Nota lepid. 13 (4) : 221-228 ; 31.XII.1990 ISSN 0342-7536

Morphology of the intromittent organ and distal male genital duct in Coleophoridae (Lepidoptera, Gelechioidea)

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Summary

A phallotheca type intromittent organ is described from the Coleophoridae. Supposed autapomorphies of the family are listed and a list of morphological terms is added.

Introduction

The coleophorid intromittent organ may be called a phallus of the phallotheca type as proposed by Snodgrass (1935). This term was also used by Matsuda (1976) and Kristensen & Nielsen (1979). The enlarged and distally extending phallobase forms a tube surrounding the aedeagus, named the phallotheca. The cited authors consider, that the anterior portion of the phallotheca is double-walled and consists of a wall or phallocrypt, and the phallotheca proper (illustrated by Kristensen (1984b) in the Agatiphagidae). They also use the term endotheca for the inner wall of the former. This interpretation is followed in the present paper. The phallotheca type of phallus is known in some other groups of insects (e.g. Trichoptera), and in the Lepidoptera has been noted in the Agatiphagidae (Kristensen, 1984b) and Heterobathmiidae (Kristensen & Nielsen, 1979). The formation in the Eriocraniidae, which was called the "duplicature ... of the ventral wall of the genital chamber" (Birket, Smith & Kristensen, 1974) has also been interpreted as a phallotheca by Kristensen (1984b). Now, for the first time, a phallotheca has been discovered in ditrysian Lepidoptera.

In the Coleophoridae the structure of the phallus is peculiar, but has never been correctly interpreted. All authors used the term aedeagus for the phallotheca (cf p. 227). Only Kuznetsov & Stekolnikov (1978) attempted to explain a process for the formation of the aedeagus, but also incorrectly.

Material and methods

The morphology of the male genitalia of *Coleophora* was studied in several Central European species, but mainly *C. lixella* Zeller, 1849, using material treated with potassium hydroxide. Histological sections were prepared from two *Coleophora* species.

Results and discussion

The phallus is situated in a slightly asymmetrical genital chamber, limited by the thin wall of the phallocrypt (Fig. 5). It is almost entirely composed of a delicate cuticle and only its lateral and ventro-lateral parts are, in the basal area, sclerotized (Figs. 1, 2). These sclerotized walls extend ventrally and distally into a V-shaped plate forming a variably developed double-walled structure, the caulis. The distal part of this sclerite attaches to the bases of the sacculi, and has small lateral emarginations or lobes which are enlarged dorsally. The edge of the fusion of the ventro-lateral walls runs for some distance along the phallotheca, forming a narrow ventral part of the genital chamber. The space formed terminates near the top of the coecum-like prominence of the base of the phallus (Figs 1, 2). The composite wall formed by the fused phallocrypt and phallotheca observed by Kristensen & Nielsen (1979), is here extremely small, or completely atrophied, especially in the dorsal part of the organ.

The *phallotheca* (Figs 1, 2, 5) is in all species a well developed sheath around the aedeagus, more or less distinctly extending beyond the apex of the latter. In primitive species the sclerotization of the phallotheca is almost uniform or gradually merges into the membranous areas. In the more developed species there appears a secondary membranisation and the sclerotized parts may form various specialised processes or lobes.

The *endotheca* (Figs 1, 5) is a thin-walled membranous sheath very close to the phallotheca. It extends proximally through the anterior opening of the latter, forming at its border a more or less distinct and complete collar-like prominence. More anteriorly the wall of the endotheca develops a more or less distinct ring-shaped sclerite (Fig. 1) ; in systematic papers this is called the annulus. Kristensen (1984a) illustrates a similar structure in *Epimartyria*. In *Coleophora* there is, however, no inner wall of the phallobase, as the aedeagus is completely membranous. The wall of the aedeagus is continuous with the endotheca just in front of the sclerite and it extends proximally as the outer tube.

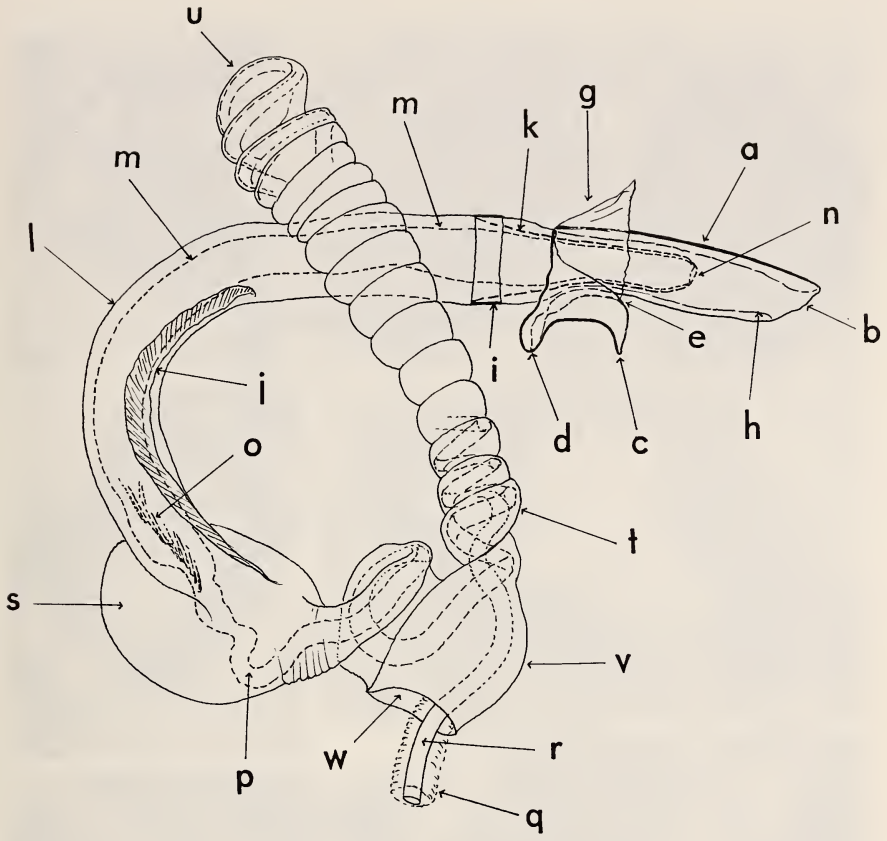
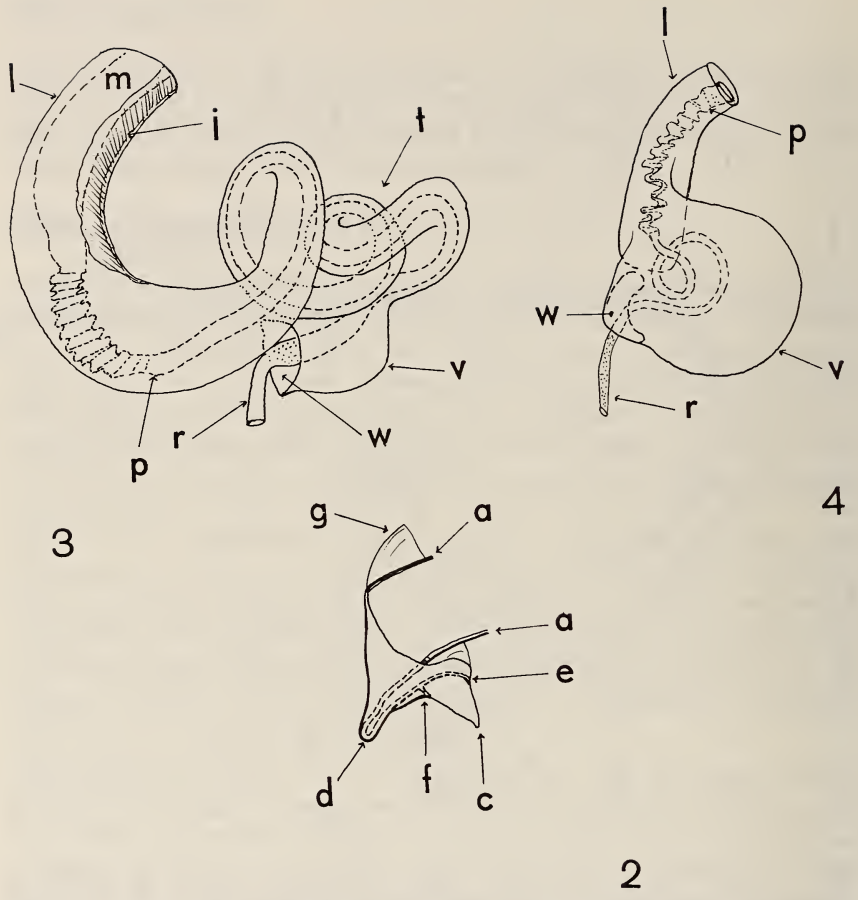


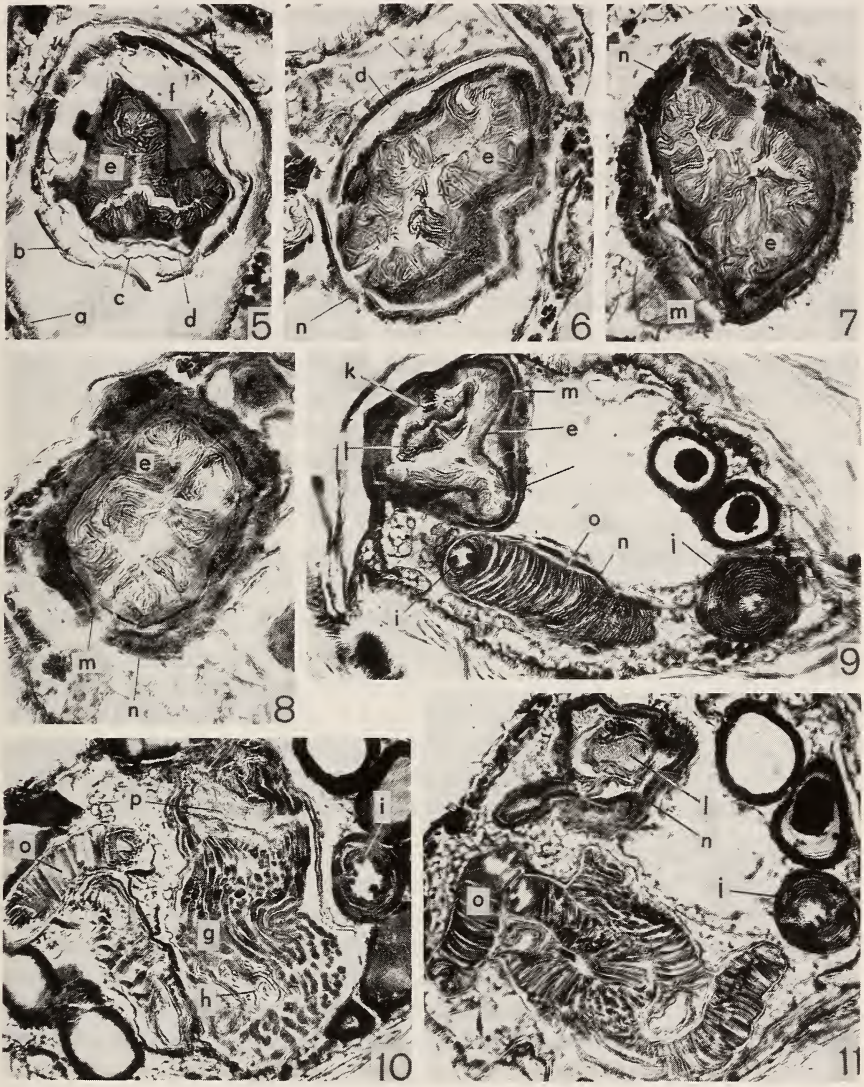
Fig. 1. Lateral view of intromittent organ and posterior parts of genital duct of *Coleophora lixella* Zeller ; a — phallotheca, b — distal opening of phallotheca, c — caulis, d — apex of pseudocoecum, e — border of fusion of walls of caulis, f — inner rib of caulis, g — wall of phallocrypt, h — endotheca, i — annulus, j — longitudinal sclerite of outer tube, k — aedeagus, l — outer tube, m — endophallus (vesica), n — secondary gonophore, o — cornuti, p — ductus ejaculatorius simplex, q — circular muscles, r — proximal part of ductus ejaculatorius simplex, s — sac of outer sheath, t — appendix, u — apical loop of appendix, v — proximal part of outer sheath, w — opening of outer sheath.

The *aedeagus* (Figs 1, 5, 6) is a thin-walled membranous tube originating at the anterior margin of the annulus (if that is present) and extending distally usually to beyond mid-length of the phallotheca. At the apex of aedeagus there is a slightly asymmetrical secondary gonophore. The distal portion of the aedeagus may slightly protrude as its wall is delicately plicate, at least in some species.



Figs 2-4. 2. Basal portion of phallus of *Coleophora lixella* Zeller, 3. Medio-proximal parts of outer sheath and ductus ejaculatorius of *Augasma aeratella* (Zeller), 4. The same, *C. spiraeella* Rebel. For abbreviations, see Fig. 1.

The *endophallus* (Figs 1, 5-9, 11) is an extremely long, densely plicate membranous tube. Inside the aedeagus there are long epidermal thickenings between the endophallus inside the aedeagus. The shape of the endophallus changes, as seen in the cross-sections (Figs 4-6). When the plication is completely extended, the length of the endophallus increases up to 7 times. In many species the cornuti are situated in the most proximal part of the endophallus. Anteriorly to them there is a weak constriction of the duct which I believe is the beginning of the endophallus.



Figs 5-11. Transverse sections: 5. At mid-length of phallotheca; 6. At base of aedeagus; 7. Near mid-length of outer tube; 8. Posterior to sac; 9. Just beyond sac; 10. Through sac; 11. Through end part of tube and appendix; a — wall of phallocrypt, b — phallotheca, c — endotheca, d — aedeagus, e — endophallus, f — anchorage of endophallus inside aedeagus, g — muscles of sac, h — tracheae, i — proximal, endodermal part of ductus ejaculatorius, j — circular muscles, k — cornuti, l — spermatophore, m — muscles of endophallus, n — outer sheath, o — transverse muscles, p — median part of ductus ejaculatorius.

Outer sheath. This term is used provisionally ; at least in coleophorid systematics it is useful. It concerns the entire ectodermal membranous structure anterior to the phallus. Anatomically it is most probably an apodemal structure formed by a complete fusion of extensions of the endothecal and aedeagal walls. In the literature I could not find any special term for this structure. Moreover, in almost all taxonomic papers the most posterior, tubular part of it is incorrectly named the ductus ejaculatorius. Callahan & Chapin (1960) and Callahan & Cascio (1963) call it a cuticular or outer tube of the ductus ejaculatorius simplex (in the Nearctic noctuid moth *Heliothis zea*) and Căpuşe (1971) calls it the "canal glandulaire" of the ductus ejaculatorius of Coleophoridae. In the latter family the outer sheath is much more complex than in other Lepidoptera examined and consists of several parts (Figs 1, 3, 4). The most posterior of these is a long, usually bent funnel called here the tube (outer tube of Callahan & Cascio). It runs medially, then dorsally in the abdomen, then more anteriorly bends downwards and distad from where the sheath broadens and coils in various ways. The inner curvature of the arch is usually strengthened by an elongate sclerite which terminates in the dorsal wall of a broadening of the sheath often developed in the form of a sac. The anterior part of the tube is more or less coiled, usually broad, especially in the most proximal portion, and terminates in a broad anterior opening. In several species a densely coiled appendix is found in the terminal portion, directed proximally, terminating in an apical loop. The shape of the tube changes to some degree, as seen in transverse sections (Figs 7-9, 11). Several tracheal branches enter through the proximal opening, some of them eventually penetrating the sac (Fig. 10).

The *ductus ejaculatorius* (Figs 1-11) is partially discussed under endophallus. Anteriorly to the endophallus, in a sac or broadening of the outer sheath, it is more or less distinctly folded and embraced by strong striated muscles (Fig. 10) ; subsequently it runs inside the coiled part or appendix, situated laterally in the latter and accompanied by several layers of transverse muscles. The proximal portion of the ductus ejaculatorius simplex is lined with a very thin intima and surrounded with strong, circular striated muscles (Figs 9-11).

Conclusions

As in some other lepidopterous families, the phallus of the Coleophoridae is of the so called phallotheca type, but differs from these other families in several characters. It is therefore considered to have evolved independently and may be treated as an autapomorphy, since this type

of phallus appears to be distributed throughout the family (over 100 species examined). The structure of the phallotheca is subject to strong variation within the family, being simple in more primitive species and specialised, with sharply differentiated sclerites, in more advanced species. However, it is suggested that the process of specialisation of the sclerites occurred independently in the coleophorids several times.

Further possible autapomorphies of the examined structures are as follows : presence of a tubular, membranous aedeagus ; complete atrophy of the coecum penis ; development of a false coecum penis ; structure of the caulis and median plate ; presence of a ring-shaped sclerite (annulus) ; very long tube of the outer sheath ; a very long densely plicate endophallus ; presence of a longitudinal sclerite of the tube ; development of a long, coiled appendix. Some of these characters are secondarily reduced in various species.

List of terms used in taxonomic papers

Aedeagus. Almost all authors use this term for the phallotheca or entire phallus.
Anellus. Căpuşe (anelius) called this the median sclerite and caulis ; Toll, the caulis.
Annulus. Ring-shaped sclerite in endotheca anterior to the phallus.
Appendix (of outer sheath). Coiled part of outer sheath.
Boulbe ejaculateur. Term used by Căpuşe for broadening of outer sheath called here 'sac of the outer sheath'.
Cornutus. Correctly termed in all papers.
Ductus ejaculatorius (excl. its distal part, the vesica). In Căpuşe's terminology it comprises the "canal-non-glandulaire", "boulbe ejaculateur" and "canal glandulaire", of which the first corresponds to the real ductus ejaculatorius simplex, the two others with the outer sheath.
Lamina ductus. Longitudinal sclerite of the tube of the outer sheath, applied by Căpuşe to the ductus ejaculatorius.
Outer sheath. Toll used the term vesica, Căpuşe the canal glandulaire (of ductus ejaculatorius).
Phallotheca. Căpuşe named it the aedeagus or penis, Toll the aedeagus.
Phallus. In Coleophoridae of the phallotheca type ; a complex consisting of the aedeagus, phallotheca and endotheca, as treated in this paper.
Sac (of outer sheath). Broadening of the outer sheath immediately beyond its tube. Căpuşe used his own term, boulbe ejaculateur (of ductus ejaculatorius), or scleriductus.

Vesica (endophallus). Toll applied this term to the distal part (tube) of the outer sheath ; Căpuşe (in part) named thus the membranous portions of the phallotheca.

Acknowledgements

I wish to express my thanks to Dr. J. Buszko, Toruń, Poland for providing some material for study, Dr. N. P. Kristensen, Copenhagen, Denmark for a fruitful discussion, Dr. E. Warchałowska, Kraków, Poland for the photomicrographs and to an anonymous referee for correcting the English text.

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