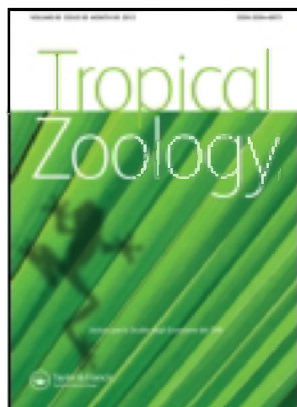


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### Interstitial fauna of the Galapagos: Duplacrorthynchinae, Macrorthynchinae, Polycystidinae, Gyratricinae (Platyhelminthes Polycystididae)

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# Interstitial fauna of the Galapagos: Duplacrorthynchinae, Macrorhynchinae, Polycystidinae, Gytratricinae (Platyhelminthes Polycystididae)

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Seven species from the Galapagos of different subfamilies of the Polycystididae are described and discussed. Four of them are new to science, three of which belong to the subfamily Duplacrorthynchinae Schockaert & Karling 1970: *Djeziraia incana* n. sp. differs from the other species of the genus by its long, thin stylet; *Phonorhynchoides haegheni* n. sp. is unique within the genus, as the prostate stylet is much shorter than the accessory stylet; *Parachrorhynchus jondelii* n. sp. is characterised by the presence of a bundle of atrial glands, paired seminal vesicles, a very large sphincter at the distal end of the female duct, and a ring of hard plates at the distal end of each ovary. Of the Macrorhynchinae Evdonin 1977, *Macrorhynchus manusferrea* n. sp. differs from the other species of the genus by the shape of the stylet and the presence of a female bursa. The subfamily Polycystidinae Schockaert & Karling 1970 is represented by *Polycystis ali* Schockaert 1982 and *Paulodora felis* (Marcus 1954). The Galapagos population of the latter species is considered a separate subspecies, *P. felis asymmetrica* n. subsp., based on differences in the female system. Finally, *Gytratrix hermaphroditus* Ehrenberg 1831 is discussed. Three colour variants of this species complex are found in the Galapagos, which represent three more species in the complex. For all new taxa, a diagnosis is given. At the end, we provide a species list of the polycystidid fauna of the Galapagos Isles.

KEY WORDS: Duplacrorthynchinae, Macrorhynchinae, Polycystidinae, Gytratricinae, Polycystididae, Galapagos, new taxa.

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INTRODUCTION

Former contributions on the polycystidid fauna from the Galapagos dealt with the subfamilies Porrocystidinae Evdonin 1977 (ARTOIS & SCHOCKAERT 1999) and Typhlopolycystidinae Evdonin 1977 (ARTOIS & SCHOCKAERT 2000). In this third contribution, members of the remaining subfamilies are described and discussed, making the survey of the polycystidid fauna of the archipelago complete. The remaining part of the Eukalyptrorhynchia (six representatives of the Koinocystididae and one of the Gnathorhynchidae) will be discussed in a later paper, which will conclude the series on the kalyptorhynch fauna of the Galapagos. The Schizorhynchia were treated by NOLDT & HOXHOLD (1984).

This contribution is part of a series of papers on the meiofauna of the Galapagos, a survey of which can be found in MIELKE (1997).

MATERIAL AND METHODS

The material from the Galapagos was collected by S. Hoxhold and P. Schmidt, who drew and photographed the live animals (for details see AX & SCHMIDT 1973). S. Hoxhold made the measurements on live animals. When sufficient animals were available, some were fixed with Bouin's fixative, embedded in paraffin and serially sectioned (4 µm sections). The sections were stained with Heidenhain's iron hematoxylin with eosin as counterstain.

Additional material of some species was collected in other localities by the authors. Some of the specimens were whole mounted using lactophenol as fixative. Specimens intended for sectioning were treated as described above.

Brief descriptions of the localities in the Galapagos are followed by a number. This number refers to the detailed descriptions of the localities by AX & SCHMIDT (1973: 21-26).

Measurements of hard parts are axial. Figures without a scale are freehand. Photographs without scale are from live material. The position of the gonopore is expressed as a percentage of body length (distance from the anterior tip of the body).

The species epithet of *Macrorhynchus manusferrea* n. sp. is copied from I. HENZE's Diplomarbeit (University of Göttingen 1987).

Type material will be deposited in the Zoological Museum of the University of Göttingen (Germany), except for that of *Phonorhynchoides haegheni*, which will be deposited in the collection of the Research Group Zoology of the Limburgs Universitair Centrum (LUC), Diepenbeek, Belgium.

## ABBREVIATIONS

*acg*: accessory glands; *ast*: accessory stylet; *b*: bursa; *bs*: bursal stalk; *db*: distal part of bursa; *de*: ejaculatory duct; *ds*: insemination duct; *e*: eyes; *fd*: female duct; *ga*: common genital atrium; *gd*: genital duct; *gg*: glands; *gp*: gonopore; *m*: mouth; *ma*: male atrium; *od*: oviduct; *ov*: ovary; *p*: proboscis; *pb*: proximal part of bursa; *pc*: prepharyngeal cavity; *ph*: pharynx; *sd*: seminal duct; *sph*: sphincter; *sr*: seminal receptacle; *st*: stylet; *t*: testis; *ut*: uterus; *va*: vagina; *vd*: vitelloduct; *vg*: prostate vesicle; *vi*: vitellarium; *vs*: seminal vesicle; *v*, *w*, *x*, *y*, *z*: see in text.

## RESULTS

## Subfamily Duplacrorthynchinae Schockaert &amp; Karling 1970

***Djeziraia incana*** n. sp. (Figs 1, 4A-B)

*Localities*<sup>1</sup>. Santa Cruz: Bahia Academy (IX. 6b). Santa Cruz: Bahia Borrero (IX. 3). Santa Cruz: Bahia Tortuga (IX. 7b). Barrington (XI. 2).

*Material*. Drawings and photographs of live animals by S. Hoxhold. Several serially sectioned specimens, one sagittally sectioned specimen designated as holotype.

*Derivation of the name*. The species name refers to the grey colour of the living animal. *Incanus* (Lat.): totally grey.

*Description*. Animals are 1-1.2 mm in length, with two eyes. They appear grey in transmitted light. The general organisation corresponds with that of *D. pardii* Schockaert 1971 in most respects, such as in the dimension of the proboscis ( $\pm 7\%$  of the body length) with three proboscis retractors and two integument retractors, in the position of the paired gonads, in the genital atrium being connected to the subterminal genital pore (at  $\pm 90\%$ ) by a long genital canal, etc. Female duct, male duct and uterus enter the genital atrium separately at the anterior side, the female duct being most dorsal.

The slender and slightly curved single-walled stylet is 162-198  $\mu\text{m}$  long (mean = 179,  $n = 3$ ) even up to 295  $\mu\text{m}$  in one specimen. The opening of the stylet is terminal. The seminal vesicle, apparently without muscle sheath, is relatively large, with a very thin epithelium with flattened nuclei. The interposed prostate vesicle is small, weakly muscular, and contains mainly a coarse-grained basophilic secretion that is sometimes supplemented with very small eosinophilic glands. The nuclei of the prostate glands are both intra- and extracapsular.

The long, narrow bursal stalk runs anteriorly, then bends backward to end in the terminal bursa. Its epithelium is rather low and anucleated, mostly ruffled ("pseudociliation"), and it is surrounded by longitudinal muscles around the distal part, and strong circular muscles around the proximal half. The short female duct enters the stalk at about its middle. This female duct (without any muscle coat) widens to a large seminal receptacle into which the oviducts enter. The insemination duct links the seminal receptacle with the proximal end of the bursal stalk.

<sup>1</sup> The type locality is Santa Cruz. The exact location remains uncertain. The holotype is labelled 31 a/b, 31 a was collected at the first locality (IX. 6b), 31 b at the second (IX. 3).

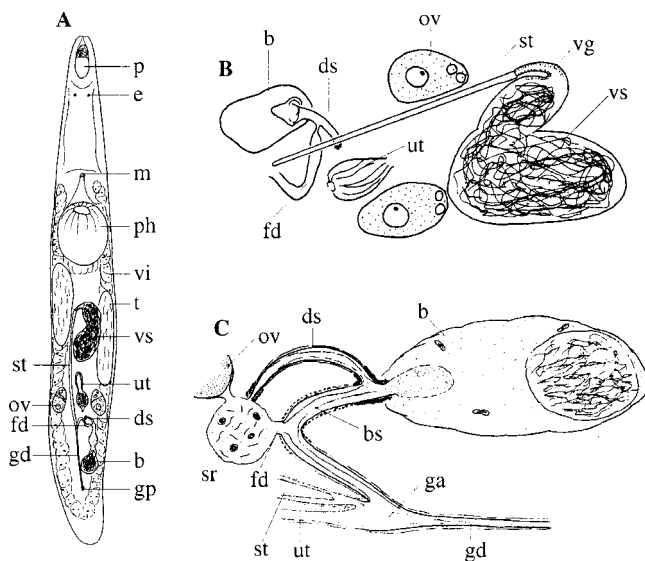


Fig. 1. — *Djeziraia incana* n. sp. A, general organisation; B, atrial organs; C, reconstruction of the female atrial organs from the left hand side (A-B from live animals).

Longitudinal muscles surround this duct, while at both ends there is also a strong circular muscle layer. The insemination duct is lined with a very low epithelium, which is mostly reduced to the basement membrane, forming a so-called pseudocuticula, especially near the seminal receptacle.

**Discussion.** *Djeziraia incana* is the third species described in this very homogeneous genus. *D. euxinica* (Mack-Fira 1971) Schockaert 1982 occurs in the Black Sea (MACK-FIRA 1971) and in the Mediterranean (Sardinia, T.J. ARTOIS pers. obs.), while *D. pardii* Schockaert 1971 is from the East African coasts. The new species can be initially distinguished by its long (162–198  $\mu\text{m}$  and up to 295  $\mu\text{m}$  in one specimen) and very slender stylet, with a terminal opening. The stylet of *D. euxinica* also has a terminal opening, but is shorter [105  $\mu\text{m}$  in the Mediterranean specimen (T.J. ARTOIS pers. obs.), 120  $\mu\text{m}$  according to MACK-FIRA (1971)]. The stylet of *D. pardii* is 84  $\mu\text{m}$  long with a subterminal opening.

The very thin-walled female duct, coming from the seminal receptacle, enters the bursal stalk at about its middle in *D. euxinica* and in *D. incana*; it is very short in the latter species. In *D. pardii* it enters the genital atrium. In all three species, the insemination duct connects to the seminal receptacle. This was in doubt in the original description of *D. pardii*. Careful observation of the type material, however, revealed that a connection of the “diverticulum” (SCHOCKAERT 1971) and the seminal receptacle does exist. A striking feature only found in *D. pardii*, is the presence of two horns at the connection. The sperm duct of *D. pardii* is highly muscular, being surrounded by a very thick circular muscle sheath, while in *D. incana* circular muscles are only present at the two ends of the duct. The situation in *D. euxinica* is not yet known<sup>2</sup>.

<sup>2</sup> Data on the internal organisation of *D. euxinica* (not given in the original description) are from an unpublished reconstruction by MACK-FIRA and KARLING, kept at the Swedish Museum of Natural History in Stockholm.

*Phonorhynchoides haegheni* n. sp. (Figs 2-3, 4C-D)

*Localities in the Galapagos.* Santa Cruz: Bahia Borrero (IX. 3). Santa Cruz: Bahia Academy: northern side (IX. 5c and IX. 5d). Bartholomé: northern side (VII. 1). Tower: Bahia Darwin (V. 1a).

*Other localities.* S. Hutchinson Island (Florida, USA), at a bridge near the park; medium fine sand taken at ca 0.5 m deep at high tide, 16.XI.1994 (type locality). S. Hutchinson Island (Florida, USA), Jensen Beach, a little bit north of “Bath Tub” at the ICH-side; medium fine sand with some detritus from ca 30 cm deep, at the foot of some rocks, near a mangrove area, 24.IX.1994.

*Material.* Several animals studied alive. Three whole mounts (Florida), one of them designated holotype (LUC no. 213), another one paratype (LUC no. 214). Three animals from Florida serially sectioned, 22 sectioned specimens from the Galapagos.

*Derivation of the name.* This species is dedicated to David Van Der Haeghen, a friend of T.J. Artois.

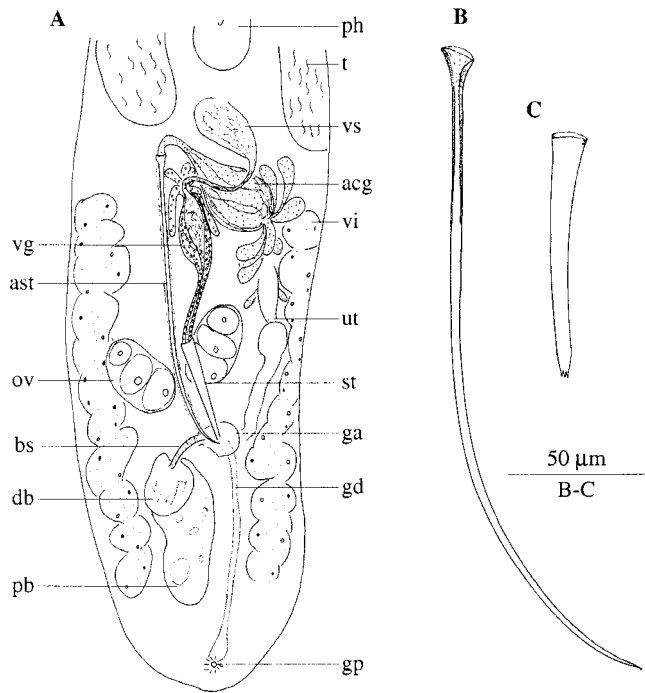


Fig. 2. — *Phonorhynchoides haegheni* n. sp. A, atrial organs; B, accessory stylet; C, stylet (A from a specimen from the Galapagos, B-C from the holotype).

*Description.* Live animals are long and slender, 1-1.4 mm, with paired eyes and a drab grey colour. The excretory system is well developed. The epidermis is 3  $\mu\text{m}$  high with cilia 2  $\mu\text{m}$  long, and with flattened, lobate nuclei, numerous optically-empty vacuoles and elongated rhabdites of length about 1/3 to 1/2 of the epithelium height. In some specimens the vacuoles are filled with a coarse-grained basophilic secretion. Caudal glands are well developed.

The proboscis is very small,  $\pm 5\%$  of the body length. The apex is barely visible in the live animal. The basal and apical epithelia of the cone are relatively high. The external musculature of the proboscis consists of eight protractors with seven to eight muscle fibres each, six fixators and a ventral and dorsal pair of retractors. The presence of the usual third, dorsolateral pair of retractors could not be established with certainty on such a small proboscis. All retractors insert on the body wall in the pharyngeal region. Additionally, a dorsal and a ventral pair of integument retractors are present.

The pharynx is situated in the first body half and is ca 70  $\mu\text{m}$  in diameter. It has the same structure as in *Phonorhynchoides somaliensis* Schockaert 1971 (see SCHOCKAERT 1971).

The general organisation of the genital system is the same as in *P. somaliensis*. The genital pore is situated ventrally, subterminally, at ca 95%. The common genital atrium has a ruffled, degenerating epithelium (pseudociliation); in some areas the epithelium has disappeared, leaving only a thick basement membrane (pseudocuticula). The genital atrium is surrounded by longitudinal muscles only. The longitudinal sclerotized ridges observed in *P. somaliensis* are lacking.

The seminal vesicle is spindle-shaped. It has a thin epithelium with some flattened nuclei and a very thin, spiral muscle sheath. The seminal duct runs axially through the ovoid prostate vesicle, which is surrounded by an almost circular muscle coat and contains a light eosinophilic secretion. Nuclei of the prostate glands are both intra- and extracapsular. The prostate stylet conducts sperm and prostate secretion, and is a straight single-walled tube, 87-98  $\mu\text{m}$  long (mean = 91,  $n = 3$ ), tapering from 12  $\mu\text{m}$  to 5  $\mu\text{m}$  in the specimens from Florida. The animals from the Galapagos have stylets 47-58  $\mu\text{m}$  long ( $n = 2$ ). The stylet lies in a narrow canal sur-

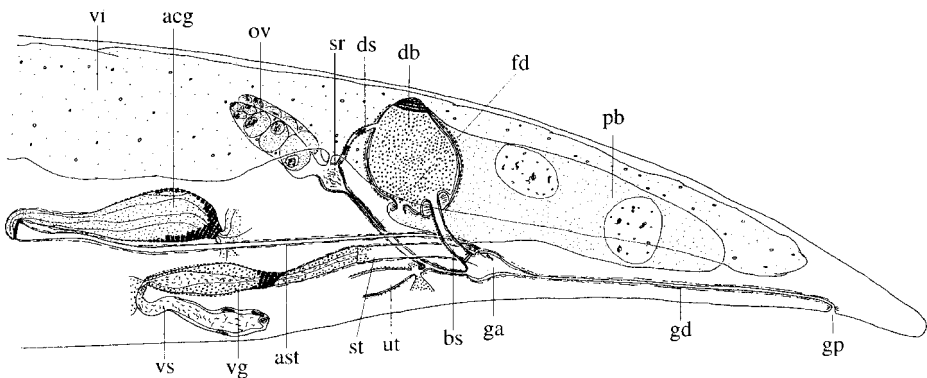


Fig. 3. — *Phonorhynchoides haegheni* n. sp. Reconstruction of the atrial system from the left hand side.

rounded by a longitudinal muscle sheath only (at least, no epithelium could be seen). This muscle sheath is continuous with the muscles of the genital atrium.

The accessory secretion reservoir, to which the accessory stylet is connected, is much larger than the prostate vesicle. It is elongated, ovoid, surrounded by a spirally-running, almost circular muscle coat and filled with a basophilic secretion. The (five?) glands that produce this secretion each have a very large extracapsular nucleated part. Towards the accessory stylet the reservoir narrows to form a broad duct. In sectioned material, the accessory reservoir is invariably orientated with its distal end in the cephalic direction, with the duct turning over  $180^\circ$  towards the accessory stylet. The accessory stylet is slender, slightly bent, and ends in a sharp point. In the specimens from Florida it is 264-325  $\mu\text{m}$  long (mean = 294,  $n = 3$ ) and 3  $\mu\text{m}$  broad in its middle. It tends to be shorter in the Galapagos individuals: 209-279  $\mu\text{m}$  ( $n = 2$ ).

The female bursa is large and divided into a muscular part and a resorbent part, connected to one another via a muscular pore. The muscular part is globular, surrounded by an outer circular and an inner longitudinal muscle coat, and is filled with an eosinophilic secretion. In some specimens it also contains some sperm. Its epithelium is reduced to a pseudocuticula, which is folded in the distal part. The bursal stalk, coming from the genital atrium, enters this part of the bursa ventrally. The distal part of the bursal wall folds back giving the impression of a thimble surrounding the proximal part of the bursal stalk. The bursal stalk is covered with a low epithelium, in some specimens reduced to a pseudocuticula, and is mainly surrounded by circular muscles and some longitudinal inner muscles near the common genital atrium. A sphincter guards the most proximal part of the stalk. Distally from this sphincter longitudinal muscles attach to the stalk and run towards the distal wall of the muscular part of the bursa. The insemination duct leaves the muscular part of the bursa dorsally and joins the seminal receptacle to which the short oviducts are connected. This duct is lined with a pseudocuticula and is surrounded by a circular muscle coat. In the specimens from Florida it is rather short, but it is somewhat longer in the Galapagos specimens. The female duct, connecting the seminal receptacle with the uterus, is long and narrow, with a very thin epithelium and mainly thin longitudinal muscles. Outer circular muscles, however, occur at both ends. The uterus joins the female duct in the proximity of the atrium.

*Discussion.* The Florida and Galapagos populations of this species exhibit some minor differences: in the Galapagos specimens the insemination duct is slightly longer and the size of the accessory glandular organ is somewhat larger. Both populations also differ in the length of the hard parts, both stylets being longer in the specimens from Florida. However, the proportions of the lengths of the prostate stylet and the accessory stylet can be considered the same. In the Florida population the main stylet is 31% of the accessory stylet on average (28-33%), while it is 22% (21-22%) in the population from the Galapagos. Similar variation in length can be found in other, congeneric species (T.J. ARTOIS pers. obs.). However, the shape of both the accessory and main stylet is the same in both populations of *P. haegheni*, and clearly separates them from the other *Phonorhynchoides* species. In other words, the differences between the two populations of *P. haegheni* are much smaller than the differences between them and the other congeneric species. Therefore, we do not consider the differences between the populations of *P. haegheni* sufficient to attribute them to two different species.

The differences with the other species of the genus are mainly to be found in the shape and length of the hard parts. In *P. somaliensis*, *P. carinostylis* Ax &



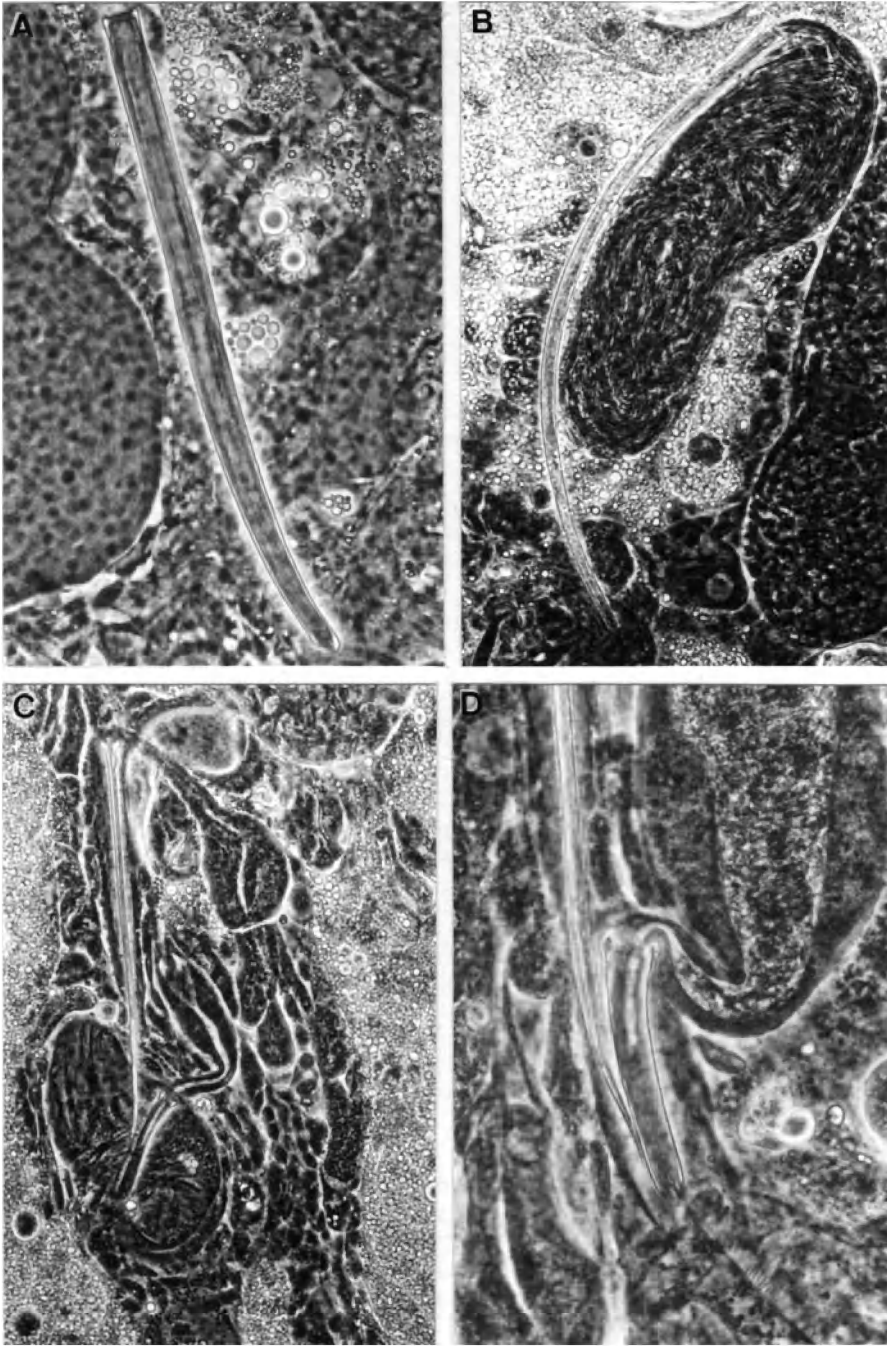


Fig. 4. — *Djeziraia incana* n. sp. A, stylet; B, exceptionally long stylet; *Phonorhynchoides haegheni* n. sp. C, atrial organs; D, stylet and distal tip of accessory stylet (all from live animals).

Armonies 1987 and *P. flagellatus* Beklemishev 1927 the main stylet is much longer than the accessory stylet. The main stylet is also more or less corkscrew-shaped in these three species, while it is straight in *P. haegheni*. The division of the bursa into a muscular and a non-muscular part is only found in *P. haegheni*.

***Parachrorhynchus jondelii* n. sp. (Figs 5-6)**

*Locations.* Santa Cruz: Bahia Academy: Southern Beach (IX. 6c) (type locality).

*Material.* Drawings and photographs by S. Hoxhold of one live animal that was later sagittally sectioned (holotype).

*Derivation of the name.* Named after Dr Ulf Jondelius (Uppsala University, Uppsala, Sweden).

*Description.* The animals are 0.7-0.8 mm long, colourless, with two eyes. The epithelium is 3 µm high with cilia 4 µm long. Rhabdites are rod-shaped, about 3/4 of the height of the epithelium in length; they are lacking around the proboscis pore and are especially numerous around the caudal end, where a more ovoid kind of rhabdites is also present. The caudal glands are well developed.

The proboscis is about 20% of the body length. An inner circular and an outer longitudinal muscle sheath surround the proboscis cavity. Neither the cone nor the proboscis cavity has intra-epithelial nuclei; nuclei are obviously insunk in the cell mass around the proboscis bulb (see SCHOCKAERT & BEDINI 1977 regarding *Polycystis naegelii*). The exact organisation of the motional muscles of the proboscis is difficult to determine, but the number of retractors and integument retractors appears to be three and two pairs, respectively.

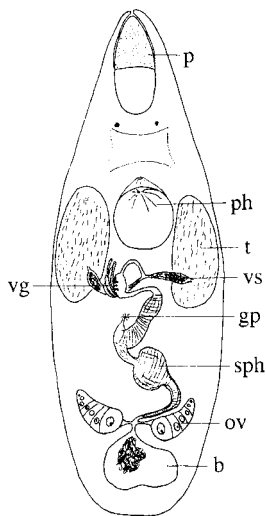


Fig. 5. — *Parachrorhynchus jondelii* n. sp. General organisation (from a live animal).

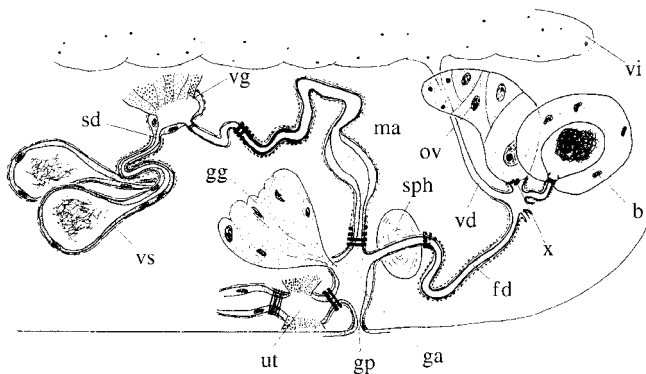


Fig. 6. — *Parachrorhynchus jondelii* n. sp. Reconstruction of the atrial organs from the left hand side.

The pharynx is situated in the first body half and is inclined slightly forwards. It is of the normal polycystidid type with the usual two kinds of glands, and the four sclerotized teeth at the proximal opening of the pharyngeal lumen. There are 24 internal longitudinal muscles.

The gonads are paired. The rather small testes lie dorsolaterally, just behind the pharynx, the ovaries just behind the gonopore. Both vitellaria extend dorsolaterally, from behind the proboscis to the caudal end of the animal. Here they are very close and may even be connected to each other. The genital pore is at 75% and surrounded by a sphincter of six to seven muscle fibres. The common genital atrium is lined by a low epithelium with very few nuclei, and surrounded by longitudinal muscles. A large bundle of eosinophilic glands enters the atrium above the uterus, which joins the atrium through the anterior wall. It is of the normal polycystidid type.

The seminal vesicles are lined with a low nucleated epithelium and have one layer of mainly longitudinal muscles. They join to form a long seminal duct, which has an anucleated epithelium and is surrounded by a thin longitudinal and a thicker outer circular muscle sheath. It enters a vesicle in which also the prostate glands empty their contents. This vesicle can be considered the prostate vesicle (in comparison with the other species of Duplacrhorhynchinae). It is lined with a high nucleated epithelium and surrounded by spiral muscles. There are two kinds of prostate glands, eosinophilic and basophilic ones, both with coarse granules. The seminal duct runs towards the male atrium, eccentrically through the prostate secretion within the prostate vesicle. The male atrium leaves the prostate vesicle (through an opening with a sphincter) and enters the common atrium dorsally on the right side. The male atrium (or male duct) is lined with a low anucleated epithelium that turns into a pseudocuticula in the narrow proximal part of the duct. Towards the common atrium the male duct enlarges. In this part, the epithelium is much higher. The male atrium is surrounded by an inner longitudinal and an outer circular muscle sheath; the latter is, however, absent around the proximal part and forms a sphincter at the entrance to the common atrium.

The female duct enters the common genital atrium caudally. Here a large globular sphincter is found. The duct is covered with a pseudocuticula and is surrounded by a thin longitudinal and a thick circular muscle coat. Proximally, it receives the oviducts and the vitelloducts from both sides and continues for some distance to end in the terminal bursa. There is a ring of (10?) knobs at the entrance of the bursa. The oviducts are very short, lined by a pseudocuticula, and surrounded by circular muscles and very weak internal longitudinal muscles, which continue around the ovaries over a short distance. At the last oocyte a ring of triangular plates (probably five: x in Fig. 6) is found. The longitudinal muscles around the oviducts and ovaries seem to converge towards these plates.

*Discussion.* Three representatives of the genus *Parachrorhynchus* are now known: *P. axi* and *P. bergensis*, both described by KARLING (1956) from the North European Atlantic coast, and *P. jondelii* n. sp. The main common features of these species are the long male atrium (sometimes referred to as the cirrus), the prostate vesicle through which the seminal duct runs eccentrically (i.e. an asymmetric conjuncta type; terminology of KARLING 1956), the terminal bursa, and the oviducts that join the bursal stalk on either side.

Only *P. bergensis* has spines in the male duct. This part can be everted as a papilla (as originally described). However this "papilla" is not a permanent struc-

ture, as was subsequently observed in a live animal by the late T.G. KARLING (pers. comm.). In *P. bergensis* there is a clearly delimited male bursa (connected to the atrium by a narrow canal), in *P. axi* there is a caudal bulge at the distal end of the male duct (with a different epithelium as well), while in *P. jondelii* there is a simple enlargement at the end of the male atrium. Sperm can be stored here in the three species (not sure for *P. bergensis*).

As in *P. axi*, there is a ring of little knobs at the entrance of the bursa in *P. jondelii*. Such knobs were not observed in *P. bergensis*, but the individual on which the description was based clearly had not reached full female maturity.

The proboscis of *P. jondelii* is about 1/5 of the total body length, the most common proportion found in Polycystididae. In the two other species it is only 7-13% of the body length, a proportion found in most other Duplacrorthynchinae (see ARTOIS & SCHOCKAERT 1999). Other striking differences are the paired seminal vesicles, the huge sphincter at the female duct and the large glands entering the common atrium. A unique feature is the ring of separate plates at the ovaries. Similar structures are found in the genus *Paulodora* Marcus 1948 (the "cuticular nozzles" of SCHOCKAERT & KARLING 1975). However, the similarities may be superficial, as the appearances in both lateral and frontal views are clearly different. In *Paulodora* the "nozzle" at each ovary looks like a small umbrella with a little stalk and it is a simple circle in frontal view with no separate plates to be found. Thus the homology of this structure in *P. jondelii* and in the *Paulodora* species is not at all certain.

Most of the characters shared by the three *Parachrorhynchus* species may be considered symplesiomorphies. Within the Duplacrorthynchinae, to which *Parachrorhynchus* belongs (see ARTOIS & SCHOCKAERT 1999), they are the only species with a copulatory organ with an asymmetrical, although interposed, prostate vesicle. This character can be put forward as a likely synapomorphy.

#### Subfamily Macrorhynchinae Evdonin 1977

##### ***Macrorhynchus manusferrea* n. sp. (Figs 7-8, 11A-B)**

**Localities.** Santa Cruz: Bahia Borrero (IX. 3) (type locality). Santa Cruz: Bahia Tortuga (IX. 7b).

**Material.** Drawings and photographs of live animals by S. Hoxhold. Two serially sectioned specimens, one of them designated as holotype (sagittally sectioned).

**Derivation of the name.** The stylet is grapnel-shaped. *Manus ferrea* (Lat.): grapnel.

**Description.** According to S. HOXHOLD's notes, the live animals are unpigmented, though orange under incident light, and filled with black-brown glands under the epidermis when seen in transmitted light. However no such glands were found in sectioned material. The animals are 0.8-1.2 mm long and have a pair of eyes. The epidermis is syncytial with numerous vacuoles, most of them empty, some filled with an eosinophilic secretion. The rhabdites are small, 1/3 of the epithelium height long, slender and spindle-shaped. The coarse-grained, basophilic caudal glands are well developed.

The proboscis, 1/5 of the body length, is of the normal polycystidid construction and has three pairs of retractors and two pairs of integument retractors.

The pharynx is situated in the first body half and is inclined forwards. More or less in the middle of the prepharyngeal cavity there is a ring of a ruffled (pseudociliated) epithelium. The rest of the prepharyngeal cavity is lined with a low, anucleated epithelium. An outer longitudinal and an inner circular muscle layer surround the prepharyngeal cavity. The latter forms a sphincter between the middle and the proximal third of the cavity, but is lacking proximal to this sphincter. The pharynx contains three types of glands: two eosinophilic and one basophilic. The basophilic one opens into the pharyngeal lumen between the two eosinophilic ones, the darkest of which opens most distally.

The topography of the gonads is shown in Fig. 7A. The gonopore is situated at about 70%. The common genital atrium is lined with a pseudociliated epithelium and surrounded by longitudinal muscles.

The long pyriform prostate vesicle contains two types of secretion: a coarse-grained basophilic one and a fine-grained eosinophilic one. The musculature of the prostate vesicle and of the proximal part of the male atrium is rather complex and comparable to that of *M. groenlandicus* (Levinsen 1879) Graff 1882 as described by SCHOCKAERT & KARLING (1975). Three muscle layers surround the prostate vesicle; each of them situated outside the membrane that borders the vesicle. The inner muscle layer is more or less circular, and only covers the prostate vesicle. The outer two layers extend further along the proximal part of the male atrium. The middle

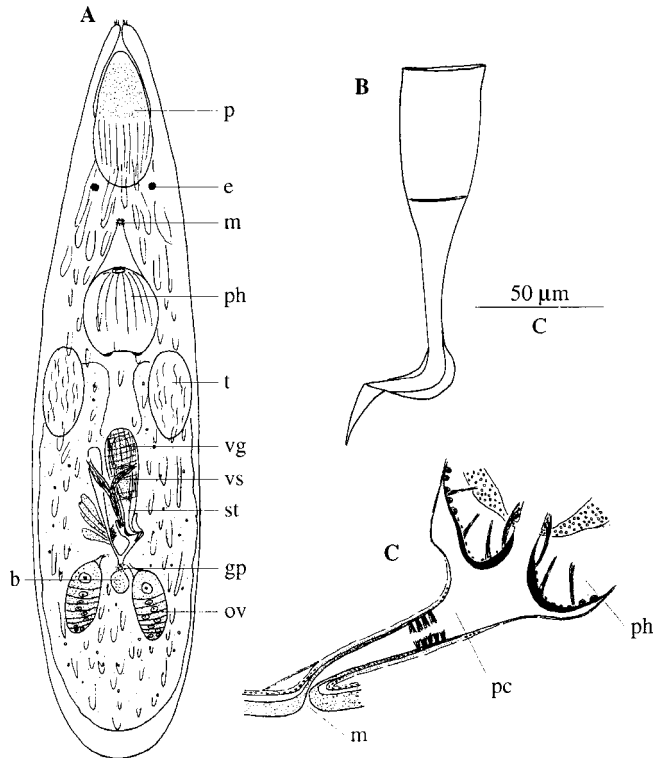


Fig. 7. — *Macrorhynchus manusferrea* n. sp. A, general organisation; B, stylet; C, section through the prepharyngeal cavity; (A-B from live animals).

layer is more or less longitudinal but becomes more spiral around the proximal part of the male atrium. The outer layer is spiral around the prostate vesicle and the major part of the male atrium, but becomes longitudinal towards the place where it attaches to the male atrium. The retraction of these fibres causes the wall of the male atrium to fold. In this fold, a strong sphincter occurs around the distal part of the stylet.

The stylet is double-walled with a 175  $\mu\text{m}$  long outer stylet and an 83  $\mu\text{m}$  long inner stylet, lying in the distal half of the outer stylet. The outer stylet is 31  $\mu\text{m}$  broad at the proximal opening, narrowing to 23  $\mu\text{m}$  in about the middle, where the inner stylet begins, and narrowing further distally to 7  $\mu\text{m}$ . The distal part of the stylet is rather complex, but has the general appearance of a hook with a gutter-shaped extension. Distally from the stylet the male atrium bends towards the common atrium, which it enters dorsally. The distal part of the male atrium is lined with a relatively high epithelium and is surrounded by a weak circular and a longitudinal muscle layer. The rest of the male atrium is covered with a pseudocuticula. A bundle of coarse-grained basophilic glands enters the male atrium dorsally at the level of the distal tip of the stylet.

The paired seminal vesicles are lined with a very low, nucleated epithelium and have a spirally-running, almost longitudinal muscle coat. The short vasa deferentia join each other under the prostate vesicle. The ejaculatory duct is relatively broad and lined with a low epithelium with flattened nuclei; it is surrounded by a circular muscle layer. It enters the male atrium ventrally through a muscular papilla close to the distal tip of the stylet. This papilla seems to end in the gutter formed by the stylet tip.

Both oviducts are very short and surrounded by a very weak circular muscle layer. Where they join, a small bursa is present, in which sperm and some necrotic nuclei were observed. The female duct is lined with a high, nucleated epithelium. It enters the common genital atrium at the same place as does the uterus,

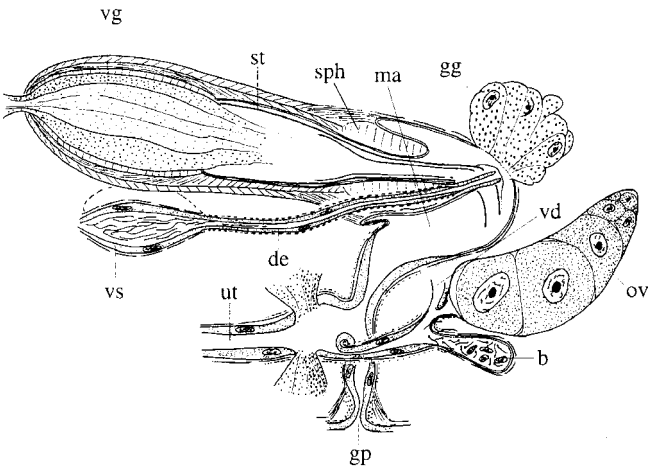


Fig. 8. — *Macrorhynchus manusferrea* n. sp. Reconstruction of the atrial organs from the left hand side.

giving the impression of a short ductus utero-communis, at least in one specimen. In one live individual the uterus contained an egg capsule with four fully-grown young (Fig. 11A).

**Discussion.** *M. manusferrea* shows the autapomorphies of the genus as given by ARTOIS & SCHOCKAERT (1998): three pairs of proboscis retractors supplemented with two pairs of integument retractors, the long stylet with a short internal stylet and complex ending. Within the genus, it most resembles *M. groenlandicus* (Levinson 1879) Graff 1882. In both species the ejaculatory duct enters the male atrium through a muscular papilla. Furthermore, in both species a bundle of glands opens in the male atrium at the distal tip of the stylet. In *M. groenlandicus* these glands are eosinophilic and rather diffuse (SCHOCKAERT & KARLING 1975), while they are basophilic with coarse granules in *M. manusferrea*. Nevertheless they may be considered homologous in the two species, and the different appearance of the secretion due either to the condition of the animals or a fixation or staining artefact.

*M. manusferrea* clearly has a female bursa, resembling that of the *Polycystis* species (see ARTOIS & SCHOCKAERT 1998). A female bursa has not been observed in *M. groenlandicus* (see SCHOCKAERT & KARLING 1975). The presence of such an organ in *M. croceus* (Fabricius 1823) Graff 1882 is mentioned by GRAFF (1905), although not in his monograph of 1882. MEIXNER (1925) explicitly denies the presence of such a bursa, and our own observations on material of *M. croceus* confirm MEIXNER's statement. It could be assumed that the female bursa is a temporary formation, formed just before or after copulation. But this is again contradicted by the observations of sperm in the oviducts and the stroma around the ovaries in *M. groenlandicus* without any trace of a bursal organ (SCHOCKAERT & KARLING 1975).

As to biogeography, *M. manusferrea* is the first *Macrorhynchus* species found outside the Atlantic, except for a doubtful record of *M. croceus* in the Adriatic Sea by GRAFF (1913) (see SCHOCKAERT & KARLING 1975). Moreover it is by far the southern most record of the genus, Massachusetts (USA) being until now the southern most boundary (SCHOCKAERT & KARLING 1975). There is one record of *M. croceus* in the Canary Islands by GRAFF (1913) but this was also considered doubtful by SCHOCKAERT & KARLING (1975).

#### Subfamily Polycystidinae Schockaert & Karling 1970

##### ***Polycystis ali* Schockaert 1982**

**Locality.** Santa Cruz: Bahia Academy: northern side (IX. 5b).

**Distribution.** East African Coast: from Somalia (SCHOCKAERT 1982) to Kenya (E.R. SCHOCKAERT pers. obs.). California (USA): several places at Pacific Grove, in tidal pools and shallow water (KARLING 1986).

**Material.** Five serially sectioned specimens and drawings of live animals by S. Hoxhold.

**Additional information.** The internal organisation of the specimens from the Galapagos does not differ from earlier descriptions (SCHOCKAERT 1982), nor from that of *P. naegelii* Kölliker 1845 (see the description by KARLING 1956).

*P. ali* has been found in three distant localities (see above), and KARLING (1986) gave the three populations different names as "formas". The Somali and Galapagos

populations are both uniformly blue-black and the stylet is almost the same size and shape. However, no whole mounts are available of the Galapagos material and a close comparison is difficult. The Californian specimens are colourless and the stylet is considerably larger. The latter population may thus represent a separate species, while the Somali and Galapagos representatives might be conspecific.

***Paulodora felis*** (Marcus 1954) Artois & Schockaert 1998 *asymmetrica* n. subsp. (Figs 9-10, 11C-D)

*Locality in the Galapagos (P. felis asymmetrica).* Santa Cruz: Bahia Academy: southern beach (IX. 6b).

*Distribution of P. felis felis.* Brazil (MARCUS 1954), Jamaica (THERRIAULT & KOLASA 1999), Mexico: Mazatlan, algae in a tidal pool on rocks in front of Hotel Valentino (4.XII.1996) (own data). Curaçao: Dam di Cabicuchi (Spaanse Water) at the side of the Spaanse Water; mixed algae (mainly *Caulerpa* and *Halimeda gantia*) with a lot of detritus on the thallus (14.XII.1998 and 30.XII.1998) (own data).

*Material.* Galapagos: drawings and photographs of live animals by S. Hoxhold. Several serially sectioned animals. Brazil: two whole mounts and three serially sectioned specimens

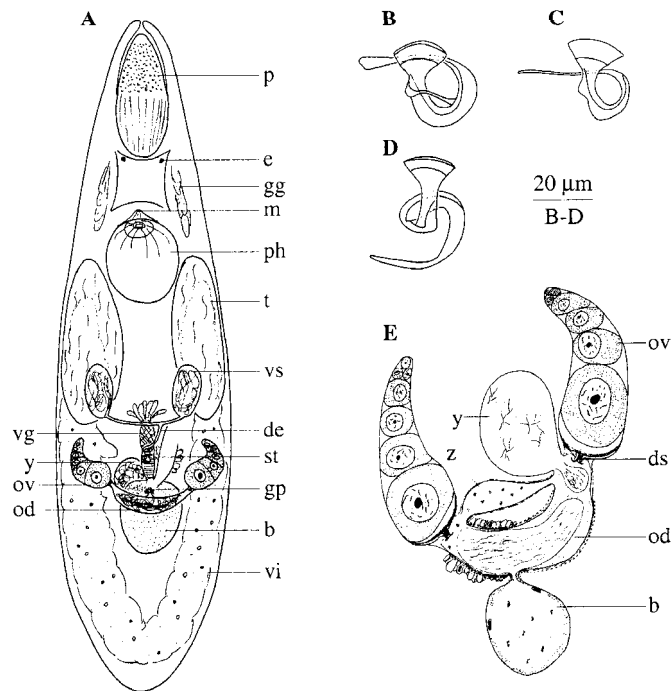


Fig. 9. — *Paulodora felis asymmetrica* n. subsp. A, general organisation; B-D, stylets of different specimens; E, reconstruction of the female atrial organs from above (bursal stalk and female duct not indicated) (A-D from live animals).



(material from E. Marcus in the Swedish Museum of Natural History, Stockholm). Curaçao: six whole mounts. Jamaica: one whole mount (leg. J. Kolasa). Mexico: three whole mounts.

*Derivation of the name.* The name of the subspecies refers to the asymmetrically-built female system.

*Description.* The stylet is almost identical in all populations examined. It is double-walled, with an inner stylet that can be observed over most of the length of the outer stylet. In its course, the stylet makes a turn of about 270°. As a result, the distal part runs perpendicular to the proximal part. When heavily squeezed, the distal part can fold downwards, giving the stylet the shape of a sickle. The outer stylet has a flap-like projection in its proximal part (sometimes difficult to observe) along which the sperm are drained. The length of the stylet is comparable in the different populations: 77-88 µm (mean = 84, n = 6) (Galapagos), 77-84 µm (mean = 81, n = 2) (Brazil), 76-82 µm (mean = 79, n = 2) (Mexico), 73 µm (Jamaica) and 81-92 µm (mean = 90, n = 6) (Curaçao). The large male bursa is connected to the male atrium by a short bursal stalk, leaving the male atrium through its caudal wall, close to the common atrium.

The female duct is rather long and narrow, lined with a high, nucleated epithelium and with a thin longitudinal muscle coat. It leaves the common atrium at the caudal side, runs forwards and bifurcates into the oviducts above the stylet. The oviducts are enlarged and filled with sperm, clearly functioning as seminal receptacles, and are surrounded by an inner longitudinal and an outer circular muscle sheath. Near the ovaries the longitudinal muscles become thinner, whereas the circular muscles are lacking completely. The female system is connected to the male bursa by a muscular pore at the bifurcation of the female duct. In the specimens from the Galapagos the female system is asymmetrically built. On the right side, the oviduct is coated by a relatively high epithelium, with some nuclei in some individuals. A large sperm-receiving vesicle (y in Figs 9-10) is connected to the oviduct by a broad pore near the ovary. In some specimens the vesicle is completely filled with a diffuse material, the epithelium is unclear, and no sperm are apparent. In other individuals it is completely filled with sperm and lined by a

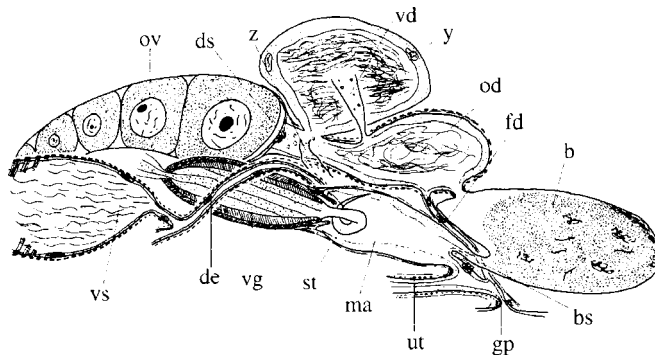


Fig. 10. — *Paulodora felis asymmetrica* n. subsp. Reconstruction of the atrial organs from the left hand side with omission of the left hand side of the female system.

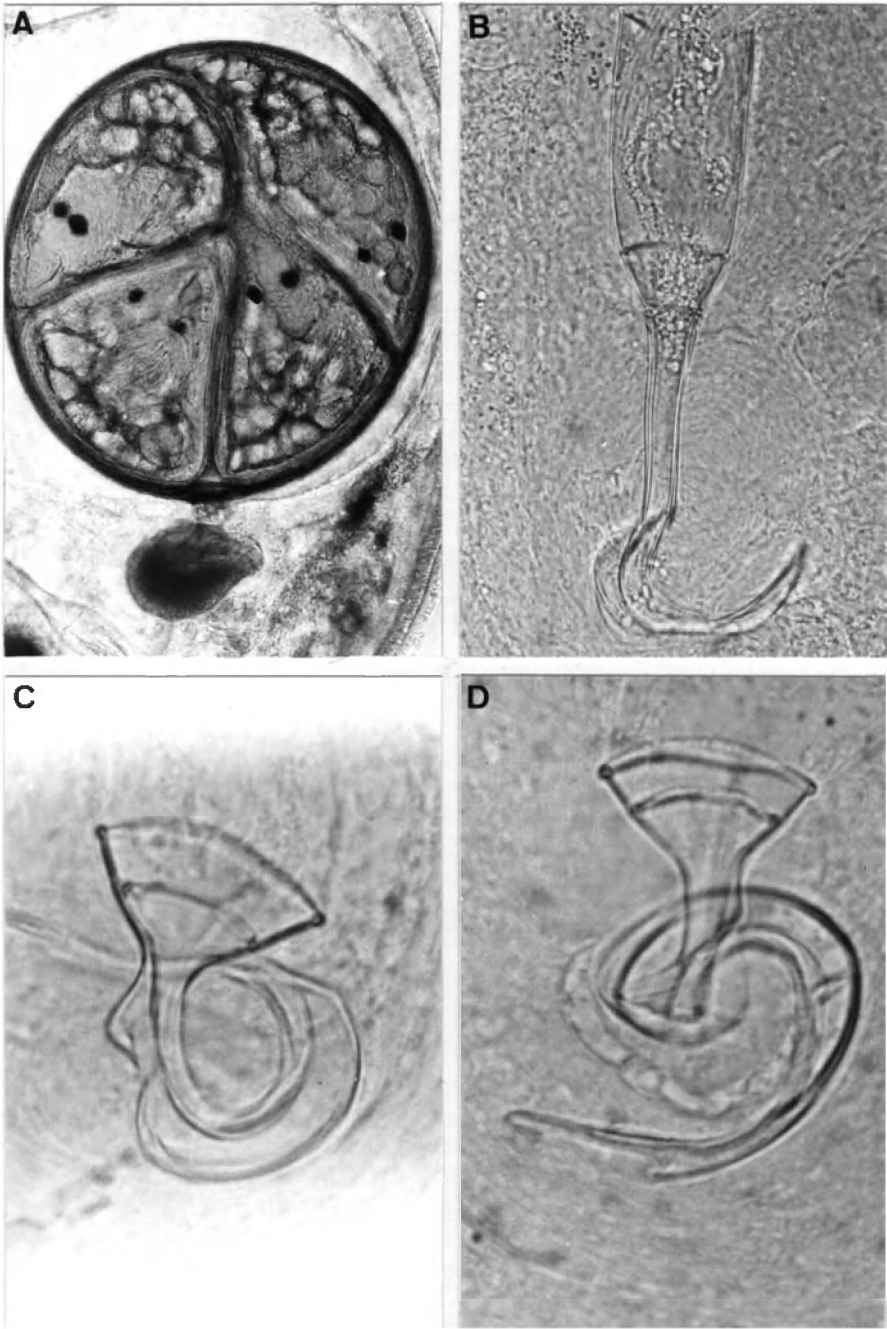


Fig. 11. — *Macrorhynchus manusferrea* n. sp. A, uterus with an egg capsule containing four young specimens; B, stylet; *Paulodora felis asymmetrica* n. subsp. C, stylet; D, stylet of another specimen (all from live animals).

high, nucleated epithelium. The left ovary always has a slightly more caudal position than the right ovary. Here a separate sperm-receiving vesicle is lacking. The left oviduct differs from the right one in that it is lined by an epithelium whose nuclei are underneath the muscles, and which probably has a secretory function. In the specimens from the Galapagos, a "bridge" (z in Figs 9-10) connects the proximal ends of the oviducts to each other. It is broad on the left side, narrow on the right side. It is surrounded by very thin longitudinal muscles, lined by a very low, nucleated epithelium and filled with fine granular, eosinophilic material, which is condensed in some places.

*Discussion.* The new subspecies differs from the nominal subspecies *P. felis felis* (Marcus 1954) in the construction of the female system. According to MARCUS (1954), the bursa enters the genital atrium from behind, with the exit of the female duct above it. Re-examination of MARCUS's material revealed that the situation is, instead, the same as described here for *P. felis asymmetrica*. There are, however, some major differences: the right and left oviducts are the same in *P. felis felis*, without the glandular epithelium on the left oviduct, nor the large vesicle on the right one. A "bridge" between the ovaries does not exist. These differences may justify giving the new taxon the status of species. However, with the material available, no differences can be found in the construction of the stylet. As the shape of the stylet is very typical for species within the genus *Paulodora* Marcus 1948 and to avoid later confusion, we prefer to keep the two taxa within the same species, even though the differences obviously can clearly be seen in living specimens that have reached full female maturity.

The two subspecies are clearly geographically separated: all individuals found on the Atlantic side of the Americas belong to *P. felis felis*. So far, *P. felis asymmetrica* has only been found in the Galapagos.

#### Subfamily Gyratricinae Graff 1905

#### *Gyratrix hermaphroditus* Ehrenberg 1831 species complex (Fig. 12)

*Localities.* (a) Colourless variant (Galapagos species I). Jervis North (VIII. 1). Santa Cruz: Playa Borrero: coarse sand in rock pools (IX. 2). Santa Cruz: Bahia Borrero: coarse sand in rock pools (IX. 3). Santa Cruz: Bahia Academy: northern side (IX. 5b). Santa Cruz: Bahia Tortuga: coarse sand in rock pools at the edge of mangroves (IX. 7). Barrington: coarse sand in rockpools (XI. 1). (b) Yellowish variant (Galapagos species II). Santa Cruz: Bahia Academy: southern beach (IX. 6b). Barrington: fine sand in rock pools (XI. 1). (c) Reddish variant (Galapagos species III). Santa Cruz: Bahia Academy: southern beach (IX. 6b).

*Other localities.* Recorded from all over the world in fresh water, brackish and marine localities.

*Material.* Several live animals studied by S. Hoxhold. Sectioned specimens: 20 colourless specimens, 5 yellowish specimens and 2 reddish specimens.

*Additional data and discussion.* This euryhaline cosmopolitan was found abundantly in several localities in the Galapagos and in three colour variants: colourless, yellowish and reddish.

The colourless and yellowish variants have eyes and their internal organisation corresponds with the descriptions found in the literature (e.g. KARLING 1963).

The colourless variant can reach a length of 1.5 mm. The measurements (n = 7) of the hard parts are: stylet 112-151  $\mu\text{m}$  (mean = 121), sheath 25-35  $\mu\text{m}$  (mean = 31), stalk of sheath 47-78  $\mu\text{m}$  (mean = 60).

The yellowish variant tends to be smaller, about 1 mm long. Measurements (n = 5) of hard parts: stylet 115-122  $\mu\text{m}$  (mean = 118), sheath 27-29  $\mu\text{m}$  (mean = 28), stalk 77-86  $\mu\text{m}$  (mean = 82).

The reddish variant is 0.8-0.9 mm long and has no eyes. The internal organisation of these specimens deviates from all former descriptions and from the other two variants from the Galapagos in the organisation of the female system. The external vagina is situated ventrally between the male and the female pore. It opens almost immediately into the bursa. Opposite the vagina, the bursa shows a flattened space with a thick sclerotized roof (w in Fig. 12). From this "roof", longitudinal muscles run in all directions towards the ventral side of the bursa and are continuous with the longitudinal muscles that surround the bursa. In the frontal part

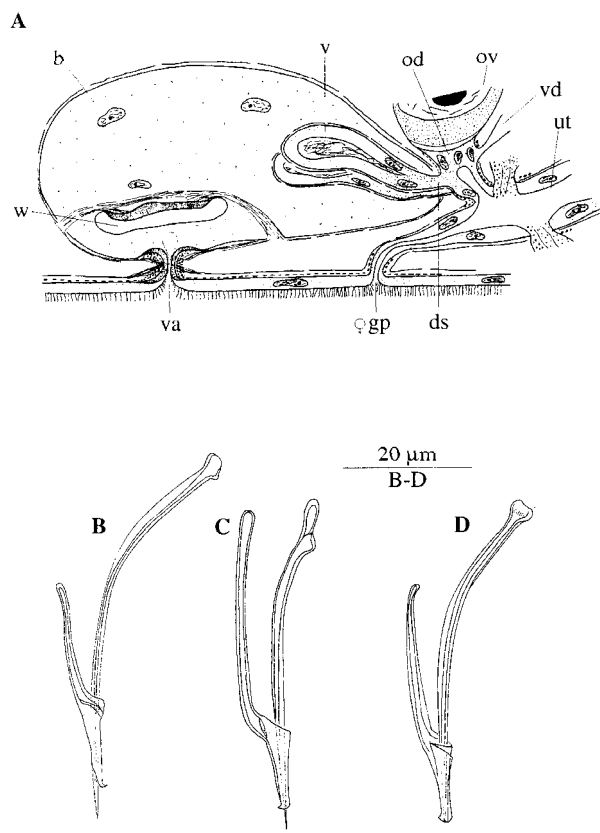


Fig. 12. — *Gytratrix hermaphroditus*. A, reconstruction of the female system from the right hand side; B, stylet of the reddish form; C, stylet of the yellowish form; D, stylet of the colourless form (B-D from live animals).

of the bursa are two separated compartments filled with sperm (v in Fig. 12). They narrow towards the frontal rim of the bursa and are connected with the oviduct by two short insemination ducts (only one in other *Gyratrix* species). A high nucleated epithelium and longitudinal muscles surround them. The epithelium of the distal, narrower part of the compartments is comparable with that of the oviduct, while the epithelium of the proximal part stains less deeply. The measurements ( $n = 2$ ) of the hard parts are: stylet 171-175  $\mu\text{m}$ , sheath 34-36  $\mu\text{m}$ , stalk 50-59  $\mu\text{m}$ .

The strong polymorphism of *G. hermaphroditus* has been known for a long time; GRAFF named a first subspecies in 1905 (*G. hermaphroditus coeca*) and a second one in 1911 (*G. hermaphroditus maculata*). Karyological studies have also revealed wide variation within the species (REUTER 1961, L'HARDY 1986, several contributions by CURINI-GALLETTI & PUCCINELLI: see references in CURINI-GALLETTI & PUCCINELLI 1998). These last authors consider the taxon as a species complex with many sibling species, some even occurring sympatrically. Karyotypes, size, and proportions of the hard parts may vary considerably. It is clear that in the Galapagos at least three "species" are present (Galapagos species I-III).

The *G. hermaphroditus maculata* of GRAFF (1911) is the only yellow variant known. However, here yellow corpuscles within the animal cause the yellow colour. In the Galapagos population the animals are uniformly yellowish. The only red variant known so far was found by DE BEAUCHAMP (1942) in the intestine (taken as food?) of some Oligochaeta from an aquarium in Rennes. Eyeless variants, *G. hermaphroditus coeca* Graff (1905), were previously only recorded from fresh water in places with little or no light: the deep waters of Lake Geneva, wells in Bohemia (Czech Republic), but also in some floods in Moscow (for references: see GRAFF 1913). The red *G. hermaphroditus* of the Galapagos is thus the first free-living marine variant that is red and without ocelli. Moreover, it also deviates in its anatomy from the other representatives of the species complex. We refrain, however, from naming it formally, avoiding further confusion, and consider it a member of the species complex that can easily be recognised on morphological grounds.

#### DIAGNOSES OF THE NEW TAXA

*Djeziraia incana* n. sp. *Djeziraia* species with a very long, slender stylet (162-198  $\mu\text{m}$ ; 295  $\mu\text{m}$ ) with a terminal opening. Short female duct entering the bursal stalk in about the middle. Sperm duct with circular muscle sheath only around both ends, and without sclerotized "horns".

*Phonorhynchoides haegheni* n. sp. *Phonorhynchoides* species with a single-walled prostate stylet; 53 (Galapagos), 91 (Florida)  $\mu\text{m}$  long. Accessory secretion reservoir very large, with a large extracapsular part. Accessory stylet single-walled: 243 (Galapagos), 294 (Florida)  $\mu\text{m}$  long. Bursa with a strong muscular distal part, connected to the proximal part by a muscular pore. Insemination duct and bursal stalk leave the muscular part of the bursa at different places.

*Parachrorhynchus jondelii* n. sp. *Parachrorhynchus* species with a proboscis  $\pm$  20% of the body length. Copulatory organ with an unarmed male atrium (cirrus), the terminal part enlarged as male bursa. Seminal vesicles paired. Bundle of atrial glands present. Female duct distally with a large sphincter. Bursal entrance sur-

rounded by small teeth. Oviducts proximally provided with a kind of closing apparatus consisting of triangular plates.

*Macrorhynchus manusferrea* n. sp. *Macrorhynchus* species in which the ejaculatory duct enters the male atrium through a ventral muscular papilla at the distal tip of the stylet. Accessory glands in the male system present. Double-walled stylet grapnel-shaped, 175  $\mu$ m long. Small female bursa present at the proximal end of the female duct.

*Paulodora felis* (Marcus 1954) Artois & Schockaert 1998. *Paulodora* species with a 73-92  $\mu$ m long stylet. The distal part of the stylet runs perpendicular to the proximal part in live animals; when squeezed it can have the shape of a sickle. The female duct is rather long, and communicates with the male bursa through a muscular pore at the level of its bifurcation into both oviducts. The oviducts function as seminal receptacles.

*P. f. felis* (Marcus 1954). Female system symmetrical, without additional sperm-receiving vesicle. Without a connection ("bridge") between the proximal ends of both oviducts.

*P. f. asymmetrica* n. subsp. Female system asymmetrical. Additional sperm-receiving vesicle connected to the proximal part of the right oviduct. Left oviduct without such a vesicle. Nuclei of the epithelium of the left oviduct insunk under the muscle sheaths. Proximal ends of both oviducts connected by a "bridge".

#### POLYCYSTIDIDAE OF THE GALAPAGOS: SPECIES LIST

##### Duplacrhorhynchinae Schockaert & Karling 1970

*Djeziraia incana* n. sp.

*Phonorhynchoides haegheni* n. sp.

*Parachrorhynchus jondelii* n. sp.

##### Macrorhynchinae Evdonin 1977

*Macrorhynchus manusferrea* n. sp.

##### Polycystidinae Schockaert & Karling 1970

*Polycystis ali* Schockaert 1981

*Paulodora felis* (Marcus 1954) *asymmetrica* n. subsp.

##### Porrocystidinae Evdonin 1977

*Austrorhynchus galapagoensis* Artois & Schockaert 1999

*Galapagorhynchus hoxholdi* Artois & Schockaert 1999

*Pygmorhynchus pygmaeus* Artois & Schockaert 1999

##### Gyratricinae Graff 1905

*Gyratrix hermaphroditus* Ehrenberg 1831

Colourless variant (Galapagos species I)

Yellowish variant (Galapagos species II)

Reddish variant (Galapagos species III)

##### Typhlopolycystidinae Evdonin 1977

*Myobulla myobulla* Artois & Schockaert 2000

*Myobulla dunata* Artois & Schockaert 2000  
*Sabulirhynchus axi* Artois & Schockaert 2000  
*Limipolycystis* sp.

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