

**THE PUPARIA OF THE EUROPEAN SPECIES OF THE FAMILY
LARVAEVORIDAE (DIPTERA) I
(SUBFAMILY SALMACIINAE, PART 1)**

JAN ZUSKA

(Caroline University, Chair of Systematic Zoology,
Department of Entomology, Praha)¹

Abstract

This paper is the first portion of a comprehensive study of the known puparia of the European species of the family Larvaevoridae. It deals with the tribes Baumhaueriini, Carceliini, Winthemini, Sturmiini, Erythroceriini and Salmaciini of the subfamily Salmaciinae (sensu Mesnil, 1939, 1944 —). Descriptions of the puparia of ten species, a redescription of the puparia of two species and notes on those of many other species are included in this paper. On the basis of the puparial, and other characters, *Carcelia dubia* (Brauer & Bergenstamm) and *Carcelia lucorum* (Meigen) are recognized as two different species (formerly they were taken for two subspecies of the same species). The general morphology of the puparia is discussed, the most reliable systematic characters are pointed out and emphasis is made on the importance of studying the puparia in order to gain a more complete knowledge of the systematics of the Larvaevoridae.

Introduction

The studying of the preimaginal stages of the family Larvaevoridae and especially of the puparia is of importance because of many factors. First, such studies are important from the standpoint of the systematics. There are very few characters in adult Larvaevoridae which are reliable for making phylogenetical conclusions, and also very few characters which do not vary considerably intraspecifically. Therefore all new characters which are of systematic importance and which give us a better understanding of the phylogeny of the family are of much value.

The larvaevorids are of such great importance in the biological control of a large number of insect pests that it is essential that all stages of the parasites be thoroughly understood. Information which will enable the researcher in applied entomology to make species identifications based upon puparia will be of much value in biological control studies.

To date comparatively few papers on the puparia of these flies have been published. Description of puparia are scattered through a great many publications and are, for the most part, very incomplete and usually lack adequate illustrations of the important structural characters. Some of the more comprehensive of the previous studies are those of

¹ Present address: Regional Museum, Cheb, Czechoslovakia.

Vimmer (1920, 1925), Greene (1921), Bisset (1938), Gardner (1940a, 1940b), Mathur (1950) and Ross (1952, 1953). The bibliography compiled by Hennig (1952) has provided the basis for all the previous work on larvaevorid puparia.

In the present literature descriptions of puparia of about two hundred species for the entire world and about seventy European species are available.

In this first portion of my study all present knowledge on the puparia of the tribes Baumhaueriini, Carceliini, Winthemiini, Sturmiini, Erythroceriini and Salmaciini of the subfamily Salmaciinae is recapitulated and the previously unknown puparia of ten species of these tribes are described and two of the previously known puparia are redescribed. (Up to this time only the puparia of nine European species of these tribes have been described; descriptions of three of those species are useless because of the nomenclatoric obscurity.) In this paper in contrast to most other works the cephalopharyngeal apparatus of the third instar larvae is figured in most of the described puparia. The structure of the posterior spiracles has been drawn from permanent slide mounts rather than from in situ specimens as has been done in other studies. For the first time the microscopic structure of the spiracular openings (orificia) has been used as a diagnostic character. The standard morphological terminology is discussed below.

Materials and methods

Only puparia from laboratory bred flies were used for this study and only emerged puparia were investigated so that they could be positively associated with the adults. After examining the external characters permanent mounts of the cephalopharyngeal apparatus and of the posterior (or also anterior) spiracles were made. A chloral hydrate medium, a modification of Liquido de Swan, was used for this purpose (gum Arabic, 15 gr; distilled water, 20 gr; chloral hydrate, 50 gr; glucose, 3 gr; acetic acid, 5 gr). The cephalopharyngeal apparatus was placed directly into the chloral hydrate medium without boiling in KOH. The spiracles were first boiled in KOH (10% or more concentrated solution) until clear.

Morphology, terminology and discussion of the most useful systematic characters

The pupa of the family Larvaevoridae is, as in other families of higher Diptera, closed in the strongly sclerotized cuticula of the third larval instar (pupa coarctata; pupa exarata according to Hinton, 1946), so that most of the characters of the full-grown larva are visible in the puparium. The number of body segments is modified in contrast to the number in the larvae. The pseudocephalon and the anterior part of the first thoracic segment are invaginated into the head cavity of the puparium and therefore only the posterior part of the first thoracic segment

is visible. Behind this segment the other two thoracic and eight abdominal segments are developed.

A secondary mouth opening is present on the first thoracic segment and above it is a pair of anterior spiracles. The anterior spiracles could be used as good diagnostic characters except that one cannot always depend upon them being present on the puparium after the adult has emerged. Since the dorsal flap with the anterior spiracles is so often broken off I have described these fully in only a few species. A pair of special organs are located laterally on the hind margin of the first abdominal segment in many species; these are called *pseudostig-*

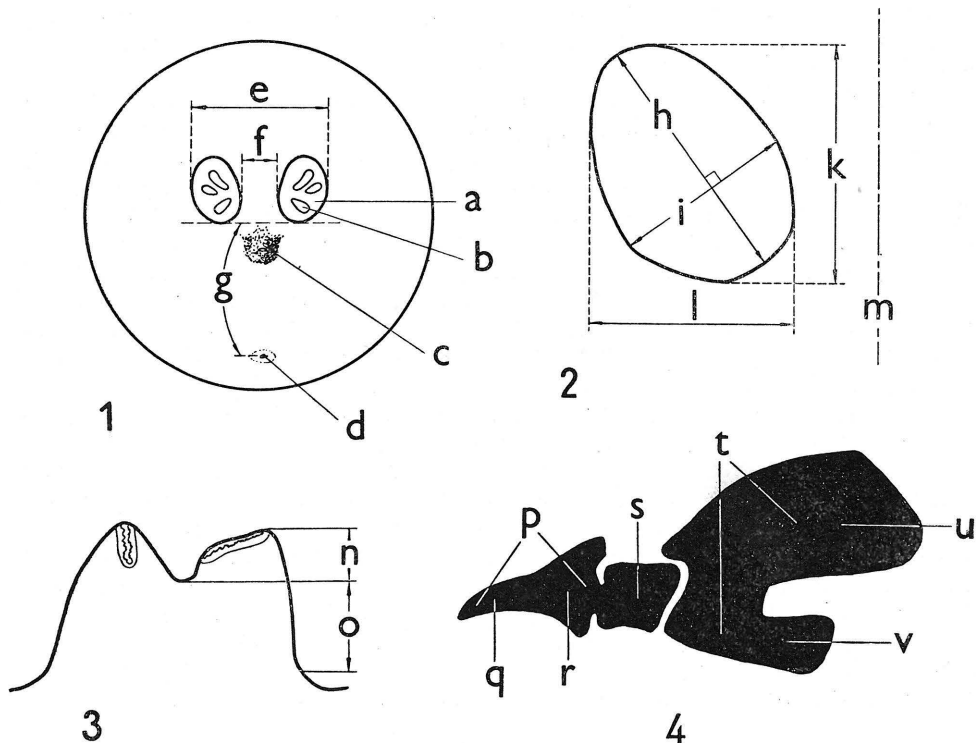


Fig. 1: Scheme of the posterior aspect of a larvaevorid puparium. — Fig. 2: Scheme of a larvaevorid posterior spiracle (situated as in fig. 1). — Fig. 3: Scheme of a larvaevorid posterior spiracle (lateral aspect). — Fig. 4: Scheme of the cephalopharyngeal apparatus of a larvaevorid third instar larva.

a, spiracular plate of the posterior spiracle; b, orificium; c, supraanal protuberance; d, anus; e, maximum distance between the posterior spiracles; f, minimum distance between the posterior spiracles; g, distance of the anus from the posterior spiracles; h, maximum diameter of the posterior spiracle; i, minimum diameter of the posterior spiracle; k, height of the posterior spiracle; l, width of the posterior spiracle; m, sagittal plane; n, orificial ridge; o, stigmatophore; p, oral part of the cephalopharyngeal apparatus; q, mouth-hooks; r, basal part; s, hypostomal part; t, pharyngeal part; u, dorsal process of the pharyngeal part; v, ventral process of the pharyngeal part.

mata (prothoracic cornicles). The function of these organs is poorly understood; Meijere (1902) first pointed out their connection with the tracheal system of the pupa. The last abdominal segment bears a pair of the posterior spiracles, and ventrally below them is located the supraanal protuberance and the anal opening (fig. 1).

The integument of the puparium shows the pattern of spinules of the third instar larva (figs. 80 to 85) and would appear to be an excellent character, especially in separating puparia of closely related species. However, this character probably slightly varies according to different hosts and other factors. Sometimes the surface of a puparium is covered with very dense, crowded, bristle-shaped spinules. On the pleural parts of puparia some segmental impressions are usually developed. The first and the last band of spinules border the anterior and the posterior spiracular fields.

Anteriorly on the puparium horizontal and vertical sutures are developed. When the fly emerges the puparium tears at these sutures and the dorsal and ventral flaps are separated (figs. 20, 25, 27, 28). The horizontal suture is located between the secondary mouth opening and the anterior spiracles and reaches to the vertical suture. This suture is located across the first abdominal segment and is mostly interrupted dorsally and ventrally, so that both the flaps are connected with the puparium at this point. On the dorsal flap the anterior spiracles remain, on the ventral flap is found the secondary mouth opening, and on the internal side intima of the atrium and stomodaeum with the cephalopharyngeal apparatus of the third larval instar are preserved.

The respiratory system of the larvae and also of the puparia is amphipneustic. Anterior and posterior spiracles have several secondary openings, which are obviously not homologous in the anterior and posterior spiracles to each other. For that reason the openings of the anterior spiracles are called pori and the openings of the posterior spiracles orificia. Anterior spiracles (figs. 52, 54; see also Meijere, 1902 and Snodgrass, 1935) are very complicated from the anatomical standpoint (a very instructive scheme cf. Snodgrass, 1935, fig. 235 A); the respiratory system communicates with the surrounding atmosphere through different number of small openings, pori. The number of pori varies often intraspecifically, especially if a great number of pori is present.

Posterior spiracles (anatomy cf. Hendel, 1928, fig. 22 and Snodgrass, 1935, fig. 235 B) have a very complicated, highly characteristic structure (figs. 42 to 51, 53, 55); they are the most important diagnostic characters found in puparia. Each spiracle consists of a spiracular plate (fig. 1, a), which is located on a more or less raised stigmatophore (fig. 3, o). The stigmatophores are mostly formed as late as during the pupation of the larva and are very strongly sclerotized. The spiracular plate, also strongly sclerotized, is perforated by three to four orificia (spiracular openings, stigmal slits; Stigmenöffnungen in German literature) (figs. 1, b; 42, 44). On the spiracular plate a cicatrix (button; Stigmannarbe) is also developed; this is the rem-

nant of the posterior spiracles of the second larval instar. Also different faintly sclerotized areas can be seen on the spiracular plate. In the puparia with a low stigmatophore the spiracular plate is mostly flat, but in the puparia with a high stigmatophore it is curved, because each orificium (or also cicatrix) is located on a more or less high protuberance. Often the orificia are located on a very high protuberance, called the orificial ridge (fig. 3, n). The orificia are not, however, the actual respiratory openings. They have their own characteristic structure which differs according to different species. Each orificium is closed by a thin sclerotized orificial membrane, in which actual respiratory openings, trachites, are located. In most species (for example *Carcelia* Robineau-Desvoidy, fig. 47) only one long and narrow trachite is developed, other species (*Salmacia* Meigen, fig. 46) have more trachites in an orificium. These trachites are so formed, that they could work as a filter but, in my opinion (on the basis of investigating posterior spiracles in many puparia), they perhaps are also closed by a clear membrane and the pupa respire only by diffusion through this membrane (this hypothesis relates to puparia only, where metabolism is very low; the trachites are probably open in larvae). Because the posterior spiracles are a very important and frequently used characters, I propose standard names for different proportions, as shown in fig. 1 and 2.

The cephalopharyngeal apparatus (figs. 66 to 79) is also an important character; it is very well preserved in emerged puparia and it is possible to mount it on a microscope slide. However, in unemerged puparia the cephalopharyngeal apparatus is more compact and is located in the original situation. The cephalopharyngeal apparatus of the full-grown larvae consists of an oral part (fig. 4, p) (consisting of mouth-hooks, Mundhaken in German literature, fig. 4, q, and of the basal part, fig. 4, r), of the following hypostomal part (fig. 4, s), which is either separated or more or less connected with the oral part and posteriorly with a distinctly separated pharyngeal part (vertical plate, fig. 4, t), with dorsal (fig. 4, u) and ventral (fig. 4, v) processes. The morphology of the cephalopharyngeal apparatus is very complicated and to date it has not been possible to work out reliably the homologies of the parts. For the identification or description of a puparium the nomenclature which I have used appears to be satisfactory since the cephalopharyngeal apparatus in full-grown larvae becomes a single structure.

The puparia of different species usually have a characteristic form, yet, on the average, they are very uniform. Only very few puparia bear outstanding macroscopic characters. The size of the puparia varies greatly and depends on the quantity and quality of the larval food. Puparial colouration is very variable. In some species a trend to the light or dark colour can be ascertained, but the colouration is not a reliable key character.

It is apparent that the structure of the posterior spiracles is the most reliable character used in the systematics of larvaevorid puparia. The

height of stigmatophores and the form of the spiracular plate are adaptive characters, which are useful only for specific diagnoses in most groups of Larvaevoridae. In my opinion the number of the orificia and probably also of the trachites may be one of the most valuable characters. However, this problem needs to be studied in much more detail before we can be sure of its usefulness. I have found that the number of the orificia or of the trachites is not dependent upon the systematic position of the particular genus, so that species with three or four orificia and with one or more trachites may belong in the same tribe. The most complicated situation is found in the genera *Drino* Robineau-Desvoidy and *Elodia* Robineau-Desvoidy (refer to the discussion under these names). I plan to make further studies to determine the systematic importance of these characters and to find out how much value they might have from a phylogenetic standpoint. Along this line the following facts should be noted: While the number of the orificia is probably a valuable diagnostic character, the number of trachites shows considerable variation. It is possible to trace a single long, narrow and strongly serpentine trachite to its breakdown into many short trachites and this breakdown need not be of phylogenetic importance since it could come about as a specific adaptation.

The shape of the trachites is very probably an important character, but its reliability and usefulness for higher taxa needs to be verified.

Because of absence of detailed facts on the anterior spiracles the systematic importance of these organs is unknown to me.

The cephalopharyngeal apparatus is very well preserved in puparia but its sclerites often are not in their natural situation. Also the mounting of the apparatus from emerged puparia is very difficult and not always successful. The shape of the cephalopharyngeal apparatus can only be used as a subsidiary diagnostic character, because of its variability. It should be very important in the future to examine in detail the variability of the cephalopharyngeal apparatus in as many species as possible. Also a detailed study on the morphology and homology of the apparatus is badly needed. However, both these studies can be made only from full-grown larvae, in place of the puparia. For the present, especially the shape of the anterior parts of the cephalopharyngeal apparatus appears to be characteristic for different species and perhaps also for different genera.

The various bionomic characters are of much diagnostic importance and should accompany the morphological characters in the systematic scheme. For example, it is important to know the host species² (Larvaevoridae are predominantly oligophagous parasites), the situation of the puparium (in the host pupa, or free living in the soil), etc. Also parasitization by different specific hymenopterous hyperparasites could be useful as a distinguishing character.

² The most comprehensive lists of hosts of the European species of the family Larvaevoridae were compiled by Baer (1921), Thompson (1943 —), Mesnil (1944 —) and especially by Herting (1960). The last of them, containing very concise descriptions of some puparia of the tribes concerned, was available to me, however, only after sending my manuscript to the editor.

Descriptive treatment

It is impossible for the time being to characterize higher taxa (tribes and subfamilies) by puparial characters. Considering the number of all the palaearctic species of the family only very few puparia are known. There we have practically no knowledge of the importance of the puparial characters for use in the systematic (of higher taxa) in the family Larvaevoridae. Those puparial characters which appear to be most important separate the species of Larvaevoridae into quite different groups than the commonly used adult characters.

As emphasized by Hennig (1943) a natural classification must include all stages in the life cycle of an insect and if species seem to fall into different groups according to the characteristics of the larvae, pupae or adults it indicates that there is an error in methods, predominantly in the evaluation of the characters. In our case, the puparial characters (especially the number of orificia, number of trachites and form of trachites) may be of slight systematic value.³ However, it is realized that the present system of the family is unnatural and not phylogenetic.

For the above reasons no general descriptions of the puparia of the tribes and subfamilies could be compiled and also no key to subfamilies and tribes is given. A complete key to known puparia of European genera of the family Larvaevoridae will be published in the last portion of this study.

Tribus BAUMHAUERIINI

A small tribe with six known European species. According to Hennig (1952) the first instar larvae (also eggs) of two species of the world are known. No puparium of this tribe has been previously described.

Histochaeta Rondani, 1859

A monotypical genus (see the discussion in Mesnil, 1956a), which parasitizes Lepidoptera and Coleoptera.

Histochaeta marmorata (Fabricius, 1805)

The puparium (figs. 5, 9) is elliptical in dorsal view, widest behind the middle, lateral sides are only slightly convex; both anterior and posterior ends are sharp, not regularly rounded. In profile the ventral side is flat in the middle part, the dorsal side is convex, especially on the posterior half, where the puparium is highest. The surface of the puparium is very rough. Numerous transverse wrinkles (the deepest on the posterior half) and many granulous structures are developed on the lateral margins; some of the granula are similar to pseudostigmata (however, no distinct pseudostigmata were found). On the dorsal part of the puparium no distinct pattern of spinules is developed (some specimens

³) It may be supposed that the morphological structure of parasitically living larvae (and therefore also of puparia) is much more modified than this of free living adults.

parts bear small spinules, but they are not clearly visible because of the rough surface of the puparium). On the ventral side each segment carries one to two compact bands, which become indistinct on the posterior segments. The band of spinules around the anterior spiracular field is (at least on the ventral side) quite distinct, the band around the posterior

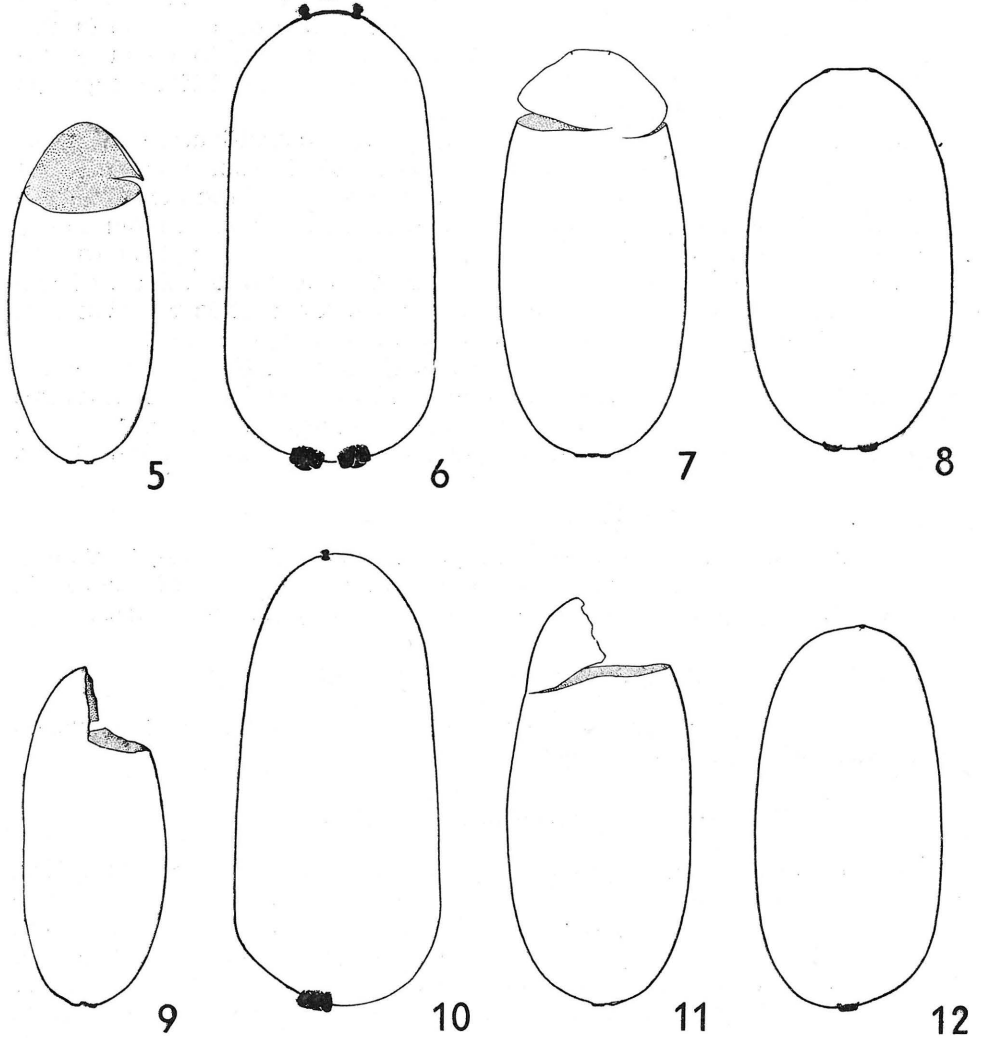


Fig. 5: *Histochaeta marmorata*, puparium, dorsal view. — Fig. 6: *Salmacia sicula*, ditto. — Fig. 7: *Ctenophorocera pavidana*, ditto. — Fig. 8: *Sturmia bella*, ditto. — Fig. 9: *Histochaeta marmorata*, puparium, lateral view. — Fig. 10: *Salmacia sicula*, ditto. — Fig. 11: *Ctenophorocera pavidana*, ditto. — Fig. 12: *Sturmia bella*, ditto. — Solid line equals 10 mm.

spiracular field is indistinct, since it is located in the area of very deep and dense wrinkles. The spinules around the posterior spiracular field are very small compared to the other spinules (figs. 83, 85).

The posterior spiracles (figs. 37, 42) are situated terminally, but are in a small and flat cavity; they are slightly higher than wide. The stigmaphore is moderately elevated (about one third as high as the spiracle), but the three orificia are separated by deep grooves. The cicatrix is strongly developed. The minimum distance between the spiracles is very small, about three-tenth as long as the width of a spiracle. Three separated orificia are developed, each with only one trachite, which is more or less straight and has a quite regular structure (fig. 60).

No pseudostigmata were found. The supraanal protuberance is strongly produced, but indistinctly bordered laterally, so that ventrally below the spiracles a large and broad swelling is developed, the top of which is on level with the tops of the posterior spiracles. The distance between the anal opening and posterior spiracles is one and two-tenth as long as the maximum distance between the latter.

The cephalopharyngeal apparatus (fig. 66) is large, with a strongly developed oral portion and with a strikingly developed dorsal process of the pharyngeal part. The pharyngeal portion is poorly developed in comparison with the anterior parts of the apparatus.

Measurements of the puparium: length, 6,5 mm; width, 2,8 mm.

Material examined: One puparium (imago det. Mesnil) ex *Arctia caja* L. (Slovakia: Banská Štiavnica, 1957, lgt. Čapek).

Tribus CARCELIINI

This tribe has many European representatives, mostly belonging in the large genus *Carcelia*. The flies of this tribe parasitize Lepidoptera. Only the preimaginal stages of the genus *Carcelia* (inclusive of some puparia) are known from Europe.

Carcelia Robineau-Desvoidy, 1830

Vimmer (1920, 1925) and Nielsen (1909, 1911) described puparia of several species of *Carcelia*, but since so much synonymy was involved, as clarified by Mesnil (1944, 1949a), those descriptions are not reliable; they are useful only in bringing out some of the generic characters of the puparia of the genus *Carcelia*.

Vimmer (1920, 1925) described as the puparium of "*Carcelia excissa* Fl." a specimen which is (by the descriptions and figures) very similar to *Carcelia lucorum* (Meigen), especially in the translocation of the posterior spiracles and in the absence of the supraanal protuberance. Nevertheless it is doubtful that Vimmer's puparium belongs to this species since according to his description the distance between the posterior spiracles is equal to the width of a spiracle. The distance of the anal opening from the posterior spiracles is only twice as great as the maximum distance between the spiracles. The puparium studied by Vimmer

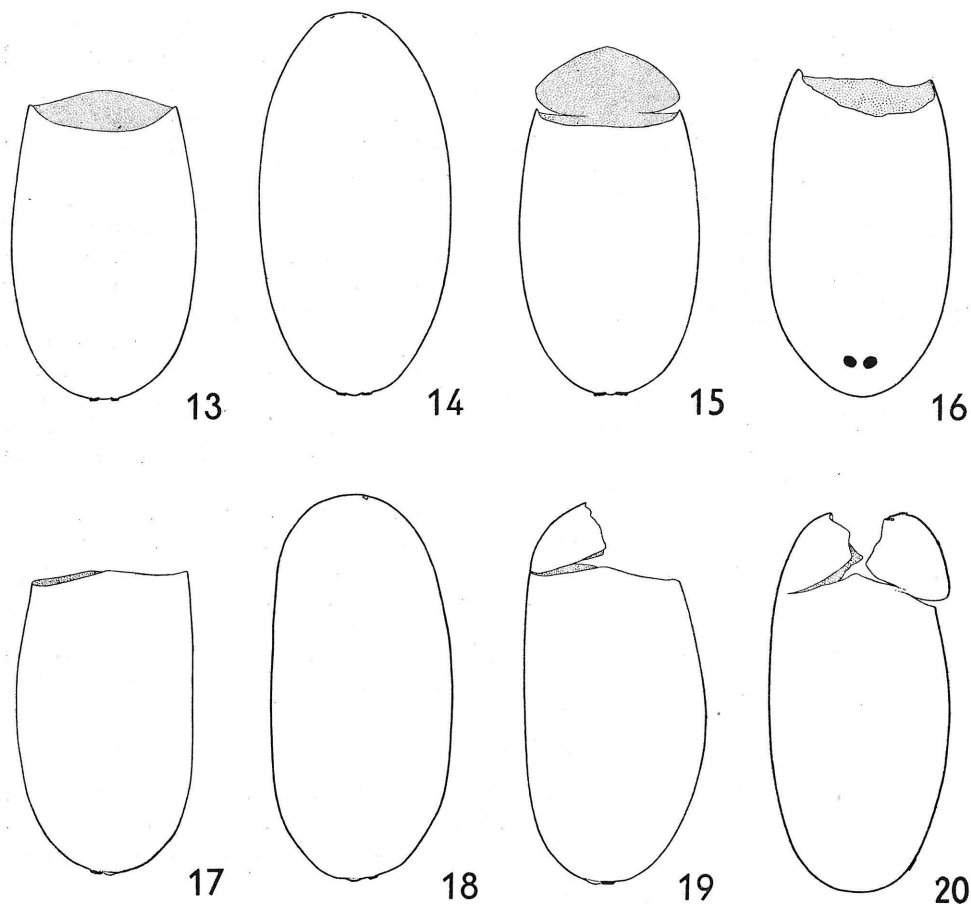


Fig. 13: *Carcelia excavata*, puparium, dorsal view. — Fig. 14: *Carcelia dubia*, ditto. — Fig. 15: *Carcelia separata*, ditto. — Fig. 16: *Carcelia lucorum*, ditto. — Fig. 17: *Carcelia excavata*, puparium, lateral view. — Fig. 18: *Carcelia dubia*, ditto. — Fig. 19: *Carcelia separata*, ditto. — Fig. 20: *Carcelia lucorum*, ditto. — Solid line equals 10 mm.

(1925) also had two- to four-toothed spines (or spinules?) and distinctly developed pseudostigmata. For that reason it is probable that this puparium belongs to another species than (but closely related to) *Carcelia lucorum*.

The puparium of the genus *Carcelia*⁴ is large, elliptical and without

⁴) Ross (1953) described puparium of *Carcelia malacosomae* Sell., bred ex *Malacosoma* spp. in British Columbia. This puparium differs very strongly from other puparia of this genus in having very long and strongly serpentine trachites. It should be very interesting to re-examine the systematic position of this species.

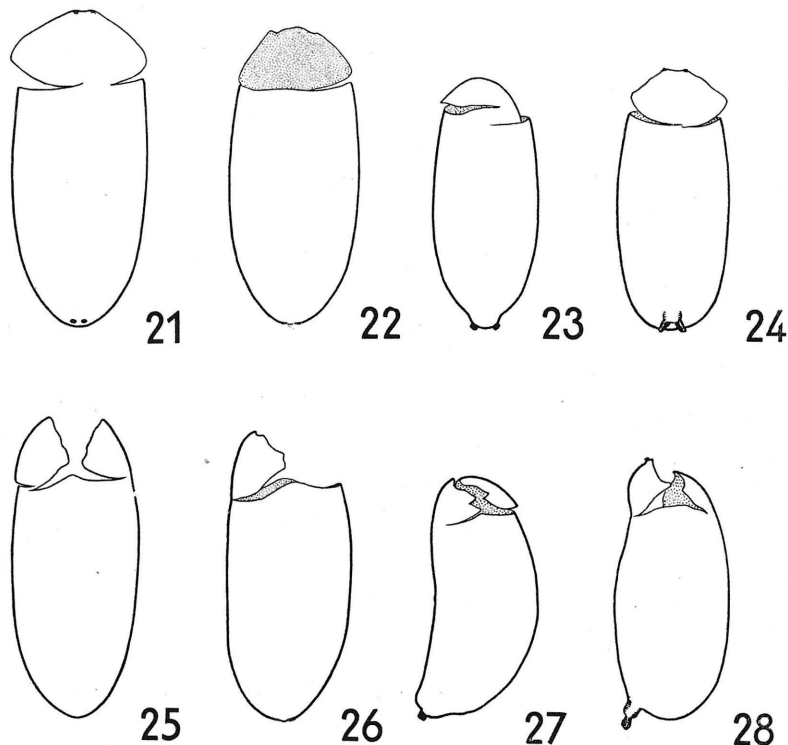


Fig. 21: *Winthemia erythrura*, puparium, dorsal view. — Fig. 22: *Pseudoperichaeta insidiosa*, ditto. — Fig. 23: *Elodia morio*, ditto. — Fig. 24: *Elodia convexifrons*, ditto. — Fig. 25: *Winthemia erythrura*, puparium, lateral view. — Fig. 26: *Pseudoperichaeta insidiosa*, ditto. — Fig. 27: *Elodia morio*, ditto (left side). — Fig. 28: *Elodia convexifrons*, ditto (right side). — Solid line equals 5 mm.

special characters. The ventral side is sometimes flat or slightly concave. The anterior spiracles are of a characteristic form, they consist of three to four hemisphere-shaped protuberances situated in a half-circle. The posterior spiracles are circular and are located relatively close to each other; they have three orificia and a distinct cicatrix. Each orificium has only one, straight or simply curved trachite; the microsculpture of the trachites is mostly regular. The stigmatophores are usually very low. The posterior spiracles are located terminally or slightly supraterminally; in *Carcelia lucorum* (Meigen) and in some Indian species (Gardner, 1940a) they are translocated dorsally. Most species have a pair of pseudo-stigmata developed laterally on the first abdominal segment. The cephalopharyngeal apparatus is medium-large. The mouth-hooks are very small, the basal part of the hooks is tiny and usually has a dorsal and a lateral processes, which are directed posteriorly. The pharyngeal part is large in comparison with the anterior parts.

Key to puparia

[Excluding *Carcelia processionae* (Ratzeburg) and *Carcelia obesa* (Zetterstedt)]

- 1 (2) Posterior spiracles translocated dorsally (fig. 16). Microsculpture of the puparial surface very fine. Supraanal protuberance absent. Pseudostigmata absent ***Carcelia lucorum*** (Meigen)
- 2 (1) Posterior spiracles not noticeably translocated (figs. 13 to 15). Pseudostigmata more or less developed. Supraanal protuberance present.
- 3 (4) Minimum distance between the posterior spiracles greater than the width of a spiracle (fig. 31). Posterior spiracles very small, nearly circular and surrounded by a circular structure. Pseudostigmata poorly developed ***Carcelia dubia*** (Brauer & Bergenstamm)
- 4 (3) Minimum distance between the posterior spiracles shorter than the width of a spiracle (figs. 29, 32). Posterior spiracles larger than in the preceding species and not always so circular in shape. Well-defined pseudostigmata developed.
- 5 (6) Puparium with a distinct pattern of spinules on the dorsal side of the middle segments (each segment with about four rows of spinules). Minimum distance between the posterior spiracles shorter than one-half the width of a spiracle (fig. 29). Spiracular plates flat. Oral part of the cephalopharyngeal apparatus strongly developed (fig. 71) ***Carcelia separata*** (Rondani)
- 6 (5) Puparium, on the dorsal side of the middle segments, practically without the pattern of spinules (only some segments with single rows of spinules). Minimum distance between the posterior spiracles longer than one-half the width of a spiracle (fig. 32). Spiracular plates slightly convex. Oral part of the cephalopharyngeal apparatus more weakly developed (fig. 67) ***Carcelia excavata*** (Zetterstedt)

Carcelia dubia (Brauer & Bergenstamm, 1891)

This species is morphologically (according to the adult) closely related to *Carcelia lucorum* (Meigen). Brauer & Bergenstamm (1891) described it as a separate species, but Mesnil (1944) has considered it as a subspecies of *Carcelia lucorum*. I feel that this is not correct and that the two are distinct species. They show sharp morphological differences, especially in the form of the male genitalia, as figured by Mesnil (1944). According to my study on the puparia of the genus *Carcelia* both the above species appear not to be closely related phylogenetically in comparison with the other species of this genus. In four species which I have examined only *Carcelia lucorum* has the posterior spiracles strongly translocated dorsally, the other three species, including *Carcelia dubia*, have the spiracles situated normally. It is to be supposed the situation of the posterior spiracles is a very important character in the specific systematics of this genus. The puparia of the two above species also differ in many other significant characters.

The puparium (figs. 14, 18) of *Carcelia dubia* is relatively large and robust, in dorsal view regularly rounded at the lateral margins; the anterior and posterior ends are somewhat extruded, not evenly rounded. The puparium is widest somewhat behind the median portion. In profile the puparium is highest slightly behind the middle, is slightly convex dorsally and approximately flat ventrally. The anterior end narrows gradually, the posterior one suddenly. The surface of the puparium bears about three horizontal rows of segmental impressions on each pleural part and also

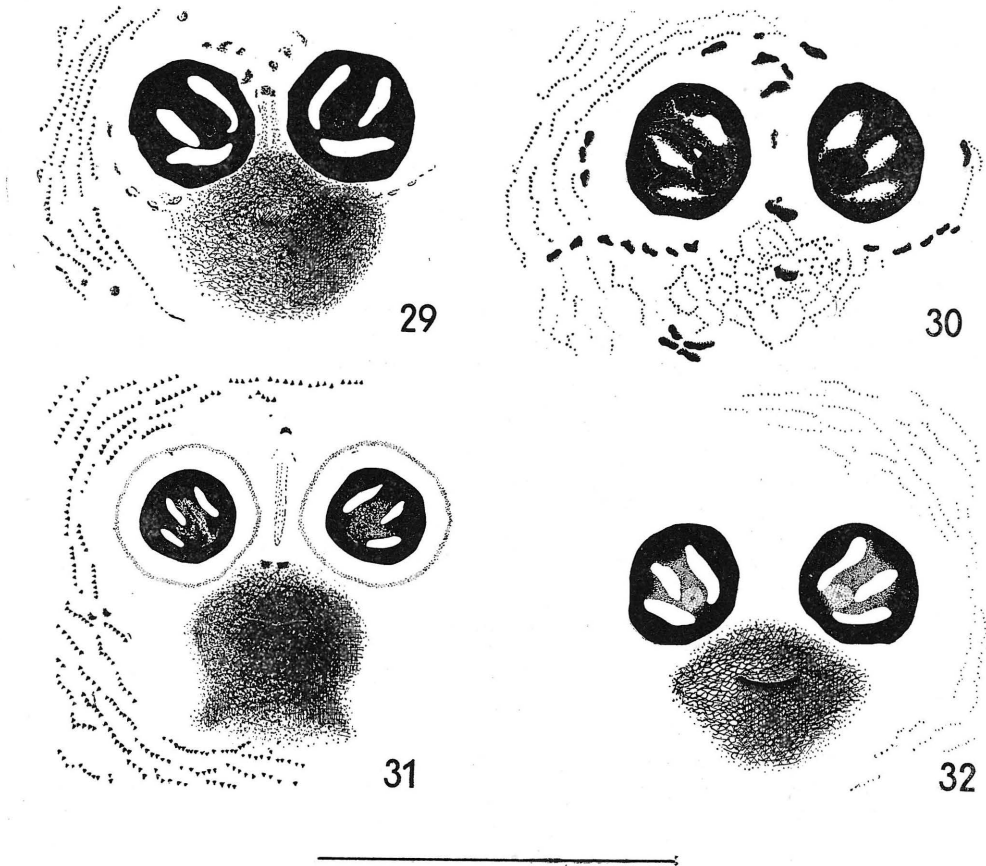


Fig. 29: *Carcelia separata*, posterior spiracular field. — Fig. 30: *Carcelia lucorum*, ditto. — Fig. 31: *Carcelia dubia*, ditto. — Fig. 32: *Carcelia excavata*, ditto. — Solid line equals 1 mm.

has a characteristic pattern of spinules. On the dorsal side a ring of spinules is developed around the anterior spiracular field, consisting of six or less rows of spinules; behind it is situated a spinulose band of the same width and another one which consists of only two rows in the middle. The next segment has only one distinct row of spinules. The following segments are practically without spinules on the dorsal surface, however, at the end of the puparium is developed a band of two rows, behind it another one with three rows and a very wide ring of spinules (about ten rows) around the posterior spiracular field; the wide posterior ring is divided ventrally into two parallel bands. On the ventral side a band consisting of about six rows of spinules is developed on each segment.

The anterior spiracles (fig. 52) are of the usual form. They consist of four hemispherical protuberances situated in a half-circle; the spiracles are scarcely raised.

The posterior spiracles (figs. 31, 51) are only slightly raised (their width is at least six times as long as the height of a stigmatophore), are very small, circular, the distance between them is one and one-half times as long as their width; each of the spiracles is surrounded by a circular structure. Each spiracle has three orificia, which are parallel and directed medioventrally; they are not separated by grooves. Each orificium has only one, nearly straight, trachite; the trachites are irregular in structure (fig. 59).

The pseudostigmata are poorly developed. The supraanal protuberance is well-defined, with an impression on the dorsal half. The distance between the posterior spiracles and the anal opening is more than three times as long as the maximum distance between the spiracles.

The cephalopharyngeal apparatus (fig. 69) is relatively small. The anterior parts (oral and hypostomal) are small and especially low, so that the hypostomal portion is twice as long as high.

Measurements of the puparium: length, 8.5 mm; width, 4.0 mm.

Material examined: One puparium (imago det. Čepelák) ex sp. indet. Lepidopterorum (Bohemia: Pardubice, 1956, lgt. Pecina).

***Carcelia excavata* (Zetterstedt, 1884)**

The puparium (figs. 13, 17) is large, glabrous, convex laterally, ventrally and dorsally. The posterior spiracles are situated slightly supra-terminally. The surface of the puparium is glabrous, slightly microsculptured. The puparial segments each have only a single row of spinules dorsally. Posteriorly the puparium has two wider bands and a following, very wide, ring around the posterior spiracular field. This ring is divided into two parallel bands ventrally; these are fairly distant from each other. Each segment has a more or less broad band of spinules on the ventral side. Before the anus there is a band consisting of about three widely separated rows of spinules.

The posterior spiracles (figs. 32, 48) are small, the stigmatophores are low, the spiracular plate is faintly convex. The minimum distance between the spiracles is about three-fourths as long as the width of a spiracle. The spiracles are slightly oval, their maximum diameter is at about 45° to the height of a spiracle. Three orificia are developed, these convergent only slightly medioventrally. In each orificium is a single trachite, which is rather regular in structure (fig. 56). The cicatrix is well-defined.

The pseudostigmata are readily visible, they are not surrounded by a swelling or by a keel. The supraanal protuberance is well developed; it is broader but lower than a spiracle and is flat, with a distinct impression. The distance of the anal opening from the posterior spiracles is about two and one-half times as long as the maximum distance between these spiracles.

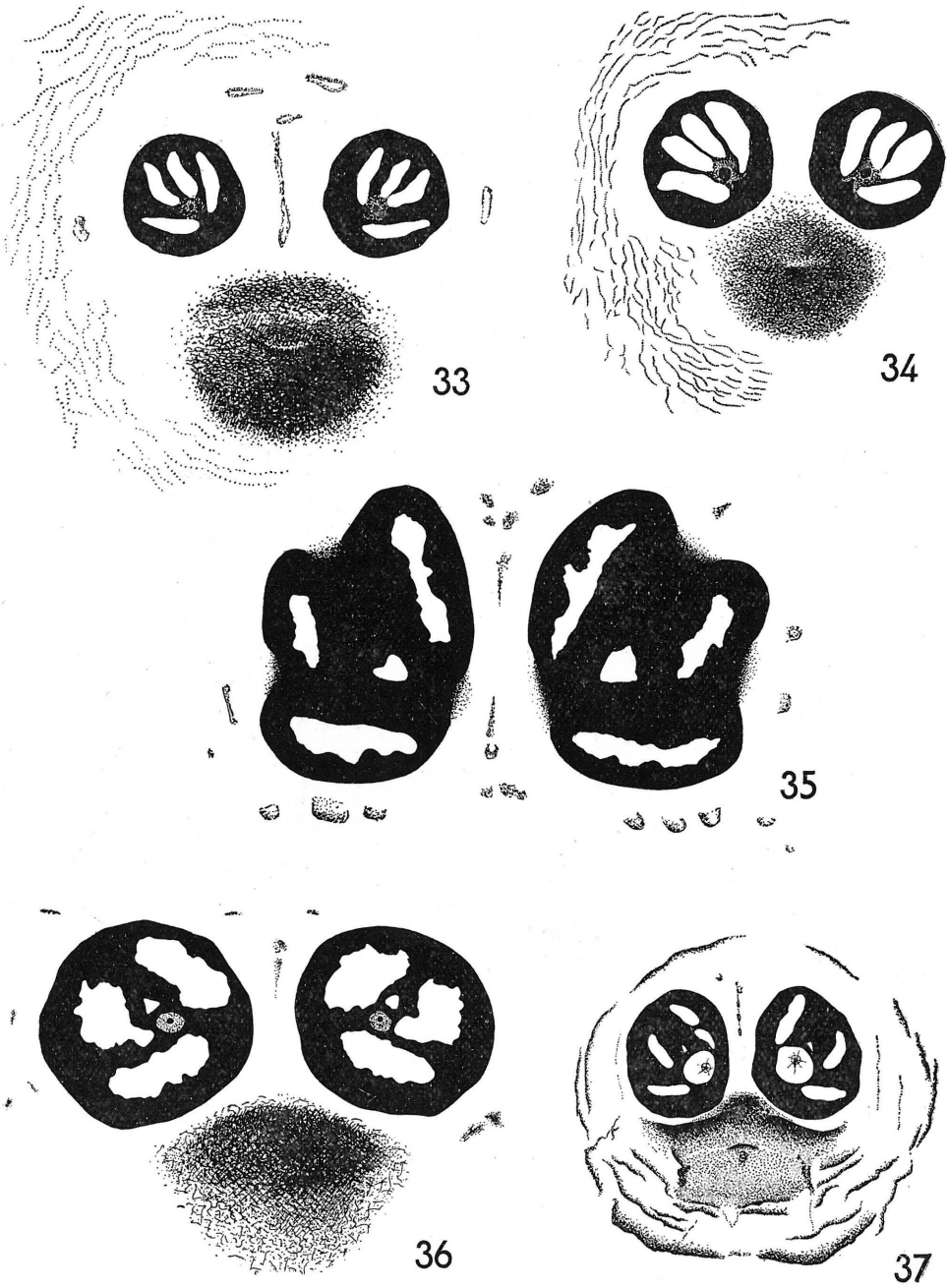


Fig. 33: *Ctenophorocera pavida* (first type), posterior spiracular field. — Fig. 34: *Ctenophorocera pavida* (second type), ditto. — Fig. 35: *Salmacia sicula*, ditto. — Fig. 36: *Sturmia bella*, ditto. — Fig. 37: *Histochaeta marmorata*, ditto. — Solid line equals 1 mm.

The cephalopharyngeal apparatus (fig. 67) has the anterior parts rather strongly developed; the basal part has two processes (a dorsal one and a ventral one) directed posteriorly.

Measurements of the puparium: length, about 7.5 mm; width, 3.8 mm.

Material examined: One puparium (imago det. Mesnil) ex *Malacosoma neustrium* L. (Slovakia: Banská Štiavnica, 1954, lgt. Čapek).

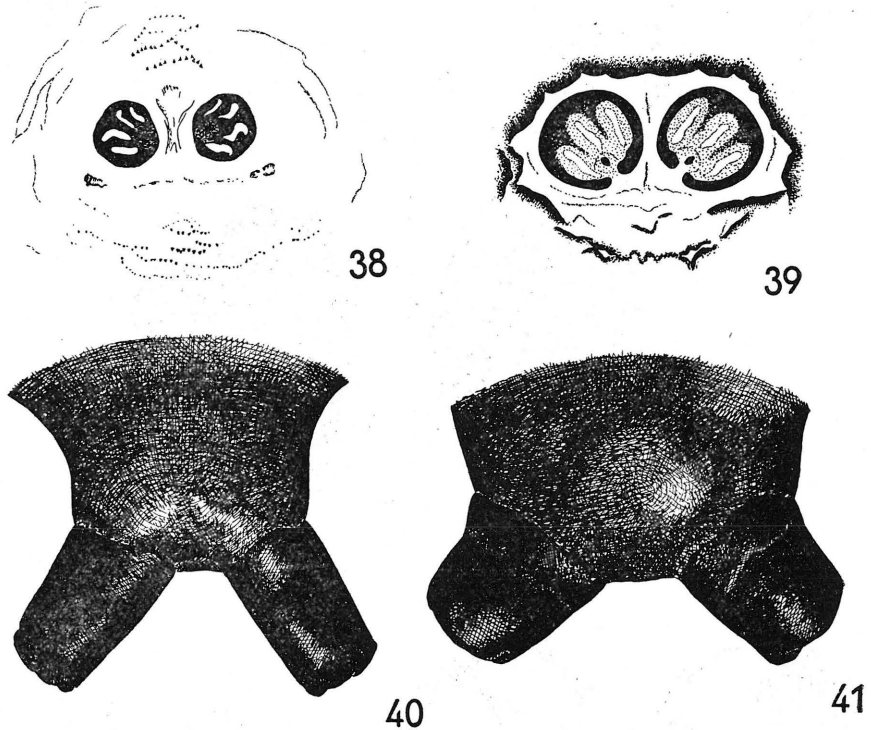


Fig. 38: *Pseudoperichaeta insidiosa*, posterior spiracular field. — Fig. 39: *Winthemia erythrura*, ditto. — Fig. 40: *Elodia convexifrons*, posterior column of the puparium, anterodorsally. — Fig. 41: *Elodia morio*, ditto, anteroventrally. — Solid line equals 1 mm.

***Carcelia lucorum* (Meigen, 1824)**

The puparium (figs. 16, 20) is rather shiny, elliptical and gently convex on all sides. The posterior end is suddenly narrowed in dorsal view and evenly rounded in profile. The anterior spiracles are situated very slightly supraterminally. The posterior pair are strongly translocated dorsally, so that their height is one-half times as long as the distance of their hind margin from the posterior apex as seen in dorsal view. The surface is smooth, glabrous, with a sparse and fine spinulous microscul-

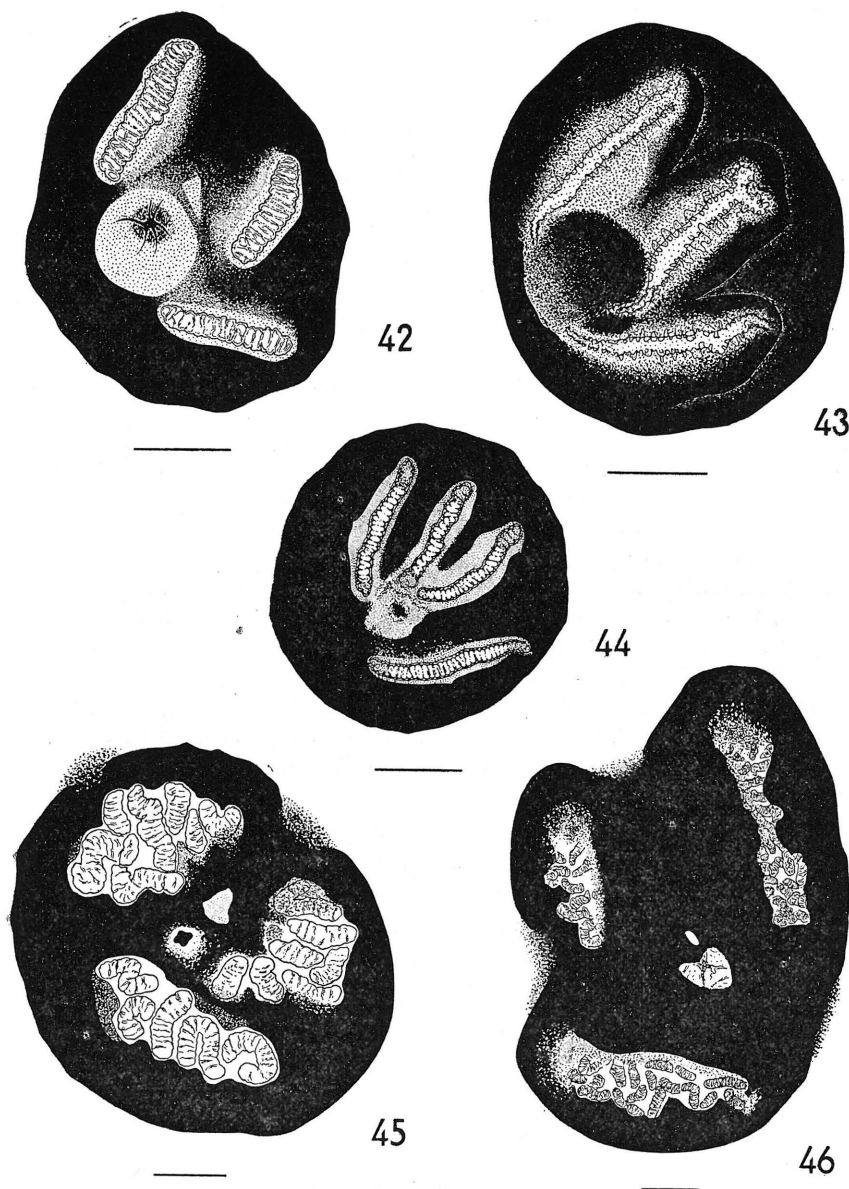


Fig. 42: *Histochaeta marmorata*, posterior spiracle. — Fig. 43: *Carcelia lucorum*, ditto.
 — Fig. 44: *Ctenophorocera pavida* (first type), ditto. — Fig. 45: *Sturmia bella*, ditto. —
 Fig. 46: *Samacia sicula*, ditto. — Solid line equals 0,1 mm.

pture (fig. 80). On each of the first three segments a broad band of spinules is developed dorsally; the first one, bordering the anterior spiracular field, is widest. Posteriorly four bands of spinules are developed, but only the last one, bordering the posterior spiracular field, is broad, the preceding bands are relatively narrow. Ventrally each segment bears a relatively narrow and single band of spinules, which are finer than the spinules of the dorsal side. The posterior band of spinules bordering the posterior spiracular field is ventrally divided into two transverse bands, which are fairly distant from each other. The anal field is bordered by a narrow transverse band of spinules at the front margin, consisting mostly of two rows.

The anterior spiracles are similar to those of *Carcelia dubia*, are not raised and appear to consist of four protuberances.

The posterior spiracles (fig. 30, 43) are strikingly translocated dorsally and lie on very low stigmatophores. The minimum distance between them is usually less than one-half the width of a spiracle. The spiracles are circular or slightly oval. The three orificia are faintly convergent and directed medioventrally. In each orificium is a single, very broad, straight (at the end more or less curved) trachite, considerably irregular in structure (fig. 57).

The pseudostigmata are not developed. The supraanal protuberance is absent, as well as the usual impression. The distance between the posterior spiracles and the anal opening is three times as long as the maximum distance between the spiracles.

The cephalopharyngeal apparatus (fig. 68) is small, with very tiny anterior sclerites; the mouth-hooks are especially short and weak.

Measurements of the puparium: length, about 8 mm; width, 3,6 to 4,2 mm.

Material examined: Five puparia (imago det. Mesnil) ex *Arctia caja* L. (Slovakia: Banská Štiavnica, 1954, lgt. Čapek).

***Carcelia obesa* (Zetterstedt, 1859)**

Klomp (1956) published a paper on the morphology and bionomy of this species. He gives only the following concise characteristics of the puparium:

„Das Tönnchen ist schwierig zu charakterisieren. Seine Ausmaße betragen durchschnittlich 7,5 × 3,7 mm. Äußerlich sind am Tönnchen die Dornenkränze, die Vorder- und Hinterstigmen, der Anus und die Einstülpungsgrube des Pseudocephalons des letzten Larvenstadiums leicht zu erkennen. Ebenso ist am Apex des Tönnchens die präformierte Bruchlinie deutlich wahrnehmbar. — Charakteristisch für das *Carcelia*-Tönnchen sind die zapfenförmige ‚Pseudostigmen‘ am ersten Abdominalsegment.“

According to Klomp the third instar larvae have following characters which are probably preserved in the puparia: Anterior spiracles with three pori. Posterior spiracles with three, only slightly curved, orificia, the situation of which is very variable. Each orificium with a single, straight or slightly curved trachite. Cephalopharyngeal apparatus (ac-

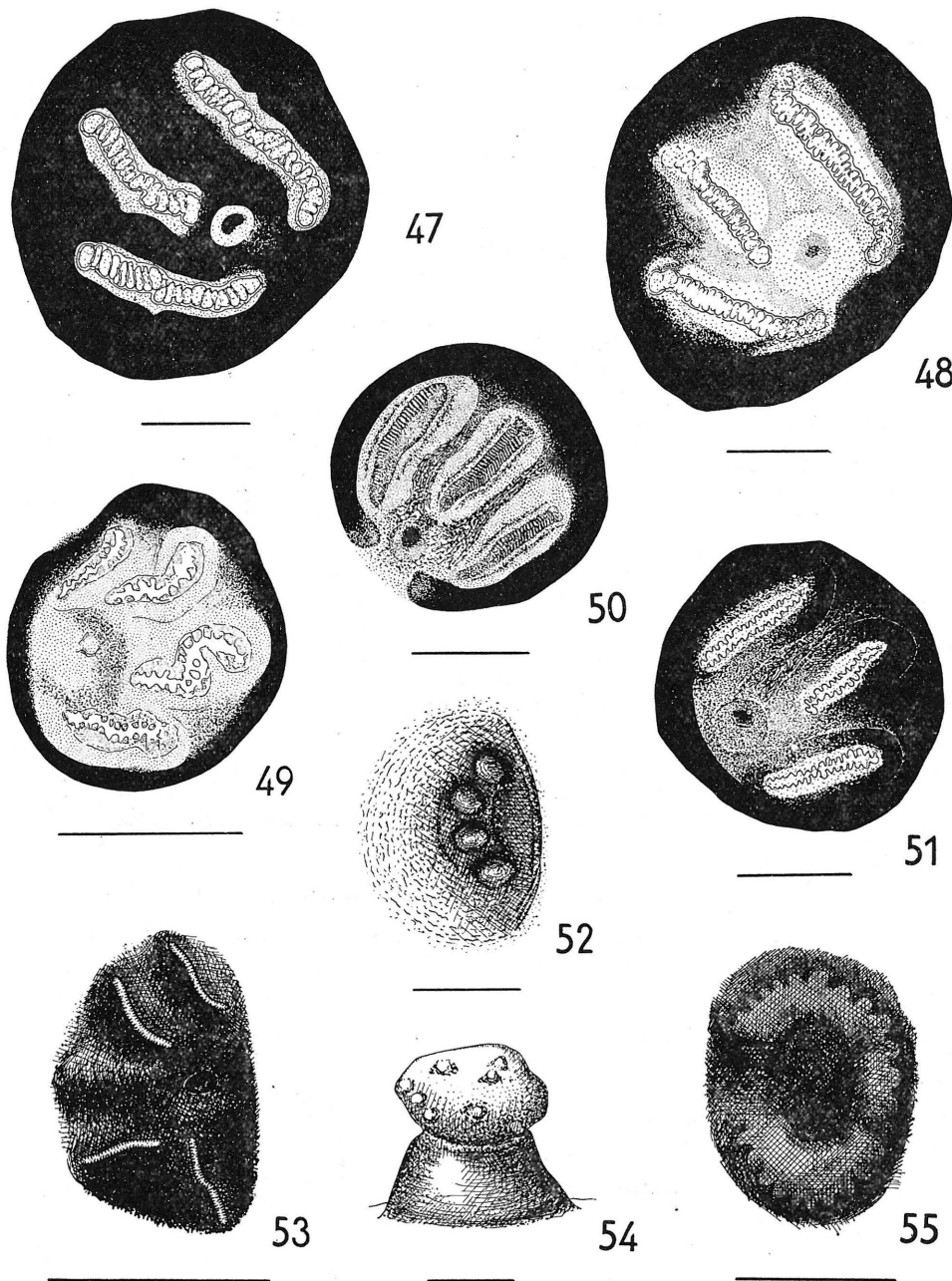


Fig. 47: *Carcelia separata*, posterior spiracle. — Fig. 48: *Carcelia excavata*, ditto. — Fig. 49: *Pseudoperichaeta insidiosa*, ditto. — Fig. 50: *Winthemia erythrura*, ditto. — Fig. 51: *Carcelia dubia*, ditto. — Fig. 52: *Carcelia dubia*, anterior spiracle. — Fig. 53: *Elodia convexifrons*, posterior spiracular plate. — Fig. 54: *Salmacia sicula*, anterior spiracle. — Fig. 55: *Elodia morio*, posterior spiracular plate. — Solid line equals 0,1 mm.

ording to a very schematized figure) without the posteriorly directed processes of the basal part.

According to Klomp the puparium is formed in the soil near the host pupa (of *Bupalus piniarius* L.).

***Carcelia processioneae* (Ratzeburg, 1884)**

The puparium of this species was partially described by Gäbler (1952), who studied this fly and its parasitism in *Cnethocampa pinivora* Tr. The following characteristics are given by Gäbler:

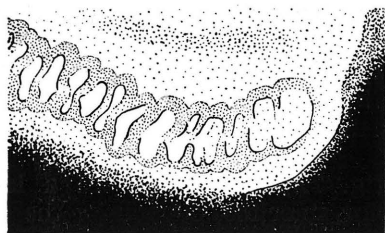
„Es wurden zahlreiche Verpuppungen beobachtet, die meist frei im Boden erfolgten. Seltener verpuppt sich die Larve in der Vorpuppe des Wirtes. 7,5 bis 9,5 beträgt die Länge des Fliegentönnchens, das anfangs hellrötlich-braun, später dunkelrot-braun gefärbt ist und meist stark glänzt. Die beiden dunkelgefärbten hinteren Stigmen liegen dicht nebeneinander. Ventralwärts von ihnen befindet sich, nur wenig sichtbar, als dünner horizontaler Strich eine Narbe. Sie kann allerdings gelegentlich auch etwas breiter sein. Am Vorderende liegen die Vorderstigmen auch auffällig dicht beieinander. Die Mundnarbe ist verhältnismäßig wulstig und glänzt meist intensiv.“

Gäbler figured puparium in anterior and posterior views, but these figures are unfortunately not of much help. However, the following characters of the third instar larvae can be supposed to be preserved in the puparia, according to the cited paper: Anterior spiracles obscure, probably with three pori. Posterior spiracles circular, with a well-defined cicatrix and with three long and broad, only very slightly curved orificia, which are almost parallel. Each orificium with a single, straight trachite. — According to Gäbler's fig. 1 the cephalopharyngeal apparatus of the third instar larvae differ strikingly from that of the other species of this genus.

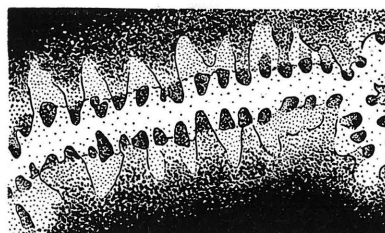
***Carcelia separata* (Rondani, 1859)**

In dorsal view (fig. 15) the lateral margins of the puparium are only very faintly convex, almost parallel, the anterior and posterior ends are evenly rounded. In profile (fig. 19) the puparium is convex dorsally, but is flat or concave ventrally. The surface is dull, the microsculpture is rough (in specimens from *Lymantria dispar* L.) or it is glabrous, lustrous, with a fine microsculpture. Dorsally the thoracic and first two abdominal segments bear transverse bands of spinules; these are gradually narrowed on the more posterior segments. The third and fourth abdominal segments have one to two (mostly one) rows of spinules and the following segments are without spinules, or with one to two rows of them. Ventrally on each segment is a very broad band of spinules and before the anus is a transverse band consisting of about four rows of spinules. The spinulose ring around the posterior spiracular field is very broad and closely borders the field; on the ventral side it is separated into two closely placed parallel bands.

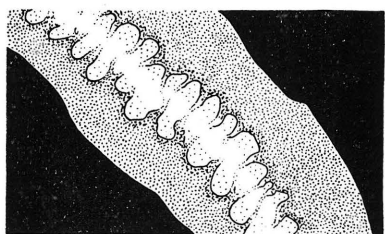
The posterior spiracles (figs. 29, 47) are situated terminally, they are not at all translocated dorsally. They are circular in shape, their minimum distance is shorter than one-half the width of a spiracle. The



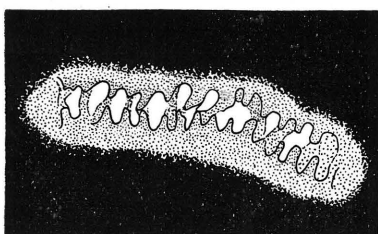
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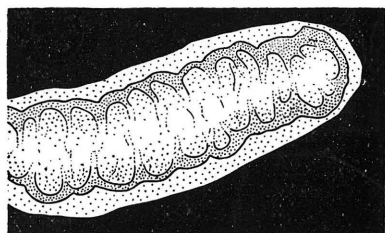
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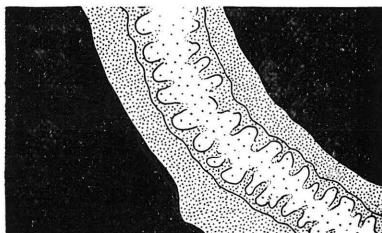
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Fig. 56: *Carcelia excavata*, structure of an orificium. — Fig. 57: *Carcelia lucorum*, ditto. — Fig. 58: *Carcelia separata*, ditto. — Fig. 59: *Carcelia dubia*, ditto. — Fig. 60: *Histochoaeta marmorata*, ditto. — Fig. 61: *Ctenophorocera pavidata*, ditto. — Solid line equals 0,1 mm.

stigmatophores are only very low as in other species of the genus *Carcelia*. Three orificia are developed; they are characteristically curved, so that they form a tulip-shaped figure; they are very narrow, with only one trachite, this is regular in structure (fig. 58). The cicatrix is well-defined.

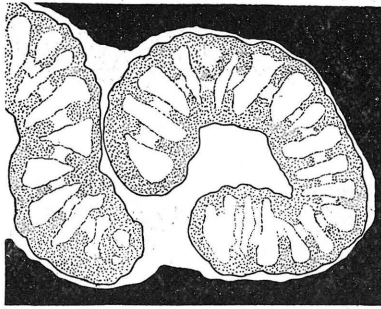
The pseudostigmata are distinctly developed, sometimes (in speci-

mens from *Drymonia querna* F.) they are enclosed by a sharp anterior keel which is parallel with the intersegmental lines. The supraanal protuberance is well-defined, strongly convex, almost hemispherical in shape, with a distinct impression. The distance between the posterior spiracles and the anal opening is twice as long as the maximum distance between the spiracles.

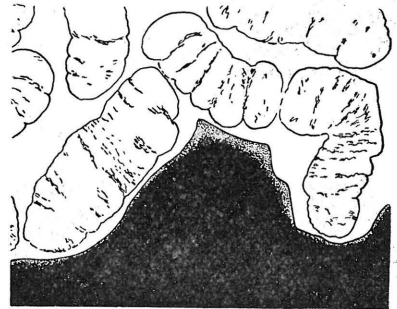
The cephalopharyngeal apparatus (fig. 71) is large, with a large pharyngeal part, but also with the anterior sclerites, especially the oral portion, strongly developed.

Measurements of the puparium: length, about 7 to about 8 mm; width, 3,4 to 4,3 mm.

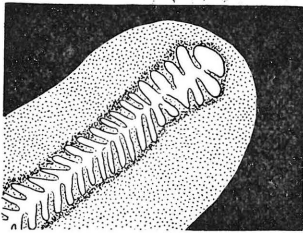
Material examined: Two puparia (imago det. Mesnil) ex *Lymantria dispar* L. (Slovakia: Tesáre n. Žit., 1954, lgt. Čapek). — One puparium (imago det. Mesnil) ex *Lymantria dispar* L. (Slovakia: Žibritov, 1955, lgt. Čapek). — Two puparia (imago det. Mesnil) ex *Drymonia querna* F. (Slovakia: Pata, 1955, lgt. Čapek).



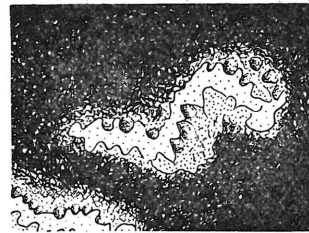
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Fig. 62: *Sturmia bella*, structure of an orificium. — Fig. 63: *Salmacia sicula*, ditto. — Fig. 64: *Winthemia erythrura*, ditto. — Fig. 65: *Pseudoperichaeta insidiosa*, ditto. Solid line equals 0,1 mm.

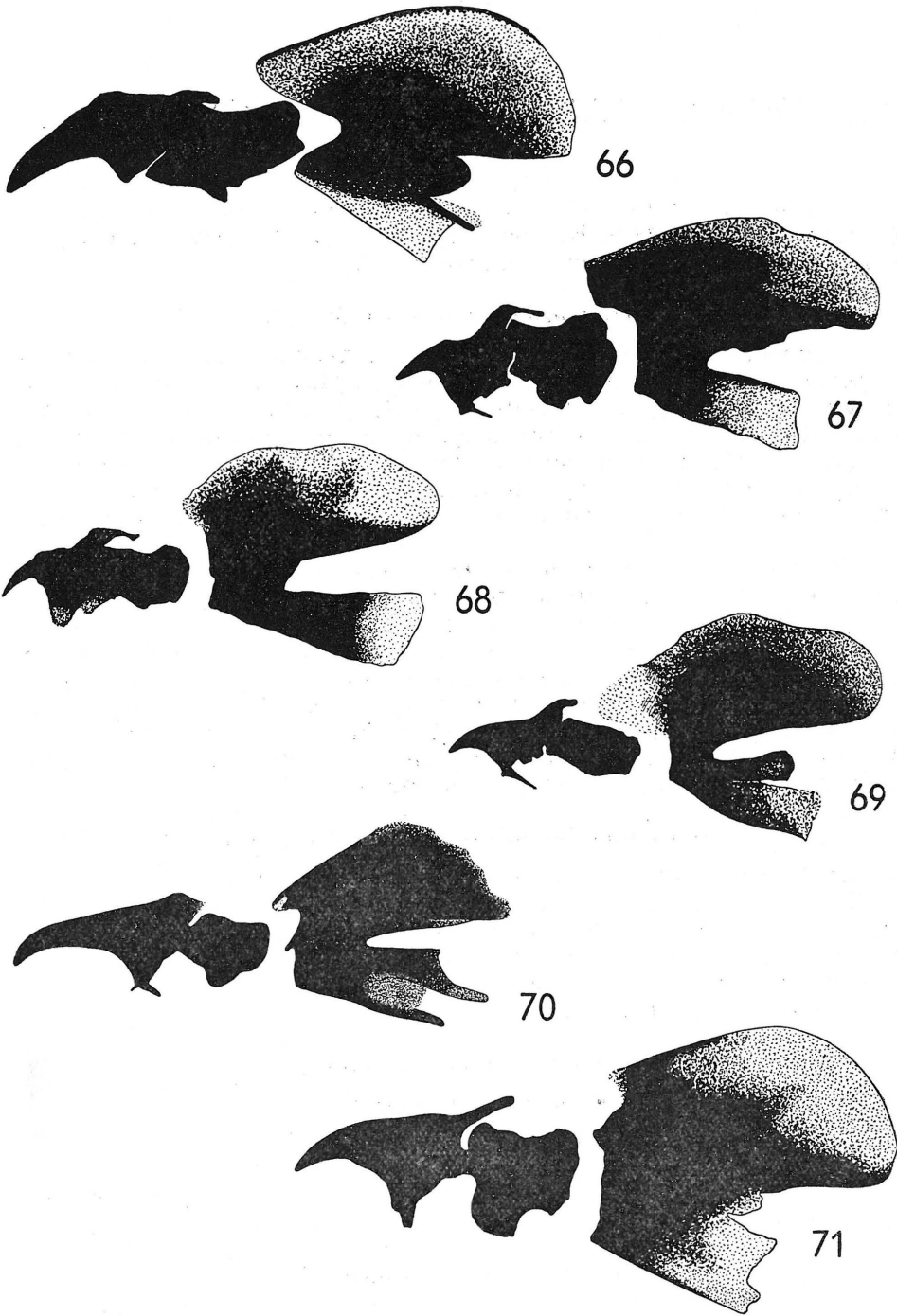


Fig. 66: *Histochaeta marmorata*, cephalopharyngeal apparatus. — Fig. 67: *Carcelia excavata*, ditto. — Fig. 68: *Carcelia lucorum*, ditto. — Fig. 69: *Carcelia dubia*, ditto. — Fig. 70: *Winthemia erythrura*, ditto. — Fig. 71: *Carcelia separata*, ditto. Solid line equals 1 mm.

Tribus WINTHEMIINI

A small, [according to Mesnil, 1949a] very homogenous group of genera with about fifteen European species. Only puparia of the genus *Winthemia* are known for the entire world.

Winthemia Robineau-Desvoidy, 1830

This genus is the largest of the tribe Winthemiini. Nevertheless, only puparia of two European and two Indian species have been described. Unfortunately, the great systematic obscurity of this genus makes many of the data published by old European and American authors uncertain. However, according to all the published facts the puparia of the genus *Winthemia* appear to be very uniform and extremely characteristic because of the structure of the orificia of the posterior spiracles (cf. figs. 50, 64).

The puparium of the genus *Winthemia* has no outstanding characters; it is elliptical in shape, with sharp or rounded ends, with evenly convex sides, and is reddish-brown to dark brown in colour. The anterior spiracles are small and obscure. The posterior spiracles are situated slightly supraterminally and next to each other. The stigmatophores are very low. The spiracular plate is circular or nearly so, with three orificia, each of which has only one slightly curved trachite. Orificia are very characteristic in structure (fig. 64). The cicatrix is well-defined. The supranal protuberance is obscure or well developed.

Winthemia bohemani (Zetterstedt, 1844)

The name *Winthemia xanthogastra* (Rondani, 1859) is a synonym of this species. Nielsen (1913) described under this name the bionomy and puparium of a fly of what he thought it was this species, but Mesnil (1949a) writes: "Nielsen (1913) hat unter dem Namen *xanthogastra* Rond. die Biologie einer *Winthemia* studiert, welche sehr wahrscheinlich *Winthemia cruentata* Rond. aus *Chaerocampa elpenor* L. ist."

Winthemia cruentata (Rondani, 1859)

See the note under *Winthemia bohemani*.

Winthemia erythrura (Meigen, 1838)

The puparium (figs. 21, 25) is small and slender and in dorsal view has slightly convex lateral margins and sharp ends (especially with the posterior one). In profile the dorsal and ventral margins are slightly convex, the puparium is highest on the anterior third of its length. The entire integument of the puparium is very rugose and has numerous transverse wrinkles and rows of spinules (fig. 81), so that the spinules are obscure. On the dorsum the third thoracic and especially the first abdominal segments each have a distinct transverse band of large spinules and the second abdominal segment has one to two rows of spinules. Ventrally each segment bears a band of spinules, which is very broad

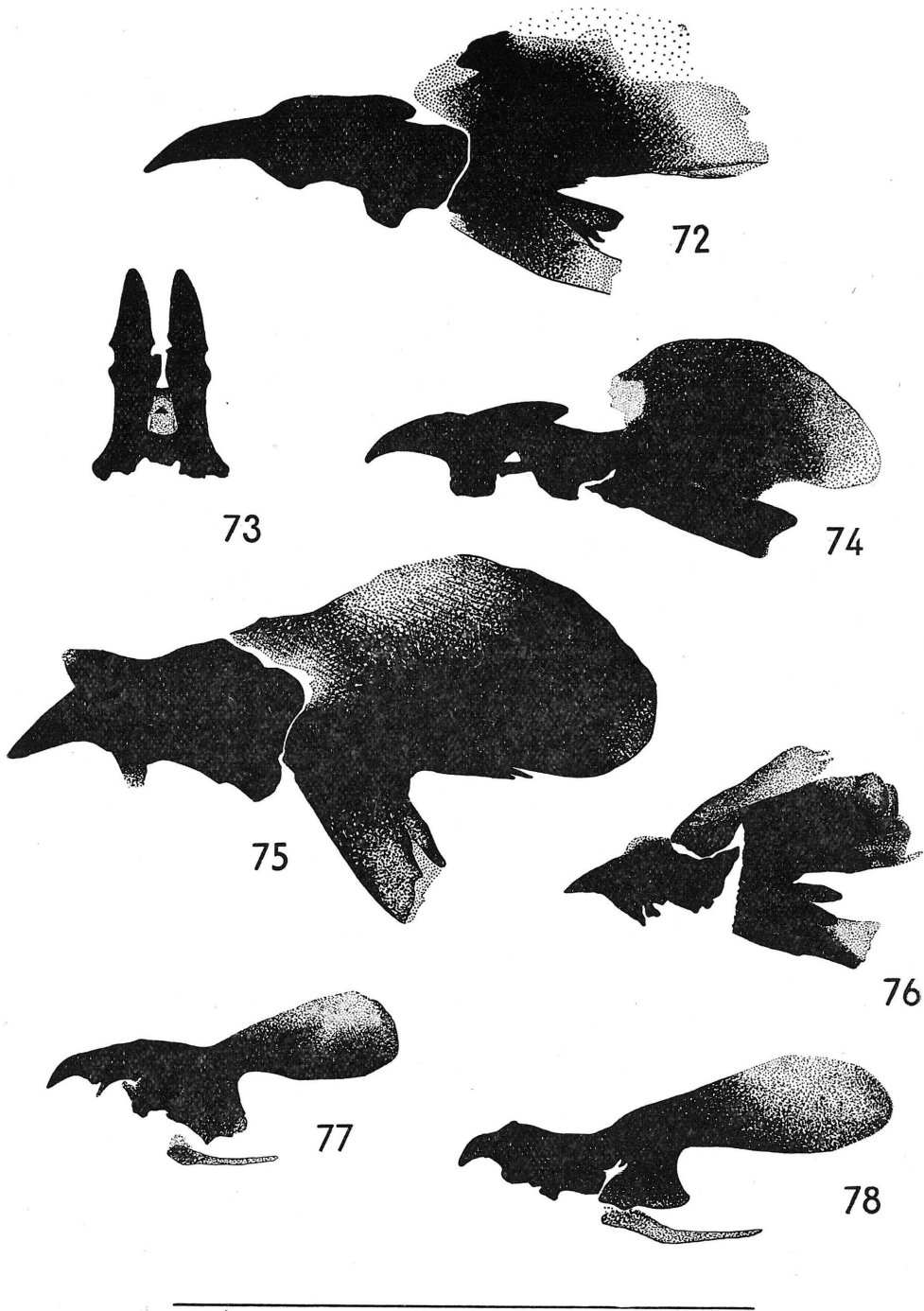


Fig. 72: *Sturmia bella*, cephalopharyngeal apparatus. — Fig. 73: *Ctenophorocera pavida*, oral part of the cephalopharyngeal apparatus, dorsally. — Fig. 74: *Ctenophorocera pavida*, cephalopharyngeal apparatus. — Fig. 75: *Salmacia sicula*, ditto. — Fig. 76: *Pseudoperichaeta insidiosa*, ditto. — Fig. 77: *Elodia convexifrons*, ditto. — Fig. 78: *Elodia morio*, ditto. — Solid line equals 1 mm.

especially on the middle and hind segments, so that the bands are almost fused.

The anterior spiracles are obscure.

The posterior spiracles (figs. 39, 50) are situated slightly supra-terminally. The posterior spiracular field is bordered by a distinct, more strongly sclerotized rim, which is obscure ventrally. Before this rim are many deep wrinkles with rows of spinules which are very closely crowded. Stigmatophores are practically absent. The minimum distance between the posterior spiracles is very short (about one seventh of the spiracular width). The spiracular plates are circular, very slightly convex; they are weakly sclerotized but bordered by a C-shaped sclerotized ring, which is interrupted medioventrally. The three orificia are practically parallel and directed medioventrally, at 45° angle to the height of the spiracles. The structure of the orificia is very characteristic. The orificium has only one trachite, the structure of which is directed obliquely and is regular in shape (fig. 64). The cicatrix is well defined.

The pseudostigmata are distinct. The supraanal protuberance is obscure. The distance between the anal opening and the posterior spiracles is twice as long as the maximum distance between the spiracles.

The cephalopharyngeal apparatus (fig. 70) has very slender and long mouth-hooks. The hypostomal part is relatively small and the pharyngeal part is not strongly developed.

Measurements of the puparium: length, 5.2 mm; width, 2.0 mm.

Material examined: One puparium (imago det. Mesnil) ex *Ennomos erosaria* Schiff. (Slovakia: Banská Štiavnica, 1954, lgt. Čapek).

Winthemia quadripustulata (Fabricius, 1794)

The puparium is described by Nielsen (1916), Greene (1921) and Allen (1925), the latter two authors have also some figures of the puparium. However, it is doubtful if these descriptions (especially these of American authors) refer to the named European species.

Tribus STURMIINI

A large tribe with many species which mainly parasitize Lepidoptera. Several species, however, parasitize larvae of saw-flies of the superfamily Tenthredinoidea (especially Diprionidae) and are extremely effective parasites of some very important pests. For that reason, a few puparia of this tribe are well-known in the literature. Many puparia of North American species of this tribe were described by Greene (1921); recently Smith, Dunn & Rosenberger (1955) have also described the puparium of a Nearctic species. Gardner's (1940a) paper deals with the puparia of a great number of Indian Sturmiini.

Mesnil (1949b; 1949a—1952) (and also Townsend, 1934—1942, according to Smith, Dunn & Rosenberger, 1955) carried out a partial generic reclassification of the tribe Sturmiini and clearly delimited some of

the genera, especially the genus *Drino* Robineau-Desvoidy [= *Zygoturmia* Townsend, 1911]. Most facts given in the literature refer to this genus and not to the genus *Sturmia* Robineau-Desvoidy (s. str.).

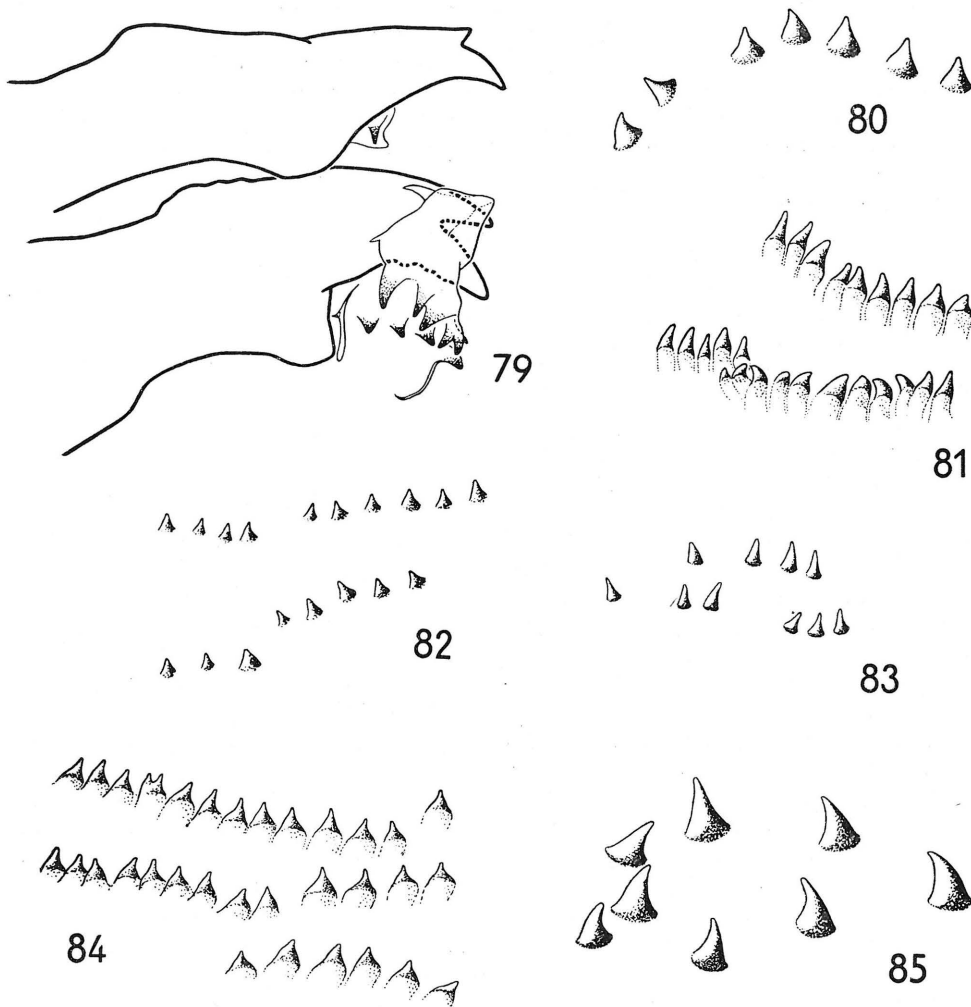


Fig. 79: *Elodia morio*, anterior parts of the cephalopharyngeal apparatus (lateroventral view). — Fig. 80: *Carcelia lucorum*, spinules on the posterior end of the puparium. — Fig. 81: *Winthemia erythrura*, ditto. — Fig. 82: *Ctenophorocera pavidia* (first type), ditto. — Fig. 83: *Histochoaeta marmorata*, spinules on the last segment of the puparium. — Fig. 84: *Ctenophorocera pavidia* (second type), spinules on the posterior end of the puparium. — Fig. 85: *Histochoaeta marmorata*, the same specimen as in fig. 83, spinules on the next to the last segment of the puparium. — Solid line equals 0,1 mm.

Ctenophorocera Brauer & Bergenstamm, 1891

A large genus, but with only two European species. Vimmer (1920,⁵ 1925) and Mathur (1950) described the puparium of an European species, *Ctenophorocera pavida* (Meigen). Gardner (1940a) described the puparium of *Ctenophorocera townsendi* (Baranov), a species distributed in China, India and Indonesia. However, the European puparia of *Ctenophorocera pavida* (according to Vimmer, 1925 and materials in my collection) differ distinctly from the Indian puparia of this species (according to Mathur, 1950), especially in the number of orificia (European specimens have four, but Indian specimens only three). This is a very important and an extremely interesting difference, in my opinion. Also the other Indian species, *Ctenophorocera townsendi*, has only three orificia in the puparia. The genus *Ctenophorocera* was recently revised by Mesnil (1950) and the relationship of *Ctenophorocera townsendi* to *Ctenophorocera pavida* was re-proved. For these reasons the puparium of *Ctenophorocera pavida* is redescribed according to the specimens from Czechoslovakia.

The following preliminary characteristics of the puparia of the genus *Ctenophorocera* can be given: The puparia are medium-large, elliptical in general shape, with broadly rounded ends, without outstanding characters. The posterior spiracles are located rather near to each other and slightly supraterminally. The stigmatophores are very low. The spiracular plate is almost circular, with three to four slightly curved orificia. The cicatrix is well-defined, not far from the centre of the spiracular plate. The supraanal protuberance is relatively large and is higher than the stigmatophores of the posterior spiracles.

Ctenophorocera pavida (Meigen, 1824)

The puparium (figs. 7, 11) is small to large and robust, considerably variable in size. In dorsal view the puparium is only slightly convex laterally, almost parallel, broadest in the median portion; the anterior and posterior ends are broadly rounded. In profile the puparium is highest beyond the middle, it is strongly convex dorsally, but slightly convex or nearly flat ventrally; both ends are broadly rounded. The surface of the puparium is glabrous, on pleural parts a row of segmental impressions are present on each side. The pattern of spinules is very fully developed. On the dorsum each thoracic segment bears a broad band of spinules, the first to third abdominal segments bear narrower bands (which narrow gradually posteriorly) consisting of two to four rows of spinules and the following segments have different numbers of extremely fine transverse rows of spinules. The seventh abdominal segment bears a broader band of very fine spinules dorsally, the last segment is almost completely covered with short and relatively sparse rows of spinules. On the anteroventral part of each segment is a broad band (broader in larger puparia) of spinules, these are bigger than the largest spinules on the dorsal surface; one to two rows of spinules are also located on

⁵ Described as "*Phorocera cilipeda* Rd."

the posterior margin of the second and following segments. Along the hind margin of the seventh abdominal segment a broader band extends around the entire segment, the last broad ring-shaped band is separated into two parallel transverse bands ventrally.

The anterior spiracles are similar to these of the genus *Carcelia*, but they are slightly raised. They probably have four pori.

The posterior spiracles (figs. 33, 34, 44) are slightly oval, almost circular in shape, their maximum diameters converge dorsally. The stigmatophores are fairly distinct, their height is one-fifth times as long as the height of a spiracle. The spiracular plate is faintly sinuate, with shallow, but distinct grooves between the orificia. Four orificia are developed, three are almost parallel and directed medioventrally, the ventral one is more or less horizontal. Each orificium has one trachite, which is straight, very narrow, and has relatively regular structure (fig. 61). The cicatrix is small, but well defined.

Two types of the puparia were found according to the distance between the posterior spiracles. The first type (probably the large puparia, fig. 33) has the minimum distance between the spiracles about as long as the width of a spiracle; these puparia have small spiracles in comparison with the length of the puparium and the spinules (fig. 82) of the ring bordering the posterior spiracular field are small and the rows are sparse. The second type (probably the small puparia, fig. 34) has the minimum distance between the spiracles about one-third as long as the width of a spiracle; these puparia have large spiracles in comparison with the length of the puparium and the spinules (fig. 84) of the ring bordering the posterior spiracular field are big and so closely crowded that they lie side by side. The puparia which I have examined show all degrees of intergradation from one extreme to the other. I suppose that the type of puparium depends on its length; further observations are needed to verify this hypothesis.

The pseudostigmata are well developed. The supraanal protuberance is slightly convex, but large and with an impression. The distance between the anal opening and the posterior spiracles is two and one-half times as long as the maximum distance between the posterior spiracles.

The cephalopharyngeal apparatus (figs. 73, 74) has compact anterior parts; the mouth-hooks are large, the basal and hypostomal parts are connected by a ventral stick-shaped sclerite, which is a process of the hypostomal part of the apparatus.

Measurements of the puparium: length, about 6,5 to about 8,5 mm; width, 3,0 to 3,8 mm.

Material examined: One puparium (imago det. Mesnil) ex *Malacosoma neustrium* L. (Slovakia: Pavlovce n. U., 1956, lgt. Čapek). — One puparium (imago det. Mesnil) ex *Thaumatopoea processionea* L. (Slovakia: Lučenec, 1954, lgt. Čapek). — One puparium (imago det. Mesnil) ex *?Polyplocia ridens* F. (Slovakia: Beluja pr. Šahy, 1955, lgt. Čapek). — One puparium (imago det. Mesnil) ex *Larentia montanata* Schiff. (Slovakia: Banská Štiavnica, 1957, lgt. Čapek). — Two puparia (imago det. Zuska) ex *Acronicta megacephala* F. (Slovakia: Šahy, 1958, lgt. Čapek).—

Four puparia (imago det. Zuska) ex *Euproctis phaeorrhoea* Don. (Moravia: Vlasatice, 1958, lgt. Dlabola).

***Sturmia* Robineau-Desvoidy, 1830**

According to above facts (see discussion of the tribe Sturmiini) the delimitation of this genus has recently been entirely changed. Therefore only one Palearctic species (according to Mesnil, 1950) belongs to this genus, the puparium of this is described here below.

***Sturmia bella* (Meigen, 1824)**

Gardner (1940a) described the puparium of this species. However, according to his figures Indian specimens differ from Czechoslovak puparia in general shape, in the form of the stigmatophores of the posterior spiracles, in the structure of the spiracular plates, etc. Therefore I give a redescription of the puparium of *Sturmia bella* according to the specimens from Czechoslovakia.

The puparium (figs. 8, 12) is big and robust, in dorsal view it is egg-shaped, broadest on the hind half and only very slightly narrowing anteriorly. In profile the puparium is highest behind the median portion, fairly convex dorsally, but slightly convex, flat or gently concave ventrally. The surface of the puparium is rugous and wrinkled, so that the spinulose pattern is obscure in spite of the large size of the spinules. Dorsally each segment has a narrow band and ventrally a broader band of spinules. The last segment has only very fine spinules.

The anterior spiracles are visible only as very small, scarcely visible protuberances.

The posterior spiracles (figs. 36, 45) are relatively large and rounded, but slightly triangle in shape, the minimum distance between them is one-fifth as long as the width of a spiracle. The spiracular plates are located on moderately elevated stigmatophores, the height of these is one-sixth to one-fifth the height of a spiracle. Three orificia are developed, they are very broad and are convergent medially. The cicatrix is small but is very distinct. Each orificium has about five to seven trachites, which are short and wide, irregularly formed but with a very regular structure (fig. 62).

Small but well-defined pseudostigmata are developed on the first abdominal segment. The supraanal protuberance is rather small, low and indistinctly bordered ventrally. The distance of the anal opening from the posterior spiracles is one and one-half times as long as the maximum distance between the spiracles.

The cephalopharyngeal apparatus (fig. 72) is long, slender, compact and strongly sclerotized. The mouth-hooks are long and slender, almost stylet-shaped; the basal part is relatively large and elongate and the pharyngeal part is medium-sized, only its dorsal process is more strongly developed.

Measurements of the puparium: length, 6,8 to about 8,5 mm; width, 3,8 to 4,6 mm.

Material examined: Ten puparia (imagines partly det. Čepelák, partly det. Zuska) ex *Nymphalis io* L. (Bohemia: Radotín, lgt. Čepelák, coll. Nat. Museum Praha). — Four puparia (imago det. Mesnil) ex *Nymphalis io* L. (Slovakia: Banská Štiavnica, 1957, lgt. Čapek).

Blepharipoda Rondani, 1856

The species of this genus are often treated in the literature as "Sturmia". The puparium of one species, *Blepharipoda zebrina* (Walker), which occurs in India, China and Japan, was described by Gardner (1940a) as *Sturmia sericariae* Cornalia.

Vimmer (1925) described and figured a larva *Blepharipoda scutellata* (Robineau-Desvoidy) with the note "dle Fiskeho"—according to Fiske, but he did not describe the puparium, as noted by Hennig (1952). Apparently the puparium of this species has not been described to date.

Drino Robineau-Desvoidy, 1830

This is the largest genus of the tribe and is of considerable economic importance because of its use in the biological control of forest pests. Several species parasitize saw-flies of the family Diprionidae.

The genus *Drino* is very difficult systematically, especially from the standpoint of the delimitation of species. The puparia, however, often possess excellent characters distinguishing species, even in closely related species (Sachtleben, 1942). In many cases the puparia show better diagnostic characters than do the adults and their use should greatly facilitate the specific classification of this genus.

In addition to the three European species the puparia of a few North American species (Greene, 1921) and a large number of the puparia of Indian species (Gardner, 1940a) have been described.

It is most interesting and significant that the reclassification of the old genus *Sturmia* Robineau-Desvoidy (see above under the tribe Sturmiini), especially the separation of *Sturmia* s. str. and *Drino* and the division of the genus *Drino* into subgenera (Mesnil, 1950, 1951) can be based also on the morphology of puparia. The following definitions may be given for various systematic units included in the old genus *Sturmia*:

Sturmia Robineau-Desvoidy s. str.

The puparium is elliptical, with broadly rounded ends. The anterior spiracles are obscure. The posterior end of puparium is very broad, evenly rounded, not truncate. The posterior end of puparium is very broad, evenly rounded, not truncate. The posterior spiracles have a low or moderately elevated stigmatophore, with three orificia. Each orificium has one strongly serpentine trachite or many trachites. [Examined: *Sturmia bella* (Meigen), specimens from Czechoslovakia; published data on *S. bella* (Meigen), specimens from India.]

Drino Robineau-Desvoidy s. str.

The puparium is elliptical or cylindrical. The anterior spiracles are probably very large, at least in *Drino lota*. The posterior spiracles have low to high stigmatophores, with three orificia; each orificium has one trachite, or two more or less parallel trachites, which is strongly serpentine. [Published data on *Drino* (*Drino* s. str.) *lota* (Meigen), *D. (D.) argenteiceps* (Macquart).]

Drino sg. **Zygobothria** Mik

It is not possible to give any characteristics of this subgenus at this time since the literature contains only sketchy information and very heterogenous data. [Published data on *Drino* (*Zygobothria*) *atropivora* Robineau-Desvoidy (Gardner, 1940a; Mathur, 1950) and *D. (Z.) convergens* (Wiedemann).]

Drino sg. **Prosturmia** Townsend

The puparium is elliptical or cylindrical. The anterior spiracles are obscure. The posterior spiracular field is bordered mostly by a ring-shaped swelling. The posterior spiracles have elevated stigmatophores, with three orificia; each orificium has one straight or slightly curved trachite. [Published data on *Drino* (*Prosturmia*) *gilva* (Hartig), *D. (P.) inconspicua* (Meigen), *D. (P.) parachrysops* (Bezzi), *D. (P.) discreta* (Wulp), *D. (P.) inconspicuoides* (Baranov).]

Drino sg. **Isosturmia** Townsend

The puparium is elliptical. The supraanal protuberance is absent. The posterior spiracles are small, with low, narrowly separated stigmatophores, which have three to four orificia. Each orificium has one trachite, which is straight or slightly curved. (Published data on *Drino* (*Isosturmia*) *nigribarbis* (Baranov), *D. (I.) chatterjeeana* (Baranov).]

General description⁶) of puparium of the genus *Drino*: The puparium is elliptical or cylindrical, without special macroscopic characters and is mostly covered with more or less dense bristle-shaped spinules. The anterior spiracles are small and obscure, or (in *Drino lota*) they are large and raised. The spiracles have many irregularly situated pori. The posterior spiracles are of various structure. The stigmatophores are low to high. Each spiracle has three (or four in *Drino nigribarbis*) orificia with one straight or serpentine trachite. The supraanal protuberance may be developed or absent.

Key to puparia⁶

- 1 (2) Anterior spiracles very large, strongly raised, with well-defined stigmatophores, the minimum distance between them is two and one-half to three times as long as the minimum diameter of a spiracle; each spiracle with about sixty pori. Posterior spiracles with very wide orificia, situated on broadly rounded ridges. Trachites strongly serpentine. Spiracles not enclosed by a ring-shaped swelling. Distance of the anal opening from the posterior spiracles about two and one half times as long as the maximum diameter of a spiracle (Müller, 1956, figs. 25—28)
Drino lota (Meigen)
- 2 (1) Anterior spiracles obscure. Trachites straight or slightly curved. Other characters not as above.
- 3 (4) Puparium cylindrical, with truncate posterior end. Supraanal protuberance very large, much larger than a spiracle and extends between the spiracles. Posterior spiracular field enclosed by a low ring-shaped swelling
Drino atropivora (Robineau-Desvoidy)
- 4 (3) Puparium elliptical, with rounded posterior end. Supraanal protuberance smaller, dorsally not reaching between the spiracles.
- 5 (6) Posterior spiracular field enclosed by a ring-shaped swelling, which may be interrupted (Sachtleben, 1942, fig. 5b). Pattern of spinules more continual (Sachtleben, 1942, fig. 6b)
Drino gilva (Hartig)
- 6 (5) Posterior spiracular field not enclosed by a ring-shaped swelling (Sachtleben, 1942, fig. 5a). Pattern of spinules less continual (Sachtleben, 1942, fig. 6a)
Drino inconspicua (Meigen)

⁶ The generic description and key to puparia have been compiled only from the published data. For a comparative discussion of the morphology of the puparia of this genus refer to Müller (1956).

Drino atropivora (Robineau-Desvoidy, 1830)

Both Gardner (1940a) and Mathur (1950) described puparia which they called *Drino atropivora* but it is obvious that they were dealing with two different species.

Drino gilva (Hartig, 1838)

The puparium was described and figured by Sachtleben (1942).

Drino inconspicua (Meigen, 1830)

The puparium of this species was described, or figured, by Webber (1932), Gardner (1940a)—from India—, Sachtleben (1942) and Belanovskij (1951). The literature on the bionomy of this species is very extensive, since *Drino inconspicua* is an effective parasite of the saw-flies of the genus *Diprion* Schr., especially of *Diprion pini* L. and of some other insect pests.

Drino lota (Meigen, 1824)

The puparium was described and figured by Müller (1956). It differs very much from the other known puparia of European species of the genus *Drino*, especially in the form of the anterior spiracles, which are very large and with numerous pori, and also in the shape of the trachites, which are very strongly serpentine.

Pseudoperichaeta Brauer & Bergenstamm, 1889

This is small genus with only one palearctic species. According to Hennig (1952) no preimaginal stages of this genus have been previously described.

Pseudoperichaeta insidiosa (Robineau-Desvoidy, 1863)

The puparium (figs. 22, 26) is shiny, small and rather slender. In dorsal view it is nearly parallel-sided, with sharp ends and in profile it is convex dorsally and flat ventrally, with sharp ends. On the dorsal side of the puparium around the anterior spiracular field is situated a very broad transverse band of spinules. The following segment has a narrower band consisting of about four rows of spinules, the next two segments have about two rows of spinules, and the following segments lack spinules or have but a single row of inconspicuous spinules. Posteriorly a transverse band is developed before the spinulous ring bordering the posterior spiracular field; the ring of spinules is very broad. On the ventral side each segment bears a wide band of large spinules. Before the anal opening only a single row of spinules is developed. Ventrally the band around the posterior spiracular field consists also of small spinules.

The anterior spiracles consist of three, slightly raised, hemispherical protuberances.

The posterior spiracles (figs. 38, 49) have practically no stigmatophores, and are very small and circular in shape. The distance between them is one-half as long as the breadth of a spiracle. The spiracular plate is flat, rather slightly sclerotized (except on the edge) and with four orificia, which are directed almost lateromedially; these are rather short, very broad and mostly curved. Each orificium has only one trachite; the structure of the trachites (fig. 65) is very rough and quite characteristic. The cicatrix is extremely large, but poorly defined.

The pseudostigmata are distinctly developed. The supraanal protuberance is absent. The distance of the anal opening from the posterior spiracles is two and one-half times as long as the maximum distance between the spiracles.

The cephalopharyngeal apparatus (fig. 76) is high and short; the oral part is high and the mouth-hooks are sharp, but short. The hypostomal part is almost as long as the oral one.

Measurements of the puparium: length, about 5,0 to about 5,5 mm; width, 1,8 to 2,4 mm.

Material examined: One puparium (imago det. Mesnil) ex *Cacoecia xylosteana* L. Slovakia: Sitno, 1957, lgt. Čapek). — Two puparia (imago det. Zuska) ex *Cacoecia xylosteana* L. (Slovakia: Banská Štiavnica, 1958, lgt. Čapek). — One puparium (imago det. Zuska) ex *Pandemis corylana* F. (Slovakia: Banská Štiavnica, 1958, lgt. Čapek).

Tribus ERYTHROCERINI

This is a small tribe with seven known European species, which parasitize Lepidoptera and also Dermaptera. No preimaginal stages of this tribe are known except for *Rhacodineura pallipes* (Fallén).

I am describing below the puparia of both the palearctic species of the genus *Elodia*. In comparing with the puparium of *Rhacodineura pallipes* (from data published by Thompson, 1928) both these genera have extremely high stigmatophores of the posterior spiracles and the species *Rhacodineura pallipes* and *Elodia morio* (Fallén) [= *tragica* (Meigen)] have secondarily modified orificia (see fig. 55 in this paper and pl. ix, fig. 39 in Thompson, 1928). According to Mesnil (1952) this tribe is very homogenous and probably forms a very natural group of species. The above similar characters may be typical for all species of this tribe. In my opinion, however, these characters are probably of no systematic importance and were brought about only by a convergent adaptation.

Elodia Robineau-Desvoidy, 1863

Two species of this genus are known from the Palearctic region. Up to this time no preimaginal stages of this genus have been described and I am presenting descriptions of both species at this time.

The puparia of the genus *Elodia* are very distinctive because of the shape of the posterior end of the puparium (see the descriptions). Both

the species have the same, but morphologically different, adaptation. The posterior spiracles are located on a broad column (figs. 40, 41), which is directed posteroventrally [in *Elodia morio* (Fallén), fig. 27], or postero-dorsally [in *Elodia convexifrons* (Zetterstedt), fig. 28]. It seems that the dorsal and ventral sides (morphologically) form different parts of the column in puparia of the two species. (From the morphological point of view also the location of the anal opening and the supraanal protuberance is of importance.) The posterior spiracles are also strongly differentiated in their shape. In *Elodia convexifrons* four narrow, straight orificia are present (fig. 53), but in *Elodia morio* one C-shaped pseudorificium is formed by the dilated and fused orificia (fig. 55). These very important differences in the same genus show that the systematic conclusions drawn from the present knowledge of larvaevorid puparia are very premature. On the other hand, these facts may be very interesting from the taxonomic standpoint, especially in a discussion of such problems as the importance of larval (or pupal) characters in the systematic scheme, the problem of convergency, etc.

The puparium of the genus *Elodia* is of a very characteristic shape. It is oval, fairly broad and as seen in dorsal view it is convex laterally. In profile it is more convex dorsally, less convex ventrally and is rounded at the anterior end. The posterior end has a broad column, directed posterodorsally or posteroventrally, on which are located large divergent stigmatophores with posterior spiracles. The pattern of spinules is faintly developed. The anterior spiracles are rather conspicuous and somewhat raised. The posterior spiracles have very high stigmatophores (especially in *Elodia convexifrons*). The spiracular plate has four straight orificia, or has a C-shaped pseudorificium. The cicatrix is large. The pseudostigmata may be developed or absent. The supraanal protuberance is large or small, but not well defined. The cephalopharyngeal apparatus is small, relatively very low. The mouth-hooks are short, the pharyngeal part (especially its dorsal process) is very large and the ventral process almost is absent. Ventrally below the basis of the pharyngeal part is developed a characteristic scale-shaped transverse sclerite.

Key to puparia

- 1 (2) Posterior column of puparium directed posterodorsally, relatively narrow and cylindric with distinct borders (fig. 40). An obscure supraanal protuberance located on the lower (proximal in relation to length axis of puparium) side of the posterior column. Anal opening located almost terminally, it is at the point of intersection of the length axis with puparial surface. Stigmatophores of posterior spiracles in anterodorsal view nearly twice as long as wide. Pseudostigmata absent (?). Four well-defined, straight, orificia are developed (fig. 53). (One puparium examined only!) ***Elodia convexifrons*** (Zetterstedt)
- 2 (1) Posterior column of puparium directed posteroventrally, broad, conical, obscurely bordered (fig. 41). An obscure to well-defined supraanal protuberance is on the lower (distal in relation to length axis of puparium) side of the posterior column. Anal opening located ventrally on the base of this column. Stigmatophores of posterior spiracles, in anteroventral view, as long as wide. Pseudostigmata developed, but often obscure. Orificia fused into C-shaped pseudorificium (fig. 55) ***Elodia morio*** (Fallén)

***Elodia convexifrons* (Zetterstedt, 1844)**

The puparium (figs. 24, 28) is shiny. In dorsal view it is slightly convex laterally, widest before the middle and it has rather strongly convex dorsal and slightly convex ventral margins. The anterior end of the puparium is broadly rounded and the posterior end has a short, broad, posterodorsally directed column (in anterodorsal view it is as long as wide), on which the posterior spiracles are located. The puparium which was examined lacked spinules except for several rows around the anterior and posterior spiracular fields. The puparium is yellow, the cuticle is extremely thin.

The anterior spiracles are very well developed, their height is equal to about three-fourth the length of their slightly oval base (in lateral view), and about five comparatively distinct pori are present.

The posterior spiracles (fig. 40, 53) have very long stigmatophores, which are (in lateral view) nearly twice as long as wide and are directed posterolaterally. The minimum distance between the bases is one-half as long as the width of a spiracle. The stigmatophores are depressed lateromedianly, in lateral view they are widest on the apical half. Four straight orificia are developed, these are directed perpendicularly to the cicatrix. The cicatrix is relatively well defined, large, and is located at the median edge of the spiracular plate. The orificia are each situated on a low ridge. (The posterior spiracles have been examined stereoscopically only, without maceration in KOH or mounting.)

Pseudostigmata were not found. The supraanal protuberance is obscure. The distance between the anal opening and the posterior spiracles is twice as long as the maximum distance between the bases of stigmatophores.

The cephalopharyngeal apparatus (fig. 77) is small and perhaps without special specific characters.

Measurements of the puparium: length, about 4.8 mm; width, 2.0 mm.

The puparium is located in the host pupa.

Material examined: One puparium (imago det. Mesnil) ex *Tinea* sp. (Slovakia: Sitno, 1956, lgt. Leontovyč).

***Elodia morio* (Fallén, 1820)**

The puparium (figs. 23, 27) is slightly shiny. As seen in dorsal view it is only slightly convex laterally. As seen in profile it is strongly convex dorsally, slightly convex ventrally. The anterior end of the puparium is rounded and the posterior end has a short and broad column posteroventrally (in posteroventral view it is as long as wide), on which the posterior spiracles are located. The latter are directed posterolaterally. The pattern of spinules is very variable. The dorsal side is practically without spinules but sometimes has a fairly broad band on each segment. The ventral side has a band of spinules on each segment.

The anterior spiracles are similar to these of *Elodia convexifrons*, but smaller. The number of pori is obscure.

The posterior spiracles (figs. 41, 55) are situated on very high stigmaphores, which are nearly as high as broad, as seen in anteroventral view. The distance between the bases of the stigmatophores is two-third as long as the width of a spiracle. The orificia are fused into a C-shaped pseudorificium. The cicatrix is large and obscure. (The posterior spiracles were examined stereoscopically only, without maceration in KOH or mounting.)

The pseudostigmata are developed, but are sometimes ill-defined. The supraanal protuberance is large, almost hemispherical and obscurely bordered. The distance between the anal opening and the posterior spiracles is one and two-tenth to one and one-half times as long as the maximum distance between the posterior spiracles; the anal opening is located at the base of the posteroventral column.

The cephalopharyngeal apparatus (fig. 78) is small (but, probably, larger than in *Elodia convexifrons*) and apparently without special specific characters. The anterior parts are not single, there is a characteristic dentation between them (fig. 79).

Measurements of the puparium:⁷ length, about 4.0 to about 4.6 mm; width, 1.6 to 2.0 mm.

The puparium is located in the host pupa.

Material examined: Five puparia (imago det. Mesnil) ex *Tortrix viridana* L. (Slovakia: Štúrovo, 1956—1957, lgt. Čapek). — Three puparia (imago det. Zuska) ex *Tortrix viridana* L. (Slovakia: Kajlovka, 1958, lgt. Čapek).

Rhacodineura Rondani, 1861

A monotypical genus containing only the species *Rhacodineura pallipes* (Fallén) [= *Rhacodineura antiqua* (Meigen)], which is a parasite of earwigs of the genus *Forficula* L. and also of Lepidoptera.

Rhacodineura pallipes (Fallén, 1820)

Thompson (1928) published an excellent study on the preimaginal stages of this species. He gave the following characteristics of the puparium:

"Dimensions: 5 mm. X 2 mm. to 6 mm. X 3 mm. Colour yellowish red, sub-shining, . . . rounded anteriorly and posteriorly; spiracles situated on the posterior extremity of the longitudinal axis, elongate, black, more or less divergent but separated at base by a distance equal to the basal diameter of one of them, anal opening situated on the under side at the anterior border of segment XI, its distance from the base of the stigmatic tubercles a little greater than the length of the latter; anterior spiracles minute . . . The pupal respiratory system . . . is complete, the prothoracic cornicles are well developed with a rather small number of respiratory orifices; the internal spiracles with over 100 respiratory papillae arranged on 7 or 8 radiating branches at the end of the atrium."

According to Thompson the posterior spiracles of the third instar larva are very similar to those of the puparium of *Elodia morio* (cf. Thompson, 1928, pl. ix, fig. 39, and fig. 55 in my paper). The spiracular

⁷ The variability of the size of the puparia is apparently much greater considering the extreme variability in length of adult flies.

plate bears orificia fused in a C-shaped orificium; the trachites (about thirty) are short and relatively wide, and are directed radially in a single row, side by side. The stigmatophores are very high (in the larvae). The cephalopharyngeal apparatus of the third instar larva is figured by Thompson (pl. viii, fig. 25).

The puparium differs from that of the genus *Elodia* especially in the shape of its posterior end. No posterior column is developed, but the stigmatophores are much more higher than in *Elodia*.

Tribus SALMACIINI

This is a small tribe with less than twenty known European species. According to Hennig (1952) some preimaginal stages are known for the genera *Salmacia* Meigen and *Spallanzania* Robineau-Desvoidy, and the puparia of two species (one European and one Nearctic) have been described.

Salmacia Meigen, 1800

This genus is the largest of the tribe Salmaciini. The species of this genus are for the most part not well defined, and a thorough study of the puparial characters would probably aid greatly in differentiating the species. The puparium of only one European species is known. I am describing below the puparium of another species, *Salmacia sicula* Robineau-Desvoidy, which is an important parasite of *Chareas graminis* L.

It is not possible at this time to give any general characteristics which are distinctive to the puparia of this genus since our knowledge of the group is so scanty and the known puparia differ highly from one another.

Salmacia capitata (Degeer, 1776)

The puparium was described by Rossikow (1909) and by Greene (1921).

Salmacia sicula (Robineau-Desvoidy, 1830)

The puparium (figs. 6, 10) is large, as seen in dorsal view the sides are almost parallel, only very slightly convergent. The anterior end is somewhat pointed, the posterior end is broadly rounded. In profile the puparium is highest posteriorly, where it is broadly rounded; on the anterior portion it narrows gradually. Both anterior and posterior spiracles are located slightly supraterminally. The surface of the puparium is densely covered with long, bristle-shaped spinules, which form a lateral band on each segment. This band extends the full length of the segment and is divided into two parallel transverse bands both on the dorsal and lateral margins. The horizontal suture is very conspicuous, strongly outstanding. The vertical suture is defined only on the lateral and ventrolateral surfaces.

The anterior spiracles (fig. 54) are about equal in height to the length of their bases. Their stigmatophores are high, conical and strongly narrowed distally. The spiracles are irregular in shape and have about ten pori.

The posterior spiracles (fig. 35, 46) are very large, their height is longer than their breadth. The stigmatophores are elevated, and each orificium is located on a very high and broad ridge. Three short and wide orificia are developed; in the area enclosed by them is a well-defined cicatrix, which is very slightly raised. Each orificium has ten to twenty irregular trachites (figs. 46, 63). The distance between the posterior spiracles is very short, about one-fourth as long as the width of a spiracle. The maximum diameter at an acute angle to the height of the spiracles is considerably longer than the minimum diameter.

The pseudostigmata are absent. The supraanal protuberance is obscure. The distance between the posterior spiracles and the anal opening is as long as the maximum distance between the spiracles.

The cephalopharyngeal apparatus is very long and high. The anterior parts are rather short but high and very compact. The pharyngeal part is strongly developed, especially its dorsal process is long and wide; the ventral process is short.

Measurements of the puparium: length, about 10.0 to about 11.0 mm; width, 4.5 to 5.2 mm.

The puparium is located in the wide anterior portion of the host pupa.

Material examined: Three puparia (imago det. Zuska) ex *Chareas graminis* L. (Bohemia occid., various localities, lgt. Šedivý).

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