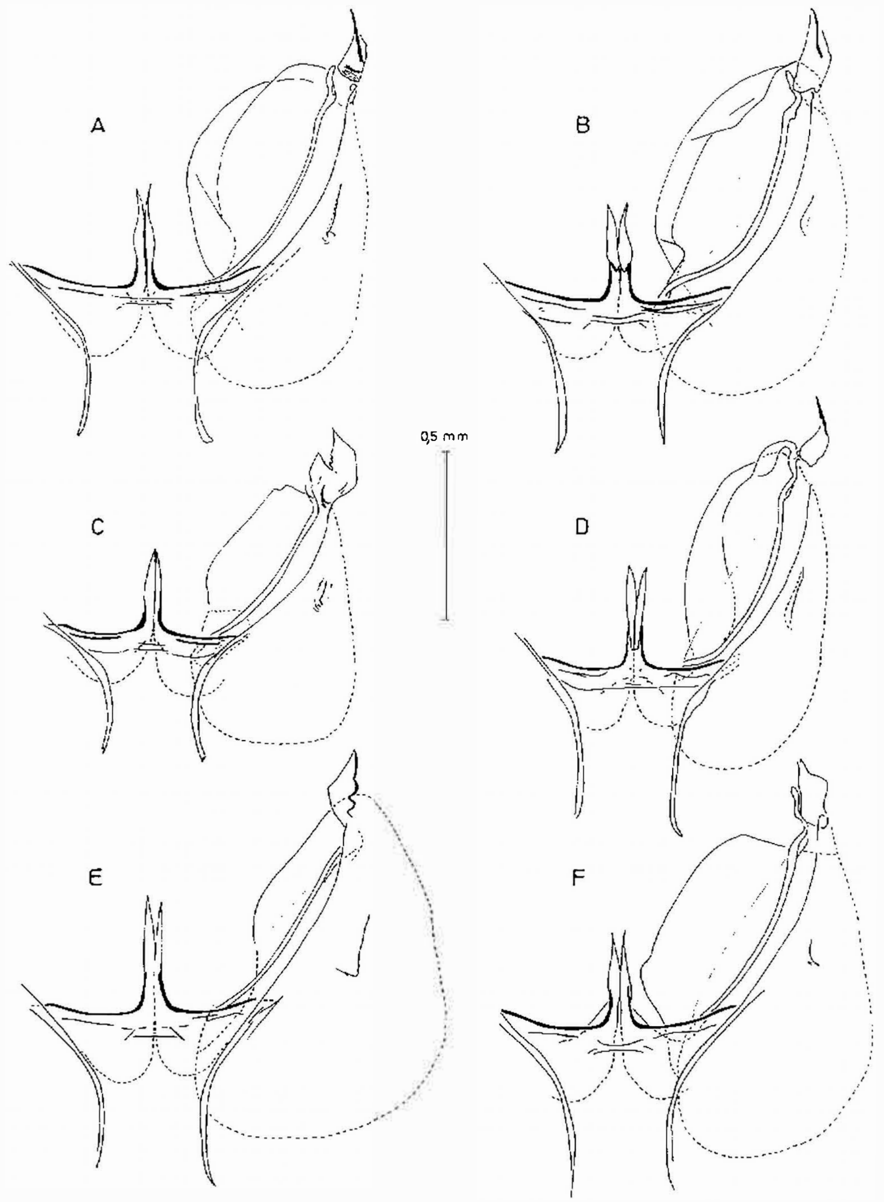


Plate 13-3. Intraspecific variability of the tympanal organs of *Achyra coelatalis*. Zaire: A, C, D; Zambia: B; Zimbabwe: F; Kenya: E.

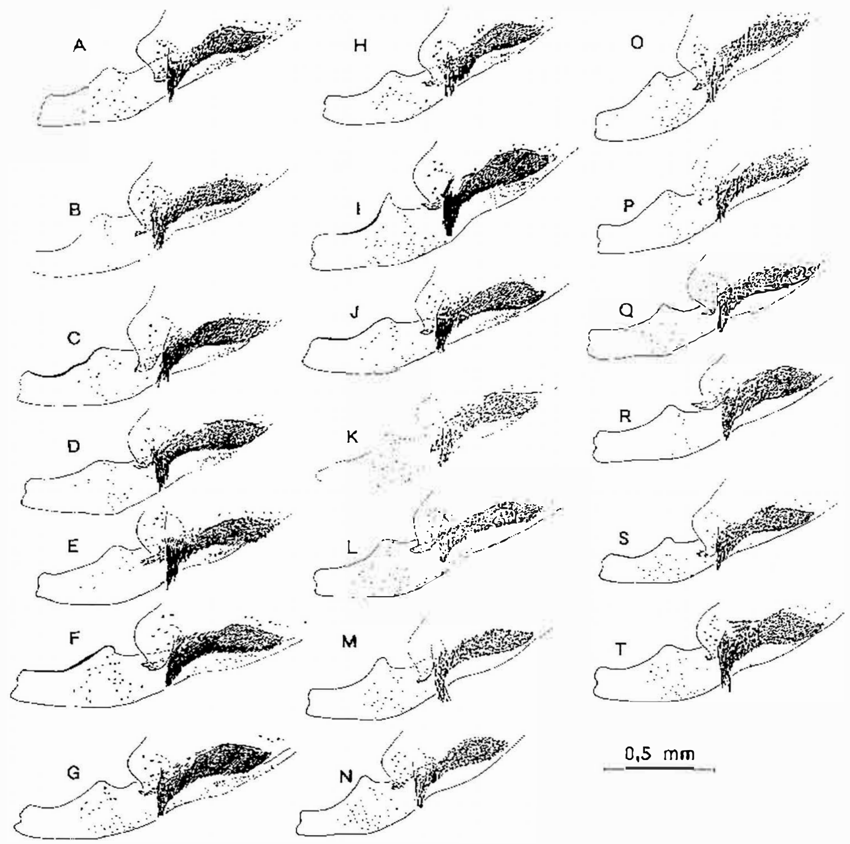


Plate 14. Intraspecific variability of the male genitalia of *Achyra coelatalis*. Rwanda: A, B, C, D, E, F, G, I; Cameroon: H, J; Zimbabwe: K, O; Zambia: L; Seychelles: M, N, Q, R, T; Kenya: P; India: S.

The valvae are paired structures articulating with the arms of the vinculum and the ventral part of the tegumen. They consist of flattened, sac-like structures and are in most cases mirror-images of each other. The internal side may be divided into a number of fields: the dorso-proximal field or costa, the central and medio-dorsal field or ampulla, the dorso-distal field or cucullus, the ventro-distal field or valvula, the central and medio-ventral field or harpe and the ventro-proximal field or sacculus.

In the Crambidae only the costa and sacculus may be recognized easily.

A number of characteristic modifications may occur on the inside of the valvae. They are best developed in the Pyraustinae-Spilomelinae complex.

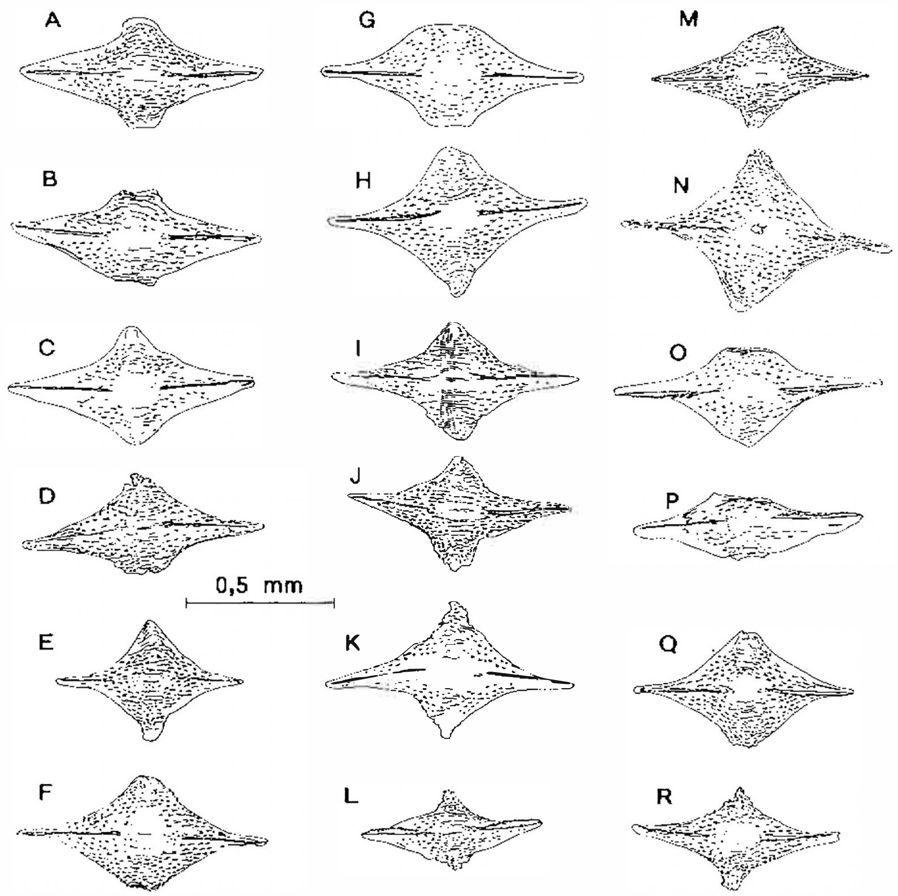


Plate 15. Intraspecific variability of the rhomboid signum of *Achyra coelatalis*. Rwanda: A, B, G, H; Cameroon: C, D, F; Zaire:E, J, K, N; Madagascar: F, Q; India: L, R; Nigeria: M; S.Africa: O; Seychelles: P.

MARION (1952, 1961) described the following structural modifications of the valvae of this group:

sella: MARION (l.c.) defines this structure as a kind of sac formed from the membrane of the valva, of very variable shape, carrying hairs, setae, spines, teeth or an editum carrying modified setae. The sella is defined here as a lobe-shaped extension originating medially from the valva and always directed towards the aedoeagus. This structure may be strongly sclerotized and bears dorsally some long setae which may be simple or modified. Sometimes a second sella may occur next to the first.

editum: associated with the sella, usually occuring above it and in general with modified setae forming lamellate structures. Typically they are flattened and incised terminally to form several teeth.

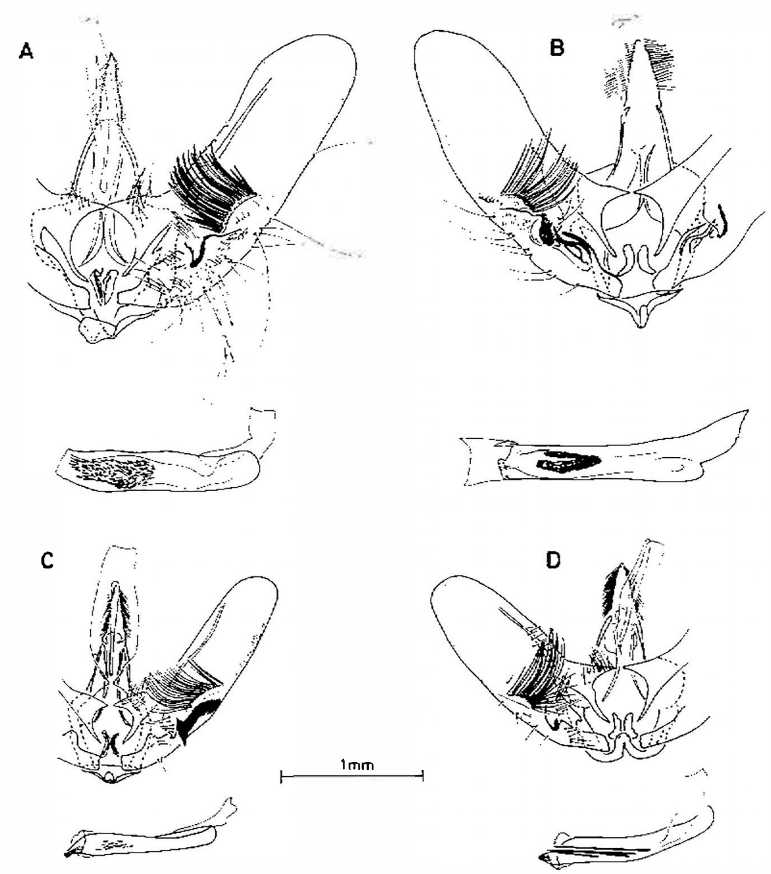


Plate 16. Male genitalia of *Achyra* species. A: *Achyra nudalis*; B: *A. rantalis*; C: *A. coelatalis*; D: *A. massalis*.

pulvinus: a modification of the sella into a cushion (MARION, 1961). This definition is considered here as a junior synonym of the editum.

cuiller: the sacullus may be prolonged distally, terminating in a point, for example in *Metasia* species.

fibula: a modification of the sella into a small conical tube (MARION, 1961). It is defined here as a lobe-shaped, strongly sclerotized structure, originating medially from the valva. The fibula is always directed towards the apex of the valva and is never assiociated with an editum.

These modifications are rather common in the Pyraustinae and Spilomelinae. Other structures also occur: a strongly sclerotized arm may occur at the base of the costa in *Stiphrometasia* ZERNY. A field bearing distinctive setae occurs medio-apically on the valvae.

Male specimens of *Eurrhypara hortulata* (LINNAEUS) bear a medio-ventral protrusion on the valvae; this is not homologous with the cuiller.

Hapalia nigrescens MOORE has two different valvae.

1.3.2. Female genitalia

MARION (1952, a.o.) did not consider the female genitalia in his studies. AMSEL (1956-1957) included the female genitalia in his work in places. Only MUNROE (1950, a.o.) and HANNEMANN (1964) made use of the female genitalia comprehensively.

These structures show less variation than the male genitalia and the number of useful diagnostic characters in them is limited.

The female genitalia of the Pyraloidea are of the ditrysian type characterised by a copulatory aperture (sinus vaginalis) on segment 8 and an ovipore on segment 9 (RICHARD & DAVIES, 1977).

The oviporal aperture, or ostium oviductus, is surrounded by a pair of papillae anales which also surround the anus. The papillae anales consist of a pair of lobe-shaped structures covered with setae and spines. They are derived from the 9th and 10th abdominal segments. The form and degree of sclerotization of the papillae anales depends upon the way the eggs are laid.

In the sinus vaginalis the ostium bursae occurs first, followed by the ductus bursae and then the bursa copulatrix. In some groups a second bursa or appendix bursae (= caput bursae, junior synonym: TUXEN, 1956) may occur. Different kinds of sclerotization may be present on the wall of the bursa copulatrix. They may be plate-like, with or without teeth, spines, scaled ridges, etc.. These structures, called signa (singular: signum) may be single or multiple.

Beneath the ostium bursae a more or less sclerotized ring, the antrum, may be distinguished. The ductus seminalis usually emerges just behind the the antrum. The ostium bursae may carry different sclerotized structures, called sterigma.

The lamella antevaginalis is the ventral plate of the ostium bursae, the lamella postvaginalis is that plate between the ostium bursae and the papillae anales.

The apophyses are internal, sclerotized apodemes which serve as muscle attachments. There are two pairs: the apophyses posteriores, emerging from the papillae anales, and the apophyses anteriores, emerging from the 8th sternite.

2. *Variability of abdominal structures*

In order to study intraspecific variation it was necessary to use a species with a wide range for which plentiful material from different localities was available. In addition, the species needed to belong to a genus with a

global distribution.

These conditions were met by the genus *Achyra* GUENÉE with species from the Palaearctic, Nearctic, Ethiopian, Oriental and Australian regions. A large number of specimens of *Achyra coelatalis* (WALKER) were available from different localities across its range. The species occurs in the Ethiopan region (Africa south of the Sahara, Madagascar and the Seychelles) and also in some parts of the Oriental region (N. India, Ceylon). Large samples were available from different localities in East and West Africa giving an idea of the variability within one population.

2.1. Tympanal organs

2.1.1. Intraspecific variability (Plate 13: 1-3)

The tympanal organs are symmetric. No sexual dimorphism occurs within this genus, nor within the subfamily containing it. The bullae tympani always appear somewhat crushed because of imperfections in the preparation technique: the strongly sclerotized flat parts of the tympanal organs are more suited to this kind of study. The zona glabra tympani and the venulae secundae may be used, as may the saccus tympani.

A series of preparations of males from Kigali (Rwanda) give an idea of the variablity within one population.

The length of the venulae secundae beyond the saccus tympani and bullae tympani is the same. One aberrant was observed: probably a malformation which occurred during the emergence of the adult, since the difference is not symmetrical. An identical form was observed in *Eurrhypara hortulata* (LINNAEUS).

The sclerotizations of the zona glabra tympani exhibit the greatest variability. In general, however, the same pattern was observed to occur within the sample: a small excavation at the level of the saccus tympani, both excavations being connected by a transverse bridge. The depth of the excavation and the length of its edges differ slightly. Specimens from Cameroon have a deeper excavation than those from other locations. Samples from other parts of the Ethiopian region do not exhibit geographic variation. After comparison with specimens from Madagascar and northern India, one may conclude that these structures are very uniform within the species.

2.1.2. Interspecific variablity (Plate 18)

The tympanal organs of *Achyra coelatalis* (WALKER) were compared with these of *A. nudalis* (HÜBNER) from the Palaearctic, *A. rantalis* (GUENÉE) from the Nearctic and *A. massalis* (WALKER) from the Australian region.

The excavation in the zona glabra occurs in all these species. The transverse bridge is easily seen in *A. nudalis* (HÜBNER). The venula secunda is well developed and always long; it extends beyond the distal end of the bulla tympani in *A. nudalis* (HÜBNER) and *A. massalis* (WALKER). The saccus tympani is deepest in *A. rantalis* (GUENÉE) and shallowest in *A. nudalis* (HÜBNER).

2.2. Pregenital segments

In the Pyraustinae the pregenital segments are not modified.

2.3. Genitalia

2.3.1. Male genitalia

The most complex modifications occur on the valva (sella, editum).

2.3.1.1. Intraspecific variation (Plate 14)

In any study of intraspecific variation the male genitalia can be observed as a whole only with difficulty: the structures are too complex and must be flattened during preparation, with possible distortion as a result. For this reason the sacculus and sella were studied; both structures are of value at the species level.

Plate 18 illustrates the intraspecific variability of these structures within the same population of *A. coelatalis* (WALKER). The protrusion on the sacculus varies from strongly flattened to sharply pointed. The sella is either rather short and blunt, or protruding and sharp. The area with a dense covering of spines is rather uniform; only the point near the sella varies slightly in length.

Specimens from the Seychelles are very uniform. The sella is always short and blunt, the area bearing spines extends slightly beyond the edge of the sacculus and the protrusion on the sella is rounded.

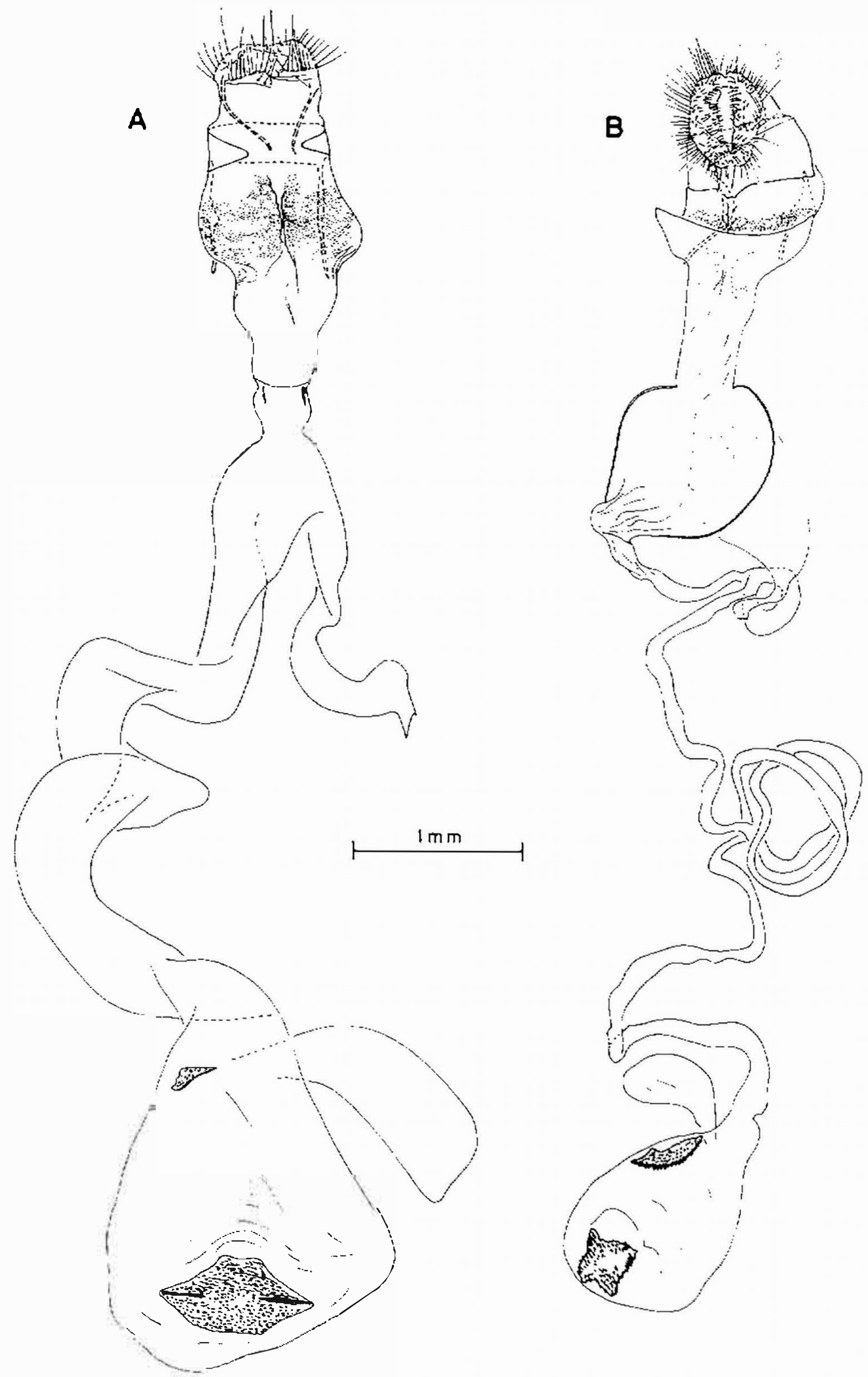
The sacculus of the specimen from Zimbabwe is blunt and different from those from other localities.

The differences between specimens from Northern India and those those from the Ethiopian region were not considered significant.

2.3.1.2. Interspecific variability

Plate 16 illustrates the male genitalia of some *Achyra* species. The uncus is simple, pointed and bears simple setae dorsally. A subscaphium is present on the tuba analis. The tegumen is broad, the vinculum U-shaped and the saccus reduced. The transtilla is well developed and a ventral arm is present. The juxta consists of two bean-shaped plates. The aedoeagus is straight. Some cornuti are present on the vesica. The valvae are simple and rounded, with a sella and an editum bearing simple setae.

Plate 17-1. Female genitalia of *Achyra* species. A: *Achyra rantalis*; B: *A. nudalis*.



The valva of *A. coelatalis* (WALKER) bears a field of spines extending both distally and ventrally from the sella.

Such a field is absent from the valvae of *A. massalis* (WALKER) and *A. nudalis* (HÜBNER). The sella of these two species is broad and bears some teeth along its edge.

In *A. massalis* (WALKER) there are some needle-shaped cornuti on the vesica. The cornuti of *A. nudalis* (HÜBNER) and *A. rantalis* (GUENÉE) are plate-like structures bearing some teeth.

On the vesica of *A. coelatalis* (WALKER) there are only a few dispersed, spine-shaped cornuti.

The sacculus is simple except in *A. rantalis* (GUENÉE) where the edge is modified to form three long spines.

2.3.2. Female genitalia

2.3.2.1. Intraspecific variability (Plate 15)

Because it is possible to achieve consistent preparations, the signum and the apophyses were chosen for study.

The corpus bursa of *A. coelatalis* (WALKER) bears two signa. The largest of them is rhomboid with a sclerotized transverse arm which is discontinued medially. Small teeth are arranged radially from the centre of the signum. The centre itself bears only very small sclerotizations or none at all. The largest teeth occur laterad of the transversal ridge. The overall sclerotization of the signum varies to give a different overall form.

The centre of the signum in specimens from the same locality may vary from naked to toothed. Specimens with a naked or only slightly toothed centre have less sclerotization over the signum as a whole than do specimens with a heavily toothed centre.

Both the apophyses posteriores and anteriores are of equal length and strongly sclerotized. The apophyses are flattened apically.

The length of the apophyses anteriores in specimens from different localities varies only slightly; they are always straight. The apophyses posteriores are more or less curved. There are some differences in length and curvature but these differences are small.

2.3.2.2. Interspecific variability (Plate 17: 1-2)

The general structure of the female genitalia of *Achyra* species is as follows: the papillae anales are weakly sclerotized. The apophyses are always well developed. The ostium bursae is apically invaginated in the 7th segment. The sinus vaginalis is surrounded by minute spines. The ductus seminalis emerges apically from the antrum, which is always present. The ductus bursae is spiraled. The corpus bursae bears two signa: a rhomboid signum and a small, ribbon-like signum composed of numerous teeth at the base of the appendix bursae.

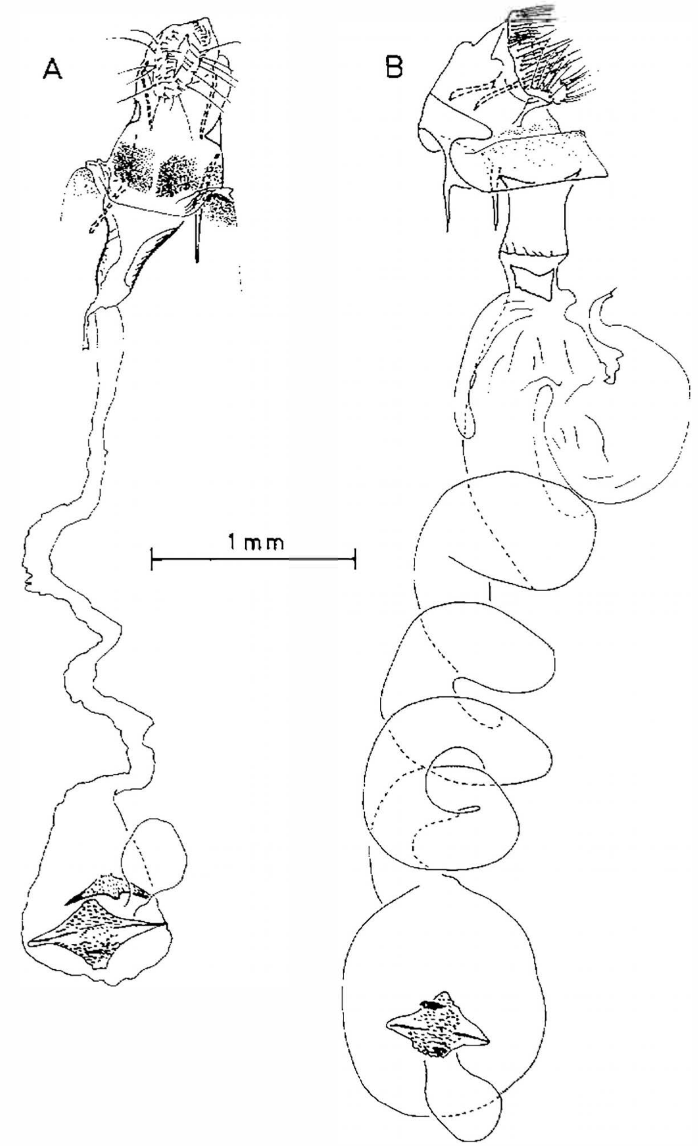


Plate 17-2. Female genitalia of *Achyra* species. A: *Achyra coelatalis*; B: *A. massalis*.

A. coelatalis (WALKER) has a broad ostium bursae, narrowing at the antrum. The ductus seminalis is slightly swollen at its base. The ductus busae is twisted but not spiraled. The second signum is large and rhomboid. The rhomboid signum is as broad as long.

A. massalis (WALKER) has a tube-shaped ostium bursae. The ductus seminalis is very broad at the antrum. Opposite the ductus seminalis, on the other side of the antrum, there is a tube-like appendix. The ductus bursae is spiraled. The second signum is very small. The four sides of the rhomboid signum are more or less of equal length.

A. nudalis (HÜBNER) has a tube-shaped ostium bursae. The enlarged part of the ductus seminalis is sclerotized. The ductus bursae is long and narrow and is enlarged just beneath the antrum. The sides of the rhomboid signum are of about equal length. The second signum is large, bent and covered with numerous teeth.

In *A. rantalis* (GUENÉE) the ostium bursae is in the form of an inverted bottle neck. The ductus seminalis is enlarged for a considerable length, but not bladder-like as in *A. nudalis* and *A. massalis*. The ductus bursae is rather short in comparison with that of other species. The edges of the rhomboid signum are rounded; the second signum is very small.

D. Discussion

The adults of the Crambidae, especially the Pyraustinae (sensu HAMPSON) have both conservative and complex morphological structures.

The morphology of the head is difficult to study (see also introduction). The basic plan varies only slightly.

The structures of the head are conservative:

- the frons is usually flat or slightly rounded. Protruberances are more common in the Odontiinae than in the Spilomelinae and Pyraustinae; their function is unknown.
- the vertex is flattened
- chaetosemata are absent in the Pyraustinae
- the maxillary palps are small and four-segmented; they are located on either side of the proboscis. There is considerable intra- and interspecific variability which renders them valueless as characters at lower taxonomic levels. In the Linostinae they are atrofied; they are present in all other Crambidae.
- the labial palps consist of three segments. They are densely scaled, with sparsely scaled palpi occurring in some high altitude species. The form and degree of scaling also varies with the age of the moth: fresh specimens are more densely scaled then older ones. The way specimens have been handled during preparation may also result in loss of scales.

The sclerotized parts of the labial palps may give some information how the genera are related. The length, form and degree of curvature may be used since they exhibit only slight intraspecific variation.

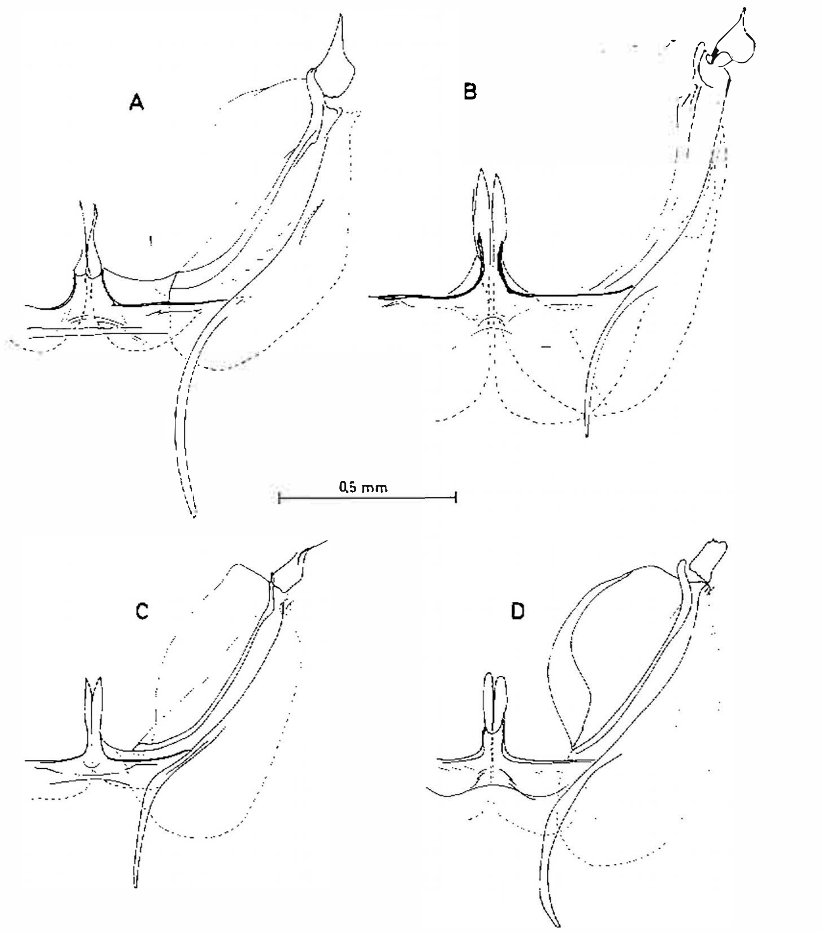


Plate 18. Tympanal organs of *Achyra* species. A: *Achyra nudalis*; B: *A. rantalis*; C: *A. coelatalis*; D: *A. massalis*.

The structure of the antennae and proboscis is somewhat more complex. This study assumes that the morphology of the proboscis is strongly influenced by their function. Within the Pyraloidea only a few variations occur. A comparison of these structures in other more distantly related groups (Geometridae, Noctuidae, Rhopalocera) indicates that they vary only slightly there too.

The antennae bear no scales ventrally; they have a peculiar net-like surface with different sensilla.

The legs are uniform. Male Pyraustinae may have the epiphyses more strongly developed than the females. Characteristic setae may be present and may be used as diagnostic characters for closely related species. Some male Pyraustinae, for instance *Pagyda* WALKER, have a brush-like structure on the mid-tibia. The spurs seem not to have taxonomic value at the lower levels.

The wing venation is very uniform and the few variations that do occur were also found in one species, therefore the wing venation is of limited taxonomic value. The wing pattern can also be misleading since sexual dimorphism and mimicry are not uncommon.

The abdomen contains the tympanal organs and genitalia. Both are complex structures which may be studied with a simple microscope.

The intraspecific variability of the tympanal organs is slight. The interspecific differences of some parts of these organs are usually obvious enough to permit species differentiation. At the specific level the zona glabra is the most useful element of the tympanal organs. Sometimes the relative length of the venula secunda/saccus tympani may be used at the specific level. Closely related genera based on other characters (genitalia) have rather similar tympanal organs while more distantly related genera exhibit greater differences.

For example: closely related genera: *Mutuuraia* MUNROE; *Algedonia* LEDERER; *Phlyctaenia* HÜBNER.

distantly related genera: *Aglaops* Warren; *Sinibotys* MUNROE & MUTUURA.

At present our knowledge of the different forms of tympanal organs within the Crambidae is only fragmentary and we do not yet have a comprehensive idea of their taxonomic value.

Within the Pyraustinae there is a strong correlation between tympanal organs and genitalia, and a combination of characters is most useful at the subfamilial level. The correlation between the genitalia and the tympanal organs was found in Pyraustinae from all zoogeographic regions. Since these complex structures are found on different parts of the body, it can be assumed that they have evolved independently. This enables the Pyraustinae to be defined as monophyletic. In typical Pyraustinae, the male genitalia are as follows: gnathos normally lacking; valva with sella and editum; apically forked setae on uncus sometimes present; tegumen parallel with the body's longitudinal axis; the female genitalia: corpus bursae with rhomboid signum and an appendix bursa, the tympanal organs with a clearly invaginated fornix tympani, which is usually narrow at the base and a more or less well developed saccus tympani. Some Pyraustinae do not have all these characters simultanously.

Since the tympanal organs seldom display sexual dimorphism, they may also be used to associate males and females with a strong sexual dimorphism in the wing pattern and colouration which have been described as different species, for example in the genus *Ulopeza* WALKER.

In summary, it is doubtful that the tympanal organs will ever be useful as generic-level characters on their own. Other structures on the body, like the genitalia are more complex, the tympanal organs do not display the numerous variations found in the genitalia. They have a rather simple basic plan on which more complex structures of various kinds may be found.

In the male genitalia the form of the valva, sella, editum, juxta, aedoeagus, vesica, cornuti and spicula exhibit the most reliable specific characters. The female genitalia on the other hand are more uniform and may provide, together with the male genitalia, reliable information at the generic level. In most cases this evidence is supported by characters found in the tympanal organs.

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E. Appendix 1

Material studied: The subfamilies, genera and species are listed by alphabetical order.

Crambidae

Cathariinae:

Catharia pyrenaealis DUPONCHEL.

Crambinae:

Agriphila inquinatella [DENIS & SCHIFFERMÜLLER]; *Agriphila tristella* [DENIS & SCHIFFERMÜLLER]; *Ancylolomia palpella* [DENIS & SCHIFFERMÜLLER]; *Ancylolomia* spec. (Ethiopian region); *Catoptria pinella* LINNAEUS; *Crambus palustrellus* RAGONOT; *Crambus pascuella* LINNAEUS; *Crambus perlella* SCOPOLI; *Crambus pratella* LINNAEUS; *Euchromius bellus* HÜBNER; *Pediasia contaminella* HÜBNER.

Cybalomiinae:

Cybalomia fractilinealis ERSCHOFF; *Cybalomia pentadalis* LEDERER; *Hyperlais nemausalis*

DUPONCHEL; *Hyperlais siccalis* GUENÉE; *Prochoristis rupicapralis* LEDERER.

Dichogamiinae:

Alatuncusia gilvicostalis HAMPSON; *Dichogama redtenbacheri* LEDERER.

Evergestinae:

Cylindrifrons succandidalis HULST; *Evergestis africalis* GUENÉE; *Evergestis forficalis* LINNAEUS; *Evergestis frumentalis* LINNAEUS; *Evergestis olivalis* WARREN; *Evergestis pallidata* HUFNAGEL; *Evergestis sophialis* FABRICIUS; *Orenaia alpestralis* FABRICIUS; *Orenaia helveticalis* HERRICH-SCHÄFFER; *Orenaia rupestralis* HÜBNER; *Reskovitsia alborivulalis* EVERSMANN.

Glaphyriinae:

Abegesta reluctalis HULST; *Glaphyria sesquistrialis* HÜBNER; *Hellula undalis* FABRICIUS.

Linostinae:

Linosta annulifera MUNROE; *Linosta sinceralis* MÖSCHLER.

Midilinae:

Midila daphne DRUCE; *Midila quadrifenestrata attacalis* WALKER; *Styphlolepis squamosalis* HAMPSON.

Noordinae:

Noorda blitealis WALKER.

Nymphulinae:

Acentria ephemerella [DENIS & SCHIFFERMÜLLER]; *Ambia ptolycusalis* WALKER; *Argyractis argentilinealis* HAMPSON; *Cataclysta lemnata* LINNAEUS; *Elophila nymphaeata* LINNAEUS; *Musotima aduncalis* FELDER & ROGENHOFER; *Nymphula stagnata* DONOVAN; *Parapoynx stratiotata* LINNAEUS.

Odontiinae:

Aporodes floralis HÜBNER; *Atralata albofascialis* TREITSCHKE; *Blepharucha zaide* STOLL; *Cynaeda dentalis* [DENIS & SCHIFFERMÜLLER]; *Epascestria pustulalis* HÜBNER; *Ephelis cruentalis* GEYER; *Euctenospila castalis* WARREN; *Eurrhypis pollinalis* [DENIS & SCHIFFERMÜLLER]; *Metamexte phrygialis* HÜBNER; *Noctuelia superbalis* HERRICH-SHÄFFER; *Orenaia alpestralis* FABRICIUS; *Orenaia helveticalis* HERRICH-SCHÄFFER; *Orenaia rupestralis* GEYER; *Tegostoma comparalis* HÜBNER; *Titanio normalis* HÜBNER.

Pyraustinae:

Achyra coelatalis WALKER; *Achyra massalis* WALKER; *Achyra nudalis* HÜBNER; *Achyra rantalis* GUENÉE; *Achyra takowensis* MAES; *Aglaops aurantialis* MUNROE & MUTUURA; *Aglaops homaloxantha* MEYRICK; *Algedonia luctualis* HÜBNER; *Anamalaia nathani* MUNROE & MUTUURA; *Anania funebris* STRÖM; *Anania verbascalis* [DENIS & SCHIFFERMÜLLER]; *Aurorobotys aurorina* BUTLER; *Aurorobotys crassispinalis* MUNROE & MUTUURA; *Callibotys hyalodiscalis* WARREN; *Carminibotys carminalis* CARADJA; *Circobotys nycterina* BUTLER; *Crocidophora pustuliferalis* LEDERER; *Crypsiptya coclesalis* WALKER; *Demobotys pervulgalis* HAMPSON; *Duzulla subhyalinalis* HAMPSON; *Ebulea crocealis* HÜBNER; *Ecpyrrhorrhoe diffusalis* GUENÉE; *Epicorsia mellinalis* HÜBNER; *Epiparbattia gloriosalis* CARADJA; *Euclasta defamatalis* WALKER; *Euclasta splendidalis* HERRICH-SCHÄFFER; *Eumorphobotys eumorphalis* CARADJA; *Eupmorphobotys obscuralis* CARADJA; *Eurrhypara hortulata* LINNAEUS; *Eusabena miltochristalis* HAMPSON; *Eutectona rubicundalis* WARREN; *Fumibotys fumalis* GUENÉE; *Gynenomis sericealis* WILEMAN; *Helvibotys helvialis* WALKER; *Hyalobathra archeleuca* MEYRICK; *Hyalobathra illectalis* WALKER; *Isocentris filalis* GUENÉE; *Isocentris unicolor* WARREN; *Lamprophaia albifimbrialis* WALKER; *Limbobotys limbolalis* MOORE; *Loxostege aeruginalis* HÜBNER; *Loxostege sticticalis* LINNAEUS; *Mabra eryxalis* WALKER; *Meridiophila fascialis* HÜBNER; *Mimetebulea arctialis* MUNROE & MUTUURA; *Mutuuraia terrealis* TREITSCHKE; *Nascia cilialis* HÜBNER; *Nephelobotys nephelistalis* HAMPSON; *Opsibotys fuscalis* [DENIS & SCHIFFERMÜLLER]; *Oronomis xanthothysana* HAMPSON; *Ostrinia incensa* MEYRICK; *Ostrinia nubilalis* HÜBNER; *Ostrinia palustralis* HÜBNER; *Pagyda salvalis* WALKER; *Paliga damastesalis* WALKER; *Paracorsia repandalis* [DENIS & SCHIFFERMÜLLER]; *Paranomis denticosta* MUNROE & MUTUURA; *Paratalanta pandalis* HÜBNER; *Paratalanta ussurialis* BREMER; *Paschiodes mesoleucalis* HAMPSON; *Paschiodes thomealis* VIETTE; *Perinephela lancealis* [DENIS & SCHIFFERMÜLLER]; *Perispasta caeculalis* ZELLER; *Phlyctaenia coronata* HUFNAGEL; *Placosaris egerialis* SNELLEN; *Prodasycnemis inornata* BUTLER; *Pronomis delicatalis* SOUTH; *Proteurrhypara ocellalis* WARREN; *Psammotis pulveralis* HÜBNER; *Pseudebulea fentoni* BUTLER; *Pseudopolygrammodes priscalis* CARADJA; *Pyrausta aerealis* HÜBNER; *Pyrausta aurata* SCOPOLI; *Pyrausta bicoloralis* GUENÉE; *Pyrausta bisignata* BUTLER; *Pyrausta castalis* TREITSCHKE; *Pyrausta cingulata* LINNAEUS; *Pyrausta gutturalis* STAUDINGER; *Pyrausta incensalis* LEDERER; *Pyrausta sanguinalis* LINNAEUS; *Sclerocona acutellus* EVERSMANN; *Sericoplaga externalis* WARREN; *Sinibotys evenoralis* WALKER; *Sitochroa palealis* [DENIS & SCHIFFERMÜLLER]; *Sitochroa verticalis* LINNAEUS; *Tenerobotys teneralis* CARADJA; *Thliptoceras cascale* SWINHOE; *Thliptoceras variabilis* WARREN; *Togabotys fusculineatalis* YAMANAKA; *Toxobotys praestans* MUNROE & MUTUURA; *Trigonuncus euergestalis* AMSEL; *Trigonuncus nissalis* AMSEL; *Trigonuncus sarobialis* AMSEL; *Trigonuncus similis* AMSEL; *Udonomeiga vicinalis* SOUTH; *Uresiphita polygonalis* [DENIS & SCHIFFERMÜLLER]; *Vittabotys mediomaculalis* MUNROE & MUTUURA; *Yezobotys ainualis* MUNROE & MUTUURA.

Schoenobiinae:

Schoenobius forficella THUNBERG; *Schoenobius gigantellus* [DENIS & SCHIFFERMÜLLER]; *Scirpophaga praelata* SCOPOLI.

Scopariinae:

Eudonia crataegella HÜBNER; *Eudonia mercurella* LINNAEUS; *Scoparia ambigualis* TREITSCHKE; *Scoparia dubitalis* HÜBNER; *Scoparia helenensis* WOLLASTON; *Scoparia idiogama* MEYRICK; *Scoparia lucidalis* WALKER; *Scoparia transversalis* WOLLASTON.

Siginae:

Siga liris CRAMER.

Spilomelinae:

Aethaloessa floridalis ZELLER; *Agathodes ostentalis* GEYER; *Agrotera nemoralis* SCOPOLI; *Amaurophanes stigmosalis* HERRICH-SCHÄFFER; *Antigastra catalaunalis* DUPONCHEL; *Apyrausta persicalis* AMSEL; *Aristebulea nobilis* MOORE; *Arnia nervosalis* GUENÉE; *Beebea guglielmi* SCHAUS; *Bocchoris inspersalis* ZELLER; *Botyodes asialis* GUENÉE; *Bradina adhaesalis* WALKER; *Ceratarcha umbrosa* SWINHOE; *Cnaphalocrocis medinalis* GUENÉE; *Deba barcalis* WALKER; *Deba milvinalis* SWINHOE; *Deba surrectalis* WALKER; *Diaphania indica* SAUNDERS; *Diasemia reticularis* LINNAEUS; *Diasemiopsis ramburialis* DUPONCHEL; *Diastictis flavibrunnea* HAMPSON; *Dolicharthria concoloralis* OBERTHÜR; *Dolicharthria punctalis* [DENIS & SCHIFFERMÜLLER]; *Ebuleodes simplex* MEYRICK; *Elbursia stocki* AMSEL; *Epactoctena octogenalis* LEDERER; *Eurrhyparodes bracteolalis* ZELLER; *Eurrhyparodes tricoloralis* ZELLER; *Eusabena setinalis* HAMPSON; *Filodes productalis* HAMPSON; *Ghesquierellana* *thaumasia* MUNROE; *Glauconoe deductalis* WALKER; *Glyphodes stolalis* GUENÉE; *Goniorhynchus gratalis* LEDERER; *Hendecasis duplifascialis* HAMPSON; *Hymenia perspectalis* HÜBNER; *Hymenia recurvalis* FABRICIUS; *Ischnurges lancealis* GUENÉE; *Lomotropa costiflexalis* GUENÉE; *Marasmia trapezalis* GUENÉE; *Maruca testulalis* GEYER; *Mecyna asinalis* HÜBNER; *Metallarcha calliaspis* MEYRICK; *Metallarcha diplochrysa* MEYRICK; *Metasia cuencalis* RAGONOT; *Metasia ophialis* TREITSCHKE; *Metasia suppandalis* HÜBNER; *Mukia nigroanalis* AMSEL; *Nomophila noctuella* [DENIS & SCHIFFERMÜLLER]; *Nosophora althealis* WALKER; *Nosophora dispilalis* HAMPSON; *Notarcha muscerdalis* ZELLER; *Omiodes indicata* FABRICIUS; *Palpita bonjongalis* PLÖTZ; *Palpita unionalis* HÜBNER; *Pardomima azancla* MARTIN; *Pardomima phaeoparda* MARTIN; *Phalanta dioramica* GHESQUIÈRE; *Plateopsis vespertilio* WARREN; *Pleuroptya aurantiacalis* FISCHER VON RÖSLERSTAMM; *Polygrammodes runicalis* GUENÉE; *Polythlipta camptozona* HAMPSON; *Psara ingeminata* MEYRICK; *Psara stultalis* WALKER; *Pycnarmon cibrata* FABRICIUS; *Pycnarmon ingeminata* Meyrick; *Pycnarmon leucodoce* MEYRICK; *Stantira variegata* WALKER; *Stiphrometasia monialis* ERSCHOFF; *Synclera traducalis* ZELLER; *Tabidia insanalis* SNELLEN; *Terastia meticulosalis* GUENÉE; *Terastia subjectalis* LEDERER; *Tetridia caletosalis* WALKER; *Udea ferrugalis* HÜBNER; *Udea hamalis* THUNBERG; *Udea lutealis* HÜBNER; *Udea olivalis* [DENIS & SCHIFFERMÜLLER]; *Ulopeza conigeralis* ZELLER; *Ulopeza ovigeralis* GHESQUIÈRE; *Zebronia perspicata* FABRICIUS; *Zeuzerobotys mirabilis* MUNROE.

Pyralidae

Pyralinae:

Endotricha flammealis [DENIS & SCHIFFERMÜLLER]; *Hypsopygia costalis* FABRICIUS; *Pyralis farinalis* LINNAEUS; *Synaphe angustalis* [DENIS & SCHIFFERMÜLLER].

Galleriinae:

Galleria mellonella LINNAEUS.

Phycitinae:

Ephestia cautella WALKER; *Ephestia elutella* HÜBNER; *Euzophera pinguis* HAWORTH; *Hypochalcia rubiginella* TREITSCHKE.

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Les manuscrits doivent être déposés en 2 exemplaires, y compris une copie des illustrations et des tableaux. Ils seront dactylographiés sur une seule face de papier de format DIN A4, en double interligne, avec une marge à gauche d'environ 3 cm; les pages seront numérotées à partir de la page de titre; les paragraphes commenceront par un alinéa net. Les auteurs respecteront les règles du Code international de Nomenclature zoologique et sont priés de prendre leurs précautions afin que les holotypes des espèces décrites dans les *Bull. & Annls* soient déposés dans un musée ou une institution officielle. Pour les descriptions de nouveaux taxons, l'établissement de nouveaux synonymes, nouveaux homonymes, nouvelles combinaisons, etc., ils emploieront les abréviations sp. n., gen. n., trib. n., syn. n., comb. n., nom. n., etc. Pour les nouvelles combinaisons, le genre d'origine sera cité. Lors de la première citation d'un taxon, le nom complet devrait toujours être suivi du nom du parrain et de la date, séparés par une virgule, avec ou sans parenthèses selon les prescriptions du Code. On évitera de citer des espèces sans faire précéder le nom spécifique d'au moins l'initiale du nom générique.

La page de titre (p. 1) comprendra le titre complet, avec entre parenthèses l'ordre et la famille du groupe traité, ainsi que le nom et l'adresse de l'auteur ou ceux des co-auteurs. La page 2 est reservée à un résumé, dans la langue de l'article, éventuellement suivi d'un résumé dans une autre langue nationale ou en anglais, de préférence de moins de 200 mots. Enfin, quelques "mots-clés" seront ajoutés pour assurer à l'article une bonne analyse bibliographique.

Le texte proprement dit commencera à la page 3. Selon les sujets traités, les chapitres suivants pourraient être développés: introduction, matériaux et méthodes, résultats, systématique, discussion. Les paragraphes commenceront par un alinéa et les noms scientifiques seront soulignés une fois (ils seront aussi publiés en italiques). Les titres de chapitres et paragraphes ne seront pas soulignés: le corps typographique sera choisi par le metteur en page.

Dans le texte, les références aux autres auteurs se feront selon les modèles suivants: SMITH (1969), (SMITH, 1969), SMITH (1969, 1985), (SMITH, 1969; BROWN, 1971), SMITH (1969) et BROWN (1976), BLACK & WHITE (1945), et, pour plus de deux auteurs: SMITH *et al.* (1979).

Dans les données de capture, il convient de citer les mois en chiffres romains (11.IV.1928); ailleurs, il est recommandé de les écrire en toutes lettres (le 11 avril 1928).

Les éventuels remerciements seront concis et précèderont la bibliographie.

Bibliographie: tout article comprendra la liste de tous les ouvrages cités dans le texte; les titres des revues seront abrégés conformément au "World list of scientific Periodicals"; pour les articles encore en cours d'impression, le nom de la revue seul sera mentionné, suivi de "(sous presse)". Les références bibliographiques seront rangées suivant l'ordre alphabétique des noms d'auteurs, et pour ceux-ci par ordre chronologique, selon les exemples suivants:

FAIN, A. & LUKOSCHUS, F. S., 1971. - Parasitic Mites of Surinam; XV. Nasal Ereynetid Mites of Bats with a key of the known species. *Bull. Annls Soc. r. belge Ent.* 107: 284-297.

HENNIG, W., 1966. - *Phylogenetic Systematics.* University of Illinois Press, Urbana, 263 pp.

On fournira les légendes des illustrations et des tableaux sur une page séparée.

Les illustrations: elles seront numérotées dans une seule série continue et les grandissements seront indiqués par une échelle ou mentionnés dans les légendes. Lors du montage, il sera tenu compte de la justification de la revue: 13,35 cm X 21 cm. Les auteurs ont intérêt à indiquer, sur le manuscrit, l'emplacement approximatif des planches ainsi que le pourcentage de la réduction. L'impression des photos et illustrations qui requièrent une technique spéciale sera portée en compte aux auteurs.