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Morphology and Vestiture of the *Tortricidae* Valva (*Lepidoptera*)

[With 8 Text-figures]

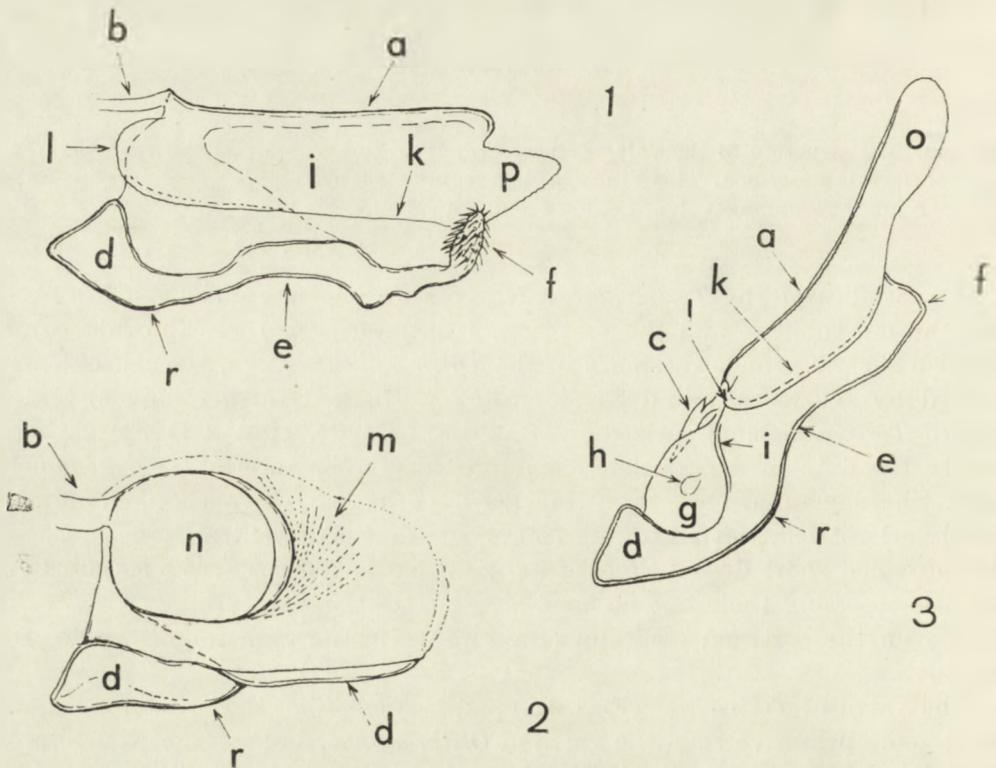
Abstract. The structure of the valva is discussed. Its regionisation and the vestiture of the inner surface is described. This study will be completed by a paper dealing with dorso-anterior juncture among valva, tegumen and vinculum.

The studies of the *Tortricidae* valva concern the morphology of its skeleton, the musculature and the vestiture. HEINRICH (1926) was the first to distinguish several groups of spines in the *Olethreutinae* valva, the muscles were studied by KUZNETSOV and STEKOLNIKOV (1973 and further papers) and in case of *Tortricinae* summarized by RAZOWSKI (1981). HORAK (1984) gathered mainly the data on the skeleton and provided some interesting own conclusions. She suggested that the primitive hypothetical valva should be rather weakly sclerotized, devoid of any complicate dorsal or ventral structures, and also provided short descriptions of its main parts, the costa, the sacculus and the disc assessing their taxonomical significance. Now, returning to my earlier studies on the tortricid genitalia (RAZOWSKI 1983) I wish roughly redescribe the valva.

The valva of *Tortricinae* (Figs. 1,2) and *Chlidanotinae* show a common plan, being more primitive than the valva of *Olethreutinae*, both in the skeleton and musculature. The longitudinal edges have developed very early in course of the evolution of the family, and now it seems difficult to find the species with the traces of that stage of valva (and not only in *Tortricidae*, hence a primitive valva should be traced in the generalized *Lepidoptera*). The simple shape of some examined valvae is resulted by a process of simplification. The more uniform

and comparatively weak degree of their sclerotization is probably of primitive character. In the primitive *Lepidoptera* and in primitive representatives of a great number of all families the number of the muscles directly or indirectly bound with the valvae is higher than in the specialized taxa and their arrangement in the latter is more specialized. The insertions of the muscles are, with a few exceptions, situated on the rigid areas, thus the structures of the primitive valva should also be strong enough. In the taxa having partially membranised valvae the muscles had changed their position and their insertions had become more specialized.

The costa and the sacculus are more or less differentiated and specialized edges of the valva. The costa is of a lesser importance in the function of clasping, thus its character is generally less advanced than that of the sacculus. It usually has a form of a semichannel having the dorsal surface variably broad and convex. The most anterior portion of the costa is often expanding dorsally, called



Figs. 1-3. Schemes of the structure of valva: 1 - *Tortricini*, 2 - *Archipini*, 3 - *Olethreutini*; a - costa, b - transtilla, c - basal process of valva, d - sacculus, e - ventral incision of sacculus, f - termination of sacculus, g - basal cavity, h - sensillar patch, i - posterior edge of basal cavity, j - disc, k - fold, l - pulvinus, m - plication of valva, n - median sclerite of disc, o - cucullus, p - brachiola, r - proximal angle of sacculus.

the basal process (processus basalis valvae, sensu PIERCE), the outer surface of basal part of costa extends ventrally to fuse with the wall of the sacculus. The sacculus is represented either by a simple convex edge, or its walls fuse at least in the basal region. Its ventral edge in plesiomorphous or secondary simplified cases is almost straight, but in more specialized ones concave medially. It also may be arched in the longitudinal surface, so its free termination extends mediad when the valvae are approached to one another. The angulation formed at the concavity is of great functional importance facilitating the clasping; the free termination of the sacculus or the prominences of its posterior part is almost similar in function. The disc is formed by a whole inner surface of the valva between the costa and the sacculus and in *Tortricinae* is almost completely membranous as a rule what enables the protractor of the aedeagus a full contraction. The caudal edge of the valva is weakly sclerotized and variably shaped. In many taxa it is more or less expanding distally, and in *Tortricini* is highly specialized having a form of a sack situated distally or externally (brachiola). Occasionally the outer margin of that area extends beyond the inner edge to form a more or less pronounced membranous lobe. The distal part of the valva, beyond the sacculus, is occasionally enlarged, resembling a structure of *Olethreutini* (cucullus) which is there much more specialized. The anterior part of disc is united with the anellus which develops various sclerites, one of which, the transtilla, is entirely fused with the anterior, inner portion of the costa sclerite, at least in the primitive type of the valva. In that region develops the apodeme of the tergal extensor of valva. In many *Polyorthini* a belt-shaped sclerite extends from the subdorsal part of the base of disc to link the juxta laterally. That apomorphy appeared in result of the peculiar function of the protractor of aedeagus or its branch attached to the inner surface of the valva. That structure may also be accompanied by an oblique slit or sclerotic belt extending towards end of the sacculus. From the ventro-caudal part of valva, beyond the sacculus runs a slight convexity of the disc membrane, being often parallel to the latter. The ventral portion of that area is often enlarged and forms a fold extending basally as far as to marginal part of the anellus, developing a lobe, the pulvinus. The inner edge of this sac-shaped lobe is membranously connected with sclerites of the anellus, e.g. with the transtilla, if present. In higher *Archipini* in which the costa of valva is completely reduced, a variably shaped, often deeply concave basal or submedian sclerite of disc develops. It raises the mechanical resistance of the valva and directly connects with the anellus sclerite, the transtilla, or the labis (in the case of a membranisation of the median part of transtilla). The fold is in those cases situated ventrally to this sclerite, and the pulvinus may be situated more anteriorly and even upturned apically. In some groups of *Tortricinae* (e.g. in *Tortricini* and *Archipini*) a tendency to a reduction of the distal part of the costa is observed and in higher *Archipini* the costa is completely atrophied.

This is treated here as a result of a reduction and not as a plesiomorphy (HORAK 1984:43). That may be supported not only by a series of gradual reductions within the subfamily but also by high specialization of the dorso-anterior part of the valva (RAZOWSKI in litt.) in the species characterized with a completely atrophied costa. The occurrence of the plication of the disc and the direction of the folds as well as the attachment of the protractor of aedeagus (cf. p. 207) confirm this point of view. The plication of the disc occurs in various groups of *Tortricinae* and has developed in course of a process of the strengthening of the valva probably in two ways. The arrangement of the plicae, vertical to the working surfaces and thus directed towards the weakly sclerotized edges speaks of mechanical importance of the plication. In lower *Archipini* the folds are rather parallel to the costa and vertical to the caudal edge of valva, in some *Sparganothini* in which the distal part of the valva is weakly sclerotized dorsally the folds are arched upwards, and in higher *Archipini* they are arranged radially towards all membranous edges of valva. The areas on which the pressure (realised by mechanical moments) is the largest become sclerotic. Thus it seems understandable that the sclerites in variably built valvae are differently situated and such characters are usually of specific importance. The second reason is that the valva can greatly enlarge its volume when filled with blood and enable better clasping. That should be, however, confirmed on the living material. It seems also possible that the work of the valva in two ways may prove complementary.

Polyorthini develop a peculiar apomorphic structure (outer split) of the external surface of valva corresponding with the coremata. It atrophies secondarily in several genera or species in a result of a reduction of the scale pencil of the end part of the abdomen. The pocket is formed by a membrane and opens dorsally having a variable length and shape.

Musculature. There are 4 pairs of muscles bound directly or indirectly with the tortricine valva (RAZOWSKI 1981). The tergal extensors (m_2) and flexors (m_4) of valvae act indirectly, whilst the protractors of aedeagus (m_5) and inner muscles (m_7) work directly. Exceptionally the retractors of aedeagus (m_6) were found to insert secondarily in the valvae (in *Anacrusis* Z., cf. RAZOWSKI 1981).

The inner muscles of valva occurring in number of 2 pairs (or one muscle only consisting of two branches) are found in *Chlidanotinae* only. One branch extends from a vertical rib situated basally in the external wall of the valva, the second inserts at the base of the saeculus; their distal parts are attached in the valva ventrally or dorsally, however, the two are always crossing. They certainly deserve as flexors of the ventral or posterior parts of the valva and show a strong tendency to reduction within that subfamily. Their presence is a plesiomorphy.

In *Chlidanotinae* and *Cochylini*, *Sparganothini*, and *Atterini* of *Tortricinae*

the valvae are moved chiefly by means of the tergal muscles which are attached to the transtilla or the apodeme situated at its base. Two tendencies are realised within higher *Tortricinae*, in which one of those pairs become finally completely reduced. In *Tortricini* only m_2 of that pair are developed whilst in higher *Archipini*, *Cnephasiini* and *Schoenotenini* exists only m_4 . A tendency of a domination of each of those pairs is treated as apomorphic, whilst the presence of a complete set of muscles is regarded as a plesiomorphy (in lower *Archipini* they are still preserved).

In all those cases, even when one of the tergal muscles is atrophied, the tergal complex of the genitalia dominates over the ventral complex and the main function of the muscle 5 is the protraction of aedeagus. That muscle is inserted on the coecum penis or partly on the caulis of one side whilst its distal attachments vary to great degree. In the primitive taxa of almost all tribes it inserts generally in the dorsal area whilst in the more advanced its attachment is more median or ventral. So, in some *Cochylini* it inserts on the transtilla, upper part of the vinculum or even on ventral portion of the pedunculus being often subdivided into 2–3 branches. It is dorsal in *Chlidanotini*, *Hilarographini*, *Polyorthini*, in *Eulia* and subdorsal in *Anacrusini* and partially in *Sparganothini*. In many genera or species at least one branch of m_5 reaches the median part of the valva, e.g. in numerous *Cochylini*, *Sparganothini*, *Cnephasiini* and *Archipini*, or even inserts on the sacculus as for instance in *Tortrix* or *Acleris* of *Tortricini* or in higher *Archipini*. It is worth mentioning that the insertion within the valva may be either external or internal. That is well visible in *Polyorthini* (external in *Cnephasitis*, internal, on the disc membrane, in *Polyortha* or *Olindia*; cf. RAZOWSKI 1981). The ventral position of the attachment of m_5 enables increased role in the clasping, the dorsal insertion is bound mainly with the protraction of aedeagus as it slightly cooperates with the tergal muscles only.

Within the family one can realise an increase of the function of the valvae in clasping what is bound with enlargement and more ventral and posterior insertion of muscle 5 and causes better sclerotization of the walls. The most important become the ventral, median and then posterior areas of the disc. Thus in those areas develop various processes, lobes or clusters of spines. The tortricine valva playing a rather secondary role in the clasping did not develop stronger sclerites of the disc and even shows a tendency to a reduction of the dorsal sclerites. The membranous disc enables muscle 5 to get easily a position almost vertical to the valva during contraction. That occasionally elevated surface cannot work in the clasping and therefore did not develop any clasping structures. It is therefore supposed that the hairs of the pulvinus play a tactile function only and do not act in clasping. HORAK (1984) suggests the pulvinus has appeared within *Tortricinae* at least 4 times, as various forms and stages of that structure are observed. One can also suppose that pulvinus

appeared early in the evolution of the family as it is found in many primitive genera of various tribes, e.g. in some *Phtheochroa* of *Cochylini*, in *Archips* of higher *Archipini*, in some *Cnephasia* of *Cnephasiini* etc. Thus its atrophy might be recognised as a reduction. The absence of the pulvinus in *Polyorthini* can be explained by a high specialization of basal region of the disc (anellus is strengthened, or a lateral link between juxta and disc is developed); similarly the lack of that structure in *Eulia* is caused by sclerotization of the dorsobasal part of the disc and its fusion with the transtilla. In some primitive *Tortricini* the pulvinus is present, in other it is situated more posteriorly, and in the species with a slender, well sclerotized valva is atrophied. Also the fold of disc is atrophying and its position is marked by a row of hairs.

Vestiture. The outer surface of the tortricine and chlidanotine valva is clothed with scales rather uniformly and thus its systematic importance is limited. In numerous species the costal and saccular hairs may take more outer position and are serving as the tactile receptors being rather uniformly distributed, however, their agglomeration is realised at the angle of the sacculus, ventral incision or distal part of costa and caudal edge of valva. Those hairs are usually longer and thicker than the remaining hairs. The vestiture of the disc is rather uniform. The hairs and setae are usually weak and play chiefly a tactile role, however, they also help in the clasping. The differentiation of the vestiture advances rather slowly. Two tactile groups are often differentiated beyond the bases of both sacculus and costa. Some other agglomerations of scales develop on the disc, e.g. on the fold or pulvinus. The groups of spines (often pectinate as in some *Tortricini* and *Schoenotenini*) are situated at the most active parts of the inner surface of valva being often accompanied by sclerotic folds, processes or convexities. More or less compact clusters of spines are thus found at the angulation of the sacculus, its subterminal or terminal parts (e.g. the spined termination in *Acleris*, or bristled end of sacculus in *Cnephasia*), beyond middle of disc (*Rhabdotenes* of *Schoenotenini*) or at the end of the valva (*Saetotenes*, *Schoenotenini* etc.).

Olethreutinae.

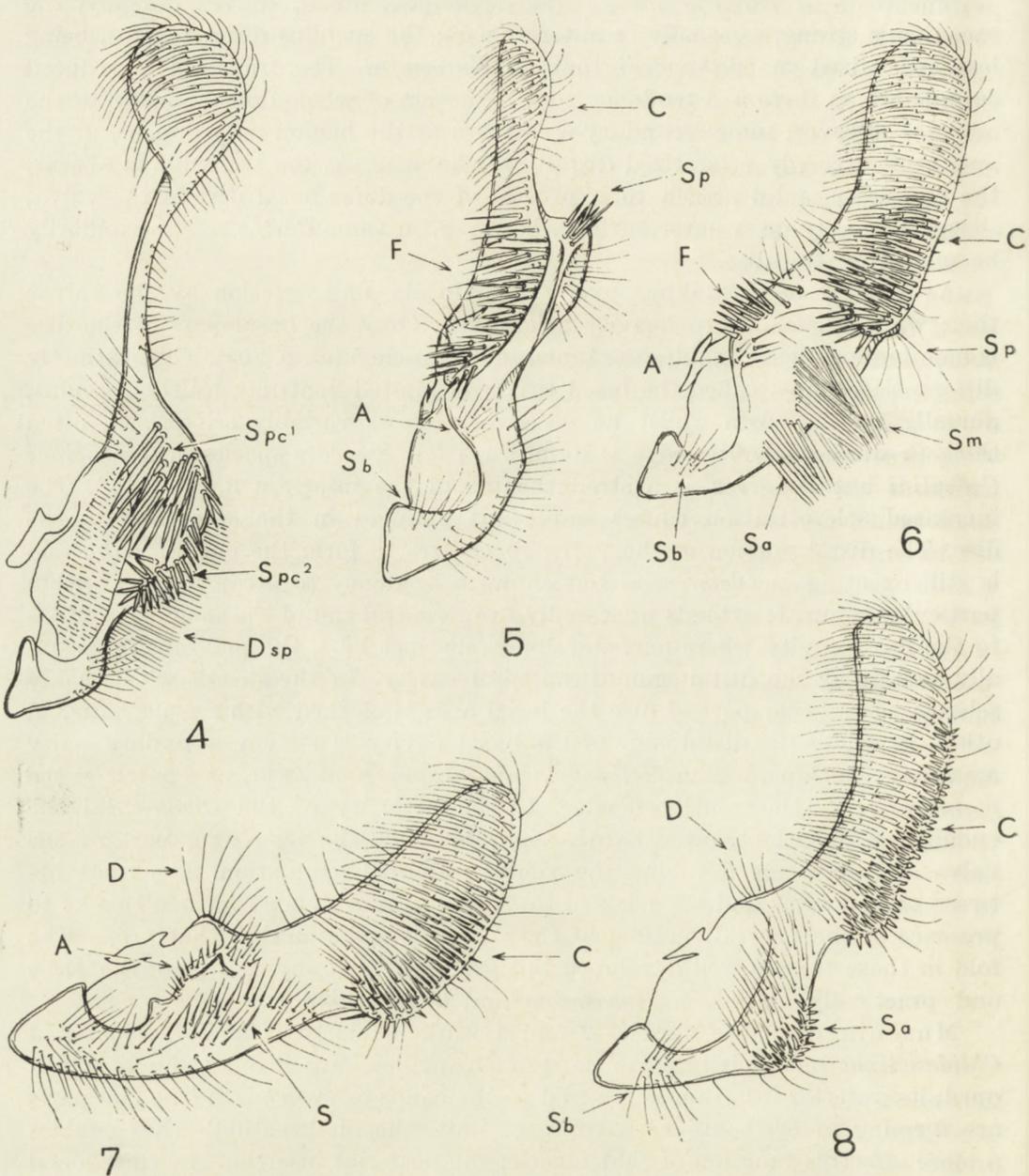
The olethreutine valva (Fig. 3) is highly specialized and shows the following progressive features: The basal cavity of the valva is developed, the apodeme of muscles 2 and 4 derives of the outer wall of the basal portion of the valva, the valva is strongly sclerotized and its ventral and distal parts play main role in the clasping and the vestiture of the disc is strongly differentiated. To the transformation series belong a gradual enlargement of the basal cavity and deep insertion of muscle 5 in the valva, differentiation of the distal part of the valva and formation of the cucullus and simplification of the vestiture.

The costa of valva is always well developed, broad, convex dorsally; the sacculus is strong, especially in anterior part; the cucullus differentiates, being less specialized in *Olethreutini* than in *Eucosmini*. The transtilla is reduced completely as there is a tendency to a reduction of whole dorsal surface of the anellus, however, some secondary structures as the henion may appear, or the anellus is strongly sclerotized distally to the zone. As the transtilla is absent, the muscles 2 and 4 attach to a process of the dorso-basal part of the valva, situated usually on a outer surface, however, in some *Bactra* may secondarily be placed on the disc.

As a result of the taking over the main clasping function by the valvae their walls become more heavily sclerotized. Only the basal part of the disc is membranous what enables the function of muscle 5 (cf. p. 207). This distinctly differentiated area called the basal cavity is limited ventrally by the sacculus, dorsally by the costa whilst its posterior edge is variably sclerotized, often thick (a similar sclerotic edge is found in a few *Stenodes* species of *Tortricinae* *Cochylini* but it serves as a strengthening of the insertion area of m_5). The increased sclerotization causes important changes in the structure of the disc. The distal portion of the valva specializes to form the cucullus; the fold is still existing in *Olethreutini* but shows a tendency to atrophy even within particular genus. It extends proximally from ventral end of the cucullus as far as to the basal cavity where may develop a distinct lobe, the pulvinus occasionally overlapping the distal edge of the basal cavity. In the species with weakly sclerotized anterior part of disc the basal area is clothed with sensile hairs, in other, in which the distal edge of the basal cavity is stiff a secondary hairy area may develop, e.g. in *Methendothenia atropunctana* ZETT. as a patch on the membrane near the mentioned edge. In the majority of the *Olethreutini* the cucullus is indistinct, often hardly separable from the remaining part of the valva and does not develop the ventro-proximal angulation. The limit between the cucullus and the neck of the valva (a narrow part formed thanks to presence of the ventral incision of the valva) is indistinct in that tribe. The fold in those taxa is well developed but gradually atrophying within the tribe and practically absent in *Eucosmina* and *Grapholitina*.

Musculature. The muscles 2 and 4 work similarly as in *Tortricinae* and *Chlidanotinae* but their importance is much smaller. Muscle 5 is strongly developed; its anterior insertion is lowered to the caulis or even juxta (the two parts are forming in *Olethreutinae* a compact unit, the olethreutoid) what enables a more effective function of that muscle; the posterior insertion is either dorsal (e.g. in *Apotomis*, *Olethreutini*), ventral or intermediate.

Vestiture is highly specialized and accompanies various sclerotic structures of the body of the valva (protuberances, lobes, processes). A primitively rather uniform vestiture is in this subfamily differentiated into groups or clusters in a result of becoming the working surfaces more efficient. Two



Figs. 4-8. Olethreutine valvae: 4 - *Pseudosciaphila* sp., symbols of spine clusters after HEINRICH 1926 - cf. p. 211, 5 - *Phiaris palustrana* (LIENIG), 6 - *Hedya ochroleucana* (FRÖL), 7 - *Epiblema* sp., 8 - *Epinotia solandriana* (L.), for explanation of the vestiture groups see p. 211-212.

usually well separable groups of sensile hairs differentiate on the costa and sacculus postbasally. The vestiture of the sacculus divides often into 3 main groups, at the angle, in the cavity and at the end of that sclerite. Along the posterior edge of the basal cavity continues another group of spines or (and) hairs; third spined and hairy area is situated on the cucullus, especially along outer edge. It extends on the fold and the surface above it as far as the proximal lobe that is often preserved even when the fold atrophies. The limits of that belt of spines are obscure as occasionally it joins secondarily with the anterior spines (of the posterior edge of basal cavity). Its ventral edge is usually well limited from the saccular spines by a hairless space. The spine group of the "fold" is, similarly as the cucullus and the fold area themselves, more or less unified. In *Eucosmini* the saccular and anterior vestitures are often simplified, so only their hairs are preserved; the group of the fold is also strongly or even completely atrophied thus the spines of the cucullus group take the main function in the clasping.

Chaetotaxy. HEINRICH (1926) was the first to propose the setal nomenclature in order to facilitate the descriptions. He proposed to distinguish the following groups of spines and gave short explanations of the symbols (Fig.4): "Dsp — spines arising from outer surface of harpe; Spc¹, Spc² — heavy spine clusters on or near sacculus of harpe; ScSp — spines on base of sacculus; x — spine group on arch of sacculus". His Spc¹ corresponds with the anterior group of spines in my system, Spc² with the group situated at the angle of the sacculus, however, not consequently; Dsp are situated in the main area of the outer surface of the valva, however, in the majority of species the outer clusters are situated submarginally on the sacculus. It is supposed that they belong to the sacculus group and secondarily changed their position from the inner for the marginal or external. However, the origin of the outer spines in *Pseudosciaphila* (Fig. 4) is unclear. The group x extending from behind a rib like edge of the distal border of the basal cavity belongs most probably in the anterior cluster. The cluster ScSp represents a basal part of the sacculus vestiture and is seldom constituted of spines.

In the terminology proposed below (Figs. 5–8) I do not distinguish between the groups of hairs and spines, however, one can introduce to their symbols the letters "h" and "s" respectively.

Sacculus group (S) is subdivided into basal (Sb), angular (Sa) and posterior (Sp). Distributed along sacculus.

Anterior group (A) is situated on the distal edge of basal cavity, often on a broad rib or on a papilla like protuberance.

Cucullus group (C) is occurring on whole inner surface of cucullus or along its caudal edge only and includes the marginal spines (Cs) extending distally and ventrally; occasionally one of those spines situated at the ventral angle is strong, and is traditionally called the pollex (Cp).

Fold group (F) — if separate, is often not distinguishable from the cucullus group, occasionally subdivided into smaller clusters.

Dorsal group (D) — vestiture of costa of valva, being often external, slightly differentiated except for postbasal agglomeration of sensile hairs.

I would like to mention that often the determination of the above groups is rather difficult as they can vary to some degree by means of secondary junctions or subdivisions. In such cases the determination is possible thanks to a comparison with some related species. The taxonomic and phylogenetic importance of the vestiture seems rather limited to some degree as often the close species differ from one another, or the chaetom is not correlated with other characters. This certainly confirms the difficulties in the building the *Olethreutinae* system based on other characters.

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STRESZCZENIE

[Tytuł: Budowa wałwy *Tortricidae* (*Lepidoptera*)]

Praca zawiera opis morfologii sklerytów, umięśnienia i chetotaksji wałw *Tortricidae*, analizę ewolucyjną niektórych ich części oraz propozycję nomenklatury wyspecjalizowanych grup szczecin.

РЕЗЮМЕ

[Заглавие: Строение вальвы *Tortricidae* (*Lepidoptera*)]

Работа содержит описание морфологии склеритов, мускулатуры и хетотаксии вальв *Tortricidae*, эволюционный анализ некоторых их фрагментов, а также предложения номенклатуры некоторых специализированных групп волосков.

Redaktor pracy — prof. dr A. Riedel