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Revision of Byrsophlebidae (Turbellaria Typhloplanoida)

Tor G. Karling

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The systematics of the family Byrsophlebidae is revised on the basis of supplementary and correcting remarks on the structure of some Byrsophlebidae, especially *Byrsophlebs graffi* Jensen and *Maehrenthalia agilis* von Graff. The genera *Byrsophlebs* Jensen, *Maehrenthalia* von Graff, *Maehrenthaliella* gen. n. and *Parabyrsophlebs* gen. n. are diagnosed. Functional and terminological remarks are made on the structure of the genital organs in the Turbellaria with special reference to Byrsophlebidae. *Maehrenthalia agilis* is new for the Pacific Ocean.

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1. Introduction

The family Byrsophlebidae von Graff, 1882, was originally (as subfamily Byrsophlebina) based on the genus *Byrsophlebs* Jensen, 1878, with *B. graffi* Jensen and *B. intermedia* von Graff, 1882, as the only species (von Graff 1882:275-276). *B. intermedia* von Graff, together with *Mesostomum agile* Levinsen, 1879 ("*Promesostoma? agile*", von Graff 1882:274), was transferred by von Graff (1905:97) to the new genus *Maehrenthalia. Typhlorhynchus* Laidlaw, included by von Graff in Byrsophlebidae, belongs to Schizorhynchidae (Karling 1981). Ax (1959:107) has eliminated *Byrsophlebs geniculata* Beklemishev from the genus *Byrsophlebs.*

This systematic revision on genus level of the family Byrsoplebidae is based on specimens in the collections of the Section of Invertebrate Zoology in the Museum of Natural History, Stockholm (SMNHI), and the basic specimens used by Luther in his classic study of *Maehrenthalia* von Graff (1936). The study of the imperfectly known and in part erroneously described species *Byrsophlebs graffi* and *Maehrenthalia agilis* is stressed. The former is known from observations of live material only (Jensen 1878:33-36; von Graff 1882:275-276). The available material is insufficient for both a phylogenetic analysis and an identification key. The lack of good whole mounts is particularly unfortunate.

2. List of species, with notes on distribution, material and main references

Byrsophlebs graffi Jensen, 1878. Figs. 3, 5-7, 23, 31-32.

European Arctic and Atlantic phytal zone. Material in SMNHI from Isle of Man, Trondheim and Skagerak (leg. Einar Westblad). New locality: USA, Mass., Nahant, East Point, Canoe Beach, tidal zone, stones, gravel and algae [July 1972, leg. Karling (TGK)]. Several sectioned and whole mounted specimens. Observations of live specimens by Westblad and TGK. — Jensen 1878:34-36; Gamble 1893:455-456; von Graff 1913:173-174, with references.

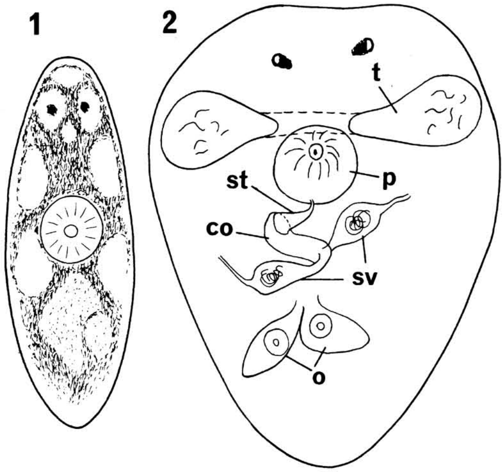
Maehrenthalia agilis (Levinsen, 1879). Figs. 1-2, 4, 8-16, 28, 33-34.

Mesostomum agile Levinsen, 1879
Promesostoma? agile (Levinsen), von Graff 1882
Maehrenthalia agilis (Levinsen), von Graff 1905

Greenland, European Arctic and Atlantic eulittoral zone. New locality: USA, California, Tomales Bay, tidal zone in *Ulva* and *Zostera* and in pools on mudflats (August 1960, leg. TGK). Several sectioned and whole mounted specimens (leg. Luther and TGK). Observations of live material by Westblad (North Sea area) and TGK (California). — Levinsen 1879:174-175; Gamble 1893:454-455; von Graff 1905:97-99, 1913:170-172, with references; Luther 1936.

Maehrenthaliella intermedia (von Graff, 1882) comb. n. Figs. 17-20, 29.

Byrsophlebs intermedia von Graff, 1882
Maehrenthalia intermedia (von Graff), von Graff 1905



Figs. 1-2. *Maehrenthalia agilis* (California). — 1. live specimen; 2. squeezed live specimen. — Free-hand drawings.

European N. Atlantic, phytal zone. Several sectioned and whole mounted specimens (leg. Westblad and Luther). Observations of live specimens by Westblad and TGK. — von Graff 1882:276, 1913:172-173; Luther 1936.

Parabyrsophlebs coeca (Luther, 1948) comb. n. Figs. 21-22.

Maehrenthalia coeca Luther, 1948
Skagerak, Gullmaren, sublittoral. Four sectioned specimens (Westblad), observations of live material by Westblad and TGK. — Luther 1948:112-117.

Byrsophlebs lutheri (Marcus, 1952) comb. n. Fig. 27.

Maehrenthalia lutheri Marcus, 1952
Brazil, phytal zone. Six slides with serial sections. — Marcus 1952:38-41.

The specimens of the following species (serial sections) are deposited in the II. Zoological Institution, University of Göttingen, FRG:

Byrsophlebs delamarei (Ax, 1956) comb. n. Fig. 24.

Maehrenthalia delamarei Ax, 1956
Mediterranean Sea, sandy shores. — Ax 1956:128-136.

Byrsophlebs simplex (Ax, 1959) comb. n.

Maehrenthalia simplex Ax, 1959
Sea of Marmara, Bosporus, shore pools, sand. — Ax 1959:108-110.

Byrsophlebs uncinata (Ax, 1959) comb. n. Fig. 25.

Maehrenthalia uncinata Ax, 1959
Sea of Marmara, sandy shores. — Ax 1959:110-112.

Byrsophlebs caligulachaena (Ehlers & Ehlers, 1981) comb. n. Fig. 26.

Maehrenthalia caligulachaena Ehlers & Ehlers, 1981
Galapagos Islands, rock pools. — Ehlers & Ehlers 1981: 6-11.

The following species are known from live specimens only:

Byrsophlebs dubia (Ax, 1956) comb. n. Fig. 30.

Maehrenthalia dubia Ax, 1956
Mediterranean Sea, sandy shores. North Sea area, Baltic Sea, phytal zone, salt marsh. Observations of live specimens by TGK. — Ax 1956:136-139; Luther 1962:38-39; Den Hartog 1966:127.

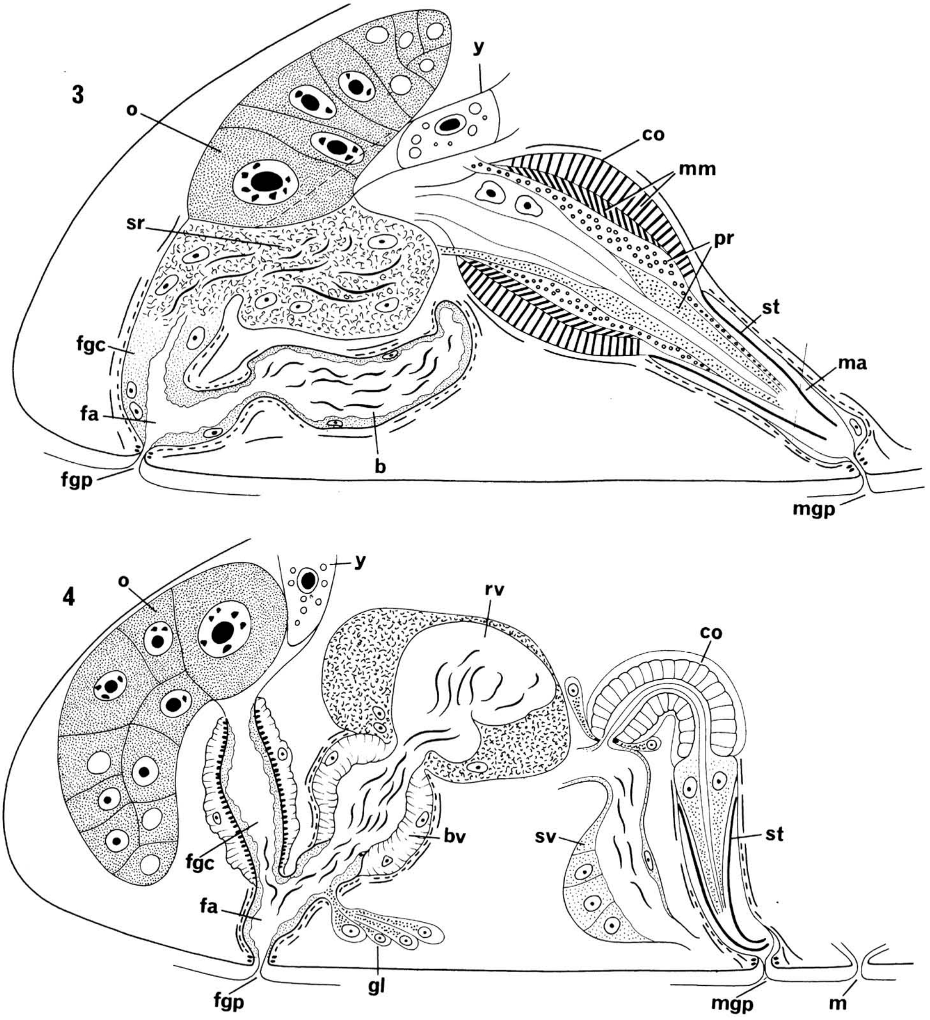
"*Maehrenthalia* spec." Ax, 1959

Bosporus, phytal zone, one live specimen. — Ax 1959: 112-113.

3. Structure of the genital apparatus

The byrsophlebids are small, plump, 0.4-1 mm long, free swimming turbellarians, anteriorly rounded or square, posteriorly bluntly pointed, colourless or brownish with paired pigmented eyes (Fig. 1), which are absent in *Parabyrsophlebs coeca* only (Luther 1948:113). In *Byrsophlebs caligulachaena* the pharynx cavity is entirely ciliated (Ehlers & Ehlers 1981:6). Otherwise, apart from the genital apparatus there are no distinct structural differences between the byrsophlebid taxa.

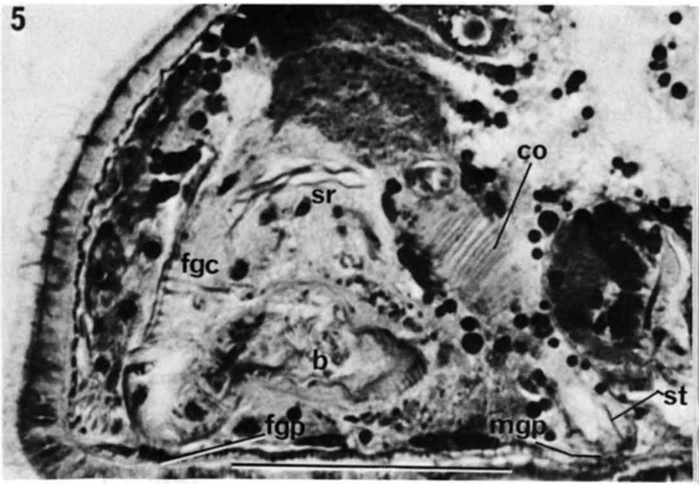
In *Parabyrsophlebs coeca* the genital pores are situated at some distance from the mouth, the female pore close behind the male one. In all other byrsophlebids the male pore lies close behind the mouth and the female one near the rear end.

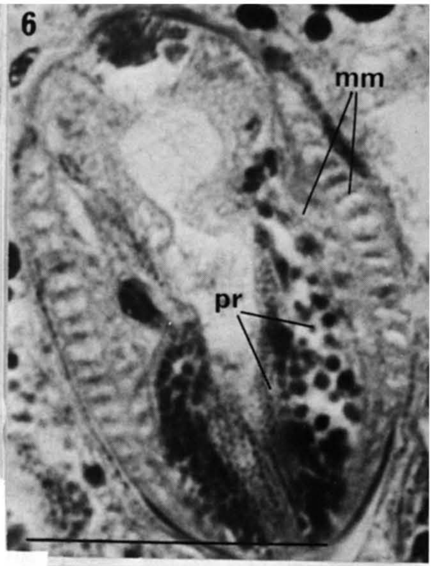


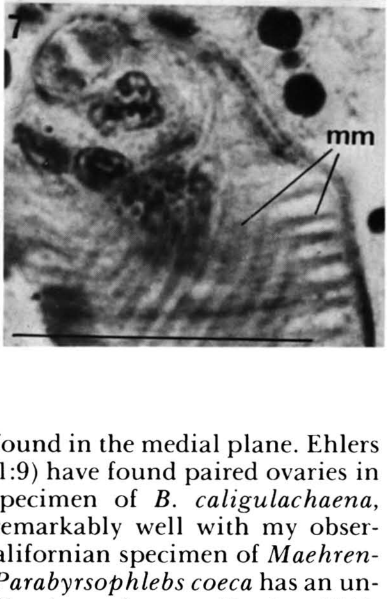
Figs. 3-4. Semidiagrammatic right side views of the genital apparatus. — 3. *Byrsophlebs graffi*; 4. *Maehrenthalia agilis* (California). — Free-hand drawings.

The paired testes are located laterally beside or in front of the pharynx. In *Maehrenthalia agilis* they are united by an anterior bridge (Figs. 2, 8) and the paired seminal vesicles are highly characteristic, globular with intracapsular glands (Figs. 4, 12, 16; Luther 1936:12).

The copulatory bulb in the *Byrsophlebs* species is globular to oviform with two layers of strong crossing spiral fibres (Figs. 3, 6, 7). A single layer is shown in a drawing of *B. lutheri* (Marcus 1952: fig. 60). In sectioned material its position is more or less vertical with an axially joined cuticular stylet. In *Maehrenthalia agilis* (Fig. 4, 10) and *Maehrenthaliella intermedia* (Fig. 20) the bulb is cylindrical, in preserved material more or less curved, covered by a layer of strong spiral fibres upon which there is a thin layer of crossing spiral fibres in the latter species. Fixation artefacts in the available sections make it difficult to verify the complicated picture given by Luther (1936:13-14) of the muscular wall of the bulb in *M. intermedia*. *Parabyrsophlebs coeca* has a small globular, weakly muscular copulatory bulb (Luther 1948: fig. 164). In all Byrsophlebidae the copu-







Figs. 5-7. *Byrsophlebs graffi*. — 5. Postpharyngeal body part, sagittal section; 6-7. male copulatory bulb, longitudinal sections. — Scale line 50 µm in Fig. 5, 20 µm in Figs. 6-7.

latory organ ends in a tubular or funnel-shaped cuticular stylet (see section 5).

The paired dorsolateral yolk glands can anastomose dorsally, sometimes appearing to be reticular in full female maturity (Luther 1936:16). The unpaired ovary in *Maehrenthaliella intermedia* is situated laterally, beside or behind the pharynx (Fig. 17) with the mature ovocytes dorsomedially as described by Luther (1936:15). Von Graff (1882:276) has seen a rudimentary ovary on the other side of the body. Owing to controversial information the condition of the ovary in *Maehrenthalia agilis* cannot definitely be established. Gamble (1893:454) and von Graff (1905:98) describe paired ovaries in that species, though with very different shapes and positions. Luther (1936:15) on the other hand describes an unpaired ovary situated mainly in the right body half. A drawing from life by Westblad (Port Erin) shows an unpaired ovary laterally behind the copulatory organ and the situation is the same in the three sectioned specimens from Norway. In all my sectioned specimens from California the unpaired, approximately globular ovary is located in the rear of the body but a (subadult?) specimen drawn from life demonstrates paired ovaries in a more anterior position (Fig. 2).

The *Byrsophlebs* species have an unpaired ovary located dorsally in the caudal body part, in sectioned (more or less contracted) specimens mostly found in the medial plane. Ehlers & Ehlers (1981:9) have found paired ovaries in a subadult specimen of *B. caligulachaena*, conforming remarkably well with my observation of a Californian specimen of *Maehrenthalia agilis*. *Parabyrsophlebs coeca* has an unpaired caudally situated ovary (Luther 1948: 116).

The provisional conclusion regarding the ovary in Byrsophlebidae is that in female maturity there is as a rule one ovary, situated caudally, and further that paired ovaries are the basic (plesiomorph) condition in the family. Luther (1936:15) also regards paired ovaries as the original condition, but it is not quite clear whether he refers to the Byrsophlebidae only or to a wider range of species.

The ovary (ovaries?) opens through a short oviduct in the proximal end of the female genital canal or in its derivative, the seminal

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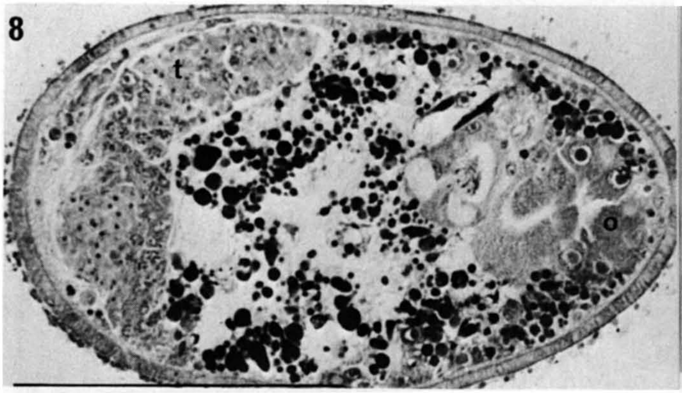

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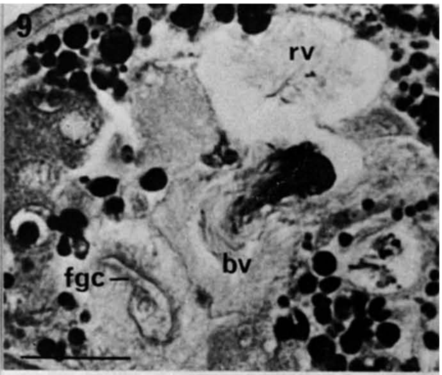

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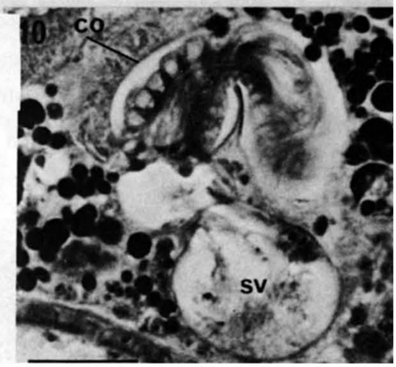


Figs. 8-10. *Maehrenthalia agilis* (California). — 8. Semi-horizontal section; 9. bursa organ and female genital canal, sagittal section; 10. proximal part of male copulatory organ, sagittal section. — Scale line = 100 μm in Fig. 8, 20 μm in Figs. 9-10.

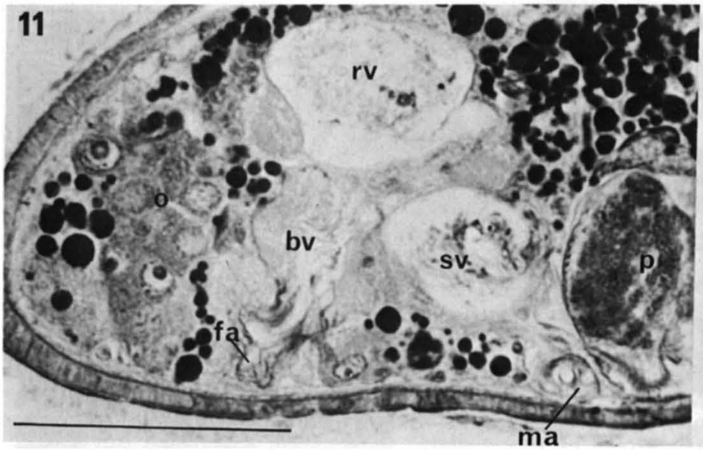
receptacle (see below). According to some records the yolk glands open separately in the female canal (Luther 1936:18, fig. 12b; Ax 1959:110), but the vitelloducts are usually missed, the most distal yolk cells being found close beside the mature ovocytes (Figs. 3-4).

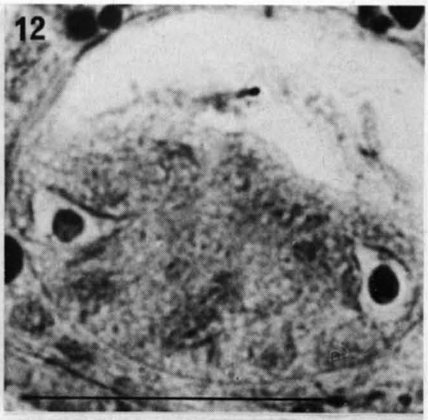
The female genital canal is a dorsal prolongation of the female antrum but otherwise there are remarkable differences between the genera in the structure of the female atrial organs. These organs are first described in *Byrsophlebs graffi* and *Maehrenthalia agilis*.

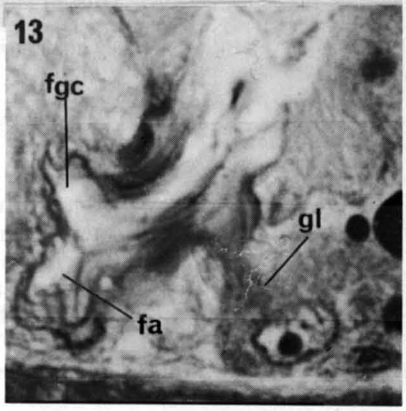
The wall of the female canal in *B. graffi* consists of a nucleated epithelium based on a thin basement membrane, covered with internal circular and external longitudinal muscle fibres. A seminal receptacle opens anteriorly in its proximal part, in the immature condition a swelling of the canal wall only. The female antrum is anteriorly provided with a bursa with the same histology as the female genital canal. Its distal enlarged part often contains alien sperm and its proximal tip was found to be constricted with strengthened basement membrane and muscle mantle (Figs. 3, 5). Contrary to the assumption by Jensen (1878:35; German translation in Luther 1936:23) there is no insemination canal (ductus spermaticus).

In *Maehrenthalia agilis* the female genital canal in the mature condition is sac-like with a strong pseudocuticular internal lining with epithelial residues, covered with circular muscle fibres (no longitudinal fibres) and a thick cellular mantle (depressed epithelium, myoblasts?). It is often found filled with sperm, but it lacks a seminal receptacle (Figs. 4, 9, 14, 15). There are secretory cells beside the canal, but their mode of discharge is uncertain.

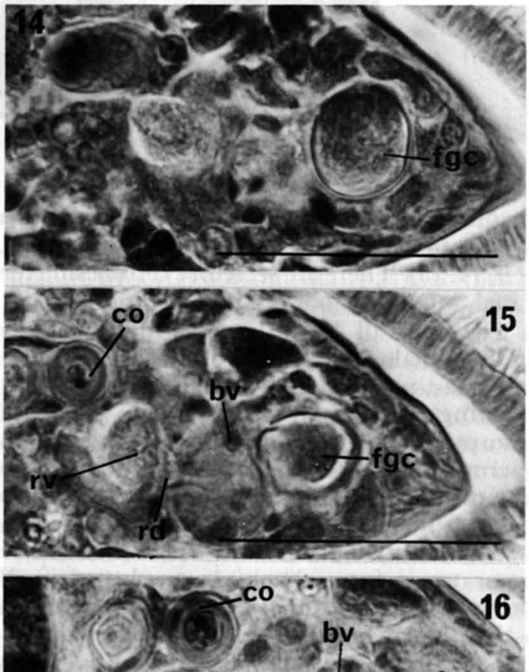
The bursa of *M. agilis*, opening anteriorly in the female antrum, consists of a distal globular sac, provisionally called bursa ventricle, opening via a resorptive duct into a typical resorptive vesicle, originally solid, later with sperm-containing vacuoles flowing together to a central cavity. The antral mouth of the bursa has a thin non-nucleated epithelium on a strong basement membrane, which proximally separates it from the high, nucleated, well preserved epithelium of the bursa ventricle on a thin basement membrane covered with internal circular and external longitudinal fibres (Figs. 4, 9, 11, 13, 15, 16). The resorptive vesicle is a derivative of the bursa, a terminal vesicle (see Karling 1963:228, 1980:264). The bursa mouth receives secretion from a ventral bundle of glands (Figs. 4, 13). Luther (1936:21) describes glands opening on both sides of the bursa ventricle ("an der Grenze zwischen Genitalgang und Receptaculum seminis" and "an der Grenze zwischen Bursa copulatrix und Genital-







Figs. 11-13. *Maehrenthalia agilis* (California). — 11. Postpharyngeal body part, sagittal section; 12. cross-section of seminal vesicle; 13. female genital antrum, sagittal secion. — Scale line = 50 µm in Fig. 11, 20 µm in Figs. 12-13.

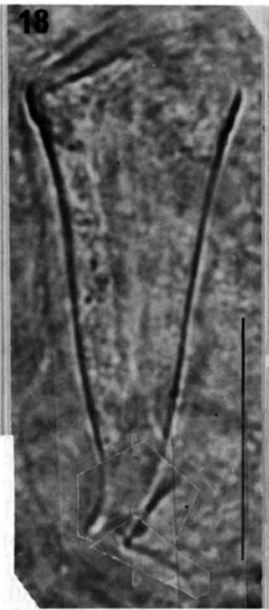


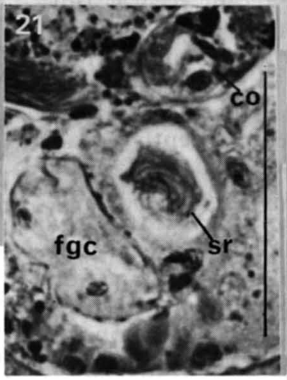
Figs. 14-16. *Maehrenthalia agilis* (North Sea). Horizontal sections of genital organs, 14. most dorsal, 16. most ventral. — Scale lines = 50 µm.

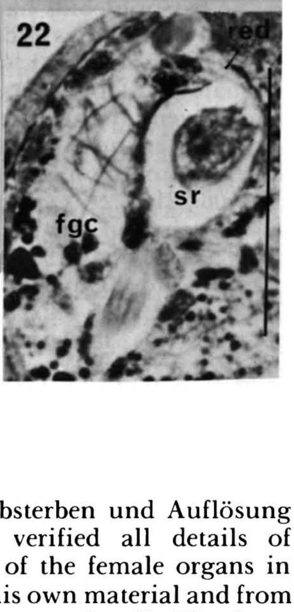
gang"). Sperm is found in both parts of the bursa organ. The origin and the function of the bursa ventricle is discussed in section 4.

Having missed the communication between the female gonads and the atrial organs, Luther (1936:21-22) interpreted the latter erroneously. He correctly describes the structure of the bipartite bursa but interprets this organ as the female genital canal with a proximally associated seminal receptacle, supposing that the female gonoducts open "am Übergang des Receptaculum in den weiblichen Genitalgang". This error led him to interpret the distal part of the femal canal as the copulatory bursa, not observing its proximal continuation.

The female atrial organs in all *Byrsophlebs* species sufficiently studied from sectioned material have the same principal construction as in *B. graffi*, with no insemination canal and with seminal receptacle and bursa located accordingly, but the state of differentiation of







Figs. 17-22. — 17-20. *Maehrenthaliella intermedia*. — 17. Dorsal view of whole mounted specimen; 18. cuticular stylet from whole mounted specimen; 19. female genital canal, sagittal section (cf. Luther 1936: fig. 9); 20. male copulatory bulb. — 21-22. *Parabyrsophlebs coeca*, semi-horizontal sections through rear body. — Scale line = 100 µm in Fig. 17, 20 µm in Fig. 18, 50 µm in Figs. 19-22.

the latter two structures varies.

According to Luther's (1936:18-20) detailed decription of the female genital apparatus in *Maehrenthaliella intermedia* the female genital pore opens through a short bulbiform tube, closed at both ends by a sphincter, into a wide female antrum expansible by dilator fibres, some of which give rise to a narrow dorsorostral pocket with doubtful function. Sperm was not found in the pocket, which, unlike the *Byrsophlebs* bursa, lacks circular muscles. The main part of the female genital canal (Luther's "*pars angustior*") has a pseudocuticular internal wall ("eine offenbar etwas festere Schicht"; Fig. 19). The proximal part of the canal (Luther's "*pars bulbosa*") is a thick-walled muscular sac opening anteriorly into a variable seminal receptacle, into the stalk of which the ovary and the yolk glands open. Sperm was found in the *pars bulbosa* and in the seminal receptacle, in a state of resorption in the latter ("im Absterben und Auflösung begriffen"). I have verified all details of Luther's description of the female organs in *M. intermedia* from his own material and from Westblad's sections (see section 2). The function of the different structures will be considered in section 4. Owing to the lack of a *Byrsophlebs* (antral) bursa and a distinct histological separation of female genital canal and antrum (see Luther 1936: fig. 11), the definition of the latter structure is controversial. I prefer to regard the well defined bulb as the female antrum (Fig. 19).

In *Parabyrsophlebs coeca* the oviduct opens into the seminal receptacle, connected with the female genital canal via a short receptacle duct. The canal is weakly differentiated with a high nucleated epithelium externally covered with a network of muscle fibres. It lacks an internal pseudocuticular lining (Figs. 21, 22). Furthermore, there is no antral bursa.

4. Remarks on function and terminology

In the old turbellarian literature written in German, a rather stable anatomical terminology was established based on Greek and Latin. This terminology is more or less anglicized in the English literature. In that respect I have followed Hyman (1951), with some exceptions. Divergences in the naming of structures according to topography, origin or function can be ocercome by further research only. These terminological issues are of current interest because of some recent records (my own and others) and are briefly clarified below. My remarks apply to the turbellarians only.

The byrsophlebids have separate male and female genital pores and consequently a male and a female antrum. Elsewhere a male atrium (or male genital canal) and a female atrium (female genital canal) are associated with a common atrium, which opens externally through a common genital pore (see von Graff 1904-08:2216-2217). There is no reason to replace "common atrium" with "common antrum" (see Hyman 1951:119).

The word "Chitingebilde" used by von Graff (e.g. 1904-08:2221) and his contemporaries was later replaced by "cuticular structures" (in German: kutikulare Gebilde, e.g. Bresslau 1933:121-122) also used by me in several papers. The terms "chitin" and "cuticula" have been used by light-microscopists in the meaning "hard", with no specification of origin or chemistry. I have described hard structures in the male copulatory organ and in the kalyptorhynchian proboscis as cuticular, a practical term, notwithstanding the various origins of these structures, established by electron-microscopists (Westheide 1978:116 with references).

The male copulatory organ in the byrsophlebids is armed with a cuticular stylet. The word "stylet" has been the accepted term for a cuticular tube or canal for the discharge of sperm and secretions though it is mostly far from stylet-shaped (e.g. Meixner 1938:53; Karling 1956:204-206). I regard it as unsatisfactory to enlarge the term stylet to include cuticular needles, hooks etc. (Hyman 1951:115; Tajika 1982:36). In that case the general term "cuticular apparatus" appears to be more correct.

In the female genital apparatus, copulatory bursa, vagina and adjacent structures are often lined with a strong, elastic membrane, stainable like muscle fibres (iron haematoxylin, eosin), in contrast to the mostly unstained "cuticular" structures. Reisinger (1924:268) gives such a membrane the name "pseudocuticula" and regards it as a product of the cell bases on the basement membrane ("von den Zellbasen gebildete Schicht"). I have modified the term pseudocuticle to apply to a strengthened basement membrane. Electron-microscopists have stated that hooks and similar structures can be derivatives of the basement membrane as well as elaborations of epithelial microvilli or cell plasma (Rieger & Doe 1975:25-32, Doe 1976:105-115, 1977:970). As far as I know the origin of the basement is not yet established in the Turbellaria, but the close connection of the basement membrane with muscle strata is the same as in "structureless" membranes of muscular septa in pharynx, proboscis, copulatory organs, etc., indicating a mesenchymatous origin (Karling 1940:139-141, 1961:272-274, 1980:262).

The existence of a pseudocuticle is an important criterion for the understanding of the function of the female atrial organs. The interpretation of the anterior diverticulum of the female antrum in *Byrsophlebs* and *Maehrenthalia* as copulatory bursa originates from Jensen's (1978:35) description of *B. graffi*, accepted by von Graff and subsequent authors. In the byrsoplebids without this diverticulum (*Maehrenthaliella intermedia, Parabyrsophlebs coeca*), the female genital canal appears to be the functional copulatory bursa, evidently an ancestral function, but, even in some *Byrsophlebs* species with a rather weakly differentiated antral diverticulum, this function of the female canal is possible (Ehlers & Ehlers 1981:9-10). The copulatory function of a part of the female canal is demonstrated by the differentiation of a pseudocuticle in both *M. intermedia* and *Maehrenthalia agilis.*

The term seminal receptacle (receptaculum seminis) is used for various weakly muscular receptors of alien sperm. Their function is material have the same principal construction fecundation of the ovocytes and resorption of excess sperm. In most byrsophlebids the proximal part of the female genital canal (e.g. the *pars bulbosa* in *Maehrenthaliella intermedia*) appears to be the original seminal receptacle, its anterior wall giving rise to a specialized seminal receptacle, obviously mainly with a resorptive function, a conclusion drawn from Luther's observation on *M. intermedia* (see above) and from figures showing inclusion of sperm in vacuoles of the receptacle tissue (e.g. Ax 1959: figs. 94, 97). In *Byrsophlebs delamarei* the receptacle is separated from the female canal by a strong sphincter (Ax 1956: fig. 33G), thus deserving the name resorptive vesicle (vesicula resorbiens, e.g. Meixner 1938:68), complying with the histogenetically different (analogous) bursa vesicle in *Maehrenthalia agilis*. These facts constitute further evidence against the formerly much debated "bursa intestinalis theory" (see Meixner 1938: 65-68, Hyman 1951:125, Karling 1958:566).

The highly differentiated antral bursa in *M. agilis* can be interpreted as a further step in the evolution of an antral bursa from the anterior wall of the female antrum. This idea implies that the copulatory function of the female canal is secondary in this species. Another evolutionary alternative could be that the main part of the bursa (bursa ventricle and resorptive vesicle) is an *ad hoc* structure (mesenchymatous?), the bursa mouth only an antral derivative like the "copulatory bursa" in *Byrsophlebs*. The distinct histological separation of bursa ventricle and bursa mouth by a basement membrane (Fig. 4) resembles the separation of uterus vesicle and uterus stalk in *Halammovortex nigrifrons* (Karling), family Dalyelliidae. Complying with my interpretation of the bursa mouth in *M. agilis*, the bursa stalk in *H. nigrifrons* has been interpreted as an atrial derivative (Karling 1943:13, fig. 12).

The bursa ventricle in *M. agilis* can be compared with the uterus in *Halammovortex*, even with regard to its function. The two vesicles have a similar wall with high nucleated epithelium and the glands opening in the bursa mouth of the former are apparently analogous with the cement glands ("Kittdrüsen") of the latter. In *Halammovortex* the function of the uterus is proved. Considering that the female genital canal appears to be the functional copulatory bursa, the function of the bursa ventricle as a uterus in *M. agilis* can be postulated. The associated resorptive ventricle does not contradict this corollary — in *Halammovortex*, too, a resorptive vesicle is associated with the uterus, though the discharge of the female cells is different in the two species.

The definite solution of the issue concerning the function of the bursa ventricle in *M. agilis* can be achieved by observations of sectioned ovigerous specimens only. As far as I know, egg formation is unknown in Byrsophlebidae. The peudocuticular internal wall of the antral diverticulum in *Byrsophlebs* species (Ax 1956:125, 1959:110, 112) indicates its function as a copulatory bursa, but the position and shape of the pocket is the same as in the uterus of many other Typhloplanoida (e.g. Ax 1956: fig. 35D; Ehlers 1972). Considering our unsatisfactory knowledge of the function of the diverticulum I have provisionally described it with the neutral term bursa.

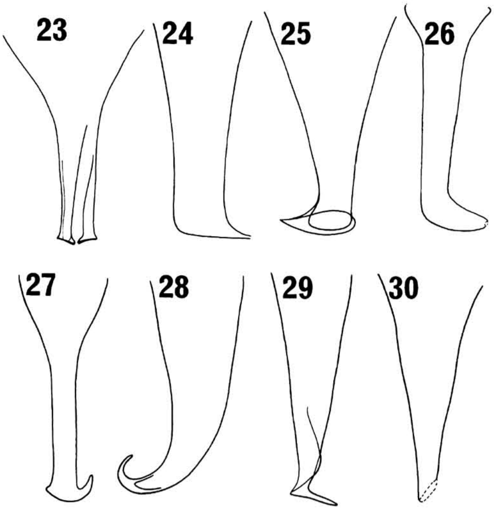
In *Maehrenthaliella intermedia*, the expansible female antrum (according to Luther's terminology) probably functions as uterus.

5. Systematics

The genus *Maehrenthalia* was diagnosed by von Graff (1905:96-97) as Byrsophlebidae with reticular vitellaries, two ovaries and no insemination canal (ductus spermaticus) as opposed to *Byrsophlebs* with two separate vitellaries, one ovary and an insemination canal. The separation of the two genera subsisted in spite of doubt as to the existence of an insemination canal in *B. graffi*, the main distinguishing diagnostic feature between the genera (Luther 1936:23, Marcus 1952:41, Ax 1959:107).

No insemination canal exists in *B. graffi*, nor in any other byrsophlebids. It has further been shown that the other diagnostic features of *Byrsophlebs* and *Maehrenthalia* are untenable. Consequently the latter genus name appears to be a junior synonym of the former. However, for other reasons *Maehrenthalia* must be considered valid, its type species *M. agilis* representing a separate evolutionary line with the synapomorphies (autapomorphies) of bulbous seminal vesicles with intracapsular glands and a bursa consisting of uterus (?) and terminal resorptive vesicle.

The genus *Byrsophlebs* is a homogeneous taxon, enclosing not only *B. graffi* but also most *Maehrenthalia* species (see below). The stylet of *B. graffi* is 36 μm (a squeezed live specimen) to about 46 μm long (a whole mounted specimen from Nahant). In agreement with the records of Jensen (1878:35, figs. II:10, 11) and von Graff (1882:275, fig. VIII:18) I have found the distal end of the stylet square with slightly thickened border and provided with a slit in the wall running obliquely proximad (Figs. 23, 31, 32). Jensen found the tip of the stylet armed with a tooth, but I have not seen



Figs. 23-30. Male cuticular stylets. — 23. *Byrsophlebs graffi*, original from a whole mounted specimen (cf. Figs. 31-32); 24. *B. delamarei*, after Ax 1956: fig. 33C; 25. *B. uncinata*, after Ax 1959: fig. 96; 26. *B. caligulachaena*, after Ehlers & Ehlers 1981: fig. 1C; 27. *B. lutheri*, after Marcus 1952: fig. 60; 28. *Maehrenthalia agilis* (California), original from live and whole mounted specimens (cf. Fig. 33); 29. *Maehrenthaliella intermedia*, original from a whole mounted specimen (cf. Fig. 18); 30. *Byrsophlebs dubia*, after Ax 1956: fig. 34C. — Length of stylets, see the text.

anything like that in my whole mounted specimens.

B. graffi, B. uncinata and "*Maehrenthalia* sp." Ax, 1959 constitute a group of closely related species with globular copulatory bulb and funnel-shaped stylet with square tip. *B. lutheri* can be placed in the same group, but the tip of the stylet appears to be more complicated (Figs. 25, 27; Marcus 1952: fig. 60 is drawn from a section and thus somewhat dubious). The stylet is 40-43 μm long in *B. uncinata*, 42 μm in "*Maehrenthalia* sp.".

In *B. delamarei, B. simplex* and *B. caligulachaena* the tip of the stylet is shoe-shaped with a narrow pore (Figs. 24, 26). The first two species mentioned have been taxonomically differentiated by the slightly different shape of the proximal part as well as the length of the stylet (35-40 versus 27-28 μm, Ax 1959:108-110), questionable diagnostic features in my opinion.

Provisionally *Maehrenthalia dubia* Ax, 1956, can be transferred to *Byrsophlebs* because of the construction of the copulatory bulb, but its internal anatomy is unknown. Its stylet is distally obliquely cut off (Fig. 30; Ax 1956: 138-139: 45-49 μm; Luther 1962:39: 54 μm).

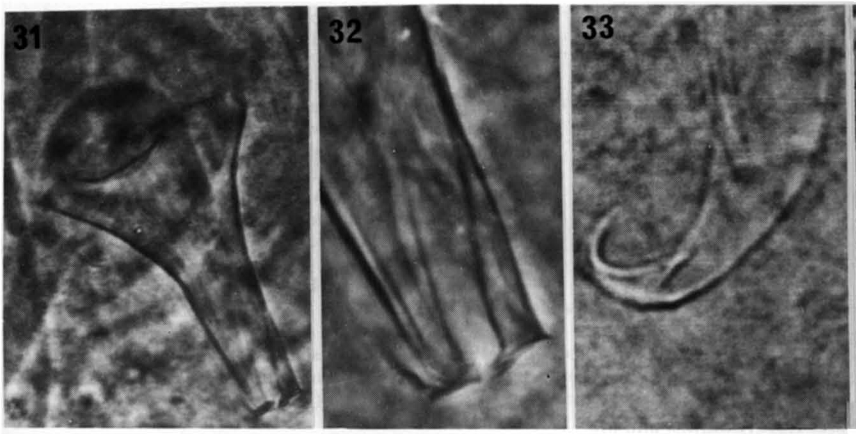
In agreement with von Graff (1905:99, t. III, figs. 5, 7) and Luther (1936:12, figs. 6, 8) I have found the stylet in the available European material of *Maehrenthalia agilis* tubiform (Luther: "ein dünnes langes Rohr"), 53 μm long (a whole mount). In the Pacific form it is a funnel with a wide base, 55-65 μm long, resembling the drawings by Levinsen (1879: fig. 5) and Gamble (1893: fig. 14). Levinsen compares the curved tip of the stylet with the horn of the chamois, and I have found it thus in whole mounted specimens from the Pacific (Figs. 28, 33) and the European Atlantic (Fig. 34), but one of my drawings from the Pacific and all previously published figures of *M. agilis* show a stylet with less curved tip.

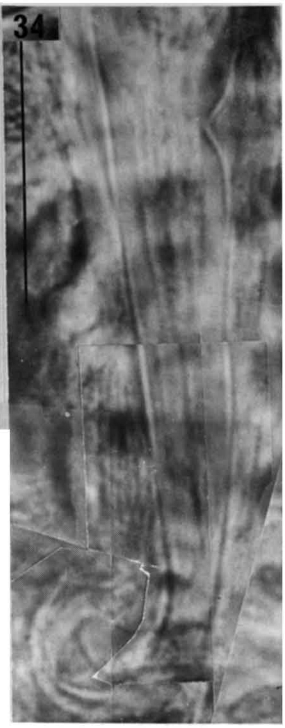
I consider *Maehrenthaliella* with the type species *M. intermedia* and *Parabyrsophlebs* with the type species *P. coeca* to be separate evolutionary lines. Both of these genera lack an antral bursa, evidently a plesiomorph feature coordinated with the function of the female genital canal as copulatory bursa.

Synapomorphies in *Maehrenthaliella* are the construction of the male copulatory bulb and the female genital canal (see diagnoses). The male stylet in *M. intermedia* is somewhat more complicated than in the *Byrsophlebs* species, distally winged (groove-shaped?) with a spur, 32.μm long (two whole mounts; Figs. 18, 29; cf. von Graff 1882: pl. VII, 17; Luther 1936: fig. 10e).

Provisionally I regard the position of the genital pores (see diagnoses) as the main synapomorphy of *Parabyrsophlebs*, but another conclusion could be drawn from Luther's opinion that the proximity of the two genital pores is a connecting feature between the Byrsophlebidae and related raxa with a common genital pore (1948:117). I interpret the weakly differentiated copulatory bulb and female genital canal (like the lack of an antral bursa) as plesiomorphies. Furthermore, the lack of pigmented eyes and the sublittoral occurrence of the type species *P. coeca* indicate a separate phylogeny (the other byrsophlebids are littoral). The stylet in *P. coeca* is straight, regularly tapering, about 55 μm long with no special distal structures (own records). It is slightly curved in Luther's figures (1948: figs. 163, 164).

The nomination of the new monotypical





Figs. 31–34. Cuticular stylets. — 31. *Byrsophlebs graffi* (Massachusetts), whole mount; 32. the same, tip of the stylet; 33. *Maehrenthalia agilis* (California), tip of the stylet, whole mount; 34. *M. agilis* (North Sea), whole mount. — Scale line = 20 μm in Figs. 31, 33 and 34, 10 μm in Fig. 32.

genera *Maehrenthaliella* and *Parabyrsophlebs*, both of them hitherto *Maehrenthalia*, is a consequence of the incompatibility of the type species *Maehrenthaliella intermedia* and *P. coeca* with the new structural and taxonomic conception of the type species *Maehrenthalia agilis*. For *P. coeca* a new genus is the only alternative. Returning *M. intermedia* to *Byrsophlebs* (see secion 2) would split this homogeneous genus.

6. Diagnoses

Family **Byrsophlebidae** von Graff, 1882

Typhloplanoida with separate genital pores, the male pore in front of the female one. Testes and yolk glands paired, ovary unpaired (occasionally paired). Male copulatory organ with tubular or funnel-shaped stylet. Female genital system with no separate insemination apparatus (ductus spermaticus), with seminal receptacle (excl. *Maehrenthalia*) and bursa (excl. *Parabyrsophlebs* and *Maehrenthaliella*, sometimes weakly differentiated). — Type genus *Byrsophlebs* Jensen, 1878.

Genus ***Byrsophlebs*** Jensen, 1878

Male genital pore close behind the mouth, female pore near the rear end. Male copulatory bulb globular-oviform with two layers of strong crossing spiral fibres. Ovary in the rear of the body. Female genital canal with seminal receptacle. Bursa without terminal resorptive vesicle, sometimes weakly differentiated. — Type species *B. graffi* Jensen, 1878. Other species, see section 2.

Genus ***Maehrenthalia*** von Graff, 1905

Genital pores as in *Byrsophlebs*. Male copulatory bulb cylindrical with a single layer of strong spiral muscle fibres. Ovary as in *Byrsophlebs*. Female genital canal without seminal receptacle. Bursa bipartite, consisting of uterus (?) and terminal resorptive vesicle. —Type (and only) species *M. agilis* (Levinsen, 1879).

Genus ***Maehrenthaliella*** gen. n.

Genital pores as in *Byrsophlebs*. Male copulatory bulb cylindrical with two layers of crossing spiral muscle fibres, the internal ones strong, the external ones weak. Ovary lateral, beside or behind the pharynx. Female genital canal with narrow medial (copulatory) part and wide distal (uterus?) and proximal parts. With seminal receptacle, without bursa. — Type (and only) species *M. intermedia* (von Graff, 1882).

Genus ***Parabyrsophlebs*** gen. n.

Genital pores removed from the mouth, the female pore close behind the male one. Male copulatory bulb small, weakly muscular. Ovary as in *Byrsophlebs*. Female genital canal (weakly differentiated) with seminal receptacle. Female antrum without bursa. (Pigmented eyes lacking). — Type (and only) species *P. coeca* (Luther, 1948).

Abbreviations in the figures

b	bursa	*o*	ovary
bv	bursa ventricle	*p*	pharynx
co	male copulatory organ	*pr*	prostatic secretion
fa	female antrum	*rd*	resorptive duct
fgc	female genital canal	*red*	receptacle duct
fgp	female genital pore	*rv*	resorptive vesicle
gl	glands of the female antrum	*sr*	seminal receptacle
m	mouth pore	*st*	stylet
ma	male antrum	*sv*	seminal vesicle
mgp	male genital pore	*t*	testis
mm	muscle mantle	*y*	yolk glands

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