

A C T A Z O O L O G I C A  
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**Phylogeny and System of *Tortricidae* (*Lepidoptera*)**

[Pp. 73—120, 1 text-fig.]

**Filogeneza i system *Tortricidae* (*Lepidoptera*)**

**Филогенез и систематика *Tortricidae* (*Lepidoptera*)**

**Abstract.** The proposed system of the family level groups of *Tortricidae* is based chiefly on the structure of male genitalia and their musculature. The phylogeny of several groups can be explained by a study of the function of male genitalia. Examination of the remaining characters utilised to date showed their limited importance. Several taxa are synonymised or their status is lowered as no constant differences were found among them or the distinguishing characters proved insufficient. In the historical review only the most important data are included because they are to be found in the synonymies of the subfamilies, tribes and subtribes.

**HISTORICAL REVIEW**

GUENÉE (1845) was one of the first to study the family group system and he divided Tortricids into ten tribes. Then several systems were proposed by STANTON (1854, 1859), MEYRICK (1882, 1895 and further works), WALSINGHAM (1897), KENNEL (1908), PIERCE and METCALFE (1922), HEINRICH (1923), DIAKONOFF (1939 and further works), OBRAZTSOV (1949, 1954), COMMON (1958, 1963, 1965), POWELL (1964) and many other authors. All names proposed by them are listed under the characteristics of the taxa on p. 87.

Comparatively few publications are devoted to the phylogeny of the Tortricids. MEYRICK (1895) considered that the *Olethreutinae* were derived from the *Tortricinae*, but subsequently (MEYRICK, 1913) changed his opinion and considered that the *Tortricinae* are a development of the *Olethreutinae* and are derived

from the *Argyroplote*-group, the *Laspeyresia*-group being the most primitive. In 1928 MEYRICK maintained his division of the *Tortricina*, treating the above-mentioned groups as families and placing the *Cochylids* before them.

HEINRICH (1923), basing his work on the structure of the genitalia, realised that Tortricids are in some respects more generalised than Olethreutids and that they could not be evolved from any present group of them. He found that there is a complete break between the two groups. In his concept the Olethreutids are more advanced, the *Laspeyresiini* being the most specialised. DIAKONOFF (1952) followed HEINRICH in the division into subfamilies but suggested that the *Enarmoniini* (= *Laspeyresiini*) are the most primitive tribe of Olethreutids. POWELL (1964) discussed mainly *Tortricinae* in which *Tortricini* are treated as the most primitive tribe and are followed by *Cnephasiini*, *Archipini* and „*Sparganothinae*”, with the suggestion that the latter group should be treated as a tribe only. In all these works the *Cochylids* are excluded and treated as a separate family.

KUZNETSOV and STEKOLNIKOV (1973) partially returned to the old systems, their study on the phylogeny of the *Tortricidae* being based on the functional morphology of the genital armatures, mainly on the musculature of the male genitalia. They divided the family into two subfamilies, viz., *Tortricinae* and *Olethreutinae*, treating the *Cochylidae* as a supertribe of the former. In their system the *Tortricinae* are divided into three supertribes, viz., the *Sparganothidii* with a single tribe, *Sparganothini*, the *Cochylidii* with the tribe *Cochylini* and the *Tortricidii* with the tribes *Cnephasiini*, *Archipini* and *Tortricini*. The *Olethreutinae* comprise the supertribes *Olethreutidii*, with the tribes *Bactrini*, *Eudemini*, *Olethreutini* and *Lobesiini*, and *Eucosmidii*, with the tribes *Ancyridini*, *Eucosmini* and *Laspeyresiini*. The division into subfamilies is based on the position of muscles  $m_5$ — $m_6$  and the status of muscle  $m_3$  (for the terminology of the muscles, see p. 79), the structure of the internal surface of the valva, and the degree of development of the tergal complex of the genital apparatus, and the valvae. The subfamilies were divided as follows. In the *Tortricinae* the authors have not examined *Sparganothidii* but supposed them to be the most primitive supertribe of the subfamily. In the *Cochylidii* they did not find any characters justifying family status, as the musculature and function of the male genitalia are typical of *Tortricinae*. However, the full number of muscles occur in the *Cochylidii*, showing the more primitive character of that supertribe when compared with the *Tortricidii*. The remaining characters (atrophy of vein *cup* in forewing, lack of gnathos etc.) are considered to be of importance only below subfamily level. The most important character which distinguishes the tribes of the *Tortricidii* is the reduction of one pair of muscles in the male genitalia (either  $m_2$  or  $m_4$ ). The *Cnephasiini* and *Archipini* always lack muscle  $m_2$  while in the *Tortricini* muscle  $m_4$  is atrophied. The authors suppose that the *Cnephasiini* are most primitive of the supertribe because the insertion of muscle  $m_5$  is on the median portion of the basal area of the valva, as in the *Cossidae*. The above divisions are further supported by additional characters, mainly in the larvae, following



the repeated work of SWATSCHEK (1958). The supertribes of the *Olethreutinae* differ in the shape of the basal process of the valva which, in the *Olethreutidii*, is lever-shaped and in the *Eucosmidii* hook- or stick-shaped. In *Olethreutidii* the vesica is functional in the fixation of the female genitalia during copulation and the signum never has a blade-shaped part; in the *Eucosmidii* the gnathos is absent, the cornuti are shed during copulation, the signa are horn-shaped, the seventh sternite of the female is often modified and the tornal ocellus of the forewing pattern is well developed. The division of the *Olethreutidii* into subtribes is based on the presence and structure (or absence as in *Bactrini*) of scent organs. In the *Olethreutini* dorsal scent organs on the hindwing and tibia are developed, in the *Eudemini* lateral abdominal groups of hair are present and the *Lobesiini* have lateral pockets on abdominal segments 1 and 2. Some minor genital and in some cases larval characters support this interpretation. In the *Eucosmidii* the authors distinguished the *Ancyloidini* as having plate-shaped, vertically directed signa, the *Eucosminii* differing in the reduction of the uncus and muscle  $m_1$ , the well developed cucullus and large basal opening of the valva. The sterigma is placed in the incision of the distal edge of the seventh abdominal sternite in the female. The *Laspeyresiini* are strongly simplified: the male genitalia lack muscle  $m_1$ , the tegumen is weak, the valva simple because of strong development of the basal opening. In the female the incision in the seventh sternite is very distinct. The tribe is divided into two subtribes, viz., *Dichroramphae* and *Laspeyresiae*.

## EVOLUTION AND SYSTEMATICS OF *TORTRICIDAE*

### Evaluation of characters

The characters which are most often utilised for separation of the family-group taxa of the *Tortricidae* are discussed below.

**Bionomy.** The bionomic characters were most precisely discussed by POWELL (1964), who supposed that the solitary deposition of eggs, the boring habits of the larva and lack of definite diapause in the Tortricid prototype are primitive characters. However, the mode of egg deposition varies throughout the family. The *Archipina* and *Sparganothina* oviposit egg-masses and cover them with a secretion from the glandulae sebaceae. This is also found in some *Tortricini*, e.g. *Tortrix viridana* L. which deposits eggs in smaller groups (usually 2 in a group) but protects them in similar way. On the other hand the data on the oviposition of very many *Archipini* are not available and one can suppose that they may deposit the eggs in both ways.

The phagisms are not of tribal character as has been sometimes supposed. Often representatives of rather closely related genera differ distinctly in this respect. Oligophagism is probably characteristic of almost all tribes of the family and monophagy is much more frequent than polyphagy.

Larval feeding habits are often characteristic of the groups of species or genera. DANILEVSKI and KUZNETSOV (1968) mention such characteristics when comparing the *Olethreutinae* with the *Tortricinae*. However, in some tribes or even genera both external and internal feeding species are found. Also internal feeding is not correlated with other characters and, being treated as a primitive feature, it is characteristic of groups supposed to be either primitive (*Cochylini*) or highly specialised (*Grapholitina*). Thus one may suppose that parallel feeding habits have developed in various groups of *Tortricidae* and this has been confirmed by COMMON (1963) in the *Cnephasiini* (= *Archipina*).

Larval characters. One of the most important works on the chaetotaxy of *Tortricidae* is that by SWATSCHEK (1958). The results of his research were noted by some authors, including KUZNETSOV and STEKOLNIKOV (1973) who used them to support their system. SWATSCHEK gives the diagnoses of 3 subfamilies and 6 tribes; one could suppose that these groups are easily distinguished. Unfortunately the main differences given by SWATSCHEK in the comments are not true as on further pages one can often find characteristics which occur in one or more of these taxa. Some characters given in particular diagnoses of the tribes, such as the position of setae III and IIIa on the mesothorax or I and III on the ninth abdominal segment which are common for all *Tortricinae*; others show differences which are only slight (e.g. the position of IV and V in the abdominal segments) or inconstant (seta VII in ninth abdominal segment). A conflicting point of view to that of SWATSCHEK was proposed by MACKAY (1959, 1962), who realised that it is impossible to distinguish some groups of *Tortricidae* on larval characters. She (MACKAY, 1962) points out that the separation of *Olethreutinae* from *Tortricinae* and *Archipini* from *Sparganothina* is impossible and that the Cnephasids are a polyphyletic group. In 1959 she gives a list of characters undergoing changes which are connected with the habits of the larva. To conclude we must assume that the importance of larval characters for the separation of the higher groups of *Tortricidae* is rather slight.

Pupal characters. Only the structure of the cremaster may provide important characters. However, the available data are very scarce (RAZOWSKI, 1966; DANILEVSKI and KUZNETSOV, 1968; KUZNETSOV and STEKOLNIKOV, 1973; YASUDA, 1972) and one can suppose that it is of no more than generic importance.

Imaginal characters. Head. In all tribes the number of segments of the maxillary palpi is 1—3. Reduction of the galea is an adaptation of innumerable species and the presence of a chaetosema and the development of the ocellus (COMMON, 1963) gives only a correlation between genera.

Wings. The shape of the wings is at most of generic importance and also the venation does not provide sufficient characters. It has been supposed that atrophy of the postcubital vein of the forewing is important for the separation of the Cochylids from the remaining *Tortricidae*. However, in some *Tortricidae* that vein is rudimentary while the Cochylids may preserve it to some degree. Some authors such as COMMON (1963), suppose that the presence of the internal vein (*M*) of the forewing median cell is an important, constant character.



It is really absent from the Australian species of his *Cnephasiini* but in some Palaearctic species of *Cnephasia* CURT. it is well developed and therefore this character is also useless, even in the separation of tribes. The wing pattern, although often showing strong variability, seems to be of greater importance. The most primitive type of pattern is that consisting of three main elements e.g. basal blotch, median fascia and external fascia or spot. This occurs mainly in the *Tortricinae*, with the exception of *Cochylini* and *Ceracina*. In the latter group a contrasting spotted pattern developed in connection with their diurnal habits, and this may be an old adaptation. Species of *Olethreutinae* are characterised by costal strigulation of the forewing and often (*Eucosmini*) by a distinct ocellus. These two characters are correlated with others found in the genitalia.

**Scent organs.** Scent organs on the wings are known in representatives of many tribes. A costal fold covering scent scales is developed in several tribes of both subfamilies and occurs in the rather primitive genera or species (for instance, *Hysterosia* STEPH. in the *Cochylini*, numerous *Archipini*, e.g. *Archips* HBN., and some *Dichrorampha* GUEN. in the *Grapholitina* etc.). Of similar importance probably are the groups of erect scales occurring in both sexes on the forewing. These scales are well developed in *Tortricini* but are found also in *Archipini*, *Cnephasiids*, *Cochylini* etc. In the hindwing of several groups of *Olethreutini* various scale tufts or folds containing scent scales are found. These were supposed to be of tribal (FALKOVITSH, 1968, KUZNETSOV and STEKOLNIKOV, 1973) or subtribal (DIAKONOFF, 1973) significance, like the abdominal scent organs. Hindwing scent organs in the form of dorsal rolls are common in *Olethreutinae* but are variably distributed. They are lacking in *Bactrae* and *Statherotides* (all taxa proposed by DIAKONOFF 1973), are developed only in part of *Gatesclarkeanae*, *Neopotamiae*, *Endotheniae* and *Zomariae*. The occurrence of tibial hair pencils on the hind leg pencils is similar as they are absent in *Bactrae* and *Rhodocosmariae* as well in some representatives of *Gatesclarkeanae*, *Gnathmoecorodides*, *Neopotamiae*, *Statherotides*, *Zomariae* and *Endotheniae*. The two characters are therefore inconstant and cannot be used for distinguishing tribes or subtribes. Although abdominal scent organs are widely distributed in the *Tortricidae* they were used for tribal (subtribal) divisions in the *Olethreutini* only. In *Cochylini* they are constantly lacking as far as we know; in *Tortricini* there are well developed coremata but as these occur only in a few species (some *Eboda* WALKER) they cannot be considered even as generic characters. They are found also in some genera of *Grapholitina*. As the division of *Olethreutini* into tribes (subtribes) was based on their presence we give their distribution in that group. They are lacking in *Bactrae*, *Olethreutae*, *Rhodocosmariae*, *Sycacanthae*, *Zomariae* and *Endotheniae* but are variously developed in the remaining subtribes (sensu DIAKONOFF, 1973). In *Gatesclarkeanae* they form ventral pockets, in *Statherotides* they are developed as typical coremata in pairs of three and in *Lobesia*, *Neopotamiae* and *Eudemini* (sensu FALKOVITSCH, 1968) are represented by groups of hairs on the sides of the abdomen (segments 1—2, 1 and tergites 1—3, segments 3—7 respectively). It is noteworthy that in *Gatesclarkeanae* and



*Statherotides* they are lacking in some representatives. Thus the above characters seem also useless for tribal division. However, DIAKONOFF (1973) used several further characters in his splitting, namely the shape and number of signa, but these are not correlated with one another.

**Sclerites of male genitalia.** The sclerites of the ninth segment are of rather slight importance for our purposes. The tegumen is more or less strong and is often developed so that apical processes or prominences partially replace the uncus. The vinculum shows at most generic characters; for instance, in the *Cochylini* in which it tends to separate ventrally into two arms.

The tenth segment consists of the uncus and gnathos. The uncus is a more or less strong, hook-shaped sclerite which tends to show parallel reduction in several groups e.g. in *Cochylini*, *Tortricini*, *Olethreutini* and *Eucosmini*. There are two types of gnathos in the *Tortricidae*; in *Archipini* and *Microcorsini* it is typical in having the form of two arms, fused terminally, which are connected with the base of the uncus. In a few cases these arms do not fuse apically but this cannot be considered as a tribal character because it occurs in two groups which apparently show parallel specialisation, viz., *Sparganothina* and *Archipina* (genus *Isotrias* MEYRICK).

In the second type of gnathos the membrane connecting the basal part of tuba analis and tegumen is weakly sclerotized. Its connection with the tegumen is more proximal than in the preceding case and may be articulated or completely fused. These two types of gnathos are of great importance in dividing the most primitive groups of *Tortricidae*.

The socii are topographically connected with the top portion of the tegumen and show a variety of forms and functions often correlated with other parts of the apparatus. All these are either of generic or specific significance only.

The eleventh segment is weakly developed and its plates are represented by sclerites of the tuba analis. It seems possible, however, that these sclerites are secondarily developed in some groups. The dorsal sclerite (scaphium) is an ill-defined plate situated subterminally while the ventral one (subscaphium) may be very strong, fused with the gnathos and provided with various ventral projections. The importance of these sclerites is great only in the *Tortricinae*, because in the *Olethreutinae* they are weaker or completely atrophied in all the tribes.

The structure of the valva is of great taxonomic importance. One can distinguish some areas within the valva, the most important of which are costa with the basal process, sacculus, cucullus and internal surface which is often provided with processes. The costa is often reduced to some degree, although rarely completely so in *Archips* HÜBNER, but, being observed only in some groups of *Tortricidae*, it is of no more than generic importance. The same may be said about the brachiola which, although found in *Cochylini* and *Archipini*, is most characteristic of *Tortricini*. The ventral area of the valva is constantly stronger than the dorsal and, undergoing no changes, is not important phylogenetically. A degree of sclerotisation, i.e. strengthening of the valva and development of the cucullus, are progressive characters. Generally the valva is weaker in

*Tortricinae* than in *Olethreutinae* and has not developed any adaptation of the basal part of the internal surface. In *Oleuthreutinae* a basal opening is formed.

The diaphragma connects to the ventro-distal part of the vinculum, the proximal edges of the internal surfaces of the valvae, the lateral parts of the tegumen and the ventral edges of the gnathos. Some important sclerites such as the anellus, juxta and transtilla are developed in the diaphragma. The structure of the juxta is of great significance in dividing the family as in the *Olethreutinae* it fuses completely with part of the anellus, the caulis. The transtilla is always absent in *Olethreutinae* while in *Tortricinae* it is occasionally lacking; the latter is connected with the insertion points of some muscles.

The aedeagus shows mainly generic and specific characters. Reduction of the cecum penis is characteristic of *Olethreutinae* but is also observed in some *Tortricinae*. In groups in which the aedeagus takes part in the fixation of the female genitalia during copulation, various adaptation are developed.

Musculature and function of male genitalia. In the male genitalia of *Tortricidae* 6 pairs of muscles occur, discounting the internal muscles of the aedeagus and tuba analis. The internal musculature of the valva is absent. In the present paper the terminology follows KUZNETSOV and STEKOLNIKOV (1973).

1. Depressors of uncus ( $m_1$ ) occur usually when the uncus is present. They are inserted on one side on the proximal edge of the tegumen (bases of pedunculi) and at the base of the uncus or terminal region of the tegumen on the other side. They are strong, broad basally, tapering towards the end and usually developed proportionately to the uncus. Exceptionally, when the uncus is atrophied, they may be well defined (*Tortricini*) because the terminal lobes of the tegumen replace the uncus functionally. Contraction of  $m_1$  lowers the uncus on top of the tegumen to hold the female abdomen between it and the gnathos or transtilla. In some *Tortricini*, e.g. in *Acleris* HÜBNER, these muscles also approach the terminal parts of the tegumen near the tuba analis. In *Cochylini* and the tribes of *Olethreutinae* one can easily notice a reduction of  $m_1$  in many of the more highly specialised genera. To conclude, neither the presence nor situation of these muscles are important for tribal division and they may be treated as of generic significance.

2. Retractors of the tuba analis enable it to return to the normal position close to the diaphragma; they also partially retract the gnathos. They are insufficiently known but it seems that they may be divided into two groups. In *Archipini* they are inserted on the oblique muscles which retract the tegumen. In *Eulia* HÜBNER the retractor is divided into three parts, one of which is inserted on the gnathos arms subterminally, the other two on the tuba analis. In *Tortricini* the true retractors of the anal tube are replaced by narrow branches of muscles  $m_1$ . The basal point of insertion of this muscle is on the proximal edge of the pedunculus medially and fused almost the entire length of the main part of that muscle. The second point of insertion is situated on the tuba analis latero-proximally as far as we can judge from an examination of representatives of the



genera *Acleris* HÜBNER and *Tortrix* LINNAEUS. In the latter that is probably the only preserved part of the depressor of the uncus.

3. The tergal extensors of the valvae ( $m_2$ ) join the lateral surfaces of the tegumen and basal processes of the valvae or diaphragma near them. They serve to raise the valvae; however, it is supposed that they may also perform other functions (raising the transtilla). The degree of development of these muscles is variable. It may be supposed that their presence is a primary character. KUZNETSOV and STEKOLNIKOV (1973) found them exclusively in *Cochylini* and *Olethreutinae* and supposed that in the *Archipini* they were atrophied because of the presence of muscles  $m_4$  (originally given as  $m_3$ !). As this muscle is also found in *Eulia ministrana* (L.) it may be supposed it occurs in other species and genera of *Archipini*. One should treat the presence of this muscle as a primitive character which, in the *Tortricidae*, has disappeared only in the majority of *Archipini*.

4. The sternal extensors of the valvae ( $m_3$ ) insert on the juxta and on the vinculum. Contraction of these muscles causes a movement of dorsal part of juxta to inside of abdomen. At same moment, due to increased turgor, the ventral portion of the juxta moves distad. As the basal parts of the valvae are fused with the juxta, they withdraw from one another and the valvae open. These muscles are of taxonomic importance and are present in *Tortricinae* but are constantly lacking in *Olethreutinae*.

5. The tergal flexors of the valvae ( $m_4$ ) extend from the basal part of tegumen (pedunculi) to the basal processes of the valvae or to the transtilla. They are antagonists to the preceding pair of muscles as their contraction approaches the valvae. Additionally the muscles  $m_4$  lift the transtilla. They are always present in *Tortricidae* except the *Tortricini*. In *Tortricinae* they are variably inserted while uniformly so in *Olethreutinae*. KUZNETSOV and STEKOLNIKOV (1973) suppose that their reduction in *Tortricini* is due to the exclusive fixation of the female abdomen by the valvae. These muscles are of great taxonomic significance at subfamily level.

6. The protractors of aedeagus ( $m_5$ ). Points of insertion of these muscles are on the coecum penis and valvae or vinculum. KUZNETSOV and STEKOLNIKOV (1973) treat a translocation of  $m_5$  from valva on vinculum as a secondary character and consider that such an insertion on the valva occurs in primitive *Lepidoptera*. In *Archipini* there is often a contemporary insertion of  $m_5$  both on the valva and vinculum; however, the greater part is always connected to the valvae. Exclusive insertion of  $m_5$  on vinculum is not confirmed. In *Tortricinae* a tendency of translocation of insertion towards the dorsal and ventral parts of valvae, e.g. costa and sacculus, is observed. That causes a subdivision of these muscles into two parts. However, these changes are at most of generic importance. The second, opposite points of insertion of  $m_5$  seem more important. In *Tortricinae*  $m_5$  is inserted on the coecum penis while in *Olethreutinae* it is always inserted on the caulis. The distance which a muscle enters inside the valva is also of



importance and is connected with morphological adaptations of the internal surface of valva. Contraction of these muscles caused protrusion of aedeagus and a contemporary approach of the valvae. At that moment the muscles are situated rather vertically to the valva, the internal surface of which should be elastic. In *Tortricinae* this is realised by membranisation of the entire area between the costa and sacculus, especially towards the base; in *Olethreutinae*, in which the valvae perform the more important role of fixation of the female abdomen during copulation, the valva has to be stiffer and more strongly sclerotised. Therefore only a limited anterior area of its internal surface, the so called basal opening remains membranous. Thus status of muscle  $m_5$  and the modifications of the valvae and complex juxta-caulis connected with it are of taxonomic importance.

7. The retractors of the aedeagus ( $m_6$ ) insert on the vinculum and coecum penis. They retract the aedeagus and indirectly open the valvae in *Olethreutinae* (replacing muscles  $m_3$ ). They are constantly present in *Tortricidae* and show only some variability in size and fusion even into an unpaired muscle. Their position on the vinculum changes only slightly. Thus they have no taxonomic value except probably at specific or generic level.

Female genitalia. The structure on the female genitalia is provided with much less important characters than those of the male. The ovipositor is adapted to the mode of deposition of the eggs and that is no more than of subgeneric importance (the floricomous ovipositor, developed in connection with covering the eggs with minute pieces of substrate, is known in *Archipini*, *Tortricini* and *Eucosmini*, the telescopic ovipositor characteristic of the species depositing their eggs in buds is also found in some tribes and even genera together with typical and floricomous ovipositors). The structure of the apophyses and eighth tergite is closely connected with the character of the whole ovipositor and therefore, is also not important for the separation of higher taxa.

The presence of a well sclerotised sterigma is of lesser importance than its connection with the apophyses anteriores. In *Tortricinae* this connection is well developed while it is atrophied in almost all *Olethreutinae* (except for *Microcorsini*), and depends on the mode of fixation of the female abdomen by the male genital apparatus during copulation.

The structure of the ductus bursae and position of the ductus seminalis are of specific or at most of generic significance, judging from the distribution of these characters in the tribes. The corpus bursae has some characters which are important at the subfamily level. One can suppose that irregular, indistinct sclerotisations of its walls are the most primitive. They occur mainly in *Cochylini* in which the signa are not specialised. Then dispersed minute spines, spined or dentate plates and eventually distinctly edged smooth sclerites could developed. A more highly specialised signum is found in many *Archipini* of the *Tortricinae* and in *Eucosmini* and *Microcorsini* of *Olethreutinae*, but it seems possible that development of tubular (funnel-shaped) signa could have been realised in various

ways. Some structures of the bursa copulatrix are insufficiently known. To that group one should include additional sacs which sometimes occur on the corpus bursae. The importance of these structures is unknown.

#### SYSTEM AND EVOLUTION

As in other *Lepidoptera*, the *Tortricidae* tend towards a simplification of structures and function of the genitalia which as can be seen from the above review, provide the most important characters.

In the most primitive Tortricid-moths the dorsal complex of the male genitalia is functionally rather balanced with the ventral complex. A tendency of supremation of the latter in the fixation of female abdomen during copulation may be observed in all the groups but it is realised in them to unequal degrees and in various ways.

Division into subfamilies is based on several characters which have developed in connection with the functional domination of the valva-aedeagus complex over the dorsal complex (tegumen-gnathos-transtilla). The process of strengthening of the ventral complex is due to the direct action of the well developed muscles  $m_2$  and  $m_4$  on the valvae and the enlargement of muscle  $m_5$ . The progressive evolution of these muscles has caused some changes in the two above mentioned complexes. While in *Tortricinae* muscles  $m_2$  and  $m_4$  often indirectly move the valvae or one of them is absent, in *Olethreutinae* they are constantly well developed and inserted in the valvae. Muscle  $m_5$  is comparatively stronger in *Olethreutinae* than in *Tortricinae* and enters deeper into the valva. This diminishes the importance of the dorsal complex in the fixation of the female abdomen and on the other hand causes some adaptative changes in the ventral complex. In *Tortricinae* this process is slower than in *Olethreutinae* as they always preserve some active parts of the tergal complex. However, the uncus of *Tortricinae* is often atrophied, but it is usually replaced functionally by the top parts of the tegumen, tuba analis or socii. Also the gnathos is, in that subfamily, typically developed and when simplified or strongly reduced its function is taken over by the transtilla in which one or two muscles are inserted. Thus there are always two parts of the dorsal complex working together between which the female abdomen may be occurred. In *Olethreutinae*, because of the above mentioned changes, the uncus plays a much slighter role and the tuba analis or the socii may only partially replace it functionally. It should be also mentioned that the transtilla is absent and the tuba analis usually weak or completely membranous. The function of the valvae and aedeagus is more precisely coordinated in *Olethreutinae* than in *Tortricinae*. In the latter the caulis is usually long and always articulated with the juxta, muscle  $m_5$  is inserted on the aedeagus near or at the level of the opening for the ductus ejaculatorius, and  $m_5$  is situated more proximally, often at the apex of the coecum penis. In the *Tortricinae* muscle  $m_3$  is inserted on the juxta; this muscle and  $m_6$  arise from the vinculum.



This arrangement of insertion points and articulation of the caulis causes a characteristic movement of the aedeagus. Contraction of  $m_5$  moves the aedeagus distad on an arch around the point of articulation mentioned above and at the time the valvae close together. Contemporary contraction of  $m_3$  causes a movement of the juxta which, with some simplification, one may treat as a rotation around its transverse median axis. The two movements together causes the aedeagus to move in an arch. The aedeagus is retracted due to contraction of muscle  $m_6$  and the valvae open when muscle  $m_3$  contracts. An increase of muscle  $m_5$  and the collaborating muscles causes increase of its antagonistic muscle  $m_6$  to retain a balance and this is probably a reason for the comparatively smaller effort of  $m_3$ . Gradual reduction of  $m_3$  leads to sclerotisation of articulation between the caulis and juxta and in this way a complete reduction of  $m_3$  appeared in *Olethreutinae* in which it is functionally replaced by  $m_6$ . This simplification is treated here as a progressive character. Further changes developed in the position of muscle  $m_5$  which, by strengthening lowered its insertion point producing a better stabilisation of the unit aedeagus-caulis-juxta. Likewise  $m_5$  which, in some extreme cases is inserted in the middle of the olethreutoid  $m_6$ , also lowers its position. Coccum penis, the place of insertion of two pairs of muscles in *Tortricinae* undergoes a gradual reduction in *Olethreutinae*. As a result of the above changes the movement of the aedeagus is much more simple in *Olethreutinae* than in *Tortricinae* and is realised on a less curved line. The complex valvae-aedeagus becomes in *Olethreutinae* more compact and unified functionally than in *Tortricinae*. Muscle  $m_5$  enters deep inside the valva which became strongly sclerotised as it takes the main part in the fixation of the female abdomen. There is a tendency of muscle  $m_5$  to obtain the optimum points of insertion in the valva. The ventral insertion is strongest and is connected with work of the sacculus and various degenerations of the costa of valva in the *Tortricinae*. In *Olethreutinae* the valva is strengthened due to sclerotisation of the internal surface between the costa and sacculus, resulting in the development of the cucullus. The sclerotisation enables the valvae to work more effectively and their distal portions are usually armed with strong setae. On the other hand it leads to an adaptation enabling muscle  $m_5$  to take a normal position vertical to the valva when contracted. To make this possible the proximal portion of the internal surface of the valva remained membranous, forming the so-called „basal opening". The basal opening is characteristic of *Olethreutinae* and is unknown in any *Tortricinae* species. The female genitalia of *Olethreutinae* are characterised by atrophy of fusion between the sterigma and apophyses anteriores. However, this is correlated with the absence of a typically developed gnathos, at least in some cases e.g. when there is no transtilla which replaces the gnathos functionally.

Evolution of *Tortricinae*. Simplification of sclerites and musculature of the male genitalia is also apparent. The most primitive forms possess all muscles of the apparatus. In the present hypothesis the most primitive are *Archipini* in which the dorsal complex plays the most important role in the



fixation of the female abdomen during copulation. In this tribe the uncus, gnathos and transtilla are well developed. The uncus is never atrophied and shows several subtribal or generic characters; the gnathos is well developed, typical, provided with the retractors or retracted indirectly, with usually a weakly sclerotised tuba analis. Muscles  $m_1$  are strong, uniform and reach the base of the uncus;  $m_4$  are always well developed whilst  $m_2$  are usually absent. Only in *Eulia* HÜBNER but probably in other unexamined genera this muscle is developed. One can therefore suppose that at least the most generalised *Archipini* are characterised by complete musculature and that in the evolution of this tribe there appeared a reduction of one muscle. Muscle  $m_5$  is variably inserted on the valva. It may be partially inserted on the vinculum, or on the valva only. There is also a tendency for this muscle to divide into two parts. The main part of the muscle is inserted in the valva and is directed ventro-medially, whilst the smaller, more or less distinctly separate arm in the dorsal part of the valva or on the vinculum.

The tribe is divided into 6 subtribes treated to date as higher taxa (subfamilies or even families). Unfortunately lack of material does not allow examination of musculature of some of them. These subtribes (*Chlidanotina*, *Polyorthina* and *Schoenotenina*) of necessity are placed in this system only provisionally.

*Archipina* are treated here as the most primitive subtribe. *Schoenotenina*, placed in the diagram (fig. 1) before *Archipina*, have not been examined. *Archipina* show great variety of shape of the male genitalia. Specialisation produced simplification of the valva and reduction of its costa. Muscle  $m_2$  is completely reduced in all genera except *Eulia* HBN. In specialised genera the signum is funnel-shaped.

*Ceracina* are an offshot of the *Archipina*-stem and differ mainly in the biology. This is a diurnal group characterised by telechromatic coloration. *Ceracina* do not show any differences to the preceding subtribe in the structure of the sclerites of the genitalia and in the musculature of the male genital apparatus except for partial change of the insertion of muscle  $m_3$  from juxta on terminal part of the caulis. This character may prove unimportant but the small amount of material examined does not allow accurate interpretation.

*Sparganothina* show no great difference from other tribes except for the peculiarly developed socii which are partially fused with the gnathos. The arms of the gnathos are usually free, rounded apically. The presence of a hair pecten on the dorsal part of vein *cu* in the hindwing is analogous to that in the *Olethreutinae* and is a specialisation of the group. An interesting but insufficiently studied character is the asymmetrical arrangement of the fused muscles  $m_3$  on the coecum penis caused by the lateral position of the ductus ejaculatorius.

*Chlidanotina* are distinguished by the presence of additional sacks in the bursa copulatrix. The musculature of the male genitalia has not been examined, therefore the position of this subtribe is doubtful and provisional.

*Polyorthina* are distinguished by the presence of coremata placed in longitudi-

nal splits of the valvae. The musculature of the male genital apparatus has not been studied.

*Cochylini* show no more than tribal characters and are placed in the subfamily *Tortricinae*. They followed a different course to that of the *Archipini*. The gnathos is strongly reduced, atypical or completely absent. The tegumen shows a variety of forms. In some genera the uncus and its depressor muscle  $m_1$  are well developed but in others (majority) it is absent. In many cases the uncus is functionally replaced by the socii but never by the tuba analis. The role of gnathos is employed by the transtilla which is often very strong. The complete number of muscles is characteristic of this tribe as far as one can judge from an examination of the representatives of 4 genera. Muscle  $m_2$  is inserted either in the transtilla or in the valva while  $m_4$  is invariably inserted in the transtilla. The remaining muscles are typical of the *Tortricinae*, although in some cases the positions of  $m_5$  and  $m_6$  may differ. Muscle  $m_5$  is usually inserted inside the basal part of the valva, either dorsally or ventrally. A rather flat insertion of  $m_5$  in the valva may prove a secondary development caused usually by the very large aedeagus. Other peculiar adaptations, such as the fixation of the female abdomen by the aedeagus and process of the juxta, by the caulis or top part of the tegumen are worth mentioning.

*Tortricini*. The reduction of the uncus was similar to that in *Cochylini*, but it was replaced mainly by the top of the tegumen and tuba analis which form a functional unit. An additional role may be fulfilled by the socii. The tuba analis is often very strong and is retracted by part of muscle  $m_1$  which only exceptionally may atrophy to some degree. Muscle  $m_2$  is present and always inserted in the valva and replaces muscle  $m_4$ . As the valva is usually well developed it works mainly by the sacculus judging from the insertion point of muscle only a small part of which reaching the base of the costa. The terminal part of the sacculus is adapted to fix the female abdomen in the development of the so-called spined termination. Muscle  $m_5$  enters deep inside the valva. An important adaptations are shortening of the caulis and the development of the strong muscle  $m_3$  which is inserted on the very large juxta which folds along its vertical axis between the vinculi.

Evolution of *Olethreutinae*. *Olethreutinae* may be divided into three tribes. The first, *Microcorsini*, is insufficiently known as its musculature has not been studied. This is the most primitive group of the subfamily and has two important characters common with the most generalised *Tortricinae*, viz., the gnathos which is thin but typically developed and the presence of a connection between the sterigma and apophyses anteriores. Other characters are typical of *Olethreutinae* but the most important are the olethreutoid and basal opening of the valva which are proportionally weakly developed. The process of sclerotisation of the internal surface of the valva is, in comparison with all *Tortricinae*, highly advanced and has caused a development of a small basal opening. Judging from its size one may suppose that muscle  $m_5$  does not enter deep inside the valva.



In the female genitalia there are two horn-like signa. As in all more primitive groups the dorsal complex is still active and may be recognised due to the well developed uncus and gnathos. One may thus suppose that *Microcorsini* is the most primitive tribe of the *Olethreutinae* derived very early from its main stock and showing some intermediate characters between this subfamily and *Tortricinae*.

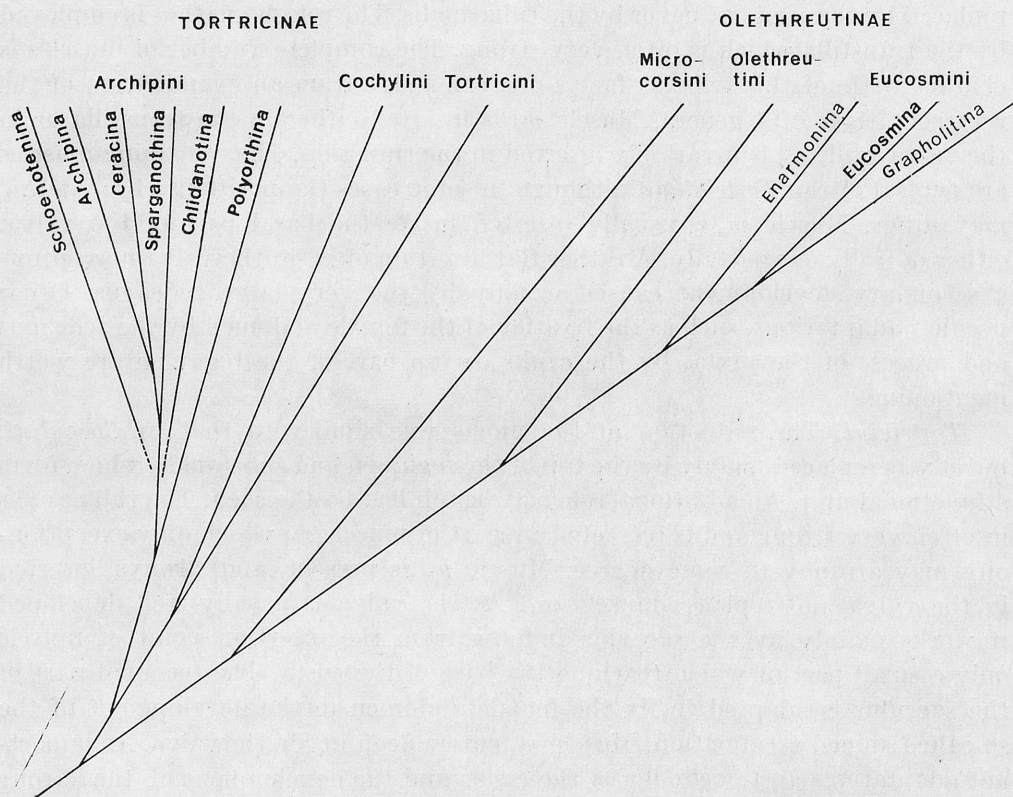


Fig. 1. Phylogenetic tree of *Tortricidae*

*Olethreutini* are characterised by the reduced gnathos two pairs of weak, narrow lateral bands fused with often well developed subscaphium. The basal opening of valva is proportionally short and muscle  $m_5$  does not enter very deep into the valva. The basal process of the valva is lever-like and the cornuti are specialised in the fixation of the female genitalia during copulation. In the forewing the costa is distinctly strigulated but the tornal ocellus is absent or ill-defined. The signa are cup- or plate-shaped. The scent organs are variably developed but their types are not correlated with other characters throughout the tribe.

*Eucosmini* are more progressive group than the *Olethreutini*. The gnathos is much weaker and often completely atrophied and the tuba analis is usually



membranous. Muscle  $m_5$  is much better developed than in the preceding tribe and enters deeper into the valva, causing a stronger development of the basal opening. The basal process of the valva is rod- or hook-shaped and the cornuti do not play a role in fixation during copulation and drop easily. The signa are plate or horn-shaped, pointed apically. In the forewing pattern the costal strigulation is well developed and the ocellus distinct. This tribe is divided into three subtribes, the most primitive of which seems to be the *Enarmoniina* which have the majority of characters common with *Eucosmina* and share some larval ones with the preceding tribe. The most important distinguishing character is the plate-shaped sharp signum.

*Eucosmina* have developed a stronger ventral complex. In the valva the cucullus is distinct and the basal opening is large. The insertion point of muscle  $m_6$  tends to be situated on coecum penis more distally towards the caulis. The gnathos is very weak and the tuba analis is usually completely membranous. In connection with the development of the cucullus the sterigma shows a tendency to move proximally. The signa are horn-like, often with broad, rounded bases.

*Grapholitina* have the tergal complex even more strongly reduced than in *Eucosmina*, with the uncus atrophied. The gnathos is vestigial and the socii are usually completely absent. Muscle  $m_1$  disappears. The valva specialises in the development of a strong, heavily bristled cucullus and a large basal opening. Muscle  $m_5$  enters deep inside the valva. In the female genitalia the sterigma is situated more proximally in an incisure of the seventh sternite. The subtribe shows slight differences to the preceding one in the larval characters (on abdominal segment 9, setae I and III on common pinaculum) but there are no differences in the pupae.

## REVIEW OF TAXA

### *Tortricoidea*

*Tortricina*: MEYRICK 1895, Handb. Br. Lepid.: 451. Type-genus: *Tortrix* LINNAEUS, 1758.

*Tortricoidea*: MOSHER 1916, Bull. Illinois Sta. Lab. nat. Hist., 12 (2): 51.

MOSHER (1916) originally included the *Epiblemidae*, *Olethreutidae*, *Tortricidae* and *Sparganothidae* in the superfamily *Tortricoidea*, basing her conclusions on the pupal characters. This arrangement was similar to that of MEYRICK (1895), who included in his *Tortricina* the *Trypanidae* (= *Cossidae*), *Phaloniidae*, *Tortricidae* and *Eucosmidae* and BOURGOGNE (1951) only two families, viz. *Tortricidae* and *Carposinidae*. For the latter family DIAKONOFF (1960) erected a separate superfamily *Carposinoidea*, leaving in the *Tortricoidea* only the *Phaloniidae* and *Tortricidae*. This interpretation of the superfamily has been commonly accepted; however, a peculiar arrangement by OBENBERGER (1964)

is worth mentioning. In his interpretation of the superfamily in question belong the *Carposinidae*, *Cyclotornidae*, *Anomologidae*, *Olethreutidae*, *Chlidanotidae*, *Tortricidae*, *Phaloniidae*, *Ochsenheimeriidae* and *Atychidae*. In the present interpretation a single family, i.e. *Tortricidae*, forms the superfamily *Tortricoidea*, but it should be mentioned that the systematic positions of some other groups has not been examined.

### *Tortricidae*

*Tortrices* LINNAEUS 1758, Syst. Nat. edit. 10: 530. Type-genus: *Tortrix* LINNAEUS, 1758.

*Tortricidae*: LATREILLE (1802—1803), [in:] SINNINI'S BUFFON Hist. nat. Gen. Crust. Ins., 3: 415 (correction of *Tortrices* LINNAEUS, 1758 — International Commission of Zoological Nomenclature, Opinion 450).

*Tortricides*: BILLBERG 1820, Enum. Insect.: 90. Incorrect formation of family name.

*Torticina*: GRAVENHORST 1834, Vergl. Zool.: 167. Incorrect formation of family name.

*Platyomidae*: DUPONCHEL 1834, Hist. nat. Lépid. Papillons Fr., 9: 5 (no type-genus designated). Described as family of *Lepidoptera*.

*Tortricites*: NEWMAN 1835, Grammar Ent.: 176. Incorrect formation of family name.

*Plicatae*: STAINTON 1858, Manual Br. Butterflies Moths, 2: 188 (no type-genus given). Proposed as family of *Lepidoptera*.

Expanse of forewings 7—60 mm, usually ca. 25 mm. Ocellus and chaetosema usually present; haustellum fairly short, naked; mandible rudimentary or absent; maxillary palpus 2—4 segmented or atrophied; labial palpus usually short, with short terminal joint.

Epiphysis present; calcaria: 0—2—4; wings well developed with exception of some micropterygous females; abdomen devoid of spines.

Male genitalia without typically developed sacculus; no internal musculature of valva.

Female typically ditrysian.

Egg of flat type.

Larva with three setae on the prestigmal plate of the prothorax and usually with developed anal comb consisting of straight spines. Crochets of the abdominal legs arranged in circles.

Pupa characterised by two rows of spines arranged on dorsum of most abdominal segments; segments 4—6 are in male and 4—7 in female movable. Cremaster often distinctly developed.

Bionomy. Larvae in shelters formed by rolling leaves, or internal feeders. Pupa protrudes from the cocoon before emergence of moth.

Distribution: all except the polar regions.

Comments. More detailed data are given under the particular subfamilies, tribes and subtribes. The characters of the larvae follow SWATSCHEK (1958: 28), those of the pupae follow MOSHER (1916: 51). About 4500 species known to date.



## *Tortricinae*

*Tortricidae*: [anonym] 1858, Accent. List Br. Lepid.: 59. Type-genus: *Tortrix* LINNAEUS, 1758. Family of *Tortricina*.

*Sciaphilidae* [anonym] 1858, ibid.: 59. Type-genus: *Sciaphila* TREITSCHKE, 1829. Family of *Tortricina*.

*Tortricinae*: FERNALD 1882, Trans. am. ent. Soc., 10: 1. Type-genus: *Tortrix* LINNAEUS, 1758. Subfamily of *Tortricidae*.

Wingspan: 7—60 mm.

Hindwing usually without cubital pecten; forewing pattern typically consisting of three main elements, e.g. basal blotch, median fascia and subapical fascia or blotch, always without costal strigulation and tornal ocellus.

Male genitalia characterised by articulation of caulis with juxta and membranous internal surface of valva. Cucullus not developed; muscle  $m_3$  present,  $m_5$  inserted on coecum penis.

Female genitalia usually with sterigma connecting apophyses anteriores; signum if present single, exceptionally two signa developed.

Larvae and pupae do not show any constant differing character from *Olethreutinae*.

Bionomy. To this family belong mainly the species whose larvae usually roll the leaves.

Distribution: as for the family.

About 2000 species known to date.

## *Archipini*

*Archipsidii* PIERCE and METCALFE 1922, Genit. Br. *Tortricidae*: XXI, 1. Type-genus: *Archips* HÜBNER, [1825]. ? Subfamily of *Tortricidae*.

Head smooth or roughly scaled; ocellus present in the majority of subtribes and species, but often small. Chaetosema developed probably in all the subtribes; maxillary palpus 1—3 jointed; tongue usually present; antenna mostly simple.

Wingspan 8—40 mm. Wings fully developed in males, sometimes strongly reduced in females. Pattern usually of cryptic type; wing densely scaled, exceptionally underside sparsely so. Venation typical of *Tortricidae*; vein *M* usually present in forewing. Occasionally cubital pecten present in the hindwing.

Male genitalia with well developed uncus and typical gnathos usually fused distally. Socius variably built, often completely atrophied; hamuli present in some genera. Costa of valva often completely reduced. Musculature fully developed only in the most primitive genera.

Female genitalia. Ovipositor variably developed; sterigma often complicated well sclerotised or almost entirely membranous. Signum plate- or funnel-shaped, if present.

Larval characters of a rather limited importance on the subtribal level (c.f. p. 76).

Bionomy. The eggs deposited in imbricated mass or solitarily. Larvae usually oligophagous (the premature stages often polyphagous). Usually they roll or fold leaves.

Distribution: as for the family.

Comments. About 700 species known to belong in the tribe. The musculature of the male genitalia not examined in *Schoenotenina*, *Chlidanotina* and *Polyorthina*. Systematic positions of the first two subtribes is doubtful and their diagnoses are based on the literature data.

The name *Archipini* proposed for the first time by PIERCE and METCALFE in an incorrect form „*Archipsidii*” was commonly in use since 1922. PIERCE and METCALFE must be recognized as the authors of this name because HÜBNER's name of strips, *Archipes*, proposed in 1825 did not include the type-genus and according to the International Code of Zoological Nomenclature Article 11e is invalid (same name by HÜBNER (1806) was included in Tentamen but this work is rejected for nomenclatural purposes by the international Commission of Zoological Nomenclature, 1926, Opinion 97, Smithsonian Misc. Collns. **73** (4): 19). However, several other names were published earlier than that by PIERCE and METCALFE but to maintain stability, an application should be made to the International Commission of Zoological Nomenclature to have *Archipini* PIERCE and METCALFE 1922 placed on the Official List of the Family Group Names in Zoology.

### *Schoenotenina*

*Schoenotenidae* DIAKONOFF, 1952, Zool. Meded. Leiden, **31**: 166. Type-genus: *Schoenotenes* MEYRICK, 1908 (*S. synchorda* MEYRICK 1908).

*Schoenoteninae*: COMMON, 1958, Proc. Xth Internat. Congr. Ent., **1** (1956): 290. Subfamily of *Tortricidae*.

*Schoenotenini* DIAKONOFF, 1960, Verh. K. ned. Akad. Wet., Afd. Nat., **53** (2): 193. Tribe of *Chlidanotinae*.

Head often roughly scaled; ocellus rarely present; chaetosema present; labial palpus 1.3—3.4; maxillary palpus 1—3 segmented, small; tongue short; antenna usually simple, in male ciliate, rarely serrulate.

Thorax occasionally with a posterior crest. Wind tibia provided with dense long scales above.

Wingspan 10—22 mm, usually ca 16 mm.

Wings with pattern typical of *Tortricinae*, often partially reduced. Costal fold only exceptionally developed. Scaling of underside of both pairs of wings sparse except on veins. This character is in some genera rather indistinct, (c.f. DIAKONOFF, 1952). Venation normally developed, well visible on underside where it is usually marked by fringes of scales. In forewing median cell often situated somewhat towards dorsum. All veins developed, occasionally last radial and first median veins stalked. Internal vein of median cell (*M*) in the majority of species well developed, long, but it may be vestigial in others.



Hindwing in some genera with usually long-stalked veins  $rr-m_1$  and partially altered median cell.

Male genitalia. Tegumen usually large; uncus variably shaped, strong, more or less elongate, often provided with various extensions, lateral or (and) median lobes situated terminally, rarely bifurcate apically. In some species it is armed with heavy setae. Gnathos usually well developed with arms fused terminally in the majority of species. It may be simple or provided with various prominences, processes or dents. Hami present in several species. Socii variable in length and shape, often absent. They are situated above bases of hami (when they are present) or fused with them. Valva elongate with costa usually well sclerotised, especially towards the base, and sacculus occasionally provided with a free termination or other processes. Internal surface of valva often with various emarginations, especially in distal area. In many species variably situated groups of bifurcate or pectinate setae present. Transtilla simple or provided with smooth or minutely spined processes. Juxta simple, rather small. Aedeagus variably shaped, simple, or armed with dents or thorns; cornuti spine-like, varying in form and size. Caulis usually short.

Female genitalia. Ovipositor typically built; papilla analis often with irregular warts; apophyses fairly short. Eighth tergite often strongly sclerotised. Sterigma usually broad and weakly sclerotised, at least partially, densely covered with minute spinulae. Often it forms a narrow lamella postvaginalis and (or) lamella antevaginalis fused to the edges of the ostium. Antrum often differentiated by large breadth; ductus bursae variable in length, often sculptured, rarely provided with small sclerites; ductus seminalis subterminal. Cestum may be developed. Corpus bursae sculptured. Signum variably formed (fold of the wall of corpus, plate- or dagger-like, funnel- or pocket-shaped) if present.

Scent organs. Three groups of erect scales in forewing. Group of scales in the costal fold of the forewing in few species.

Sexual dimorphism slight.

Larva insufficiently known. Only COMMON (1965) gives a description of the setal arrangement of three Australian species.

Pupa: no data.

Bionomy insufficiently known. COMMON (1965) gives some data on Australian genera. Larvae of *Proselena* MEYRICK are miners in early stages, then they spin leaves together and pupate therein; larva of *Tracholena* COMMON tunnels in the bark. Food plants: deciduous and coniferous trees.

Distribution. The subtribe is known mainly from Australia and New Guinea. Some species are confined to the Oriental Region (from India to Indonesia). The species described from Madagascar (DIAKONOFF, 1947) are in fact *Archipina* as stated by DIAKONOFF (1972, as „*Tortricinae*”).

Comments. The group is still insufficiently known. It seems noteworthy to mention that some characters treated by DIAKONOFF as peculiar of *Schoenotenina* are in fact shared with other *Archipini*. These are sparse scaling of under-side of the wings, absence of ocelli, presence of hami, pectinate setae in the male

genitalia etc. Some of them are widely discussed by COMMON (1965). The status of this group has been changed several times; besides the data in the above synonymy *Schoenotenina* were treated as a subfamily of *Tortricidae* by DIAKONOFF (1972, 1973, 1974) and as a tribe of *Chlidanotinae* (DIAKONOFF, 1960).

About 200 species known to date.

### *Archipina*

*Archipes* HÜBNER, [1825], Verz. bekannter Schmett.: 388. No type-genus included; invalid.

*Sciaphilidi* GUENÉE, 1845, Annls Soc. ent. Fr., (2) 3: 163. Type-genus: *Sciaphila* TREITSCHKE, 1829. Established as tribe of *Tortrices*.

*Aphelidi* GUENÉE, 1845, ibid.: 305. Type-genus: *Aphelia* HÜBNER, [1825]. Tribe of *Tortrices*.

*Sciaphilidae*: MORRIS, 1868, Nat. Hist. Br. Moths. 3: 161 (include various tribes of *Tortricidae*).

*Aphelidae*: MORRIS, 1868, ibid.: 223.

*Exapatidae* STANTON, 1854, List Specimens Br. Animals Br. Mus., 16: 10, 11. Type-genus: *Exapate* HÜBNER, [1825]. Family of *Tineina*.

*Cnephasidae* STANTON, 1858, Manual Br. Butterflies Moths, 2: 188; 1859: 255. Type-genus: *Cnephasia* CURTIS, 1826. Family of *Tortricina*.

*Tortricodidae* STANTON, 1859, ibid.: 277. Type-genus: *Tortricodes* GUENÉE, 1845. Family of *Tortricina*.

*Chimatophilidae* KIRBY, 1897, LLOYD'S nat. Hist., 5 (3): 282. Type-genus: *Chimatophila* [sic!] STEPHENS, 1829. Family of *Tortrices*.

*Cnephasidii*: PIERCE and METCALFE, 1922. Genit. Br. *Tortricidae*: XXI, 9.? Subfamily of *Tortricidae*.

*Cnephasiinae*: HESLOP, 1938, Cat. Br. Lepid.: 71. Subfamily of *Tortricidae*.

*Chresmarchidii* DIAKONOFF, 1939, Zoöl. Meded. Leiden, 21: 135. Type-genus: *Chresmarcha* MEYRICK, 1910. Subfamily of *Tortricidae*.

*Cacoecidii* DIAKONOFF, 1939, ibid.: 151. Type-species: *Cacoecia* HÜBNER, [1825] = *Archips* HÜBNER, [1825]. Tribe of *Tortricinae*.

*Archipsinae*: BUSCK; 1940, Bull. Sth Calif. Acad. Sci., 39: 91.

*Cnephasiades*: DIAKONOFF, 1941, Treubia, 18: 215. Given as suprageneric group in *Tortricidae*.

*Chresmarchides* DIAKONOFF, 1941, ibid.: 35.

*Cacoeciades* DIAKONOFF, 1941, Treubia, Hors sér., 1 (1): 31.

*Zacorisoides* DIAKONOFF, 1941, ibid.: 36. Nomen novum for *Chresmarchidii*.

*Archipsini*: OBRAZTSOV, 1942, Dt. ent. Z. Iris, 56: 157. Tribus of *Tortricinae*.

*Cnephasiini*: OBRAZTSOV, 1949, Entomon. 1: 201. Tribe of *Tortricinae*.

*Zacorisini*: OBRAZTSOV, 1949, ibid.: 201. Tribe of *Tortricinae*.

*Cacoecini* DIAKONOFF, 1952, Verh. K. ned. Akad. Wet., Afd. Nat., (2) 49 (1): 99.

*Epitymbiinae* COMMON, 1958, Proc. 10. int. Congr., 1 (1956): 291. Type-genus: *Epitymbia* MEYRICK, 1881. Subfamily of *Tortricidae*.

*Epitymbiini* COMMON, 1963, Austral. J. Zool., 2 (1): 85. Tribe of *Tortricinae*.

*Niasomini* POWELL, 1964, Univ. Calif. Publ. Ent., 32: 66. Tribe of *Tortricinae*. Not described.

Head usually roughly scaled. Ocellus probably developed in all species, but in some somewhat reduced. Antenna simple or dentate, in males often densely bristled, rarely with paired, rather long subbasal processes on each



segment of flagellum. Pedicel occasionally with a concavity. Labial palpus varying in length, in some species up to 6 times longer than diameter of the eye. Maxillary palpus usually 3-segmented.

Wingspan ca 10—40 mm.

Forewing well developed with exception of few micropterigous females. In males of numerous species a distinct costal fold present. Venation typical of *Tortricidae*, with a tendency to fusion of some veins, mostly  $m_3$  and  $cu_1$ , occasionally the former vein absent. Internal veins of median cell developed to varying degrees. Vein *pcu* well developed or completely absent with many intermediate forms. In the hindwing veins  $rr-m_1$  and  $m_3-cu_1$  separately from common points or stalked, often  $m_3$  absent.

Scale-cover usually dense, some scales of forewing appressed, or larger groups of scales erect. Pattern typical of *Tortricinae* with a tendency to reduction or transformation of basal blotch and subterminal marking. Brown and grey colours predominate, refractive pattern in some species developed.

Male genitalia with strong tegumen and uncus. The latter greatly varies in breadth, being often bifurcate. Base of uncus often broad with produced lateral parts. Various spines and setae occur in ventral surface of uncus, mainly distally. Gnathos typically developed, strong, terminating in a hook-like or plate-shaped process, and often with lateral or distal processes of the lateral arms. Exceptionally the lateral arms are not fused terminally. Socii vary greatly in size, being often completely reduced. Usually they are hairy, but in some cases strong bristles or dents are to be found. Vinculum well developed, broad ventrally, usually strongly sclerotised throughout. Valva broad or distinctly elongate, with well developed or completely atrophied costa. Sacculus provided with free, termination or various processes or in form of smooth sclerotisation of ventral edge of valva. Distal edge of valva usually rounded, rarely with well developed brachiola. Various hairs and bristles occurring especially on internal surface of valva. Transtilla in majority of the species well developed, provided with various processes, indentations or minute bristles or other sculpturing, often median or lateral parts distinctly differentiating. In other species transtilla membranous or only partially more strongly sclerotised. Juxta plate-shaped, uniform, more or less incised in middle of dorsal edge, often provided with small hairy patches dorsolaterally. Aedeagus greatly variable in shape and size, with well developed, rarely shortened coecum penis which occasionally may be bilobed apically. Distal part of aedeagus usually tubular often partially membranous dorsally or dorsolaterally. In many species and genera various dents, thorns, plates or bifurcation of distal part of aedeagus occur. Vesica large, extrusible, with or without cornuti or sculpturing. Cornuti mainly spine-like or capitate, rarely plate-shaped, single or numerous, minute or very large.

Musculature of male genitalia. In the most primitive species all muscles preserved, but in the majority of the representatives of the subtribe muscle  $m_2$  absent. Muscle  $m_1$  invariably well developed,  $m_2$  inserted on proximal process of valva,  $m_4$  short and broad, inserted on transtilla near base or medially,  $m_6$

typically developed and inserted. Muscle  $m_5$  varies in size and shows a tendency to divide into dorsal and ventral arms. In some species, main part of this muscle is inserted on dorsal part of valva basally and on dorsal portion of vinculum, in other ones the muscle is directed towards ventral portion of valva and inserted on sacculus dorso-medially and partially (the dorsal part of muscle) on dorsal part of vinculum. Occasionally this muscle is inserted in median part of valva. Muscles  $m_3$  are inserted on upper part of juxta and show a tendency to move towards the caulis or fuse with one another. Muscles of tuba analis and gnathos are variable in size and form, being often divided into three arms.

Female genitalia. Usually ovipositor typically developed, but floricomous and telescopic forms occasionally occur. Papillae anales in the two latter types of ovipositor petal-shaped or narrow and coalescent. Apophyses in telescopic ovipositor very long, especially the apophyses posteriores. The apophyses anteriores in some species very short. Sterigma variably developed and sclerotised to varying degrees. Often only lamella postvaginalis or lamella antevaginalis present, but in some genera both fused lamellae or indistinct sclerites surrounded by variously formed scobinate or minutely bristled membrane occur. Sterigma connected with the apophyses anteriores by narrow linkages situated laterally which exceptionally are ill-defined or completely atrophied. Ostium bursae placed medially in sterigma, often on the bottom of a concavity and leading into antrum, if differentiated. Ductus bursae varying in length, often provided with cestum or sclerotisations of outer surfaces. Ductus seminalis variably positioned, very often subterminally. Corpus bursae often sculptured, occasionally provided with more strongly sclerotised areas. Signum, if present, plate-shaped (smooth or dentate) or funnel-like, often with well developed capitulum.

Scent organs: usually groups of androconial scales hidden by costal fold of male forewing and probably groups of erect scales of forewing in both sexes. Coremata occurs in innumerable genera.

Sexual dimorphism appearing mainly in size, the females being often almost twice as large as the males, coloration and pattern of forewing. Rarely females micropterigous.

Larva. There is no possibility of giving any characteristics of the chaetotaxy without repeating the data common for *Sparganothina* and even some *Olethreutinae* (cf. MACKAY, 1962). SWATSCHKE (1958) provides a diagnosis based on European species which is also defective. One can suppose that the following characterise the *Archipina* larvae to some extent. Bristles IV and V diagonally arranged on all abdominal segments, bristles I and II on separate warts on 9th abdominal segment, group VII consists of 3 setae on 7th and two setae on the two first abdominal segments. In the mesothorax IIIa is situated dorso-cranially to III. Often seta VI absent from 9th abdominal segment.

Pupa. Terminal portion of abdomen produced or short, cremaster consisting of a pair of hooks directed dorsally, or smooth.

Bionomy. Newly hatched larvae of some species mine in the leaves. Other larvae feed in the buds, roll or bind leaves or flowers, are solitary and rarely



gregarious. They utilise all sorts of dicotyledonous and many monocotyledonous plants, being mainly oligophagous or monophagous. A few species are polyphagous. Hibernation in various instars, mainly as the egg or caterpillar. The larvae often build hibernacula. In temperate zones the species of *Archipina* are usually mono- or bivoltine; however, several multivoltine species are known. In the tropics the generations are more numerous.

Distribution: as for *Tortricidae*.

Comments. Of the above listed synonyms three need special attention. These are the names of groups treated during the last 50 years as separate taxa.

*Cnephasiini* was erected as a family *Cnephasidae* by STANTON in 1856 and subsequently variably treated, mainly as a tribe. Two years earlier STANTON also described *Exapatidae* with type-genus *Exapate* HBN. which is very close to *Cnephasia* CURT. and commonly placed in *Cnephasiini*. The name *Exapatidae* was, however, neglected. OBRAZTSOV (1954) who treated *Cnephasiini* as a tribe hardly found characters to differentiate them from the *Archipini*. According to that author the uncus in *Cnephasiini* is slender and the signum if present, is a dentate plate. However, these characters are shared with *Archipina*, and partially also with *Schoenotenina*, *Ceracina* and *Tortricini* and therefore cannot be taken into consideration. COMMON (1963) found that Australian *Cnephasiini* differ from remaining tribes in having a well developed internal vein (*M*) of the forewing median cell and from *Archipini* in the shape of the transtilla. In his *Cnephasiini* many species occur with a broad, often bifurcate, uncus which basically does not fit OBRAZTSOV's diagnosis. KUZNETSOV and STEKOLNIKOV (1973) based the diagnosis of *Cnephasiidi* mainly on OBRAZTSOV's work but also added some characters of the musculature of the male genitalia, based on an examination of *Exapate congelatella* (CLERCK). The main character differing this tribe from *Archipini* was after these authors position of the muscle  $m_4$  which is inserted on the transtilla submedially. A similar position of this muscle is known, however, in other groups of *Archipini*, e.g. in *Sparganothina* and it varies in *Cnephasiini*, being more or less situated laterally. It seems possible that in some *Archipina* species having a median prominence of the transtilla, this muscle is also positioned more medially. Because of lack of any other character differentiating the group of genera closely correlated with *Cnephasia* CURT., I sink this name as a synonym of *Archipina*.

The *Chresmarchidii*, also known under the name *Zacoriscini*, were separated on the presence of the corethrogynae i.e. an area (7th sternite) surrounding the ostium bursae covered with very strong hair or scales and coremata developed in some abdominal segments. COMMON (1958) found corethrogynae in some Australian species which apparently do not belong in this group, and DIAKONOFF (1952) realised that *Zacoriscini* and *Archipinae* intergrade. COMMON (loc. cit.) suggests that *Zacoriscini* are only a highly specialised group of *Archipinae* and DIAKONOFF (1970) mentions *Zacorisca* and its allies as belonging in *Archipini*. I am also treating *Zacoriscini* as synonymous with *Archipina*.

*Epitymbiinae* was described by COMMON as a subfamily of *Tortricidae* close to

*Cnephasiinae* and *Archipinae*. It should differ from them in having heavily sclerotised genitalia and different ornamentation of the sacculus and aedeagus in the male. Some additional characters mentioned by that author are also of slight importance and cannot be treated as a support even for a subtribal division. It is noteworthy that in the discussed Australian group of *Archipina* corethrogyne, treated by COMMON as being homologous with that in *Zacorisca*, may develop.

About 700 species known to date.

### *Ceracina*

*Ceraciinae* COTES and SWINHOE 1889, Cat. Moths India 6: 699. Type-genus: *Cerace* WALKER, 1863. Described as subfamily of *Tortricidae*.

*Ceracidae*: MEYRICK 1908, Rec. Indian Mus., 2: 395. Family of *Tortricina*.

*Ceracidi*: DIAKONOFF 1939, Zoöl. Meded. Leiden, 21: 128. Given as subfamily of *Tortricidae*.

*Ceraciini*: OBRAZTSOV 1949, Entomon, 1: 201. Tribe of *Tortricinae*.

*Ceracini*: DIAKONOFF 1960, Verh. 11. int. Kongr. Ent. Wien: 125. Correct formation of the tribe name.

Head smooth-scaled; ocellus developed; antenna ciliate, especially distinctly in male; labial palpus fairly short (usually ca 1.5); maxillary palpus two-segmented.

Thorax and legs smooth-scaled. Expanse of wings 30—60 mm. Forewing elongate, often elongate-ovate, sometimes with apex concave at vein  $r_5$ . Costal fold absent. All veins separate but  $m_3$ — $cu_1$  in hindwing from one point. In forewing internal veins of median cell developed, chorda extending from beyond base of  $r_1$  reaching  $r_3$ , often long median stem ( $M$ ) present, terminating at  $m_2$ . Postcubital vein fully developed or partially atrophying in median portion, always thin. Coloration telechromatic; pattern consisting of rows of spots fusing occasionally with one the other.

Male genitalia with well developed tegumen and strong hooked uncus broadening basally. Gnathos typically developed, strong, with pointed apex. Tuba analis with fairly well developed subscaphium. Socius large, drooping, hairy. Vinculum broad. Valva elongate with distinct costa and sacculus. Strong bristle-like hairs on internal surface of valva terminally. Aedeagus simple; caulis fairly short; juxta well sclerotised plate. Transtilla band-shaped, or ill-defined, membranous.

Musculature of male genitalia (*Cerace xanthocosma* DIAKONOFF examined). Muscle  $m_1$  strong, typically inserted with large area of insertion on pedunculus and on lateral parts of base of uncus;  $m_4$  short, very broad, curved, inserted on end of pedunculus;  $m_5$  large, entering deep into valva with dorsal edge reaching middle breadth of valva and inserted along dorsal edge of sacculus;  $m_6$  strong, fused at coecum penis;  $m_3$  well developed, partially inserted on terminal portion of caulis.

Female genitalia. Papilla analis normally developed. Degree of sclerotisation of the sterigma varying and often its distal portion is strongly sclerotised or



process of membranisation is even more advanced. Ostium broad, protruding ventrally and antrum incised in the eighth sternite. Ductus bursae membranous except for distal portion which may be sculptured or somewhat more strongly sclerotised. Signum plate-shaped, partially invaginated, dentate.

Larva little known. Chaetotaxy (after YASUDA, 1965, based on 2 species) is as follows. On 8th abdominal segment, III and IIIa on common pinaculum, on 8th segment, I dorsal to II, III anterior to and, IIIa ventral to spiracle. In abdominal segments 1, 2, 7, 8 and 9 group VII numbering 3:3:3:2:2. Proleg crochets triordinal, numbering 53—68. Other characters insufficiently known or not important.

Pupa with long cremaster expanding at the top laterally; provided with knife-shaped setae.

Bionomy. Larva rolling the leaves or tying tops of shoots of coniferous and deciduous trees. One or two generations yearly. Hibernation (in Japan) in early larval instars. The larvae do not build hibernacula and feed occasionally in warmer winter days. Moth diurnal.

Distribution: Oriental Region and eastern part of Palaearctic Region.

Comments. About 50 species known to date. This group, described as a distinct family, was lately (DIAKONOFF, 1970) treated as a tribe of *Tortricinae*. In the mentioned work the characters distinguishing *Ceracina* from other groups of the subfamily were the diurnal habits of life of the imago and length of some setae in the larvae. These characters seem insufficient to preserve tribal status for Ceracid moths. The differences in the structure of the genitalia are very slight compared with other *Archipini*. The diurnal activity of imagines, vivid coloration and smooth scaled head is known in some other *Archipini* e.g. in *Atteria* WALKER and *Zacorisca* MEYRICK. I am thus lowering the group to subtribal status because the only difference from the *Archipina* is the position of muscle  $m_3$ , part of which is inserted on the caulis. However, additional study is needed to solve the problem of importance of this character which most probably is shared with other *Archipini*.

### *Sparganothina*

*Sparganothidae* DRUCE, 1912, Entomologist's mon. Mag., **48**: 133. Type-genus: *Sparganothis* HÜBNER, [1825]. Described as family of *Microlepidoptera*.

*Sparganothidae* WALSINGHAM, 1913, Biologia cent. am., Zool. *Lepid. Heterocera*, **4**: 206. Described as new family.

*Sparganothiinae*: BUSCK, 1940, Bull. Sth. Calif. Acad. Sci., **39**: 91, 94. As subfamily of *Tortricidae*.

*Atteridae* BUSCK, 1932, Boll. biol., **21**: 43. Type-species: *Atteria* WALKER, 1863. Family of *Microlepidoptera*.

*Sparganothinae* OBRAZTSOV, 1944, Dt. ent. Z. Iris, **57**: 68. Erected as a new subfamily of *Tortricidae*.

*Atterini*: DIAKONOFF, 1959, Ark. Zool., (2) **12** (13). 165. Tribe of *Ceracinae*.

*Sparganothidinae*: DIAKONOFF, *ibid.*: 165.

*Sparganothidini*: DIAKONOFF, 1961, Verh. 11. Int. Kongr. Ent. Wien: 126. As tribe of *Tortricinae*.

*Sparganothidina*: DIAKONOFF, 1961, *ibid*: 126. As subtribe of *Sparganothidini*.

*Anacrusina* DIAKONOFF, 1961, *ibid*: 126. Type-genus: *Anacrusis* ZELLER, 1877. Erected as subtribe of *Sparganothidini*.

*Sparganothini*: MACKAY, 1962, *Can. Ent., Suppl.*, **28**: 5, 72. As tribe of *Tortricinae*.

*Atteriini*: POWELL, 1964, *Univ. Calif. Publ. Ent.*, **32**: 66. As tribe of *Tortricinae*.

*Anacrusiini*: OBRATSOV, 1966, *Proc. U.S. Natn. Mus.*, **118** (3535): 575. Correct formation of the tribe name.

*Sparganothidii*: KUZNETSOV and STEKOLNIKOV, 1973, *Trudy ènt. vses. Obsheh.*, **56**: 39. As supertribe of *Tortricinae*.

Head with ocellus strongly reduced or absent; antenna simple or serrate, in males distinctly ciliate. Labial palpus up to 6; maxillary palpus 2—3 segmented. Thorax without crest.

Wingspan ca 16—30 mm. Forewing in male often with costal fold. Venation: in forewing  $r_4$ — $r_5$  stalked, internal vein of median cell developed in more primitive genera. In the hindwing  $rr$ — $m_1$  short stalked,  $m_3$ — $cu_1$  separately or from one point. A hair pecten in basal portion of upper side of cubital arm of median cell well developed in most specialised forms. Pattern typical of *Tortricinae*, ground colour often glossy.

Abdomen with well developed mensis dorsalis.

Male genitalia. Tegumen broad, laterally partially indistinctly sclerotised. Uncus broad basally, then very thin, usually not broadening apically. Gnathos well developed, often not fused terminally. Socii broad, often produced dorsally, in ventral parts fused with arms of gnathos. Tuba analis rather weakly sclerotised or with ill-defined subscaphium. Vinculum uniform. Valva large, weakly sclerotised distally, with rather delicate distal part of costa and simple sacculus. Juxta proportionally small, plate-shaped, sometimes folding along median axis. Transtilla well developed, provided with single or bipartite median prominence. Aedeagus proportionally short with well developed coecum penis. Orifice for ductus ejaculatorius situated on left side of coecum penis. Cornuti numerous, developed in form of spines with lateral prominences subbasally for fixing in the vesica. Caulis very short.

Musculature of male genitalia (examined in *Sparganothis pilleriana* (DEN. & SCHIFF.) only) with muscle  $m_1$  strongly developed,  $m_4$  thick, inserting on median part of transtilla;  $m_2$  absent. Muscle  $m_3$  typically developed,  $m_5$  consisting of two parts, the smaller inserting on the basal part of the costa of the valva, the larger (main part) inside the valva and along the edge of vinculum. Muscles  $m_6$  fused with one another, asymmetrical, reaching on the left side of coecum penis the opening for the ductus ejaculatorius.

Female genitalia typically developed. Sterigma consisting of fairly large lamella postvaginalis and weak lamella antevaginalis, between which a pocket-like concavity is formed with the ostium bursae at the bottom. Position of ductus seminalis characteristic specifically. Signum plate-shaped or represented by a row of granules along middle part of corpus bursae.

Scent organs developed in form of androconial scales covered with costal fold.



Sexual dimorphism occurring in size and often in shape of forewing (females often very large with somewhat narrowed wing).

The larva does not show any differences from that of *Archipina*. Pupa insufficiently known.

Bionomy. The eggs are deposited in groups each imbricate and covered with a substance which hardens on exposure to the air. Larvae live solitarily or in small groups, binding or rolling leaves, shoots or flowers as well as boring in buds, fruits, stems or bark. Polyphagous. Number of generations depends on climatic conditions, in temperate zones usually 1—3. Hibernation occurring as, small larva which constructs a hibernaculum.

Distribution. The subtribe is abundantly represented in the Nearctic and Neotropical Regions, scarcely so in Palaearctic, Oriental and Australian.

Comments. About 150 species. This subtribe may be divided into two groups. DIAKONOFF (1961) proposed its division into *Sparganothidina* and *Anacrusina*, but earlier BUSCK (1932) had erected *Atteridae*. OBRAZTSOV (1966) distinguished in the latter some genera belonging in *Archipina*, *Polyorthina* and proposed the transfer of *Atteria* WALKER to *Anacrusiini* (treated as a tribe). However, the name by BUSCK has priority and in this paper I resurrected it, treating *Atteria* WALKER and *Anacrusis* ZELLER only as a group of genera *Atteriae* equivalent to *Sparganothides*. The *Atteriae* show some common characters (c.f. DIAKONOFF, 1961: 126) the most important of which are presence of uniform gnathos and lack of hair pecten of the hindwing cubital vein. The species of *Anacrusis* ZELLER are characterised by cryptic coloration while those of *Atteria* WALKER resemble the species of *Ceracina*. This group is limited exclusively to the Neotropical Region.

### *Chlidanotina*

*Chlidanotidae* MEYRICK 1906, J. Bombay nat. Hist. Soc., 17: 412. Type-genus: *Chlidanota* MEYRICK, 1906. New family in *Tortricina*.

*Chlidanotinae*: DIAKONOFF, 1960, Verh. K. ned. Akad. Wet., Afd. Nat., (2) 53 (3): 192. Subfamily of *Tortricidae*.

*Chlidanotini*: DIAKONOFF, 1960, ibid.: 193. Tribe of *Chlidanotinae*.

Head with appressed scales; ocellus small; chaetosema present. Antenna simple, distinctly ciliated in male; labial palpus 1.3—2; maxillary palpus 1—2 segmented.

Legs often with long loose scales on tibia. Forewing without costal fold but with a subapical line of weakness (at rest tip of wing bent upwards).

Expanse ca 8—30 mm.

Venation: in forewing one of radial veins usually absent; *pcu* vestigial or absent; internal veins of median cell not developed or a trace of chorda exceptionally preserved. Two or three last radial veins with tendency to stalk. In hindwing *rr*—*m*<sub>1</sub> on long stalk, *m*<sub>3</sub>—*cu*<sub>1</sub> separately, from one point or stalked. Cryptic coloration; scales probably invariably not appressed. Ground colour

of forewing usually whitish, pattern brownish consisting of a fascia extending from middle of dorsum to apex. Often all the area beyond this fascia is suffused. Dorsum suffused or spotted, postbasal and median blotches at costa more or less distinct. Often costal strigulation developed.

Male genitalia. Tegumen broad; uncus slender; gnathos typically developed or completely atrophied; hami present; socii membranous, hairy. Vinculum sometimes „expanded to form a short broad saccus” (COMMON, 1965: 710). Valva elongate with well developed costa and usually simple sacculus. Juxta rather small, plate-shaped; transtilla strongly developed provided with pair of dorsal or (and) ventral processes or lobes. Aedeagus slender, simple, provided with rather short coecum penis and often very long caulis. Cornuti in form of numerous thin spines or single stronger spine, if present.

Musculature of male genitalia unknown.

Female genitalia. Ovipositor typically developed. Sterigma membranous or in form of lamella antevaginalis or postvaginalis, or both plates fused. Antrum distinct, well sclerotised; ductus bursae slender; ductus seminalis from anterior part of ductus bursae or corpus bursae, the latter provided with an additional sac with which it is connected by a duct. At the base of the duct a ring- or cup-shaped signum present. In first case from the edges of the signum numerous long spines arise.

Scent organs: no data.

Larva and pupa unknown. The bionomic data are insufficient to characterise the group.

Distribution: Oriental, Australian and Ethiopian Regions (Madagascar).

Comments. About 50 species known. *Chlidanotidae* were erected by MEYRICK (1906) for *Chlidanota* MEYRICK as a distinct family and this status was accepted by DIAKONOFF (1949 and further papers) and CLARKE (1955). Only in 1960 DIAKONOFF decided to lower the status of this group to subfamily *Chlidanotinae*. This author included in *Chlidanotinae* two tribes, viz., *Schoenotenini* described in 1952 by himself as a separate family of *Tortricoidea* and *Chlidanotini* s. str. COMMON (1965) accepted the tribal status of the two groups, commenting, however, on their only superficial similarity and placing as equivalent tribes of *Tortricinae*. It seems that the hami developed in this group independently and an exceptional reduction of the typical gnathos is a secondary character. The position of this subtribe cannot be fixed without further study especially of the musculature of the male genitalia.

### *Polyorthina*

*Polyorthini* OBRATSOV, 1966, Proc. U. S. natn. Mus., **118** (3535): 578. Type-genus: *Polyortha* DOGNIN, 1905. New tribe in *Tortricinae*.

Head with more or less appressed scales. Ocellus developed. Antenna simple, often biciliate. Tongue short; labial palpus 1.5—5. Thorax often with posterior crest.



Wingspan 12—32 mm. Forewing somewhat expanding terminally or elongate-ovate, without costal fold in males. Venation: in forewing all veins separate or last two radial veins and  $m_3-cu_1$  stalked, rarely one radial vein absent. Chorda and internal median vein of median cell variably developed, if present. In hindwing veins  $rr-m_1$  and  $m_2-cu_1$  with tendency to stalk. Coloration either vivid, or typically cryptic, characteristic of *Tortricinae*. Wing surface smooth or numerous raised scales or appressed tufts present.

Male genitalia. Tegumen strong; uncus well developed, slender, hooked. Gnathos typical, rather delicate; socii drooping weakly sclerotised; tuba analis membranous. Valva large or very large, externally rather weakly sclerotised, provided with large longitudinal split reaching at least to two-thirds its length that opens dorso-laterally. Costa and sacculus usually weak. Vinculum complicated, broad. Juxta plate-shaped; transtilla large, partially membranous, band-shaped or paired. Aedeagus varying in breadth and length to a great degree, often slender with coecum almost completely reduced, terminating with a process. Caulis strongly reduced. Cornuti, if present, in form of thorns or plates, often developed as a row of short spines (cuneus).

Musculature of male genitalia unknown.

Female genitalia. Ovipositor normally developed. Sterigma cup-shaped with more or less distinctly developed lamella postvaginalis, rarely resembling that of the *Tortricini* with produced proximal corners. In case of stronger reduction of plates the membrane surrounding the ostium provides various sculptures and small sclerites. Ductus bursae normally developed, or very broad; antrum usually differentiated; corpus bursae often distinctly sculptured, if present. Signum plate-shaped, often with a distinct fold or shallow invagination, rarely in form of a bunch of spines.

Scent organs. Large coremata of eight abdominal segment. A pencil-like cluster of scales fit in longitudinal split of the valva. Exceptionally the cluster is lacking; however, the split in the valva is developed. In several species, groups of erect scales occur in the forewings.

Sexual dimorphism (occurring mainly in the size) known in majority of the species.

Early stages: no data.

Bionomy: no data except on the time of collection of some species.

Comments. About 60 species known to belong here. The group was constantly treated as a tribe. OBRAZTSOV (1966) supposed it to be rather close to the *Cnephasiini* while DIAKONOFF (1974) considered it as a link between *Tortricinae* and *Chlidanotinae*. In this paper it is treated as a subtribe, being probably the most specialised group closely correlated with *Archipina*. Until the musculature of the male genitalia is examined the position of the *Polyorthina* cannot be fixed.

## *Cochylini*

*Cochylidi* GUENÉE, 1845, Annls Soc. ent. Fr., (2) 3: 297. Type-genus: *Cochylis* TREITSCHKE, 1829. Described as a tribe of *Tortrices*.

*Lozoperidae* STANTON, 1858, Manual Br. Butterflies Moths, 2: 188; 1959: 265. Type-genus: *Lozopera* STEPHENS, 1829. Described as family of *Tortricina*.

*Cochylidi*: STEPHENS, 1852, List. Spec. Br. Anim. Coll. Br. Mus., 10: 76, 96. Subfamily of *Tortricidae*.

*Cochylidae*: MORRIS, 1868, Nat. Hist. Br. Moths, 3: 209. Family of *Tortricina*.

*Conchylinae*: COTES and SWINHOE, 1889, Cat. Moths India, 6: 695. Type-genus: *Conchylis* TREITSCHKE, 1830 (emedation of *Cochylis* TREITSCHKE, 1829).

*Conchylidae*: MEYRICK, 1882, Proc. Linn. Soc. N.S.W., 6: 413, 693. Family of *Tortricina*.

*Phaloniadae* MEYRICK, 1895, Handb. Br. Lepid.: 543. Type-genus: *Phalonia* HÜBNER, [1825] = *Aethes* BILLBERG, 1820. Described as family of *Tortricina*.

*Phaloniinae*: REBEL, 1901 [in:] STAUDINGER and REBEL, Cat. Lepid. pal. Faunengeb., 2: 94 (correction of *Phaloniadae* MEYRICK).

*Commophilidae* HAMPSON, 1918, Novit. zool., 25: 387. Type-genus: *Commophila* HÜBNER, [1825]. Replacement name for *Phaloniadae*.

*Phaloniidae*: MEYRICK, 1906, J. Bombay nat. Hist. Soc., 17: 137 (correction of family name *Phaloniadae* MEYRICK, 1895).

*Phaloniadii*: PIERCE and METCALFE, 1922, Genitalia *Tortricidae* Lepid. Br. Islands: 24 (status not mentioned; probably subfamily).

*Hysterosiinae* HESLOP, 1938, Cat. Br. Lepid.: 70. Type-genus: *Hysterosia* STEPHENS, 1852. Given as subfamily of *Phaloniidae*.

*Lozoperinae*: HESLOP, 1938, ibid.: 70. Subfamily of *Phaloniidae*.

*Aetheinae* OBRAZTSOV, 1946, Z. wien. ent. Ges., 30 (1945): 22. Type-genus: *Aethes* BILLBERG, 1820. Proposed as subfamily name of *Tortricidae* to replace *Phaloniinae*.

*Hysterosiini* OBRAZTSOV, 1944, Dt. ent. Z. Iris, 57: 68. Type-genus: *Hysterosia* STEPHENS, 1852. Described as new tribe of *Phaloniinae*.

*Agapetidae* OBRAZTSOV, 1950, Ent. News, 61: 198. Type-genus: *Agapeta* HÜBNER, [1825]. Proposed as the correct name of family *Phaloniidae*.

*Cochylini*: KUZNETSOV and STEKOLNIKOV, 1973, Trudy vses. ènt. Obsheh., 56: 21. Tribe of *Cochylidii*.

*Cochylidii*: KUZNETSOV and STEKOLNIKOV, 1973, ibid.: 37. Supertribe of *Tortricinae*.

Head usually roughly scaled; antenna simple, ciliate; tongue and remaining parts of the mouth normally developed. Ocellus present.

Thorax often with crest. Wingspan 8—34 mm. Forewing usually with costa weakly curved outwards basally, termen never deeply sinuate. Costal fold in males of few species not characteristic generically. In the venation of forewing there is a tendency for the last radial veins to develop into of short stalk. Postcubital vein absent or strongly reduced; median cell with occasionally well developed internal vein (chorda). In hindwing veins  $rr-m_1$  and  $m_3-cu_1$  run separately, from common point or are stalked. Pattern of forewing with usually distinct dorsal blotch extending towards middle of wing accompanied by opposite costal spot with it may connect. Basal blotch and subterminal fascia, sometimes reduced to two spots at costa and tornus, occur. Refractive pattern usually well developed.

Abdomen typically developed, often with elongate pregenital tergite.



Male genitalia. Tegumen broad, often rather weakly sclerotised. In the most primitive species uncus well developed, often very strong, but in the majority of genera completely atrophied and terminal portion of tegumen membranous. Rarely distal part of tegumen elongate, resembling the uncus. Gnathos reduced to very weak lateral sclerites or, usually, completely atrophied. Socii variable in shape and size: in some species heavily sclerotised, long or provided with processes, in others almost completely atrophied. Tuba analis membranous. Vinculum typically developed or consisting of a pair of arms connected by a membrane ventrally; exceptionally ventral portion strong produced anteriorly. Valva varying in length; costa well developed, in some genera separated from main part, provided with apical dents and directed upwards. Sacculus usually well developed, often with terminal process. Exceptionally, distinct processes of internal surface of valva or thin brachiola occur. Juxta plate-shaped, varying in size to some degree, transtilla well developed, chiefly with median identate prominence or process. Aedeagus usually very large, with strong coecum penis and proportionally short distal portion. Often lateral or dorsal processes occur. Vesica large, extrusible; cornuti in form of various thorns, spines or plates, often in great number. Caulis in the majority of species short or very short, but in some very large, dentate.

Musculature of male genitalia. All muscles preserved. Muscle  $m_1$  varies in size to a great degree, being often completely atrophied,  $m_2$  inserted on proximal process of valva or on transtilla more or less laterally. Similar variable position of the insertion points on valva and transtilla concern muscle  $m_4$ . Muscle  $m_3$  is typically inserted, often submedially on juxta. While muscle  $m_5$  has a rather constant insertion on the coecum penis, muscle  $m_6$  may be strongly moved distally beyond the opening for the ductus ejaculatorius.

Female genitalia. Ovipositor normally developed, rarely telescopic; papilla analis always narrow. Apophyses very long in the genitalia with telescopic ovipositor, especially the apophyses posteriores. Sterigma in form of a plate accompanied by minutely spined or bristled membrane, sometimes without any sclerite. In case of well sclerotised lamellae the linkages to apophyses anteriores well developed. Antrum often very broad and heavily sclerotised; ductus bursae in majority of species broad with variably positioned ductus seminalis. Corpus bursae sometimes hardly broader than the ductus bursae, provided often with additional sacs. Signa, if present, irregular groups of spines and/or diffused plate-shaped sclerites.

Scent organs: as in *Archipina* except for coremata.

Sexual dimorphism slight; seasonal dimorphism occurring in size also indistinct.

Larva differing slightly in chaetotaxy from that of *Archipini* and other *Tortricinae*, mostly by presence of single crowns of crochets in the abdominal legs; however, that character is to be found also in some *Archipini*. Following SWATSCHEK (1958) the diagnosis may be completed as follows: in 9th abdominal segment bristle VI absent and bristles VIII more distantly placed from one

another than in 8th segment, or seta  $Frl_1$  closer to  $Frl_2$  than to  $F_1$ . Sutura coronalis usually not longer than the breadth of adfrontalia at the level of apex of clypeus.

Pupa as in some representatives of *Archipina* but with 4 or 8 thorns (STEKOLNIKOV and KUZNETSOV, 1973).

Bionomy. The larvae spin together flowers and seeds of various plants, boring inside them or in stems, roots or bark of various dicotyledonous plants, mainly *Umbelliferae*. One or two generations each year in the temperate zone; no data from the tropics. Hibernation in the Palaearctic Region probably in the pupal stage.

Distribution. The majority of the species are known from the Holarctic Region, but according to available material one can suppose that they are common also in the Oriental, Ethiopian and Neotropical Regions. Only one species is known from Australia.

Comments. Ca 500 species belong here. Because of some superficial characters the group was recently treated as a distinct family. The synonymy has been discussed in several papers including that of RAZOWSKI (1970).

### *Tortricini*

*Tortricidi* GUENÉE, 1845, *Annls Soc. ent. Fr.* (2) 3: 136. Type-genus: *Tortrix* LINNAEUS, 1758. Tribe of *Tortrices*.

*Tortricidae*: STANTON, 1858, *Manual Br. Butterflies Moths*, 2: 188. Family of *Tortricinae*.

*Peroneidae* STANTON, 1859, *ibid.*, 2: 229. Type-genus: *Peronea* CURTIS 1824 = *Acleris* HÜBNER, [1825].

*Tortricinae*: WALSINGHAM, 1897, *Trans. ent. Soc. Lond.*, 1895: 59.

*Peroneidii*: PIERCE and METCALFE, 1922, *Genitalia Tortricidae* Lepid. Br. Islands: 16 (?subfamily of *Tortricidae*).

*Tortricidii*: FILIPPIEV, 1931, *Ezheg. zool. Mus.*, 31 (1930): 500. Proposed as nomen novum for *Peroneidii*. Tribe of *Tortricinae*.

*Peroneinae*: HESLOP, 1938, *Cat. Br. Lepid.*: 72. Subfamily of *Tortricidae*, includes also *Sparganothis* HÜBNER.

*Peroneidii*: DIAKONOFF, 1939, *Zoöl. Meded. Leiden*, 21: 217. Incorrect formation of subfamily name.

*Peroneades*: DIAKONOFF, 1941, *Treubia*, 18: 431.

*Tortricini*: OBRATZSOV, 1949, *Entomon*, 1: 201. Tribus of *Tortricinae*.

*Peroneini*: DIAKONOFF, 1953, *Verh. K. ned. Akad. Wet., Afd. Nat.*, (2) 49 (3): 82.

Head with usually rough scales; antenna simple, ciliate; ocellus present; haustellum well developed; labial palpus fairly short; 1.3—3; maxillary palpus weak, at most consisting of 3 partially fused segments.

Wingspan ca 8—30 mm. Forewing usually with distinctly convex costal edge, rarely elongate-ovate, without costal fold. Venation typical of *Tortricinae*. In forewing veins separate, rarely  $r_4$ — $r_5$ , or  $r_3$ ,  $r_4$ ,  $r_5$  stalked; veins  $m_3$ — $cu_1$  show similar tendencies. In hindwing all veins separate or  $rr$ — $m_1$  and (or)  $m_3$ — $cu_1$  from common point or stalked. Usually cryptic coloration occurs, but in some species distinct refractive pattern developed.



Plates of abdomen typical, rarely subterminal sternite with long anterior process or row of strong distal bristles.

Male genitalia. Tegumen usually well developed; in primitive genera uncus well developed, in more advanced ones atrophied and then top part of tegumen provided with strong processes. Gnathos invariably absent in the typical form, in some genera rather strong, lateral, band-like sclerites in membrane connecting base of tuba analis are developed. The latter well sclerotised ventrally to form a subscaphium provided with various terminal projections. Socii varying in shape and size to a great degree, usually simple, sometimes, however, complicated, well sclerotised and long with terminal parts hairy. Vinculum slender, uniform. Valva elongate, usually with long, rarely strongly shortened, costa, well developed brachiola and strong sacculus provided in majority of species with spined, free termination. Juxta large, usually folded along vertical axis; transtilla if present in form of a narrow transverse fascia. Aedeagus proportionally small, tubular, partially membranous, often provided with various thorns or processes, with short coecum penis and very short or almost completely reduced caulis. Cornuti in form of short capitate spines, and plates.

The musculature of the male genitalia is characterised by the constant lack of  $m_4$ . Muscle  $m_1$  is, in all examined species, well developed and if reduced its median portion inserting on the tuba analis is preserved. Muscle  $m_2$  inserts invariably on the processus basalis of the valva, and is proportionally weak. Muscle  $m_6$  is typically developed,  $m_5$  with strong ventral portion inserting on the sacculus inside the valva. Its dorsal insertion on the costa is small. Muscle  $m_3$  is very strong, typically inserted.

Female genitalia. Papilla analis and ovipositor of the three types known in *Tortricidae* (the floricomous the rarest). Sterigma plate-shaped or deeply concave medially. The ostium bursae is placed at the bottom of the concavity and the lateral parts of it are produced to form proximal processes. Antrum often differentiated; ductus seminalis variably positioned on ductus bursae; cestum absent; corpus bursae with plate-shaped or dentate signum, if developed.

Scent organs: groups of erect scales on forewing and probably rows of costal bristles in basal portions of both wings occurring in few species as well as variably developed coremata. Exceptionally a bunch of scales present on upperside of forewing.

Sexual dimorphism rather slight, occurring in size, shape of wings and occasionally in pattern. Seasonal dimorphism in some species very distinctly expressed in wing shape, coloration and size.

The larva shows some differences from the remaining tribes. SWATSCHEK (1958) gives the following diagnosis. „Double crowns of crochets. On 9th abdominal segment bristles I and III on separate pinacula, when exceptionally fused on the abdominal segments IV and V almost equally long and sutura coronalis distinctly longer than breadth of adfrontalia. Group VII consists of 3 bristles on 2nd abdominal segment and two bristles on the seventh segment. On 9th abdominal segment, VI is developed, and setae VIII is further removed than

on 8th segment (with exception of one species)." The diagnosis by MACKAY (1962) is somewhat different: „seta III being on its own pinaculum separate from that of IIIa on most, if not all of abdominal segments 1—7; the VII group on segments 1, 2, 7, 8, and 9 numbering 3:3:2:2:2, or if less, then highly unstable; seta I on segment 9 on its own pinaculum in most species, or if on the same pinaculum as IIIa, then with VIII on 9 more or less twice as far apart as those on 8; the presence of an anal fork". The first diagnosis concerns the Palaearctic, the second, the Nearctic species. Unfortunately no data on larvae of the tropical *Tortricini* are available.

The pupa is characterised by a pair of hooks on cremaster directed ventrally.

Bionomy. The larvae roll or spin the leaves, rarely boring in the fruits, exceptionally feeding on coccids. Most commonly the dicotyledonous plants (mainly *Rosaceae*) are utilised, and only a few species are known to feed on coniferous plants. Usually the *Tortricini* are mono- or oligophagous. Hibernation very often in the adult stage; however, also eggs, larvae and pupae hibernate. One to three generations yearly are noted.

Distribution. The tribe is distributed in all regions, but very little is known from the Neotropical Region (1 species only). The most primitive species are from the Oriental, Ethiopian and Australian Regions.

About 300 species known to belong in this tribe.

### *Olethreutinae*

[*Olethreutae* HÜBNER, 1806, Tentamen....: 2. Type-genus: *Olethreutes* HÜBNER, 1806. Names included in rejected work].

*Olethreutae* HÜBNER, 1822, Verz. bekannter Schmett.: 374. No type-genus included, thus invalid.

*Grapholithidae*: MEYRICK, 1882, Proc. Linn. Soc. N. S. W., 6 (1881): 413. Type-genus: *Grapholitha* TREITSCHKE, 1830 = *Grapholita* TREITSCHKE, 1829.

*Grapholithinae*: MEYRICK, 1882, Trans. am. ent. Soc., 10: 27.

*Trichophoridae* WALSINGHAM, 1895, Trans. ent. Soc. Lond., 1895 (4): 517. No type-genus included. Mentioned as a group of *Tortricidae* [sic!] to be replaced by *Olethreutinae*.

*Olethreutinae* WALSINGHAM, 1895, ibid.: 517. Type-genus: *Olethreutes* HÜBNER, 1822. Proposed as a correction of the name *Olethreutae* HÜBNER, 1806.

*Epiblemidae* MEYRICK, 1895, Handb. Br. Lepid.: 453. Type-genus: *Epiblema* HÜBNER, [1825]. Family of *Tortricina*.

*Eucosmidae* MEYRICK, 1907, J. Bombay nat. Hist. Soc., 17: 731. Type-genus: *Eucosma* HÜBNER, [1823]. Family of *Tortricina*.

*Epibleminae*: KENNEL, 1907 [in:] SPULER, Schmett. Eur., 2: 263.

*Olethreutidae* WALSINGHAM, 1918, Biologia cent. am., Zool., Lepid.- Heterocera, 4: 224.

*Eucosmiidae*: HAMPSON, 1918, Novit. zool., 25: 387.

*Eucosminae*: FORBES, 1923, Mem. Cornell Univ. agr. exp. Stat., 68: 387.

*Eucosmiadae*: DIAKONOFF, 1947, Mem. Inst. scient. Madagascar, (A) 1 (1): 28. Incorrect formation of the family name *Eucosmidae* MEYRICK, 1907.

Wingspan 8—30 mm. Pattern of forewing with usually well developed costal strigulation and often tornal ocellus. Hindwing with cubital pecten dorsally, rarely without it.



Male genitalia. In more primitive forms uncus well developed, but in the most specialised ones completely atrophied. Gnathos typically developed only exceptionally, in the majority of species reduced to a pair of letaral band-like sclerites connecting base of tuba analis, or completely unsclerotised. Socii and occasionally dorsal processes of tegumen variably developed; tuba analis usually membranous; however, a subscaphium may occur. Vinculum simple; valva elongate, varying considerably in shape. Basal opening of valva invariably present, more or less long, processus basalis present. Distal part of valva forming a more or less distinct cucullus; various prominences of sacculus and spines or bristles of inner surface of valva developed. Juxta fused with caulis to form so called olethreutoid. Transtilla completely atrophied. Aedeagus simple with strongly shortened coecum penis. Cornuti, if present, usually spine like.

Musculature of male genitalia. Muscle  $m_1$  variably developed, very often strongly reduced or absent;  $m_2$  inserted on tegumen and basal process of valva;  $m_4$  on pedunculus and basal process of valva. Muscle  $m_3$  absent,  $m_5$  large, inserted on olethreutoid, muscle  $m_6$  showing similar tendency to move on to olethreutoid or on coecum penis distally.

Female genitalia with various types of ovipositor but mainly with a typically developed one; sterigma only exceptionally fused with apophyses anteriores, very often in form of weakly sclerotised membrane surrounding the ostium bursae. Two signa present, or corpus bursae without any.

Larva. The diagnosis is common to all *Tortricidae*. This subfamily does not show any constant characters and share them with the representatives of *Tortricinae*.

Pupae little known; no subfamily characters.

Bionomy. The larvae very often boring in stems, fruits, or roots; however, very many of them roll the leaves like members of *Tortricinae*.

Comments. About 2500 species known to date. The musculature of the male genitalia have not been examined in *Microcorsini*.

Comments. WALSINGHAM (1895) was the first to use the name *Olethreutinae* for this subfamily mentioning that it is a correction of HÜBNER's stirps' name *Olethreutae* (1806). However, HÜBNER's work (Tentamen...) is rejected for the nomenclatural purposes (cf. p. 90). In 1825 HÜBNER used again name *Olethreutae* but did not include its type-genus and therefore the name must be treated as invalid (International Code of Zoological Nomenclature, Article 11e). Prior to WALSINGHAM, MEYRICK proposed name *Grapholithinae* (in 1882) and *Epibleminae* (1895) for this subfamily but *Olethreutinae* have become consolidated thanks to several monographs, e.g., by HEINRICH (1923, 1926), KUZNETSOV and STEKOLNIKOV (1973) and DIAKONOFF (1973). To maintain stability, an application should be made to the International Commission of Zoological Nomenclature to have *Olethreutinae* WALSINGHAM, 1895 placed on the Official List of the Family Group Names in Zoology.

### *Microcorsini*

*Microcorsini* KUZNETSOV, 1970, Ènt. Obozr., 49: 442. Type-genus: *Microcorsus* WALSINGHAM, 1910. Described as tribe of *Olethreutinae*.

Labial palpus 1.5—2, head roughly scaled.

Wingspan 16—22 mm. Forewing pattern rather typical of *Tortricinae* without or with ill-defined costal strigulation. Ternal ocellus absent. Venation typical of *Tortricidae*, with all veins separate. In the forewing internal veins of median cell developed (i.e. radial and median branches) and *pcu* well developed but interrupted. No cubital pecten in hindwing in the majority of species.

Male genitalia. Uncus developed; gnathos typical but thin; tuba analis membranous; socii minute. Vinculum fairly large; valva with well developed costa and simple sacculus. Basal opening of valva very short, small; basal process of valva minute. Transtilla atrophied; juxta proportionally small, fused with ill-defined caulis. Aedeagus large with strong coccum penis.

Musculature of male genitalia unknown.

Female genitalia. Ovipositor normally developed; sterigma in form of rather well developed lamella antevaginalis and with distal membrane minutely bristled. Ostium bursae at the bottom of a concavity formed by middle part of sterigma. Antrum may be well sclerotised; ductus seminalis rather medially; corpus bursae provided with pair of horn-like, often asymmetrical signa. Sterigma connected with apophyses anteriores by thin linkages.

Scent organs. Androconia of hindwings in form of bunch of long scales hidden in a fold among veins  $a_1$  and  $a_2$  dorsally. Often costal fold covering scent scales occurs, or scent organs not found.

Sexual dimorphism mainly in size (females much larger than males).

Morphology of early stages and bionomy unknown.

Distribution (after KUZNETSOV, 1970): eastern part of Palaearctic region, Oriental, Australian and Neotropical regions.

Comments. About 20 species. This tribe, originally described in *Olethreutinae*, was subsequently transferred by its author to *Tortricinae* (KUZNETSOV, 1973). On genital characters one can suppose that *Microcorsini* are the most primitive tribe of *Olethreutinae*. The gnathos is preserved in the typical form while the valva is already developed its basal opening.

### *Olethreutini*

*Penthinidi* Guenée, 1845, Annls Soc. ent. Fr., (2) 3: 151. Type-genus: *Penthina* TREITSCHKE, 1830. Described as tribe of *Tortrices*.

*Sericoridi* GUENÉE, 1845, *ibid.*: 156. Type-genus: *Sericoris* TREITSCHKE, 1830. Described as tribe of *Tortrices*.

*Penthinidae*: R. L. [anonym], 1858, Accent. List. Br. Lepid.: 63. Family of *Tortricina*.

*Sericoridae*: R. L. [anonym], 1858, *ibid.*: 64. Family of *Tortricina*.

*Olethreutidii*: PIERCE and METCALFE, 1922, Genitalia Br. *Tortricidae*: XXI, 38.



Major group of *Tortricidae*, probably subfamily; should be treated as correction of *Olethreutinae* WALSINGHAM, 1895.

*Sericorina*: HESLOP, 1938, Cat. Br. Lepid.: 72. Subfamily of *Eucosmidae*.

*Argyroplocini* DIAKONOFF, 1953, Verh. K. ned. Akad. Wet., Afd. Nat., (2) 49 (3): 88. Type-genus: *Argyroploce* HÜBNER, [1825]. Described as tribe of *Eucosminae*.

*Eudemini* FALKOVITSH, 1962, Ent. Obozr., 41: 882. Type-genus: *Eudemis* HÜBNER, [1825]. Described as tribe of *Olethreutinae*.

*Olethreutini*: FALKOVITSH, 1962, ibid.: 883. Type-genus: *Olethreutes*, HÜBNER, 1822. Tribe of *Olethreutinae*.

*Lobesiini* FALKOVITSH, 1962, ibid.: 883. Type-genus: *Lobesia* GUENÉE, 1845. Tribe of *Olethreutinae*.

*Bactrini* FALKOVITSH, 1962, ibid.: 884. Type-genus: *Bactra* STEPHENS 1834. Tribe of *Olethreutinae*.

*Olethreutidii*: KUZNETSOV and STEKOLNIKOV, 1973, Trudy vses. ènt. Obsheh., 56: 38. Supertribe of *Olethreutinae*.

*Gatseclarkaeanae* DIAKONOFF, 1973, Zoöl. Monogr. Rijksmus. nat. Hist., 1: 5. Type-genus: *Gatesclarkaeana* DIAKONOFF, 1966. Described as subtribe of *Olethreutini*.

*Gnathmocerodides* DIAKONOFF, 1973, ibid.: 25. Type-genus: *Gnathmocerodes* DIAKONOFF, 1968. Subtribe of *Olethreutini*.

*Rhodocosmariae* DIAKONOFF, 1973, ibid.: 35. Type-genus: *Rhodocosmaria* DIAKONOFF, 1973. Subtribe of *Olethreutini*.

*Zomariae* DIAKONOFF, 1973, ibid.: 39. Type-genus: *Zomaria* HEINRICH, 1926. Subtribe of *Olethreutini*.

*Sorolophae* DIAKONOFF, 1973, ibid.: 47. Type-genus: *Sorolopha* LOWER, 1901. Subtribe of *Olethreutini*.

*Sycacanthae* DIAKONOFF, 1973, ibid.: 105. Type-genus: *Sycacantha* DIAKONOFF, 1959. Subtribe of *Olethreutini*.

*Statherotides* DIAKONOFF, 1973, ibid.: 179. Type-genus: *Statherotis* MEYRICK, 1909. Subtribe of *Olethreutini*.

*Neopotamiae* DIAKONOFF, 1973, ibid.: 295. Type-genus: *Neopotamia* DIAKONOFF, 1973. Subtribe of *Olethreutini*.

*Endotheniae* DIAKONOFF, 1973, ibid.: 363. Type-genus: *Endothenia* STEPHENS, 1852. Subtribe of *Olethreutini*.

*Bactrae*: DIAKONOFF, 1973, ibid.: 336. Subtribe of *Olethreutini*.

*Lobesiae*: DIAKONOFF, 1973, ibid.: 373. Subtribe of *Olethreutini*.

*Olethreutae*: DIAKONOFF, 1973, ibid.: 393. Subtribe of *Olethreutini*.

Head roughly scaled; ocellus usually present; labial palpus 1.2—3. Thorax often with a crest.

Wingspan ca 9—30 mm. Wing pattern with usually well developed costal strigulation and often with tornal ocellus. Venation typical of *Tortricidae*, with all veins separate or with some stalked or beginning at common points (especially  $rr-m_1$  and  $m_3-cu_1$  of the hindwing). Cubital pecten of hindwing usually well developed.

Male genitalia with tegumen more or less strongly developed and with uncus often strong, curved downwards, but in some cases completely reduced. Socii varying in size and form if preserved. Tuba analis in the majority of the species membranous, occasionally developing a subscaphium. Gnathos membranous or in form of weak, lateral, band-like sclerites connecting base of tuba analis or a transverse plate. Vinculum well developed. Valva showing great variety

of forms, often very long, with more or less distinctly formed cucullus, variously shaped sacculus and usually long costa. Various thorns, spines or hooks developed in internal surface of valva. Basal opening distinctly developed but often short. Olethreutoid well developed; aedeagus simple, often very short, with rather short coecum penis. Cornuti, if present, spiniform.

Musculature of male genitalia. Muscle  $m_1$  may be either well developed or completely atrophied;  $m_6$  on coecum penis;  $m_2$  and  $m_4$  on basal process of valva; however, the latter may be ill-defined. Other muscles typical for *Olethreutinae*, but  $m_5$  may enter rather flat into valva.

Female genitalia. Ovipositor typically developed. Sterigma in form of a plate or thick membrane surrounding the ostium bursae, being minutely spined throughout or partially more strongly sclerotised. Ostium often at the bottom of a cup-like concavity. No linkages between sterigma and apophyses anteriores. Ductus bursae varying in shape and length; ductus seminalis variably positioned. Antrum often well differentiated and heavily sclerotised. Corpus bursae provided with plate-shaped, cup-like, cornute or variably shaped, scobinate types of signum. One or two signa developed, or no signum present.

Scent organs very variably developed. The abdominal organs are in the form of pockets situated ventrally or developed as bunches of hair-like scales laterally on segments 1, 2, 3—7 or on tergites 1—3. Sometimes three pairs of coremata occur. The hindwing organs are also variable, often weakly developed, in other cases very strong, usually in form of a dorsal roll. On hind tibia various hair pencils or groups of scales are developed. In some genera all three types of scent organs are present, in others two or only one is developed.

Sexual dimorphism often distinct, occurring mainly in size and shape of the wings.

Larva. The chaetotaxy does not render any special character. The diagnosis of the tribe given by SWATSCHEK (1958) includes the characters of *Enarmoniina*. In 9th abdominal segment setae I and III are on separate or fused pinacula and group IV consists of 2 setae in known cases.

Pupa insufficiently known. Cremaster rather long and almost straight provided with indentations and flattened bristles. Other characters are seemingly shared with those of *Eucosmini*.

Bionomy. The eggs are deposited singly or in small groups. Larvae roll the leaves or bore the stems and roots, utilising various plants mainly dicotyledonous. They are mainly mono- and oligophagous species. Hibernation mainly in egg or larval stage.

Distribution: as for *Tortricidae*.

Comments. Approximately 1300 species belongs in this tribe. The tribes and subtribes described by FALKOVITSCH (1962) and DIAKONOFF (1973) are treated in this paper as groups of species only. They were differentiated mainly on the basis of scent organs and female genitalic structures. But there is no constant character distributed throughout the tribe and in some cases very close species may differ in the scent organs, structure of signum or sterigma.



### *Eucosmini*

*Eucosmidii*: KUZNETSOV and STEKOLNIKOV, 1973, Trudy vses. ènt. Obsheh., 56: 38. Supertribe of *Olethreutinae*.

Head usually roughly scaled; labial palpus 1.2—3.5; antenna simple, ciliate. Ocellus developed; tongue present. Thorax often with well developed crest.

Wingspan 8—30 mm. Wings with typical venation; pattern of forewing with costal strigulation and usually distinct ocellus at tornus. Cubital pecten of hindwing developed.

Male genitalia as in *Olethreutini* but uncus more often reduced. Socii usually weakly sclerotised, drooping; tegumen occasionally producing distal or ventral processes some of which are probably homologous to hami. Valva much more simple than in preceding tribe, with well differentiated cucullus, distinct costa and basal process, rather simple sacculus and large basal opening. Various spines and thorns and strong bristles in internal surface of valva. Aedeagus usually short; coecum penis short; olethreutoid well developed. Cornuti often in rather great numbers, spiniform, capitate, forming a bunch.

Musculature as in *Olethreutini*, but muscle  $m_1$  usually weaker and more often atrophied.

Female genitalia with ovipositor usually typically developed, rarely telescopic or floricomous. Sterigma varying in shape and degree of sclerotisation, often positioned in an incision of pregenital sternite. Signa usually in form of pair of funnel-like sclerites, rarely blade-shaped.

Scent organs developed as wing androconia or coremata.

Larval characters close to those of *Olethreutini*. Pupae often with distinct cremaster.

Bionomy. The larvae feed mainly in stems and roots of various plants, although several species are known to feed in spun leaves.

Comments. About 1200 species known to date. The tribe is divided into three subtribes of which *Enarmoniina* are the most differentiated.

*Eucosmini*, the name of the tribe, is based on the family-group name *Eucosmidae* MEYRICK, 1907. It has been used commonly during over 50 year, however, *Spilonotidi* of GUENÉE was published much earlier. The latter name has not been used as a senior synonym for over 50 years, and according to the International Code of Zoological Nomenclature (Article 23b) is treated as nomen oblitum. The same concerns *Anchyloperidae* STANTON, 1858.

### *Enarmoniina*

*Anchyloperidae* STANTON, 1858, Manual Br. Butterflies Moths, 2: 188; 1959: 217. Type-genus: *Anchylopera* STEPHENS, 1829. Family of *Tortricina*.

*Ancylisidii* PIERCE and METCALFE, 1922, Genitalia Br. *Tortricidae*: XXI, 52. Type-genus: *Ancylis* HÜBNER, [1825]. Described as group of *Tortricidae*, probably treated as subfamily.

*Enarmoniini* DIAKONOFF, 1953, Verh. K. ned. Akad. Wet., Afd. Nat., (2) 49 (3): 87, 161 (as tribe of *Eucosminae*). Type-genus: *Enarmonia* HÜBNER, [1825]. Placed on Official List of Family Group Names in Zoology (1955), Opinion 349.

*Ancyliidini*: KUZNETSOV and STEKOLNIKOV, 1973, Trudy vses. ènt. Obsheh., 56: 33. Tribe of *Olethreutidii*.

Head typical of *Olethreutinae*, labial palpus 1.3—2.

Wingspan 10—22 mm. Forewing often with acute, curved apex. Venation typical for the tribe.

Male genitalia. Tegumen rather delicate; uncus often developed, bifurcate or completely reduced. Gnathos atrophied. Socii usually pair of drooping soft, hairy pads, rarely fused with apical part of tegumen. Vinculum delicate. Valva long with long costa, usually prominent sacculus and variably formed cucullus. Basal opening of valva rather short; however, in more specialised forms it may be distinctly elongated and large. Aedeagus slender; cornuti numerous, deciduous.

Musculature of male genitalia characterised by the well developed muscle  $m_2$  and short muscle  $m_4$ . Muscle  $m_1$  completely atrophied. Muscles  $m_5$  and  $m_6$  well developed, long, the former inserted on olethreutoid.

Female genitalia. Ovipositor typical, sterigma rather delicate, often in form of membranous, sculptured plate; antrum usually well differentiated and sclerotised; ductus bursae slender; signa a pair of blade-shaped plates directed to the inside of corpus bursae. Pregenital sternite broad, variably shaped. Scent organs: not found.

Dimorphism. The sexes differ mainly in size.

Larva hardly differing from that in *Olethreutini*.

Pupa with distinct cremaster and row of thorns on tenth abdominal segment.

Bionomy. Larva in spun leaves of various plants, mainly deciduous trees. Hibernation in larval stage. In temperate zones there are 1—2 generations yearly.

Distribution. Palaearctic, Nearctic and Oriental regions.

Comments. Approximately 50 species belong here. The representatives of this subtribe have usually been placed in *Eucosmini*, except *Eucosmomorpha* OBRAZTSOV which was treated as a member of *Grapholitina*. Only KUZNETSOV and STEKOLNIKOV (1973) have placed them correctly, separating them from other subtribes on the basis of the very characteristic signum.

### *Eucosmina*

*Spilonotidi* GUENÉE, 1845, Anns Soc. ent. Fr., (2) 3: 154. Type-genus: *Spilonota* STEPHENS, 1859. Tribe of *Tortrices*.

*Spilonotidae*: R. L. [anonym], 1858, Accent. List Br. Lepid.: 61. Family of *Tortricinae*.

*Epiblemidii*: PIERCE and METCALFE, 1922, Genitalia Br. *Tortricidae*: XXI, 56. Major group of *Tortricidae*, treated probably as a subfamily.

*Eucosminae*: HEINRICH, 1923, Bull. U.S. natn. Mus., 123: 10. Subfamily of *Olethreutidae*.



*Eucosmini*: OBRAZTSOV, 1946, Z. wien. ent. Ges., **30** (1945): 23. Tribe of *Olethreutinae*.

*Eucosmini*: KUZNETSOV and STEKOLNIKOV, 1973, Trudy vses. ent. Obsheh., **56**: 38. Tribe of *Eucosmidii*: KUZNETSOV and STEKOLNIKOV, 1973.

Head, thorax and wings typical for the subfamily. Labial palpus 1.2—3.

Wingspan 10—30 mm. Venation typical often with one or two (chorda and median stem) internal veins of median forewing cell developed.

Male genitalia. Tegumen well developed; uncus in more primitive forms strong, often bifurcate, in others in various stages of reduction or completely atrophied. Gnathos weak or completely membranous; tuba analis usually weakly sclerotised. Socii varying considerably in form and size, being usually semi-membranous, drooping. In some species latero-apical processes of tegumen present. Valva showing a variety of shapes, provided with distinct cucullus, long costa and rather simple sacculus. Internal surface of valva well sclerotised, armed with various spines or setae, especially on cucullus. Basal process and basal opening well developed. Aedeagus usually simple and rather short with short coecum penis; olethreutoid strong. Cornuti consisting of numerous slender spines, easily shed during copulation.

Musculature of male genitalia with muscle  $m_1$  present, often well developed,  $m_2$  and  $m_4$  strong. Muscle  $m_5$  very large, entering deep inside valva, inserted on olethreutoid. Point of insertion of  $m_6$  has also moved distad on aedeagus, often even on olethreutoid.

Female genitalia. Ovipositor usually normally developed; however, several species are known to have developed telescopic or floricomous ovipositors. Sterigma mainly in form of a lamella postvaginalis, varying in shape and degree of sclerotisation, being more or less distinctly placed anteriorly in the incision of the pregenital sternite. The latter is well sclerotised, varying morphologically. Antrum often well sclerotised and ductus bursae with a well sclerotised ring. Signa a pair of narrow pockets, often with broadened bases, in many cases asymmetrical, sometimes one or both being atrophied.

Scent organs developed in form of androconial scales covered by costal fold of forewing. Sometimes variously formed coremata occur.

Sexual dimorphism expressed mainly in size and shape of wings; seasonal dimorphism mainly in size of specimens.

Larva showing no constant characters which differ from those of other tribes or subtribes of the subfamily in question. In the 9th abdominal segment, I and III always on fused pinacula. Other characters given by SWATSCHEK (1958).

Pupa with atrophied cremaster replaced by group of short thorns and hook-like setae.

Bionomy. Eggs deposited singly or in small groups. Larvae feed either in spun leaves or in stems or roots, with a preference for the first type of feeding. No larva lives under bark; only rarely do they feed in seeds. Food: mainly dicotyledonous plants. Hibernation probably in egg, larval or pupal stages. One to three generations yearly in the temperate zones.

About 700 species known to date.

## Grapholitina

*Grapholithidi* GUENÉE, 1845, Anns Soc. ent. Fr., (2) 3: 169. Type-genus: *Grapholitha* TREITSCHKE, 1830 = *Grapholita* TREITSCHKE, 1829. Described as tribe of *Tortrices*.

*Grapholithidae*: R. L. [anonym], 1858, Accent. List. Br. Lepid.: 66. Family of *Tortrices*.

*Stigmonotidae* STANTON, 1858, Manual Br. Butterflies Months, 2: 188; 1859: 236. Type-genus: *Stigmonota* GUENÉE, 1845. Family of *Tortricina*.

*Carpocapsidae* STANTON, 1858, ibid.: 188, 1859: 250. Type-genus: *Carpocapsa* TREITSCHKE, 1829. Family of *Tortricina*.

*Ephippiphoridii* PIERCE and METCALFE, 1922, Genitalia Br. *Tortricidae*, XXI, 74. Type-genus: *Ephippiphora* DUPONCHEL, 1834. Described as group of *Tortricidae*, probably treated as subfamily.

*Lipoptychidii* PIERCE and METCALFE, 1922, ibid.: XXI, 93. Type-genus: *Lipoptycha* LEDE-  
RER, 1859. Described as group of *Tortricidae*, probably treated as subfamily.

*Stigmonotinae*: HESLOP, 1938, Cat. Br. Lepid.: 72. Subfamily of *Eucosmidae*.

*Laspeyresinae* HEINRICH, 1923, Bull. U.S. natn. Mus., 123: 10. Type-genus: *Laspeyresia* HÜBNER, [1825] = *Cydia* HÜBNER, [1825].

*Melanalophidae* DIAKONOFF, 1941, Treubia, 18 (2): 437. Type-genus: *Melanalopha* DIA-  
KONOFF, 1941. Described as distinct family.

*Laspeyresiini*: OBRATSOV, 1946, Z. wien. ent. Ges., 30 (1945): 23. Tribe of *Olethreutinae*.

*Melanalophinae*: OBRATSOV, 1949, Entomon, 1: 201. Subfamily of *Tortricidae*.

*Grapholitidae* PASTRANA, 1952, An. Soc. cient. Argent., 152: 65.

*Dichroramphae* DANILEVSKI and KUZNETSOV, 1968, Fauna SSR, Nasekomye Tchesnuekry-  
lye, 5 (1): 4, 142. Type-genus: *Dichrorampha* GUENÉE, 1845. Described as subtribe of  
*Laspeyresiini*.

*Laspeyresiae*: DANILEVSKI and KUZNETSOV, 1968, ibid.: 6, 235. Subtribe of *Laspeyresiini*.

Head and thorax typical for the subfamily; labial palpus 1—2.5.

Wingspan 8—24 mm. Forewing sometimes with costal fold; pattern with well developed costal strigulation and tornal ocellus; very often a dorsal pale blotch or stripes present. Venation typical for the subfamily, with similar constant tendency to fusion of basal parts of some veins of hindwing ( $rr-m_1$  and  $m_3-cu_1$ ). Internal veins (chorda and median stem) usually well developed; *pcu* rudimentary exceptionally fairly well developed.

Male genitalia. Tegumen rather delicate; uncus absent; gnathos membranous; tuba analis without sclerites. Valva elongate with well differentiated setose cucullus, long costa and variably formed sacculus. Basal opening and processus basalis well developed. Aedeagus fairly long, often bent, sometimes provided with dents or processes. Coecum penis short; cornuti variable in form and number. Olethreutoid strong or with delicate dorsal portion.

Musculature of male genitalia. Muscle  $m_1$  absent;  $m_2$  well developed,  $m_4$  short, both typically inserted. Muscle  $m_5$  very large, entering deep into valva;  $m_6$  proportionally large. Points of insertion of these two muscles moved distally, but  $m_5$  is fixed in upper part of olethreutoid.

Female genitalia. Ovipositor normally developed. Sterigma simple plate-shaped (lamella postvaginalis) varying greatly in degree of sclerotisation, being often almost completely membranous. Ostium bursae large, surrounded by the edge of usually well developed and sclerotised antrum. Ductus bursae in



majority of species short, sclerotised around entrance of ductus seminalis. Two funnel-like, basally broad, sometimes asymmetrical signa in corpus bursae. Seventh sternite varying considerably in shape, being usually deeply incised in middle of distal edge.

Scent organs. Androconia occurring in some species are covered by costal fold of forewing; androconial organs of hindwing are often developed. These are groups of variably shaped scales contained in concavities or folds of the wing membrane in anal and subcubital areas dorsally. Abdominal scent organs are found in 7th and 8th segments between 4th and 5th tergites and as typical coremata invaginated in the 7th and 8th segments.

Sexual dimorphism rather slight, occurring mainly in size and shape of wings, more rarely in coloration.

Larva as in *Eucosmina*, with setae I and III of 9th abdominal segment situated on common pinaculum. According to SWATSCHEK (1958), group VII of that segment consists of one or exceptionally, two setae.

Pupa as in *Eucosmina*.

Bionomy. Two ecological groups may be differentiated, viz. dendrofilous (restricted to deciduous trees) and connected with shrubs. The larvae of *Grapholitina* utilise various plants, including conifers. They are typically endophagous, feeding rarely in spun leaves; many larvae are carpophags or live in galls. *Grapholitina* are mostly monophagous, partially oligophagous. One to three generations yearly in temperate zones; hibernation in larval stage (insufficient data).

Comments. Approximately 500 species belong in this tribe. Hitherto the group has been treated as a tribe; however, KUZNETSOV and STEKOLNIKOV (1973) found that it is very close to *Eucosmini* and placed them in a common supertribe *Eucosmidii*. DANILEVSKI and KUZNETSOV (1968) differentiated two subtribes, viz., *Dichroramphae* and *Laspeyresiae* which differ in the form of the antrum (fused with pregenital sternite in the former group) and in bionomy. The two are treated in this paper as groups of species only.

The name *Laspeyresiinae* was used for the first time by HEINRICH (1923) and became consolidated thanks to several works, e.g., OBRAZTSOV (1946), and DANILEVSKI and KUZNETSOV (1968). However, this name cannot be kept in use because its type-genus *Laspeyresia* HÜBNER, [1825] is preoccupied by *Laspeyresia* R. L. (anonym), 1817 (emendation of *Laspeyria* GERMAR 1810, *Noctuidae*). The oldest family group name is *Grapholithidi* GUENÉE, 1845 used further on in several publications. This name (emended for *Grapholitina* as the type-genus is *Grapholita* TREITSCHKE, 1829 not *Grapholitha* TREITSCHKE, 1830) is proposed to replace *Laspeyresiinae*.

*Melanalophidae* described as a distinct Tortricid family was synonymized by OBRAZTSOV (1958) with *Laspeyresiini* and consequently included in this paper in *Grapholitina*.

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Praca zawiera propozycję nowego układu systematycznego taksonów szczebla rodzinnego zwójkówek i próbę wyjaśnienia ich filogenezy w oparciu o budowę, funkcję i tendencje rozwojowe narządów kopulacyjnych skorelowane z innymi cechami. W przeglądzie historycznym omówiono najważniejsze dotychczasowe systemy *Tortricidae*. Przegląd wykorzystywanych cech bionomicznych i morfologicznych zawiera ich charakterystyki i omówienie przydatności. Nowy system i filogeneza zostały szczegółowo przedstawione i uzasadnione. Do *Tortricoidea* zaliczona została tylko jedna rodzina, a mianowicie *Tortricidae*, do której włączono *Cochylidae* i *Chlidanotidae*, uznawane ostatnio za osobne rodziny, a status licznych grup traktowanych jako podrodziny lub plemiona (np. *Ceracinae* i *Polyorthini*) został obniżony. W nowym układzie *Tortricidae* dzielą się na dwie podrodziny, a te z kolei na plemiona i podplemiona (porównaj rys. 1). W przeglądzie systematycznym scharakteryzowano wszystkie taksony szczebla rodzinnego zwójkówek podając ich synonimikę. Liczne nazwy zostały zsynonimizowane. Celem stabilizacji zaproponowano utrzymanie nazw *Archipini* i *Olethreutini*, chociaż okazały się one starszymi synonimami. Ponadto konieczne okazało się wprowadzenie nazwy *Grapholitina* na miejsce preokupowanej nazwy *Laspeyresiini* i przywrócenie zatwierdzonej przez Komisję Nomenklatoryczną nazwy *Enarmoniina* zamiast używanej ostatnio *Ancyloidini*.

## РЕЗЮМЕ

Работа содержит предложение новой систематики таксонов семейства листовёрток и попытку выяснения их филогенеза на основании строения и направления развития копулирующих органов коррелированных с другими признаками. В историческом просмотре изложено важнейшие классификации листовёрток. Просмотр используемых бионических и морфологических признаков содержит их характеристики и изложение пригодности. Новую систему и филогенез подробно представлено и обосновано. К *Tortricoidea* отнесено лишь одно семейство, а именно листовёртки, к которому отнесено, признаваемые за последнее время как отдельные семейства, *Cochylidae* и *Chlidanotidae*, а статус многочисленных групп трактуемых, как подсемейства и трибы (нпр. *Ceracinae* и *Polyorthini*) — понижен. В новой систематике *Tortricidae* делятся на два подсемейства, которые в свою очередь делятся на трибы и подтрибы (ср. рис. 1). В систематическом просмотре дано характеристику всех таксонов семейства листовёрток и их синонимы. С целью стабилизации предложено удержать названия *Archipini* и *Olethreutini*, хотя они оказались старшими синонимами. Кроме того, оказалось необходимым введение названия *Grapholitina* вместо ранее употребляемого названия *Laspeyresiini* и возвращение утверждённого Номенклатурной комиссией названия *Enarmoniina* вместо употребляемого в последнее время названия *Ancyloidini*.





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