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# Abdominal scent organs in Tortricidae (Lepidoptera)

[With 74 text-figs.]

Odwłokowe narządy zapachowe Tortricidae (Lepidoptera)

Abstract. Scent organs developed on the non-genital segments of the abdomen and some accompanying structures are described and illustrated. Their probable evolutionary trends and systematic implications are discussed.

Various, more or less distinct groups of scales situated on the abdomen are suspected to be of scent importance. In this paper only more specialized agglomerations of scent scales building up rather advanced organs often accompanied by additional structures are presented. The scent structures situated on the genitalia (e.g. tufts of scales of the pedunculus and valva in males and groups of scales of the sterigma in females) are omitted. The function of some organs remains, at least partially, unclear, but I am including them in this publication.

#### SYSTEMATIC REVIEW

# Females

Distinct pouches connected with the subgenital sternite are already found in Cnephasiini nad Eucosmini (Razowski, 1981, 1987). They are recognized as scent structures although no scent scales occur in them. In Xerocnephasia Leraut there are two lateromedian cavities of the eighth sternite and a single pouch situated just before its distal edge and open proximally (fig. 1). Doloploca punctulana (Denis & Schiffermüller), and probably its allies possess a pair of large lateral pouches situated anteriorly to the stigma and well separate from the eighth sternite (fig. 2). In Amphicoccia phasmatica (Mexrick) the scent organ is also paired, but more anterior, protected by sternite and accompanied by additional lateral hollow pouches bound with the tergite. The lateral region of this segment is strengthened by an elongate sclerite, slender posteriorly, expanding anteriorly and originating from the dorsal plate

of the abdomen. The scent organ of A. adamana (Kennel) consists of a pair of large, rounded concavities originating at the anterior corners of the eighth sternite and accompanied by indistinct anterior folds of membrane. A similar organ is found in Eucosmini genus Thiodia Hübner. In Th. citrana (Hübner) two pouches (fig. 5) are developed in the intersegmental membrane at the proximal corners of the eighth sternite. Homological structures are also found in two European species of Spilonota Stephens. A shallow invagination filled with slender scent scales is found at posterior part of subgenital sternite in Semnostola Diakonoff and much deeper concavities at the median portions of that segment in Enarmonopsis major (Walsingham). These concavities (fig. 6) enter beneath the sternite. Indistinct, elongate concavities situated between tergites and sternites of that segment (fig. 7) are realized in Antichlidas holocnista Meyrick. The outer edges of the pouches are fringed with short scent scales.

Various groups of scales, occasionally arranged characteristically, often situated at the distal edge of the subgenital sternite or on its ventral surface (e.g. in Archips HÜBNER) may prove to be of scent importance.

### Comments

The organs described above developed probably in the intersegmental membrane between sternites 7 and 8 being more or less lateral. In some species they are bound with anterior part of the subgenital sternite, in others, however, are situated near its lateral edges. They might have developed independently in some taxa as one can judge from a formation of an additional pouch in the subtergal region in phasmatica or a curious structure in Xeroenephasia rigana (Sodoffsky) which developed an unusual additional pouch in distal portion of subgenital sternite. Thus the pouches situated in posterior part of the subgenital segment may be developed independently of the membrane between sternite and tergite. In all known Archipinae the pouches are devoid of any scales; scent scales are, however, found in several Olethreutinae. It seems evident that the organs possessing scent scales have developed by a depression of the areas with glands, but there are no grounds to confirm that the simple scaleless pouches evolved from them directly. Such membranous pouches or sacs are already developed on the venter of the abdomen in Micropterigidae, so those in Tortricidae could also appear independently.

## Males

### Chlidanotinae

Polyorthini. In Olindia schumacherana (Fabricius) (figs 8, 9) the tegumen is simple but large, broadly rounded posteriorly, forming large posterior lobe with parallelly-situated intersegmental membrane extending proximad to be-

fore middle length of the plate. The sternite forms a pair of large sublateral lobes and is distinctly sclerotized anteriorly. The scent organ is developed as an elongate plate folding longitudinally, with inner wall and the major part of the bottom sclerotized and the outer wall membranous. The dorsal part of this structure is attached to the posterior edge of the tergite, the inner wall with the genitalia and the outer wall by a long membrane with the adominal plates. The scent gland is situated in the ventral portion of this structure. The scent scales are very long, thread-like, forming a bunch kept in a slit of the outer surface of the valva. The scent organ of Polyortha viridescens (MEYRICK) (figs 10-12) is more complicate than in Olindia Guenée. The tergite is large, rounded posteriorly and its membrane extends proximally as far as to its base; the lobes of the sternites are shorter and their inner walls are distinctly sclerotized on the same distance as the outer walls. Lateral parts of the tergite and sternite are connected by a complicate sclerotic structure of the scent organ. Its anterior portion extends proximally as a sclerotic belt of the inner portion of the scent sac, almost reaching its bottom. In distal part the sclerite along its long axis and forms a cup-like base from which extends a sclerotic plate directed proximally and fused with inner membranes of the tergite and sternite. The cup-like part of the sclerotic structure is firmly connected to the tergite and membranously so to the sternite. The scent cells are distributed in outer portion of the sac and in its bottom part where they are most dense. This differentiation leads to a development of two distinct groups of scent cells forming two more or less distinctly separate scent glands, with two groups of variably long scales. In Ardeutica sphenobathra (Meyrick) this separation is well advanced. In other genera of Neotropical Polyorthini, e.g. in Monortha RAZOWSKI the form of the scent organ is very similar, and the differences are expressed in the size of the sac, form of the sclerotic structure and development of the scent gland and its scales.

Hilarographini. The scent organ in Hilarographa plectanodes MEYRICK (fig. 13) is similarly built as in Polyorthini, but seemingly more advanced. The tergite is rather weak, the sternite is large, broadly extending laterally to form lobes homological to those described in Polyorthini. The scent organ is connected with the tegumen, what is a synapomorphy of all Chlidanotinae tribes, and consists of a deep membranous pocket strengthened with long inner sclerite tapering towards its bottom and bifurcate distally. The dorsal branch of the latter is broad, rounded apically, attached to the tegumen, the ventral part fused with the lateral portion of the sternite. The distal borders of the sac fuse with the vinculum and the abdominal plates. In the bottom of the sac there is a compact scent gland with non-differentiate, thread-like, very long scales.

The genus Orthocomotis Dognin included by me in Chlidanotinae on the basis of the genital characters developed deep cavities in the basal area of the abdomen but is devoid of the scent organ typical of the tribe. In the membrane above sternites 1+2 there is a membranous pouch provided with a pair of

reversible elongate areas of thick scent scales flanking a much longer tapering proximally surface of dense sensillae. Ill-defined groups of identical sensillae are also situated before and beyond the latter (O. aphanisma Razowski & Becker, figs 14, 15). Its distal, rounded part is concave, the remaining portions weakly so. An additional element of the organ is a small, deeply concave punctured area situated antero-ventrally to the dorsal scaled area. The organ varies within the genus in the size and proportions of its elements and is absent in some species (e.g. in O. attonsa Razowski). Its shape and accompanying scales of the anterior part of the abdomen in O. pseudolivata Clarke is figured for comparison. This organ certainly fulfils the scent function, but the presence of the sensillar areas points to its additional receptorical importance.

# Tortricinae

Cochylini. In this tribe the scent organs are scarce but occasionally highly specialized. The most primitive genera (e.g. Phteochroa Stephens) or the primitive species within other genera have no scent organs on the abdomen. In some species the distal portions of some sternites are somewhat extending posteriorly, clothed with scent scales. In Mielkeana gelasima RAZOWSKI & BEC-KER (fig. 17) there is a short median prominence of sixth sternite and much larger, expanding terminally process of the seventh sternite. In Lasiothyris cnestovalva Razowski & Becker (fig. 18) a large, bifid process is situated on sternite 6 and on the following sternite the prominence of the posterior edge is very small. The atrophy of the latter is observed within this genus and in L. ficta RAZOWSKI & BECKER it is almost completely reduced. The shapes of the sternal process of the sixth segment are variable, often being of specific importance (cf. L. diclada Razowski & Becker, fig. 19). In Saphenista Wal-SINGHAM this organ appears in several species and is variably shaped and reduced. Usually it is preserved on sternite 6 (e.g. in S. orichalcana Razowski & BECKER, S. eranna RAZOWSKI & BECKER) but also is occasionally found in sternite 7, but in vestigial form (S. consona Razowski & Becker). Homologous organ of sixth sternite is also discovered in Mimeugnosta Razowski. The described organ is only known in the Neotropical genera forming a rather compact group and is treated as homological in all of them. The ventral and partially lateral surfaces of the processes are well sclerotized whilst the dorsal area is membranous. Some rather little-differentiated scales treated as the scent scales and some bristles are occasionally present.

In Eupoccilia Stephens the subgenital sternite is highly specialized in some species, e.g. in E. ambiguella (Hübner) (fig. 20). The distal edge of the sternite is somewhat protruding what reminds the conditions in the preceding genera and in Henricus Busck, covered with fairly broad scales. Along the middle of the sternite runs a delicate convexity forming a distinct bulb at the proximal edge. The scales of this organ are differentiated, the longest expanding terminally are situated proximally, followed by a small number of somewhat

slenderer scales; the remaining scales clothing the median rib are short, very broad. In another species (probably n.sp., from Tibet, figs 21, 22) very close to the preceding one, the posterior prominence of the sternite is broad, the median rib is weak and the proximal swollen portion is rounded. The scales are also different in shape but show a similar character. In the two cases the proximal edge of the sternite is similarly shaped as the costal selerotization consists of two narrow lateral portions. In ambiguella a weak scent structure is also found in the preceding sternite (scales broken off during preparation). It consists of two ventral elevated areas extending from beyond middle lenght of sternite to its distal edge. This organ is treated as an autapomorphy of Eupoecilia; it is observed that in some species (e.g. E. angustana (HÜBNER)) it may be completely atrophied.

The subgenital segment of the New World genus Henricus Busck is strongly altered being functionally included in the genital scent organ (figs 23-28). The tergite of this segment is enlarged, convex dorsoposteriorly, strengthened by a lateral sclerotic belt laterally. The distal area of the tergite is more or less concave and contains scent glands from which groups of slender scales extend. The distal edges of the sternites 6 and 7 are more or less extending posteriorly similarly as in Saphenista and its allies. The scent scales of those prominences are specialized, longer than the cover scales of the remaining surfaces. In H. powelli Razowski (fig. 23) in a postbasal concavity of the median portion of the sternite there are some similarly shaped scales, probably also of scent importance. As mentioned above, the subgenital segment is included in the elaborate scent armature. The sternite is weak, with atrophied costal belt whilst the tergite is very strong, with large dorsolateral cavities. In the lower portion of each cavity a large group of completely fused scent scales is located, in the upper area a long bunch of scales is placed. The lower bunch consists of long scales completely fused in their distal halves or thirds but separable anteriorly. The two clusters originate in the membrane of the outer surface of the valva posteriorly to the vinculum as shown for H. ophyrodes (MEYRICK) (fig. 27). The upper cluster is compact and its scales are invisible, impossible to separate (fig. 28). It easily breaks off leaving distinct sockets on the valva membrane.

Tortricini. The scent organs are developed at least in a few more generalized genera and they are rather insufficiently known in result of the lack of material for study. Some of the bunches of scent scales are certainly attached to the tegumen. In Accra Razowski and most probably in all allied genera (e.g. the Etiopian Sanguinograptis Razowski) the scent glands are situated in a pocket developed externally to the articulation between tegumen and valva. In Accra (fig. 29) a weakly specialized scent organ is situated in the membrane just before the genitalia and consists of long, usually bipectinate scales (the longer placed externally to the smaller ones) accompanied by short, deeply incised scales. Ventral surface of the membrane is armed with two belts of minute spines directed distally, not reaching its posterior part. The sub-

genital segment bears peculiar lateral structures most probably of scent importance. Its distal edge is deeply concave medially, fringed with elongate, basally-thin scales; from the middle of the anterior edge extends a long rod like process tapering towards base. On each side of the sternite an elongate semifunnel structure is present. Most probably it developed from the marginal part of the sternite and is connected with it by a ventral membrane invaginating medially. The anterior portion of this structure is directly fused with the sternite, the posterior juncture is, however, realized by a slender belt. Distal portion of that organ extends far beyond the remaining parts of the sternite and is covered by rigid, sharp, transformed scales. Similar but shorter scales are present more proximally, being partially covered by usual pectinate scales laterally and very short, ovate scales at the base.

Paratorna cuprescens Falkovitsh has little-specialized plates of the subgenital segments but its scent organ situated at the end of the subgenital membrane is much more advanced than in Accra. It consists of two glandular areas covered with long scales slightly broadening apically. The upper, small, rounded area is situated just above the juncture between the tegumen and vinculum immediately above the lateral elongate area running along the vinculum arm and reaching almost its ventral line of symmetry. The scales of the two areas slightly differ as seen in fig. 30.

The scent organ in *Vellonifer doncasteri* Razowski from the Oriental Region (Razowski, 1968) consists of an elongate structure that bears two groups of scales of which the ventral one is built of a number of rather short, expanding apically scales and the lateral one of numerous thread like very long ones.

In Eboda smaragdinana Walker the scent organ is bound with the sternal region and composed of two parts. The tergite is rather weakly sclerotized. convex posteriorly. The sternite forms two distal prominences marked with irregular ribs fringed by a row of rigid, bifurcate transformed scales (only the innermost scales are spiniform). Between the tergite and sternite two deep lateral sacs are developed entering the sixth segment. The inner portions of the sacs extend along the pedunculi edges and terminate around the plate-shaped process of their bases dorsally. Each sac is suspended on a long ventral rigid but transparent and flexible process originating on proximal broadening of the upper portion of the vinculum. The process is fused with the sac in its posterior (basal) third. The scent gland is situated in the bottom of the sac and is accompanied by long, thread like scales. Along the distal edge of the vinculum extends a belt of thin scales terminating submedially. The outer portions are broadening to form rounded patches from which extend much longer scales. The scales of the two parts of the scent organ protrude through the same opening.

Tuck (1986) illustrates the scent organ of his *Latibulocornis curiosa* from Brunei describing it as belonging to 6th segment. It consists of the pair of sublateral sacs clothed with cilia and provided with apical bunch of scales. This

organ is unknown to me and is not included in table 1 as no exact location is

given.

Archipini. In the more generalized generalike Epagoge Hübner the scent organs are not differentiated. Their subgenital sternite is rather uniformly and weakly sclerotized and its covering scales are little differentiated. In the more specialized generathe abdominal plates, chiefly the sternites, are more or less specialized and their scent scales distinctly differ from the covering scales.

In Aphelia pallorana (Robinson) the subgenital sternite is rather simple, with weakly differentiated proximal portion, which is well sclerotized. The scent scales are grouped along distal edge being agglomerated chiefly ven-

trally (fig. 34).

The subgenital sternite in *Meridenis vietorum* Razowski (fig. 35) is subdivided by a semimembranous area into the anterior, broad sclerite and crescent-shaped posterior, rather distinctly sclerotized part. The scent scales are grouped in transverse rows on the distal rib like prominences behind which the sternite develops two subtriangular lobes directed dorsad.

The structure of the subgenital segment of *Electraglaia izosona* (Meyrick) (fig. 36) is much more advanced. The tergite is well sclerotized anteriorly and broadly so along middle as far as to posterior prominence clothed with fairly broad scales. The sternite is not membranized postbasally, however, its proximal edge is strongly sclerotized, marked with median process directed anteriorly. In the distal portion of the sternite a pair of lateral pockets is present. The scent scales are rather uniformly shaped, the longest being situated medially.

Neocalyptis krzeminskii Razowski (fig. 37) and most probably all its allies are characterized by large sclerotic posterior area of the tergite connected with the proximal sclerite by a slender median belt. The proximal edge of its sternite is strongly sclerotized, very slender, marked by median anterior broadening and a subterminal thorn-like process directed medially. All the remaining area is membranous except for two lateral shallow concavities with posterior edges somewhat emarginate, directed ventrally. Besides the scent scales densely clothing the concavities there occur some lateral tactile bristles. A similar structure of the sternite is found in some other genera, e.g. in Clepsis Guenée.

In Diplocalyptis apona Diakonoff the process of specialization also concerns the two plates of the eighth segment. The tergite is membranized immediately beyond the anterior sclerite and the scent scales occur beyond another sclerotized area developed submedially and extending laterally. The structure of the sternite is very complicate; the proximal sclerite and the membrane are fully developed, followed by lateral concavities the edges of which are well sclerotized and provided with fairly long scales. The longest broad posteriorly scent scales are grouped submedially. The posterior portions of the sternite are connected with the processes of the vinculum by means of a delicate membrane.

Further specialization of the subgenital segment is realized in *Isodemis illiberalis* (Meyrick) (fig. 41) in which the proportions of the tergal sclerites

are quite different than in all preceding genera. The process of membranization of the sternite is advanced to such a degree that only the proximal sclerite remained distinct. To fulfil its role it becomes broader posteriorly and its proximal process is long. The scent glands are situated in lateral oblique concavities becoming shallow towards middle and followed by a plicate median structure connecting it with the genitalia. The scent scales of the concavity are differentiated: in the shallow parts they are simple, small, in the submedian portion larger, in the deepest very long. Some long, fairly broad scales of probably same importance are found proximally to the scent organ.

In Leptochroptila daratua Diakonoff (Diakonoff, 1939) there are large groups of scent scales on the lateral parts of the eighth tergite. Diakonoff also illustrates a sternite in which besides the proximal sclerite there are at least three specialized areas being most probably the scent organs. Horak (1984) illustrated the sternite of an undescribed allied genus with long tuft of scent scales originating in the outer patches and a bilobe median area. Unfortunately the descriptions and drawings in the two papers are insufficient for a more accurate discussion.

The tergite of the eighth segment is weak in Archips Hübner, but in A. seminubilus (Meyrick) (fig. 44) there is a distinct proximal plate accompanied by a weak posterior sclerotization. The sternite of this genus has a strong anterior plate with distinct median process membranously connected with a complicate posterior plate. The latter is semicircular, emarginate anteriorly and laterally, with well-expressed posterior portion directed dorsad. Scent scales of three types are situated on the folded areas and the tactile hairs are distributed on the ventral surface. The distal portion of the posterior plate may also bear some scent scales as shown in fig. 42 (A. compitalis Razowski). In this species the scent scales form a large lateral tuft on the up-curved portions of the posterior plate of the sternite and are differentiated as in some other species of this genus, forming two indistinctly separated groups.

The abdominal scent organs in *Pandemis* Hübner are represented by subgenital structures and basal pockets. The eighth segment is strongly altered in its ventral region whilst the tergite is simple with all the surface except anterior edge uniformy and rather weakly sclerotized (fig. 46); the posterior scales may prove to be of scent function. In *P. heparana* (Denis & Schiffermüller) (figs. 45, 46) the proximal portion of the sternite is plate-shaped, the median portion is completely membranous, scarcely scaled and the distal part built of a pair of two deep pouches. Their posterior edges are membranous except for submedian, strongly sclerotized triangular plates membranously connecting the vinculum. In the inner part of the pocket the scales are fairly short, much broader than the main group of thread-like scales originating on the gland in the bottom of the pocket.

In *P. corylana* (FABRICIUS) the posterior plates are rather shallow and their posterior sclerites are slenderer than in *heparana* provided with subtriangular prominences contacting the vinculum (fig. 47). The scent scales are

also differentiated and form three groups, of which the longest are situated externally, and the anterior become gradually longer towards the middle. That structure is similar in shape in *P. cerasana* (HÜBNER) (cf. RAZOWSKI, 1978).

In the latter species a complicate scent organ (figs 49, 50) is located in the basal area of the abdomen, ventrally. It consists of a pair of fairly deep pockets separated from one another by sternites 1+2, deepening lateroposteriorly, filled with a great number of broad scent scales. Posteriorly to those cavities extends a transverse narrow area of strongly transformed scales (fig. 50). There is no support to treat them as scent scales; however, they build up a compact morphological unit with the preceding structure. The sternite of the following segment is elongate and its anterior prominences touch two ovate fenestrae developed in a thin membrane.

The saes of this type are found in already-mentioned corylana (fig. 47); however, they are strongly reduced having a form of shallow concavities with innumerous small scent scales. Another species, P. phaiopteron RAZOWSKT (figs 51—53) has a peculiar basal organ. In the ventrolateral region of the base of the abdomen a deep cavity is developed and subdivided into rather shallow dorsal portion and a deep ventral part. Just above the latter a wart-shaped prominence armed with slender scales is developed. Proximal process of the sternites 1+2 is strongly enlarged, elongate, directed dorsally.

# Olethreutinae

Olethreutini. Falkovitsh (1962) separated his Eudemini on basis of the presence of scent scales of the particular abdominal segments. Then Diakonoff (1973) illustrated groups of thin scales in segments 3—8 in Sorolopha chortodes (Diakonoff). He also provided a drawing of the abdomen of Sycacantha ostracachtys Diakonoff with similar but weaker groups of delicate scales originating probably in the lateral membrane of segments 3—6. In four posterior segments of the abdomen of the Australian Statherotis amoebea (Lower) the same author shows groups of scales, on small segment 5 and large on segments 6—8. In Ophiorrabda favillosa Diakonoff he figures distinct convexities of segments 4—8 provided with groups of thin scales, and described them as a pair of lateral coremata on segment 6, and pairs of dorso-lateral coremata on the two following segments. He also mentions that in Metendothenia Diakonoff there are "sometimes coremata on 7th segment in male". Unfortunately those structures have not been examined by me so I did not include them in the table 1.

Distinct dorsal scent organ situated beyond transverse sclerite of 6th tergite is found in *Statheromantis pietana* (Kuznetsov). It consists of a rather weakly sclerotized area clothed with pectinate scales, situated in a membrane. The following tergite is similar, but devoid any scent area.

Of Gatesclarkeanina at least two species developed peculiar abdominal organs (Gatesclarkeana idia Diakonoff and Asymmetrarcha iograpta (Meyrick)). In first of those species (fig. 54) the organ is developed in the ventral region of the segment 3 and is anteriorly limited by a collar like median fold concave in middle proximally, extending distad posteriorly partially separating two large shell-shaped structures. The proximal portions of their ovate covers reach to middle of sternite 1+2, the distal ones are extending beyond the border of third sternite being approached medially. The inner and partially outer edges of those sclerites are fringed with scales expanding posteriorly, probably of scent importance. Beneath posterior parts of the covers there are slender, elongate-ovate sclerites extending mediad into short processes that touch one another. These sclerites limiting the posterior space formed beneath the "shells" are membranously connected with an irregularly-folded inner membrane and with a transverse vertically-arranged structure. The latter, being membranous anteriorly, is distally strengthened by a pair of trapezoidal sclerites, the lateral surfaces of which are folded; the shorter are proximal.

In Ukamenia sapporensis (Matsumura) (figs 55, 56) the distal portion of the second segment is in major part membranized ventrally. In the following sternite there is a pair of anterior deep capsules opening towards the anterior edge of the sternite and extending in form of slender prominences to inside of the membrane of the preceding sternite. The walls of the capsules are rather weakly sclerotized, strengthened by concentric ribs between which some minute structures of undefined importance occur. Diakonoff (1973) illustrates very similar but directed laterally organs in Sycacantha ostracachtys Diakonoff from New Guinea terming them the scent pouches.

In Lobesia Guenée and Lobesiodes Diakonoff (Lobesiina) a pair of lateral, pouches situated in the membrane above sternites 1+2 (figs 57, 58,) are developed. Their scent areas are provided with small, broad scales.

Eucosmini. In the subtribe Eucosmina the abdominal scent scales are weakly differentiated or absent. In some species, as in Hendecaneura impar Walsing-Ham (fig. 59), they form an indistinct group in distal portion of the subgenital sternite, laterally.

In *Grapholitina* the abdominal scent organs are very common, often highly specialized. The group of genera closely related to *Pammene* Hübner is characterized by dorsal scent scales arranged in groups near the anterior edges of the tergites. In *P. christophana* Möschler and *P. argyrana* (Hübner) the scent organs are preserved on tergites 6 and 7 in form of transverse belts of long scent scales in the latter species and are accompanied by a subdorsal pencil of scales situated in the membrane beyond eighth tergite (fig. 60). In *P. trauniana* (Denis & Schiffermüller) scent organs (fig. 61) are preserved only on sixth tergite.

Pammenodes galucana (Kennel) has similar scent organs on tergite 4 and 5. They consist of fully developed transverse areas of short scales situated in semimembranous portions of the tergite. Similar membranous areas developed

beyond sclerotic anterior edges are figured by Danilevski & Kuznetsov, 1968 also in tergites 6—8, however, without scent scales.

The scent organ of *Pseudopammene fagivora* Komai (figs 62, 63) consists of the anterolateral pocket of the subgenital tergite filled with a large group of very slender scent scales, weakly differentiated group of scales on the distal portion of that sternite and a group of broad, large scales situated in the membrane at the end of the intersegmental sclerite (compare at *Grapholita Treitschke*). The tergite of this segment is altered in connection with its scent function, so its anterior separable portion is elevated, strongly sclerotized.

The of *Parapammene selectana* (Christoph) (fig. 64) is similar in shape to that in *Pseudopammene* Komai but its scent organ is atrophied. There is, however, a distinct organ bound with the intersegmental sclerite composed of ovate scent area extending ventrally in a subtriangular piece, and large bunch of long scales.

Strophedra nitidana (Fabricius) developed the scent organ situated in the lateral corner of the subgenital tergite. It is accompanied by a postbasal row of broad scent scales. Some longer scales are also in distal portion of the sternite, but no postsegmental bunch of scales is realized, although the postsegmental sclerite is present.

The scent region in Leguminivora glycinivorella (MATSUMURA) (fig. 67) is bound with the eighth sternite, the anterior portion of which is strongly sclerotized, incised in middle anteriorly, distinctly produced posteriorly. In its most distal portion there are some short, fairly broad scales. Laterally to that sclerite, along the anterior sclerotization extends a concave area of very dense, uniformy broad dark, scent scales. A bunch of much longer scales (accompanied by some broad but shorter ones) originate in a rounded concave scent area situated at the end of the costal sclerotization of the tergite.

The large genus *Grapholita* TREITSCHKE preserved only one scent organ, viz., the bunch of specialized scales placed at the dorsal top of a sclerite developed in postsegmental membrane, between eighth sternite and the vinculum of the genitalia. It is variably attached to the sclerite, usually by means of a short membrane. The scent gland is situated at its dorsal, often expanding portion. The sclerite together with its membranes may be retracted to the eighth segment. The shape of the scales and their groups are characteristic specifically; the whole structure of *G. funebrana* (TREITSCHKE) is illustrated in fig. 68.

There are two types of scent organs in Selania. In S. leplastriana (Curtis) (fig. 69) there is a small tergal scent area clothed with slender scales and a ventral group of long scales on the whole (very slender) sternite. The postsegmental sclerite is fully developed yet unaccompanied by scales. In S. resedana (Obraztsov) (fig. 70) after Danilevski & Kuznetsov (1968) the scales of the subgenital segment are not specialized, the postsegmental sclerite is present, but not expanding dorsally and in the postsegmental membrane there is a large, strongly altered scale replacing the typical bunch of scent scales of the preceding genus.

Elaborate and compound scent organs are in Matsumuraeses Issiki. In

M. falcana (WALSINGHAM) (fig. 71) it consists of two pencils of scales developed in the intersegmental membrane, subtergally. The more anterior one of them originates in the membranous fold beneath distal edge of seventh tergite, the second is more posterior and dorsal, situated just before the following tergite. Whilst the scales of first pencil are completely free, those of the second are stuck to before middle, forming a distal fan hidden in an oblique pocket of the lateral area of the subgenital tergite. Beneath the fold of the first scale tuft there runs a longitudinal depression in which small, broad scales occur. The seventh sternite is distinctly altered, semimembranous, except the proximal sclerotic edge divided into two lateral parts. In the middle of the lateral surface of the segment there is a large, elevated circular area full of long scent scales. The scales of very small eighth sternite are also of scent type. In the membrane beyond this segment a distinct postsegmental sclerite is developed. DANI-Leyskij & Kuznetsov (1968) illustrated the scent organs of M. ussuriensis (CARADJA). It differs from that in falcana by having the distal pencil of scales situated at the postsegmental sclerite, by the lack of the lateral scales of seventh sternite and by the lack of scent scales beneath the tergite of same segment. At the end of that tergite there is a simple bunch of thread-like scales located in the oblique slit of the subgenital tergite.

The most complicate scent apparatus consisting of several scent areas and altered sclerites is found in *Cryptophlebia* Walsingham, showing well-defined specific differences.

In C. ombrodelta Lower (figs 72, 73) the plates of the segment 7 are strong, the tergite forming a distinct costal sclerite. The costa of the subgenital tergite is arched, also well-sclerotized. A folded lobe of the posterior sclerite of the tergum the distal edge of which is fringed with short, transformed scales forming two lateral groups, is membranously attached in the median area of costa. On each side of that sclerite there is an elliptic, concave structure filled with long scales. From its proximal part extends a process terminating in a scaled patch. The sternite of this segment is very short, somewhat extending posteriorly, provided with sublateral rigid processes proximally. The processes contact with the sclerite of the postsegmental membrane. The median portion of the latter is strongly extending distally to connect the sternite, whilst the lateral parts are long, slender, coalescent with the scent area apically. The scent area is bordered with a fairly distinct sclerotic edge and located in a shallow, transverse pocket of the lateral portion of the intersegmental membrane.

In *C. yasudai* KAWABE (fig. 74) groups of long, thread like scales form in tergite 1 a submedian and in the following at least 4 tergites median pairs of scent structures. The anterior sclerite of the subgenital tergite is strong, constricted medially. Into the latter area enter anterior fold of the posterior sclerite which is concave distally and extends laterally. Those lateral parts are limited by shallow depressions bearing scent scales and more laterad and anteriorly flanked by much deeper pockets provided with very long scales. The postsegmental membrane contains ill-defined sclerites extending ventrad. The subgenital

sternite is small, slightly extending in middle posteriorly, clothed with long scales. Its proximal edge is rigid, provided with lateral, rounded prominences. The postsegmental sclerite is large, complicate, extending posteriorly and forming lateral wing-shaped parts. Of each end of them a small, elongate sclerite accompanied by scent area is attached.

#### DISCUSSION

There are two main types of scent organs in the tortricide abdomen: more or less concave or even invaginate areas of the segmental plates or intersegmental membranes and the pouches of its basal or ventral regions.

In the examined *Tortricidae* various reductions obscure the evolutionary trends. The scent cells were probably distributed originally in various parts of the abdomen surface and grouped in the areas most convenient for scent distribution, mainly in the ventral and posterior regions. Then they became more or less specialized, forming the organs which included the surrounding surfaces both membranous and selerotic. Their secondary specialization led to a development of even highly advanced structures. The most effective position was at the end of the abdomen, thus one can observe the subgenital segment is in many cases very strongly altered.

In the ventral surface the scent organs developed in the majority of Archipini, some Tortricini, Cochylini and most advanced Olethreutinae, mainly in Grapholitina. The most economic position for the ventral scent organs is the distal portion of the abdomen, especially the eighth sternite and its postsegmental membrane. In *Cnephasiini* and *Sparganothini* as well as in many genera and species of all remaining tribes this sternite is not modified and is uniformly and rather weakly sclerotized, scaled analogically to the preceding sternites. Only the scales of its posterior edge are much longer than the other scales and mainly play a protective function. In the process of the development of the sternal scent organs, the anterior region of the plate becomes rigid. It then forms a distinct transverse sclerite whilst the posterior area is less sclerotized. In the latter part of the segment the scales begin to specialize and group mediolaterally or laterally. In some genera as in Meridemis the distal portion of the segment is almost uniform, and the scent scales are grouped laterally on an oblique fold. The position of the latter became bent in such a way that the scaled surface was exposed distad. In Archips the scent glands are situated mainly on the dorsal emargination of the sternite, laterally. However, some scent scales are placed as in Meridemis but that posterior area becomes more specialized forming a narrow, transverse belt directed vertically to the main surface of the sternite. Parallel process of a membranization of the surface between the proximal and posterior areas of the sternite is observed causing some secondary changes in the two regions. It was probably involved by the

trend to the most favourable exposition of the scent area realized by the function of the segmental muscles. The changes in the anterior region of this segment are defined by simple response to mechanical factors. In Neocalyptis, Clepsis and several other genera of advanced Archipini the process of membranization is strong, even between already-developed, distinct scent areas. In Isodemis the entire distal area becomes membranized and the scent organ is situated in a pair of concavities. The membranization of the whole posterior area involved a contemporary process of strengthening expressed in a plication of the membrane vertically to the forces acting on the whole unit. In Pandemis the scent glands are in much more depressed areas which form rather distinct pouches situated as in the preceding genera. The distal parts of them are secondarily sclerotized what enabled the preservation of their normal shape. That is a different way of realization of the same problem (mechanical resistance) as in Isodemis Diakonoff. In Electraglaia Diakonoff the situation is quite different: the sternite is short, uniformly sclerotized, sufficient to support the scent organs. The process of sclerotization seems to be secondary in this case. Another specialization is observed in Diplocalyptis Diakonoff in which the sclerotization concerned only some portions of the eighth sternite. In all mentioned genera there is a tendency to stabilize the anterior part of the sternite by a formation of a median process at its anterior edge. The shape of lateral arms of the costal sclerite is also adapted to this function.

In Archipini, similarly as in the other tribes of Tortricidae, there is a tendency to the differentiation of the scent scales both within the whole region and in its particular elements. The scales of the pouches are often of 2 or 3 types of size, the smaller, usually broad scales are situated in the inner parts of the

pouches, the longest in their outer portions.

Simple ventral scent organs are observed in some cochyline species. In Henricus they are found in distal parts of the sternites in form of small protuberances. They are developed on the sternites and that of 7th sternite is certainly homological with the prominence of eighth sternite of Eupoecilia and most probably with those on segments 6 and 7 in several genera allied with Saphenista. In some species they are small, simple, in the other very large, usually bifid. Their scent scales are slightly specialized. Those simple prominences are probably closest to the primitive scent organs of the hypothetical tortricine moths and could develop on several sternites. The trend of specialization was, however, completely different from that in other tribes of this family. The increase of the organ was possible (because of its weight) in the segments of the median region of the abdomen only. In the more posterior segments they are small, if present. In Eupoecilia the scent organ is more complicate by development of additional, more anterior structures. Analogical apomorphic structures are expected in other cochylids.

Sternal scent organs have been realized neither in *Olethreutini* nor *Eucosmina* of *Eucosmini*; however, a group of lateral scales of the subgenital sternite of *Hendecaneura* Walsingham is most probably of scent function.

In Grapholitina some primitive organs are found in the subgenital sternites formed by transverse rows of scent scales or usually median tufts situated posteriorly. Only in Matsumuraeses there is a large lateral organ in segment 7, and in Leguminivora Obraztsov a large scent area occupies the postbasal portion of the subgenital sternite. It is supposed that the scent organ of eighth sternite of Grapholitina has a common origin with the organ of Tortricinae, but that it has remained unspecialized or weakly advanced because of a quite different trend in development of the organ situated in the membrane beyond that segment discussed on p. 533.

The ventral scent organs in *Tortricini* are bound with the postsegmental membrane being very close to the vinculum at least in *Paratorna* Meyrick. This type, variable in form, appears most probably in several other genera of this tribe but they require an reexamination as in some other taxa a similarly-situated organ originating of the pedunculus (e.g. in *Acera* Razowski) is present. Apart from this rather simple organ, attached to the proximal edge of the vinculum the fully-developed coremata are discovered in *Eboda* Walker. They also originate from the postsegmental membrane. The corema consists of a large sac attached to distal plates of the subgenital segment and extending proximally as far as inside the sixth sternite and the scent gland situated in its preximal portion accompanied with long scent scales. It occupies a ventrolateral position but is bound with the ventral region as one can gather from the presence of a rod-like ventral suspensorum originating in the vinculum.

Chlidanotinae also developed distinct coremata in the membrane between the subgenital segment and the genitalia but its sac is armed with a sclerite attached to the tergite and most probably originating from it. Because of the large size of the sac it occupies whole lateral area of the segment. The scent apparatus partially consists of the genitalia as the scale tuft is located in the outer slit of the valva. In Olindia Guenée the sac of the corema is very shallow, flattened laterally, partially sclerotized, and its scent gland is situated ventrally. That seems to represent a primitive than an advanced position. In Hilarographini the lateral sclerite rather strengthens the whole length of the inner body of the sac and has a bilobe basal portion. In Polyortha that sclerite is funnel-shaped and its base is more or less complicate, accompanied by a vertical additional plate. This most probably illustrates the evolution of the coremata within the subfamily, as in Chlidanotini that structure seems very close (unfortunately not reexamined for this paper).

There are some grounds to suppose that the scent organs of the membrane situated beyond the subgenital segment appeared in the three subfamilies (Chlidanotinae, Tortricinae: Tortricini and Olethreutinae: Olethreutina and Grapholitina) independently. In Grapholita and some related genera that organ is closer to that segment than to the genitalia and bound with an apomorphous selerotization of the ventral portion of the membrane. Thus there developed a quite distinct way of retraction of the scent organ in that segment. The presence of that sclerite in some genera without scent scales allows to suppose

that the scent organ disappeared in the course of a secondary reduction and that this character is an apomorphy of the subtribe. Such bunches of scent scales certainly appeared several times within the family, what supports the presence of additional scale pencils in *Matsumuraeses* (see p. 532) belonging to the same tribe as *Grapholita*. In *Cryptophlebia* the size of that scent organ is diminished because of the enlargement of the dorsal unit occasionally incorporated in the highly specialized intersegmental sclerite.

The dorsal region of the abdomen developed some analogical scent organs to these on the ventral surface, but their number is much lower, what supports the opinion that the distribution of scent is more easily realized by the former. In almost all Archipinae the scales of the eighth tergite extend distally serving mainly as a cover for the genitalia and their scent scales, if present, usually do not build up any specialized organ. The sclerites of this tergite are often elaborate. In Diplocalyptis the proximal edge is strongly sclerotized, separate from the large posterior part by a membrane. Some scales of its distal area are seemingly of scent importance. In Leptochroptila Diakonoff belonging to advanced Archipini large lateral tufts of scent scales are present. In Cochylini the dorsal scent organs found in Henricus are certainly apomorphic. No other well-defined scent organ was found in Tortricinae and Chlidanotinae, whilst of Olethreutinae, a great variety of dorsal scent organs has developed within the subtribe Grapholitina.

The most primitive organs are in Pammene Hübner and its allies. These are the transverse belts of scent scales situated on membranous areas beyond anterior edges of some tergites. The highest number of segments with preserved scent organs is 2; in Pammene they are situated on the sixth and seventh tergite and may degenerate on the latter. In Pammenodes Danie. & Kuzn. they are found on segments 4 and 5 but the subcostal, membranous areas are also present on the tergites 6 and 7, what suggests that the primitive condition is the presence of scent areas on segments 4—7. Analogically to the eighth sternite, the tergite of the same segment is more specialized that the preceding ones. The subcostal area of this tergite is also membranous in many taxa, however, scent scales were only found in Strophedra. Judging from the variation in shape and size of the scent areas, one can suppose that long, slender, lateral, elevated areas touching one another dorsally are most primitive.

In Strophedra there is an additional organ in this tergite, developed in form of a small rounded scent area provided with a fan like group of scales situated laterally. It is supposed that the additional group originates either independently or as a part of the longitudinal transverse belt. This may be supported by the presence of a similar but more advanced structure in Pseudopammene, having the form of anterolateral pocket with long scales in similar position accompanied by the scent organ of postsegmental membrane discussed below. The structure of the tergal sclerites in Pseudopammene and in Parapammene Obraztsov allows to suppose that in the latter the lateral bunch of scent scales is completely atrophied. The elaborate structure of the tergal

region of this segment of *Cryptophlebia* Walsingham is treated as an advanced stage of the same evolutionary trend. The apomorphic characters are the separation of the basal and median sclerites and the lateral pouches, more or less differentiated in particular species.

The scent organs of the intersegmental membrane of the distal portion of the abdomen appeared only in one *Grapholitina* genus, *Matsumuraeses*, independently and secondarily to the development of the tuft of scales of the scent gland attached to the postsegmental sclerite. The single or double organ is situated beneath tergite 7 and/or anteriorly to the eighth tergite and the posterior of them just before that tergite.

The pouches of the basal portion of the abdomen are identically located in Chlidanotinae (Orthocomotis), Archipina (Pandemis) and Lobesiina (Lobesia, Lobesiodes), but there is no support for their being of common origin. All of them developed small scent scales inside the pouches but the organs show various reductions and complications even within particular genera. In Orthocomotis the scent areas are accompanied by large groups of sensillae of unknown function, in Pandemis the organ may be reduced to various degrees, provided with additional, highly specialized scales, or the scent scales are situated in specialized areas. The scent organs of Lobesiina are rather simple and little variable. That all gives no support to judge whether the pouches of the abdomen base developed early in the evolution of the family and then became reduced in the majority of taxa, or if they appeared as complementary organs when other scent structures were insufficient to the scent requirements of some of them.

There are also organs of two peculiar types that need a separate discussion, both evolved in Olethreutini and known in a small number of genera only. The organ of Ukamenia Oku is certainly homological with that in Sycacantha Diakonoff. As concerns its function I follow the opinion of Diakonoff (1973) who treated it as of scent importance in the latter. To explain it a study on fresh material is needed. The peculiar abdominal organs of Gatesclarkeana Diakonoff and Asymmetrarcha Diakonoff at least partially performs a scent role as suggested by the presence of the specialized scales. A production of scent substances may also be located inside the shell-like structures and their covers can be temporarily open to release them and distribute by the scales. In case of both organs it is supposed they appeared independently and are treated here as autapomorphies.

The scent system in *Tortricidae* developed to various degrees in the family level taxa, being completely reduced in *Cnephasiini*, or very complicate as in *Grapholitina*. The abdomen scent organs must be assessed as a part of that complex (see table 1). This differentiation can be understood, that some groups either do not require a highly specialized scent system, or the organs they have are satisfactorily efficient. In almost all the groups some reductions are observed, especially within the most specialized genera. The only exception are *Grapholitina*, which both preserved some primitive organs and developed some others.

Distribution of scent organs in Tortricidae

scent organ on:	8th sternite	7th sternite	6th sternite	5th sternite	subgenital membrane	intersegmental sclerite	dorsal subgenital sac	ventral subgenital sac	4th—7th tergite	8th tergite	base of abdomen	3rd sternite	peduncus	valva	socius	forewing costal fold	hindwing anal roll	hindwing surface	legs	8th female segment
Polyorthini	_	-		_	+	_	+			_	_			_					_	_
Hilarographini				_	+	_	+		_	_			_	_			_		_	
Chlidanotini	_	-		_	+	_	+	_		_		_				_				=
Orthocomotis					_	_	_	_	_	_	+	_				_	_			_
Cochylini	+	+	+	+	-	_		_	_	+			+	_		1	_	_		
Tortricini	(+)				+	_	_	+	_			_	+	_	(+)		_			
Sparganothini		_			_		_	_		_		_	+	+	+	+				_
Cnephasiini		-	_			_		_	_	_			+	_		_	_			+
Archipini	+	-						_			+		+	+	_+_	+		_	+	
Olethreutini			_				_	_			+	+	+			+	+	+	+	_
Eucosmina	(+)	_			_		_	_		_	_		+	_		+	_	+	_	+
Grapholitina	+	1+			_	+		-	+	+	-			-		1+1		+1		

(+) — ill-defined or unique structures

# SYSTEMATIC IMPLICATIONS

The structure of the coremata is one of the most important systematic characters of *Chlidanotinae*. They are bound with the eighth tergite and the scale tuft is located in the outer slit of the valva. However, in several species and some more specialized genera, both elements, or only one of them, are reduced. Other scent structures, except for small groups of scales of the forewing, are missing. In two Neotropical genera, *Orthocomotis* Dognin and *Paracomotis* Razowski, secondary scent organs are developed in the basal region of the abdomen, most probably replacing usual coremata. The distribution of similar scent organs in *Tortricidae* does not support their identification as a distinct tribe.

Among the remaining *Tortricidae*, the fully developed coremata of the subgenital region are found only in *Tortricini*. Their structure is, however, different from that in *Chlidanotinae* as the base of the sac is not connected with the tergite by any sclerotic structure. Several representatives of this tribe developed a peculiar scent organ bound with the pedunculus and usually located at its articulation with the valva and vinculum certainly functionally replacing the coremata of the above type. In several other taxa of this tribe the posterior scent organs are bound with the genitalia or are developed in

the membrane beyond the subgenital segment. Of all other examined *Tortricinae* groups, *Tortricini* differ in the absence of the scent organs of the particular segments or they are quite different (in *Accra*) from those in *Archipini* and other tribes. So, the structure of the abdominal scent organs may be treated as an important tribal character.

The presence of primitive ventral scent organs of *Cochylini* suggests their generalized character. However, similar primitive scent organs are found in other groups. In *Archipini*, their specialization is characteristic of the tribe and they are treated as an autapomorphy.

In Sparganothini and Cnephasiini no male abdominal scent organs have been found in the course of this study. In males of Cnephasiini no scent organ has been found to date, and in Sparhanothini the only distinct groups of scent scales are those on the socii and valvae. Their males bear costal folds of the forewing and this is recognized as a primitive character shared by the representatives of almost all tribes.

The advanced Archipini have abdominal scent organs situated on the subgenital segment only; mainly on the sternite. They evolved in various ways: however, only few evolutionary trends are realized. The structure of the specialized organs is autapomorphic, in many cases, characteristic of particular genera or their groups. Contrarily to Sparganothini, the trend to develop scent scales of the socii is weak and probably convergent. Archipini developed specialized groups of scent scales (and scent areas distinctly differentiated) on the valvae. If in this tribe the scent organs are in form of pouches, they are located only in the segmental plates (mainly in sternites) and not in the intersegmental membranes.

Olethreutini did not develop any distal abdominal scent organs, but their scent requirements are realized by the organs situated on both pairs of wings and on the legs, and in a limited part by autapomorphic anterior organs of the venter. The latter organs may be used as additional systematic characters. In the systematic review I mention some structures described by Diakonoff (1973) but unfortunately I had no opportunity to reexamine them. As their situation is not accurately known I do not try comment on their systematic importance. Most probably they appeared independently from similar structures in other tribes.

Grapholitina is a tribe with the greatest variety of the scent organs within Tortricidae. It was usually treated either as a tribe of Olethreutinae or a subtribe of Eucosmini. Some genera have been treated as of indefined systematic position and located variably in the Eucosmina, Grapholitina or Enarmoniina. The differing characters among those groups were inconstant and insufficient. The presence of the intersegmental sclerite is probably an apomorphy of this subtribe and permits an easy separation of the two subtribes as well as an inclusion of some genera unplaced to this date. The absence of that sclerite in Pammene is, however, a weak point of this hypothesis. It is supposed that the postsegmental sclerite degenerated in that genus and its function was ta-

ken by the enlarged, primitive dorsal scent structures. Reexamination of some primitive species of *Pammene* may solve this problem. In *Eucosmina* the function of the discussed organ is performed by a more primitive structure, an agglomeration of scent glands and scales on a lower part of the pedunculus, treated as a primitive character (distributed throughout the family).

## NOTE ON TERMINOLOGY

PIERCE (1914) introduced the term corema (-ata) for a paired scent structure of eighth segment in Geometridae then adapting it for the scent organs (sac and scent scales) of some other segments. Diakonoff (1939) described it as "lateral extension of pleura [sic!] of segment" and located it in the seventh segment. Tuxen (1970) followed Pierce's diagnoses mentioning segments 7-9. HORAK (1984) used it for any scent structure of sternite 8. I prefer to use the more general term, scent organ, until the differences between the structures of the segmental plates and those of the intersegmental membranes are definitely explained and preserve the term coremata for deep invaginations of the membranes provided with scent glands and scales. Diakonoff's term "pencil" is useful to describe "long, slender tuft of hairs" as originally expressed. I would only like to add that in the Totrtricidae the "pencils" are exclusively built of scales and not of hairs. Two further terms of that author are the mensis and the scopa. Mensis (dorsalis and ventralis) is originally defined as "chitinised caudal edge of the 8th abdominal segment in male" and this meaning is accepted by Tuxen and other authors. Only Horak (1984) suggested that it concerns the anterior sclerite of the segment. Scopa (also dorsalis and ventralis) is after Diakonoff a "long, dense hairs [= scales] at the 8th abdominal segment in male" and that is named by Horak as coremata. That corrects Tuxen's interpretation of mensis also based on Diakonoff's description of the scopa which are , the hair-brushes on those [= mensis dorsalis and mendis ventralis] parts".

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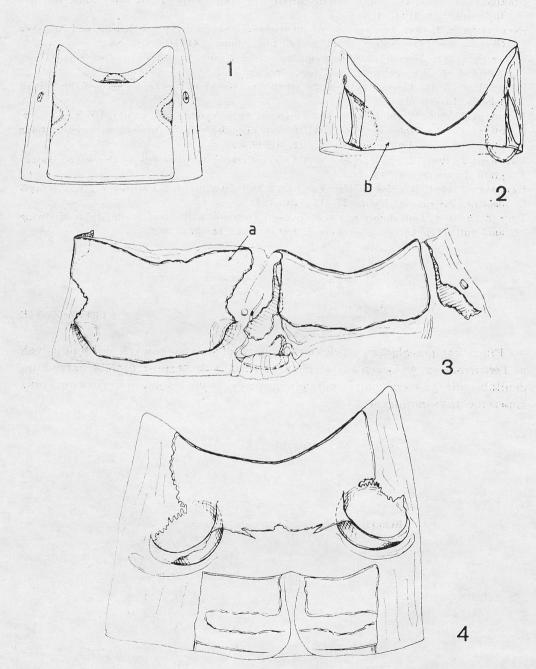
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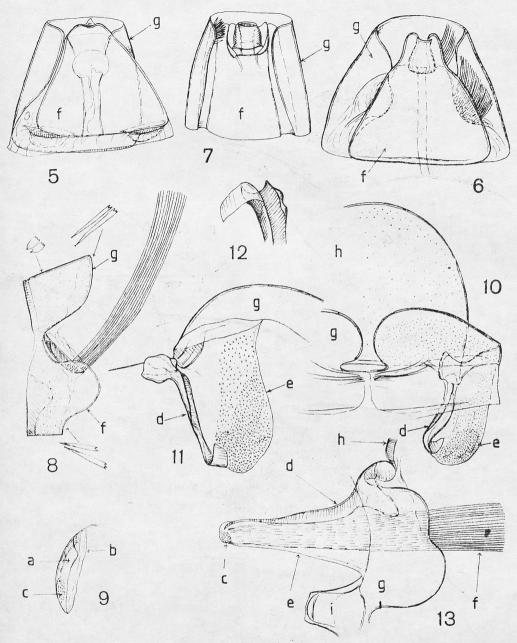
STRESZCZENIE

Praca jest przeglądem odwłokowych narządów zapachowych występujących u *Tortricidae*, z wyłączeniem struktur związanych bezpośrednio z narządami genitalnymi. Zawiera opisy narządów, próbę wyjaśnienia ich rozwoju oraz znaczenie taksonomiczne.

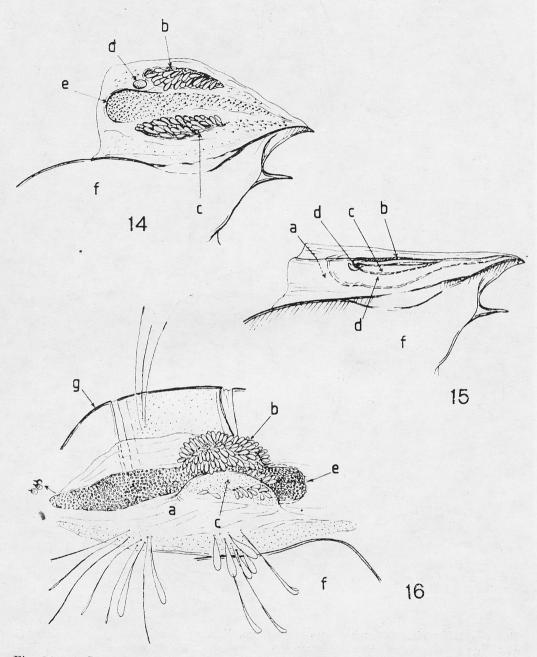
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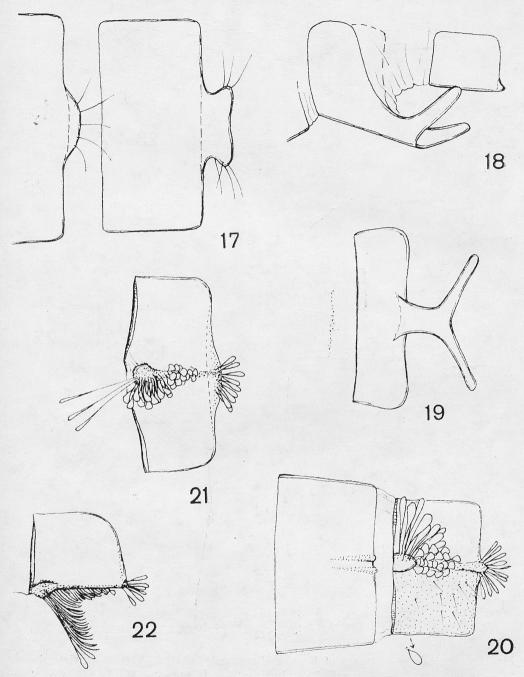
Figs 1—4. Female scent organs of *Cnephasiini*, ventral view of subgenital sternites: 1 — Xerocnephasia rigana (Sodoff.), Germany, after Razowski, 1981; 2 — Doloploca punctulana (Den, & Schiff.), Germany, after Razowski, 1981; 3 — Amphicoecia phasmatica (Meyr.), China; N. Yunnan; 4 — A. adamana (Kenn.), Altai Mts; a — tergite, b — sternite



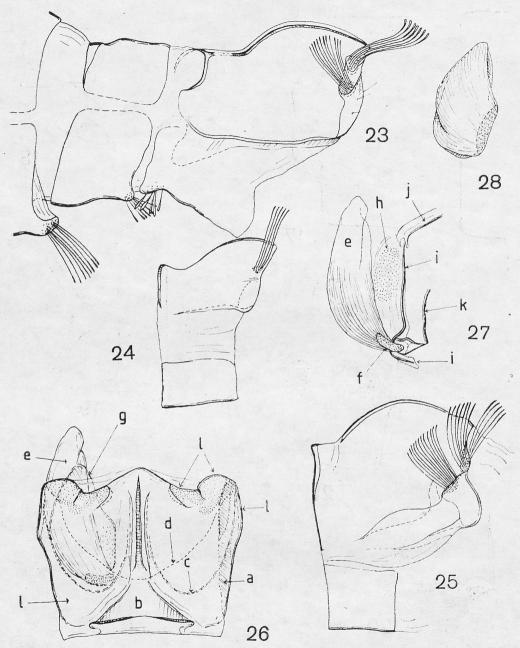
Figs 5—13. Female (5—7, with parts of genitalia, Eucosmini) and male (8—13, Chlidanotinae) scent organs, ventral view except for 8, 9 (lateral): 5 — Thiodia citrana (Hübn.) Poland, 6 — Enarmonopsis major (Walsm.), Japan; 7 — Antichlidas holocnista Meyr., Japan; 8 — Olindia schumacherana (F.), Polyorthini, Poland, 9 — same species, scent organ; 10 — Polyortha viridescens Meyr., Brazil: Paraná; 11 — same species, scent organ, enlarged; 12 — same species, terminal part of lateral sclerite of corema; 13 — Hilarographa plectanodes Meyr., Hilarographini, Costa Rica; a — inner wall, b — outer wall, c — scent gland marked by sockets of scent scales, d — lateral sclerite of corema, e — sac of corema, f — scale pencil, g — sternite, h — tergite



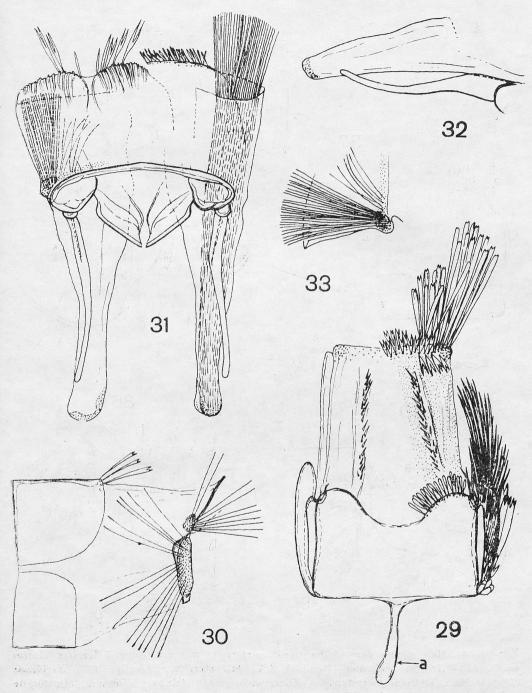
Figs 14—16. Scent organs of Orthocomotis Dogn., lateral view, with examples of scales; 14—15—0. aphanisma RAZ. & BECK., Mexico: Veracruz; 16—0. pseudolivata CLARKE, Brazil: Paraná; a—lateral cavity, b—dorsal scent area, c—ventral scent area (in fig. 16 everted), d—ovate sensory pit, e—elongate sensory area, f—sternite, g—tergite



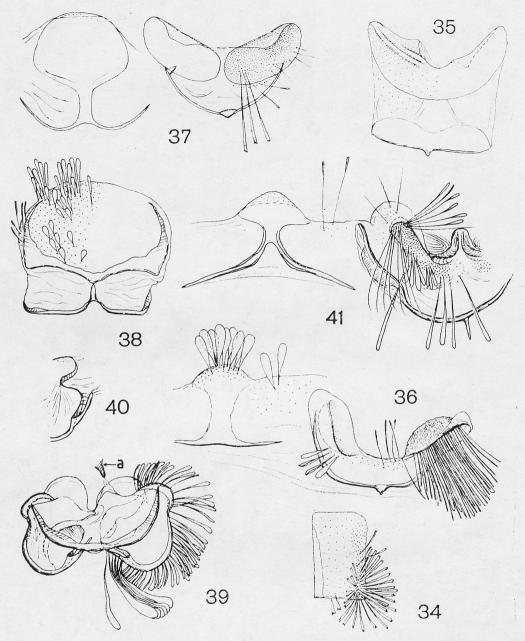
Figs 17—22. Male scent organs of *Cochylini*, ventral (17, 19—21) and lateral (18, 22) view: 17— *Mielkeana gelasima* RAZ. & BECK., Brazil.: Paraná; 18— *Lasiothyris cnestovalva* RAZ. & BECK., Costa Rica; 19— *L. dielada* RAZ. & BECK., 6th sternite, Costa Rica; 20— *Eupoccilia ambiguella* (HÜBN.), Poland: 21, 22— *E.* sp., Tibet, 8th sternite



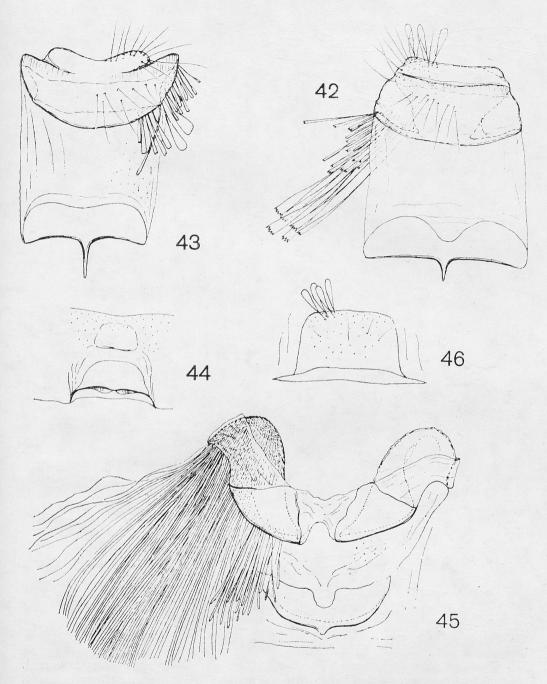
Figs 23—28. Male scent organs of Henricus Busck, Cochylini; 23—25, 27, 28, lateral view 26—dorsal view: 23—H. powelli Raz., Mexico; 24—H. cognatus (Walsm.), Mexico; 25—H. melanoleucus (Clarke), Mexico; 26—27—H. ophyrodes (Meyr.), Mexico; 28—upper scale cluster of same species; a—lateral sclerite of 8th tergite, b—anterior sclerite of 8th tergite, c—anterior edge of scent cavity, d—posterior edge of 8th sternite, e—lower scale cluster, f—glandular area of upper scale cluster, g—lower scale cluster, h—glandular area of lower scale cluster, i—vinculum, j—costa of valva, k—sacculus, l—sternite



Figs 29—33. Male scent organs of *Tortricini*; 29, 31, 33—ventral view, 30, 32—lateral view: 29—*Accra viridis* (Walsm.), Nigeria; 30—*Paratorna cuprecens* Falk., URSS: Primorsk; 31—*Eboda smaragdinana* Walk.; 32—same species, lateral tuft of scent scales; 33—same species, sac of corema; a—anterior process of 8th sternite



Figs 34—41. Male scent organs of Archipini, on sternites, ventral view and tergites (dorsal view): 34—Aphelia pallorana (Rob.). U.S.A., 8th sternite, laterally; 35—Meridemis vietorum Raz., Vietnam, sternite; 36—Electraglaia isozona (Meyr.), Vietnam, 8th tergite and sternite; 37—Neocalyptis krzeminskii Raz., Vietnam, 8th tergite and sternite; 38—Diplocalyptis apona Diak., Vietnam, 8th tergite; 39—same species, 8th sternite; 40—same species, end of lateral sclerite; 41—Isodemis illiberalis (Meyr.). Vietnam, 8th tergite and sternite; a—vinculum



Figs 42—46. Male scent organs on 8th sternites and 8th tergites of Archipini: 42 — Archips compitalis RAZ., Vietnam; 43 — A. seminubilus (Meyr.), Vietnam; 44 — same species, 8th tergite; 45 — Pandemis heparana (Den. & Schiff.), Poland; 46 — same species, 8th tergite

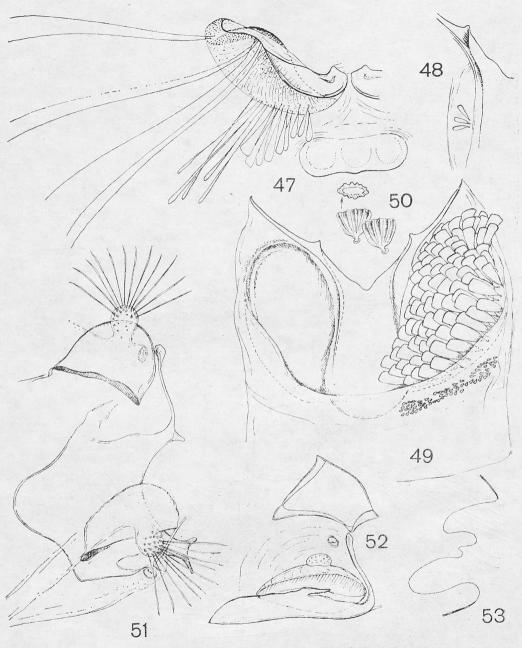
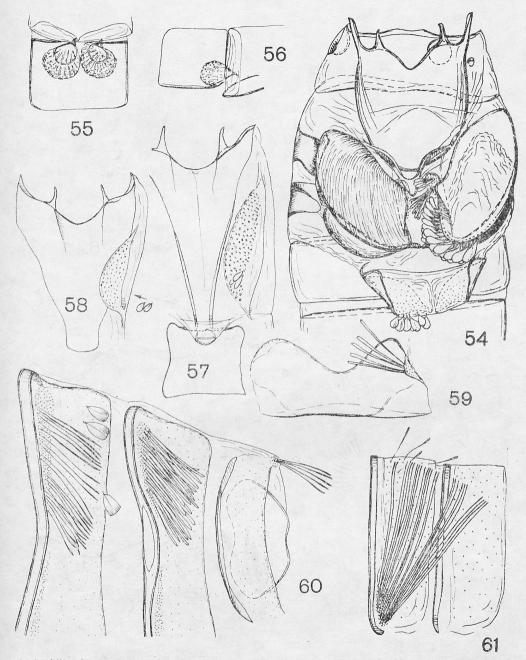
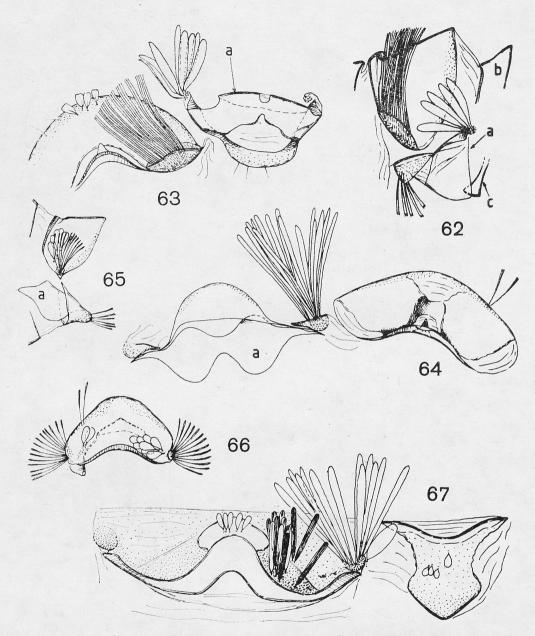


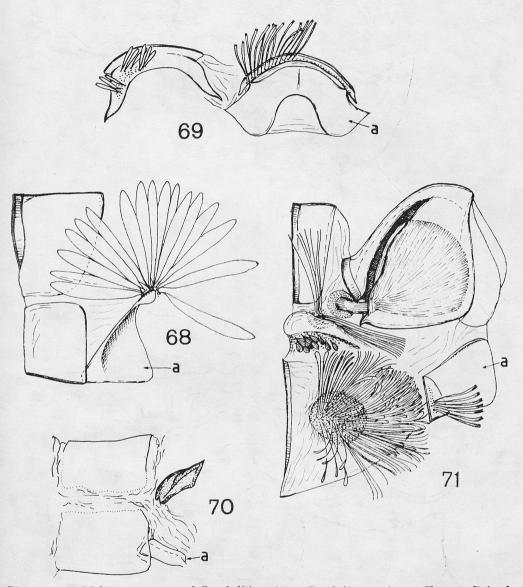
Fig. 47—53. Male scent organs of Pandemis Hübn.: 47—P. corylana (Den. & Schiff.), 8th sternite; 48—same species, basal abdominal pouch; 49—P. cerasana (Hübn.), Poland, base of abdomen, ventral view; 50—same species, transformed scales of anterior row, magnified; 51—P. phaiopteron RAZ., China: S. Shansi, ventral view of base of abdomen; 52—same species, same area, lateral view; 53—same species, transverse section of the organ, outline



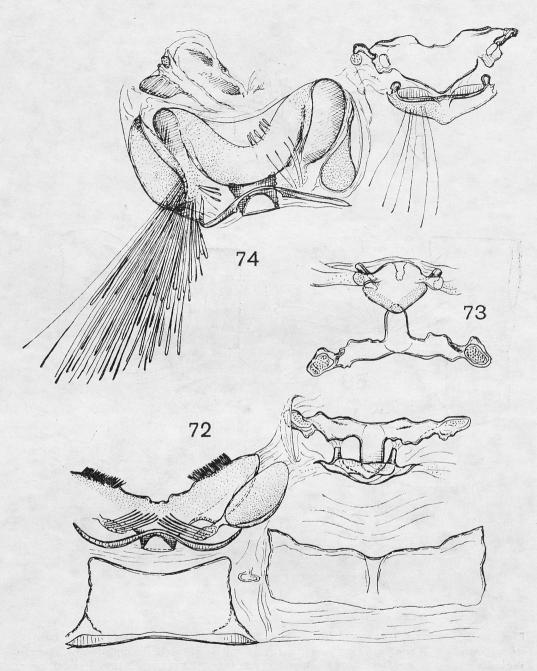
Figs. 54—61. Male scent organs of: 54— Olethrentinae Gatesclarkeana idia Diak., Olethreutini, Japan, ventral view of anterior part of abdomen; 55— Ukamenia sapporensis (Mats.), Olethreutini, Japan, anterior sternites of abdomen, ventral view; 56— the same, lateral view; 57— Lobesia reliquana (Hübn.), Lobesiina, Poland, anterior sternites of abdomen, ventral view; 58— L. bicinctana (Dup.), Poland, the same; 59— Hendecaneura impar (Walsm.), Eucosmina, Japan, 8th sternite, ventral view: 60— Pammene argyrana (Haw.), Grapholitina, Poland, 6th—8th tergites, dorsal view; 61— P. trauniana (Den. & Schiff.), Poland, 6th and 7th tergites, lateral view



Figs 62—67. Male scent organs on subgenital segment of Grapholitina: 62 — Pseudopammen fagivora Komai, Japan, lateral view; 63 — same species, tergite dorsally, sternite seen from the inside; 64 — Parapammene selectana (Chr.), Japan, sternite in ventral view, tergite in dorsal view; 65, 66 — Strophedra nitidana (F.), Poland, tergite, dorsal view; 67 — Leguminivora glycinivorella (Mats.), N. Korea, sternite in ventral view, tergite in the dorsal, with end directed backwards; a — intersegmental sclerite, b — tegumen, c — vinculum



Figs. 68—71. Male scent organs of Grapholitina: 68 — Grapholita functiona (Treit.), Poland, lateral view; 69 — Selania leplastriana (Curt.), Yugoslavia, tergite in dorsal view, sternite ventrally; 70 — S. resedana (Obr.), after Danilevskij & Kuznetsov, 1968, lateral view, simplified; 71 — Matsumuraeses falcana (Walsm.), Japan, lateral view; a — intersegmental selerite



Figs 72—74. Male scent organs of Cryptophlebia Walsm., Grapholitina: 72 — two distal abdominal segments of C. ombrodelta Walsm., Vietnam, 73 — subgenital sternite and intersegmental sclerite of same specimen; 74 — subgenital sternite and tergite with intersegmental sclerites of C. yasudani Kaw., Japan