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Assessment of taxonomically significant structures in Tortricinae (Lep., Tortricidae)¹

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The taxonomically significant structures of adult Tortricinae, including male and female genitalia, are assessed from a phylogenetic point of view on a world-wide base. For each character a short literature review is given, followed by a discussion based on material examined for the present study. A list of all taxa considered is provided, and many structures are illustrated by photographs or drawings. As far as possible the groundplan character state for the subfamily is inferred for each structure and apomorphic conditions are discussed in relation to their systematic significance.

The present study has grown unpremeditatedly from my taxonomic and systematic work on Papuan Tortricinae, from the purely practical need to evaluate the characters used in classification. Though there is a tradition, implicitly agreed upon, of how certain characters are to be considered in tortricid taxonomy, the subject has never been consequently studied, let alone general agreement reached on the matter. Examination of selected tortricine taxa on a world-wide base soon made it obvious that several preconceived notions will have to be revised, with eventual consequences for tortricid classification. Extensive discussions with colleagues led to the decision to publish the results of this character assessment, originally intended just to help understand the evolution of a few puzzling characters. It is, however, not meant to present the final conclusions but rather to provide a documented base for further arguments and studies on tortricine morphology, with relevance to the systematics of the group.

For the understanding of relationships between higher taxonomic categories Hennigian phylogenetics (HENNIG, 1966; ASHLOCK, 1974) has in recent years proved to be an indispensable tool. The process of quantum speciation followed by adaptive radiation, which is reargued recently to be often at the origin of higher taxa (STANLEY, 1979), may easily lead to such a marked divergence in phenetic appearance that relationships can no longer be recognized simply by judging from the degree of similarity. Adaptations to similar conditions, on the other hand, may result in superficially surprisingly similar appearance in organisms from widely different groups. The only means of establishing kinship in such cases is to demonstrate the monophyly of the group concerned.

By definition a monophyletic group includes only and all the descendants of a given ancestor and is recognized by specific characters acquired by the ancestor and passed on to all descendants. Thus only the shared possession of a derived character by two or more taxa, of a synapomorphy, serves as an indication of their

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kinship, symplesiomorphies being without consequence for the determination of a monophyletic group. The correct determination of the sequence of several succeeding stages of an evolving character (i. e. the polarity of character states) is therefore the crucial prerequisite for a successful reconstruction of the phylogeny.

Before it can be decided which of two character states compared with each other is more derived, it has to be established that both states belong to the same series of transformations, i. e. that they represent succeeding stages in the development of the same structure. If a recognized transformation series comprises more than two subsequent conditions the same state can both be plesiomorphic (compared to the more derived states) or apomorphic (relative to the more primitive states).

HENNIG provides four criteria to help reconstruct the character phylogeny but only his «criterion of correlation of series of transformations» is applicable to the evaluation of the different character states within the Tortricinae. Thus if a character state whose level of development is obscure is very frequently associated with the plesiomorphic state in other characters, the surmise that the character in question represents also a plesiomorphy is justified until the contrary can be demonstrated. But it must be borne in mind that such a deduction in itself can never prove a case, although many indications pointing in the same direction may help considerably in understanding the evolution of an obscure structure. The construction of a cladogram with as little parallelism, convergence and reversal as possible will be a test for the correctness of the inferred polarities.

Though the Tortricidae are a clearly defined group, rich in typical characters, it has already been pointed out by previous authors that in only very few instances have genuinely new structures appeared below the family level. TURNER (1918) and HEINRICH (1923), as well as DIAKONOFF (1973), recognized that most of the development consists of reductions. This observation is in perfect agreement with the recently reconsidered and modified ideas of a possible origin of higher taxa by quantum speciation, i. e. a genetic revolution in an extremely small population leading to fundamental restructuring of the genotype and dramatic changes in the morphology. Once a new genetical equilibrium has been reached and the new phenotype is successful enough to spread through an adaptive radiation, further morphological change will be due to regulatory processes rather than to the creation of new genetic information.

This is very much what we see in the Tortricidae: the sudden appearance of a morphologically well defined family whose further evolution occurs without many additionally acquired characters, but through several often parallel trends of reduction which results eventually in quite diverse types. It was a great surprise during the present study to find out just how many structures previously considered derived proved to be only plesiomorphies. Apart from a few scattered and very generalized taxa they are often retained in only one otherwise highly developed group for which they were regarded to be the typical apomorphy (scaled *socii*, long palpi, strongly ciliate antenna).

In trying to reconstruct the phylogeny of the Tortricinae we are thus faced with the difficulty that most apomorphies will be reductions, very likely independently occurring several times in different places. In the absence of convincingly new structures only a careful analysis of several apomorphic reductions and their correlation will allow the recognition of monophyletic groups, assuming that the reversibility of these reductions is negligible. If we were to accept the view expressed by RAZOWSKI (1976), who for taxonomic reasoning completely dismisses

all characters showing parallel development in any degree, we would be left with far too little evidence to ever understand the phylogeny of a group.

There is probably some tacit agreement on the polarity of most of the character states currently considered taxonomically significant in the Tortricidae, but surprisingly few authors clearly define their deductions or assumptions. A review of the literature in this respect, with a comparative morphological analysis of as many potentially meaningful structures as possible of representatives throughout the Tortricinae, seemed the obvious first step towards a study of the phylogeny of the subfamily. Special attention was given to taxa known or suspected to be rich in plesiomorphies.

HISTORICAL REVIEW OF CHARACTER EVALUATION IN THE TORTRICINAE

HEINRICH (1923), DIAKONOFF (1939, 1961), FREEMAN (1958) and POWELL (1964) all provide historical reviews of the development of taxonomy in the Tortricidae. FALKOVICH (1962) gives an apt summary of the progressive incorporation of new knowledge and methods which are usually at first relied upon exclusively to construct a modified system, disregarding previously considered structures that, however, often become integrated again with their due weight by more balanced views at a later stage. As the aim of the present study is to establish the relevance of the characters used for classification, not the merits of any one system, the literature is briefly reviewed only with regard to character evaluation in the Tortricidae.

The earliest attempts at grouping tortricid species into higher categories are based on wing pattern and coloration only, and GUENÉE (1845) gives no reasons for his arrangement. HERRICH-SCHÄFFER (1849–1856) provides figures of several morphological features and discusses their value but eventually considers for his classification only the antenna and the shape of the wing, with some very basic aspects of wing venation unsuitable for subdivision within the Tortricidae. He therefore subdivides the family on the basis of differences in wing shape and colour pattern. The subsequent studies by LEDERER (1859) and HEINEMANN (1863) are both based on a thorough discussion of the general morphology with regard to suitable structures for classification. Both recognize the prime taxonomical importance of the cubital pecten, but while LEDERER erects several genera on the strength of secondary sexual characters, HEINEMANN completely rejects their use and consequently synonymizes the genera concerned. A comprehensive and critical analysis of the external characters of the Tortricidae is provided by PEYERIMHOFF (1876), but it remains purely descriptive without any indication of a phylogenetic concept. MEYRICK (1888 etc.) utilizes external morphology and especially wing venation as completely as possible for his taxonomic work, probably also supported by good intuition. His attempts, however, at rendering the phylogeny of the Tortricidae (MEYRICK, 1895) are completely untenable and severely criticized by KENNEL (1908).

From the discussion of the different morphological structures of the Tortricidae, and especially from the well-founded criticism of MEYRICK's phylogenetic diagrams, it is obvious that KENNEL had a clear and correct concept of phylogeny and character evolution. He considers a venation with all veins arising separately and equally spaced to be the most primitive state. With sound reasoning he deduces that the absence of a costal fold in Tortricidae constitutes a derived condition and considers it unlikely that such a specialized structure, not obviously

under adaptive pressure, should have arisen at least five times independently within the Palearctic Tortricidae.

Apart from an isolated attempt by MEYRICK (1895) DAMPF (1908) initiated the use of genitalic characters for taxonomic purposes in the Tortricidae, but his paper remained largely unnoticed. Within a short period PIERCE & METCALFE (1922), HEINRICH (1923, 1926) and PHILPOTT (1928) present comprehensive studies of male and partly also female genitalia of large groups of Tortricidae. The papers by PIERCE & METCALFE on the English and by PHILPOTT on the New Zealand Tortricidae are confined to descriptions and illustrations of the morphology without any phylogenetic deductions. The former authors explicitly mention that genitalia are strongly generic in nature but shed very little light on the historic relationships of the genera. HEINRICH, on the other hand, in his revision of the North American Eucosminae, Laspeyresinae and Olethreutinae, analyzes the development of genitalic characters from a phylogenetic viewpoint, considering them in combination with the external morphology and mostly reaching interpretations and conclusions still valid today. Instead of enumerating useful and useless characters, as previous authors had done, he defines the circumstances that make a certain character taxonomically meaningful, e.g. «In this family, strange as it may seem, it is necessary to know what species constitute a group before the taxonomic value of any single character can be established» (HEINRICH, 1923 :4). He also realizes that most evolution below family level consists of reductions, often with parallel tendencies in different groups, but that such trends can still be used for classification as long as one compares members of the same genetic lineage only. However, he searches only for characters that may serve to separate groups, the concept of a synapomorphy being entirely lacking.

DIAKONOFF (1939), OBRAZTSOV (1954–1957), FREEMAN (1958) and YASUDA (1972, 1975) base extensive revisions of local tortricid faunas on combined consideration of genitalic structures and external morphology, but at times show rather less phylogenetic awareness than did HEINRICH in his well-reasoned discussions. In a brief review COMMON (1958) presents an outline of the higher classification of the Australian Tortricinae, founded on characters explicitly identified as primitive or derived, thus meeting an important prerequisite for a phylogenetic classification. Powell (1964) introduces a wealth of new and significant information into the discussion of tortricid phylogeny by emphasizing carefully analyzed biological aspects and his study contains a brief evaluation of taxonomic characters. But though phylogenetic considerations are given increasingly more weight, often with careful appreciation of developmental series of selected characters (DUGDALE, 1966), the principles of HENNIG's phylogenetic systematics have never been consistently applied to tortricine taxonomy, except for a recent publication by TUCK (1981) on Chlidanotini. Failure to do so has especially thwarted some of the conclusions drawn by KUZNETSOV & STEKOLNIKOV (1973) from their fine comparative study of the musculature of the male genitalia, because several of their groupings are due to mere symplesiomorphies. However, it must be stated here that it was impossible to obtain a comprehensive translation of this important Russian publication. Many of the arguments and conclusions presented there may therefore have escaped attention and will unfortunately have to be ignored in the present study. This may well also apply to KUZNETSOV's (1978) treatment of the Tortricidae. RAZOWSKI (1976) largely accepted KUZNETSOV & STEKOLNIKOV's line of reasoning and, in a comprehensive discussion of most of the features ever used in the higher classification of the Tortricidae, he unconditionally disputes the

usefulness of all those showing any parallel development, even in rather distant groups, not recognizing the potential validity of such characters in an argumentation system strictly conforming with cladistic tenets.

CHARACTERS CONSIDERED AND METHODS USED

The characters considered in the present study are mainly those already used previously or currently, for taxonomic work in the Tortricidae. It is not the aim to give a general description of tortricid morphology – a task that has been accomplished by PEYERIMHOFF (1876), KENNEL (1908) and others – but to assess the taxonomic value of the structures concerned. Thus, only morphological features showing variations demonstrated to be relevant for classification are discussed here, those without recognized past or present taxonomic importance being omitted. With the hope of finding useful characters, especially for the delineation of higher categories in the structure of the body sclerites, macerated integuments of representatives of several tribes were carefully compared, but with disappointing results. Characteristically it is ZIMMERMAN (1978) who, after having written a series of monographs on non-lepidopterous insects, reproaches lepidopterists in his volume on the Hawaiian Microlepidoptera for neglecting any possibly taxonomically useful feature that might be obscured by scaling. But it seems that at least in the Tortricidae very little additional information can be gained by a study of the body sclerites.

It is of great importance that comparative morphological studies are based on results obtained by similar methods. Statements on the degree of reduction of wing veins in Lepidoptera are a good example. Their evaluation depends greatly on whether the venation is studied *in situ*, where only tubular veins can be recognized, or by means of stained microscopic preparations showing vestigial veins as well. The following observations and conclusions are all based on wing preparations made according to a technique developed by I. F. B. COMMON, as outlined by ZIMMERMAN (1978) and on genitalia slides conforming to the method required for material from the British Museum (Natural History) (ROBINSON, 1976; ZIMMERMAN, 1978).

TAXA CONSIDERED

The Tortricidae are structurally a remarkably uniform family, a fact that has earned them a reputation for being a difficult group. There are few obvious divisions; even the distinct and undoubtedly monophyletic Olethreutinae cannot be defined by larval characters (MACKAY, 1959). Depending on the importance ascribed to typical and often conflicting features another classification is proposed or the relative rank of a group assessed differently. ZIMMERMAN (1978) gives a vivid picture of the confused situation in the higher taxonomy of the Tortricidae.

Much more work is needed before tortricid taxonomy can be fully understood. Attempts at higher classification can no longer be restricted to one isolated fauna on one continent and must be based on thorough cladistic analyses. Immediate decisions, however, on which classification to adopt, were needed for the present study to have clearly defined groups available for the discussion of character states. As neither RAZOWSKI'S (1976) nor KUZNETSOV & STEKOLNIKOV'S (1977) systems are satisfactory, a more conservative classification, based mainly on OBRAZTSOV (1954), COMMON (1958) and DIAKONOFF (1977a & b) for the Tortrici-

nae and on HEINRICH (1923) and KUZNETSOV (1970) for the Olethreutinae has been adopted, with the conviction that a reasonably established system should be changed only on very convincing evidence. The appropriate taxonomic level of a group can probably only be finally assessed once the entire system is understood. For the time being it seems sensible to retain well-defined groups like the Epitymbiini and Cnephasiini as distinct tribes until their rank and relationships are established beyond doubt.

Three subfamilies of the Tortricidae are recognized, the Chlidanotinae (Chlidanotini, Hilarographini, Polyorthini), the Tortricinae (Phricanthini, Tortricini, Ceracini, Cnephasiini, Epitymbiini, Archipini, Cochylini, Sparganothini, Atteriini, Schoenotenini), and the Olethreutinae (Microcorsini, Eucosmini, Olethreutini, Grapholitini). Whereas there are good reasons to consider the Chlidanotinae and Olethreutinae to be monophyletic groups (TUCK, 1981 - Chlidanotinae; CLARKE, 1955 - Olethreutinae) the Tortricinae probably represent a paraphyletic assemblage. The Schoenotenini are here included in the Tortricinae in agreement with the view of COMMON (1965) (see p. 25). In his discussion on the taxonomic position of the Phricanthini, DIAKONOFF (1981) suggests that this tribe arose before the Tortricinae and Chlidanotinae originated. But until this can be proved the tribe is most reasonably placed within the Tortricinae. KUZNETSOV & STEKOLNIKOV's amalgamation of Sparganothini and Cochylini mainly on the strength of a sympleiomorphy (see p. 34) and the separation of these two tribes from the remaining Tortricinae cannot be accepted; until their kinship is established they are both considered distinct tribes of the Tortricinae. As discussed below (pp. 25, 38, 46 & 58) the Sparganothini are restricted according to their original definition by BUSCK (1940) and OBRAZTSOV (1944), and the Atteriini treated as a separate tribe of generalized Tortricinae in accordance with OBRAZTSOV (1966). The Archipini clearly are a polyphyletic group that will have to be further subdivided into monophyletic entities. But until an acceptable cladogram can be produced no new tribal names should be created as the delineation of monophyletic genus-groups serves the same purpose equally well.

List of taxa considered. The arrangement of tribes, genera and species is in alphabetical order. Taxa of doubtful systematic relationship are usually retained in their generally accepted position. In only very few instances are they listed at the end of the subfamily under «*incertae sedis*». No material has been examined from genera or species marked with an asterisk, conclusions have there been drawn on the base of literature (with the most important source, if not the original description, mentioned in brackets after the name). The most relevant revision of the non-Palaeartic taxa discussed is given for most tribes previous to the list of taxa. The author and year of publication are as according to LERAUT (1980) for Palaeartic taxa.

Tortricinae

Archipini

Adoxophyes MEYRICK, 1881: *orana* (FISCHER VON RÖSLERSTAMM, 1834). *Acropolitis* MEYRICK, 1881: *xuthobapta* TURNER, 1945. *Anisotenes* DIAKONOFF, 1952. *Aphelia* HÜBNER, [1825]: *viburnana* ([DENIS & SCHIFFERMÜLLER], 1775). *Archips* HÜBNER, 1822: **inopinatanus* (KENNEL, 1901) (RAZOWSKI, 1977); *oporana* (LINNAEUS, 1758); *podana* (SCOPOLI, 1763); **purpurana* CLEMENS, 1865 (OBRAZTSOV, 1956); *rosana* (LINNAEUS, 1758). «*Argyrotoxa*» *pompica* TURNER, 1925. *Automaema* TURNER, 1916: *pentacosma* (LOWER, 1900). «*Batodes*» *jactatana* WALKER, 1863. «*Capua*» *belophora* TURNER, 1945. «*Capua*» *leucostacta* MEYRICK, 1910. *Carphomigma* DIAKONOFF, 1953. *Chionotremma* DIAKONOFF, 1952. *Choanograptis* MEYRICK, 1938. *Chresmarcha* MEYRICK, 1910. *Clepsis* GUENÉE, 1845: *rogana* (GUENÉE, 1845). **Cornusacula* DIAKONOFF, 1960. *Cryptoptila* MEYRICK, 1881: *australana* (LEWIN, 1805). *Ctenopseustis* MEYRICK, 1885: *obliquana* (WALKER, 1863). *Cuspidata* DIAKONOFF, 1960: Subgenus *Pilophorica* DIAKONOFF, 1960: *leptozona* DIAKONOFF, 1960. **Digitosa* DIAKONOFF, 1960. *Epagoge* HÜBNER, [1825].

Epalxiphora MEYRICK, 1881: *axenana* MEYRICK, 1881. «*Epichorista*» *emphanes* (MEYRICK, 1902). *«*Epichorista*» *perversa* MEYRICK, 1912 (CLARKE, 1958). *Epichoristodes* DIAKONOFF, 1960: Subgenus *Epichoristodes*: *apiletica* DIAKONOFF, 1960. *Epiphyas* TURNER, 1927: *postvittana* (WALKER, 1863). *Gonioiorna* MEYRICK, 1933: Subgenus *Gonioiorna*: *erratica* (DIAKONOFF, 1947). *Harmologa* MEYRICK, 1883. *Hiceteria* DIAKONOFF, 1953. *Homona* WALKER, 1863: *coffearia* (NIETNER, 1861). *Homonoides* DIAKONOFF, 1960: *euryplaca* (MEYRICK, 1933). *Isochorista* MEYRICK, 1881: *encotodes* MEYRICK, 1910; *panaeolana* MEYRICK, 1881; *parmiferana* (MEYRICK, 1881); *ranulana* MEYRICK, 1881. *Isotenes* MEYRICK, 1938: *miserana* (WALKER, 1863). *Leptochroptila* DIAKONOFF, 1952. *Lozotaenia* STEPHENS, 1829: *forsterana* FABRICIUS, 1781. **Lozotaeniodes* OBRAZTSOV, 1954. *Mesocalyptis* DIAKONOFF, 1953. **Panaphelix* WALSINGHAM, 1907 (ZIMMERMAN, 1978). *Pandemis* HÜBNER, [1825]: *cinnamomeana* (TREITSCHKE, 1830). *Paradichelia* DIAKONOFF, 1952. *Paramesia* STEPHENS, 1829: *gnomana* (CLERCK, 1759). **Parapandemis* OBRAZTSOV, 1954 (DIAKONOFF, 1960b). **Paraptila* MEYRICK, 1912 (CLARKE, 1958). *Philedone* HÜBNER, [1825]: *geringana* ([DENIS & SCHIFFERMÜLLER], 1775). *Planotortrix* DUGDALE, 1966: *pictoriana* (FELDER & ROGENHOFER, 1875). *Pseudargyrotoza* OBRAZTSOV, 1954: *conwagana* (FABRICIUS, 1775). **Ptycholoma* STEPHENS, 1829 (OBRAZTSOV, 1954). *Ptycholomoides* OBRAZTSOV, 1954: *aeriferanus* (HERRICH-SCHÄFFER, 1851). «*Teras*» *incessana* WALKER, 1863. *Thrincoptera* MEYRICK, 1881: *dryinodes* (MEYRICK, 1910); *signigerana* (WALKER, 1863). «*Tortrix*» *incompta* TURNER, 1927. *Tremophora* DIAKONOFF, 1953. *Williella* HORAK, in press. *Zacorisca* MEYRICK, 1910.

Atteriini (see DIAKONOFF, 1961; OBRAZTSOV, 1966)

Anacrusis ZELLER, 1877: *piriferana* (ZELLER, 1877); «*Tortrix*» *stapiana* FELDER & ROGENHOFER, 1895. «*Ctenopseustis*» *lurida* MEYRICK, 1912. *Templemania* BUSCK, 1940: *animosana* (BUSCK, 1907).

Cnephasiini (see COMMON, 1963)

Arctophora MEYRICK, 1881. *Cnephasia* CURTIS, 1826: *interjectana* (HAWORTH, 1811). *Eana* BILLBERG, 1820: *argentana* (CLERCK, 1759); *osseana* (SCOPOLI, 1763). *Eulia* HÜBNER, [1825]: *ministrana* (LINNAEUS, 1758). **Paraphyas* TURNER, 1927 (COMMON, 1963). *Sphaleroptera* GUENÉE, 1845: *alpicolana* (FRÖLICH, 1830).

Cochylini

Aethes BILLBERG, 1820. *Cochylis* TREITSCHKE, 1829. **Trachysmia* GUENÉE, 1845 (as *Hysterosia* STEPHENS, 1852 in RAZOWSKI, 1970).

Epitymbiini (see COMMON, 1958)

Aeolostoma MEYRICK, 1910. *Aplastoceros* DIAKONOFF, 1953. *Cleptacaca* DIAKONOFF, 1953. *Meritastis* MEYRICK, 1910. *Rhomboceros* MEYRICK, 1910.

Phricanthini (see COMMON, 1965; DIAKONOFF, 1981)

Phricanthes MEYRICK, 1881: *asperana* MEYRICK, 1881. *Scolioplecta* MEYRICK, 1881: *molybdantha* MEYRICK, 1910.

Schoenotenini (see DIAKONOFF, 1954a; 1960a; COMMON, 1965)

**Diactenis* MEYRICK, 1907 (DIAKONOFF, 1954a). *Epitrichosma* LOWER, 1908. **Homalernis* MEYRICK, 1908 (CLARKE, 1958). *Palaeotoma* MEYRICK, 1881: *styphelana* MEYRICK, 1881. **Proactenis* DIAKONOFF, 1941 (DIAKONOFF, 1954a). **Proselena* MEYRICK, 1881 (COMMON, 1965). **Protarchella* DIAKONOFF, 1956. *Rhabdotenes* DIAKONOFF, 1960. **Syncratus* COMMON, 1965. *Tracholena* COMMON, 1965: *sulfurosa* (MEYRICK, 1910).

Sparganothini (see LAMBERT, 1950)

Amorbia CLEMENS, 1860: *cuneana* (WALSINGHAM, 1879). *Coelostathma* CLEMENS, 1860: *disco-punctana* CLEMENS, 1860. *Heterochorista* DIAKONOFF, 1952. *Lambertiodes* DIAKONOFF, 1959: *harmonia* (MEYRICK, 1908). *Platynota* CLEMENS, 1860: *flavedana* CLEMENS, 1860. *Sparganothis* HÜBNER, [1825]: *pillariana* ([DENIS & SCHIFFERMÜLLER], 1775). *Synnoma* WALSINGHAM, 1879: *lynosyrana* WALSINGHAM, 1879.

Tortricini (see COMMON, 1965; RAZOWSKI, 1966)

**Accra* RAZOWSKI, 1964 (RAZOWSKI, 1966). *Asterolepis* RAZOWSKI, 1964. *Beryllophantis* MEYRICK, 1938. *Eboda* WALKER, 1866. **Paratorna* MEYRICK, 1907 (RAZOWSKI, 1966). *Pareboda* RAZOWSKI, 1966. **Polemograptis* MEYRICK, 1910 (RAZOWSKI, 1966). *Sclerodisca* RAZOWSKI, 1964. *Spatalistis* MEYRICK, 1907. *Tortrix* LINNAEUS, 1758: *viridana* LINNAEUS, 1758. **Vellonifer* RAZOWSKI, 1964 (RAZOWSKI, 1966).

Taxa incertae sedis

Drachmobola MEYRICK, 1907. *Proeulia* CLARKE, 1962: species cf. *aethalea* OBRAZTSOV, 1964; species cf. *chrysopteris* (BUTLER, 1883); **tenontias* (MEYRICK, 1912). *Protopterna* MEYRICK, 1908. *Pternozuga* MEYRICK, 1908. *Taeniarchis* MEYRICK, 1931.

Chlidanotinae

Chlidanotini (see COMMON, 1965; TUCK, 1981)

**Caenognosis* WALSINGHAM, 1900 (COMMON, 1965). **Chlidanota* MEYRICK, 1906 (TUCK, 1981). **Daulocnema* COMMON, 1965. **Iconostigma* TUCK, 1981.

Hilarographini (see DIAKONOFF, 1977a & b; HEPPNER, 1982)

**Hilarographa* ZELLER, 1877: **swederiana* (STOLL, 1782) (DIAKONOFF, 1977b). **Mictocommosis* DIAKONOFF, 1977. **Mictopsichia* HÜBNER, [1825] (DIAKONOFF, 1977b): **callicharis* MEYRICK, 1921 (CLARKE, 1969). **Thaumatographa* WALSINGHAM, 1897 (DIAKONOFF, 1977b).

Polyorthini (see DIAKONOFF, 1974; RAZOWSKI, 1981)

Isotrias MEYRICK, 1895. **Lopharcha* DIAKONOFF, 1941 (DIAKONOFF, 1974). **Lophoprora* MEYRICK 1930 (DIAKONOFF, 1974). **Lypothora* RAZOWSKI, 1981. *Olindia* GUENÉE, 1845. **Polylopha* LOWER, 1901 (DIAKONOFF, 1974). **Polyortha* DOGNIN, 1905 (DIAKONOFF, 1974). **Pseudatteria* WALSINGHAM, 1913 (OBRAZTSOV, 1966). **Scythalognatha* DIAKONOFF, 1956.

Olethreutinae

Eucosmini (see HEINRICH, 1923)

**Blasthestia* OBRAZTSOV, 1960. *Epinotia* HÜBNER, [1825]. **Gretchena* HEINRICH, 1923. **Gypsonoma* MEYRICK, 1895 (HEINRICH, 1923). *Peridaedala* MEYRICK, 1925. *Zeiraphera* TREITSCHKE, 1829: *diniana* (GUENÉE, 1845).

Grapholitini (see HEINRICH, 1926)

Cydia HÜBNER, [1825]: *pomonella* (LINNAEUS, 1758). **Dichrorampha* GUENÉE, 1845 (OBRAZTSOV, 1958). **Ecdytolopha* ZELLER, 1875 (HEINRICH, 1926). *Grapholita* TREITSCHKE, 1829. **Matsumuraeses* ISSIKI, 1957 (OBRAZTSOV, 1960). **Melanolopha* DIAKONOFF, 1941.

Microcorsini (see KUZNETSOV, 1970)

Cryptaspassa WALSINGHAM, 1900. **Microcorses* WALSINGHAM, 1900 (KUZNETSOV, 1970).

Olethreutini (see DIAKONOFF, 1973)

Asaphystis MEYRICK, 1909. *Endothenia* STEPHENS, 1852. *Eudemis* HÜBNER, [1825]. *Hedya* HÜBNER, [1825]: *nubiferana* (HAWORTH, 1811). *Olethreutes* HÜBNER, 1822. *Statherotis* MEYRICK, 1909.

Taxa incertae sedis

Anathamna MEYRICK, 1911. *Eucosmomorpha* OBRAZTSOV, 1951: *albersana* (HÜBNER, [1813]). *Metaselena* DIAKONOFF, 1939.

ASSESSMENT OF STRUCTURES

Head

Vestiture: The vestiture of the head is of little value for classification, modifications being either not pronounced enough or only occasionally expressed, like the often striking secondary sexual characters on the frons of some male Epitymbiini. The head of Ceracini and of *Zacorisca* is smooth-scaled and shiny, but as the nocturnal *Isotenes*, very closely related to *Zacorisca*, has a roughly scaled head like the remainder of the family, the appressed scales of the former two groups are probably linked to their diurnal habits as suggested by DIAKONOFF (1970).

In his unpublished thesis R. LAMBERT (1950) considers a tuft of projecting scales on the frons to be typical for his «Sparganothidinae». However, PEYERIMHOFF (1876) had already noted the frequent coincidence of very large palpi and

such a frontal tuft and my impressions would confirm the assumption that the two characters are causally linked to some degree.

From his observations on the Hawaiian fauna ZIMMERMAN (1978) reports that squamae on the lower part of the face directed dorsad instead of ventrad is a trait encountered among Microlepidoptera only in Tortricidae, many Cossidae, and some genera of Tineidae.

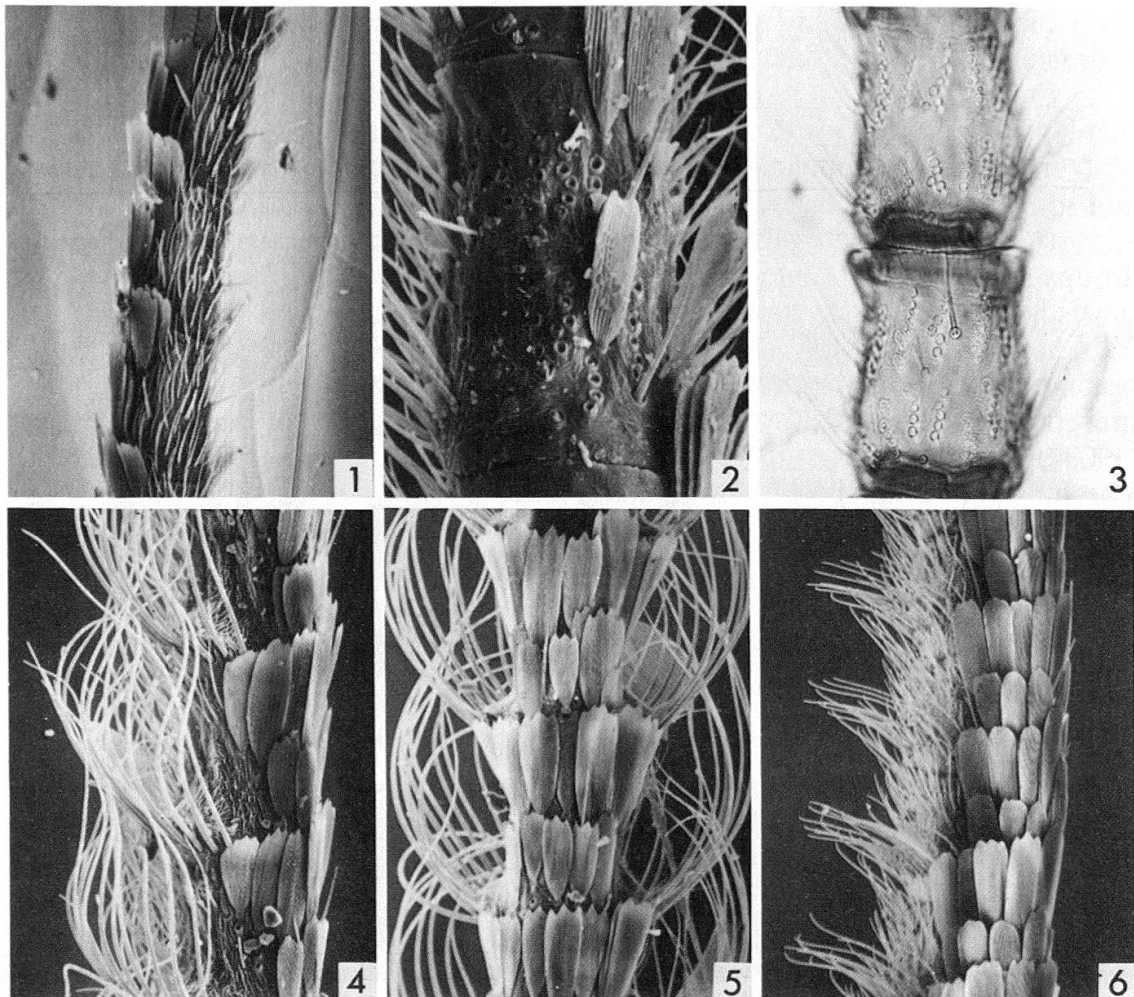
Ocellus: A progressive reduction of the ocelli can be observed in several groups and is very pronounced in the Schoenotenini, but they are present, at least in vestigial condition, in some genera of this tribe as well.

Antenna: LEDERER (1859) considered the antenna to be of only limited taxonomic value, but nevertheless made use of the degree of ciliation and the presence of an antennal notch in his generic key, a practice followed by KENNEL (1908) and by MEYRICK (1913) and, to a lesser degree, also by OBRAZTSOV (1954). The transition from short to long setae is gradual, however, and any assessment of the ciliation is thus to some extent arbitrary. In addition, large sexual differences may exist. The antenna has therefore become largely ignored for taxonomic purposes (DIAKONOFF, 1939).

No structures of the scape and pedicel of tortricid antenna are currently used for taxonomic differentiation, apart from a pecten reported from the scape of *Melanolopha*. Obvious secondary sexual modifications of the flagellum are found in Tortricinae (*Pandemis*, *Rhomboceros*) as well as in Olethreutinae (*Peridaedala*). They have obviously arisen independently several times and are of only limited systematic value. Scanning electron microscopic studies have been carried out on the flagellar sensilla of several tortricids, e. g. *Choristoneura fumiferana* (CLEMENS, 1865; ALBERT & SEABROOK, 1973) and *Cydia rusticella* (CLERCK, 1759) (WALL, 1978; as *Cydia nigricana* (FABRICIUS, 1794)), but such information is still too scattered for its value in phylogenetic reconstruction to be assessed. PEYERIMHOFF (1876) points to an apparently basic dissimilarity in the arrangement of scales on the flagellum of his «Thricides» (Olethreutinae) and «Athricides» (Tortricinae) without however recognizing its cause. To the best of my knowledge this observation has never been confirmed, but a random sample of male antennae revealed an apparently consistent difference between the two groups, enabling recognition of a representative of the Olethreutinae just on the basis of an antenna at least in the male sex.

It seems reasonable to consider randomly distributed scales intermixed with sensory setae (sensilla trichodea and sensilla basiconica) over the entire flagellum segment to be the primitive condition for the lepidopterous antenna. The development of an anterior (on the horizontally extended antenna) sensory area devoid of scales with an often parallel reduction of sensory setae on the scaled posterior face (except for the sensilla chaetica) represents an obvious adaptive modification, having occurred independently several times. The formation of processes to enlarge the area bearing sensory organs is subject to the same pressures and may lead to such convergences as the bipectinate antennae.

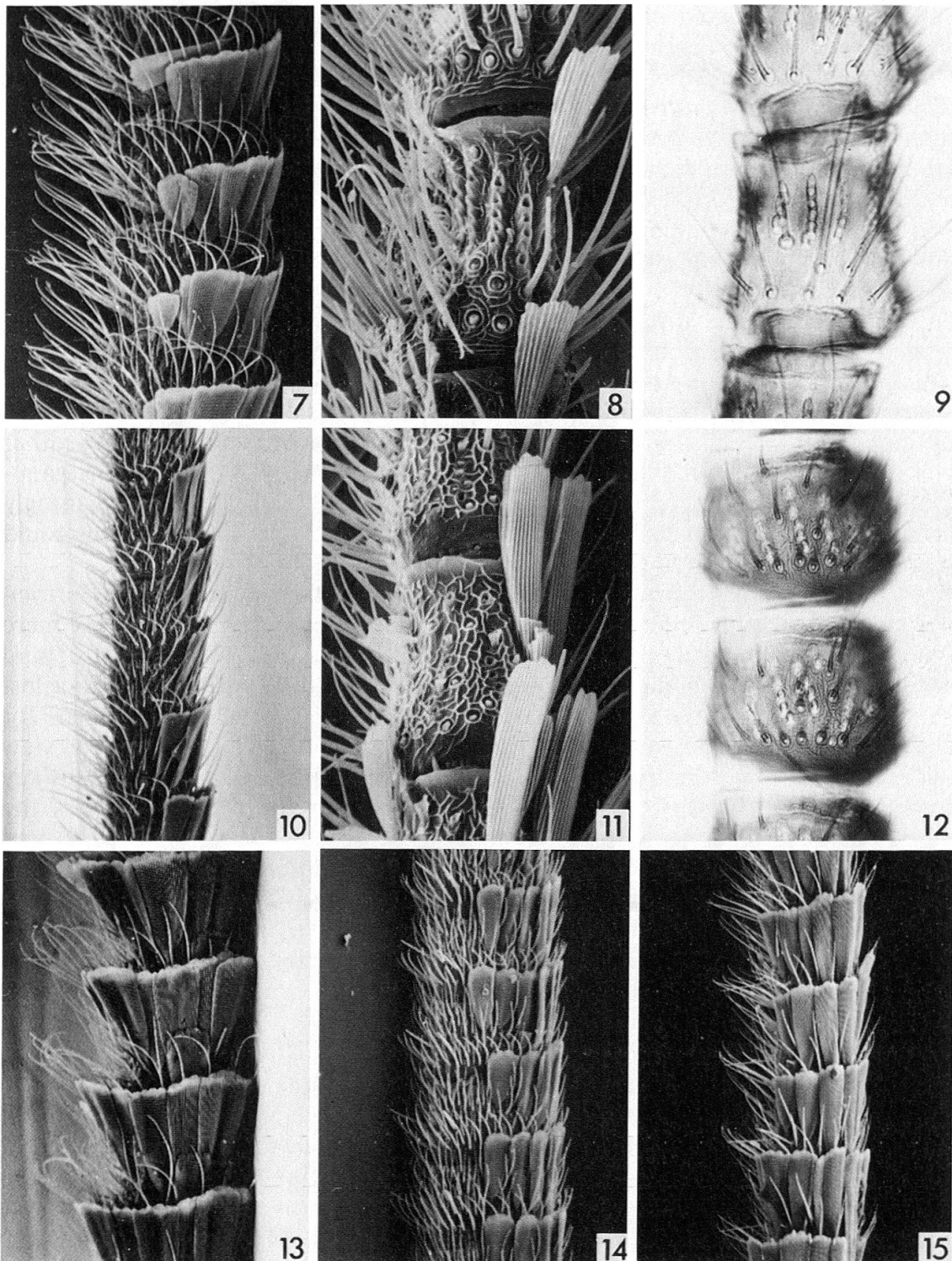
In all tortricids examined the sockets of scales on the flagellar segments are arranged in rows parallel to the axis of the antenna, the length of the apically following scales decreasing within each row, so that each such tuft of several scales of graduated length lying closely against one another appears, under low magnification, like a single scale. The assumption that a distribution of scales without apparent pattern is the more plesiomorphic condition than an alignment of these tufts of scales into neat rings around each segment, as in Tortricidae, is



Figs. 1-6: Scale arrangement on male antenna (Figs. 1, 4-6, antenna intact; Figs. 2, 3, antenna descaled) of: 1, 2, *Tortrix viridana*; 3, «*Batodes*» *jactatana*; 4, 5, *Amorbia cuneana*; 6, *Anacrusis piriferana*; (Figs. 1, 2, 4-6, with scanning electron microscope; Fig. 3, with optical microscope).

supported by the irregular scaling on the cossid flagellum (DANIEL, 1960). In all male Olethreutinae studied the scales over the entire length of each segment are incorporated in a single bunch, arranged in a well-defined ring around each segment, superficially giving the impression of a single row of scales inserted just below the middle of the short and stout segment, and hardly protruding past its apical margin (Figs 10-14). In Tortricinae and Chlidanotinae the flagellar scaling is divided into two distinct areas at the base and at the apical part of the rather elongate segment, in the initial arrangement forming two clear-cut, parallel rows often enhanced by different scale colouring (Figs 1-6). The scales of the apical row usually reach past the joint and enclose the base of the next segment like a collar - the characteristic PEYERIMHOFF seized upon to distinguish between the two subfamilies. BARTOLONI (1951) gives a figure of a similar arrangement of flagellar scales in two zones on each segment for *Phthorimaea operculella* ZELLER (Gelechiidae), the scales, however, appearing randomly scattered and not grouped in vertical rows. Possibly in conjunction with an enlargement of sensory setae, the scaling in the basal half of the segment becomes gradually reduced in the Tortricinae (Fig. 4) and is in the male of *Sparganothis* finally lost entirely, leaving only one

row of scales (Figs. 7-9). A comparison of denuded flagella of *Sparganothis* (Figs. 8-9) and Olethreutinae (Figs. 11-12) shows, however, a fundamental difference in these superficially similar conditions.



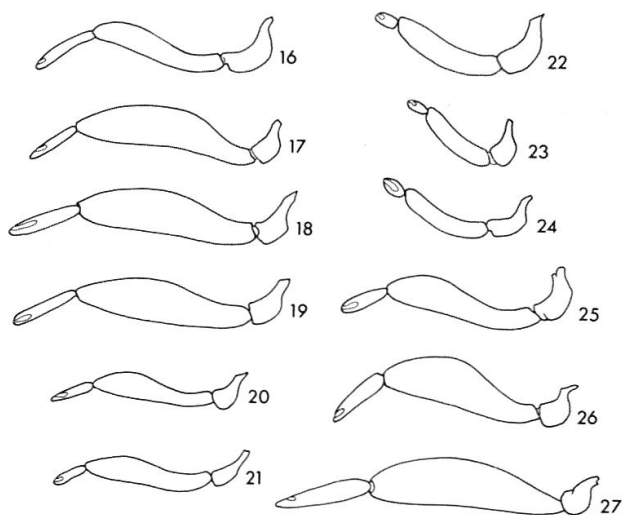
Figs. 7-15: Scale arrangement on male antenna (Figs. 7, 10, 13-15, antenna intact; Figs. 8, 9, 11, 12, antenna descaled) of: 7-9, *Sparganothis pilleriana*; 10, 11, *Olethreutes lacunana*; 12, *Epiblema fanfarae*; 13, *O. lacunana*; 14, *Cydia pomonella*; 15, *Sparganothis pilleriana*; (Figs. 7, 8, 10, 11, 13-15, with scanning electron microscope; Figs. 9, 12, with optical microscope).

While the Olethreutinae seem to be more conservative in largely retaining sensory setae among the scales of the posterior face of the flagellum several derivative trends to enlarge the sensory area and to separate it from the dorsal vestiture can be observed, especially in the males of the Tortricinae. In the original condition setae are intermixed with scales on the dorsal face and only a narrow anterior band is devoid of scaling, bearing setae of equal and moderate length (*Phricanthes*, *Tortrix* (Figs. 1-2), *Sphaleroptera*, *Eana*, *Isochorista*, *Choanograptis*, *Rhomboceros*, *Adoxophyes*, *Clepsis*). A general lengthening of the sensory setae (*Cryptoptila*, *Ctenopseustis*), a predominance of those in the basal part of each segment (*Anacrusis* (Fig. 6), *Coelostathma*, *Synnoma*) and either their retention around the entire segment (*Heterochorista*, «*Batodes*» *jactatana* (Fig. 3), «*Teras*» *incessana*), often with increasing suppression of the basal row of scales (*Aphelia viburnana*, *Lambertiodes*, *Sparganothis* (Figs. 7-9), *Platynota*), or their multiplication through a development of pectinations (*Amorbia* (Fig. 4), certain Patagonian Tortricinae, *Templemania*, *Philedone gerningana*) are modifications frequently encountered in quite distant groups or the last two both occurring in closely related taxa. Perhaps contrary to the alignment of scales into a certain pattern which might to some extent be a *ludus naturae* modifications of sensory setae are seemingly so much affected by adaptive pressure that similar configurations have developed repeatedly. It is of note, however, that most Archipini retaining rather plesiomorphic venation and male genitalia, as well as the Atteriini and Sparganothini, are all characterized by an antenna with a prominent basal row of strongly developed long cilia on each segment. Only further analysis will show if this could represent a synapomorphy joining the entire group.

Labial palpus: Compared with other families the labial palpi of the Tortricidae show remarkably little variation, the more pronounced cases often being mere secondary sexual developments. Moreover, much of the observed structural difference is due to modification of scaling only and is thus easily obscured or lost in worn specimens. LEDERER (1859) deemed them to be completely worthless for characterization, as differences are not consistent and distinct enough, a view basically shared by PEYERIMHOFF (1876) and KENNEL (1908). As reflected in his key to the genera of Tortricidae, MEYRICK (1913) initiates the extensive use of the labial palpi for generic division, a practice accepted by DIAKONOFF (1939) and OBRAZTSOV (1954). But whilst with experience it is undoubtedly possible to recognize types and characteristics one is already familiar with, even in the usually rather worn specimens available for comparison, it is an entirely different matter to describe these often subtle differences. A feature often employed is the position of the palpi, «porrected» (horizontally extended), «sub-ascending», «ascending» or «appressed» (to the face), which is the sum of three often independent variables: 1) shape of naked palpus, 2) its vestiture, and 3) the relative direction of the first segment. Of these only the shape of the denuded palpus is suited for objective and consistent comparison.

According to KRISTENSEN (1968) «three labial palp segments is the primitive number in insects and the usual number in Lepidoptera» and the sensory pit on the apical segment (organ of von Rath) seems to belong to the ground plan of the Lepidoptera. Since the various shapes of the palpus are the result of only differential growth processes no fundamental differences can be expected. The great range within many genera (e. g. *Trachysmia*) shows that mere increase or reduction in size of the entire organ is the taxonomically most insignificant variation, while a change in the relative size of the three segments and/or of their individual shape

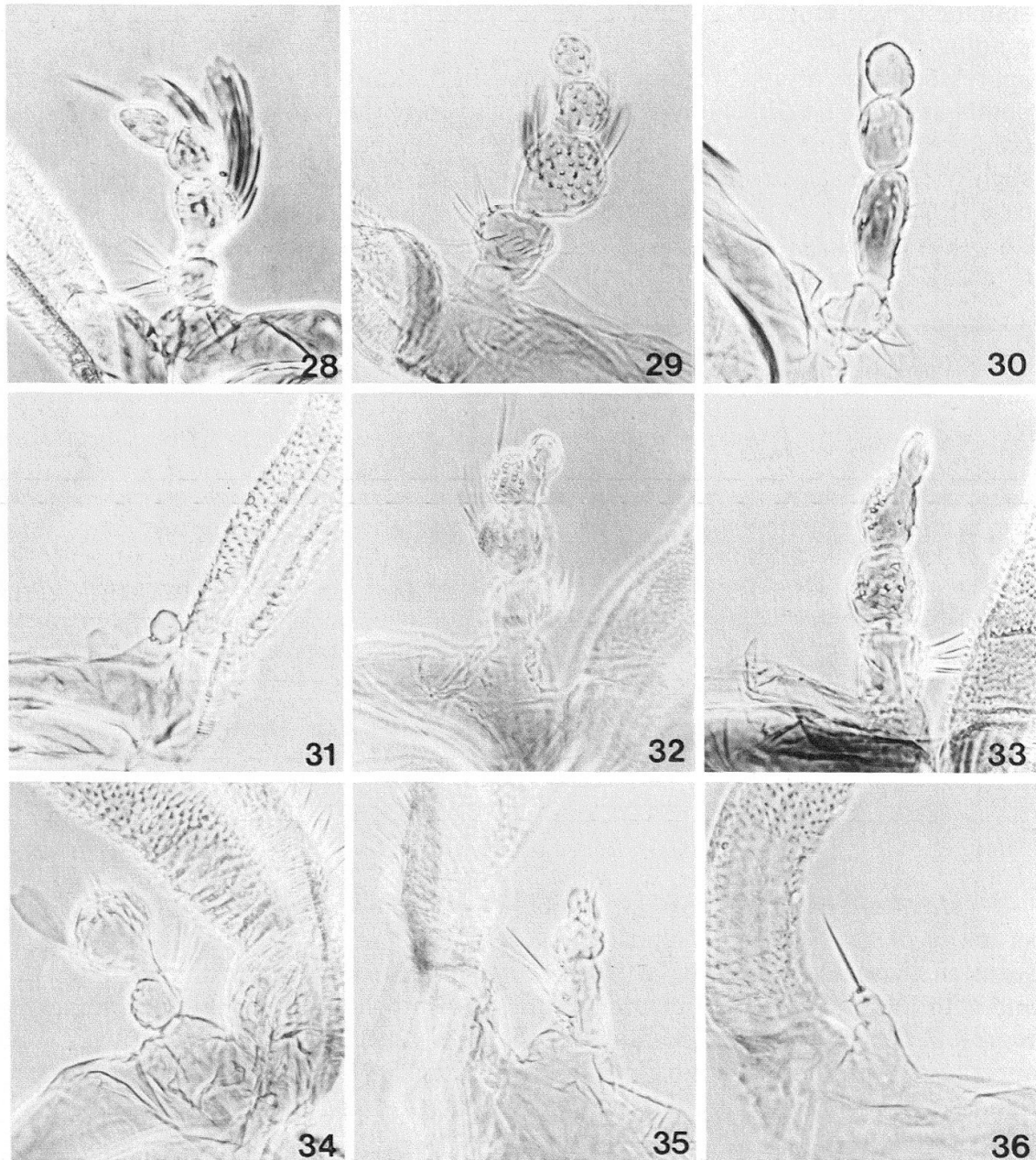
expressed in a different length/width ratio would be much more meaningful. Judging from their wide distribution and prevalence among rather generalized groups (Cnephasiini (Fig. 16), Schoenotenini, Cochylini, *Zacorisca*, certain Patagonian Tortricinae (Fig. 17), «*Teras*» *incessana*, «*Batodes*» *jactatana* (Fig. 18), *Ctenopseustis obliquana* (Fig. 19), *Isotenes* (Fig. 20), *Epichoristodes apiletica*, *Heterochorista* (Fig. 21) and *Dichrorampha*) relatively long and slender palpi with a sinuate second and rather long third segment probably represent the ground plan condition of the family. The elongate palpi of the Sparganothini (Figs. 25–27) have long been considered a derived feature typical of this group, but, apart from those of some species of *Sparganothis* (Fig. 27) with an enlarged and basically dilated apical segment, the proportions of the palpi in this group conform well to the generalized state. A modification of the second segment, from a sinuate shape with a strongly sinuate upper margin to a distinctly upwardly curved segment with an upper margin concave to its apex, is the cause for the development of ascending or appressed palpi, an observation mentioned by KENNEL (1908). The third segment points in the same direction as the apical portion of the median segment, and thus enhances the either sinuate or upwardly curved shape of the second segment. It is slightly drooping, seemingly at an angle with the remaining palpus in the former case (Figs. 16–21, 25–27), and ascending in a continuation of the curved palpus in the extreme development of the latter case (*Templemania* (Fig. 22), *Homona* (Fig. 23), *Cydia pomonella* (Fig. 24)).



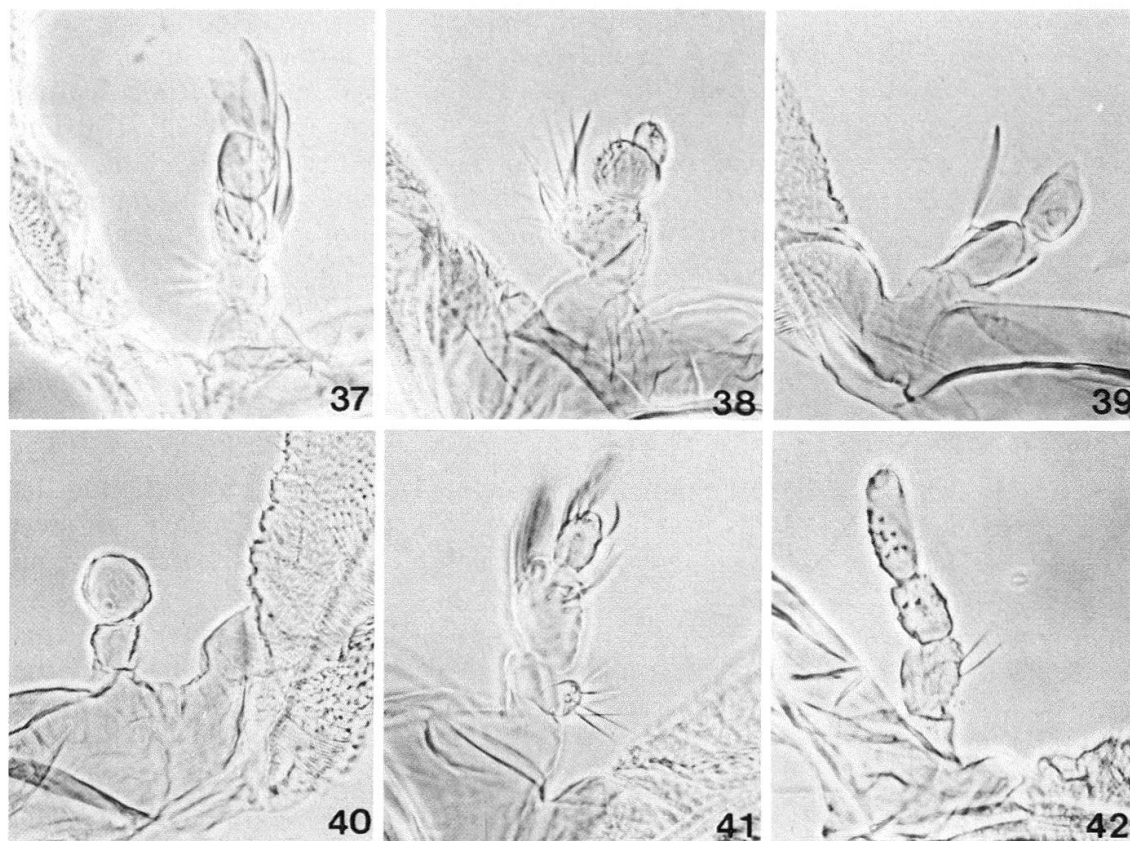
Figs. 16–27: Labial palpus of male of: 16, *Eana argentana*; 17, South American Tortricinae of unknown genus; 18, «*Batodes*» *jactatana*; 19, *Ctenopseustis obliquana*; 20, *Isotenes miserana*; 21, *Heterochorista melanopsigma*; 22, *Templemania animosana*; 23, *Homona coffearia*; 24, *Cydia pomonella*; 25, *Lambertiodes harmonia*; 26, *Platynota flavedana*; 27, *Sparganothis pilleriana*.

Maxillary palpus: DUGDALE (1966) gives a comprehensive discussion of the structure of the maxillary palpus in the New Zealand Tortricinae, assuming a 4-segmented, scaled palpus with the apical segment smaller than the penultimate and with the basal segment bearing a tuft of a few erect setae on the inner face to represent the ground plan condition for the family. As he points out, however, it is apparent from the illustrations given by PHILPOTT (1927) that the setose patch on the basal segment is a feature shared with numerous other families in the Ditrysia, not a characteristic of the Tortricidae. The scaled, 4-segmented palpi of *Phricanthes asperana* (Fig. 28), *Eana argentana* (Fig. 29) and *Sphaleroptera alpicolana* (Fig. 30) with a typically developed basal segment illustrate this plesiomorphic condition.

Modifications from the ground plan usually involve reductions (Fig. 31), in the overall size of the organ, in the number of segments and as loss of scaling, trends that have obviously been effective repeatedly in different lineages and thus are of little value in establishing relationship, except as indicators of degree of derivation. DUGDALE (1966) distinguishes four derivative tendencies: reduction in number of segments; loss of scales, and reduction in size of organ; enlargement of the apical segment (regardless of number of segments); palpus raised on pedicel. With the possible exception of the raised palpus of the Schoenotenini mentioned by DUGDALE and confirmed by my studies none of these developments results in a unique apomorphy that could help to identify a phylogenetic entity. Assuming



Figs. 28-36: Maxillary palpus of male of: 28, *Phricanthes asperana*; 29, *Eana argentana*; 30, *Sphaleroptera alpicolana*; 31, *Isochorista ranulana*; 32, *Thrincoptera dryinodes*; 33, *Acropolitis xuthobapta*; 34, *Archips podana*; 35, *Lambertiodes harmonia*; 36, *Sparganothis pilleriana*.



Figs. 37-42: Maxillary palpus of male of: 37, *Ctenopseustis obliquana*; 38, «*Batodes*» *jactatana*; 39, *Choanograptis* sp.; 40, *Mesocalyptis* sp., 41, *Adoxophyes orana*; 42, *Anisotenes* sp.

that decrease in number of segments is irreversible, the degree of reduction of the palpus can, however, provide some measure for overall derivation and may serve to give an indication of the phylogenetic sequence of related taxa. The 3-segmented palpus of *Lambertiodes harmonia* (Fig. 35) and the small, unsegmented remnant in *Sparganothis pilleriana* (Fig. 36) illustrate such a sequence. *Thrincochora dryinodes* (Fig. 32) and *Acropolitis xuthobapta* both have retained a 4-segmented palpus close to the ancestral condition, the fourth segment being however partly fused with the third in a slightly subapical, eccentric position, suggestive of a possible synapomorphy linking the two genera. Apart from a few clearly generalized taxa like *Ctenopseustis obliquana* (Fig. 37) and «*Batodes*» *jactatana* (Fig. 38), the general trend for reduction of the maxillary palpus is much more pronounced in the archipine genera possessing a simple valva with a straight costa than in the *Clepsis* group with its strongly derived, plicate valva. *Mesocalyptis* (Fig. 40) and *Choanograptis* (Fig. 39) thus retain only two strongly reduced segments, often lacking the setose patch on the basal joint. The fact that *Clepsis rogana*, *Adoxophyes orana* (Fig. 41), *Epiphyas postvittana* and *Anisotenes* (Fig. 42) all have rather well-developed, 3-segmented palpi with a strong basal patch of setae, corresponding with a much weaker tendency for stalking of R₄ and R₅ would make it hardly feasible to consider the Archipini with plicate valva to be directly derived from ancestors of those representatives of the tribe with simple valva. *Pandemis cinnamomeana* with three palpus segments and *Archips podana* with only two segments represent a possible further development series, thus supporting the suggestion that the Archipini are a polyphyletic assemblage.

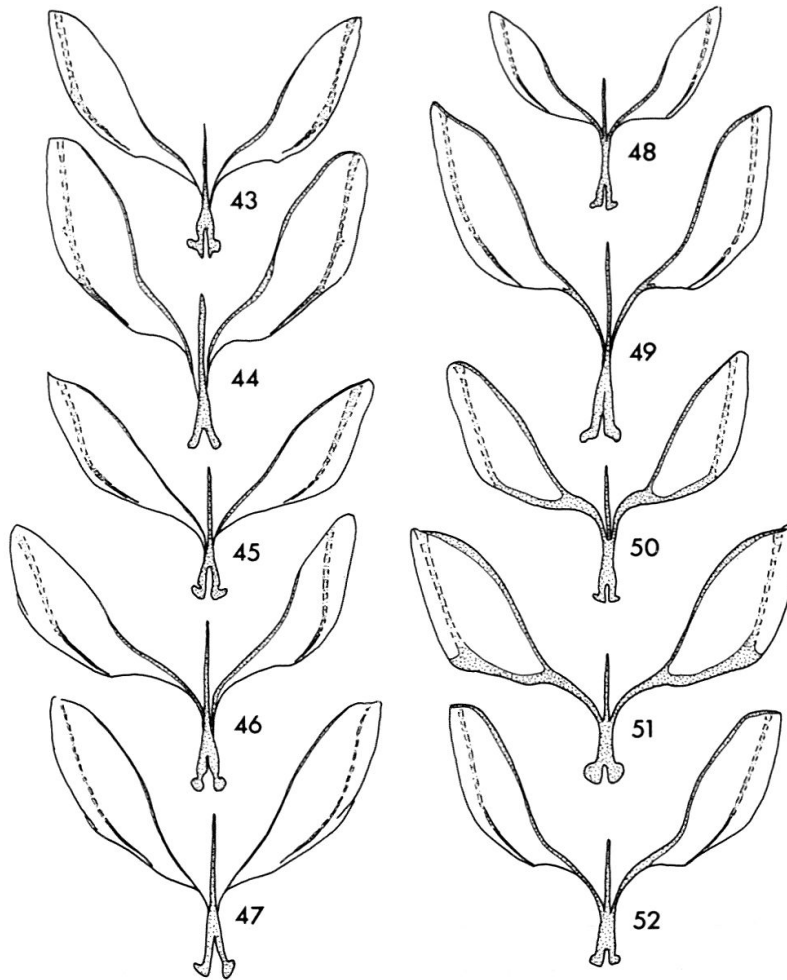
Thorax

Vestiture: The thorax may be either entirely smooth-scaled or possess a variably developed, single or bifid dorsal posterior crest of raised scales, a feature frequently used by MEYRICK to separate genera in his key (MEYRICK, 1913). The loose scales of the crest, however, are easily lost in otherwise only little worn specimens or during pinning, without the damage being necessarily apparent. Apart from the Chlidanotini (COMMON, 1965), Sparganothini (LAMBERT, 1950), Ceracini (OBRAZTSOV, 1954) and Hilarographini (DIAKONOFF, 1977a), at least a small posterior crest is reported from some genera in all remaining tribes of the Tortricinae and Chlidanotinae. The very frequent occurrence of this structure throughout the Olethreutini and Eucosmini and its presence in only *Ecdytolopha*, considered by HEINRICH to be the most primitive genus of his Laspeyresiinae which otherwise have a smooth thorax, suggest that a posterior thoracic crest has arisen very early in the development of the Tortricidae or must be ascribed to the groundplan. PEYERIMHOFF (1876) mentions that the occurrence of a posterior crest is correlated with a tuft of similarly enlarged scales at the base of the inner margin of the forewing.

Thoracic sclerites: BROCK'S (1971) discussion of thoracic morphology seems not to be relevant within the Tortricidae and a preliminary comparison of the thoracic sclerites of a representative of each of most tortricid tribes yielded no obviously significant differences apart from the development of the metepisternum for which the small sample studied suggests different development trends in the Olethreutinae and Tortricinae. The two extremes are exemplified by *Cydia pomonella* where the metepisternum appears abruptly constricted and its dorsal and ventral margins fuse well before reaching the furcasternum, and by *Adoxophyes orana* with a metepisternum evenly tapering and nearly reaching to the furcasternum. This dissimilarity is due not only to the outline of the episternum but also to the development of its ventral margin, strengthened by a continuous rim in most Olethreutinae studied (*Zeiraphera diniana*, *Cydia pomonella* (Fig. 51) and *Cryptaspasma* (Fig. 50)) which is medially lacking in all Tortricinae examined (*Tortrix viridana* (Fig. 43), *Eana osseana*, *Aethes* sp., «*Batodes*» *jactatana* (Fig. 44), *Isochorista ranulana*, *Automaema pentacosma*, *Thrincochora dryinodes*, *Cryptoptila australana*, *Isotenes miserana* (Fig. 46), *Archips* sp., *Ptycholomoides aeriferanus*, *Adoxophyes orana* (Fig. 45), *Meritastis* sp., *Lambertiodes harmonia*, *Sparganothis pilleriana* (Fig. 47) and *Tracholena sulfurosa* (Fig. 48)), leading to a gradually tapering episternum. *Hedya nubiferana* (Fig. 52) and *Phricanthes asperana* (Fig. 49) represent an intermediate condition with a metepisternum not reaching to the furcasternum but medially devoid of a strengthened ventral margin. This, and a rather cursory examination of one representative each of the Psychidae, Gelechiidae and Yponomeutidae, all three with an episternum recalling *Cydia pomonella*, could suggest that the Olethreutinae and *Phricanthes* have retained the more ancestral state.

Legs: Apart from secondary sexual characters in the Olethreutinae, discussed by FALKOVITCH (1962), no group specific variations have been recognized in the structure of the tortricid legs before YASUDA'S comparative study of the tarsal setae (YASUDA, 1972). He reports consistent differences in the numbers of setae on the tarsal segments 1-4 in the Japanese representatives of the four tribes Ceracini, Cnephasiini, Archipini and Tortricini.

A very superficial investigation of this character shows a group of three apical setae on each segment from the first to the fourth to be the most widely



Figs. 43–52: Metepisterna of male of: 43, *Tortrix viridana*; 44, «*Batodes*» *jactatana*; 45, *Adoxophyes orana*; 46, *Isotenes miserana*; 47, *Sparganothis pilleriana*; 48, *Tracholena sulfurosa*; 49, *Phricanthes asperana*; 50, *Cryptasasma* sp.; 51, *Cydia pomonella*; 52, *Hedya nubiferana*.

distributed condition, encountered in all Olethreutinae examined (*Hedya nubiferana*, *Zeiraphera diniana* and a second Eucosmini, *Cydia pomonella* and *Cryptasasma* sp.), in «*Batodes*» *jactatana*, «*Teras*» *incessana* and three Patagonian Tortricinae of yet uncertain tribal affinity but generalized genitalia and venation, and in *Isochorista ranulana*, *Aethes* sp. and *Sparganothis pilleriana*. Reduction in numbers obviously occurred in different groups (*Pseudargyrotoza*, *Drachmobola*), leading to complete absence of tarsal setae in the Tortricini (YASUDA, 1972) and *Phricanthes asperana*. Some Cnephasiini (*Eana*, *Cnephasia*), *Lambertiodes* and numerous Archipini and Epitymbiini (*Meritastis*) on the other hand possess additional setae, from a single fourth subapical one (*Adoxophyes*, *Meritastis*) to a large group of up to 20 setae at least on the first segment, scattered over nearly its entire inner surface (*Eana*, *Cryptoptila australana*, *Ptycholomoides aeriferanus*) or rather fewer arranged more apically in indistinct rows (*Lambertiodes*, *Archips*, *Isotenes*). Exemplified by the different conditions in the closely related *Sparganothis* and *Lambertiodes* the distribution of tarsal setae seems partly to be the result of parallel trends, and it is doubtful if this character is as reliable for group distinctions as YASUDA supposes. The apical row of numerous setae in the Ceracini, however, suggests a possible autapomorphy for this group.

Vestiture: Whilst the first attempts at classification in the Tortricidae relied heavily on wing pattern, this feature later became increasingly disregarded in favour of morphological characters. But unless the wing design is under adaptive influence like mimicry or strong cryptic behaviour, one could imagine that especially in a mostly dusk- and night-flying group like the Tortricidae the wing pattern is, like the genitalia, a field where random developments have a chance to persist, suitable colouring alone could make a given design cryptic enough to survive. More recently revised presumably monophyletic genera in the Tortricidae are usually characterized by a set of essentially similar markings variously expressed or obscured on the species level. RAZOWSKI (1976) asserts the importance of the forewing markings for the higher classification in the Tortricidae, the costal strigulation (PEYERIMHOFF, 1876) typical for the Olethreutinae and a pattern with three transverse elements widely encountered in the Tortricinae. Considered in this context the pronounced costal strigulation of the Chlidanotini and the at least vestigial presence of this feature in the Phricanthini is probably taxonomically meaningful. OBRAZTSOW (1954) interprets a faint maculation on the lower surface of the hindwing as traces of a more primitive pattern, an explanation supported by the strongly maculated hindwings of many rather generalized taxa (*Heterochorista*, *Ctenopseustis*, *Epalxiphora*, «*Batodes*» *jactatana* and «*Teras*» *incessana*) and the Ceracini. In *Epinotia*, however, pale mottling of the hindwing appears to be derived (R. L. BROWN, pers. comm.).

Costal fold: Because of its wide distribution throughout the Olethreutinae and Tortricinae it has been early accepted that a costal fold belongs to the ground plan of the Tortricidae (KENNEL, 1908; HEINRICH, 1923). It has frequently been lost at various taxonomic levels, however, in some species within a genus as in *Sparganothis*, *Choristoneura*, *Homona*, *Paradichelia* etc., or in entire tribes as in the Phricanthini, Tortricini, Ceracini, Schoenotenini and probably in all Chlidanotinae. KENNEL (1908) gives a detailed description of the different stages of reduction of the costal fold and uses it as an example to criticize MEYRICK'S (1895) phylogenies. On the base of comparative studies R. L. BROWN (pers. comm.) questions the general assumption that the costal fold is a homologous structure throughout the Tortricidae. This cautionary comment may well apply to the Tortricinae. An especially elaborate costal fold is found in *Cryptoptila australana* where the vein Sc for nearly its entire length gives rise to a broad lamella directed anteriorly and appressed to the wing surface, completely enclosed by the flap of the costal fold. Long scent scales are thus concealed in a double pocket between the wing membrane and the outgrowth of vein Sc, anteriorly closed by the costal fold.

Cubital pecten: The taxonomic importance of the cubital pecten for separating Olethreutinae and Tortricinae has been recognized by LEDERER (1859). Its presence in a few Tortricinae rich in plesiomorphies (*Ctenopseustis obliquana*, *Epalxiphora axenana*, *Cryptoptila*) and in many Sparganothini, with their generalized male genitalia, suggests that this structure is part of the tortricid ground plan, a view implied by MEYRICK (1911) when he ascribes the occurrence of a cubital pecten in several taxa of the Tortricinae to reversion, and expressed by POWELL (1964) in his diagram of phylogenetic relationships in the Tortricinae. The concept of a possible attavism rather than a continuous persistence of the cubital pecten in the Sparganothini is supported by its absence in *Lambertiodes harmonia*, a close precursor of *Sparganothis* in many other characters.

Venation: (Nomenclature according to COMMON, 1970; see Fig. 53). LEDERER (1859) is the first to make use of some venational characters for subdivision in the Tortricidae. PEYERIMHOFF (1876) gives an extremely detailed but purely descriptive account of tortricid venation. Venation is the basis of MEYRICK'S classification, but his attempts at reconstructing the phylogeny of the tortricid families (MEYRICK, 1895) demonstrate that he had no notion of an evolution of this character from ancestral to more derived conditions except for his recognition of «parting veins» as primitive characters which probably led him to postulate a descent of the Tortricidae from the Eucosmidae. Only a little later KENNEL (1908) shows a clear concept of the development of tortricid venation from a wing with all veins separate and more or less equally spaced to connate, stalked or even congruent veins. Citing examples of venational dissimilarities within apparently natural genera he cautions against a too strong reliance on this character only for classification as practiced by Meyrick.

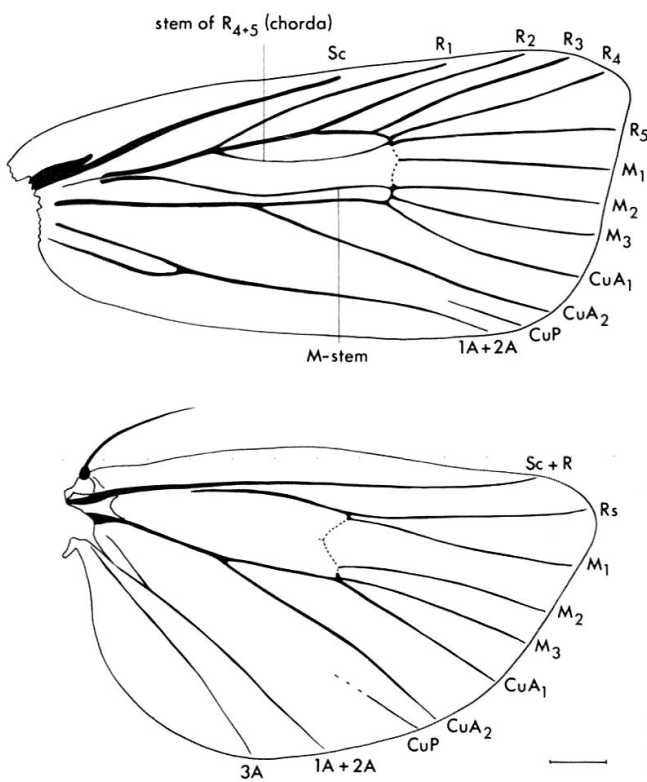
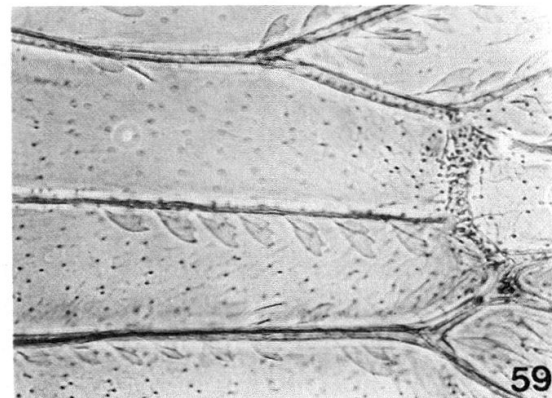
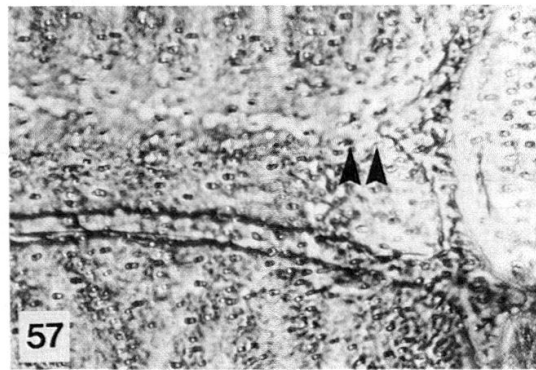
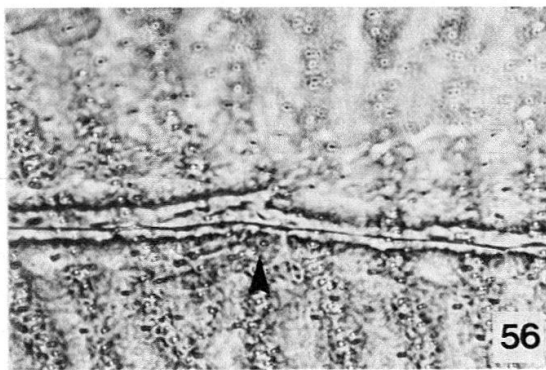
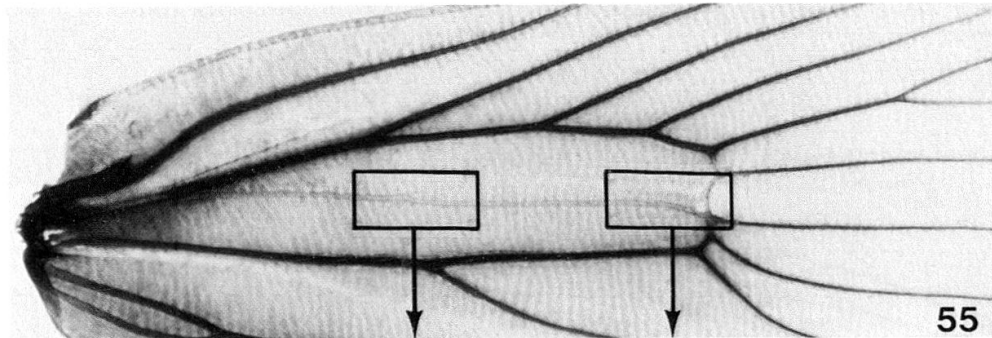
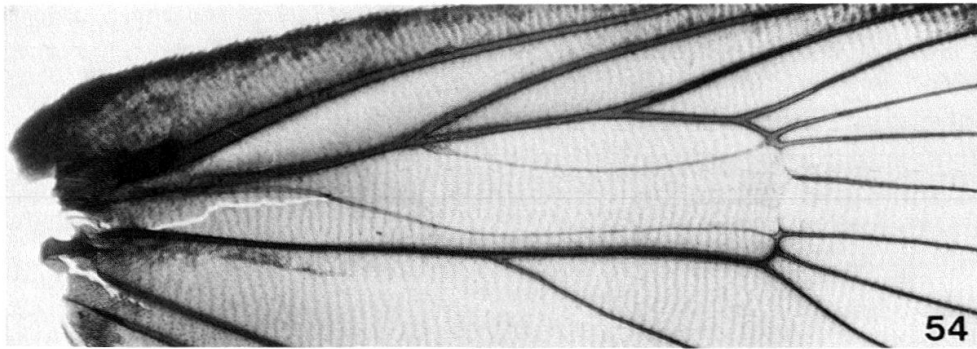


Fig. 53: Wing venation of male *Anacrusis piriferana* (Scale = 1 mm).

HEINRICH'S (1923) observation that the taxonomic value of any single character depends on the group concerned is especially pertinent for wing venation. Experience shows that stalking of the same veins can be very significant in one tribe and quite trivial in another; no general evaluation can therefore be given. There is, for example, a strong tendency in some Papuan Epitymbiini for R_3 , R_4 and R_5 to become stalked, and the end point of the development with all three branches borne on the same stalk has probably been reached repeatedly, while the large *Epiphyas/Isotenes* group in the Archipini has only in few instances produced taxa with stalked R_{4+5} , though the group is otherwise strongly derived. Until the contrary has been proved it seems reasonable to assume that the stalking and

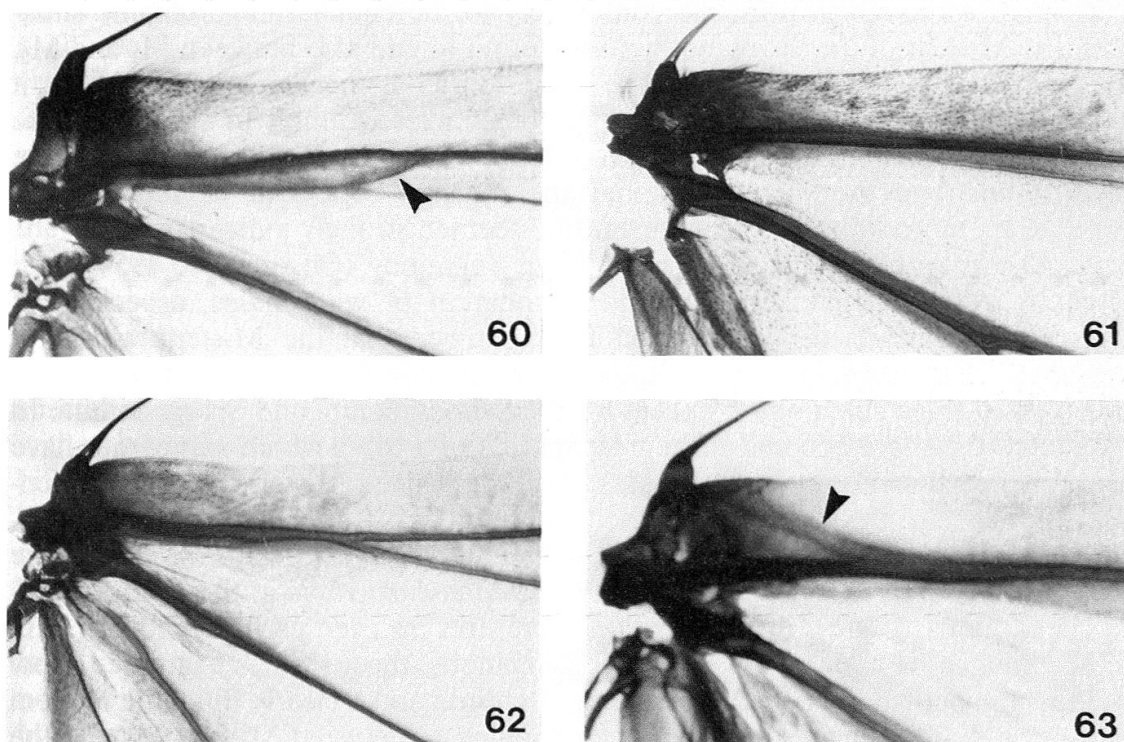


Figs. 54–59: Forewing of: 54, *Anacrusis piriferana*; 55, *Sparganothis pilleriana*; 56, 57, details of Fig. 55 (▲ bifurcation of M-stem; ▲▲ juncture of anterior branch of M with crossvein inter-M); 58, *Cryptoptila australana*; vestigial M-stem with sensillum campaniforme (▲); 59, *Epitrichosma* sp.

coincidence of veins are essentially irreversible processes, probably more so than simple obsolescence of a vein. Reduction and modification of the stem of R_4 and R_5 (chorda) and the M-stem in the forewing, and reduction and obsolescence of CuP are still, or have once been, considered of importance for the higher classification of the Tortricidae, and are reviewed extensively below after a few short remarks on some interesting points of tortricid wing venation that seem to have escaped attention till now.

Granted the assumption that separate and equally spaced veins represent the ancestral state, the widely separate R_s and M_1 in the hindwing of the more generalized Polyorthini (*Isotrias*, *Lophoprora*) and Hilarographini (*Mictocommosis*) and in *Dichrorampha* would represent the plesiomorphic condition of a character modified elsewhere in the Tortricidae so as to constitute a characteristic feature of the family. OBRAZTSOV (1958) reaches a similar conclusion on the base of the venation of *Dichrorampha* and some New World Grapholitini and therefore accepts MEYRICK'S and DIAKONOFF'S (1953) opinion that the Grapholitini are the most generalized tribe of the Olethreutinae.

In the groundplan of the Tortricidae $Sc + R_1$ and R_s were probably both developed and separate for their entire length, though parallel and somewhat approximate towards the base and connected by the crossvein R_1 (*Anacrusis* (Figs. 53, 61), *Adoxophyes* (Fig. 60), *Cryptoptila*). Development occurs along two different lines: the base of R_s becomes increasingly reduced and finally disappears together with the crossvein, or $Sc + R_1$ and R_s draw closer together, lying side by side touching along the basal section (*Lambertiodes*, *Amorbia cuneana*, *Coelostathma discopunctana*, *Scolioplecta molybdantha*, *Phricanthes asperana*, *Goniotorna* (*G. erratica*)) or even merge completely, leading to outrightly stalked $(Sc + R_1) + R_s$



Figs. 60-63: Hindwing base of: 60, *Adoxophyes orana* (▲ anastomosing R_1); 61, *Anacrusis piriferana*; 62, *Sparganothis pilleriana*; 63, *Templemania animosana* (▲ recurrent vein).

(*Sparganothis pilleriana* (Fig. 62), *Platynota flavedana*, *Synnoma lynosyrana*). Though the tendency for the basal convergence of these two veins is apparent in several groups, it might indicate a significant difference between the Sparganothini and the superficially very similar, rather plesiomorphic Atteriini (*Anacrusis piriferana* (Fig. 61), *Templemania animosana* (Fig. 63)). *Templemania animosana* shows a well-developed recurrent vein at the base of the hindwing (Fig. 63), strongly suggesting a humeral vein, a possible plesiomorphy that can also be detected as a very weak trace in some of the generalized Patagonian Tortricinae, but which seems to have disappeared in most other Tortricidae.

In a comparative study of cossid wing venation TURNER (1918) discusses in detail modification and progressive degeneration of the M-stem, with a short remark on the condition in the Tortricidae, and COMMON (1958) recognizes the importance of its plesiomorphic persistence in the forewing of some of the Australian Cnephasiini. DUGDALE (1966) gives a detailed discussion of the differences in the course of M in the discal cell within the Tortricidae, based on comparison with the often more conservative pupal integument venation. In agreement with COMMON (1965) he concludes that the cnephasiine-archipine line and the Schoenotenini have retained a different branch each of a more ancestral forked M-stem, as exemplified in the Cossidae and most tortricine pupal venations. Accordingly, the schoenotenine M-stem ending between M_1 and M_2 represents the anterior branch of a formerly forked M-stem, while the Cnephasiini have retained the posterior branch ending between M_2 and M_3 , conditions that could be derived from *Cossodes* WHITE, 1841 and *Dudgonea* HAMPSON, 1908 among the most primitive Cossidae (TURNER, 1918).

Extensive comparisons of stained wing preparations of representatives of most tortricid tribes and some pupal cases confirmed the basic difference in the structure of the schoenotenine M-stem with regard to all the other Tortricidae examined. Although in principle conforming to the cnephasiine-archipine situation, the M-stem of the Sparganothini was found to end also between M_1 and M_2 , thus superficially suggesting the same condition as in the Schoenotenini, and it became obvious that the difference cannot be expressed simply in terms of where the M-stem meets the discal vein. An attempt to understand the schoenotenine modification and to evaluate whether the unusual course of M represents a genuine apomorphy of the Sparganothini seemed strongly indicated.

A survey of published tortricid wing venations (OBRAZTSOV, 1954-1968; YASUDA, 1972; LAMBERT, 1950) and examination of wing slides, especially of equivocal or supposedly generalized taxa, showed that the M-stem whenever present at least vestigially, nearly always ends between M_2 and M_3 or at the origin of M_2 in all three subfamilies, except for the Schoenotenini and Sparganothini. In particular, the more generalized representatives of a tribe, which sometimes have also retained the chorda, often possess a well-developed M-stem: many representatives in each of the four tribes of the Olethreutinae; *Arotrophora* in the Cnephasiini; *Isotrias* in the Polyorthini; *Templemania* and *Anacrusis* (Figs. 53, 54) in the Atteriini; a more vestigial M-stem in *Hilarographa swederiana* in the Hilarographini (DIAKONOFF, 1977b). Pupal venation represents an even earlier condition and, in accordance with DUGDALE's (1966) observations, most species examined show in the empty pupal integument a developed chorda and a clearly bifurcate M-stem with the usually weaker anterior branch running to between M_1 and M_2 and the posterior one to between M_2 and M_3 , even though these veins have become atrophied in the corresponding moth. A careful examination of the descaled and

stained adult wing membrane, however, often reveals at least a short stump of the posterior branch usually still associated with the appropriate sensillum campaniforme a little below the discal vein (Fig. 58), and a characteristic small and sharp inward bend of the discal vein between M_1 and M_2 where the anterior branch once originated. DIAKONOFF (1939) and OBRAZTSOV (1954) report the presence of a forked M-stem in the adults of some Ceracini, both acknowledging the primitive nature of this condition.

In the Sparganothini the posterior branch has moved costad to between M_1 and M_2 , a development even more strongly expressed in the pupal integument of *Sparganothis pilleriana* where both branches of the forked M-stem join the discal vein closely together between M_1 and M_2 . The adult wing of a specimen of *S. pilleriana* with a M-stem better developed than usual for this species (Figs. 55–57) demonstrates its bifurcation and the course of the two branches. This could be a modification in connection with the early reduction of the chorda in this group, the pupa of *S. pilleriana* being the only one examined without any trace of this vein. In the pupa of *Adoxophyes orana*, with only a faint mark of the pupal chorda, the posterior branch of the M-stem also joins the discal vein costad of M_2 , while in all other pupae examined (*Cnephasia interjectana*, *Thrincochora dryinodes*, *Eulia ministrana*, *Aphelia viburnana*, *Archips rosana* and *A. oporana*) the chorda is well developed and the posterior branch of the M-stem ends between M_2 and M_3 or at most at the origin of M_2 . This consistently more costad position of the posterior M-stem branch between M_1 and M_2 thus seems to represent an autapomorphy for the Sparganothini, distinguishing them from the Atteriini, but it certainly is a trend present in some Archipini as well, though obliterated there as this vein becomes atrophied in the moth.

There are several indications that the superficially similar course of the M-stem in the Sparganothini and Schoenotenini is a convergence reached through basically different modifications, though perhaps for similar reasons. Any trace of a chorda is notably absent even in the most conservative schoenotenine wing venation (*Proactenis*, *Diactenis*) and in the pupae examined by DUGDALE (1966), a fact that, as in the Sparganothini, could favour a costad displacement of the M-stem for static reasons. COMMON'S (1965) and DUGDALE'S (1966) conclusion that in the Schoenotenini the anterior branch of the M-stem has been retained instead of the posterior one is supported by the complete lack of any indentation of the discal vein between the M-stem and M_1 in the Schoenotenini examined (*Palaeotoma styphelana*, *Tracholena sulfurosa*, *Epitrichosma crymodes* and *E. sp.* (Fig. 59)). Thus there is no trace pointing to the former presence of a more anterior branch. The absence of a sensillum campaniforme apically on the M-stem in all four species is equally notable. However, the fact that even in *Proactenis* and *Diactenis* with a hindwing M-stem conspicuously forked there is apparently no trace of a bifurcation of this vein in the forewing, and that DUGDALE (1966) reports no branching in the schoenotenine pupae he examined, could suggest that the two branches have become coincident already as a groundplan condition in this tribe. The course of the M-stem in the Schoenotenini certainly contrasts strongly with that of the Hilarographini and Polyorthini. The taxonomic position of the tribe will have to be reconsidered because the only structure providing a link to the Chlidanotinae, the hami (DIAKONOFF, 1960b), are absent in the more generalized genera by which the systematic position must be judged, as COMMON (1965) correctly notes. An inclusion of the group as a subtribe among the Archipini (RAZOWSKI, 1976), however, is equally unconvincing.

In the Tortricidae CuP had generally persisted at least towards the wing margin in both wings, and the Cochylini have long been treated as a separate family, mainly because in their forewing CuP has become completely atrophied and CuA₂ originates from a more apical position than is usual for the Tortricidae. Though in his *Microlepidoptera Palaearctica* volume RAZOWSKI (1970) still strongly argues for the family rank of the Cochylini he later accepts (RAZOWSKI, 1976) their inclusion in the Tortricinae, mentioning that further Tortricidae show a similarly rudimentary CuP as the Cochylini, but giving no examples.

In the closely related genus pair *Scoliopecta molybdantha* and *Phricanthes asperana* CuP of the forewing is well-developed towards the wing margin in the former and reduced without leaving a trace in the latter taxon. Both conditions occur within the one genus in *Heterochorista* (Sparganothini). Forewing CuP is lacking in the Chlidanotini and according to COMMON (1965) in *Asterolepis* in the Tortricini and *Diactenis* in the Schoenotenini. The degree of persistence of CuP in the hindwing, i. e. how far from the wing margin the vein still appears to be tubular, seems to some extent to be a measure of the overall level of derivation.

Abdomen

Before the taxonomic value of the genitalia became apparent, the tortricid abdomen was considered unimportant for classification; PEYERIMHOFF (1976: 586) states laconically: «L'abdomen des Tordeuses est dénué de caractères...». The proximal abdominal structures studied by BÖRNER (1939) and BROCK (1971) are taxonomically relevant only above the family level, and therefore cannot contribute to phylogenetic reconstruction within the Tortricidae, but the situation typical for the family will be briefly described. The development of the male 8th segment, however, shows apparently consistent modifications within the Archipini.

Preabdomen: BROCK (1971) considers the typically invaginated «tortricoid apodemes» (Fig. 97) to be a derived feature, a development probably linked with the disappearance of the caudal portion of the sternal rods. Fully developed so-called «tineid rods» would thus belong to the ditrysian groundplan. No trace of even vestigial sternal rods has been found in any of the Tortricinae examined. Many Olethreutinae, however, have caudal apodemes on the second sternite (R. L. BROWN, pers. comm.), but whether these are homologous with BROCK's «tineid rods» remains to be resolved.

A small, strongly sclerotized area ventrally towards the anterior margin of the second sternite, varying from an ill-defined, roughly triangular reinforcement of the sternite to a small, but distinct, caudally raised and vaulted plate (Fig. 97), seems to represent a plesiomorphic structure as it appears to be more pronounced in generalized Tortricinae. If the sclerite is recognizable, at least its caudal edge is well-defined and often bears remnants of filaments even in macerated specimens, suggesting a muscle attachment. In a figure caption RAZOWSKI (1959: Figs. 130–136) refers to obviously the same structure as «thympanal organs of Cnephasiini», without further elaboration in the text. This seems, however, a highly unlikely interpretation.

Dorsal pits: Some Archipini (*Archips*, *Homona*, *Panaphelix*, *Tremophora*) and Sparganothini (*Amorbia*, *Coelostathma*) possess single or paired dorsal pits on the second and often third abdominal segments. RAZOWSKI (1977) reports five pairs of dorsal pits on segments 2–6 in *Archips inopinatanus*. DIAKONOFF (1955) gives a detailed description and illustrations of the «dorsal organs» in *Tremophora*. Sec-

tions of dried abdomens soaked in water shed no light on their function. The possibility that they are either tympanal organs, scent organs or mite chambers are all considered to be unlikely. On the basis of the literature OBRAZTSOV (1957) assumes that the dorsal pits of *Archips* and *Amorbia* are of the same nature as those of *Tremophora*. As dorsal cavities are present also in the pupa of *Archips* and *Amorbia*, even if they are lacking in the moth (*Archips purpurana*), he concludes that they must be primarily structures of the pupa leaving their imprints on the adult abdomen.

As long as their function remains obscure it is difficult to decide whether the presence of such pits in different groups represents a synapomorphy. Those of *Tremophora* are conspicuously deeper, invaginations rather than shallow depressions as in the other groups, and at least superficially not suggesting a homology. LAMBERT'S (1950) description of the number and position of the dorsal pits in his «Sparganothidinae» is equivocal, but it appears that only the species of his genus IV possess paired pits on the dorsum of the second segment like *Archips*. All other genera have a single round depression medially on the second tergite, those with so-called double pits one on the second and third segments each. Figures of these «dorsal fovea» of the pupae of *Panaphelix* and *Amorbia* by ZIMMERMAN (1978: Figs. 302A, 327) strongly suggest that they represent the same structure in both cases, two separate pits in *Panaphelix* which have become approximated and fused in *Amorbia*. It has to be left open for the time being whether these structures represent a shared derived feature of some Archipini and Sparganothini, or a mere parallelism.

Structure of the eighth abdominal segment in the male: So-called coremata associated with the eighth segment are described for the males of many groups of all three subfamilies, but as they often are developed only in some of the representatives of a genus or tribe, and in taxonomic discussions usually have been lumped regardless of their often basically different structure in different groups, their taxonomic importance has repeatedly been disclaimed (DUGDALE, 1966; RAZOWSKI, 1976). Possession of eversible abdominal scales is obviously an adaptive improvement, but the same advantage has been attained by different methods in different groups – a situation probably producing meaningful characters for a phylogenetic analysis. The partial disappearance of such coremata within a group does not lessen their relevance for higher classification which is based on the morphological details evaluable where the structure is present. Their complete lack in a group, however, can always mean either its plesiomorphic primary absence or a secondary reduction of any of the possible derived states, and thus in itself allows no taxonomic conclusions.

The hair-pencil present on the eighth segment of some Chlidanotini, Hilargraphini and Polyorthini and fitting into an invaginated valva has often been referred to as corema. TUCK (1981) in his discussion of this structure, a synapomorphy for the Chlidanotinae, refrains from doing so and thus underlines its basic dissimilarity to scale pockets associated with the eighth segment elsewhere in the Tortricidae. Among the Olethreutinae *Grapholita*, *Matsumuraeses* and a number of New World Grapholitini possess a pair of eversible lateral scale tufts on the eighth sternite.

At least two different kinds of coremata have developed within the Tortricinae, one in some Tortricini and the second in parts of the Archipini. RAZOWSKI (1966) figures coremata for most genera of the Tortricini. Observations on *Beryllorphantis* (HORAK & SAUTER, 1979) show that these dorso-lateral ribbons of very

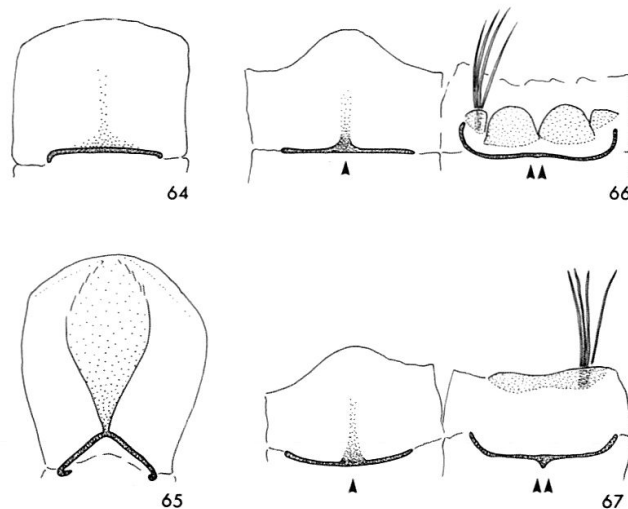
long scales are rather ephemeral and easily lost during slide preparation. They seem to be a development either of the posterior edge of the eighth tergite or of the subsequent intersegmental membrane, but at least some species of *Eboda* possess conspicuously complicated coremata consisting of four separate scale tufts associated with the seventh and eighth abdominal segments according to RAZOWSKI (1966). While further careful observation will be needed to understand the coremata structures within the Tortricini, the conditions in different archipine groups proved to be taxonomically significant and are discussed below.

Coremata can be recognized only if genitalia preparations are made and while PIERCE & METCALFE (1922) note their presence for *Pandemis*, DIAKONOFF (1939) is the first author to give a description of their structure in the Tortricinae. He does not identify them as coremata, a term he restricts in this paper to modifications of the seventh segment according to PIERCE (1914) and accepts for scale-pockets of the eighth segment only in subsequent publications. DIAKONOFF uses the term *scopa dorsalis* and *scopa ventralis* for the scale-brushes on the eighth tergite and sternite, and *mensis dorsalis* and *mensis ventralis* for narrow, crescent-shaped sclerites at the base of the eighth segment. He originally considers the possession of *menses dorsales* and *ventrales* with the associated coremata to be a taxonomically important modification, and his new subfamily «Chresmarchidii» is designed to comprise all archipine genera characterized by strongly developed *menses* and *scopae* and strongly folded, partly membranous valvae. Unfortunately *Chresmarcha* was erroneously included in this group on the base of a deceptively similar-looking female specimen of *Chionotremma patarea* (MEYRICK, 1924), which was originally described by MEYRICK as the female of *Chresmarcha sybillina* MEYRICK, 1910. *Zacorisca* was suppressed in favour of *Chresmarcha* because of this misidentification. In his monograph on the Microlepidoptera of New Guinea, however, DIAKONOFF (1952) divides his former «Chresmarchidii», considering the presence or absence of a corethrogyne in the female (see p. 29) to be taxonomically more meaningful than the shared possession of highly developed coremata in the male. COMMON (1958) treats a *mensis ventralis* of the eighth abdominal sternite as a significant development of the more derived Archipini.

A simple, evenly sclerotized sternite and tergite without any scale-bearing invagination is probably the original condition of the male eighth segment in the Tortricidae. Many of the more generalized Archipini (*Thrincoptora*, *Cryptoptila*, certain Patagonian Tortricinae, *Ctenopseustis obliquana*, «*Batodes*» *jactatana*, *Epalxiphora axenana* (Fig. 64), the Sparganothini and the Epitymbiini examined have retained the simple sternite, strengthened however by a narrow, sclerotized bar along its anterior edge, usually with an equally sclerotized dorsal posterior process. In *Anacrusis*, *Templemania* and «*Ctenopseustis*» *lurida* this development has reached an extreme condition in a strongly enlarged and apically projecting, hood-like eighth tergite with an angulate basal rod and a long, triangular, sclerotized dorsal projection, strongly expanded apically but constricted at its origin (Fig. 65). The basal rod and, to a lesser extent its dorsal projection, can be traced on the preceding segments, becoming more faint towards the base of the abdomen. In all taxa mentioned above, the eighth sternite remains unmodified, at most with two small, ear-like lobes at the caudal margin in *Anacrusis*.

Coremata have developed probably more than once within the Archipini, apparently parallel with the trend leading to the typical archipine valva with a reduced costa and a plicate, membranous disc, but are restricted to the ventral part of the abdomen as elsewhere in the family. In the Tortricidae coremata consist in

principle always of an invaginated membranous fold or pocket of diverse shape, filled with enlarged scales which are displayed if the abdomen is extended and thus the folds or pockets turned inside out. The shallow fold along the apical margin of the eighth sternite in the Malagasy *Epichoristodes* could be an earlier state of the series leading to the deep, semicircular invagination in *Archips*. Presumably another line of development culminates in the complicated ventral coremata of *Leptochroptila* and related genera (Fig. 66), divided into three or four separate pockets filled with scales. While in *Leptochroptila* the eighth tergite has become modified as well, covered with conspicuously modified scales, it conforms to the condition described above for the generalized Archipini in *Anisotenes* and *Isotenes*, genera with an eighth tergite (Fig. 67) belonging to the same transformation series as that of *Leptochroptila*, but representing earlier, less modified states.



Figs. 64-65: Tergum VIII of: 64, *Epalxiphora axenana*; 65, *Anacrusis piriterana*.

Figs. 66-67: Tergum and sternum VIII with coremata of: 66, genus near *Leptochroptila* with divided coremata; 67, *Anisotenes* sp. (▲ mensis dorsalis, ▲▲ mensis ventralis).

The sclerotized rod along the anterior margin of the eighth tergite (mensis dorsalis, Figs. 66, 67) which medially gives rise to the dorsal sclerotized process in *Anisotenes*, *Isotenes* and *Leptochroptila* is probably homologous to the very similar-looking structure in the generalized Archipini, and is thus a plesiomorphic feature not associated with the development of coremata. The equivalent structure of the eighth sternite (mensis ventralis, Figs. 66, 67) has so far been observed only in genera also possessing coremata (*Anisotenes*, *Isotenes*, *Leptochroptila*) and thus could indeed be linked to this modification. But it seems more reasonable to treat the coremata as the primary apomorphy, as their gradual evolution is obvious.

Corethrogyne: While many Cnephasiini cover their eggs with dirt and debris (POWELL, 1964) with the aid of their specialized ovipositor pads (floricomous ovipositor), several rather distant groups in the Epitymbiini, Archipini and Atteriini obviously protect their eggs with scales derived from a strongly modified seventh segment. DIAKONOFF (1944) suggests the term corethrogyne for tufts or brushes of densely set, modified scales on the seventh segment in the female and employs this structure for characterization of his Zacoriscini (*Zacorisca*, *Chionotremma*, *Isotenes*). Similarly modified scale patches on the seventh segment are however present in some Australian Epitymbiini and Archipini (COMMON, 1958) and in *Anacrusis* and *Templemania*. J. A. POWELL (pers. comm.) observed that

Isotenes, *Anacrusis* and *Templemania* all surround their egg masses at some distance with a fence of upright scales. That he found the same behaviour also in *Cryptoptila australana*, though this species lacks a modified seventh segment and the scales are probably derived from the well-developed dorsal portion of the anal tuft, suggests that this behaviour might have arisen independently several times due to adaptive advantages or else at an early stage of tortricine development, subsequently becoming lost again in most branches.

Genitalia

Though he later resisted the use of genitalia for classification, it was MEYRICK (1895) who originally introduced them into tortricid taxonomy in his key for the families of the Tortricina where the couplet separating his Epiblemidae and Tortricidae contains the references «uncus not developed» and «uncus developed». KENNEL (1908) rightly criticizes the generalization but then states his similarly sweeping opinion that the genitalia are so strongly diverse that they may be valuable for separation of closely related taxa but useless for higher classification. DAMPF (1908) refutes this view by his careful analysis of the genitalia of *Rhopobota naevana* HÜBNER, [1817], the first comparative study appreciating the taxonomic value of tortricid genitalia. But utilization of this new source of information becomes possible only with PIERCE & METCALFE'S (1922), HEINRICH'S 1923, 1926) and PHILPOTT'S (1928) descriptions and illustrations of a representative sample of the family, which immediately led to a much more adequate higher classification. Once the use of genitalia structures was accepted and considered in combination with superficial characters, rapid further advances were made in tortricid taxonomy especially by DIAKONOFF (1939, etc.) in the Oriental fauna and by ORAZTSOV (1954, etc.) for the Palearctic region. CLARKE'S (1958) monumental work made the genitalia of a large part of MEYRICK'S tortricid types available and allows preliminary comparison on a nearly worldwide basis.

DAMPF (1908) mentions phylogenetic considerations only in a few passing remarks, and PIERCE & METCALFE (1922) refrain from drawing any such conclusions, pointedly stating that «a phylogenetic tree, from the genitalic point of view, is not yet possible». In his revision of the Olethreutinae HEINRICH (1923, 1926) evaluates genitalic structures together with the more conventional superficial characters, and through very apt and critical reasoning reaches a basically correct conception of the evolution of tortricid genitalia. He correctly recognizes that most development consists of reductions which, moreover, are often expressed as trends only and can proceed at different rates in different lineages, and often by distinct ways as he demonstrates for the disappearance of the uncus within the Eucosmini. DIAKONOFF (1939), in his synopsis of the Indo-Malayan and Papuan Tortricinae, provides a detailed description of the genitalic apparatus based on the definitions given by PIERCE & METCALFE (1922), but he refrains from any discussion of its phylogeny.

The unpublished Ph. D. thesis by LAMBERT (1950), an extensive and detailed study of the «Sparganothidinae» contains a most interesting chapter on «phylogeny and evolution of the subfamily» where the author gives a description of the surmised common ancestor of the Archipini and Sparganothini. To avoid having repeatedly to cite his views with regard to every structure discussed below, and also to give due credit to LAMBERT'S contribution to tortricid phylogeny which remained largely unnoticed, the full text of the pertinent passage is here given:

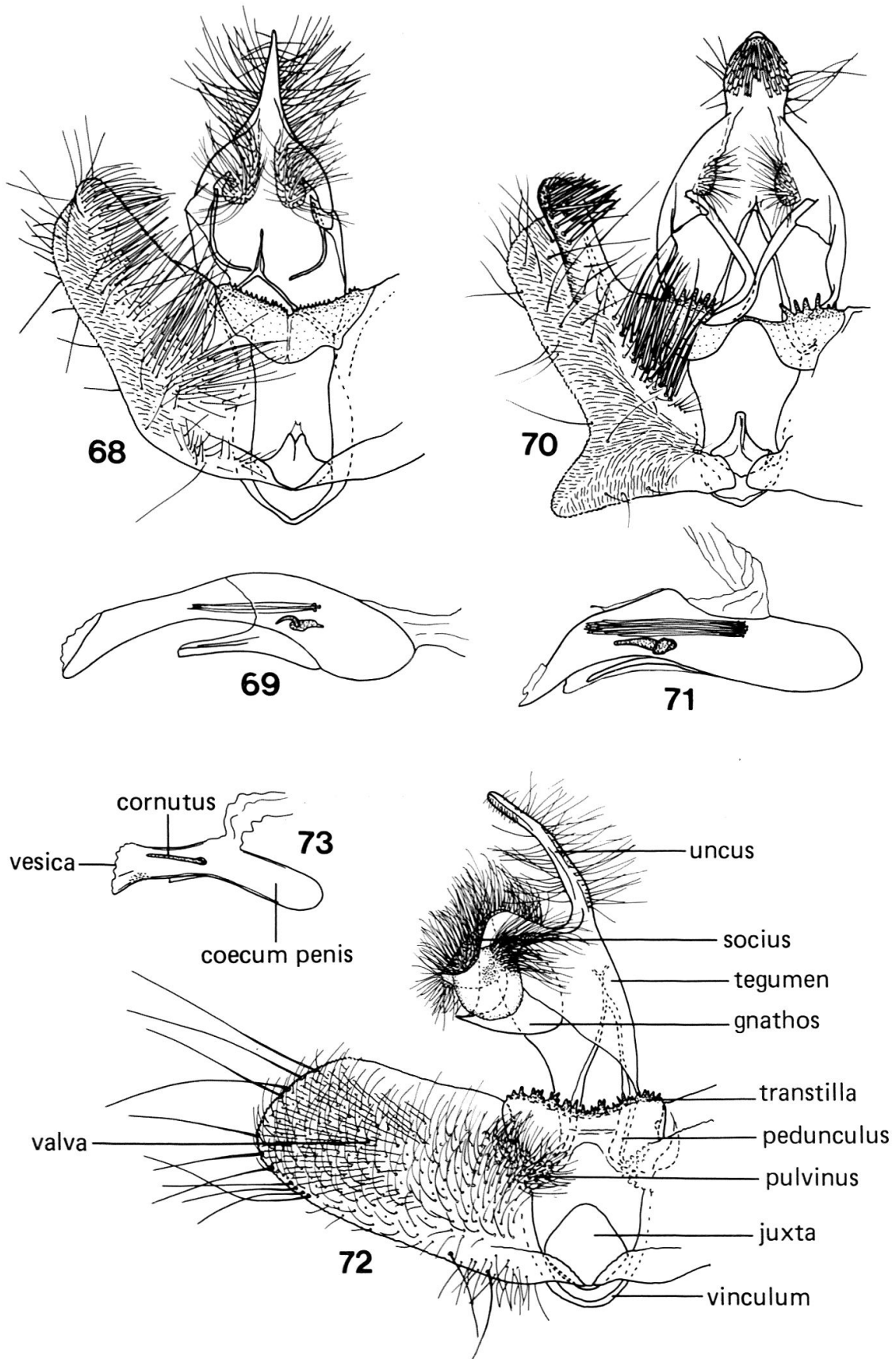
«I imagine that the two subfamilies Sparganothidinae and Archipinae may have had a similar ancestor recalling *Ctenospseustis lurida* MEYR., with an uncus similarly curved at apex, but blunt and not forked. The highly developed socii would have been attached to the uncal plates and the sides of the tegumen; the gnathos thin, united at apex, with a ventral plate; the transtilla wide and spined; the harpes long; the labides poorly developed; the anellus wide; the aedeagus thin and curved; the cornuti curved at base; and the vinculum U-shaped. As to the external characters. the palpi would have been moderate and porrect; the front convex, covered with drooping scales; the ocelli small; the tongue relatively short; and the antennae fasciculate. In the fore wing the costal fold would have been long, and the veins 7 and 8 separate at the end of the cell, with approximate bases. Such an ancestor would have formed by its evolution into two opposite directions, the two allied subfamilies.»

OBRAZTSOV'S (1954, 1955) revision of the Palaearctic Tortricinae contains a wealth of detailed information but while bringing decisive progress for tortricid taxonomy through subdivision of largely superficially assembled groups into natural, monophyletic genera, it does not bring new insights into the evolution of the family. On the contrary, OBRAZTSOV still insists on regarding the Grapholitini as the most primitive tribe of the Olethreutinae, despite HEINRICH'S convincing arguments. As has been noted already for some superficial characters, COMMON'S (1958) brief outline of his concept of tortricine classification shows also for genitalic structures a keen appreciation of phylogenetically relevant developments, and his conclusion that the Tortricinae must have stemmed from a cnephasiine-like stock is demonstrated by the fact that no clear dividing-line can yet be drawn between genuine Cnephasiini and some overall plesiomorphic Tortricinae which apparently lack apomorphies linking them to a specific tribe (*Taeniarchis*, *Eulia*, *Cryptoptila*, some South American Tortricinae). POWELL (1964) reconstructs the phylogenetic relationships within the Tortricinae, mainly with the help of his extensive knowledge of tortricid biology, and apart from relegating the origin of the Tortricini to the very base of the subfamily he reaches conclusions agreeing with those of COMMON. His inclusion of the Sparganothini in the Tortricinae next to the Archipini for biological reasons supports LAMBERT'S suggestion of a common ancestor for the two groups in the recent past.

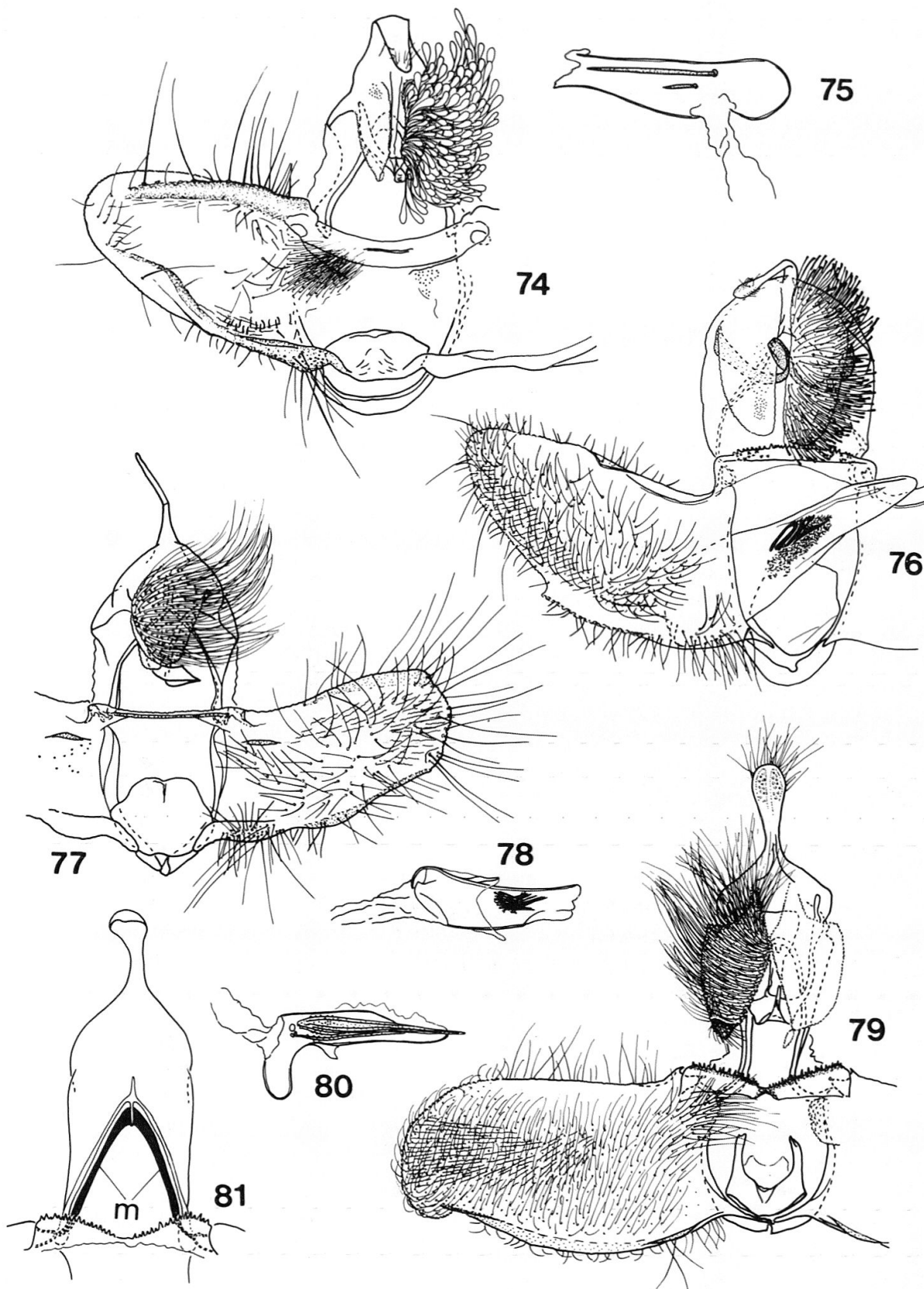
An entirely new approach to genitalia study by KUZNETSOV & STEKOLNIKOV (1973, 1977) through comparison of development and position of male genitalic musculature which reflects the function of the different parts during copulation led to two recent reconstructions of tortricid phylogeny (KUZNETSOV & STEKOLNIKOV, 1973; RAZOWSKI, 1976), differing in basic aspects from previous classifications, but not congruent with each other. As KUZNETSOV & STEKOLNIKOV'S publications are in Russian with no translation available so far, only the greater lines of their arguments could be grasped, and the critical discussion of the conclusions drawn from genitalic musculature has to be considered in this light.

Male genitalia

The technical terms used for most genitalic structures in the Tortricidae (Figs. 72, 73) are by now so generally accepted that with few exceptions no reference will be made to the authors initiating their use. Several glossaries provide this information; see KLOTS (1970) for a comprehensive review, PIERCE (1914) for the original definitions of many terms, and DIAKONOFF (1939, 1954b) and RAZOWSKI (1966, 1970) for discussion of the condition in the Tortricidae.



Figs. 68-73: Male genitalia of: 68, 69, *Thrincoptera signigerana*; 70, 71, *Acropolitis xuthobapta*; 72, 73, *Cryptoptila australana*.



Figs. 74-80: Male genitalia of: 74, 75, «*Batodes*» *jactatana*; 76, *Williella angulata*; 77, 78, «*Teras*» *incessana*; 79, 80, *Heterochorista melanopsygma*.

Fig. 81: Tergal extensor muscle of valva (m) in *H. melanopsygma*.

Musculature of the male genitalia: In a series of papers on the functional morphology of the male genitalia of different lepidopterous families, KUZNETSOV & STEKOLNIKOV (1973, 1977) studied male tortricid genitalic musculature and suggest a revised phylogenetic concept of the family. As it was impossible to have the Russian publications translated their results could be appreciated and applied only inasmuch as they could be deduced from the excellent illustrations of the original papers and from their discussion by authors familiar with Russian (DIAKONOFF, 1973; RAZOWSKI, 1976).

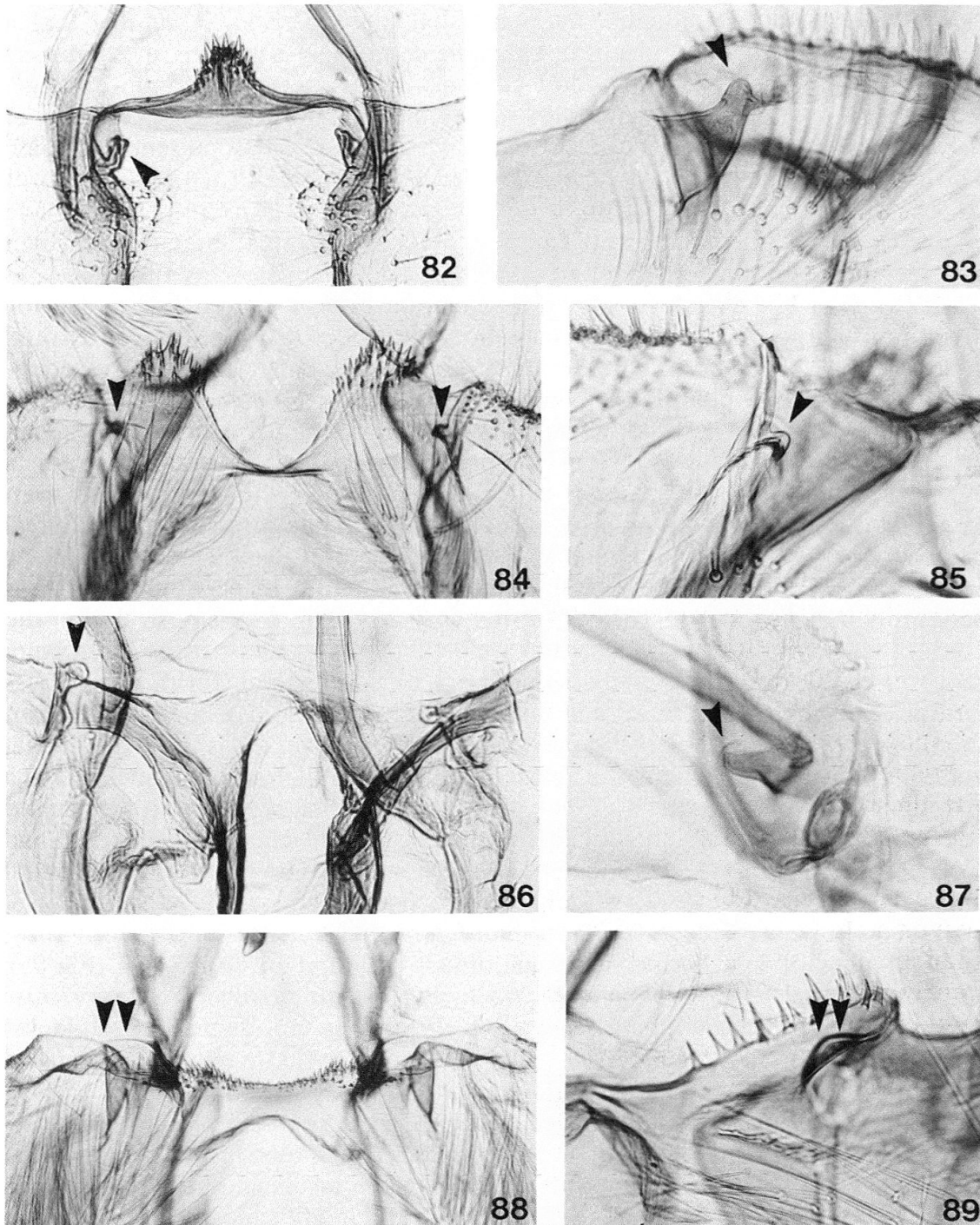
In order to understand the evolution of the different parts of the male tortricid genitalia their function was studied through comparison of position and development of their musculature. As for other morphological structures it was confirmed also for the genitalia and their musculature that most evolution below family level means reduction. In the case of the male genitalia a general trend in all groups is for the valvae to become strengthened and to take over a greater share of the clasping function as the tergal complex becomes reduced. This process involves parallel modification in the musculature, the most obvious changes being loss of muscles in the tegumen and displacement of their attachment in the valva.

The plesiomorphic condition with a well-developed tegumen as found in generalized members of several tribes (Archipini, Sparganothini, Cochylini, Olethreutini, Eucosmini) is characterized by basically the same set of muscles which therefore can be considered to represent the groundplan for the family (KUZNETSOV & STEKOLNIKOV, 1977: Fig. 6). Reduction of the tergal musculature affects different muscles in different groups, and is expressed as trends leading to repeated, parallel disappearance of the same muscle in different branches of a clade. Each of the three main tergal muscles can become atrophied. Many derived Olethreutinae (*Eucosmomorpha albersana*, *Cydia pomonella*) have the uncus depressor (m_1) reduced, all Tortricini are said to lack the tergal flexor of the valva (m_4) and the tergal extensor of the valva (m_2) has been lost several times in the Tortricinae (most Archipini, at least some Cnephasiini, Ceracini, presumably also Epitymbiini). Though properly preserved material is generally needed to examine the musculature, at least the point of attachment of m_2 on the valva is often apparent even in macerated genitalia (Figs. 81–87).

The conclusions drawn from comparative examinations of genitalic muscles however can be weakened by two fallacies. As atrophy of a certain muscle is demonstrably a trend effective in a group often without being expressed in all its branches, the shared loss of a muscle does not necessarily mean that the taxa concerned are phylogenetically closer than some others retaining it. Joint possession of a full set of muscles on the other hand is merely a symplesiomorphy and thus no argument for kinship. KUZNETSOV & STEKOLNIKOV's Cochyliidii appear to be an artificial assemblage based mainly on such a symplesiomorphy, the shared retention of the tergal extensor muscle of the valva (m_2) (Fig. 81) in the Sparganothini (Fig. 82), Cochylini and *Eulia*.

The presence of a tergal extensor in tortricine taxa has, in the present study, been treated as an indication of their rather archaic nature, a generalization supported in the Palaearctic fauna by *Eulia* and *Pseudargyrotoza*, both with a complete set of tergal muscles and underived venation with M-stem and chorda developed in *Pseudargyrotoza* and at least the latter indicated in *Eulia*. Through projections of the caudo-dorsal angle of the valva between transtilla and pedunculus serving as attachment for the tergal extensor, obvious even in macerated genitalia, the pres-

ence of this muscle can be inferred for further archipine taxa like «*Capua*» *leucostacta* (Fig. 87), *Isochorista* and *Epichoristodes* (Figs. 84, 85) and the sparganothine *Heterochorista* (Fig. 83). On the evidence of macerated genitalia *Ctenopseustis obliquana* (Fig. 89) and *Carphomigma* (Fig. 88) hold an intermediate position, the



Figs. 82-87: Attachment point (▲) of tergal extensor muscle of valva of: 82, *Sparganothis pilleriana*; 83, *Heterochorista melanopsigma*; 84, *Epichoristodes apiletica*; 85, enlarged detail of Fig. 84; 86, *Taeniarchis* sp.; 87, «*Capua*» *leucostacta*.

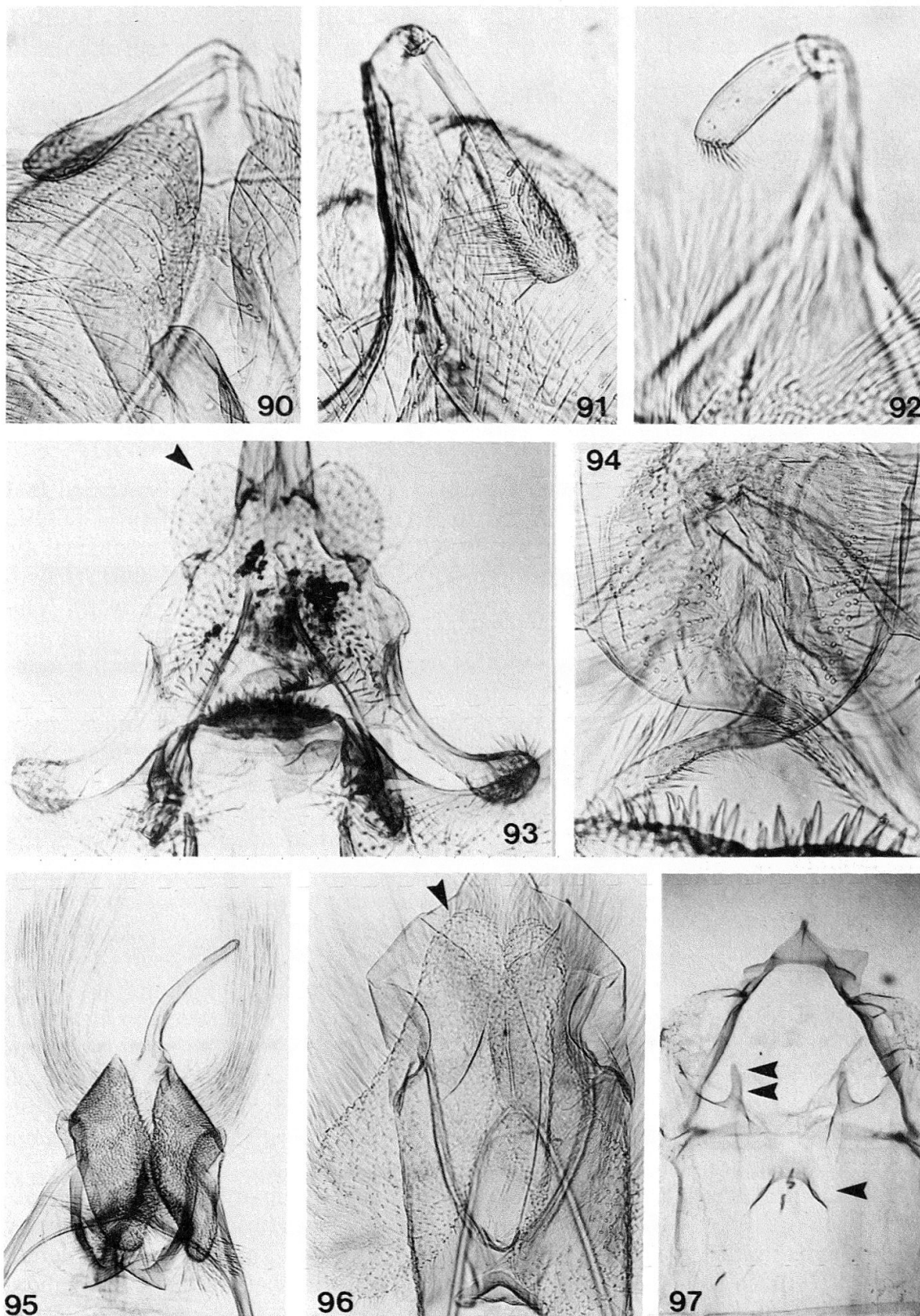
Figs. 88-89: Presumably non-functional vestige of former attachment point (▲▲) of: 88, *Carphomigma* sp., 89, *Ctenopseustis obliquana*.

deep invagination of the internal surface of the valva just lateral to the transtilla which once served as attachment for the tergal extensor muscle is still present, but apparently no longer functional. In *Heterochorista* (Fig. 83) this cone-like pit ends in a drawn-out attachment point often with some residual fibres, but in *C. obliquana* and *Carphomigma* there remains only an evenly rounded pocket which is almost completely atrophied in «*Epichorista*» *emphanes* and *Planotortrix*, taxa closely related to *Ctenopseustis* but somewhat more derived. Assuming that a muscle does not reappear once it has become completely atrophied, the Malagasy *Epichoristodes* with its unspecialized tegumen without uncus brush and with large, scaled socii combined with modified valvae strongly suggesting a precursor of *Archips*, is a further argument for the polyphyletic nature of the present Archipini. The simple ventral coremata of *Epichoristodes*, similar in structure to those of *Archips*, further support inclusion of *Epichoristodes* and *Archips* in the same clade as opposed to at least one phylogenetic line of the Archipini characterized by a simple, not plicate valva with well-developed costa, lacking any coremata.

Tegumen: The structures of the tegumen have been largely disregarded for taxonomic purposes, though its articulation with the vinculum and valva could conceivably provide valuable information. The conspicuously club-shaped pedunculi of certain Epitymbiini (*Rhomboceros*, *Aplastoceros*, *Cleptacaca*) (DIAKONOFF, 1953: Figs. 270, 281, 282) are a possible synapomorphy of this primarily Papuan group. A small process with residual filaments projecting cephalad from the dorsal angle formed by the anterior margins of the two halves of the tegumen can, even in genitalia slides, give a strong indication for the original presence of the tergal extensor muscle of the valva which is often attached at this point.

Uncus: The uncus was the first genitalic structure to be used in tortricid taxonomy in MEYRICK'S (1895) key for the families of his Tortricina as part of the couplet separating his Tortricidae and Epiblemidae. The alternatives given were however based on an ill-advised assumption as by no means all Tortricinae possess an uncus or all Olethreutinae lack one. HEINRICH'S (1923) detailed discussion of the different ways the uncus disappears within the Eucominae shows clearly that without his stating it explicitly he already considers a well-developed uncus to be a primitive feature. LAMBERT'S (1950) description of the uncus of his surmised ancestral form broadly agrees with the conclusions reached in this study, and COMMON (1958) recognizes a widening of the uncus and development of a ventral apical brush as derived trends within the Tortricinae.

A well-developed but rather undifferentiated uncus, long and narrow, apically more or less hooked but unadorned, as found in *Taeniarchis* (Fig. 95), *Proselena*, *Polylopha*, *Arotrophora*, *Trachysmia*, some *Heterochorista*, «*Teras*» *incessana* (Fig. 77) and «*Capua*» *leucostacta* presumably represents the groundplan condition for the Tortricinae and Chlidanotinae. The extremely thin uncus of many Sparganothini with its swollen base and the strong, tapering but naked hook of *Cryptoptila* (Fig. 72), *Carphomigma*, *Homonoides*, *Epichoristodes* and «*Batodes*» *jactatana* (Fig. 74) are both but little derived. Development from the ancestral state takes apparently two opposite routes: reduction as in the Tortricini and Cochylini or a general broadening of the uncus and modification of its apex either into some club-like structure (*Anacrusis*, many Schoenotenini) or through acquisition of a ventral brush (Archipini, Epitymbiini, Ceracini), both perhaps means of increasing barb-style function of the uncus. The so-called «typical archipine uncus» with a ventral brush at its apex is obviously a developmental trend which has become expressed several times in different lineages, perhaps as a con-



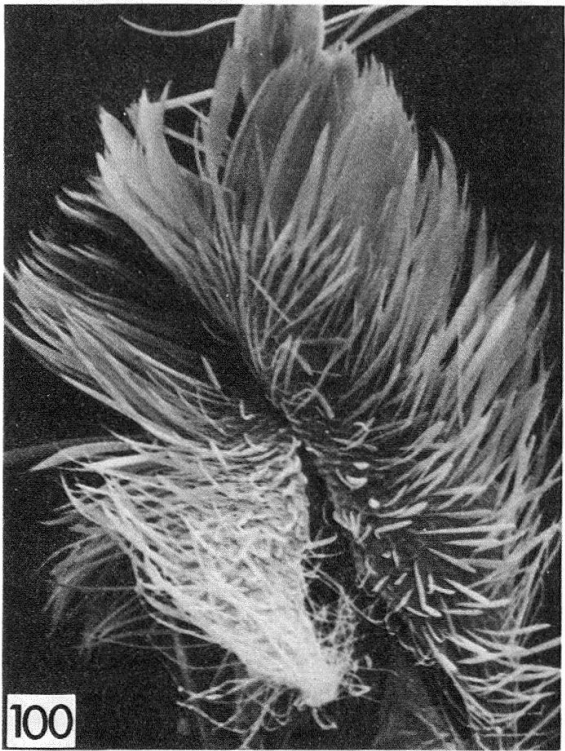
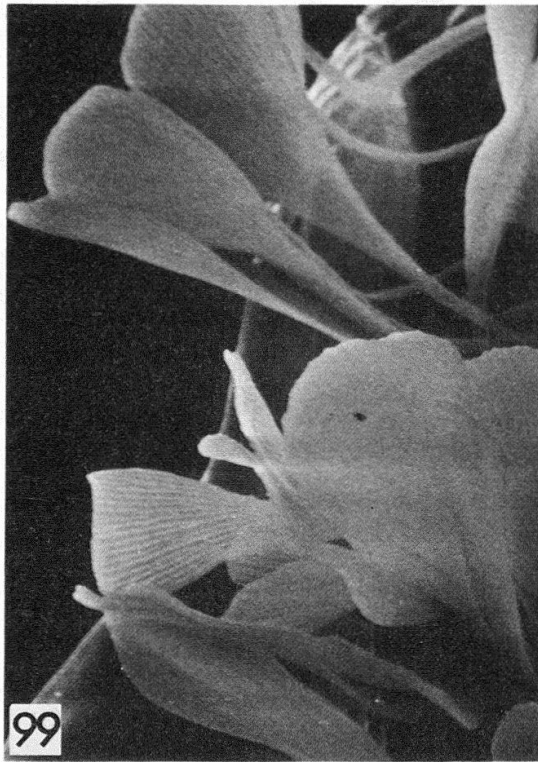
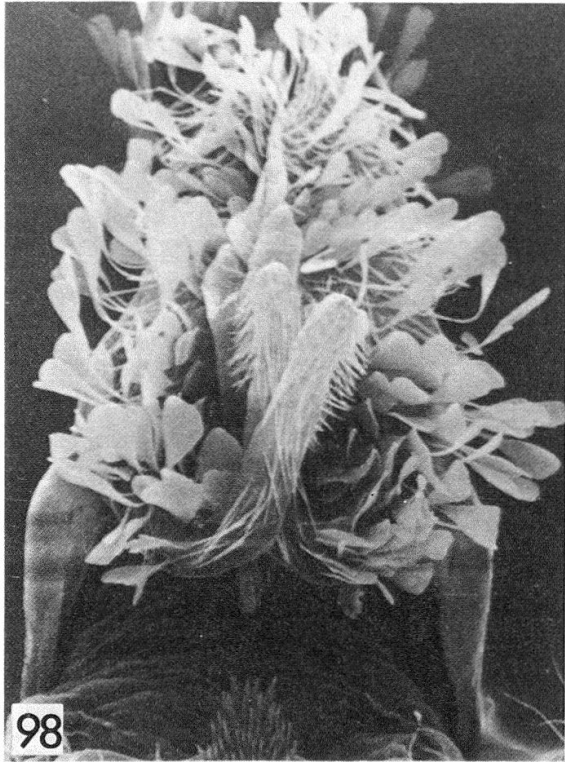
Figs. 90-92: Uncus of: 90, *Williella angulata*; 91, *W. sauteri*; 92, «*Tortrix*» *incompta*.
 Figs. 93-94: Fused socius and gnathos in Sparganothini of: 93, *Synnoma lynosyrana* (▲ free caudal lobe of socii); 94, *Lambertiodes harmonia*.
 Figs. 95-96: Socii of: 95, *Taeniarchis* sp.; 96, *Heterochorista* sp. (▲ free caudal lobe).
 Fig. 97: Base of abdomen of «*Batodes*» *jactatana* (▲ presumed muscle attachment, ▲▲ tortricoid apodeme).

vergence in response to similar adaptive pressure, but probably rather as parallelisms due to an underlying apomorphy. The gradual development of an uncus brush can be observed within the *Thrincochora*/*Acropolitis* complex, two closely related genera linked by several obvious synapomorphies. While *Thrincochora* (Fig. 68) has a tapering, ventrally naked uncus, a series of *Acropolitis* species bear an increasingly developed ventral brush of scales on the enlarged apex of their uncus, ranging from a small tuft of a few scales to a dense brush (Fig. 70). *Williella* (Figs. 76, 90, 91) and «*Tortrix*» *incompta* (Fig. 92) seem to be further taxa with an uncus brush in statu nascendi, and the Malagasy Archipini suggest another at least superficially independent appearance of the same character. The shared possession of an uncus brush can therefore not be treated simply as a synapomorphy, and is for example not a valid argument for the inclusion of the Epitymbiini in the Archipini.

Socii: The frequent observation that in any given group relatively large socii are found in the rather generalized members (HEINRICH, 1923; LAMBERT, 1950; DIAKONOFF, 1952; DUGDALE, 1966) has led to an early acceptance of well-developed, large socii as the groundplan condition. Careful observations revealed that scaled socii, a feature long considered to be a derived condition typical for the Sparganothini, must also be ascribed to the groundplan of the Tortricinae. Its frequent occurrence in overall plesiomorphous taxa of different lineages (*Heterochorista*, *Williella*, *Epichoristodes*, *Anacrusis*, «*Capua*» *leucostacta*, «*Capua*» *belophora*, «*Tortrix*» *incompta*, «*Batodes*» *jactatana*) but in only one highly developed branch, the Sparganothini, leaves only this explanation. In some species of *Heterochorista* and other Sparganothini (Figs. 98–100), in *Anacrusis* and «*Batodes*» *jactatana* (Fig. 101) the scales have probably become strongly spatulate as a secondary derivation, and in a rather cursory examination only socii bearing such conspicuous scales would be recognized as scaled. Because several taxa in different tribes (*Acropolitis*, a possible new genus in the Epitymbiini, «*Capua*» *belophora*, «*Argyrotoxa*» *pompica*) have scales instead of the usual bristles in the uncus brush, the question whether in such a context bristles or scales represent the more ancestral state could perhaps be raised in a more fundamental way.

Even if the scales on the socii can no longer be treated as an exclusive feature of the Sparganothini, the tribe is still characterized by two apomorphies in the socii. While typically plesiomorphic socii are simple, large pendant flaps which at their top are attached to the tegumen (*Taeniarchis* (Fig. 95), «*Batodes*» *jactatana*, «*Teras*» *incessana*, *Cryptoptila*, *Ctenopseustis obliquana*, *Homonoides*) all sparganothine socii have an erect caudal lobe rising well above the junction of the socii with the tegumen (Fig. 93), a modification that is the main reason for their cushion-like appearance. The superficially very similar *Anacrusis* and *Templemania* genitalia lack this apomorphy, a further argument against their inclusion in the Sparganothini. Sparganothine socii with a free caudal lobe are however a characteristic feature of some *Heterochorista* (Fig. 96) and thus a probable synapomorphy of this generalized Papuan genus with the Sparganothini. The position and significance of *Orthocomotis melania* CLARKE, 1955, also with sparganothine socii and a cubital pecten, both unusual features in *Orthocomotis* DOGNIN, 1905, will have to be reconsidered once the female becomes available.

A further apomorphy of the Sparganothini consists of a very characteristic fusion of the gnathos and socii. *Lambertiodes* (Fig. 94) seems to represent an earlier stage in this development where the apically separated gnathos arms have each become completely fused to the lower edge of the socii, but without any



Figs. 98-101: Scaled socii of: 98, 99, *Sparganothis pilleriana* (Fig. 99, detail of socii scales); 100, *Heterochorista* sp.; 101, «*Batodes*» *jactatana*.

further differentiation as the entire organ is covered with scales and bristles to the pointed tip without any interruption. The apices of these compound structures apparently become more specialized, developing into small knobs (*Sparganothis*) or round plates (*Synnoma*, Fig. 93), covered with bristles and separated from the

rest of the socii by a naked neck obliterating the origin of the apical bristles on the gnathos. The socii are joined with the gnathos also in *Anacrusis*, but as both structures have a very different development in the two groups it seems doubtful that the loose connection in *Anacrusis* is homologous to the fusion in the Sparganothini. HEINRICH (1923) describes fusion of gnathos and socii also for some Eucosmini (*Gypsonoma*, *Gretchena*, *Epinotia*).

The porrect, beak-like, paired and bristled apical processes of the Phricanthini have generally been regarded as socii; but the superficially strong overall similarity of phricanthine genitalia to those of some Cossidae might warrant a closer examination, especially a study of the muscle attachments.

Hami: The phylogenetic origin of the hami (DIAKONOFF, 1948) is of interest in deciding whether these structures in the Chlidanotini and Hilarographini on the one hand, and the Schoenotenini on the other, are homologous to each other and a possible synapomorphy to include the Schoenotenini in the Chlidanotinae, as suggested by DIAKONOFF (1960b). As no Hilarographini and Chlidanotini could be examined, some questions already raised by COMMON (1965) are reconsidered purely theoretically in the light of published information on Chlidanotini, Hilarographini and Schoenotenini. If the hami represent a synapomorphy for the three groups one would expect their presence at least in the more generalized members of all three tribes. COMMON (1965) draws attention to the fact that the schoenotenine genera with the greatest genitalic specialization (*Epitrichosma*, *Rhabdotenes*) have often retained a more plesiomorphic state of their venation and maxillary palpi than some with generalized genitalia of more tortricine form which have lost the M-stem in the forewing (*Proselena*, *Palaeotoma*). But the fact that possession of hami is always correlated with a clearly derived uncus, socii and gnathos, and that both *Proactenis* and *Diactenis*, the genera with the most plesiomorphic schoenotenine venation, lack this structure carries more weight, and strongly suggests the appearance of hami as an autapomorphy within the Schoenotenini. A similar evaluation of the Hilarographini and Chlidanotini would be needed to understand the origin of the hami in these tribes; a very superficial investigation of the Chlidanotini yields conflicting results. While *Caenognosis*, the genus with the apparently most plesiomorphic venation with all veins except CuP present in the forewing possesses well-developed hami, the New Caledonian *Iconostigma*, the only chlidanotine genus retaining the abdominal hairpencil which together with an invaginated valva is an important synapomorphy of this tribe with the Hilarographini and Polyorthini, shows no traces of hami. But as the dorsal genitalic complex of *Iconostigma* is otherwise rather derived through a reduction of the gnathos and sclerotization of the socii, the absence of hami could in this case be a secondary development. As the remarkable signum with its accessory sac closely links those Hilarographini usually possessing hami (*Hilarographa*, *Thaumatographa*) with the Chlidanotini, it seems reasonable to assume common ancestry for both these derived structures. Should this prove correct, the position of *Mictocommosis* and *Mictopsichia* will have to be reconsidered.

Gnathos: A gnathos with ventrally joined arms is so frequently found, especially among the lower Ditrysiina, that it can safely be assumed to have arisen in this form previous to the branching off of the Tortricidae. While this plesiomorphic state persists with only slight modification in most groups of the Tortricinae, except for the Tortricini and Cochylini, and often develops into a prominent, heavily ornamented structure usually ending in a flattened plate (among Cnephasiini, Archipini, Schoenotenini), there is a much stronger trend for reduction of

the gnathos in the Olethreutinae. *Microcorses*, however, a member of the presumably most archaic tribe of the Olethreutinae, still possesses a very slender, but essentially tortricine gnathos, while this organ is present in a strongly modified state only in some Olethreutini (*Eudemis*, *Statherotis*), and as a weak and undifferentiated band in the more generalized Eucosmini.

A relatively slender but well sclerotized gnathos, ventrally joined to form a flattened plate or trough, seems to have been the groundplan condition for the Tortricinae, and probably also for the Chlidanotinae. Secondary separation of the two gnathos arms has obviously occurred independently several times, at least once in the Sparganothini, the Polyorthini (*Isotrias*, *Olindia*) and the lower Archipini (*Thrincochloa*, Fig. 68). As has been described for the development of the uncus brush, the separation of a typically archipine gnathos into two free arms can be observed within the genus *Thrincochloa*.

The gnathos often becomes connected with the anal tube, a development that in Tortricinae has so far had no bearing on taxonomic considerations. Fusion between gnathos and socii, on the other hand, is considered of much more importance for classification and is discussed above in the section on socii.

Tuba analis: A modification of the anal tube may occur parallel to a reduction of the gnathos, its ventral surface becoming sclerotized and as subscaphium, usually connected with the remnants of the gnathos, possibly taking over the function of this organ. In the Tortricinae this development is evident in the Tortricini (RAZOWSKI, 1966).

Vinculum: In the large majority of Tortricinae the vinculum is a well-sclerotized, ventrally firmly fused band joined to the base of the valva and providing the connection to the tegumen through the pedunculi. It is generally agreed that Tortricidae lack a saccus, but there are a few significant exceptions to this rule. Nearly all Phricanthini have a large, apically tapering saccus which in length often exceeds the width of the valva. A ventrally widened vinculum, strongly suggesting a vestigial saccus, is present elsewhere in the Tortricinae, in «*Capua*» *leucostacta* and some South American Tortricinae. COMMON (1965) and TUCK (1981) report a short, truncate saccus from *Daulocnema* and *Iconostigma*, both Chlidanotini. It is probably no coincidence that for entirely different reasons nearly all these taxa are counted among the generalized members of their tribe or even their subfamily, as in the case of the Phricanthini. A partial persistence of the saccus, a plesiomorphic feature widely distributed among the lower Ditrysiinae, seems a more logical explanation for its sporadic occurrence than repeated origin at the base of several branches within the Tortricidae.

Vinculum arms which are ventrally not firmly fused but only lightly joined by a membranous connection appear to be a less fundamental modification than the retention of a saccus, and are present in some rather generalized taxa («*Teras*» *incessana*, «*Argyrotoxa*» *pompica*) as well as in more derived ones (*Cochylis*, *Aethes*). Ventrally free arms of the vinculum may develop into enlarged, rounded terminations as in *Aethes*.

Valva: A number of terms are available for every area of the valva, but the origin and homology of structures referred to by the same term in different groups are often obscure as KLOTS (1970) points out in his review. The tortricine valvae possess few differentiated regions, and for the present discussion a division into costa and sacculus for sclerotized rims or more complicated structures along the dorsal and ventral margin of the valva, and the general term disc for its central part, will suffice. The presence of a pulvinus and its shape are important enough

for certain groups of the Tortricinae to warrant a special term for this structure. Furthermore, comparative studies show that at least in the Tortricinae the pulvinus is derived from the valva, and the term «lateral process of the transtilla» used by KLOTS is therefore not appropriate. A special term also seems justified for the brachiola in the Tortricini (RAZOWSKI, 1966), an obvious apomorphy of this tribe, though similar structures are found elsewhere in a very few instances (RAZOWSKI, 1976).

The differences between olethreutine and tortricine valvae have been discussed repeatedly since DAMPF's (1908) and HEINRICH'S (1923) initial observations. DAMPF draws attention to the dissimilarity in the connection between tegumen, valva and vinculum in the two subfamilies, and HEINRICH adds to this the basal opening of the valva as a characteristic of the Olethreutinae. OBRAZTSOV (1958) rightly criticizes HEINRICH'S use of «opening» for the basal excavation of the olethreutine valva which is closed by a transparent membrane, but failing to recognize this modification in *Eucosmomorpha* he too lightly dismisses its taxonomic importance. Referring to DANILEVSKI & KUZNETSOV'S (1968) conclusion DIAKONOFF (1973) gives a detailed description of the morphology of the tortricine and olethreutine valvae. A summary of results obtained from comparative studies of the functional morphology of tortricid genitalia by RAZOWSKI (1976), drawing on KUZNETSOV & STEKOLNIKOV'S (1973) work, contains a plausible explanation for the development of the typical olethreutine valva.

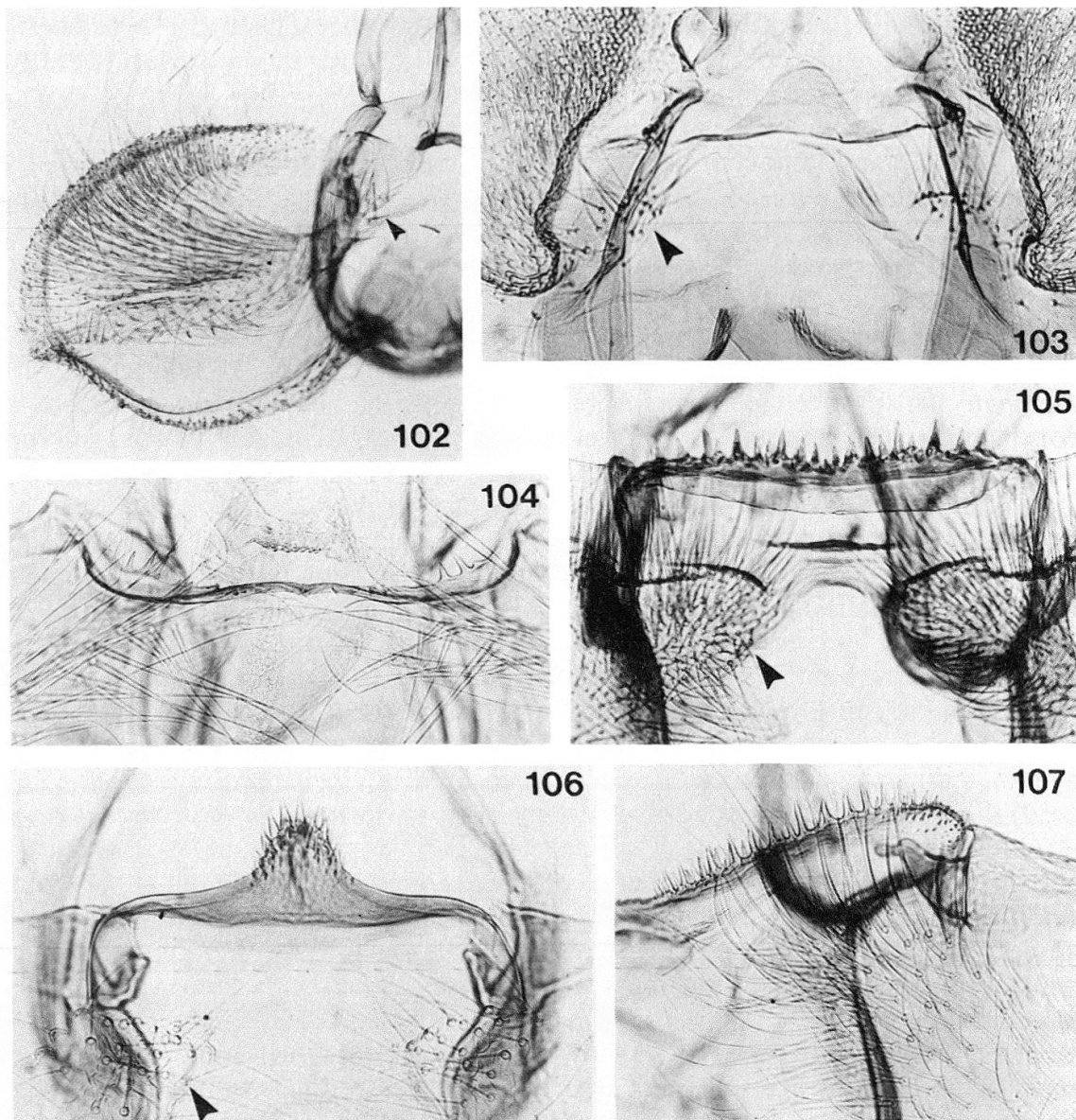
Reviewing the literature on tortricine genitalia one is left with the impression that the essential difference between a simple valva like the one of *Epagoge* and those with a wrinkled or even plicate disc as in *Archips* or *Clepsis* has for a long time not been sufficiently appreciated. COMMON (1958) was the first to provisionally subdivide the Archipini in such a way that those genera with plicate valva are grouped together, but this has not been followed up since. In the course of the study of the rich and diverse Papuan fauna the impression that the Archipini in their current composition must represent a polyphyletic group grew, together with the suspicion that a simple valva on the one hand, and a valva with a plicate disc on the other, indicate a very basic division within the tribe. Closer examination of the Malagasy *Epichoristodes* and *Homonoides* revealed in these genera a combination of a very plesiomorphic dorsal genitalic complex with a typically wrinkled valva recalling *Archips*, a finding that confirmed the notion of a polyphyletic nature of the present Archipini.

A survey of the Tortricinae leaves no doubt that a simple, unadorned valva, weakly and evenly sclerotized, with a straight costal and ventral edge without an apically differentiated sacculus represents the groundplan condition. Relatively simple valvae are found in the Phricanthini, Ceracini, among the lower Schoenote-nini (*Synchratus*, *Tracholena*), Cnephasiini (*Arotrophora*), Archipini (*Ctenopseustis*, *Cryptoptila*, «*Teras*» *incessana*, «*Capua*» *leucostacta*) and the Sparganothini *Hetero-chorista*, *Lambertiodes*). Judging from the range of derived forms the ancestral valva was probably as membranous as the least sclerotized ones found today, as in *Cryptoptila* (Fig. 72) or *Heterochorista* (Fig. 79), and probably longitudinally wrinkled in a similar manner. Different development trends, either singly or in combination, seem all to have led to a more robust valva, firm enough to be moved by one pair of muscles only, allowing the tergal extensor to become eventually atrophied. This is accomplished either by a stronger sclerotization of the entire valva (*Ctenopseustis*), the development of a rod-like costa (*Anacrasis*) and a strong sacculus, often with a free termination (*Tortricini*, *Cnephasiini*), or an

increasing folding of the membranous disc (*Anisotenes*). The dense brushes of scales on the greatly enlarged surface of such plicate valvae conceivably add to their stability and especially to their clasping ability.

Development of a sacculus is of such general occurrence that it is largely irrelevant to taxonomic considerations at least on the higher level. Modifications of the costal margin of the valva are much less frequent and thus of more consequence for assessing kinship. In *Proeulia tenontias* and several undescribed congeneric species a well-defined, broad area along the costa is much more strongly sclerotized than the remainder of the valva, except for the solid sacculus. A similarly sclerotized, but much narrower band along the entire costa is found in *Anacrusis*, *Templemania* and many Sparganothini. It seems that in *Lambertiodes* and *Platynota* the lower edge of such a band-like costa has become prominent as a conspicuous rod, running slightly below and parallel to the costal edge of the valva.

References to the strongly modified valva of higher Archipini usually mention its reduced or atrophied costa rather than its wrinkled or plicate disc. If the inference is correct, however, that the groundplan valva is only little sclerotized, it follows that the absence of a sclerotized costa in *Archips*, *Anisotenes* etc. is merely a plesiomorphy and not a modification. The derived feature of such valvae consists in the characteristically wrinkled (*Archips*) or folded (*Anisotenes*) disc. A rough grouping of the different archipine valvae yields three basic types: 1) the plesiomorphic groundplan condition, flat or with longitudinal wrinkles along the margin, subrectangular and with a straight costa as in *Cryptoptila* or *Choanograptis*; 2) the triangular to rounded *Archips*-type (Fig. 102) with a curved costal edge, a smooth ventral part whose lower half develops into the sacculus and a central area of dense, parallel wrinkles which, gradually converging, run in an even curve from along the entire dorsal margin towards the base of the transtilla; and 3) the extreme forms like *Anisotenes* and *Clepsis* (Fig. 108), where the membrane of the inner surface forms pocket-like folds if it is pressed to lie flat. It is not yet possible to decide if the *Archips*- and *Clepis*-types represent two different lines of development or just two different states in the same transformation series, but there is good evidence from two sides that separation of the Archipini with a wrinkled or plicate valva from the generalized stock took place at an early stage in the evolution of the tribe. Those Papuan and Australian archipine genera with the valva folded in the most elaborate way possess some surprisingly plesiomorphic features like predominantly unstalked R_4 and R_5 and a well-developed maxillary palpus of three segments, and this in contrast to the bulk of those Archipini with a simple, flat valva (*Epagoge*, *Choanograptis*, *Hiceteria* etc.) which have R_{4+5} stalked and generally much more reduced maxillary palpi. The combination of a simple, unmodified valva with a venation with R_4 and R_5 separate is found mostly in isolated and small taxa (*Cryptoptila*, *Pseudargyrotoza*, *Lozotaenia*) clearly representing relicts judging by their generally plesiomorphic nature. In the New Zealand fauna, however, this element is well represented (*Harmologa*, «*Epichorista*» *emphanes*, *Planotortrix*), in itself possibly an argument for its relative old age. The ancestors of the genera with a plicate valva must obviously have branched off from the main stem of the Archipini at a time when R_4 and R_5 were still separate and the maxillary palpi at least 3-segmented. Malagasy Archipini (*Homonoides* (Fig. 102), *Epichoristodes*) with an *Archips*-type valva but otherwise very plesiomorphic genitalia further suggest an early evolution of this character (see DIAKONOFF, 1960b). *Homonoides* and *Epichoristodes* both have an uncus without ventral brush



Figs. 102–107: Pulvini of: 102, *Homonoides euryplaca*; 103, *Archips piceana*; 104, «*Grapholita*» *pictoriana* (= *Planotortrix*); 105, *Cryptoptila iubata*; 106, *Sparganothis pilleriana*; 107, *Heterochorista melanopsigma*; (in some Figs. pulvinus indicated with ▲).

and very large *socii*, scaled in *Epichoristodes*. In genitalia slides of *E. apiletica* the attachment points of the tergal extensor muscle are clearly visible below the transtilla (Figs. 84, 85), and as there can be no doubt that this characteristic group is monophyletic it follows that it must have separated from the main stock before the uncus brush arose and the tergal extensor of the valva became atrophied. The valva of *Homonoides* with its narrow, faintly sclerotized sacculus and continuous, curved band of bristles from the tip of the valva to the base of the transtilla (Fig. 102), without a differentiated pulvinus, represents an early stage of the transformation series leading to the valva of *Archips*. *Epichoristodes* and *Coniotorna* illustrate the progressive development of a broad sacculus, *G. erratica* already with an indication of a free termination in the shape of a sharply projecting ridge, characteristically along the dorsal margin of the sacculus as in *Archips*. As an

exactly parallel development can be observed in the transtilla of these Archipini (see p. 48), the assumption that these African taxa are derived from an earlier, more widely distributed facies, and could thrive especially in the relative isolation of Madagascar, seems justified. This archaic group is now apparently absent from the Oriental/Australian region, but whether it never extended its range to this area or became extinct there later must be left open.

No valva of an obviously transitional condition between the two types represented by *Archips* and *Anisotenes* was recognized in the present study. Among the Australian and Papuan Archipini with the external characters of *Anisotenes* variably folded valvae are found, differing in the manner of arrangement of their folds as well as in the degree of their plication. Some can be arranged in short series, each with a distinct principle of folding but increasing in complexity. Parallel development is thus clearly occurring in the most recent branches.

DIAKONOFF (1977a) and TUCK (1981) both comment on the apomorphic nature of the invaginated valva and the corresponding abdominal hairpencils of the Chlidanotinae. While DIAKONOFF implies a parallel development of a split valva in the Polyorthini and Hilarographini, TUCK convincingly argues that this feature must represent a synapomorphy of the three chlidanotine tribes, which may, however, be obscured in some genera through secondary loss. Such genera as *Caenognosis* and *Chlidanota*, which possess an invaginated valva without a hair pencil, can only be logically accounted for by partial atrophy of a once functional unit. If we accept an invaginated valva for the common ancestor of the Hilarographini, Polyorthini and Chlidanotini the position of *Mictopsichia* and *Mictocommosis* must be reconsidered also for this reason. With their tortricine male and female genitalia both taxa could at most be regarded as very generalized Hilarographini, a position which would then however strongly imply the retention of such a synapomorphy as the invaginated valva.

A patch of flattened, pencillate bristles on the inner surface of the valva is a very characteristic feature of the higher Schoenotenini, but as they are lacking in the more generalized genera they cannot belong to the groundplan of the tribe. COMMON (1965) points out that similarly modified bristles are found also among the Tortricini in *Asterolepis* and *Sclerodisca*, and they also occur in such isolated groups as *Mictopsichia* (Hilarographini) and an undescribed epitymbiine genus with strongly derived venation from New Guinea. This suggests independent development of this apomorphy sporadically several times within the Tortricinae and Chlidanotinae, and it thus can have no bearing on the relationships between the tribes.

A pulvinus crops up often in a very similar shape in widely different groups beyond the Tortricidae, and in the Tortricinae is present in the Sparganothini, many Archipini and Tortricini. It is quite conceivable that possession of a bristled pad at the base of the valva is of advantage as it may facilitate clasping of the female during copulation or fulfil some sensory function. Attempts at understanding relationships among the Sparganothini, Archipini, Cnephasiini and Atteriini led to a more detailed inquiry into the evolution of the pulvinus as its distribution in these four tribes seemed to confirm some surmised kinships that could at the time not be proved with more tangible arguments. It became apparent that at least in the Tortricinae the pulvinus is derived from the bristles of the inner surface of the valva and is only secondarily connected with the transtilla and then integrated into a functional unit in the higher Archipini.

A pulvinus is lacking in the Olethreutinae (with the possible exception of *Microcorses*), the Chlidanotinae and the Phricanthini, Ceracini, Cnephasiini, Epitymbiini, Cochylini and Atteriini except for «*Ctenopseustis*» *lurida* which possesses a bristled ridge of questionable homology. *Ctenopseustis obliquana* and *Homonoides euryplaca* (Fig. 102) presumably illustrate an early situation in the development of the tortricine pulvinus: the bristles on the inner surface of the valva reach close to the basis of the transtilla in a curved and narrow band. In the more derived relatives of *H. euryplaca* the bristles at the end point of this band, next to the transtilla, become increasingly more numerous and finally form a distinct pad (*Cornusaccula*, *Parapandemis*) together with the supporting membrane (DIAKONOFF, 1960b) as in *Archips* (Fig. 103). In the higher Archipini (*Anisotenes*, Fig. 114) the transtilla has become separated into two lateral, toothed knobs only loosely connected with each other, but each half is joined closely with the small but strongly raised pulvinus which carries only a few bristles (peniculus in DIAKONOFF, 1952) and whose origin from the inner surface of the valva has become entirely obliterated.

The development of discrete pulvini from the bristles on the inner surface of the valva cannot be observed as consistently in the Archipini with a simple valva as in the example described from Madagascar, but the initial state in *Ctenopseustis*, *Planotortrix* (Fig. 104) and «*Capua*» *leucostacta* and the derived condition in *Cryptoptila* (Fig. 105) and «*Batodes*» *jactatana* (Fig. 74) strongly suggest a similar process. Development of *Sparganothis*-type pulvini (Fig. 106) occurs within the genus in *Heterochorista* (Fig. 107). This means that a pulvinus has appeared at least four times within the Tortricinae, if the Tortricini are included, and further instances of its development cannot be ruled out. The monophyly of a group has therefore to be established on the strength of other autapomorphies before the significance of the presence or absence of a pulvinus can be judged. *Cryptoptila*, «*Batodes*» *jactatana* and *Heterochorista* all possess a pulvinus, but its very different structure in the first two genera, together with the radically differing signum in *Cryptoptila*, the derived valva of «*Batodes*» *jactatana* and the stalked R_{4+5} in *Heterochorista* - to mention only the most obvious discrepancies - render it highly unlikely that the shared possession of a pulvinus indicates monophyly for these three genera. The very similar-looking pulvinus in *Heterochorista* and all other Sparganothini on the other hand carries much more weight as in both cases it is associated with conspicuously modified socii with an erect caudal lobe. The most parsimonious hypothesis is to ascribe both apomorphies to a common ancestor of both groups. The consistent presence of a well-developed pulvinus in the Sparganothini and its absence in all Atteriini (except perhaps in «*Ctenopseustis*» *lurida*, where a bristled, ridge-like structure is present in the usual position of the pulvinus) is a further argument against merging the two groups despite their superficial resemblance due to symplesiomorphies.

Transtilla: PIERCE (1914) mentions that the transtilla becomes a highly complex part in the Tortricidae in his original definition of this structure, and OBRATSOV (1954) employs it under the term *fultura superior* in an attempt at subdividing his Archipsini. In his concept, briefly summarized, a band-like transtilla is considered to be the primary condition. It gradually becomes medially separated and reduced, and is in *Clepsis*, *Adoxophyes* etc. functionally replaced by the two so-called *processus basales* of the valvae, allegedly protuberances of the dorso-caudal corners of the valva which become fused medially and are thus not homologous with the transtilla. *Ptycholoma* is said to have retained traces of the original transtil-

la beside the processus basales. The fact that the original transtilla in *Archips* as well as the supposedly newly developed basal processes in *Adoxophyes* are attached in a similar manner to exactly the same muscle (KUZNETSOV & STEKOLNIKOV, 1973 & 1977) led very early in this study to doubts about the accuracy of OBRAZTSOV'S concept. It is hardly conceivable that a muscle attachment could move from one sclerite to another, and it certainly could never pass through the diaphragm to reach a processus caudally of this membrane.

In the Tortricidae not only the shape of the transtilla itself but the entire complex of the many connections originating in the dorso-caudal angle of the valva provide very valuable information for a taxonomic assessment. This area serves as attachment point for the pedunculi, the tergal extensor muscle, the vinculum and the transtilla. Depending on the development of each of these structures the entire complex, and particularly the transtilla, may become modified. Especially in the Tortricinae a thorough understanding of its morphology may be a prerequisite for a phylogenetic classification. No attempt has been made here to homologize these parts in the three subfamilies, careful studies especially in the Microcorsini would be required first, but the suggested homology of the processus basalis (costal hook) in the Olethreutinae with the lateral knob of the transtilla in higher Archipini (OBRAZTSOV, 1958) is an incorrect simplification. According to KUZNETSOV & STEKOLNIKOV (1973, 1977) the basal process in the Olethreutinae serves as attachment for two muscles, the tergal extensor of the valva and its tergal flexor. In the Tortricinae, the former muscle, if present, is connected by a small process to the valva itself, and the latter to the transtilla. This seems to imply that the basal process in the Olethreutinae comprises both the transtilla and the adjoining part of the valva carrying the muscle attachment.

A transtilla is usually present in Chlidanotinae and Tortricinae, while in the Olethreutinae it has become reduced and probably incorporated in the processus basalis, as briefly outlined above. In its original condition the transtilla was presumably a simple, lightly sclerotized, smooth or finely spined band-like structure as still found in many generalized taxa (*Ceracini*, *Arotrophora*, *Phricanthes*, «*Batodes*» *jactatana*, «*Teras*» *incessana*, «*Capua*» *leucostacta*, *Epalxiphora*, *Heterochorista* (Fig. 107). The transtilla of *Lambertiodes* is only slightly more derived. In most other Sparganothini (Fig. 106) the teeth are confined to the raised median portion of the transtilla, but still reveal the relatively plesiomorphic nature of this organ (see diagram Fig. 108).

Within the Archipini only those characterized by a combination of a simple, unmodified valva with several further plesiomorphic traits seem to possess an uninterrupted, dorsally dentate, band-like transtilla (*Cryptoptila* (Fig. 105), *Heterochorista*, *Isochorista*, «*Tortrix*» *incompta*, *Williella*). From the initial band-like condition at least two developmental series led to the formation of a bipartite, toothed transtilla, a process tentatively sketched in diagram Fig. 108. In the first modification series (*Ctenospseustis*, *Planotortrix*) the teeth are retained on the transtilla but its median portion becomes constricted till the transtilla consists of two spined, loosely connected halves. The second series, represented by Malagasy relatives of *Archips*, seems to initiate from a smooth, band-like transtilla whose central part becomes twisted. Two lateral horn-like processes (*Homonoides*) secondarily develop into toothed (*Goniotorna*) to hand-like structures fused with the pulvini, while the median connection weakens increasingly. The *Clepsis*-type transtilla could be a further derivation of either of the two transformation series or represent a third development.

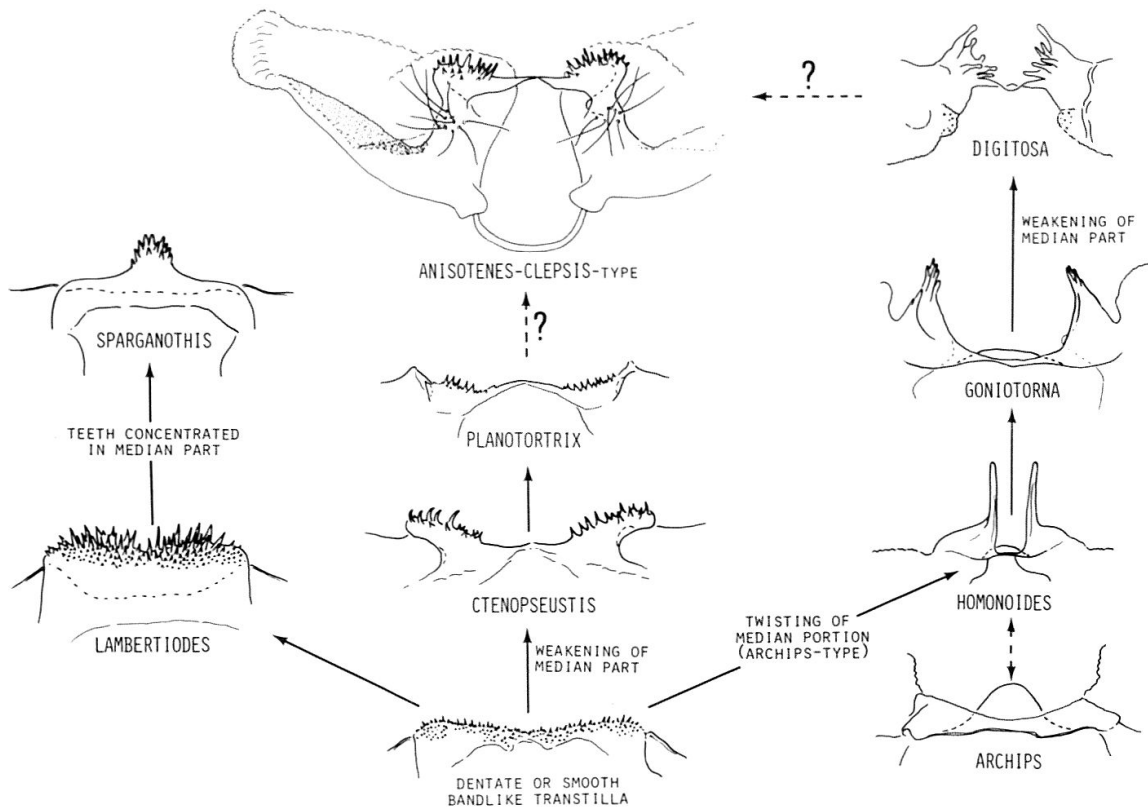
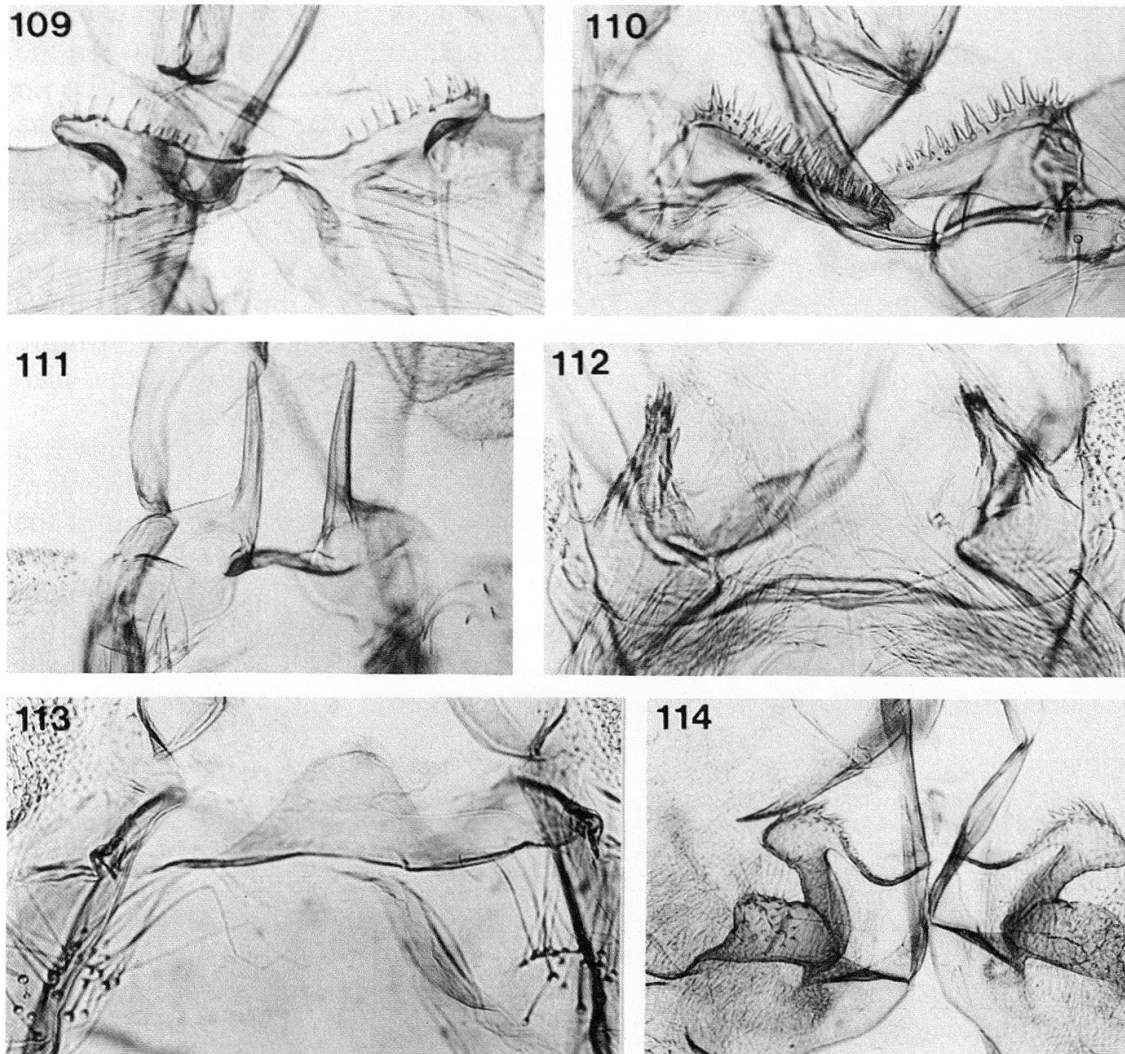


Fig. 108: Diagram of evolutionary trends in the development of archipine and sparganothine transtilla (transtilla of *Digitosa* redrawn from DIAKONOFF, 1960b).

The conclusion that the divided *Ctenopseustis* transtilla (Fig. 109) with its large but rather delicate teeth and its weak association with the pulvinus can be but little derived is strengthened by the overall plesiomorphic nature of *Ctenopseustis* (simple valva, separate R_4 and R_5 , cubital pecten). There can be no doubt about the close relationship of *Ctenopseustis*, «*Epichorista*» *emphanes* and *Planotortrix*, though the latter two taxa are clearly more derived. The Palearctic *Paramesia*, *Lozotaeniodes* and *Lozotaenia* possibly belong in the same grade as these New Zealand genera, representing an archaic feature in the Palearctic Archipini.

Lozotaenia shares with *Planotortrix* and «*Epichorista*» *emphanes* a curiously composite transtilla consisting of an only slightly sclerotized, medially constricted, toothed dorsal part and a strong, simple, ventral rod, either fused (*Planotortrix* (Fig. 104), *Lozotaenia*) or as two separate bands («*Epichorista*» *emphanes*, Fig. 110). OBRAZTSOV (1954) interprets this state in *Lozotaenia* as having originated through fusion of the dorsal «processus basales» with the ventral fultura superior (transtilla). Examination of the muscle attachment will be required to understand this modification. DIAKONOFF (1960b) figures a double transtilla also for *Cuspidata* (*Pilophica*) *leptozona* with its *Archips*-type valva, but dissection of the paratype did not confirm this observation.

The initial representatives in the second transformation series, *Homonoides euryplaca* (Fig. 111) and *Epichoristodes apiletica* (Fig. 84) also show several plesiomorphies mentioned previously (p. 45) confirming their generalized nature. The transtilla of *Homonoides* has, apart from the two lateral processes, the same



Figs. 109–114: Transtilla of: 109, *Ctenopseustis obliquana*; 110, «*Epichorista*» *emphanes*; 111, *Homonoides euryplaca*; 112, *Goniotorina* (*G.*) *erratica*; 113, *Archips piceana*; 114, *Anisotenes* sp.

structure as that of *Archips* (Fig. 113): it is essentially a smooth, subtriangular band with the ventral, medially projecting point bent cephalad (turned upward in slide, Fig. 113), giving the transtilla a characteristically twisted appearance. The two lateral horns in *Homonoides* might at first sight obliterate the basic similarity. A comparison of the transtilla of *Epichoristodes* (Fig. 84), *Goniotorina* (Fig. 112) and *Digitosa* (Fig. 108) strongly suggests homology of the toothed lateral processes in these genera with the smooth horns in *Homonoides*. The overall markedly more plesiomorphic aspect of *Homonoides* supports a concept of a progressive development of the transtilla from the *Homonoides*-type towards conditions with sharply toothed lateral processes and a reduced median connection as in *Goniotorina* and *Digitosa*, also the most logical sequence in this character transformation for purely morphological reasons.

Until intermediate conditions are found it cannot be decided whether the highly developed *Clepsis*-type transtilla (Fig. 114) with its strongly developed lateral knobs fused to the pulvini is the end point of one of the two transformation series outlined above, or if it has arisen independently.

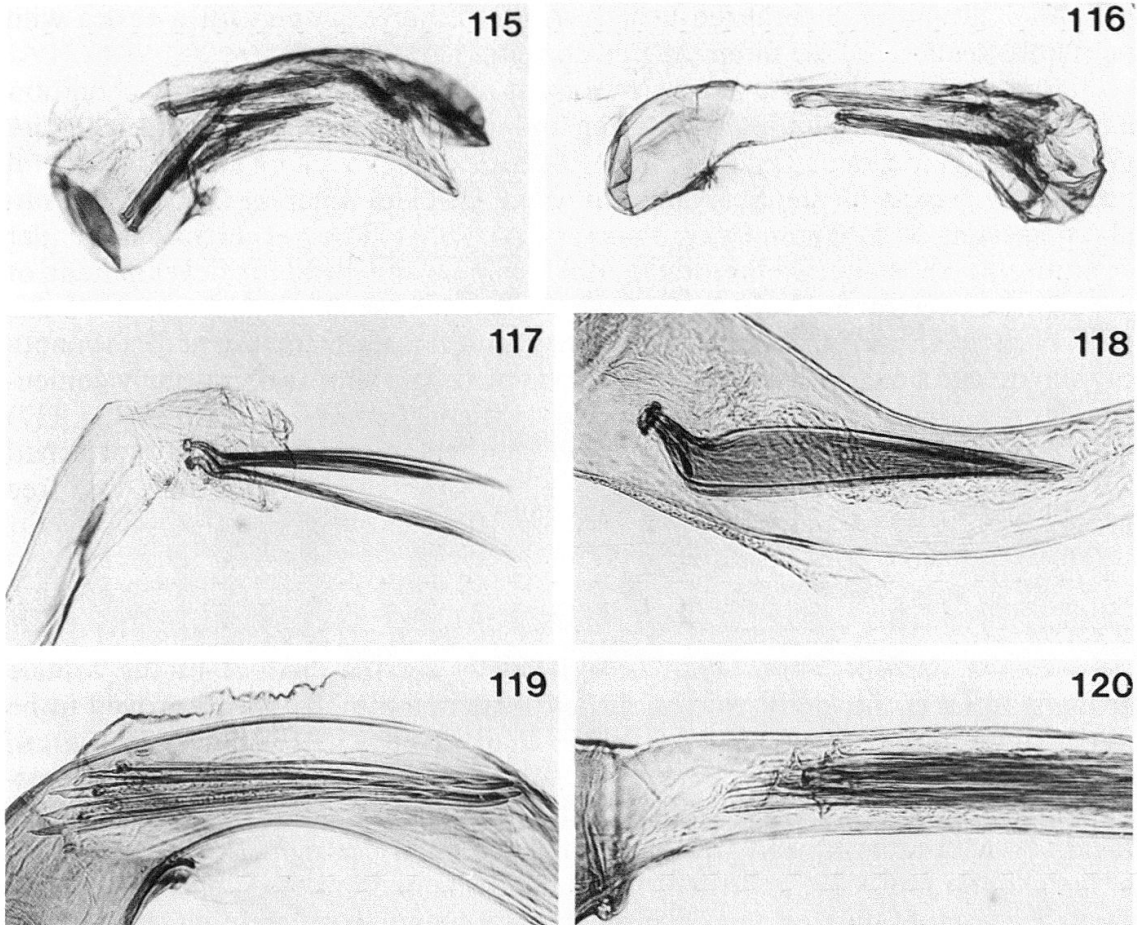
Juxta: The shape of the juxta, and especially its mode of articulation with the caulis/aedeagus-complex, is one of the most fundamental differences between the Olethreutinae and the other two subfamilies of the Tortricidae. There can be no doubt that the loosely hinged connection in the Tortricinae and Chlidanotinae represents the more plesiomorphic condition as pointed out by HEINRICH (1923). He recognizes the apomorphic nature of the firm fusion between juxta and caulis in the Olethreutinae and argues that therefore the Olethreutinae have to be derived from the tortricid stem, and not vice versa as MEYRICK had suggested. No great modifications of the juxta have taken place within the Tortricinae and there are few consistent differences which could be recognized as apomorphies. A more or less shield-shaped, rather delicate plate presumably represents the ground-plan condition, and most variation is found in the shape of its dorsal edge.

Aedeagus: PIERCE & METCALFE (1922) state that a pistol-shaped penis is a very distinctive character in the Tortricidae but do not mention at all its divergent form in the Olethreutinae. However, comparison of the muscle attachments of the tortricid aedeagus in the Tortricinae and Olethreutinae (KUZNETSOV & STEKOLNIKOV, 1973) reveals basic structural differences in this organ in the two subfamilies. As a conclusion from such studies, RAZOWSKI (1976) treats the reduction of the coecum penis as a characteristic development of the Olethreutinae (occasionally also encountered in the Tortricinae) while he concedes only generic or specific importance to modifications of the aedeagus within the Tortricinae. A diagram of the progressive modification of the aedeagus musculature by KUZNETSOV & STEKOLNIKOV (1977) summarizes the loss of the coecum penis in the Olethreutinae and the gradual displacement of the muscle attachment from the coecum to the caulis.

The presumably most generalized Olethreutinae – the Microcorsini – have a strong coecum penis (RAZOWSKI, 1976). Its sporadic absence in the Tortricinae and Chlidanotinae seems to be of random occurrence, not more frequent among the less derived groups. This strongly suggests that a coecum penis pertains to the groundplan of the Tortricidae, has been lost secondarily in the Olethreutinae and has become accentuated in some Tortricinae and Chlidanotinae.

A relatively large, rather undifferentiated and often weakly sclerotized aedeagus could well be the more generalized condition within the Tortricinae. Examples are provided by the Phricanthini, some Papuan Epitymbiini (*Rhombo-ceros*), the South American *Proeulia* (Figs. 115, 116) and especially the Cochylini. A smaller, but similarly unstructured aedeagus is found in many Tortricini, *Williella* (Fig. 76) and «*Teras*» *incessana* (Fig. 78). The number of basic forms of an organ as simple as the aedeagus is necessarily very limited and the same shape must have resulted several times. There are two very characteristic types in the Tortricinae: 1) the above-mentioned pistol-shaped aedeagus with coecum and distal part both more or less straight but at a distinct angle to each other, considered typical for the Archipini but occurring frequently elsewhere as well, and 2) the rather evenly curved aedeagus found in most Sparganothini (Fig. 119).

The vesica of the tortricid aedeagus usually bears fixed and/or deciduous cornuti of various shape and number. If they are deciduous they are a most valuable tool for the correct association of male and female, and in genera with strongly dimorphic sexes and well differentiated cornuti (*Heterochorista*) are often the only means to do so on a morphological basis. But as pointed out for the aedeagus similar forms can easily have arisen independently several times also in the cornuti, and care has to be taken if they are employed for taxonomic purposes.



Figs. 115–116: Aedeagus of: 115, *Proeulia* sp. close to *P. aethalea*; 116, *Proeulia* sp. close to *P. chrysoptervis*.

Figs. 117–120: Cornuti of: 117, *Goniotorna* (*G.*) *erratica*; 118, *Homonoides euryplaca*; 119, *Sparganothis pilleriana*; 120, *Templemania animosana*.

Laterally attached cornuti in the Atteriini as well as the Sparganothini have, for example, served as an important argument to join the two groups into one tribe (DIAKONOFF, 1961) but as this shared character is contradicted by several other, more convincing ones, its weight must be reconsidered.

A trend parallel to the development of a more complex aedeagus from a generalized, simple type is possibly indicated for the number of cornuti in vesica. Several pairs of closely related species in which the overall more plesiomorphic one possesses numerous cornuti which are reduced and often clearly fused in the generally more derived one, suggest that this process might be of general or at least frequent occurrence. The two species of *Williella* illustrate the fusion of a part of countless minute cornuti into a large, possibly not deciduous compound structure in the species with the more derived valva. Similarly a species of *Proeulia* close to *aethalea* with a rather plesiomorphic valva has about 10 slender, smooth cornuti (Fig. 115), while *P. tenontias*, *P. chrysoptervis* and a related unidentified species (Fig. 116), all with protruding sacculus, have 2–4 large, unequally sized, irregular cornuti which must have originated through fusion of several simple ones. *Arotrophora*, «*Teras*» *incessana* (Fig. 78), «*Tortrix incompta* and «*Capua*»

belophora, all rather generalized taxa, provide further examples for a vesica with numerous scattered, little differentiated cornuti.

Simple, smooth, spine-like cornuti must represent the groundplan condition and flattening, acquisition of sculpturing and possibly also of a distinct socket are derivations. Very characteristic cornuti attached to the vesica by a subbasal lateral process are typical for the Sparganothini (Fig. 119) and Atteriini (Fig. 120), strongly suggesting a synapomorphy. OBRAZTSOV (1958) however mentions similar cornuti also for some Olethreutinae, obviously an independent development of the same modification. This permits assumption of a separate appearance of this specialization also for the Atteriini and Sparganothini, as its treatment as a synapomorphy would be conflicting with other evidence. The subbasally strongly geniculate cornuti of *Homonoides euryplaca* (Fig. 118) and *Goniotorna erratica* (Fig. 117) could represent an intermediate condition between apically and laterally attached cornuti, if one imagines the point of this elbow to increasingly protrude as a free process.

Female Genitalia

PIERCE & METCALFE (1922) relied largely on the signum of the female genitalia to form the larger groups of their system, a method which proved to be much more successful in the Tortricinae than in the Olethreutinae. HEINRICH, after having entirely disregarded the female genitalia in his revision of the Eucosmini (1923) criticizes in his treatment of the Laspeyresiini and Olethreutini (1926) PIERCE & METCALFE's nearly exclusive reliance upon the signum for subdivision of the Olethreutinae. He points out that the transitions from the supposedly typical forms are gradual, clearly marked at most at the generic level and thus not suitable for higher classification. He gives however, in this second volume, figures and descriptions also of the female genitalia. DIAKONOFF (1939) provides a detailed description of the female tortricid genitalia and introduces the terms limen, colliculum and cestum. OBRAZTSOV (1954) recognizes four basic types of signa (lamina dentata) in the Archipini, but refrains from any phylogenetic interpretation. COMMON (1958) is the first to consider this aspect, observing that recognizably polarized evolutionary trends like reduction of socii, loss of M-stem and specialization in the valva are correlated in the Tortricinae with a transformation in the form of the signum from a dentate patch to a thorn, spine, hook or dagger. RAZOWSKI (1976) presents a more detailed account of the phylogenetic development of the structures on the wall of the bursa from irregular, indistinct sclerotizations over dispersed minute spines to distinctly edged sclerites. He cautions that similar structures - as tubular signa - may have been realized independently several times. DIAKONOFF (1973) employs the female signa as a leading character for subdivision of the Olethreutini into subtribes, without however considering their phylogeny.

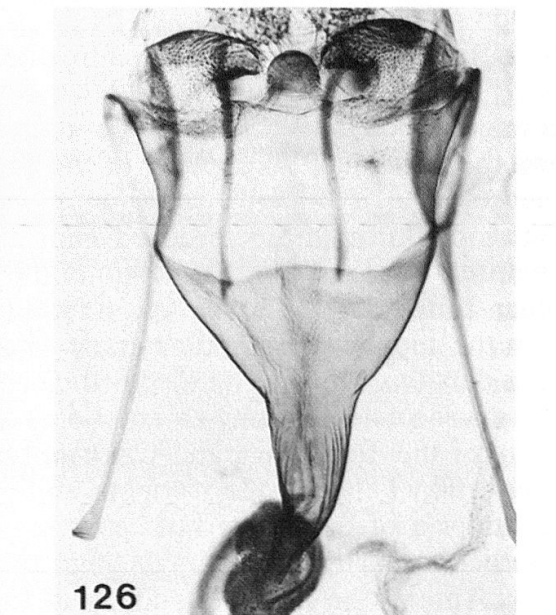
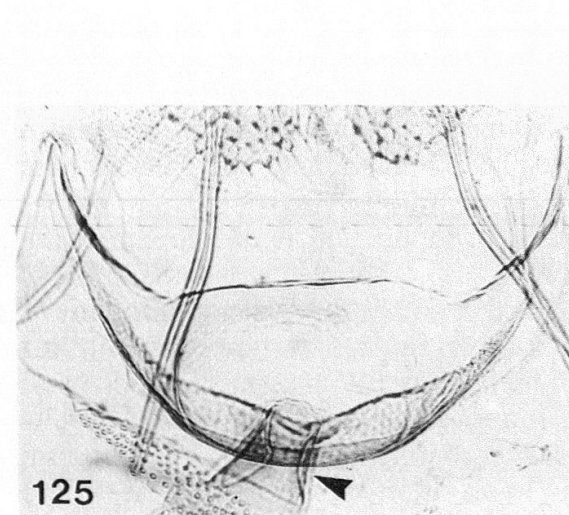
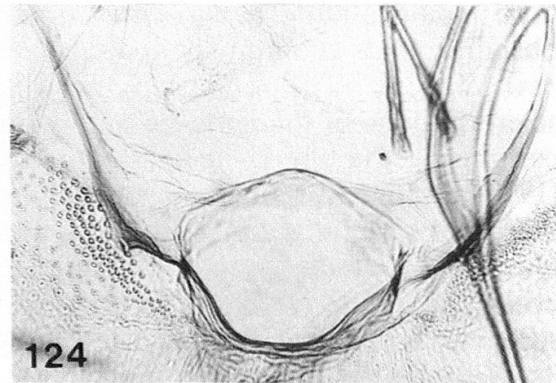
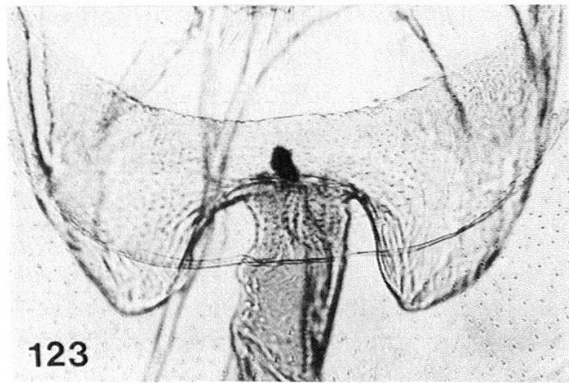
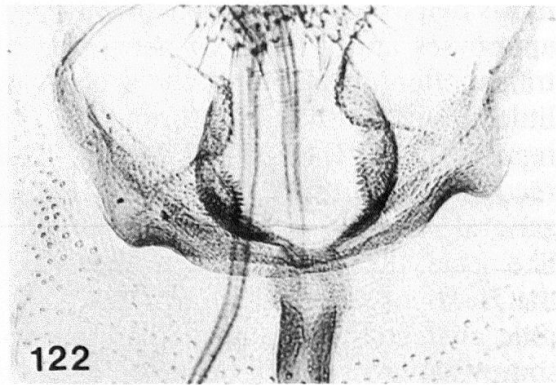
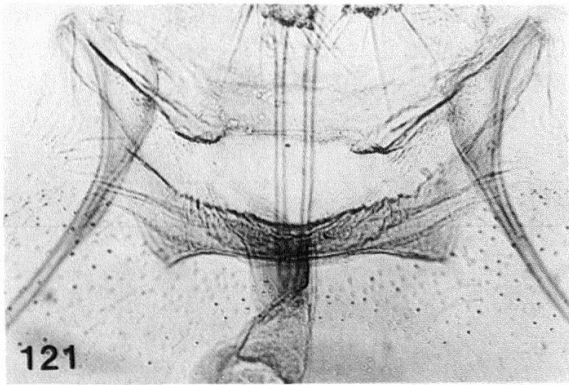
Papillae anales: It is generally acknowledged that the structure of the papillae anales and apophyses depends greatly on the mode of oviposition and is therefore of little taxonomic consequence (RAZOWSKI, 1976). A pair of large, simple, flat and posteriorly usually pointed and widened lobes, soft and strongly setose, is the most frequently encountered condition, found in all tribes and certainly belonging to the groundplan of the family. Modifications have occurred repeatedly either in connection with oviposition in crevices or buds (telescopic ovipositor) or to facilitate covering of exposed eggs with debris or scales (florico-

mous ovipositor). Telescopic ovipositors with the corresponding lengthening of the apophyses and a frequent narrowing of the papillae anales are found in several tribes, often developed at the species level only (*Metaselenia*, *Aethes*), and provide little if any taxonomic information. Floricomous ovipositors also have appeared repeatedly (Cnephasiini, Tortricini, Archipini), but as POWELL (1964) points out, recognizably distinct types have developed in different tribes though of the same general principle with distally enlarged, concave papillae anales bearing nailhead-like setae. If present they can therefore serve as valid apomorphies, especially for the Holarctic Cnephasiini which are otherwise characterized mainly by plesiomorphic character states. A median constriction of the papillae anales resulting in a somewhat cross-like appearance of the two ovipositor lobes is an obvious but rare third modification (*Pternozyga*, *Protopterna*, «*Epichorista*» *perversa*). Its function is obscure and its taxonomic importance cannot be assessed.

Sterigma: The term sterigma will be used here in a very wide sense for sclerotizations of the lamellae antevaginalis and postvaginalis as well as for those comprising the sinus vaginalis (DIAKONOFF, 1954b). In accordance with KLOTS (1970) the term ostium is restricted just to the opening into the ductus bursae. Sterigmal structures are so varied in the Tortricidae that it is at present impossible to reliably separate homologies from parallelisms and to reconstruct the pattern of evolution in different lineages. But the complexity and diversity of a more derived sterigma can possibly provide valuable clues for phylogenetic reconstructions once its development is understood. A few possible evolutionary trends suggested by the present study are presented below, mainly as hypotheses for further considerations, to be falsified or confirmed by future observations.

With the exception of the Microcorsini there is an essential difference in the connection of the sterigma and apophyses anteriores between the Olethreutinae and the remaining Tortricidae. In the Tortricinae, Chlidanotinae and Microcorsini the sterigma is laterally continuous with the ventral branch of the apophyses anteriores through a sclerotized band. No such connection is developed in the Olethreutinae, and the bifurcation of the apophyses anteriores characteristic for all other Tortricidae is absent. KUZNETSOV (1970) recognizes that the sterigma linked with the apophyses anteriores in the Microcorsini is unusual for the subfamily but considers this similarity to the Tortricinae to be convergent. This seems unlikely as the microcorsine apophyses anteriores are branched in exactly the same way as those of the Tortricinae and Chlidanotinae. RAZOWSKI'S (1976) conclusion that a connection between the sterigma and apophyses anteriores must belong to the groundplan of the family but has in the Olethreutinae been retained only in the Microcorsini is the more convincing explanation.

Among the numerous kinds of tortricine sterigmata three basic types and variations on their principle are especially frequent and conspicuous: 1) The ostium is surrounded by an aciculate membrane and becomes invaginated at the bottom of a pocket or pouch (*Heterochorista*, Fig. 121) which evolves into an increasingly complex structure. The aciculate dorsal wall of this pocket can develop into a second shallow, blind pouch as in *Sparganothis* (Fig. 122) or its antero-lateral corners may extend cephalad beyond the ostium to form projecting lobes (many Tortricini, *Amorbia* (Fig. 123), *Templemania*). 2) The ostium is situated in a smooth but often strongly sclerotized concave transverse band (*Adoxophyes*) or elliptic to crescent-shaped, trough-like sclerite (*Ctenopseustis obliquana* (Fig. 125), «*Batodes*» *jactatana*, *Planotortrix*, *Lozotaenia forsterana*) firmly contiguous with the apophyses anteriores. 3) The ductus bursae opens into the bottom



Figs. 121–126: Sterigma of: 121, *Heterochorista* sp.; 122, *Sparganothis pilleriana*; 123, *Amorbia cuneana*; 124, *Paradichelia* sp.; 125, *Ctenopseustis obliquana* (▲ split colluculum); 126, *Archips piceana*.

of a strongly sclerotized, funnel-shaped structure (*Pandemis*, *Archips*, Fig. 126). Though these three basic types certainly have arisen independently several times, and by no means comprise all modifications of the membrane surrounding the ostium, they can with appropriate caution be included in considerations of kinship. Often one has to do so when females only can be considered, especially if their signum is lacking. Genera revised with stringent standards show sterigmata conforming to a basic pattern in an often remarkable way.

Within the frame of the Tortricinae the simple, aciculate, membranous pocket of *Heterochorista* and the sclerotized, smooth, transverse, trough-like sclerite of *Ctenopseustis obliquana* presumably represent plesiomorphic states. Though it is not yet possible to infer the groundplan condition for the family a few tentative conclusions may nevertheless be risked. The conspicuously similar sterigma of the Atteriini and Sparganothini is not a strong argument for closer relationship between the two tribes as it probably represents a symplesiomorphy. The plesiomorphic band-like sterigma of *Lozotaenia forsterana*, characteristic of the most generalized New Zealand Archipini, is one more feature pointing to the rather archaic nature of this taxon. The remarkably simple sterigma of *Isotenes*, *Anisotenes*, *Paradichelia* (Fig. 124) and allied genera, just two narrow bands forming the lamellae antevaginalis and postvaginalis, stands in marked contrast to the funnel-shaped structure in *Archips*, *Homona* and their Malagasy relatives. If the *Clepsis/Isotenes* group with its strongly folded valva is derived from ancestors of the *Archips* group, this must have happened before the sinus vaginalis developed into a sclerotized funnel.

Bursa copulatrix: The division of the bursa copulatrix into ductus bursae and corpus bursae is somewhat arbitrary and the two often intergrade imperceptibly. Homologization of sclerites in these organs across different tribes can thus be difficult. In the following account, one or two small sclerites just below the ostium are regarded as colliculum, an elongate sclerotized band or scobination in the ductus as cestum, and sclerites in the bursa – with few exceptions even if they are located at the entrance of the ductus – as signa.

A colliculum, usually consisting of a bent, small, dorsal plate (split colliculum, Fig. 125) or of two separate lateral sclerites, and only rarely of a complete ring, is present in several tribes of all three tortricid subfamilies, not restricted to the Archipini only. It is impossible to infer the groundplan condition for the Tortricinae or even the entire family, but a few generalizations as far as they are possible might help to elucidate the position of single females. While even very generalized Archipini possess a well-developed colliculum either ventrally split (*Ctenopseustis obliquana* (Fig. 125), *Epalxiphora*, *Thrincochora*, *Cryptoptila*) or consisting of two lateral sclerites (*Isochorista*, *Planotortrix*, *Lozotaenia*), this structure, if at all present in the Palaearctic Cnephasiini (OBRASZTSOV, 1955) and the Epitymbiini, consists usually of a complete, undifferentiated ring. A ventrally split colliculum seems to be the rule among the higher Archipini. Sparganothini and Atteriini, as far as studied, both possess a colliculum of two lateral plates. The strong ring or collar in many Cochylini referred to as antrum (RAZOWSKI, 1970) is a sclerotization of essentially the same region of the bursa just below the ostium and thus most likely homologous to the colliculum.

Sclerotizations of the ductus bursae sporadically occur in all three subfamilies, but in those groups with contiguous ductus and corpus bursae (Cochylini, Epitymbiini, *Proeulia*) cannot be differentiated from structures of the corpus bursae itself. Among the Tortricinae a typical band-like cestum is usually considered a characteristic feature of the Archipini, but in a few instances it is found elsewhere, as in some generalized Schoenotenini (*Tracholena*, *Protarchella*) and in the Sparganothini as a small sclerite close to the opening of the ductus into the corpus bursae in *Coelostathma*. Rather generalized Archipini (*Ctenopseustis*, *Epalxiphora*, *Planotortrix*, *Lozotaenia*) as well as derived groups like *Archips* and related genera or *Clepsis*, *Zacorisca* and *Isotenes* all may possess a cestum, suggesting that the ability to develop such a structure is present throughout this tribe.

It is in practice often of great value to help differentiate female archipine genera from those of other Tortricinae.

In the Tortricinae a simple sac- or pear-shaped bursa copulatrix not separated into ductus and corpus bursae can be considered plesiomorphic for two different reasons. Such a bursa is 1) usually present either in overall rather plesiomorphic taxa like *Eulia*, *Proeulia* and the Cochylini or in the more generalized members of a tribe (*Protarchella*, *Proselena* in the Schoenotenini; *Arotrophora* in the Cnephasiini) and 2) very frequently covered with undifferentiated scobination or spines (*Eulia*, *Proeulia*, *Paraptila*, Cochylini, *Rhomboceros*, *Protarchella*) in the place of well-defined signa.

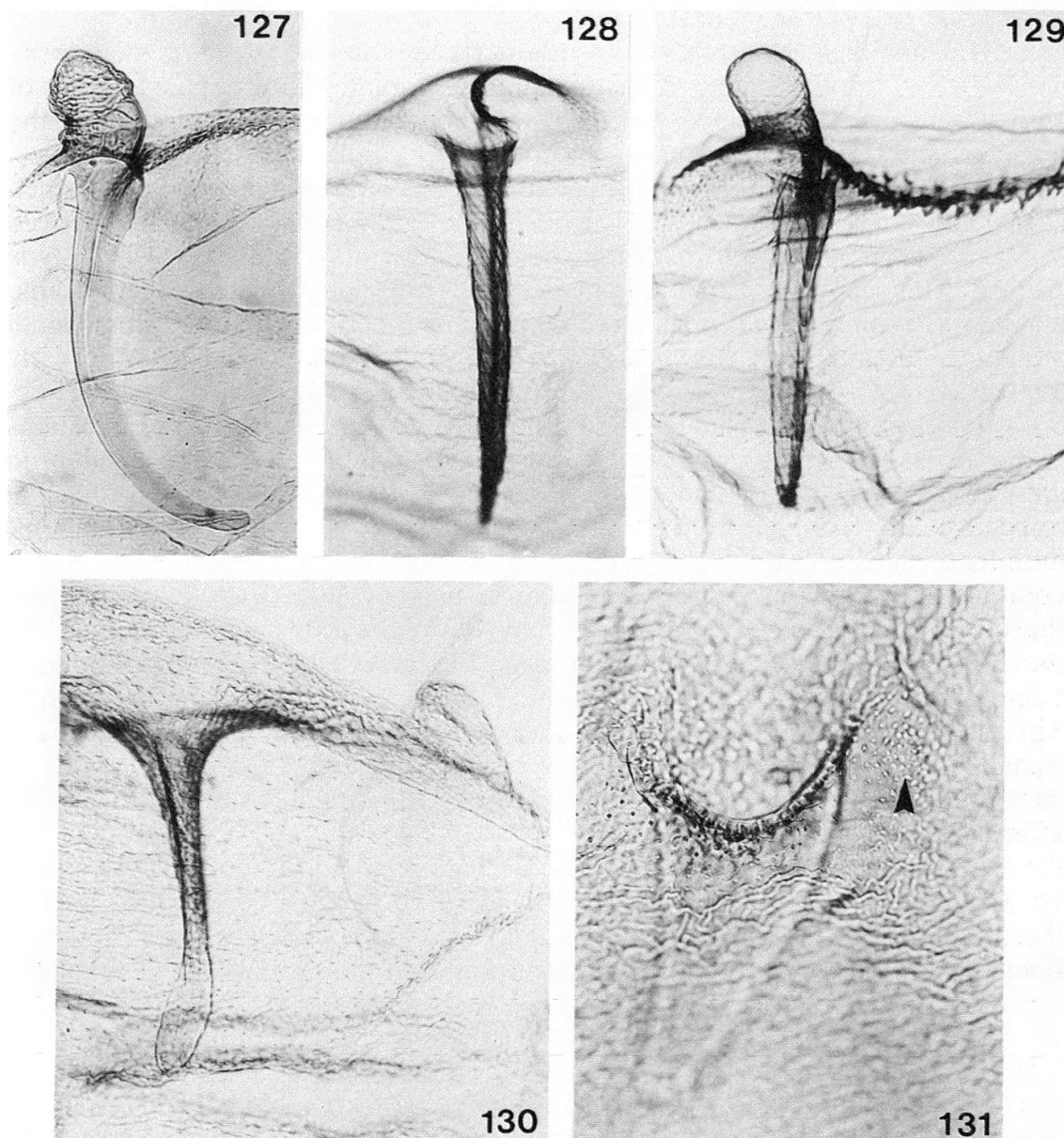
The above-mentioned observations support RAZOWSKI'S (1976) assumption that irregular, indistinct sclerotization and spinules of the bursa wall are the most plesiomorphic condition in the transformation series leading to definite signa. This state has not been preserved in the Olethreutinae, but many signa in the Olethreutini still appear to consist basically of an enlarged scobination (*Olethreutes*, *Asaphistis*, *Statherotis*). The dentate band- or plate-shaped signum typical of the Cnephasiini and Tortricini is but little derived, an enhanced expression of the basic structure but restricted to a limited area only. Further development to fold-, horn- or dagger-shaped signa protruding into the corpus bursae always seem to involve invagination and sclerotization of the bursa wall itself, with the possible exception of the Cochylini and *Proeulia*, where even large spines seem to be structures entirely inside the bursa, not originating from folds in the membrane. Tubular, funnel-shaped signa certainly have appeared independently several times, not only separately in the Olethreutinae and Tortricinae but also repeatedly within the latter subfamily where, within the Schoenotenini, the entire development from a bursa covered with scattered spines (*Protarchella*) to a large, invaginated, blunt horn (*Epitrichosma*) can be observed.

Two signa in the Olethreutinae and one in the Tortricinae and Chlidanotinae are the usual numbers, and apparently also the groundplan condition for the respective subfamilies, but numerous modifications occur. Doubling of the number of signa is presumably a genetically simple process. *Isochorista* is a case in point, comprising species with one minute thorn-like signum only (*I. parmiferana*) together with several others possessing four such thorns (*I. panaeolana*, *I. encotodes*). *I. ranulana* generally has one signum only, but some specimens showing traces of a second one suggest an originally intermediate position for this species. The polyorthine *Lopharcha* similarly contains species with both single or paired signa. The cnephasiine *Paraphyas*, the schoenotenine *Syncratus* and *Homalernis*, and *Drachmobola* and some *Aeolostoma* of unclear epitymbiine or archipine affinity are all examples of Tortricinae with two signa. Reduction or loss of one of the normally paired olethreutine signa has possibly occurred even more frequently: *Dichrorampha* (Grapholitini), *Blastesthia* (Eucosmini) and *Endothenia* (Olethreutini) are just a few examples. Complete lack of any signum is of such frequent occurrence in all groups that it can never serve as an argument for kinship.

A signum positioned at the origin of the ductus, directly at its entrance into the corpus bursae, as in the Ceracini, suggests that it may represent the remnant of a former cestum instead, like the irregular sclerites in *Metaselena* and *Anathamna*. This suspicion is especially pronounced in «*Capua*» *leucostacta* which additionally possesses two small, distinct areas of scobination which could well represent the signa. However, a comparison between *Thincophora signigerana* and species of *Acropolitis* demonstrates two things: 1) The proper signum may indeed be located

exactly at the entrance of the ductus into the corpus bursae, as in *Acropolitis*, and 2) its position (and shape) can, even in two closely related genera, vary to a considerable degree.

A dagger-shaped signum with a capitulum (Figs. 127–129) has long been recognized as a diagnostic feature of the Archipini. Unless the capitulum is shown to be of adaptive value it seems reasonable to assume that such a complex structure has arisen only once and represents a reliable apomorphy indicating monophyly. Its presence in such generalized taxa as *Ctenopseustis* and *Epalxiphora* in the typical and most complete condition with an associated toothed band (Fig. 129) strongly suggests that it forms part of the groundplan of the tribe. Such signa or derivations of it are, however, encountered also in taxa on the borderline to or outside of the Archipini, and demand either reconsideration of the apomor-



Figs. 127–131: Signum of: 127, *Heterochorista* sp.; 128, *Archips piceana*; 129, *Ctenopseustis obliquana*; 130, *Anacrusis* cf. «*Tortrix*» *stapiana*; 131, *Templemania animosana* (▲ vestige of capitulum).

phic nature of this structure or reevaluation of some taxonomic assignments. For all such considerations the frequent secondary loss of the capitulum, even within a genus (*Heterochorista*), has to be borne in mind. Signa with a secondarily reduced capitulum become indistinguishable from the originally horn-shaped, more plesiomorphic condition. One signum complete with capitulum in an otherwise demonstrably monophyletic group is however sufficient to treat this character as an apomorphy for the entire group.

Such typically archipine signa, dagger-shaped and with a capitulum, are present in genera with a simple valva and well-developed costa (*Ctenopseustis*, *Planotortrix*), as well as in both groups with modified valva, *Archips* and its relatives and *Isotenes* and allied genera. One therefore has to assume a common ancestor for these three groups. Evidence of a different nature than only primary or secondary lack of the capitulum will be needed to separate convincingly the remaining genuine Archipini from the Epitymbiini, Cnephasiini and possibly some other taxa of uncertain affinity.

The large Papuan genus *Heterochorista* has an interesting intermediate position between the Archipini and Sparganothini, combining apomorphic features of both tribes: a well-developed, typically archipine signum with capitulum in the female (Fig. 127) and in the male socii with a free callosal lobe, strongly reminiscent of the Sparganothini. If both these characters are indeed apomorphies which arose only once within the Tortricinae then *Heterochorista* is probably derived from ancestors of the recent Sparganothini before they lost their *Archips*-type signum. The second possibility, that a caudally free lobe of the socius became secondarily reduced again in all Archipini, seems much less feasible. The overall plesiomorphic aspect of *Heterochorista* would entirely agree with such an early derivation.

Associated with a blade-shaped signum some Atteriini show modifications of the bursal wall which strongly suggest a capitulum either in statu nascendi or in the process of becoming reduced. A specimen of *Anacrusis* cf. «*Tortrix*» *stapiana* has, at a short distance from the signum, an inconspicuous, entirely membranous, rounded protrusion of similar shape and structure as a capitulum, covered with concentric rings of impressions like hammer-marks (Fig. 130). A scarcely raised round spot of concentrically arranged scobination next to the signum seems to be the equivalent in *Templemania animosana* (Fig. 131). This suggests a common origin also for Atteriini and Archipini, or a branching off of one from the other at some stage of their development. The sexual dimorphism of the forewing shape in *Anacrusis* leading to female forewings modified in exactly the same way as in *Archips* and *Homona* provides a further connection between the two tribes, shared with many Epitymbiini.

Mictocommosis and *Mictopsichia*, according to illustrations (DIAKONOFF, 1977b), possess signa recalling the most generalized Archipini-type with a dentate band, and *Mictopsichia callicharis* apparently also has a well-developed capitulum (CLARKE, 1969). This signum casts further doubt on the justification of the inclusion of these taxa in the Hilarographini.

A second clearly apomorphic and very characteristic signum is found in the Chlidanotinae, most typically developed in the Chlidanotini and most Hilarographini as a large bunch of long, slender, tapering spines, associated with an accessory sac to the bursa opening from the edge of the signum. As no material was available for the present study from these groups the following remarks are based on the literature only. While this signum complete with the accessory sac seems to

be the rule in the Chlidanotini, it is present in only part of the Hilarographini and Polyorthini. The Hilarographini fall into two groups: those with a typically chlidanotine signum (if present) and an accessory sac branching off from the corpus bursa (*Hilarographa*, *Thaumato-grapha*), and those with an archipine signum without an accessory sac from the corpus bursae (*Mictocommosis*, *Mictopsichia*). Much more variation is found in the structure of the bursa and signum in the Polyorthini, and the chlidanotine type is nowhere expressed so perfectly as in the other two tribes. In the majority of genera the bursa has no diverticle and the signum is very variably shaped from a single, small plate (*Polyortha*, *Lophoprora*) over a large, deeply W-curved sclerite (*Polylopha*) to paired, large blunt horns (*Lyphothora*). Only the Papuan *Scythalognatha* and some of the Oriental *Lopharcha* possess a diverticle of the bursa and a single or paired signum of chlidanotine affinity, one or two variably shaped bunches of long spines. DIAKONOFF'S (1974) suggestion that a scobinate signum could be the precursor of the spined one eventually points to the very plesiomorphic bursa copulatrix of *Olindia* and *Pseudatteria* with their little differentiated, small and often scobinate single or paired signum as the most ancestral state. These observations seem to imply a gradual development of the chlidanotine signum and the appearance of an accessory sac to the bursa in the Oriental/Papuan branch of the Polyorthini.

SUMMARY

1. The taxonomically significant structures of adult Tortricinae, including male and female genitalia, are assessed from a phylogenetic point of view on a world-wide base. For each character a short literature review is given, followed by a discussion based on material examined for the present study. A list of all taxa considered is provided.
2. The following plesiomorphic character states are inferred for a surmised generalized member of the Tortricinae: *Head*: Ocelli present; antennae with two rings of scales per segment; labial palps 3-segmented, sinuate, elongate; maxillary palps 4-segmented, scaled. *Forewing*: Costal fold probably present; all veins separate beyond cross-veins R-M, inter-M and M-CuA₁; CuP present; M-stem developed, its posterior branch intercepting crossvein inter-M between M₂ and M₃; stem of R₄₊₅ (chorda) present. *Hindwing*: Cubital pecten present; all veins separate; Sc and R-stem separate to base, connected by R₁; Rs and M₁ probably widely separated; humeral vein possibly present. *Male genitalia*: Uncus long, thin and naked; socii large, pendant, covered with scales instead of bristles; gnathos with ventrally joined arms; valva simple, weakly sclerotized, without differentiated costa, sacculus or pulvinus; transtilla band-like, smooth or dentate; saccus probably developed; juxta and aedeagus loosely hinged; aedeagus undifferentiated, sac-like, with numerous cornuti. *Female genitalia*: Sterigma little developed, simple, but connected to apophyses anteriores; ductus bursae not distinctly set off from corpus bursae; undifferentiated scobinations or spines on the bursa wall instead of well-defined signa.
3. Shared retention of the tergal extensor muscle of the valva in *Eulia*, the Cochylini, Sparganothini and some generalized Archipini is merely a symplesiomorphy and thus no valid argument for kinship.
4. The following are the systematically most relevant apomorphies:
 - 4.1. Loss of one of the initial two rings of scales per segment on the male antennae has occurred in Olethreutinae and some Sparganothini, but possibly in different ways in the two groups.
 - 4.2. Several reduction series are apparent in the maxillary palps within the current Archipini, indicating parallel development within separate lineages.
 - 4.3. In the forewing of the Schoenotenini and Sparganothini the course of the M-stem has become modified, intercepting cross-vein inter-M between M₁ and M₂ or opposite M₂. This apomorphic condition in the two tribes is, however, only superficially similar, as the distal portion of the M-stem in the Schoenotenini appears not to be homologous to the corresponding part in the Sparganothini.
 - 4.4. Absence of CuP in the forewing is noted for some Phricanthini, Archipini, Tortricini, Schoenotenini as well as for the Chlidanotini and Cochylini.
 - 4.5. The tendency for stalking of Sc and R-stem in the hindwing, apparent in several groups, is strongly expressed in the Sparganothini. This may be of use to differentiate between Ateriini and Sparganothini.
 - 4.6. The «uncus brush» has demonstrably been developed several times, either as an underlying apomorphy or due to convergence.

- 4.7. The apomorphic features of sparganothine socii are not their scales, as has been assumed, but their protruding caudal lobes and the characteristic fusion between socii and free gnathos arms.
- 4.8. The development of modified valvae, either the wrinkled *Archips*-type or the plicate *Clepsis*-type, indicates one or two major divisions within the Archipini. It cannot yet be decided whether both modifications belong to the same transformation series or represent two separate lineages.
- 4.9. The invaginated valva with the corresponding abdominal hair-pencils found in Chlidanotini, Hilarographini and Polyorthini probably represents an apomorphy for the entire subfamily, though it has been secondarily lost again several times.
- 4.10. The tortricine pulvinus is initially derived from bristles of the inner surface of the valva. It seems to be of use in separating Sparganothini from Atteriini and possible other generalized Tortricinae.
- 4.11. At least two transformation series, both leading to a bipartite archipine transtilla, are recognized, parallel to the development of a modified valva.
- 4.12. Absence of the connection between sterigma and apophyses anteriores is diagnostic for female Olethreutinae (except Microcorsini).
- 4.13. A dagger-shaped signum with a capitulum must have arisen early in the development of the Archipini (or even prior to this) as it is present in many of the most generalized representatives of this tribe as well as in *Heterochorista*, which also possesses sparganothine apomorphies. Traces of a capitulum are also found in some Atteriini.

ZUSAMMENFASSUNG

1. Die taxonomisch bedeutungsvollen Strukturen von adulten Tortricinae, einschliesslich der männlichen und weiblichen Genitalien, werden aus phylogenetischer Sicht auf weltweiter Basis beurteilt. Auf eine kurze Literaturübersicht folgt jeweils eine Diskussion, die auf eigens für diese Studie zusammengetragenes Material gründet. Alle berücksichtigten Taxa sind in einer Liste zusammengestellt.
2. Die folgenden plesiomorphen Merkmale werden einem rekonstruierten, ursprünglichen Vertreter der Tortricinae zugeschrieben: *Kopf*: Ozellen vorhanden; Antennen mit zwei Schuppenringen pro Segment; Labialpalpen dreigliedrig, s-förmig, lang; Maxillarpalpen viergliedrig, beschuppt. *Vorderflügel*: Kostalumschlag vorhanden; alle Adern getrennt; CuP vorhanden; M-Stamm entwickelt, der hintere Ast zwischen M_2 und M_3 in Querader mündend; Anhangszelle vorhanden. *Hinterflügel*: Kubitalpekten vorhanden; alle Adern getrennt; Sc und R-Stamm bis zur Basis ausgebildet und getrennt, nur durch R_1 verbunden; R_s und M_1 wahrscheinlich weit getrennt; Humeralader möglicherweise vorhanden. *Männliche Genitalien*: Uncus lang, dünn und nackt; Socii grosse, hängende, mit Schuppen besetzte Lappen; Arme des Gnathos ventral zu gemeinsamer Spitze verschmolzen; Valve einfach, schwach sklerotisiert, ohne differenzierte Costa, Sacculus oder Pulvinus; Transtilla bandförmig, glatt oder gezähnt; Saccus wahrscheinlich vorhanden; Juxta und Aedeagus nur gelenkartig lose miteinander verbunden; Aedeagus undifferenziert, sackförmig, mit zahlreichen Cornuti. *Weibliche Genitalien*: Sterigma nur schwach ausgebildet, einfach, aber mit Apophyses anteriores verbunden; Ductus und Corpus Bursae nicht deutlich voneinander abgesetzt; Bursa gleichmässig bestachelt anstelle von klar umschriebenen Signa.
3. Das Vorhandensein des tergalen Extensormuskels der Valve bei *Eulia*, den Cochylini, Sparganothini und einigen ursprünglichen Archipini ist nur eine Symplesiomorphie und daher kein gültiges Argument für eine nähere Verwandtschaft der vier Gruppen.
4. Die folgenden Apomorphien erscheinen systematisch besonders bedeutungsvoll:
- 4.1. In der männlichen Antenne der Olethreutinae und einiger Sparganothini ist von den ursprünglich zwei Schuppenringen pro Segment nur noch einer vorhanden. Diese Reduktion ist aber möglicherweise in den beiden Gruppen auf verschiedene Weise vor sich gegangen.
- 4.2. Innerhalb der Archipini können mehrere Reihen paralleler Reduktion der Maxillarpalpen beobachtet werden.
- 4.3. Der M-Stamm ist bei den Schoenotenini und Sparganothini costad verschoben und mündet zwischen M_1 und M_2 oder gegenüber von M_2 in die Querader. Diese Apomorphie ist aber nur oberflächlich betrachtet gleicher Natur in den beiden Triben, der distale Teil des M-Stammes der Schoenotenini scheint dem entsprechenden Abschnitt in den Sparganothini nicht homolog zu sein.
- 4.4. CuP im Vorderflügel fehlt nicht nur bei den Cochylini und Chlidanotini, sondern auch bei einzelnen Gattungen der Phricanthini, Archipini, Tortricini und Schoenotenini.
- 4.5. Sc und der R-Stamm im Hinterflügel zeigen bei verschiedenen Gruppen eine Tendenz zu Stielung. Dies ist besonders ausgeprägt bei den Sparganothini und möglicherweise nützlich zur Unterscheidung von Sparganothini und Atteriini.
- 4.6. Eine «Uncusbürste» ist offensichtlich mehrmals parallel entstanden, entweder auf Grund einer nur teilweise ausgeprägten, einmaligen Apomorphie oder durch Konvergenz.

- 4.7. Die apomorphen Merkmale der Sparganothini-Socii sind nicht ihre Schuppen, wie bisher angenommen, sondern ihre abstehenden, caudalen Fortsätze und die charakteristische Verschmelzung von Socii und getrennten Gnathosarmen.
- 4.8. Die Entstehung einer modifizierten Valve, des gerunzelten *Archips*-Typus ebenso wie des gefalteten *Clepsis*-Typus, bedeutet eine entscheidende Verzweigungsstelle innerhalb der Archipini. Vorläufig kann nicht entschieden werden, ob beide Modifikationen derselben Evolutionsreihe zuzuschreiben sind oder ob sie zwei getrennte Entwicklungslinien verkörpern.
- 4.9. Die charakteristisch modifizierte Valve mit der tief eingeschnittenen Falte und zugehörigen abdominalen Haarpinseln, wie sie bei den Chlidanotini, Hilarographini und Polyorthini gefunden werden kann, scheint eine Apomorphie für die gesamte Unterfamilie der Chlidanotinae darzustellen, obwohl sie sekundär mehrmals wieder zurückgebildet worden ist.
- 4.10. Der Pulvinus gewisser Tortricinae hat sich offensichtlich aus der Behaarung der inneren Valvenfläche entwickelt. Sein Vorhandensein scheint zur Abtrennung der Sparganothini von den Atteriini und möglichen andern ursprünglichen Tortricinae geeignet zu sein.
- 4.11. Es können mindestens zwei Evolutionsreihen unterschieden werden, die beide zu einer in zwei Teile gegliederte Transtilla führen. Sie decken sich mit parallelen Entwicklungslinien in der Valvenausbildung.
- 4.12. Das Fehlen einer Verbindung von Sterigma und Apophyses anteriores ist diagnostisch für Weibchen der Olethreutinae (mit Ausnahme der Microcorsini).
- 4.13. Ein dolchförmiges Signum mit Capitulum muss sehr früh in der Entwicklung der Archipini entstanden sein, oder sogar vorher, da es bei den meisten ursprünglichen Vertretern der Tribus bereits ausgebildet ist, ebenso bei *Heterochorista*, einer Gattung, die Merkmale der Sparganothini und der Archipini vereint. Andeutungen eines Capitulum sind auch bei gewissen Atteriini vorhanden.

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