Primary homology assessment of structures in the female atrial system among species of the Polycystididae (Rhabditophora, Eukalyptorhynchia)

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Abstract. The female atrial system of members of the Polycystididae has been studied at the light microscopical level and compared among the constituent taxa. Based on the criteria of position and conjunction, hypotheses of homology are put forward and compared with the assessments of homology found in earlier literature. Contradictory terminology is synonymized and adapted to fit new findings that recognize homology among structures in different taxa. Based on differences in position and structure, 2 types of female duct are recognized: female duct type I and female duct type II. The term "female bursa" is restricted to a sperm resorbing organ at the proximal end of the female duct type I and/or at the end of a common oviduct. Some species have bundles of glands at the place where the oviduct(s) enter the female duct type I, which are considered homologous among these species. Different types of seminal receptacles are recognized. The term "insemination duct" is restricted to the ducts which in some species, in addition to the oviducts, connect the ovaries with the female duct type I. A single muscular duct, the common oviduct, connects the joined oviducts with the female duct type I in species of *Duplacrorhynchus* and is considered homologous with the similar duct present in some other species. A uterus is always present, entering the common genital atrium through its frontal wall, or entering a female duct type II. This morphological review of the female atrial system reveals a mosaic distribution of characters if applied to previous phylogenies that are based primarily on the male reproductive system.

Additional key words: Platyhelminthes, Turbellaria, morphology, genital system

Not only is the taxon Polycystididae the largest taxon of Kalyptorhynchia (free-living flatworms with a prehensile proboscis), but it is also undoubtedly the most varied with respect to internal morphology. Because the reproductive system, in particular, exhibits astonishing complexity and variability, it has long been considered the most important source of evidence for assessing evolutionary relationships within the Polycystididae. However, divergent ideas exist on the homology of organs of the genital system, and have led to conflicting hypotheses of relationships (see Meixner 1925; Karling 1956; Evdonin 1977) and, in many cases, to the description of new genera and species (e.g., Karling & Schockaert 1977; Artois & Schockaert 1998). However, a cladistical approach has yet to be applied to evolutionary relationships of the Polycystididae.

Before characters and character states can be introduced in a character–species matrix and subsequently used to reconstruct phylogeny, a sound assessment of the possible homology of the structures concerned must be undertaken, based on positional and structural data (the "primary homology": Remane 1952; Patterson 1982; de Pinna 1991; Brower & Schawaroch 1996). Each of these hypotheses of homology (primary homologies) is a cladistical character and is represented by a column in the data matrix. A cladistical analysis will show which of these primary homologies are true homologies (= synapomorphies). In an earlier contribution (Artois & Schockaert 2003), we discussed the conjectures of homology of several characters pertaining to the male atrial organs, resulting in the recognition of a greater diversity of types of stylets and glandular vesicles than was suggested in earlier literature (e.g., Karling 1956; Schockaert 1974). Because of these surprising results, we deemed it necessary to also examine the female system in more detail, as it could reveal characters useful in cladistical analyses.

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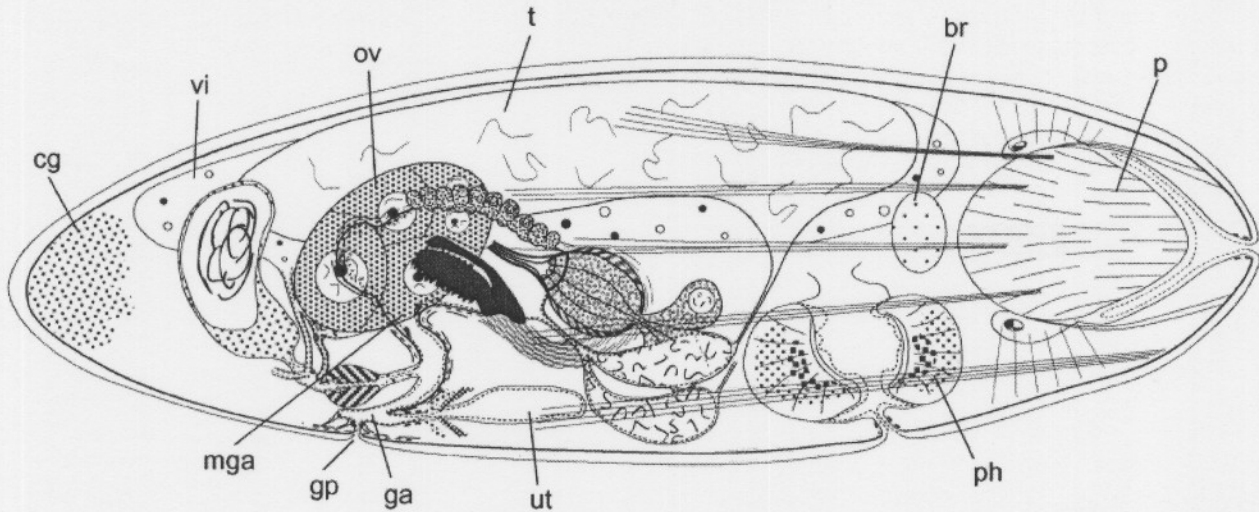   E-mail: tom.artois@luc.ac.be

Fig. 1. Schematic reconstruction of a specimen of *Austrorhynchus,* seen from the right and showing the proboscis with its internal and external musculature, the pharynx, the brain, and the caudal glands. The male genital system consists of a pair of testes (of which only the left one is shown), and the organs associated with the male genital atrium (for details, see Artois & Schockaert 2003). The female genital system consists of a pair of ovaries (where the egg cells are produced), a pair of vitellaria (where the yolk cells are produced), and the female atrial organs (organs associated with the common genital atrium, such as the uterus). The genital atrium opens through the common genital pore. (See Methods for key to abbreviations.)

In this paper, the female atrial organs are discussed and hypotheses of homology put forward. Within the term "atrial organs," we include all structures that are associated with the genital atrium; all elements of the reproductive system except the gonads (see Fig. 1). Karling introduced the name, atrial organs, in his seminal work of 1956, in which he made an extremely detailed analysis of the male atrial organs of the Kalyptorhynchia. Although the female system was recognized as taxonomically important, it has never been used as an important source of characters for inferring relationships. Characters of the female system were considered just additional characters in the diagnosis of taxa, which were defined primarily on characters of the male system. Superficially, the female atrial organs do indeed seem less complex and varied than those of the male system.

The lack of a thorough study on the possible homology of structures in the female system has led to confusing and inconsistently used terminology. The same term has been applied to structures that may not be homologous, and different names have been used to denote the same structure. The data from the literature thus do not offer a firm basis for assessment of the primary homologies, and a thorough analysis is needed. In this paper we present the results of such an analysis, and propose a new terminology based on the new insights. This analysis and terminology is not only useful when describing taxa and discussing relationships within the Polycystididae, but it also

forms a solid base for morphological analyses of taxa within the Kalyptorhynchia or even within the Rhabdocoela. Moreover, the results presented in this paper, together with other data, can be used in cladistical analyses of the Polycystididae. Such an analysis is outside the scope of this contribution, but is planned by the first author.

Methods

Microscopy

Serial sections of 77 out of the 143 known species of Polycystididae were examined using light microscopy. These species are listed in Table 1. For most species, several specimens were studied.

For the other 66 species, we did not find any sectioned material or only material of very poor quality. For the sake of completeness, we also studied material of many undescribed species.

Material (including the type material) of species described by us in the past and of species yet to be described is deposited in the collections of the Limburgs Universitair Centrum. All other useable material was loaned to us by either the Naturhistorisk Riksmuseet (Stockholm, Sweden) or the II. Zoologischen Institut der Universitaet zu Göttingen (Germany).

In our analysis, we mainly refer to the figures without mentioning specific taxa. The presence or absence of structures in the genital atrium is summarized in

Table 1. Matrix summarizing the occurrence of the different structures of the female system within the Polycystididae (for abbreviations see Methods).

	fd-I	b	id	gl	fd-II	cod	duc
Acrorhynchides caledonicus (Claparède 1861) Strand 1928 *A. styliferus* Schockaert & Karling 1975	×	−	−	−	−	−	−
Acrorhynchides robustus (Karling 1931) Strand 1928	×	−	×	×	−	−	−
Albertorhynchus amai Schockaert 1976	×	×	×	−	−	−	−
Alcha evelinae Marcus 1949	×	−	×	×	−	−	−
Annalisella bermudensis Karling 1978	−	×	−	−	×	×	×
Annulorhynchus adriaticus Karling 1956	−	−	−	−	×	−	×
Antiboreorhynchus novzelae Karling & Schockaert 1977	×	×	−	−	−	−	−
Austrorhynchus galapagoensis Artois & Schockaert 1999 *A. hawaiiensis* Karling 1977 *A. magnificus* Karling 1952 *A. pectatus* Karling 1952 *A. spinosus* Karling 1977	×	×	×	−	−	−	−
Cincturorhynchus karlingi Schockaert 1982 *C. ruber* Evdonin 1970	×	×	×	×	−	−	−
Danorhynchus duplostylis Karling 1955	−	−	−	−	×	−	×
Danorhynchus gosoeensis Karling 1955	−	×	−	−	×	×	×
Djeziraia incana Artois & Schockaert 2001 *D. pardii* Schockaert 1971	×	×	−	−	×	×	−
Duplacrorhynchus heyleni Artois & Schockaert 1999 *D. major* Schockaert & Karling 1970 *D. megalophallus* Artois & Schockaert 1999 *D. minor* Schockaert & Karling 1970	×	×	−	−	−	×	−
Galapagorhynchus hoxholdi Artois & Schockaert 1999	×	×	×	−	−	−	−
Gallorhynchus mediterraneus Schockaert & Brunet 1971 *G. simplex* Schockaert & Brunet 1971	−	×	−	−	×	×	×
Gyratricella attemsi (Attems 1897) Karling 1955	−	×	−	−	×	×	×
Gyratrix hermaphroditus Ehrenberg 1831 *G. proavus* Meixner 1929	−	×	−	−	×	×	×
Hawadlia papii Schockaert 1971	×	×	−	×	−	−	−
Koinocystella inermis Karling 1952	×	×	−	−	−	−	−
Lagenopolycystis peresi (Brunet 1965) Artois & Schockaert 2000	×	×	−	−	−	−	−
Limipolycystis curvitubo Schilke 1970	×	×	−	−	−	−	−
Macrorhynchus croceus (Fabricus 1826) Graff 1882 *M. groenlandicus* (Levinsen 1879) Graff 1882	×	−	−	−	−	−	−
Macrorhynchus manusferrea Artois & Schockaert 2001	×	×	−	−	−	−	−
Myobulla dunata Artois & Schockaert 2000 *M. myobulla* Artois & Schockaert 2000 *M. swedmarki* (Karling 1978) Artois & Schockaert 2000	×	×	−	−	−	−	−
Neopolycystis tridentata Karling 1955	−	−	−	−	×	−	−
Parachrorhynchus axi Karling 1956 *P. bergensis* Karling 1956 *P. jondelii* Artois & Schockaert 2000	×	×	−	−	−	−	−
Paraustrorhynchus elixus (Marcus 1954) Karling & Schockaert 1977 *P. pacificus* Karling & Schockaert 1977	×	−	−	×	−	−	−
Paulodora asymmetrica Artois & Schockaert 2001 *P. contorta* (Schockaert & Karling 1975) Artois & Schockaert 1998 *P. dolichocephala* (Pereyaslawsewa 1892) Artois & Schockaert 1998							

Table 1. (Continued).

	fd-I	b	id	gl	fd-II	cod	duc
P. felis (MARCUS 1954) ARTOIS & SCHOCKAERT 1998							
P. fredelyna (MARCUS 1948) ARTOIS & SCHOCKAERT 1998							
P. matarazzoi MARCUS 1948							
P. subcontorta (SCHOCKAERT 1982) ARTOIS & SCHOCKAERT 1998	×	−	−	−	−	−	−
Phonorhynchoides haegheni ARTOIS & SCHOCKAERT 2001							
P. somaliensis SCHOCKAERT 1971	×	×	−	−	×	×	×
Phonorhynchus helgolandicus (METSCHNIKOW 1865) GRAFF 1905	×	×	×	−	−	−	−
Polycystis ali SCHOCKAERT 1982							
P. hamata KARLING 1986							
P. naegelii KÖLLIKER 1845	×	×	−	−	−	−	−
Polycystis gabriellae (MARCUS 1948) KARLING (1952)	×	−	−	−	−	−	−
Porrocystis assimilis (LEVINSEN 1879) KARLING (1952)	×	×	×	−	−	−	−
Progyrator mamertinus (GRAFF 1874) REISINGER 1926				See text for discussion			
Psammopolycystis bidens MEIXNER 1938							
P. bondensis KARLING 1956							
P. bredungensis KARLING 1956							
P. falcata KARLING 1956	×	×	−	−	−	−	−
Pygmorhynchus pygmaeus ARTOIS & SCHOCKAERT 1999	×	×	×	×	−	−	−
Rogneda anglica KARLING 1953							
R. capulata KARLING 1953							
R. gallica AX 1956							
R. hibernica (SOUTHERN 1936) KARLING 1953							
R. minuta ULJANIN 1870							
R. westbladi KARLING 1953	×	−	−	×	−	−	−
Sabulirhynchus axi ARTOIS & SCHOCKAERT 2000	×	×	−	−	−	−	−
Scanorhynchus forcipatus KARLING 1955							
S. limophilus KARLING 1955	−	×	−	−	×	×	×
Typhlopolycystis coeca KARLING 1956							
T. coomansi SCHOCKAERT & KARLING 1975	×	×	−	−	−	−	−
Yaquinaia microrhynchus SCHOCKAERT & KARLING 1970	×	×	−	−	−	−	−

Table 1. The figures are semi-diagrammatic representations of the female atrial organs of species chosen as examples. All figures are reconstructions of the animal seen from the right, i.e., with the anterior to the right of the diagram and the gonopore situated ventrally (unless indicated otherwise). Where gonads are paired, the figures indicate whether left, right, or both ovaries, oviducts, and vitelloducts are depicted; otherwise only one ovary is present.

Abbreviations

Abbreviations used in figures are: (b) bursa, (br) brain, (cg) caudal glands, (cod) common oviduct, (duc) ductus utero-communis, (fd-I) female duct type I, (fd-II) female duct type II, (ga) common genital atrium, (gl) glands, (gp) gonopore, (lid) left insemination duct, (lod) left oviduct, (lov) left ovary,

(lvd) left vitelloduct, (mb) male bursa, (mga) male genital atrium, (mo) morula-shaped appendage, (od) oviduct, (ov) ovary, (p) proboscis, (ph) pharynx, (rbd) right bursal duct, (rod) right oviduct, (rov) right ovary, (rvd) right vitelloduct, (sph) sphincter, (sr) seminal receptacle, (t) testis, (ut) uterus, (vi) vitellarium, (vd) vitelloduct.

Results

Morphological analysis and homology assessments

The female atrial system consists of all genital structures, except the gonads proper and their ducts (see Fig. 1). It is situated in the posterior half of the body of the animal, which itself is 0.5–3 mm long, depending on the species. There are 1 or 2 ovaries, and 1 or 2 vitellaria (yolk glands). The vitelloducts

always end in the oviducts near the ovaries. The connection of the oviducts with the common genital atrium is provided by 1 or 2 female ducts (female duct type I and/or II). In some species, the oviducts join each other and form a common duct before entering a female duct type I. In other species, a second connection, in addition to the oviduct, connects the ovary with a female duct type I (insemination ducts). To store alien sperm after copulation, some species have special organs such as a female bursa and/or seminal receptacles. In some species, the junction of the oviducts with the female duct type I is surrounded by large bundles of glands. A uterus is always present and enters the common genital atrium through its frontal wall or through the distal part of a female duct type II. The part distal from the junction is then termed "ductus utero-communis." These structures and assessments of homology are discussed below. The results are summarized in Table 1; if species of the same genus are identical with respect to the characters discussed, they are cited in a single row.

Ovaries, vitellaries, and their ducts. Polycystidid flatworms have 1 or 2 ovaries, each with an oviduct, and (mostly) paired vitellaria, each with a vitelloduct. The oviduct and vitelloduct are a continuation of the tunic that surrounds the ovary and the vitellarium, respectively, and are thus lined with a membranous epithelium. Near the last ovocyte, the vitelloduct joins the oviduct (which in fact becomes the ovo-vitelloduct) (Figs. 2–5). In species with a single ovary and paired vitellaria, the 2 vitelloducts fuse before joining the oviduct. Except for the number of gonads and the number of their ducts, there is no variation in structure or position of these initial ducts, and their homology is well supported. These ducts are not considered parts of the organs of the atrial system.

Female duct type I. In the simplest organizational pattern of the female atrial organs, the two oviducts (= ovo-vitelloducts) join each other forming a common duct, the female duct, that continues towards and enters the posterior side of the genital atrium (Figs. 2–4, 5A). When a bursa is present (see below), it enters the duct at its most proximal end, and the oviducts (if paired) enter the duct at either side. This duct is surrounded by muscles, which can be very thick compared to the thickness of the underlying epithelium (Fig. 4A–C). It can vary greatly in length compared with the length of the oviduct, from very long (Fig. 3D) to very short, almost immediately splitting into both oviducts (Figs. 3A, 4B). This duct has been called different names: simply "female duct," sometimes "ductus communis," and when it is highly muscular it is referred to as the "vagina" (e.g., in *Austrorhynchus;* see Karling 1952). We consider this type of duct, which is very muscular, enters the genital atrium through its posterior wall, and has the bursa (if present) at its proximal end, as homologous in all species where it occurs. We give it the name "female duct type I." If a bursa is present, the part of this duct in between the bursa and the entrance of the oviducts is called "bursal stalk."

Female bursa. Proximal to the entrance of the oviducts in the female duct type I or at the terminal end of the common oviduct (see further), a bursa can occur. It is absent in some species (e.g., some species of *Macrorhynchus, Alcha evelinae,* species of *Paulodora;* see Figs. 2A, 4C,D). In others it is very small, even inconspicuous (e.g., species of *Polycystis;* Fig. 2B), but in the vast majority of the Polycystididae, it is a large vesicle, often with irregular form (Figs. 3, 4A,B, 5). In individuals at full female maturity, the bursa, after copulation, mostly contains sperm, which is
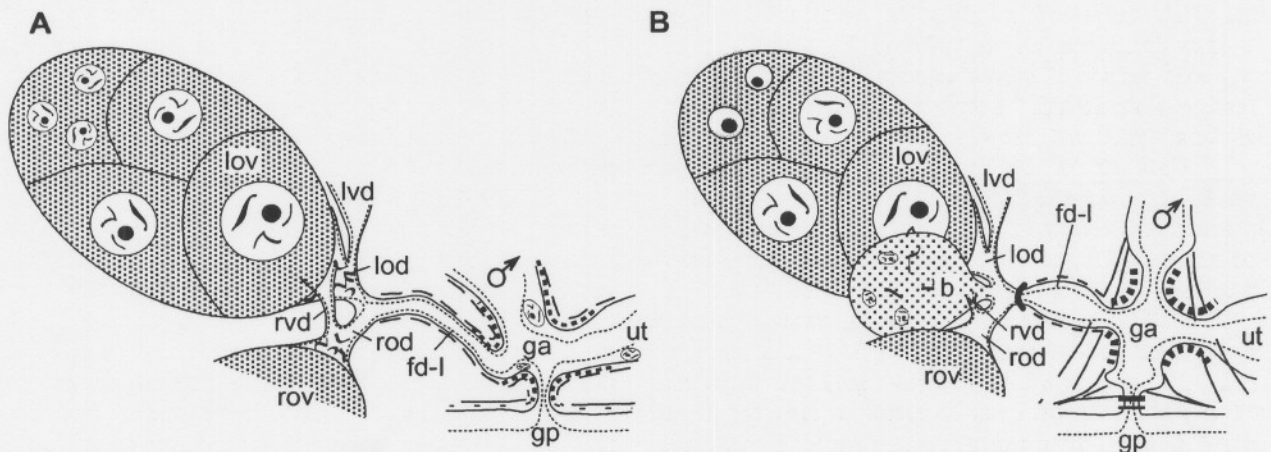

Fig. 2. Schematic representation of the female atrial organs of **A.** *Macrorhynchus croceus* and **B.** *Polycystis naegelii.*
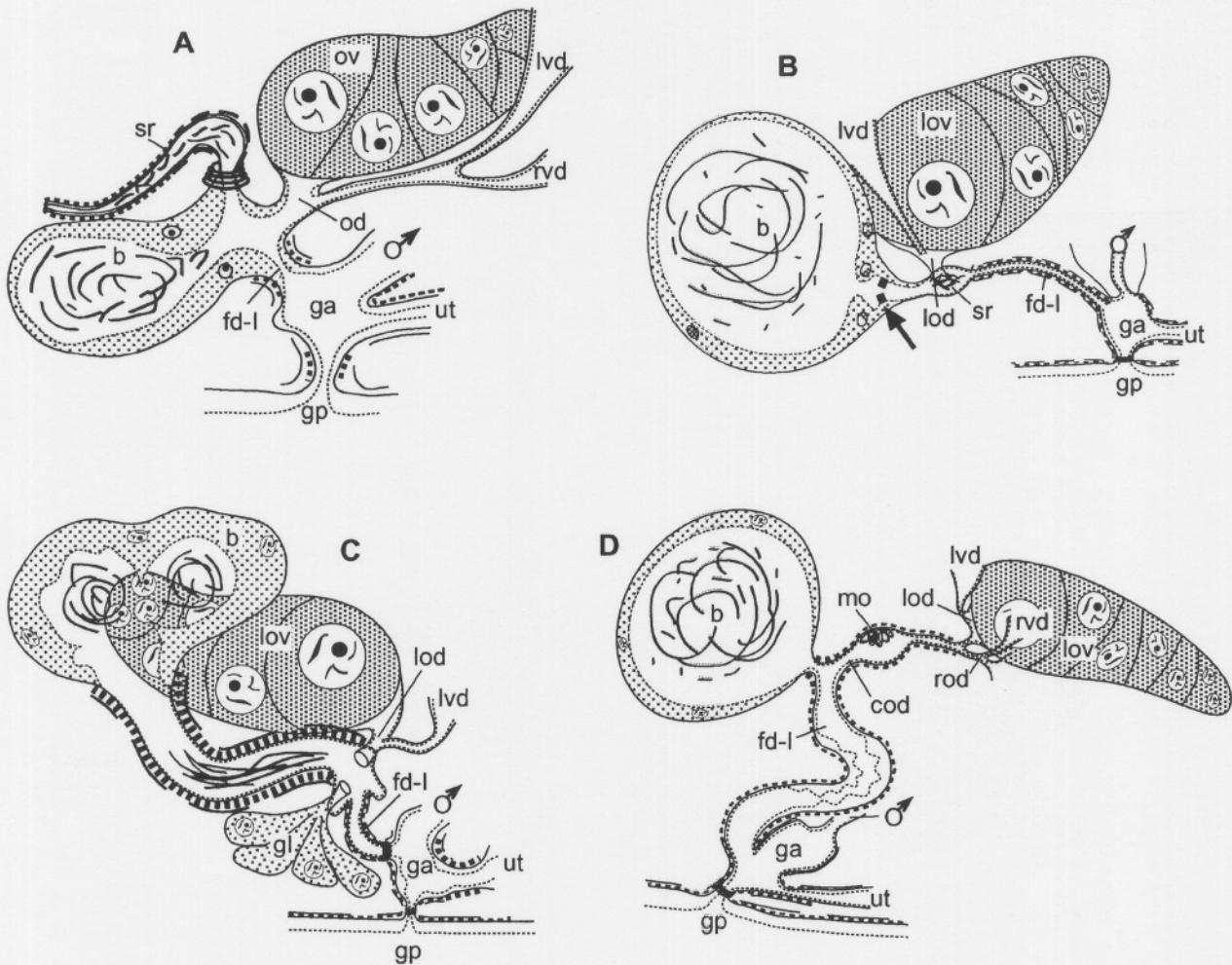
Fig. 3. Illustration of the female atrial organs. **A.** *Typhopolycystis coeca.* **B.** *Yaquinaia microrhynchus* (arrow indicates the sclerotized knobs at the entrance of the bursa, see text). **C.** *Hawadlia papii.* **D.** *Duplacrorhynchus minor.*

clearly degenerating. Often the bursal tissue is divided into large cavities that contain sperm (and often also prostate secretions) in various phases of digestion. This sperm is obviously excess sperm received at copulation (see Vreys et al. 1997). This bursa has received various names: "bursa copulatrix," "bursa resorbiens," or "bursa seminalis" (referring to its function, see Hyman 1951: p. 120), "bursa terminalis" (referring to position, see Meixner 1925), and "bursa parenchymalis" (referring to the presumed origin, see Karling 1955). We prefer to use a neutral term, female bursa, for the vesicle at the proximal end of the female duct type I. The "bursa" in *Annulorhynchus adriaticus* and in *Neopolycystis tridentata* has a different position and structure (immediately connected to the common genital atrium, lacking morphology consistent of resorption and surrounded by muscles) (see Karling 1955) and is thus

not considered homologous with the female bursa in the other Polycystididae. In a few species (*Parachrorhynchus axi*, *P. jondelii*, and *Yaquinaia microrhynchus*), a ring of sclerotized knobs occurs at the entrance of the bursa (Fig. 3B). These cannot be considered homologous with the morphologically similar hard knobs found in all species of *Phonorhynchus*, because here they are situated anteriorly from the entrance of the oviducts in the female duct type I.

Seminal receptacles. Donated sperm that will be used for fertilization can be temporarily stored in a seminal receptacle. These sperm are actively moving in the living animal; in sections they are few, and show no sign of degeneration, clearly different from the sperm seen in the bursa. A seminal receptacle for each ovary, or a common seminal receptacle, may be present. In many species, the narrow space in the ovary where the oviduct exits (Figs. 2A, 4A), or the
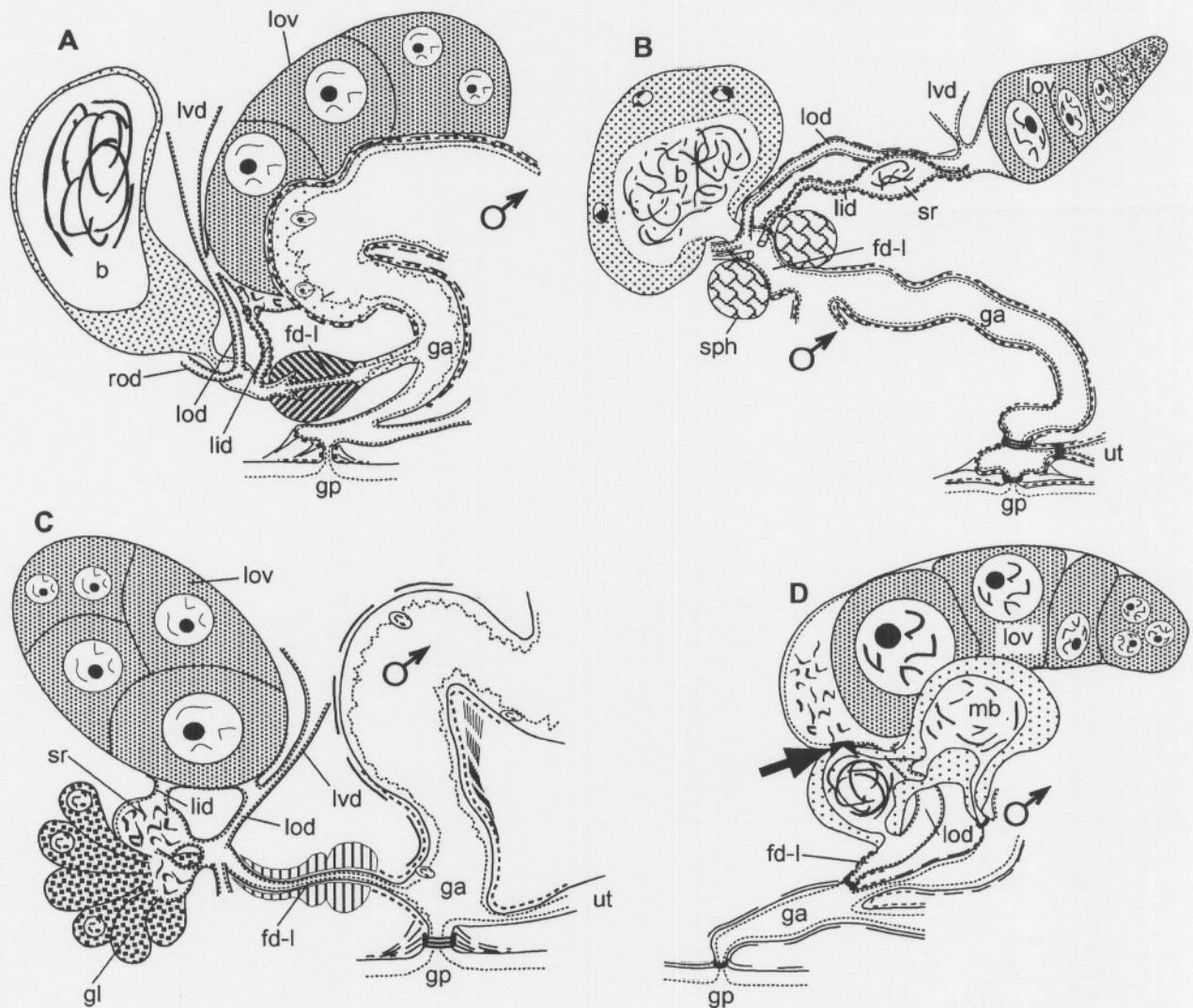
Fig. 4. Schematic illustration of the female atrial organs. **A.** *Austrorhynchus magnificus.* **B.** *Galapagorhynchus hoxholdi.* **C.** *Alcha evelinae.* **D.** *Paulodora contorta* (arrow indicates the "nozzles"; see text).

oviducts themselves, function as the storage location. In some species, the junction of both oviducts (Figs. 3B, 5A) or the part of the female duct type I distal from this junction (Fig. 3C), is enlarged, and functions as a seminal receptacle. Also, the insemination ducts (see below) can be enlarged and form seminal receptacles (Fig. 4B,C). Although all these vesicles have the same function, because of variation in anatomical position and structure they clearly cannot be considered homologous and should be scored as different characters in a data matrix.

A typical seminal receptacle is found in *Limipolycystis curvitubo, Lagenopolycystis peresi, Sabulirhynchus axi,* and species of *Myobulla* and *Typhlopolycystis.* Although it is morphologically dissimilar in different taxa, it should, nevertheless, be considered as the same character, as it occupies exactly the same position in all the taxa mentioned: connected to the dorsal wall of the "bursal stalk," i.e., the part of the female duct type I proximal from the entrance of the single oviduct.

Insemination ducts. In most cases, sperm that will fertilize the eggs simply reach the ovocyte via the oviduct. However, separate insemination ducts do occur in some species, also called spermatic ducts or ductus spermatici (Fig. 4A–C). These ducts can always be distinguished from the oviducts, even if they look similar, since they never connect to the vitelloduct. They are found only in species with a female duct type I. They may be short and rather inconspicuous (Fig. 4A), or long and muscular (Fig. 4B), and they
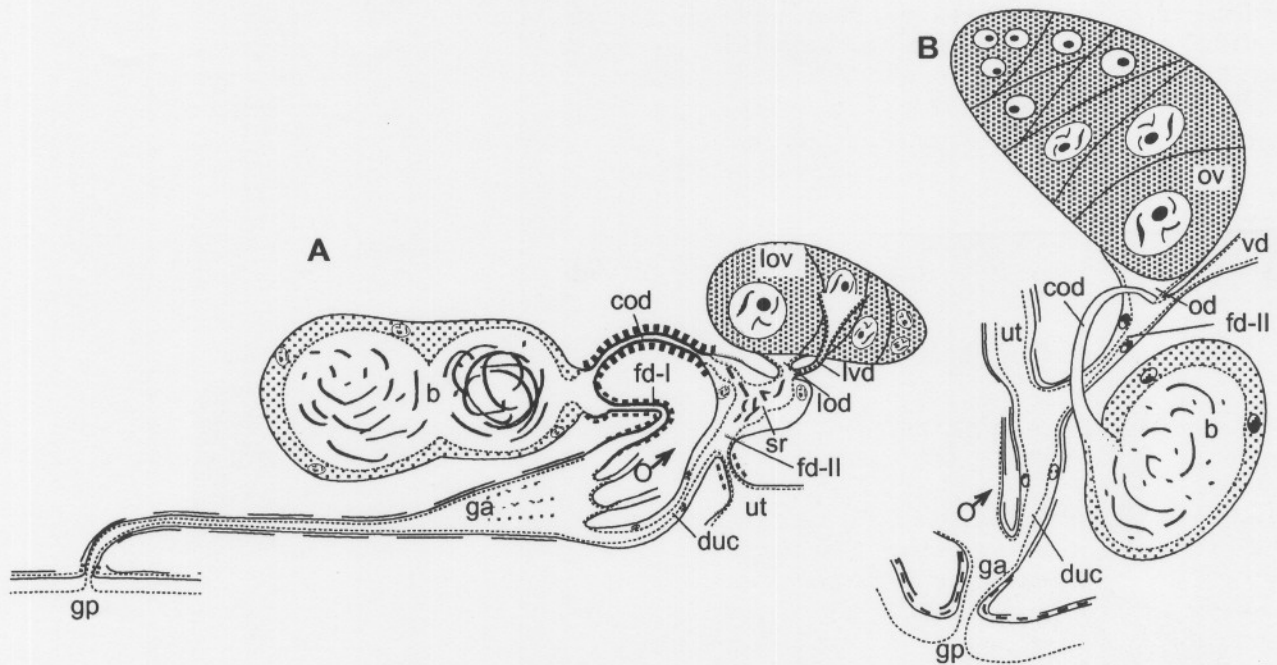
Fig. 5. Schematic representation of the female atrial organs. **A.** *Phonorhynchoides somaliensis*. **B.** *Scanorhynchus forcipatus* (from horizontal sections, gonopore situated terminally, anterior end of the animal to the top of the diagram).

can be enlarged to form seminal receptacles (Figs. 4B,C). Insemination ducts are also clearly visible in *Acrorhynchides robustus* and *Albertorhynchus amai,* 2 species for which the occurrence of these ducts is not reported in earlier literature.

The term "insemination pore" has sometimes been used to denote the narrow connection guarded by an umbrella-shaped structure of sclerotic elements (the "nozzles") between the male bursal system and each ovary in all species of *Paulodora* (Fig. 4D) (see Schockaert & Karling 1975). These structures are in no respect comparable with the insemination ducts discussed above, as they have a completely different position (within the oviduct and not connected to the female duct type I) and structure (umbrella-shaped, sclerotized). Therefore, they clearly cannot be considered homologous with the insemination ducts of other Polycystididae.

Glands. In a number of species, bundles of glands enter the female duct type I. When the bursa is absent, these glands are found at the terminal end of the female duct (Fig. 4C); when it is present they are displaced ventrally (Fig. 3C) at the junction of the two oviducts. Because of their similar position, we consider these glands as homologous among the species where they occur.

Female duct type II. In a small number of species, a duct leaves the common genital atrium from its rostroventral wall and connects the atrium with the ovaries. If the ovaries are paired, it always ends at the junction of both oviducts, and this junction is mostly widened and contains sperm (=seminal receptacle, see above). The same kind of widening, but less obvious, is also found in some species with only 1 ovary. No or very thin muscles surround this duct. In none of these species is this duct connected to the bursa, if present, and no glands enter this duct. Because of these differences in structure and position, we do not consider this duct homologous with the female duct type I, and name it "female duct type II" (Fig. 5).

In some species with a female duct type II, the bursa is connected to the atrium by a muscular canal that is often called the "bursal stalk" in earlier literature. We consider this canal to fit the criteria that define the female duct type I (muscular, entering the genital atrium through its posterior wall and with the bursa at its proximal end) (Fig. 5A). The co-occurrence of these two types of ducts in some species confirms that they cannot be considered homologous.

Common oviduct. In species of *Duplacrorhynchus* (Fig. 3D), a muscular duct runs from the bursa to the common genital atrium, clearly a female duct type I. Another narrow muscular duct connects the oviducts, from the point of their confluence, to the female duct at the entrance of the bursa. Since this
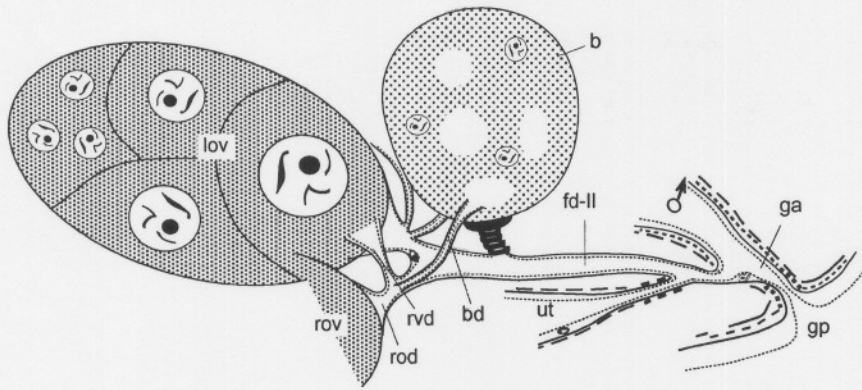
Fig. 6. Schematic representation of the female atrial organs of *Progyrator mamertinus* (seen from the left).

narrow tube is proximal of the bursa, we do not consider it the female duct type I, nor part of it, and name it the "common oviduct." In *Duplacrorhynchus,* it is locally swollen and contains a "morula-shaped appendage" typical of the species in this genus (see Schockaert & Karling 1970). In species of *Djeziraia* or *Phonorhynchoides* (Fig. 5A), we find exactly the same situation: the female duct type I connects the bursa to the atrium, and the common oviduct connects the female duct type I with the seminal receptacle. However, the seminal receptacle is also connected to the atrium by the female duct type II. The common oviduct probably now functions as an insemination duct, which is clearly a completely different structure from the insemination ducts discussed earlier. In other species with a female duct type II, the connection atrium–bursa (the female duct type I) is absent (Fig. 5B), and sperm is injected into the bursa by dermal impregnation or through a permanent "vagina" (a simple pore at the bursa) as in species of *Gyratrix*. The connection bursa–ovary (the common oviduct) is still present as an "insemination duct," sometimes sclerotized, and sometimes double as in *Gyratricella attemsi* and in one of the populations of *Gyratrix hermaphroditus* from the Galapagos (see Artois & Schockaert 2001).

Uterus and the ductus-uterocommunis. Most polycystidids flatworms have a uterus that enters the genital atrium anteriorly and separately from the other atrial organs, and this entrance is surrounded by two sets of glands. In a few species, the uterus and the female duct (always a female duct type II) join each other before they enter the genital atrium. The part of the female duct distal from this junction is then referred to as "ductus utero-communis" (Fig. 5).

The case of *Progyrator mamertinus*. *Progyrator mamertinus* has such an aberrant construction of the female system that it hardly can be compared with that of other polycystidids (see Fig. 6). A thorough description is provided by Meixner (1925). Both ovaries are situated anteriorly to and ventrally from the other atrial organs. Both oviducts join each other to form a female duct, which receives the uterus through its anterior wall and continues towards the common genital atrium as a ductus utero-communis, entering the common genital atrium anteriorly. The narrow and muscular bursal stalk, regarded as the female duct ("weibliche Genitalkanal") by Meixner (1925), leaves the dorsal wall of the female duct. Proximally, the bursal stalk ends in the large bursa through a muscular pore. Just proximal to this pore, two "bursal ducts" connect the bursa with the ovaries.

Discussion

Classical polycystidid classifications are mainly based on features of the male system and on the number of gonads. In the most recent classification of Evdonin (1977), 10 subfamilies are recognized. The new insights in the morphology and homology of structures we have proposed above, however, seem to contradict some of the relationships proposed by Evdonin (1977). For instance, the female duct type II occurs in three of his subfamilies:

1. in all members of the Gyratricinae (*Danorhynchus duplostylis, D. gosoeensis, Gyratricella attemsi, Neopolycystis tridentata,* and the species of *Gyratrix* and *Scanorhynchus*);

2. in some members of the Duplacrorhynchinae (species of *Djeziraia* and *Phonorhynchoides*), including *Annalisella bermudensis* (see Karling 1978), but not in the species of *Duplacrorhynchus*; and

3. in some representatives of the Psammopolycystidinae (*Annulorhynchus adriaticus,* species of *Gallorhynchus*), but not in *Phonorhynchella biarcuata* nor in species of *Psammopolycystis*.

On the other hand, a common oviduct occurs not only in species of *Duplacrorhynchus,* in all species of *Djeziraia* and *Phonorhynchoides,* and in *A. bermudensis,* but also in all species of *Gyratrix* and *Gyratricella* as well as in *A. adriaticus* and species of *Gallorhynchus.* Moreover, the latter species have a ductus utero-communis, as have some species of Gyratricinae and some species of Duplacrorhynchinae.

From these examples only, it becomes clear that a "system" based solely on the male system causes a "mosaic-like" distribution of other characters, and that as many characters as possible (including molecular data) should be used in a phylogenetic (cladistical) analysis. Not only will this lead to more correct hypotheses of relationships, but will also reveal which of the primary homologies discussed in this paper are corroborated, and which show homoplasy. An analysis of the male system of the polycystidids (Artois & Schockaert 2003) will be used together with the characters discussed above and with characters of other systems in a cladistical analysis of the Polycystididae. Moreover, the characters and terminology presented above can also be used in the study of other Kalyptorhynchia (or even Typhloplanoida), which clearly would facilitate communication about and comparison of species of different taxa. This would also facilitate the construction of useful data matrices for analyses on a higher taxonomical level.

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