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Taxonomy and phylogeny of the Archimonocelididae Meixner, 1938 (Platyhelminthes, Proseriata)

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Abstract

The family Archimonocelididae Meixner, 1938 has been revised. The family contains two subfamilies, each comprising two genera: the Archimonocelidinae with *Archimonocelis* Meixner, 1938 and *Meidiama* Marcus, 1946, and the Calviriinae subfam. nov. with *Asilomaria* Karling, 1966 and *Calviria* gen. nov. with 20, 2, 1, and 3 species, respectively, 13 of which are new to science.

The type species of the family is redescribed. Material of all the Archimonocelididae genera has been studied and supplementary remarks are made on some known species. The karyotype of 14 species is described.

Archimonocelis has a cosmopolitan distribution while *Meidiama* is restricted to the South American coast, *Calviria* to the Mediterranean, and *Asilomaria* to the Pacific North American coast.

The phylogenetic relationships within the family are analysed.

Résumé

La famille des Archimonocelididae Meixner, 1938 a été revisée. La famille contient deux sousfamilles qui chacune couvrent deux genres: les Archimonocelidinae avec *Archimonelis* Meixner, 1938 et *Meidiama* Marcus, 1946, et les Calviriinae, nouvelle sousfamille, avec *Asilomaria* Karling, 1966 et *Calviria*, nouveau genre. Les genres contiennent respectivement 20, 2, 1, et 3 espèces dont 13 sont nouvelles et qui sont décrites.

L'espèce type de la famille est redécrite. Plusieurs espèces, dans chacun des différents genres, sont également étudiées et des données supplémentaires sur plusieurs espèces connues sont dispensées. Le caryotype de 14 espèces est décrit.

Archimonocelis a une distribution cosmopolite. Les autres genres montrent une distribution très réduite: *Meidiama* habite les côtes Sud-Américaines, *Calviria* est connue de la mer Méditerranéenne tandis que *Asilomaria* est trouvée sur la côte Est de l'Amérique du Nord.

Les relations phylogénétiques dans la famille sont également analysées.

Introduction

Meixner (1938) subdivided the Monocelididae Hofsten, 1907 into the Monocelidinae, Coelogynoporinae, and Archimonocelidinae. The latter subfamily contained the two genera *Archimonocelis* and *Monotoplana*, for which a new family was erected by Ax (1958). Karling (1966a) elevated the Coelogynoporinae to the family level and grouped all other Monocelididae into one taxon. In 1978, he introduced the subfamily Minoninae, provisionally keeping all remaining monocelids in the subfamily Monocelidinae. The taxon Archimonocelidinae sensu Meixner had thus disappeared.

E.M. studies of the hard structures of the copulatory organ of the Proseriata (E. Martens, 1984), as well as karyological studies (Curini-Galletti et al., 1984), suggested that *Archimonocelis* should be removed from the Monocelididae.

A systematic revision of the Monocelididae revealed that the genera *Meidiama* Marcus, 1946 and *Asilomaria* Karling, 1966 could not be placed in that family (as already suggested by Karling, 1966a). For the three genera mentioned above, excluded from the Monocelididae, and for a new genus, the taxon Archimonocelidinae Meixner, 1938 was reintroduced at a family level (Martens & Schockaert, 1988).

The relationships within this family have already been traced by Martens & Schockaert (1988), however, only the apomorphies of the different taxa on which the new system was based were dealt with.

In the present paper the morphological data on which the system is based are presented in more detail, together with the description of new taxa and redescription of some species.

Material and methods

Animals were collected by the authors in sandy habitats, from the intertidal to sublittoral areas. Extraction, preservation, and histological techniques as routinely adopted for Proseriata were used (see P. Martens, 1984 and Martens et al., 1988).

The karyotype was determined in lactic-acetic orcein stained spermatogonial mitoses, as described by Curini-Galletti et al., 1989. Relative lengths (r.l. = length of chromosome × 100 / total length of haploid genome) and centromeric indices (c.i. = length of short arm × 100 / length of entire chromosome) were obtained from measurements of camera lucida drawings of 5–10 metaphase plates for each species. Idiograms (Figs. 17, 27) are based on karyometrical data presented in the karyotype formula: haploid genome absolute length in μm, fundamental number, relative length and centromere index of each chromosome; chromosome nomenclature between parentheses (m = metacentric; sm = submetacentric; st = subtelocentric; t = acrocentric). The fundamental number (NF) is according to Matthey (1949) and chromosome nomenclature is according to Levan et al. (1964).

Type material of new species is deposited in the Zoological Collection of the Department SBG, Limburgs Universitair Centrum (ZC-LUC), Diepenbeek, Belgium.

Abbreviations used in the figures

a : atrium
ag : accessory glands
aco : accessory glandular organ
acsp : accessory spines
b : bursa
br : brain
cn : cnidoblast
co : copulatory organ
dp : diaphragm
en : intestine
fd : female duct
fg : female glands
fp : female pore
frg : frontal glands
gic : genito-intestinal canal
gis : genito-intestinal system
hg : adhesive glands
kd : cephalic gut
mp : male pore
od : oviduct
ov : ovary
pcg : prepenial glandular complex
pg : prostate glands
ph : pharynx
phg : pharyngeal glands
pp : penis papilla
s : stylet
sd : seminal duct
sev : subepidermal vesicles
sp : spines
spi : spiculae
sta : statocyst
t : testes
v : vagina
vg : prostate vesicle
vi : vitellary
vs : seminal vesicle

Taxonomic account

Archimonocelididae Meixner, 1938

Diagnosis. – Proseriata with statocyst, without pigmented eyes, with cephalic gut and brain capsule. Pharynx in second half of body. Male and female genital pores separate. One pair of ovaries in front of pharynx, at its base, or anterior to vitellaria. Common female duct present. With or without vagina and genito-intestinal "connection". Copulatory organ with or without a stylet, either with or without spines. Vesiculae seminales paired or single, lying outside the bulbus. Hard structures of intracellular origin. With or without an accessory glandular organ (prostatoid).

Type genus: *Archimonocelis* Meixner, 1938.

Subfamily **Archimonocelidinae** Meixner, 1938

Diagnosis. – Archimonocelididae with a pharynx with or without a strongly developed oesophagus. Ovary in front of vitellaria and lateral to testes. With or without cnidosacs in epidermis. Copulatory organ with stylet. Accessory glandular organ, if present, not separated from male atrium. Long common female duct present.

Type genus: *Archimonocelis* Meixner, 1938.

Key to the genera

– With cnidosacs and a horizontal slender pharynx .... *Archimonocelis* Meixner, 1938
– Without cnidosacs and with a vertical short pharynx .... *Meidiama* Karling, 1966

Genus *Archimonocelis* Meixner, 1938

Diagnosis. – Archimonocelidinae with cnidosacs lying in one median, dorsal row. With a long tubiform, horizontally oriented pharynx. Copulatory organ with a stylet that may be surrounded by spines. With or without accessory glandular organ.

Type species: *Archimonocelis mediterranea* Meixner, 1938.

Key to the species (see also the pictoral key (Fig. 14))

1. – With one vesicula seminalis 2
   – With two vesiculae seminales 6
2. – With accessory glandular organ .... *A. meixneri* sp. n.
   – Without accessory glandular organ 3
3. – Copulatory organ with many spines (> 100) .... *A. carmelitana* sp. n.
   – Copulatory organ with much less than 100 spines 4
4. – Spines all alike, with a distal long, arched hook on the outside of the straight tip ....*A. koinocystis* Karling, 1966
   – With different kinds of spines 5
5. – With two different kinds of spines: two large, hooked spines with curved tip as long as stylet (± 63 μm) and about twelve straight spines gradually increasing in length (37–58 μm), without curved tip and with a subterminal hook .... *A. crucifera* sp. n.
   – All spines with curved tip and subterminal hook; two of them large and almost as long as stylet (54–59 μm); others (10–16 in number) smaller and of similar length (about 35–38 μm) .... *A. puertoricana* sp. n.
   – All spines with curved tip and subterminal hook; four spines nearly as long as stylet (45–48 μm), two of them being distinctly broader. Six to eight smaller spines (about 32 μm long) .... *A. inopinata* sp. n.
6. – With accessory glandular organ 7
   – Without accessory glandular organ 10
7. – With more than 5 accessory spines 8
   – With about 70 spines and only 3–4 accessory spines ... . *A. semicircularis* Karling, 1966
8. – With small stylet ± 50 μm long, accessory spines of four different kinds .... *A. oostendensis* Martens & Schockaert, 1981
   – Accessory spines of almost same shape 9
9. – Stylet curved, ± 100 μm long, 2 large spines and about 25 smaller ones, with about 20 accessory spines ....*A. staresoi* sp. n.
   – Stylet straight, ± 77 μm long, with 27–35 spines slightly differentiated in shape and about 10 accessory ones ... . *A. sabra* sp. n.
10. – Without spines 11
    – With spines 12
11. – With a short, ± 28 μm long, straight stylet ....*A. keke* Martens & Curini-Galletti, 1989
    – With curved stylet, about 68 μm long, with a 35 μm broad base .... *A. itoi* Tajika, 1981
    – With curved stylet, about 75 μm long, with a 12 μm broad base .... *A. glabrodorsata* sp. n.
12. – With only 4 spines 13
    – With more than 4 spines 14
13. – With stylet curved over 180°, about 65 μm long, spines slender, about 20–22 μm long .... *A. hasanuddin* Martens & Curini-Galletti, 1989
    – With slightly curved stylet about 70 μm long, spines about 40–50 μm long and with a broad weakly sclerotized base .... *A. helfrichi* Karling et al., 1972
14. – With stylet about 150 μm long and with a curved distal end, spines (more than 90–100) about 45 μm long .... *A. coronata* Karling, 1966
    – With less than 90 spines 15
15. – With straight stylet about 50–65 μm long and with all spines of same kind, with curved tip and subterminal hook, about 45–60 μm long .... *A. monicae* sp. n.
    – Spines of different kinds 16
16. – With slightly curved stylet, ± 112 μm long, with at least 2 stronger spines with hook, other spines slender and straight with curved tip . *A. bathycola* (Westblad, 1952)
    – Stylet straight, with three different groups of spines ... 17
17. – Stylet about 65 μm, 6 needle-like spines with curved tip (± 45 μm long) and 6 spines with curved tip and subterminal hook, 2 of them ± 45 μm long and 4 ± 53 μm long ... . *A. rhizophoralis* Martens & Curini-Galletti, 1989
    – Stylet about 55 μm long, with 14 spines all with subterminal hook: 2 long spines about 45 μm long with straight tip, 6 medium spines about 36 μm long and 6 smaller spines about 30 μm long ..... *A. mediterranea* Meixner, 1938

Archimonocelis mediterranea Meixner, 1938 (Figs. 1, 14N)

Distribution and material. – Mediterranean Sea: Italy, Napoli (type locality) (Meixner, 1938). Type material was stored in the Zoological Museum of Berlin and destroyed during the Second World War. Corsica, Bay of Calvi, Revellata, 35–40 m, poorly sorted medium sand with 2–6% mud and 2–5% gravel, May, June, July, November 1983 and April 1984.

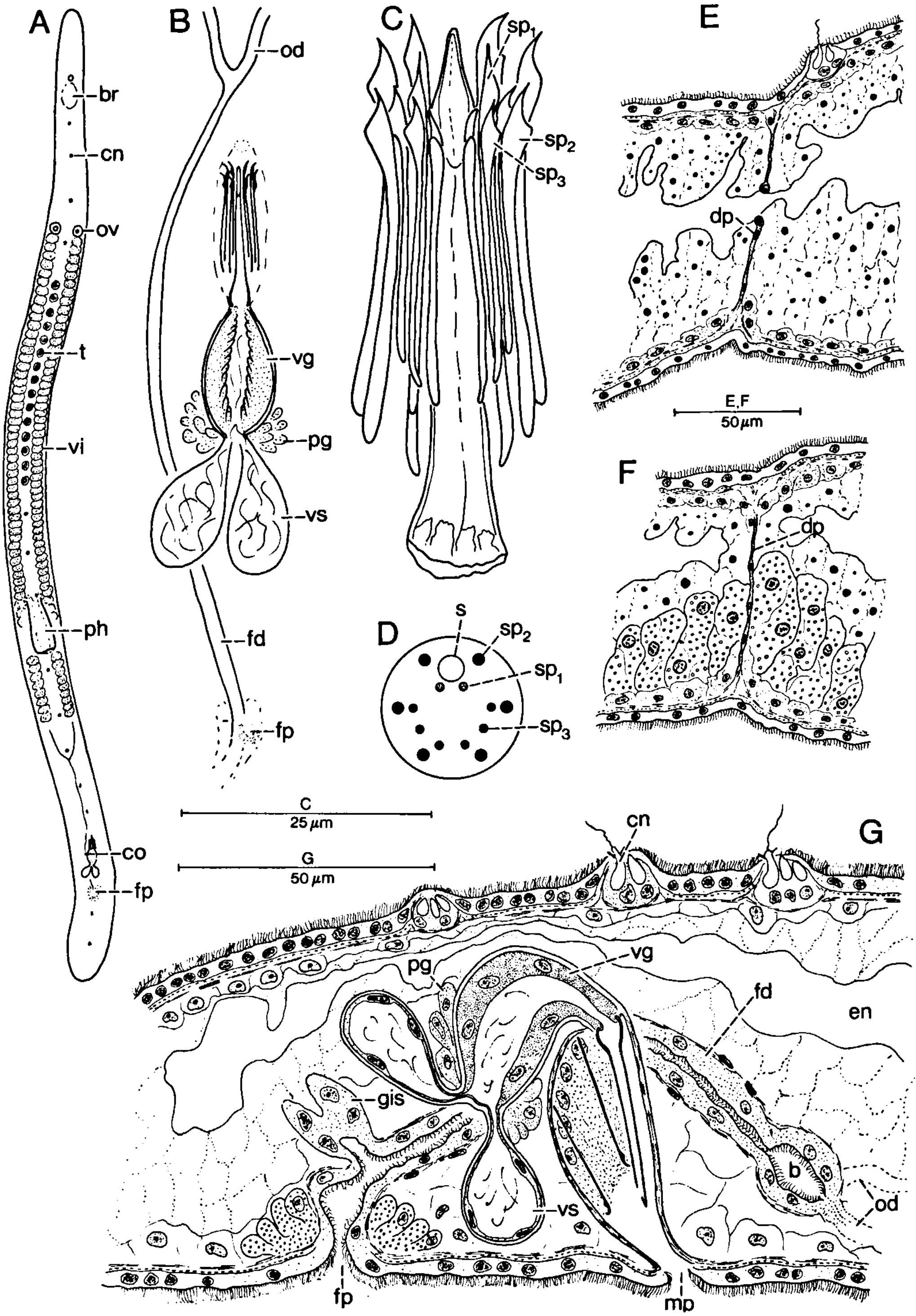

Fig. 1. Archimonocelis mediterranea Meixner, 1938: A, habitus; B, general organization of the copulatory organs in live animals; C, stylet and spines; D, organization of stylet and spines in a transversal section; E–F, reconstruction of the postpharyngeal septum from serial sagittal sections: E, mediosagittal, F, laterosagittal; G, reconstruction of the genital organs from serial sagittal sections.

Several animals studied alive; some of them preserved as whole mounts, one serially sectioned and one semi-thin sectioned.

Description. – Body filiform, about 2.5–3.5 mm long, colourless and without eyes. Cnidosacs well visible on live material and located between epidermis and sub-epidermal musculature. A parenchymatic septum containing a weakly muscular diaphragm is present behind the pharynx. On live material this postpharyngeal septum is not always visible.

Fifteen to twenty testes in one median row in front of the pharynx. The copulatory organ consists of paired vesiculae seminales, a prostate vesicle and a stylet surrounded by 14 spines. The bulb is formed by a muscular wall which surrounds the prostate vesicle and the stylet with the spines. The prostate glands enter the bulb together with the seminal vesicles. The stylet, 55–58 µm long, is tubiform, narrowing distally into a point. The distal orifice is ovoidal and about 12 µm broad. On live material the spines seem to be all of the same kind. However, in strongly squeezed slides three groups of spines can be recognized: two long spines, 45 µm, with flattened subterminal hook and straight tip lying closely to the stylet (sp1), an outer ring of six larger spines (sp2), about 36 µm long, and an inner half ring formed by six smaller spines (sp3) of about 30 µm. The two latter groups of spines are hooked and have a slightly curved tip. Stylet and spines lie in the male atrium, which has a strong muscular wall. On light microscopic sections it is clearly visible that stylet and spines have an intracellular origin. In addition to the spine-forming cells, the epithelium of the male atrium is also provided with secretory cells which open between the spines. An accessory glandular organ is absent.

The ovaries lie in front of the vitellaria in the first fifth of the body. The common female duct is provided with a ciliated epithelium with intraepithelial nuclei. Directly after fusion of the oviducts, the common duct widens slightly to form a small bursa. A vagina is not present. A genito-intestinal connection is present posterior to the copulatory organ, consisting of a bursa of the resorbing type, which is connected with the female common duct and the gastrodermis. A permanent genito-intestinal canal was not observed in the material examined.

Karyotype. – With $n = 12$ and a distinctly larger metacentric chromosome; the smallest chromosomes of the set about ¼ the length of the largest.

Karyotype formula: 19.5 µm; 19; I: 19.98, 40.20 (m); II: 12.31, 36.73 (sm); III: 9.53, 21.27 (st); IV: 8.08, 34.23 (sm); V: 7.66, 20.23 (st); VI: 7.36, 30.0 (sm); VII: 6.77, 34.22 (sm); VIII: 6.43, 18.83 (st); IX: 6.01, 17.26 (st); X: 5.98, 33.60 (sm); XI: 4.98, 20.39 (st); XII: 4.89, 27.34 (sm).

Archimonocelis bathycola (Westblad, 1952)
Fig. 14I)

Syn. – *Monocelis bathycola* Westblad, 1952.
Archimonocelis bathycola (Westblad, 1952); Karling 1966a.

Distribution, material, and description. – Atlantic Ocean: Norway, Korsfjord, 600–700 m, mud, summer 1951 (type locality).

One sectioned specimen (holotype) and one whole mount (Swedish Museum of Natural History, Stockholm: SMNH). Norway, Norwegian Channel, 400 m; Bergen, Mangerfjord, 350 m and Drøbak, Digerud's depth, 100–150 m.

See the original description of Westblad (1952) and the additional notes of Karling (1966a).

Archimonocelis koinocystis Karling, 1966
(Fig. 14M)

Distribution, material, and description. – Norway, Bergen, Korsfjorden, Bondisholmen, 17 m, fine shell sand, August 1964 (type locality).

Two sectioned specimens, one of them deposited in the Museum of Bergen (Norway) (holotype: two slides) and the other in the SMNH. One whole mount (SMNH).

See the original description of Karling (1966a).

Archimonocelis semicircularis Karling, 1966
(Fig. 14C)

Distribution, material, and description. – West coast USA, Pacific Grove, Hopkins Marine Station, tidepools, from shell gravel, stones and seaweed, September 1960 (type locality); Bodega Bay, Second Sled Road, tidepools, August 1960.

Eight sectioned specimens, one of them chosen as holotype (SMNH).

See the original description of Karling (1966a).

Archimonocelis coronata Karling, 1966 (Fig. 14J)

Distribution, material, and description. – West coast USA, Bodega Bay, Second Sled Road, tidepools, August 1960 (type locality).

Three sectioned specimens, one of them chosen as holotype (SMNH).

See the original description of Karling (1966a).

Archimonocelis helfrichi Karling, Mack-Fira & Dörjes, 1972 (Fig. 14P)

Distribution, material, and description. – Hawaii, Coconut Island, Oahu, Kaneohe Bay, in mixed sediments among coral outcrops (type locality).

Three whole mounts, one of them chosen as holotype (SMNH).

See the original description of Karling et al. (1972).

Archimonocelis oostendensis Martens & Schockaert, 1981 (Figs. 14A, 17, 18E)

Distribution and material. – North Sea: Belgium, beach of Oostende, fine to medium sand (type locality); several localities in northern France, Belgium, and Holland (Martens & Schockaert, 1981 and Schockaert et al., 1989); Germany, sublittorally around the island of Sylt (Wehrenberg & Reise, 1985).

Many whole mounts from different localities (one of them chosen as holotype, ZC-LUC No. 128) and thin and semi-thin sectioned material from E. Martens, all in the ZC-LUC.

Description. – See the original description (Martens & Schockaert, 1981).

Some additional data can be given. The structure of the copulatory organ is similar to that of *A. staresoi* (see below). E. Martens (1986) has given some information about the ultrastructure of the copulatory organ. A genito-intestinal canal is present.

Karyotype. – With $n = 6$; chromosomes can be arranged in three sets, each comprising two chromosomes of similar length.

Karyotype formula: 17.8 μm; 10; I: 21.99, 45.73 (m); II: 21.57, 43.01 (m); III: 15.93, 43.51 (m); IV: 15.19, 22.21 (st); V: 12.66, 41.97 (m); VI: 12.64, 22.11 (st).

Archimonocelis itoi Tajika, 1981 (Fig. 14R)

Distribution, material, and description. – Japan, Ishikari Bay, Oshoro, sub- and medio-littoral, sand (type locality).

Many whole mounts and serially sectioned specimens (one of them chosen as holotype) (Institute of Zoology of the University of Hokkaido).

See the original description of Tajika (1981).

Archimonocelis hasanuddin Martens & Curini-Galletti, 1989 (Fig. 14Q)

Distribution, material, and description. – Indonesia, South-West Sulawesi, Soreang, fine volcanic sand, just below the water line (0.25 m deep), September 1984 (type locality).

One whole mount (holotype, ZC-LUC No. 124).

See the original description of Martens & Curini-Galletti (1989).

Archimonocelis keke Martens & Curini-Galletti, 1989 (Fig. 14S)

Distribution, material, and description. – Indonesia, South Sulawesi, Kudingareng Keke, coral sand, littoral, October 1984 (type locality).

One whole mount (holotype, ZC-LUC No. 126).

See the original description of Martens & Curini-Galletti (1989).

Archimonocelis rhizophoralis Martens & Curini-Galletti, 1989 (Figs. 14O, 17)

Distribution, material, and description. – N. Australia, Darwin N.T., Ludmilla creek, fine sand with mud, intertidal in mangroves, September 1987 (type locality).

One whole mount (holotype, ZC-LUC No. 127), several specimens studied karyologically.

See the original description of Martens & Curini-Galletti (1989).

Karyotype. – With $n = 5$ and rather evenly sized chromosomes.

Karyotype formula: 15.2 μm; 8; I: 22.66, 41.26 (m); II: 22.57, 46.53 m); III: 20.59, 22.46 (st); IV: 17.28, 10.26 (t); V: 16.88, 39.48 (m).

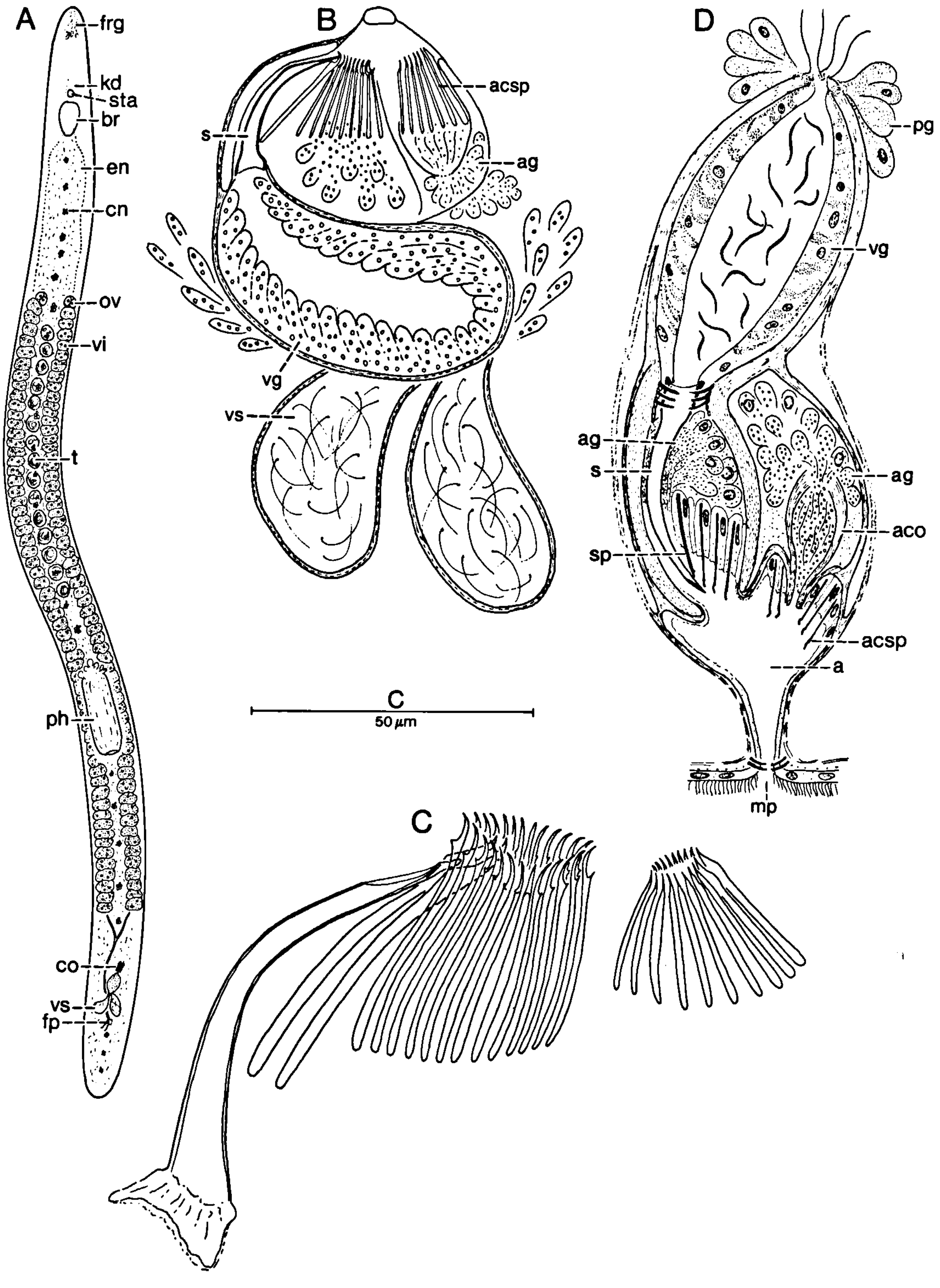

Fig. 2. Archimonocelis staresoi **sp. n.: A, habitus; B, general organization of the copulatory organ from live animals; C, stylet, spines and accessory spines; D, reconstruction of the male copulatory organ from transversal sections.**

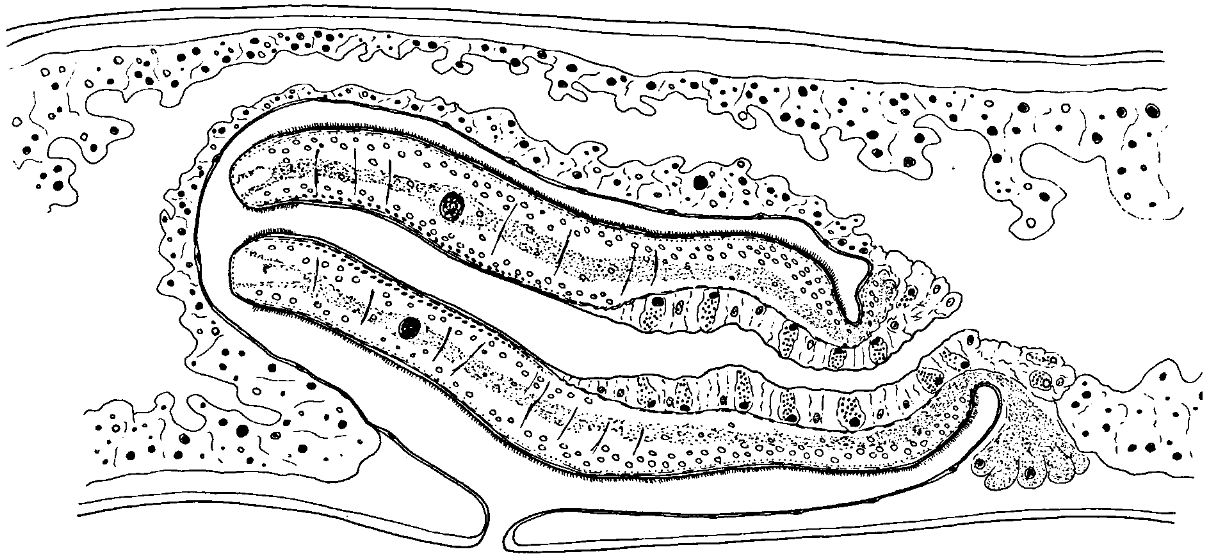

Fig. 3. Archimonocelis staresoi sp. n., reconstruction of the pharynx from serial sections.

Archimonocelis staresoi sp. n.
(Figs. 2–4, 14B, 15E, 17, 18D)

Distribution and material. – Mediterranean Sea: Corsica, Bay of Calvi, 10–15 m, coarse sand with gravel, May 1983, January and April 1984 (type locality). Israel, Haifa, Shiqmona beach, intertidal in coarse sand, April 1988, February 1989; Atlit, low water line in medium sand plus gravel, April 1988; Italy, Punta Ala (Grosseto), low intertidal in coarse sand with gravel, December 1990, April, May 1991; Capraia Island (Livorno) 15–20 m, medium sand, November 1991, February, March, and November 1992; Porto Cesareo (Lecce), low intertidal in coarse sand with gravel, March 1991; Greece, Cassandra Peninsula, low intertidal in coarse sand with gravel, February 1991.

Numerous animals from each locality studied alive, six animals sectioned serially (one of them chosen as holotype, ZC-LUC No. 173), several strongly squeezed whole mounts and one animal semi-thin sectioned.

Etymology. – The species name refers to the STARESO, Station de Recherches Sous-Marines et Océanographiques (Calvi, Corsica).

Description. – *A. staresoi* is 6–10 mm long and 0.3 mm broad. Calcareous spiculae can be spread all over the body. The cnidosacs are easily visible on live material. They lie between the epithelium cells and the basal lamina (A-type, see Karling 1966b) and are particularly numerous at the level of the copulatory organ.

The long slender pharynx lies in the second half of the body and is posteriorly oriented. The pharynx has the same morphology as in the other *Archimonocelis* species (see Fig. 3). External and posterior internal epithelia are ciliated. The tip and most of the inner epithelium is not ciliated. The posterior half of the internal epithelium has sunk nuclei and is flat; the anterior half is lined with a high secretory epithelium with intraepithelial nuclei. The glands are unicellular, and lie between the non-secretory epithelium cells. This anterior part of the epithelium constitutes the oesophagus. At the basis of the pharynx the oesophageal epithelium is connected with the gastrodermis. Outside the pharynx there are pharyngeal glands whose necks run through the pharynx parenchyma and discharge in the non-ciliated tip of the pharynx. A weakly developed muscular diaphragm is present behind the pharynx (seen on sectioned material).

Fifteen to thirty testes are located in one median row in front of the pharynx. The copulatory organ consists of one pair of seminal vesicles, a bulbus with the prostate vesicle, a stylet surrounded by spines, and an accessory glandular organ. At the distal end of the prostate vesicle the muscular wall is separated into an inner and an outer layer. The inner layer forms the last part of the ductus eja-

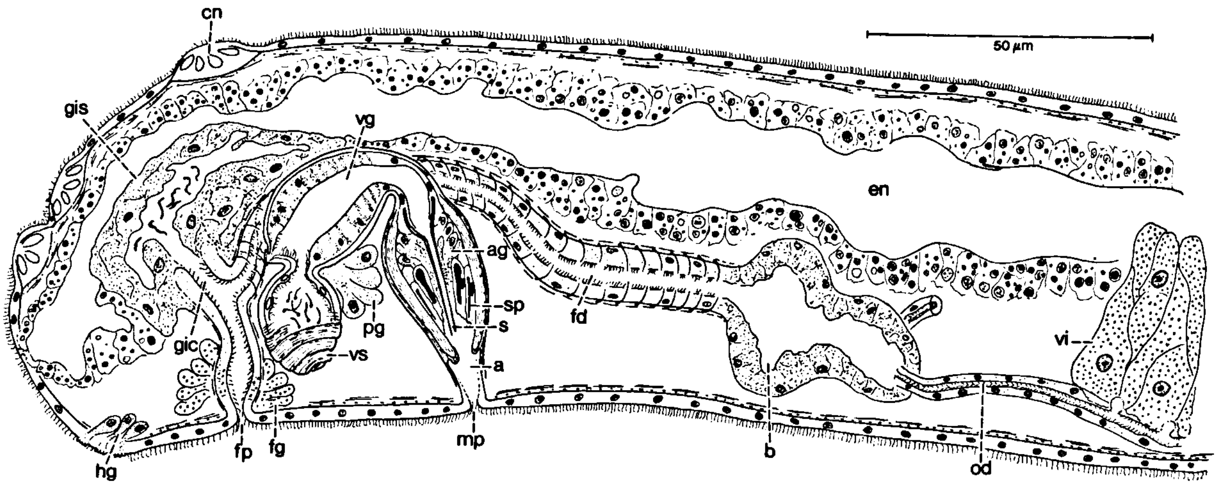

Fig. 4. Archimonocelis staresoi sp. n., reconstruction of the genital organs from transversal sections.

culatorius (male atrium). The outer layer forms a bulbus around the ductus ejaculatorius and the accessory organ.

The stylet is about 100 µm long, slightly curved, with an oval, subterminal aperture. The stylet is surrounded by two larger spines, about 60 µm long and by a girdle of 25 smaller spines (40–50 µm long). Necks of glandular cells (atrial glands) open into the male atrium between the spine-forming cells. The accessory glandular organ lies in a diverticle of the male atrium and is surrounded by its own muscular wall. The organ consists of a prostatic bulb in which the necks of glandular cells discharge (accessory glands); their cell body lies between the inner and the outer muscular wall, and also outside the bulb. The aperture of the prostatic bulb is surrounded by 18–20 spines (about 28–33 µm long), which have a slightly curved tip; the spines lying opposite to the stylet are provided with a subterminal hook.

The vitellaria extend from ¼ of the body length till slightly before the copulatory organ. The oviducts fuse behind the vitellaria and form a bursa which continues in the female common duct and opens into the female pore. The last part of the female duct is surrounded by (female) glands. The epithelium of the female duct and oviducts is ciliated. The epithelium of the bursa is high, not ciliated and probably secretory. Behind the copulatory organ the female duct gives rise to a diverticle: the genito-intestinal system. This system lies in the gut and is surrounded by its own tissue; here the gastrodermis is lacking. This tissue has an evident lumen in which degenerating sperm is present. This genito-intestinal system is to be considered as a bursa of the resorbiens type. A connection with the gut, as observed in some other species, was not present.

Karyotype. – With $n = 5$, and rather evenly sized markedly heterobrachial chromosomes.

Karyotype formula: 16.4 µm; 5; I: 22.82, 6.00 (t); II: 21.46, 5.15 (t); III: 20.03, 5.57 (t); IV: 18.62, 6.02 (t); V: 16.96, 7.66 (t) (data from specimens from Haifa). Specimens from Punta Ala and Porto Cesareo had nearly identical karyometrical values.

Archimonocelis meixneri sp. n.
(Figs. 5, 14D, 17, 18J)

Syn. – *Archimonocelis* sp. 1 (Martens et al., 1989)

Distribution and material. – Mediterranean Sea: Corsica, Bay of Calvi, 30–50 m, moderately well sorted medium sand, 2–5% mud and 2–5% gravel, April 1980 and March 1985 (type locality).

Four animals studied alive, two of which prepared as whole mount (one of them chosen as holotype, ZC-LUC No. 152), one used for serial sections and one for karyology.

Etymology. – The species is dedicated to J. Meixner, author of the genus *Archimonocelis*.

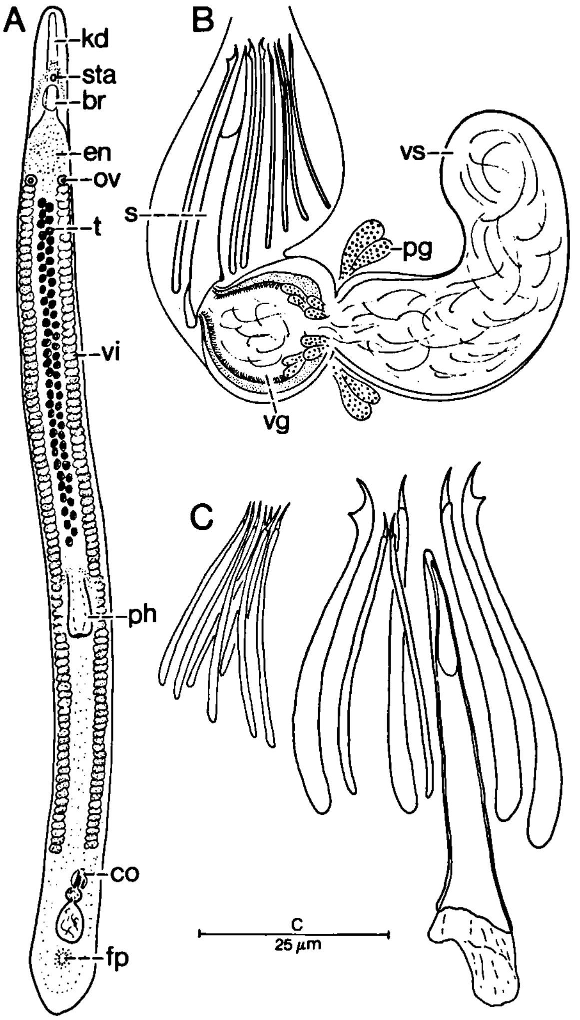

Fig. 5. Archimonocelis meixneri sp. n.: A, habitus; B, general organization of the copulatory organ from live animals; C, stylet, spines, and accessory spines.

Description. – Long slender species with typical *Archimonocelis* habitus. About 60 testes lying medially in front of the pharynx. The copulatory organ consists of a seminal vesicle, a prostate vesicle, a stylet surrounded by spines, and an accessory glandular organ provided with spines. The stylet, about 61 µm long, narrows slightly to the distal tip which has a terminal oval aperture, 16 µm broad. The stylet is surrounded by four large spines (42–52 µm long) and two small spines (about 37 µm). The accessory organ contains seven spines of almost similar shape (25–35 µm).

The ovaries lie in front of the vitellaria, which run from 1/6 of the body till the copulatory organ. Beside these organs only the female pore was recognized.

Karyotype. – With $n = 6$, and chromosomes considerably differing in length, with the smallest approximately half the length of the largest.

Karyotype formula: 21.0 µm; 10; I: 21.14, 35.49 (sm); II: 19.62, 7.28 (t); III: 17.22, 35.71 (sm); IV: 16.00, 7.68 (t); V: 13.49, 39.11 (m); VI: 12.56, 44.20 (m).

Archimonocelis carmelitana sp. n.
(Figs. 6–7, 14K, 16D, 17, 18C)

Distribution and material. – Mediterranean Sea: Israel, Haifa, Cape Carmel, low intertidal in medium to coarse sand, April 1988 (type locality); Atlit, low intertidal in medium sand plus gravel, April 1988; Caesarea, low intertidal in coarse sand, April 1988. Italy, Porto Cesareo (Lecce), low intertidal in coarse sand, March 1991.

Three whole mounts (one of them chosen as holotype, ZC-LUC No. 169); several karyological slides with squeezed hard parts.

Etymology. – Named after the type locality.

Description. – Animals long, about 12 mm, with a clearly visible cephalic gut. Circular bands, regularly spaced along the body, are clearly evident on live animals (see Figs. 6A and B). These bands are areas in which the epithelium is provided with small adhesive glands. The pharynx lies in the posterior third of the animal. About 100 testes, irregularly arranged in one row, lie in front of the pharynx. The ovaries are situated approximately at the level of the 12th testicular follicle. The vitellaria extend from the ovaries to the bursa. The oviducts fuse to form a muscular bursa, which is provided with a vagina. In live material, it was possible to observe a genito-intestinal connection at the end of the female duct.

The male copulatory organ is provided with a seminal vesicle, a prostate vesicle and a rather straight stylet which is 97–105 µm long. Along with the stylet there are more than 100 spines, which are 52–66 µm long, slender and not distinctly curved at the tip. Only in highly squashed preparations it is

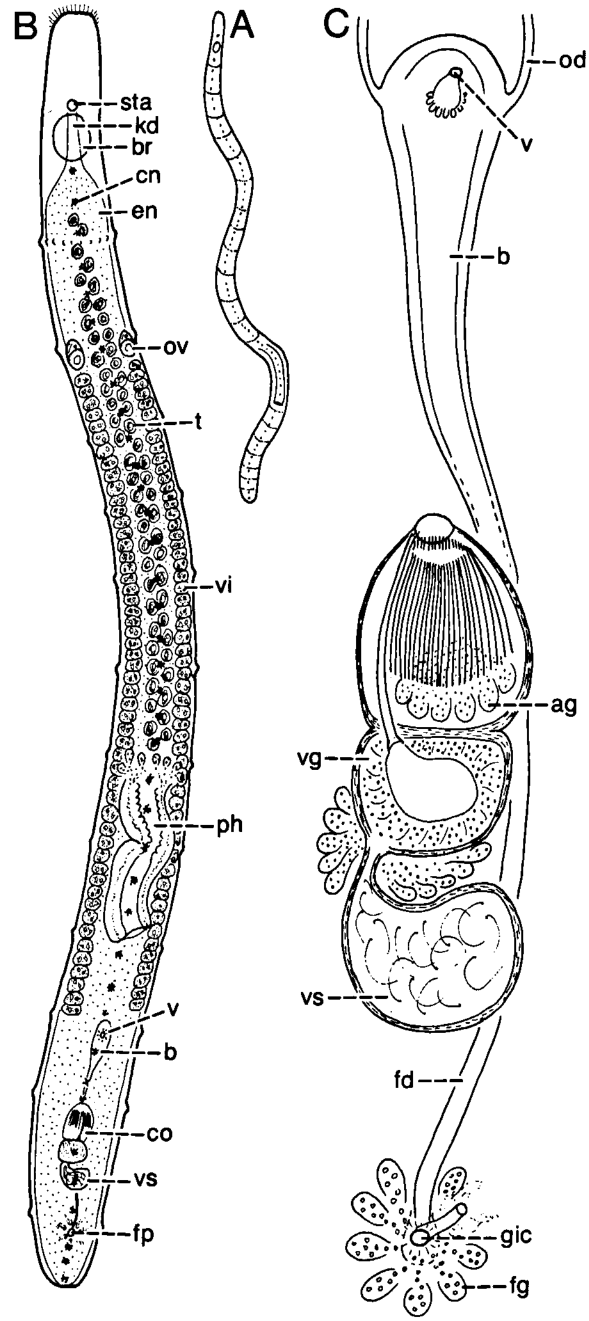

Fig. 6. Archimonocelis carmelitana sp. n.: A, habitus; B, general organization of a live animal; C, general organization of the copulatory organs from live animals.

possible to observe that the tip is slightly curved and provided with a subterminal hook (Fig. 7B).

Karyotype. – With $n = 9$. Chromosomes can be arranged in a regularly decreasing set, with the smallest one being half the length of the largest chromosome; all chromosomes are markedly heterobrachial.

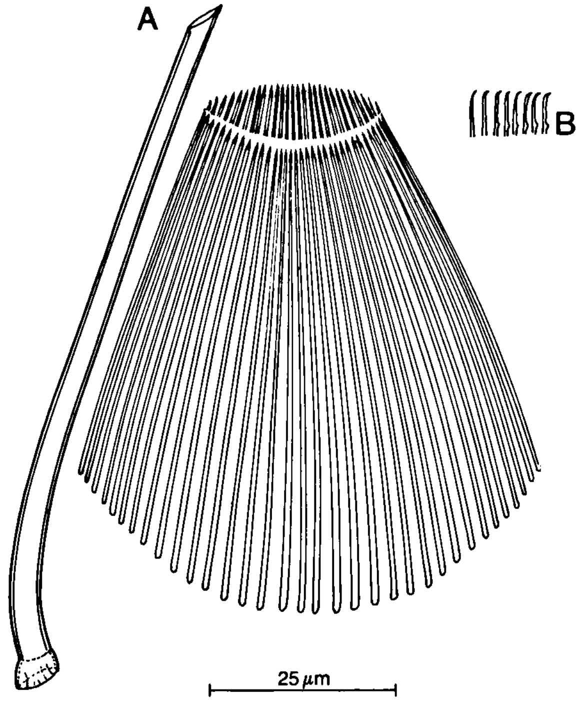

Fig. 7. Archimonocelis carmelitana sp. n.: A, stylet and spines; B, detail of tips of some spines.

Karyotype formula: 21.0 µm; 9; I: 14.15, 6.59 (t); II: 12.85, 5.90 (t); III: 12.37, 5.39 (t); IV: 11.69, 7.85 (t); V: 11.13, 5.64 (t); VI: 10.6, 6.60 (t); VII: 10.33, 5.62 (t); VIII: 9.70, 6.23 (t); IX: 7.18, 10.12 (t) (data from Haifa specimens).

Archimonocelis crucifera sp. n.
(Figs. 8, 14F, 15B, 16C, 17)

Distribution and material. – Mediterranean Sea: Israel, Atlit, near the Crusaders' Castle, low intertidal in medium sand, April 1988 (type locality). Crete, Pachià Ammos, –20 cm, medium sand; Francocastelo, near the Crusaders' Castle, low intertidal in medium sand, April 1990. Italy, Paraggi, Genova, low intertidal in coarse sand, December 1990.

Numerous whole mounts (one of them chosen as holotype, ZC-LUC No. 170); three serially sectioned animals.

Etymology. – The specific epithet (from *crux*, cross and *fero*, carry) refers to the species' occurrence close to the Crusaders' Castle and to the particularly distinct presence of cross-like spiculae in its body.

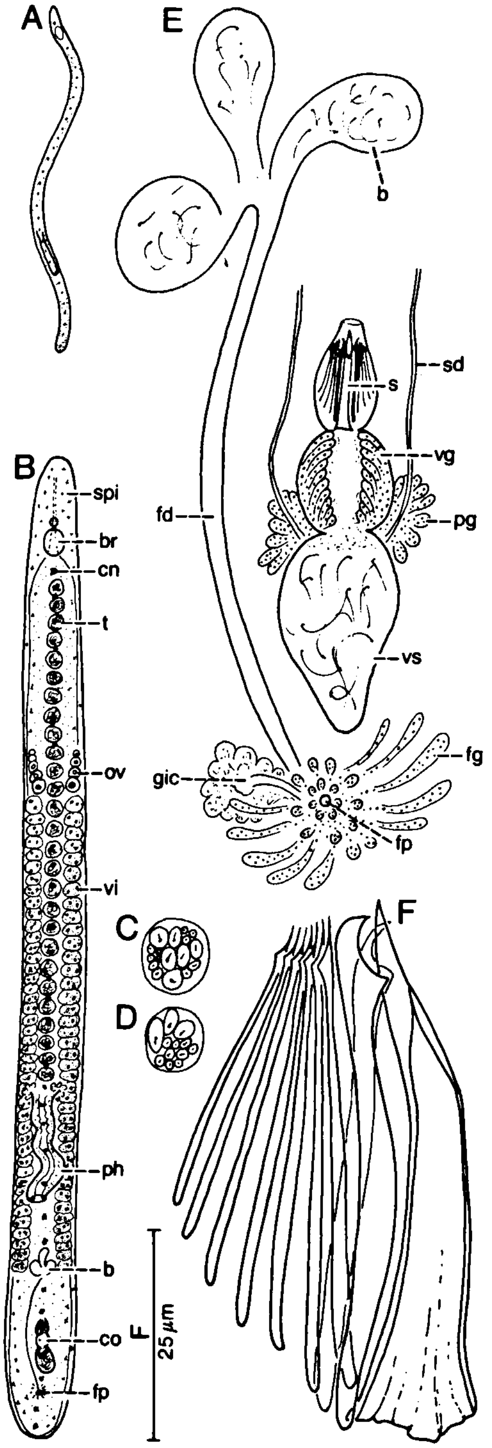

Fig. 8. Archimonocelis crucifera sp. n.: A, habitus; B, general organization of a live animal; C–D, cnidosacs; E, general organization of the copulatory organs from live animals; F, stylet and spines.

Description. – Large animals, about 15 mm long. In live animals the cephalic gut is visible, as well as the very numerous calcareous spiculae which are spread all over the body. In live animals it was also possible to observe some ovoidal masses of sperm in different regions of the body; whether they are the results of hypodermal impregnations could not be ascertained. The long tubular pharynx lies in the last third of the body. About 30 to 40 testes lie in one medium row in front of the pharynx. About 10 testes lie in front of the ovaries. The vitellaria extend from behind the ovaries to the bursa. In only some mature specimens the female duct was developed into a bursa. The bursa appeared to be vacuolar and was filled with spermatozoa. A vagina was never observed. The end of the female duct is provided with a genito-intestinal connection.

The copulatory organ consists of a straight stylet, 63 µm long, surrounded by 10–14 spines. Two of these spines, on either side of the stylet, are curved near the tip and provided with a strong subterminal hook. The two spines are as long as the stylet, while the other ones decrease in length from 58 to 37 µm, the largest spines being closest to the stylet. They are straight and their subterminal hook is not particularly strong. The seminal vesicle is single.

Karyotype. – With $n = 11$; one metacentric chromosome distinctly larger than the others, about four times the size of the smallest.

Karyotype formula: 22.3 µm; 17; I: 19.64, 45.22 (m); II: 11.60, 37.57 (m); III: 10.41, 34.57 (sm); IV: 9.00, 31.24 (sm); V: 8.36, 18.06 (st); VI: 8.09, 37.02 (sm); VII: 7.72, 29.11 (sm); VIII: 7.12, 22.17 (st); IX: 6.57, 16.05 (st); X: 6.10, 18.07 (st); XI: 5.37, 17.62 (st) (data from Atlit specimens). Specimens from Crete and Paraggi had a nearly identical karyotype.

Archimonocelis monicae sp. n.
(Figs. 9, 14L, 15C, 17, 18F)

Distribution and material. – Red Sea: Israel, Eilat, near the Underwater Observatory, – 1/ – 6 m, sheltered area with *Halophila*, fine sand (type locality), April 1988, February 1989.

Several animals studied alive; two of them prepared as whole mounts (one of them chosen as holotype, ZC-LUC No. 167) and another used for karyology.

Etymology. – Named after the first author's wife,

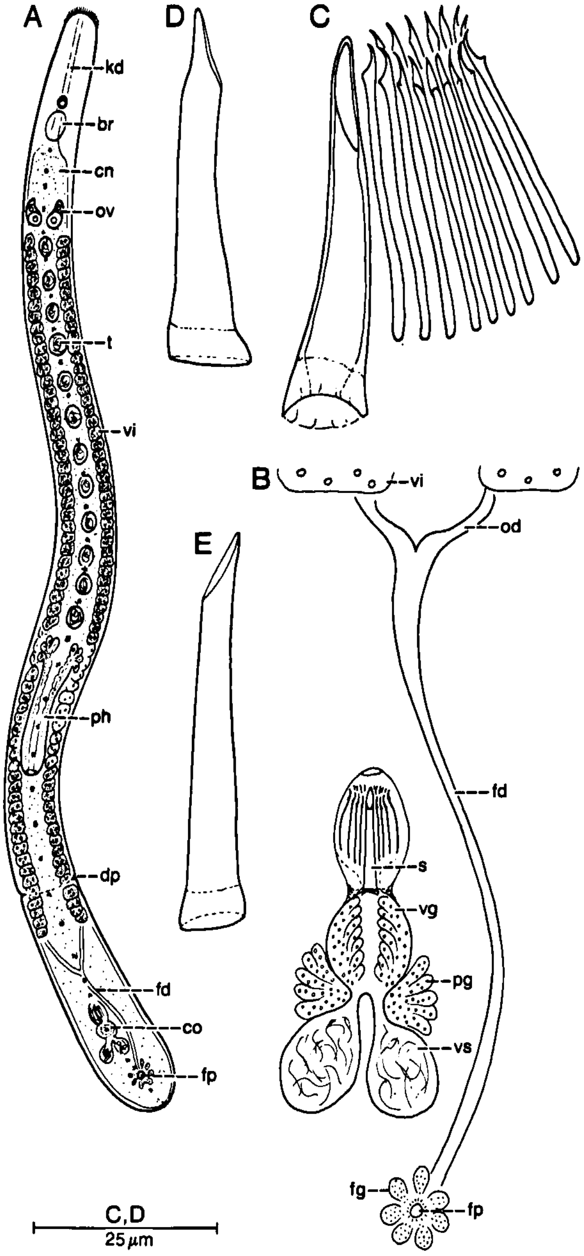

Fig. 9. Archimonocelis monicae sp. n.: A, general organization of a live animal; B, general organization of the copulatory organs from live animals; C, stylet and spines; D–E, stylet in slightly squeezed slides.

in recognition of her cooperation and patience during the preparation of this paper.

Description. – This species can reach a length of 20 mm. The presence of a postpharyngeal diaphragm can easily be seen in live animals. The pharynx lies in the last third of the body. The exact number of testes could not be discerned; they seem to lie in a single, median row. The ovaries lie in front of the first testes and the vitellaria run from behind the ovaries to just behind the diaphragm. The oviducts fuse in front of the copulatory organ to form a common female duct. Neither a bursa nor a genito-intestinal connection has been observed.

The copulatory organ is provided with two seminal vesicles and a straight stylet of 50–65 μm, surrounded by 11–16 spines. In individual specimens, the spines have all about the same length and shape. Among different specimens, however, we observed a variability in length of the spines, ranging from 45 to 60 μm.

Karyotype. – With $n = 7$, with two larger metacentric chromosomes and the others markedly heterobrachial; the smallest chromosome is less than ⅓ of the size of the largest.

Karyotype formula: 15.7μm; 9; I: 25.52, 41.48 (m); II: 20.40, 45.21 (m); III: 14.89, 4.32 (t); IV: 11.92, 5.46 (t); V: 10.22, 5.77 (t); VI: 9.30, 7.12 (t); VII: 7.75, 7.01 (t).

Archimonocelis sabra sp. n.
(Figs. 10–11, 14E, 15D, 16G, 17, 18G)

Distribution and material. – Red Sea: Israel, Eilat, near the Underwater Observatory, about –3 m at the basis of a *Millepora* reef, fine sand (type locality), April 1988.

Four animals studied alive, two prepared as whole mounts (one of them chosen as holotype, ZC-LUC No. 166) and two used for karyology.

Etymology. – Named after the nickname for people born in Israel.

Description. – Animals about 10 mm long. In live animals some calcareous spicules, spread all over the body, were observed. The pharynx lies in the last third of the body. Only a few testes could be observed, due to the content of the gut; they seem to lie in a single median row. The ovaria lie closely behind the brain and the vitellaria run to the bursa. The oviducts fuse immediately behind the last vitelline follicle to form the common female duct. The first part of this duct is slightly enlarged and forms a bursa, which is not provided

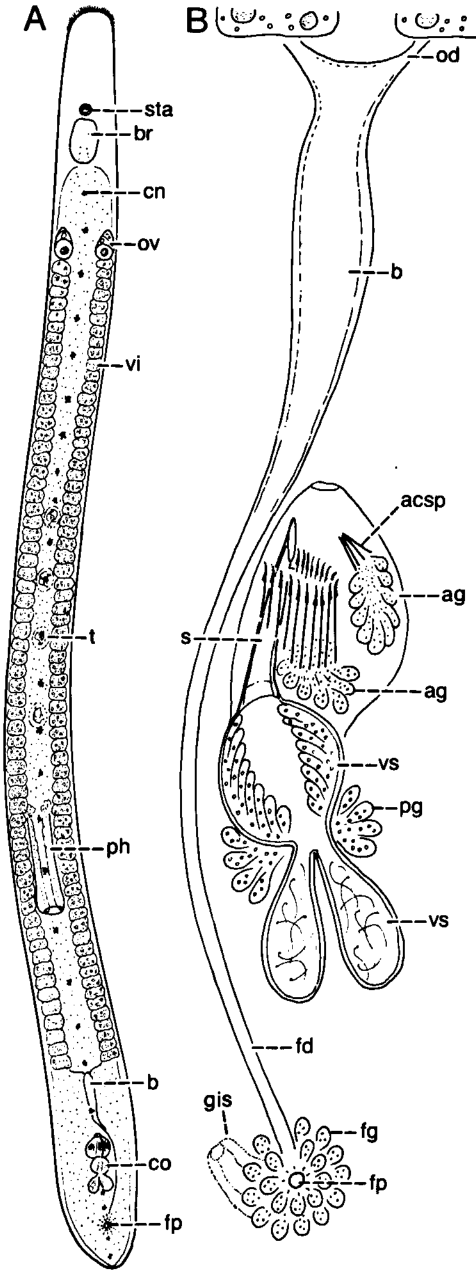

Fig. 10. Archimonocelis sabra sp. n.: A, general organization of a live animal; B, general organization of the copulatory organs from live animals.

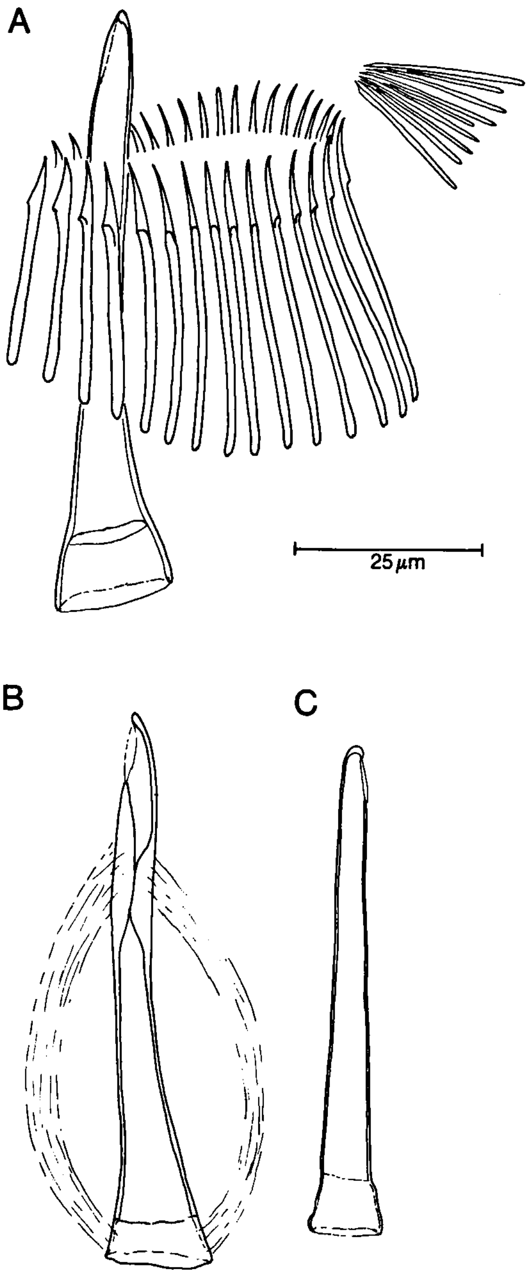

Fig. 11. Archimonocelis sabra sp. n.: A, stylet, spines and accessory spines; B, stylet in a strongly squeezed slide; C, stylet in a slightly squeezed slide.

with a vagina. A genito-intestinal connection is present.

The copulatory organ consists of two seminal vesicles and a 77 µm long stylet which is surrounded by 27–35 spines. These spines vary in length from 26 to 46 µm. In strongly squashed slides fibre-like structures could be observed, running from the basis of the stylet to well-sclerotized parts just below the opening of the stylet (Fig. 11B). The spines closest to the stylet are short and broad; the more outwards located spines are long and slender. The spines are gutter-shaped, in their distal part the sides converge to form a conical tip. Many atrial glands discharge between these spines. The copulatory organ is provided with an accessory glandular organ which bears about 10 needle-shaped spines, about 21 to 24 μm long.

Karyotype. – With $n = 7$, with two larger metacentric chromosomes and the others markedly heterobrachial; the smallest is about ⅓ the length of the largest.

Karyotype formula: 15.9 μm; 9; I: 26.05, 45.19 (m); II: 20.72, 45.80 (m); III: 13.42, 11.28 (t); IV: 11.51, 11.91 (t); V: 10.58, 10.62 (t); VI: 9.53, 12.00 (t); VII: 8.34, 9.55 (t).

Archimonocelis puertoricana sp. n.
(Figs. 12A–C, 14G, 16E–F, 17, 18B)

Distribution and material. – Caribbean: Puerto Rico, Isla Magueyes, about –10 m, in poorly sorted medium sand among coral outcrops, December 1988 (type locality).

One whole mount (holotype, ZC-LUC No. 171) and two karyological slides with strongly squeezed hard parts.

Etymology. – Named after the type locality.

Description. – Animals about 10 mm long. On some live animals, spiculae were observed, spread all over the body. The pharynx lies in the second third of the body and the cephalic gut runs up to the anterior tip. About 10 to 15 testes lie in the median part of the body, in front of the pharynx. The ovaries lie at the level of the anteriormost testes, and the vitellaria run up to the copulatory organ. In front of the copulatory organ a small, non-vaginal bursa is present which may contain sperm. A genito-intestinal connection was not observed.

The copulatory organ has one seminal vesicle and is provided with a stylet that is surrounded by 12 to 18 spines. The stylet is 55–61 μm long and slightly curved. The spines with a subterminal hook are curved at the tip and arranged in a circle around the stylet. The two broad spines next to the stylet are 54–59 μm long; the others are narrow and about 35–38 μm long.

Karyotype. – With $n = 7$; five metacentric and two acrocentric chromosomes.

Karyotype formula: 22.3 μm; 12; I: 17.68, 45.5 (m); II: 16.38, 45.26 (m); III: 15.11, 44.64 (m); IV: 14.05, 8.40 (t); V: 13.49, 41.57 (m); VI: 11.97, 9.27 (t); VII: 11.49, 45.37 (m).

Archimonocelis inopinata sp. n.
(Figs. 12D, 14H, 15A, 17)

Distribution and material. – Caribbean: Puerto Rico, Isla Magueyes, about –5 m in channels among coral outcrops, poorly sorted coarse sand, December 1988.

Two whole mounts (one of them chosen as holotype, ZC-LUC No. 172) and two karyological slides, with strongly squeezed hard parts.

Etymology. – The name reflects the unexpected (Latin, *inopinatus*) finding of this species.

Description. – Examination of karyological slides and permanent mounts of specimens identified at low magnification as *A. puertoricana* revealed some individuals which were consistently different from that species in morphology of the hard parts and the karyotype.

The basis of the stylet is elongated to one side; the longer side of the stylet measures 47–54 μm in length, the shorter is about 39 μm long. Four of the spines are large, 45–48 μm long, arranged in two symmetrical pairs, one at each side of the stylet. Each pair of spines consists of a distinctly broad spine and a spine with the same morphology as the smaller spines. Even in the extremely squeezed slides it is apparent that the members of these pairs are connected at their base. The smaller spines are 6–8 in number and are 29–34 μm long.

Karyotype. – With $n = 7$; two metacentrics, two submetacentrics, two subtelocentrics and one acrocentric.

Karyotype formula: 21.4 μm; 11; I: 18.09, 34.48 (sm); II: 17.63, 40.99 (m); III: 14.77, 23.22 (st); IV: 13.81, 11.21 (t); V: 13.80, 38.38 (m); VI: 11.93, 30.92 (sm); VII: 10.44, 14.93 (st).

Archimonocelis glabrodorsata sp. n.
(Figs. 13, 14T, 15F)

Distribution and material. – Caribbean: Puerto Rico, Isla Magueyes, –12, –16 m, at the basis of coral outcrops, poorly sorted medium sand, December 1988.

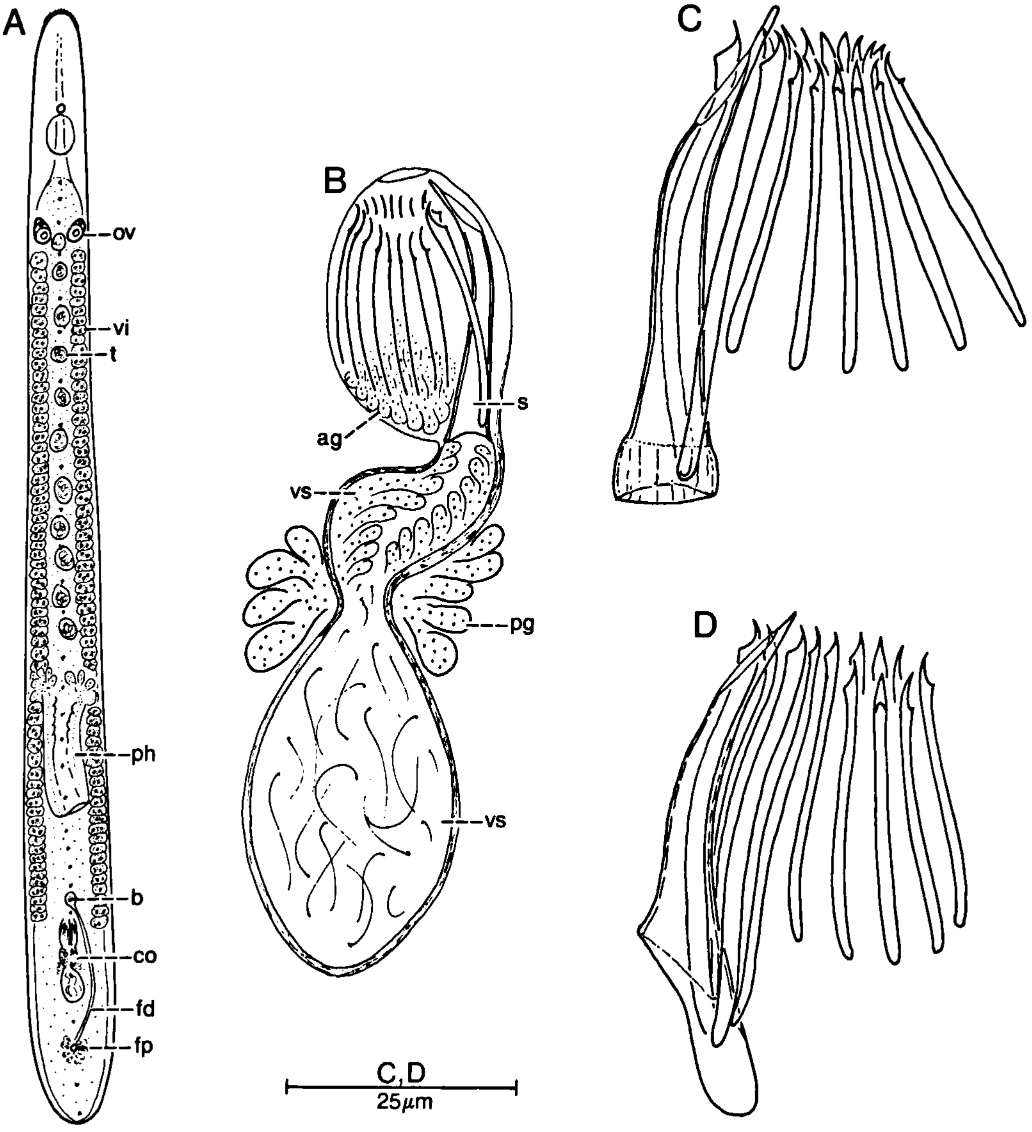

Fig. 12. A–C, *Archimonocelis puertoricana* sp. n.: A, general organization of a live animal; B, general organization of the male copulatory organ from live animals; C, stylet and spines. D, *Archimonocelis inopinata* sp. n., stylet and spines.

One whole mount (holotype, ZC-LUC No. 168) and one animal semi-thin sectioned.

Etymology. – The name reflects the peculiarity of the species' ciliation (from the Latin *glaber*, glabrous and *dorsum*, back).

Description. – This peculiar species is about 7 mm long. The habitus of live animals did not make them immediately recognizable as *Archimonocelis*, because cnidosacs were not clearly visible. In the posterior part of the body, at the level of the copulatory organ, many cnidocysts (about 70–80) can be seen, which are not neatly packed in cnidosac-like structures. A very elongated pharynx with well-developed oesophagus lies in the second half of the body. About 12 testes lie in one median row in front of the pharynx. The ovaries lie at the level of the posteriormost testes. The vitellaria run from behind the ovaries up to the bursa. In front of the copulatory organ the female duct widens, forming a muscular bursa provided with a vagina. A genito-

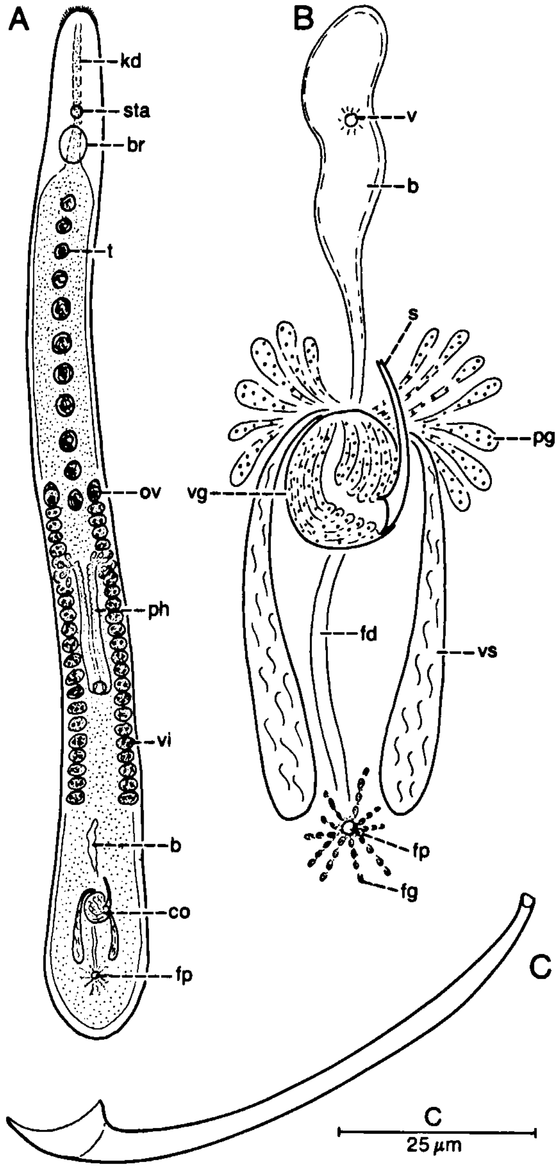

Fig. 13. Archimonocelis glabrodorsata sp. n.: A, general organization of a live animal; B, general organization of the copulatory organs from live animals; C, stylet.

intestinal connection could not be observed in live specimens.

The copulatory organ contains two elongated seminal vesicles, which enter the prostate vesicle at the anterior side. The prostate vesicle is spherical, with a diameter of about 50 μm. Only a stylet, without spines, is present; it is slightly curved and about 75 μm long. The proximal opening of the stylet is about 13 μm wide, while the distal opening has a width of about 2 μm.

Some additional data from sectioned material can be given. The nuclei of the epidermis are intraepithelial. The dorsal, non-ciliated epidermis is about 3–5 μm high, while the ventral epithelium is 7–10 μm high. The cephalic gut runs over the brain and the statocyst. Frontal glands are present between the cephalic gut and anterior tip. Cnidoblasts, not visible in live animals, are present mediodorsally over the whole length of the animal. They are more or less grouped but never surrounded by a tunica forming a cnidosac, and are laying beneath the body wall musculature. These facts probably obscure their observations in live animals.

Discussion of the genus Archimonocelis

Twenty species of this nearly cosmopolitan genus are known so far. Differentiation among them is possible mainly on the basis of the morphology of the hard structures (see identification key of the genus and pictorial key). The genus is characterized by the presence of cnidosacs, absence of vitellaria in front of the ovaria, and a long slender pharynx with a strongly developed oesophagus.

The type species of the genus is known only from drawings of sagittal reconstructions (see Meixner, 1938) and has never been reported subsequently. Of the five *Archimonocelis* species we found in the Mediterranean, only one resembles the original drawing of *A. mediterranea,* since it shows paired seminal vesicles, a stylet encircled by few spines, absence of an accessory glandular organ, and lack of vagina. Therefore we consider this species as *A. mediterranea.*

Within the genus *Archimonocelis* different states are present for some characters, viz. the number of seminal vesicles, the bursa,,the vagina, spine number and morphology, absence of accessory glandular organ, and karyotype. Groupings based on these characters are conflictual and therefore some of them need to be considered as homoplasous.

From outgroup comparisons, the presence of a tubular stylet with simple terminal opening and numerous spines curved at tip and all similar in shape, and the presence of the accessory glandular organ can be considered as the plesiomorphic condition, since this configuration is also present in

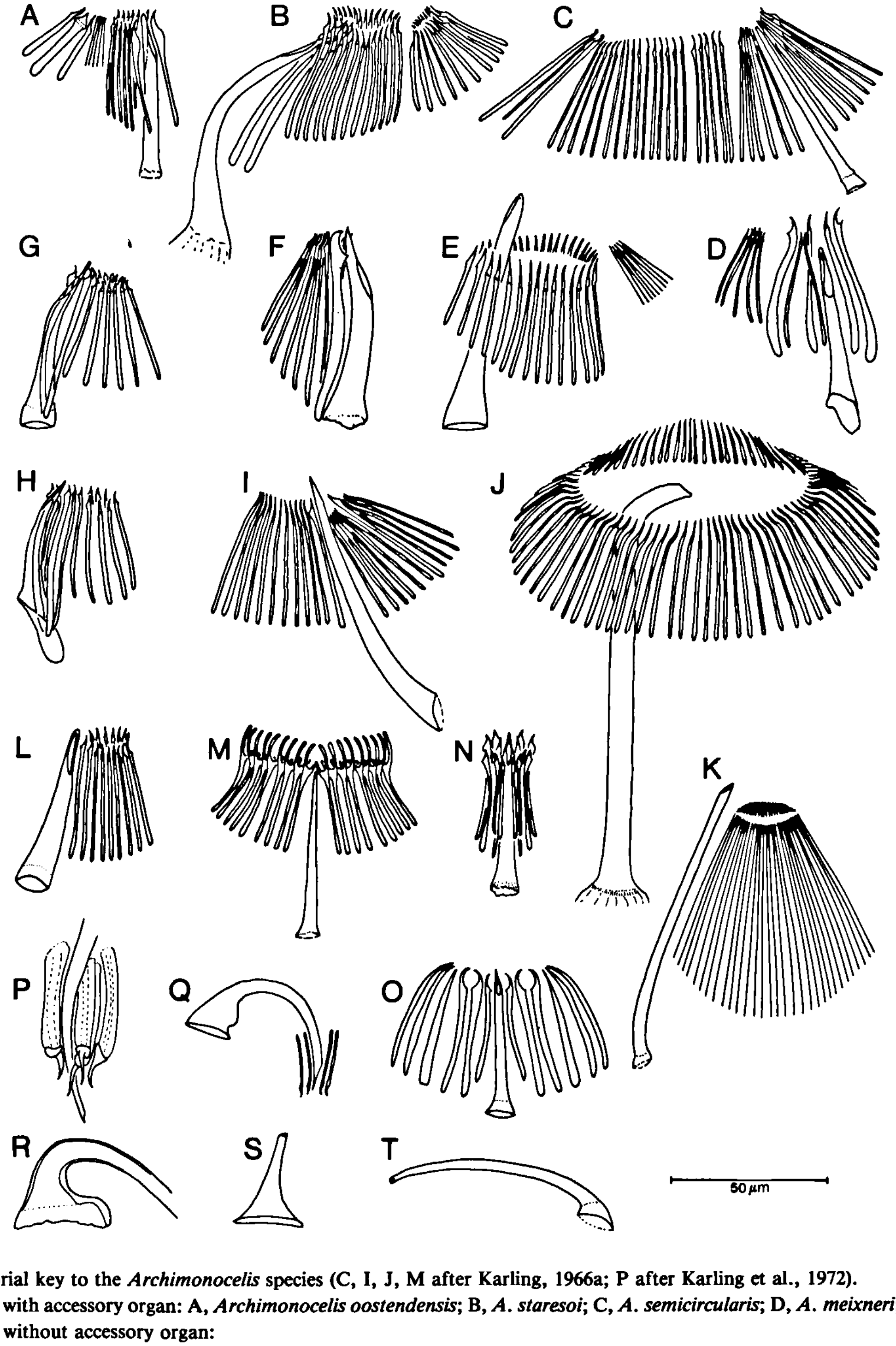

Fig. 14. Pictorial key to the *Archimonocelis* species (C, I, J, M after Karling, 1966a; P after Karling et al., 1972).
A–E. Species with accessory organ: A, *Archimonocelis oostendensis*; B, *A. staresoi*; C, *A. semicircularis*; D, *A. meixneri*; E, *A. sabra*.
F–T. Species without accessory organ:
F–I. With two large hooked spines: F, *A. crucifera*; G, *A. puertoricana*; H, *A. inopinata*; I, *A. bathycola*.
J–K. With more than 90 spines: J, *A. coronata*; K, *A. carmelitana*.
L–O. With more than 4 spines: L, *A. monicae*; M, *A. koinocystis*; N, *A. mediterranea*; O, *A. rhizophoralis*.
P–Q. With 4 spines: P, *A. helfrichi*; Q, *A. hasanuddin*;
R–T. Without spines: R, *A. itoi*; S, *A. keke*; T, *A. glabrodorsata*.

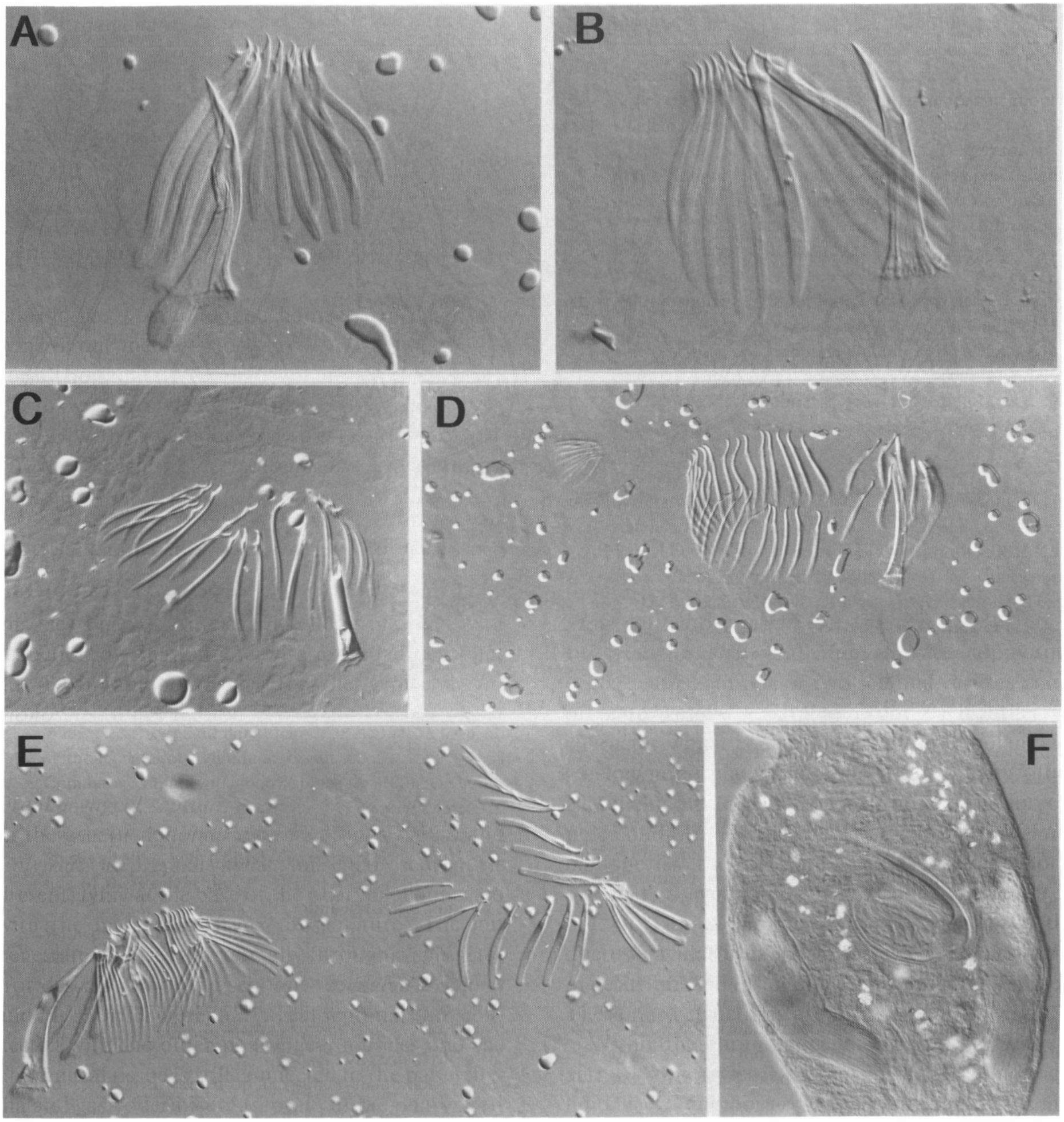

Fig. 15. Hard structures of the copulatory organ of some *Archimonocelis* species: A, *A. inopinata*; B, *A. crucifera*; C, *A. monicae*; D, *A. sabra*; E, *A. staresoi*; F, *A. glabrodorsata*.

related taxa (see character discussion). Based on the morphology of the hard parts, some groupings can be proposed; they are indicated in the pictorial key (Fig. 14), in which all the hard structures of the known species are given. Whether these groupings have some phylogenetical implications cannot be ascertained because they are not congruent with the distribution of other characters (see above).

The karyotype of eleven species of the genus *Archimonocelis* is known. Within the genus *Archimonocelis* the haploid chromosome numbers range from 5 to 12, the largest intrageneric variation

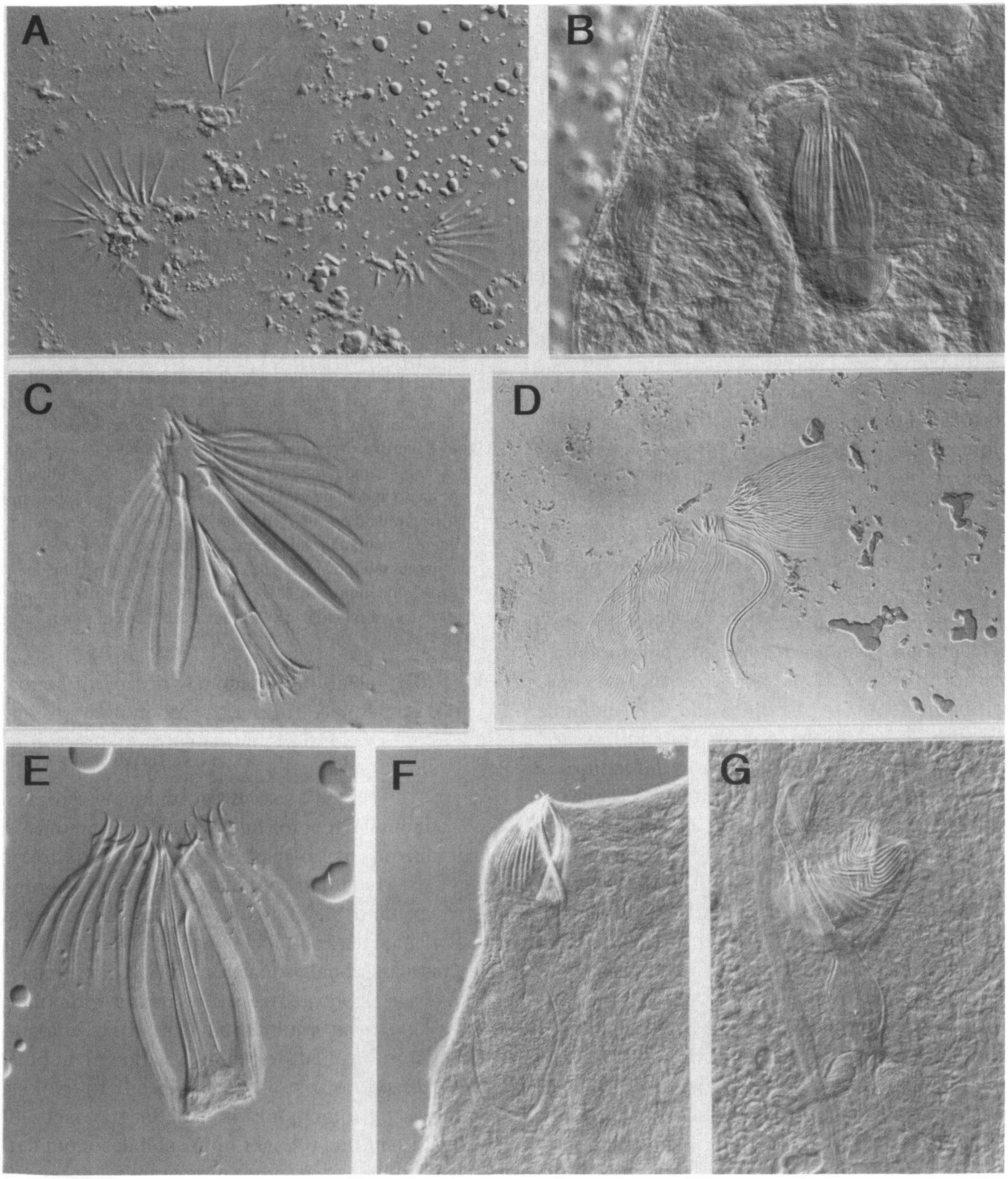

Fig. 16. Hard structures of the copulatory organ of *Calviria banyulensis* (A), *Meidiama schockaerti* (B) and some *Archimonocelis* species: C, *A. crucifera*; D, *A. carmelitana*; E, *A. puertoricana*; F, *A. puertoricana*; G, *A. sabra.*

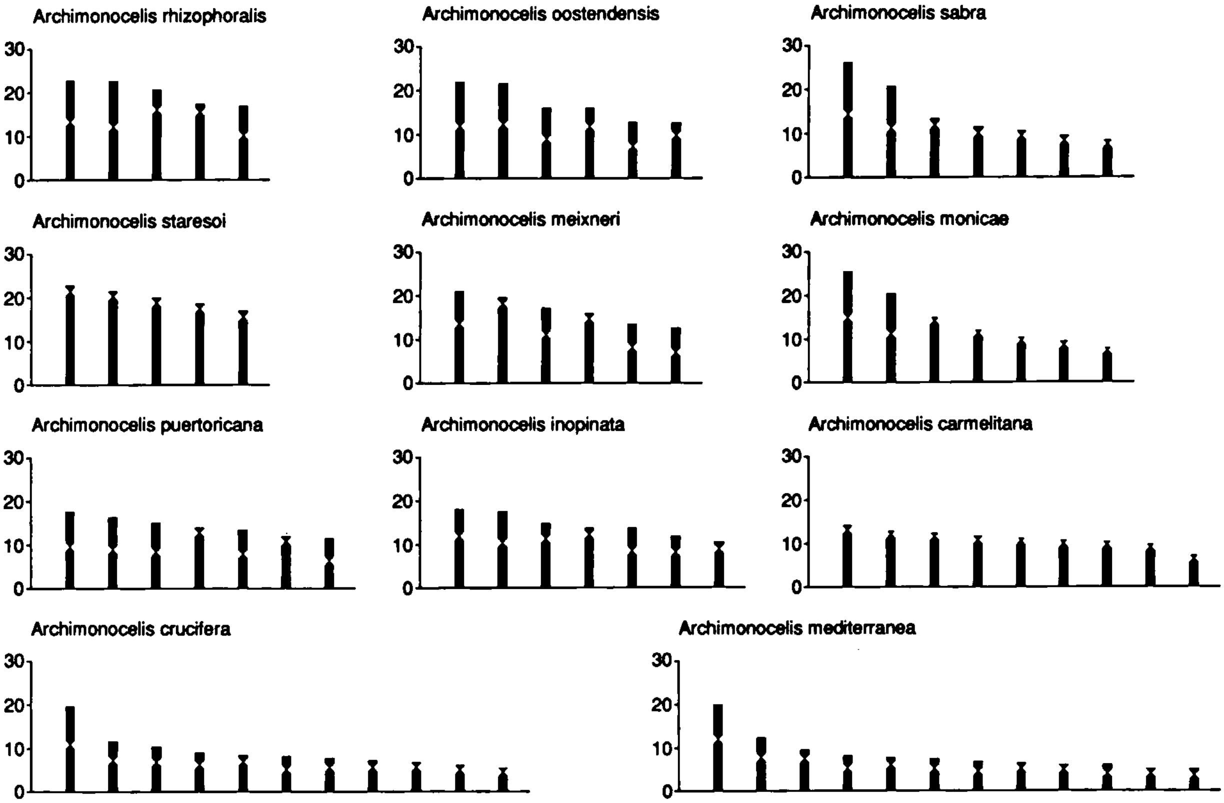

Fig. 17. Idiograms representing the haploid sets of *Archimonocelis* species, based on data reported in species descriptions.

known so far among the Proseriata. The basic condition for the Paramonocelidida is $n = 6$ (see character discussion); this number is shown by *A. oostendensis* and *A. meixneri*. Both these species have an accessory glandular organ; this observation strengthens the hypothesis that presence of an accessory organ is the presiomorphic situation.

Chromosome numbers different from $n = 6$ must be interpreted as apomorphic features, caused by Robertsonian mechanisms of chromosome fission(s) or fusion. There are evidences that the above mechanisms may have happened independently in different species; therefore the use of mere chromosome numbers for reconstructing phylogenies is questionable. An example is the case of the species with $n = 7$, deriving from one fission. Four species have this character: *A. sabra* and *A. monicae*, from the Red Sea, and *A. puertoricana* and *A. inopinata*, from the Caribbean. Analysis of their karyotypes reveals that the two species in each area are closely related, while they differ from the other pair for any other karyometric parameter considered (chromosome absolute and relative length, centromeric index) showing that at least two independent events of fissioning have occurred. Because of the similarities in karyotype, we consider members of each pair as sister species, possibly the result of sympatric speciation.

Genus *Meidiama* Marcus, 1946

Diagnosis. – Archimonocelidinae without cnidosacs. Pharynx short and ventrally oriented. Ovaria just in front of the pharynx, vitellaria postpharyngeal. Copulatory organ with stylet and spines. No accessory glandular organ. The prostate vesicle is anteriorly oriented and the seminal vesicles enter the vesicle at its anterior side.

Type species: *Meidiama lutheri* Marcus, 1946.

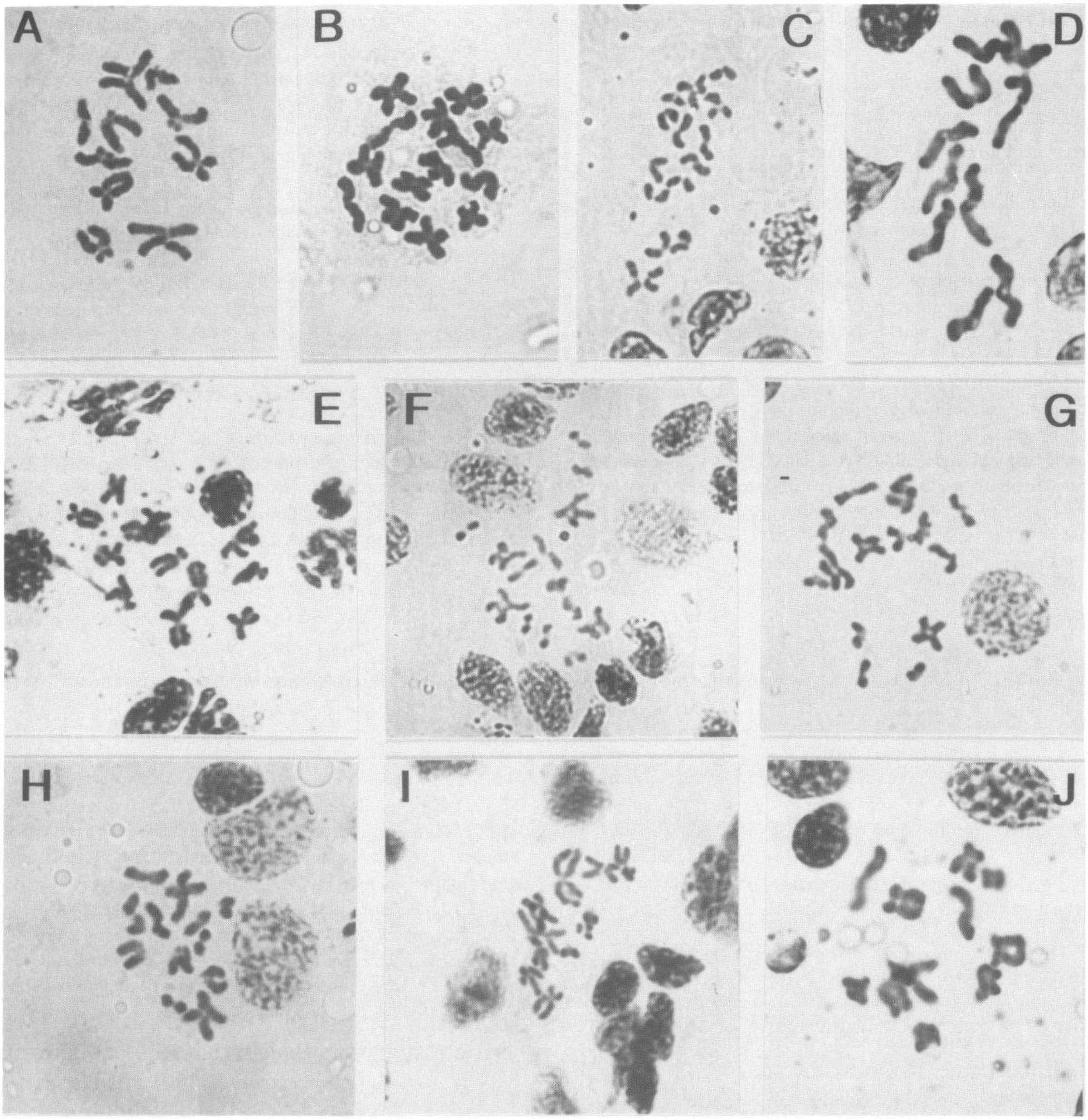

Fig. 18. Plates of spermatogonial mitoses: A, *Calviria banyulensis*; B, *Archimonocelis puertoricana*; C, *A. carmelitana*; D, *A. staresoi*; E, *A. oostendensis*; F, *A. monicae*; G, *A. sabra*; H, *C. sublittoralis*; I, *C. solaris*; J, *A. meixneri*.

Key to the species

– Stylet straight, about 60 μm long; spines 45–50 μm long ... . *M. schockaerti* sp. n.
– Stylet curved, about 60 μm long; spines about 30 μm .... *M. lutheri* Marcus, 1946

Meidiama lutheri Marcus, 1946
(Fig. 19D)

Distribution, material, and description. – Brazil, beach of Guarujá, near Santos, coarse shell gravel (type locality).

One whole mount (designated by us as lectotype) and one

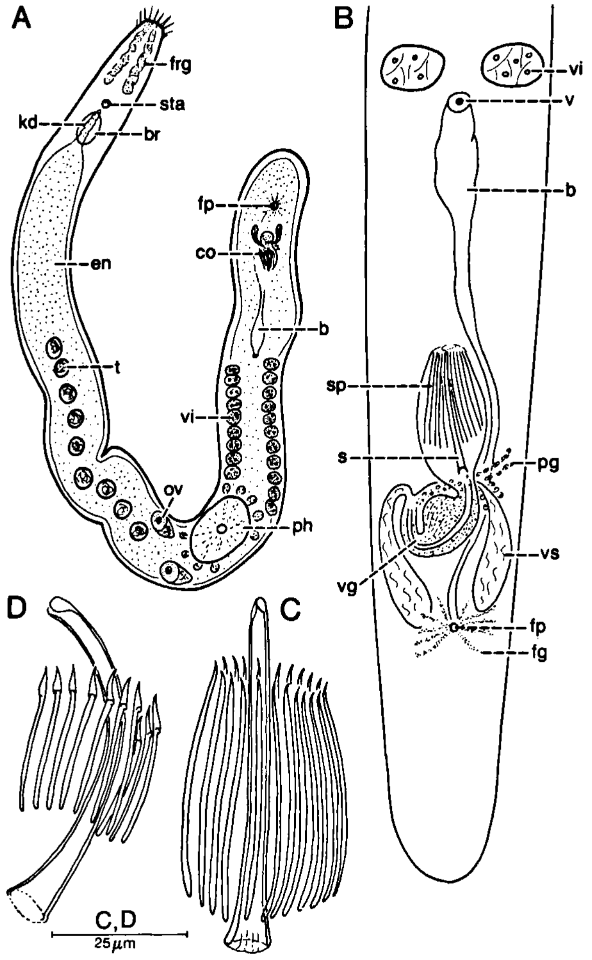

Fig. 19. A–C, *Meidiama schockaerti* sp. n.: A, general organization of a live animal; B, general organization of the copulatory organs from a live animal; C, stylet and spines. D, *Meidiama lutheri* Marcus, 1946, stylet and spines.

slide with many serially sectioned specimens (SMNH).

For an extended description, see the original account of Marcus (1946). We have studied the type material and our observations agree with the original description. Though Marcus mentioned the presence of 12 spines, we could observe only 10 spines in the lectotype (Fig. 19D).

Meidiama schockaerti sp. n.
(Figs. 16B, 19A–C)

Distribution and material. – Argentina, Punta Arenas, beach of Pinginnerias, coarse sand and gravel, January 1989 (type locality).

Two whole mounts (one of them chosen as holotype, ZC-LUC no. 153).

Etymology. – The specific epithet refers to Prof. Dr. E. Schockaert, who collected the material of this species.

Description. – Long slender animal with almost the same habitus as *M. lutheri.* In whole mount the animal is 2–3 mm long and 0.5 mm broad. The anterior tip is provided with long sensory bristles. In front of the statocyst two glandular-like structures ending in the anterior tip were observed (frontal glands). The brain is encapsulated.

The short, ventrally oriented, pharynx lies just in front of the last third of the body. The anterior part of the gut runs over the brain and forms a cephalic gut.

Testes lie in one median row in front of the pharynx. About 9 testes could be counted; however, they were difficult to observe and a more exact number can not be given. The copulatory organ consists of a pair of seminal vesicles, a prostate vesicle and a stylet surrounded by about twenty spines. The stylet is straight and about 60 µm long. The spines have all the same shape, are about 45–50 µm long, not hooked, and slightly curved at the tip.

Ovaries lie in front of the pharynx, vitellaria behind it. Just behind the last vitelline follicles the female ducts fuse to form a well visible bursa with a vaginal pore surrounded by some muscles. From the bursa, the female duct continues posteriorly over the copulatory organ and opens to the exterior through the female pore, which is surrounded by many glands.

Discussion of the genus Meidiama

The two known species are very similar. The main differentiating characters are the number of testes (much less in *Meidiama schockaerti* than in *M. lutheri*) and the hard structures of the copulatory organ. In *M. schockaerti* the stylet is straight (about 60 µm long), while in *M. lutheri* the stylet is curved (also about 60 μm long). In *M. schockaerti* there are about 20 spines which are ± 45–50 μm long, while in *M. lutheri* there are only 12 spines which are about 30 μm long.

Meidiama species are superficially very similar to most *Archimonocelis* species. Marcus (1946) considered the presence of a vagina as the discriminating character with the genus *Archimonocelis*. However, at present a vagina is known for many species of the genus *Archimonocelis* as well.

Karling (1966a) considered the localization of the ovary, the shape of the pharynx, which is short and ventrally oriented, the presence of a postpenial bursa and the absence of cnidosacs as characteristics of the genus *Meidiama*. He mentioned that the postpenial bursa of *Meidiama* corresponds with the genito-intestinal duct in *Archimonocelis*. In some *Archimonocelis* species the genito-intestinal duct is also a non-permanent structure and in these animals the morphology of the postgenital bursa is rather similar to *Meidiama*. The presence of a postpenial bursa can therefore no longer be considered as a discriminating feature.

Therefore, the main differentiating characters for the genus *Meidiama*, as compared to *Archimonocelis*, are: (1) the absence of cnidosacs, (2) the short, ventrally oriented pharynx, (3) ovaria just in front of the pharynx as well as in front of the vitellaria, which are restricted to the postpharyngeal region, and (4) the anterior orientation of the prostate vesicle. All these characters are synapomorphies for the two species, with the exception of the absence of cnidosacs and the position of the ovaries (see also phylogenetic conclusions). The known distribution of the genus is limited to South America, from Brazil to Magellan Strait, an area from which no *Archimonocelis* species have been reported so far.

Subfamily **Calviriinae** subfam. n.

Diagnosis. – Archimonocelididae with a septum at the base of the pharynx. This septum is dorsally provided with a diaphragm through which the intestine penetrates. Ovaria just in front of the pharynx and vitellaria anterior to the ovaria. Copulatory organ without a stylet. With an accessory glandular organ, which is partly or completely separated from the male atrium. Short common female duct present and vagina absent.

Type genus: *Calviria* gen. n.

Key to the genera

- Accessory glandular organ communicates with the male atrium; with a postpenial invagination .... *Asilomaria* Karling, 1966
- Accessory glandular organ does not communicate with the male atrium .... *Calviria* gen. n.

Genus *Calviria* gen. n.

Diagnosis. – Calviriinae with a simple penis papilla pointing into the male atrium, which is provided with numerous spines. An accessory glandular organ with spines lies in front of the penis; this organ is not connected with the male atrium and has its own pore. A glandular complex is located medioventrally in front of the accessory organ. Secretory ducts run laterally from the accessory organ and open into two ventrolateral invaginations. With large subepidermal vesicles spread over the whole body.

Type species: *Calviria solaris* sp. n.

Etymology. – The genus name refers to the place (Calvi, Corsica) where species of the genus have been found for the first time.

Key to the species

1. – With more than 80 atrial spines arranged in two groups: one group consisting of two lateral rows of spines and one group arranged semicircularly around the penis papilla .. .. *Calviria solaris* sp. n.
   – With one group of atrial spines surrounding the penis papilla 2
2. – About 20–30 spines, all of about the same size (± 60 μm) .... *Calviria sublittoralis* sp. n.
   – About 30 spines, ranging in length between 12 and 30 μm .... *Calviria banyulensis* sp. n.

Calviria solaris sp. n.
(Figs. 18I, 20–22, 25A, 26A–B, 27)

Syn. – Nov. gen. sp. 1 (Martens et al., 1989).

Distribution and material. – Mediterranean Sea: Corsica, Bay of Calvi, poorly sorted medium sand, littoral, May 1983 (type locality). Livorno, beach near Cantieri Orlando, medium to coarse sand, about 20 cm deep, January 1991. Elba Island, Marina di Campo, city beach, coarse sand, about 15 cm deep, December 1990. Lecce, beach of Acquatina, medium sand, about 30 cm deep, March 1991.

Many animals studied alive, four specimens sectioned serially (one of them chosen as holotype, ZC-LUC No. 176), three squeezed whole mounts and one animal semi-thin sectioned. Several karyological slides.

Etymology. – The specific epithet refers to the radial arrangement of the spines around the copulatory organ.

Description. – Large specimens are about 5–10 mm long and 0.5 mm broad. Without pigment or eyes. The anterior tip is rounded. Hyaline subepidermal vesicles are spread over the whole body. In live animals the brain capsule is anteriorly trilobated, while in sectioned material the brain is spherical as a result of fixation. The statocyst in front of the brain is surrounded by a capsule similar in aspect to the brain capsule.

The epidermis with intraepithelial nuclei is 2.5–3.5 μm high and ciliated over the whole body. Cilia are 3.5–5 μm long. The epidermis as well as the cilia are higher ventrally than dorsally. Rhabdites are absent. Frontal glands lie behind the brain and run ventrally to the anterior part of the body, where they open subterminally.

Subepidermal vesicles are spread over the whole body. In live animals these vesicles seem to be empty and connected to the outside through a small canal. In sections these vesicles consist of a single large, vacuolated cell, of which the vacuole seems to be empty. The cell has a neck which pierces the epithelium to open to the exterior. The vacuole extends inside the neck. In the spherical part of the cell there is a peripheral, more densely stained area which corresponds to a dense cytoplasm with nucleus.

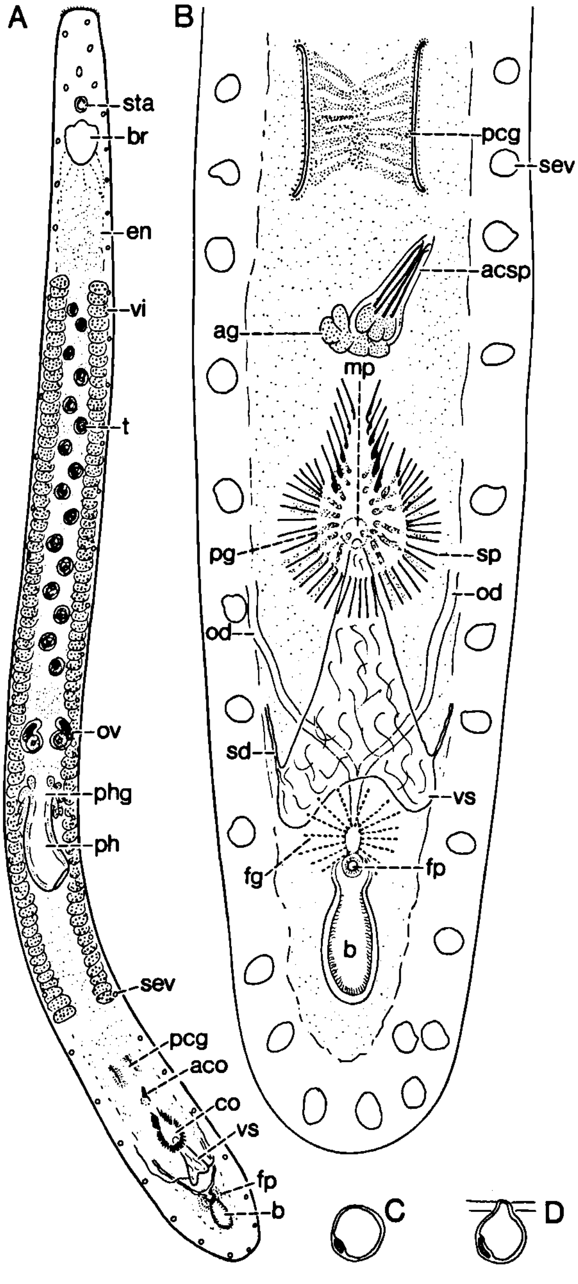

Fig. 20. Calviria solaris sp. n.: A, general organization of a live animal; B, general organization of the copulatory organs from live animals; C–D, sections of subepidermal vesicles.

The intestine runs from behind the brain up to the end of the copulatory organs. The cephalic gut reaches the statocyst. The horizontal, tubiform pharynx lies just in front of the last third of the body. In sections, the pharynx is about 125 μm

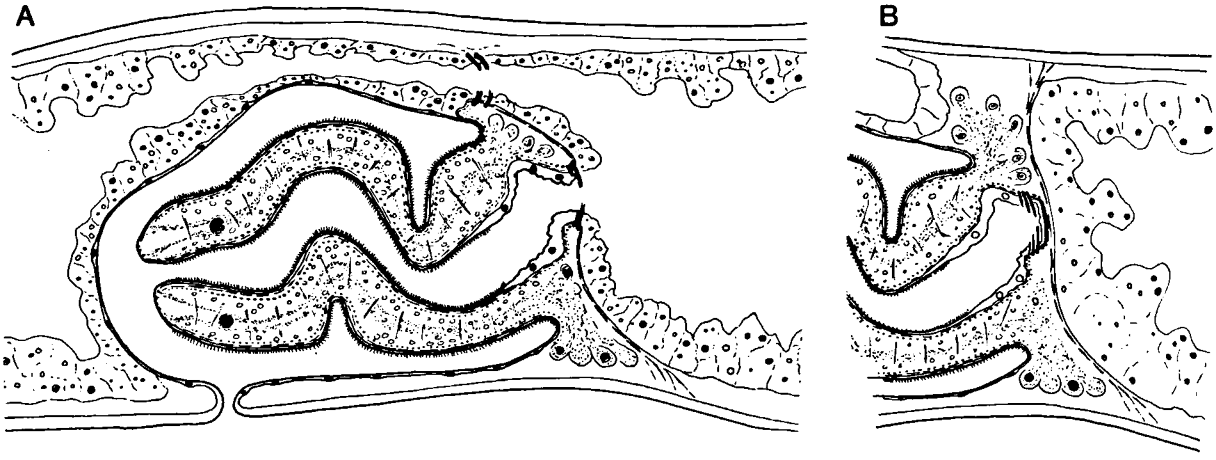

Fig. 21. Calviria solaris sp. n., sagittal reconstruction of the pharynx: A, mediosagittal; B, laterosagittal.

long. The pharynx muscles are arranged as in the other Archimonocelididae: beneath the epithelium there is an outer layer of longitudinal muscles and an inner layer of circular muscles. Within the parenchyma several transversal muscle fibers are present. The epithelium has insunk nuclei and is ciliated except at the anterior tip, where glands discharge to the exterior.

The oesophagus is weakly developed. Only 1/8 of the pharynx length is provided with a nonciliated epithelium with intraepithelial nuclei. This epithelium shows no secretory activity. Proximally, at the base of the pharynx, some circular muscles are well developed, forming a sphincter around the lumen of the pharynx (see Fig. 21). At the base of the pharynx a septum ("prepharyngeal septum") separates the gastrodermis from the pharynx. This muscular septum is constituted by muscles originating from the internal longitudinal muscles of the pharynx, which are connected with the body musculature. The gut penetrates this septum dorsally to the pharynx; in this diaphragm some circular muscles are present, constituting a sphincter. Numerous glands lie in the parenchyma at the basis of the pharynx; their cell necks run through the pharynx parenchyma and discharge at the distal tip of the pharynx.

In front of the ovaria there are 15–20 medial testes in two alternating rows. The copulatory organ consists of a large, lobated, anteriorly oriented seminal vesicle, which is scarcely muscular and continues into a penis papilla. Prostatic glands were not observed. There are, however, numerous glands which open in the atrium together with the penis papilla. This atrium is lined with a high epithelium, in which intraepithelial spines are formed. The atrial spines can be separated into two groups: one group, with 60–80 spines of about 55–75 μm long, lies around the penis papilla. A second group, consisting of two lateral rows, each containing about 20 spines each of 70 to 80 μm long, lies rostrally to the penis papilla. The spines of the lateral rows and some of the semicircular group are curved at the tip and are provided with subterminal hooks. Tip and subterminal hook can be both irregularly serrated.

In front of the male atrium, there is an anteriorly oriented accessory glandular organ embedded in the parenchyma. This accessory organ consists of a muscular bulb, containing four spines (85 to 90 μm long), which are straight and only slightly curved at the tip. Cell necks, from glands which are located outside the bulb, lie between the spines. A connection between the accessory glandular organ and the exterior was never observed.

A large glandular complex (prepenial gland complex) is present in front of the accessory organ; it consists of two groups of glands, which open in-

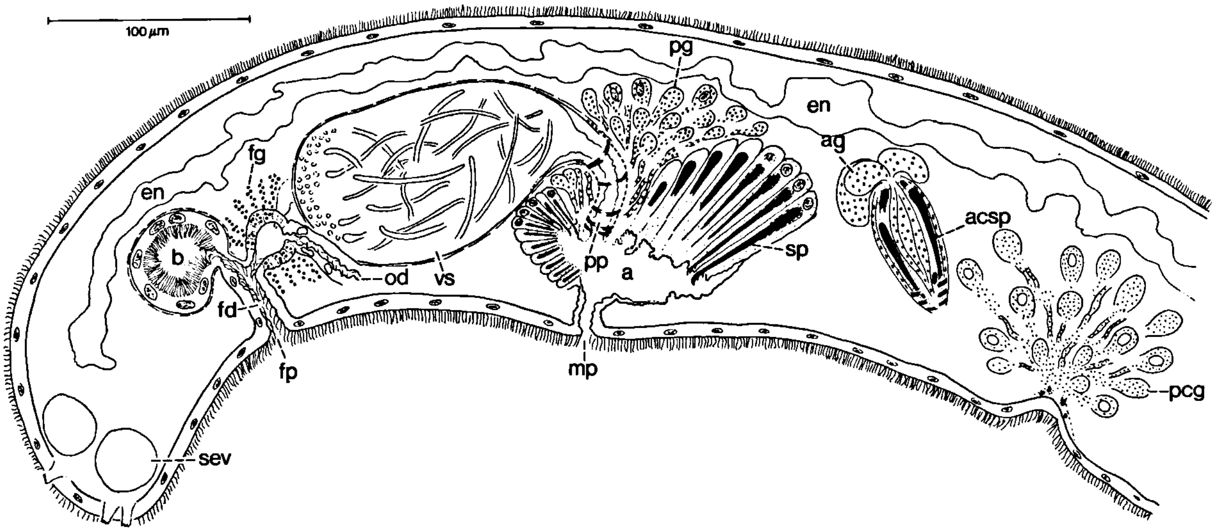

Fig. 22. Calviria solaris sp. n., reconstruction of the copulatory organs from serial sagittal sections.

dependently in two lateroventral invaginations of the epidermis. Due to muscle contraction, the shape of the opening of the invaginations is variable.

Vitellaria lie laterally and run from the first fifth of the animal to the copulatory organ. One pair of ovaria lies just in front of the pharynx, medially to the vitellaria. The paired germovitelloducts are ciliated, and run lateroventrally to behind the seminal vesicle, where they fuse to form the female common duct. This duct is very short and opens to the exterior through the female pore. At the point of fusion of the oviducts, the glandular female duct broadens, and is devoid of cilia. Distally from this broadening, the female duct is ciliated and is connected with a bursa, which is provided with a well-developed ciliated epithelium with intracellular nuclei. This last distal part, together with the bursa, is only well developed in fully mature animals.

Karyotype. – With $n = 6$, one large submetacentric, three medium-sized meta- to submetacentric and two small chromosomes, about ¼ the size of the largest.

Karyotype formula: 17.8 μm; 11; I: 29.89, 34.83 (sm); II: 20.04, 38.79 (m); III: 17.29, 33.53 (sm); IV: 17.00, 40.58 (m); V: 8.48, 38.77 (m); VI: 7.37, 13.77 (st) (data from the Calvi population). Specimens from Elba Island showed an almost identical karyotype.

Calviria sublittoralis sp. n.
(Figs. 18H, 23, 24, 25B, 26C–D, 27)

Syn. – Nov. gen. 2 (Martens et al., 1989).

Distribution and material. – Mediterranean sea: Corsica, Bay of Calvi, 6–36 m, poorly sorted medium to coarse sand with gravel, March 1983 (type locality).

Several whole mounts (one of them chosen as holotype, ZC-LUC No. 175). Two specimens serially sectioned, one in male and one in female maturity.

Etymology. – The specific epithet refers to the sublittoral habitat of the species.

Description. – In general organization this species is very similar to *C. solaris*. It is, however, slightly smaller and the anterior tip in front of the statocyst is comparatively shorter. The cephalic gut runs up to the statocyst. In sectioned material transversal muscles appear particularly well developed all over the body. The pharynx is the same as in *C. solaris*.

In *C. sublittoralis* only specimens with male or female maturity were found. The copulatory organ contains a prostate vesicle, clearly visible in the live animal, as well as in sections. A large seminal vesicule is connected to the prostate vesicle through a small muscular sphincter. Cell bodies of the

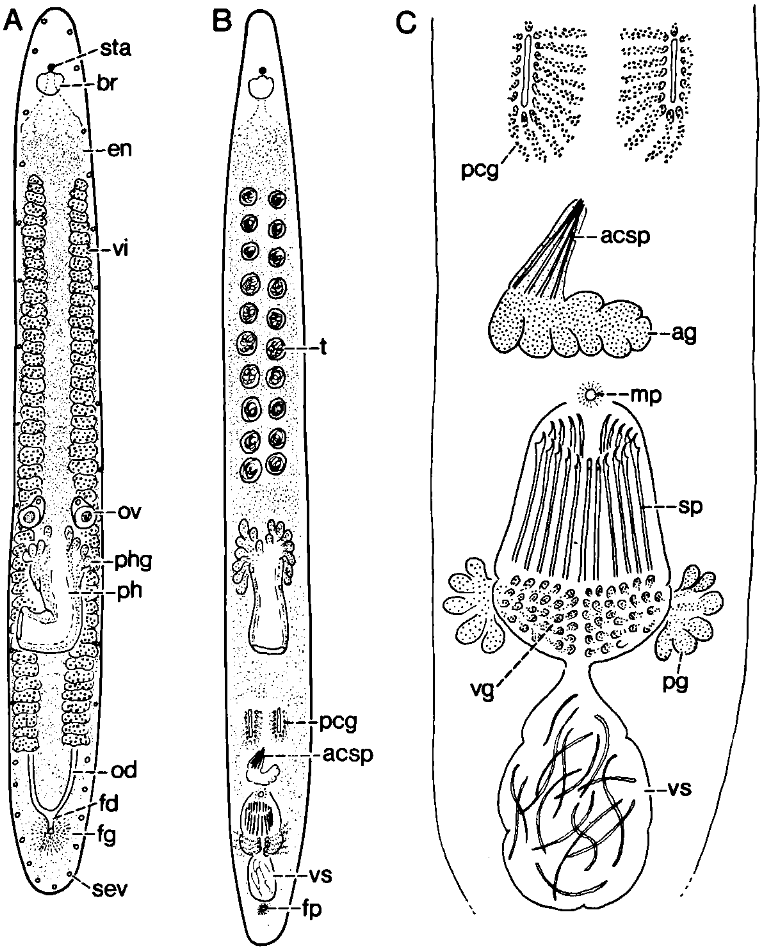

Fig. 23. Calviria sublittoralis sp. n.: A, general organization of a live animal with female maturity; B, general organization of a live animal with male maturity; C, general organization of the copulatory organs of a live animal with male maturity.

prostate glands lie inside and outside the bulbus. The prostate vesicle ends into a penis papilla which opens into the male atrium; the papilla is surrounded by 20–30 spines. These spines are formed intracellularly and are about 60 μm long. Some of the spines have distinctly curved tips and are provided with subterminal hooks; both the tip and the hook can be serrated. The accessory glandular organ contains four spines, about 70 μm long, with a slightly curved tip. In sectioned material the accessory organ seems to open into an atrium, which narrows in the direction of the prepenial gland complex; there is probably a connection with both gland ducts. The two gland ducts of the prepenial gland complex are short, as in *C. solaris*, and open into two ventrolateral invaginations of the body wall.

The female copulatory organ is similar to that of *C. solaris*. The two long, ciliated oviducts fuse behind the seminal vesicle, forming the short female duct which is surrounded by many glands. Neither a bursa nor a genito-intestinal connection were observed. In sections of specimens in male maturity, the female channel was also present.

Karyotype. – With $n = 6$, one large metacentric and five acrocentric chromosomes; the smallest is about ¼ the size of the largest.

Karyotype formula: 17.0 μm; 7; I: 32.15, 45.33 (m); II: 18.12, 9.11 (t); III: 16.35, 8.43 (t); IV: 14.13, 6.79 (t); V: 10.62, 7.54 (t); VI: 8.61, 9.57 (t).

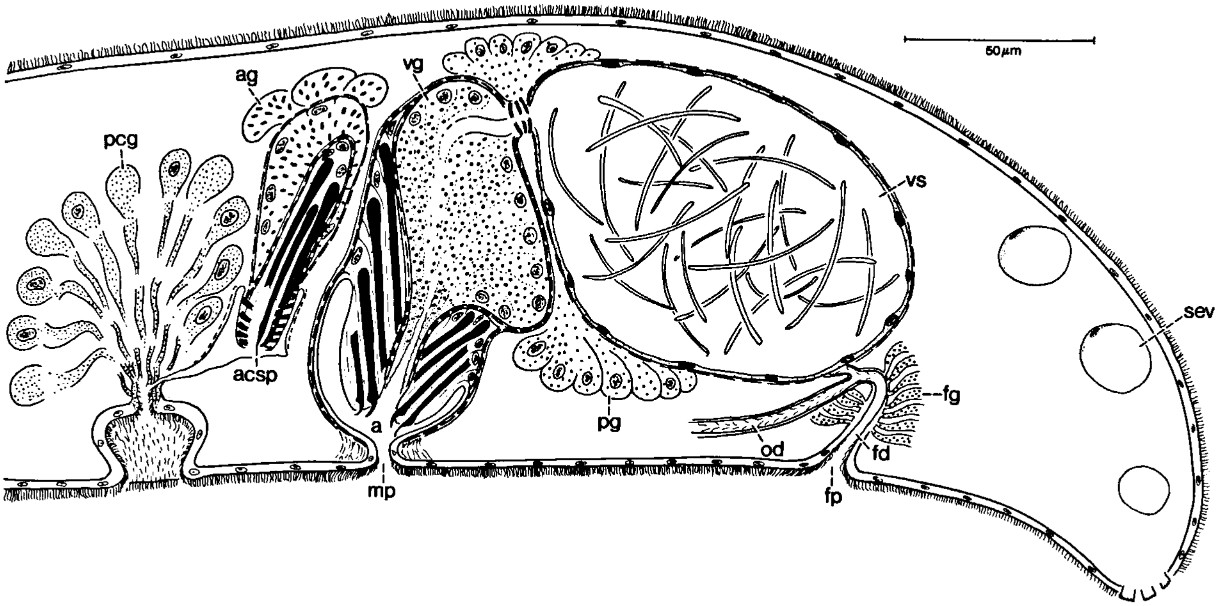

Fig. 24. Calviria sublittoralis sp. n., reconstruction of the copulatory organs from serial sections of an animal with male maturity.

Calviria banyulensis sp. n.

(Figs. 16A, 18A, 25C, 27)

Distribution and material. – Mediterranean: France, Banyuls-sur-mer, 6 m deep in coarse sediment in front of the Laboratoire Arago, October 1987 (type locality).

Three karyological slides with squashed hard structures, one of them chosen as holotype (ZC-LUC No. 174).

Etymology. – The species is named after the sampling locality.

Description. – At a low magnification, the animals looked similar to *C. sublittoralis* and have been held for that species. During the karyological study, however, differences in karyotype as well as in hard structures made evident that the animals belong to a distinct species.

The hard structures contain 30–32 atrial spines and 4 accessory spines. The atrial spines surround the penis papilla in a semi-circular corona. The spines are different in length: at the periphery they are about 30 µm long, whereas in the central part they are shorter, i.e. about 12 µm. The spines are provided with a coarsely serrated terminal part, which is shaped differently in each spine; due to the serration in most of the spines, a distinction between curved tip and hook is not apparent. The accessory glandular organ contains 4 spines, about 25–27 µm long, straight, with the tip curved at a right angle.

Karyology. – With $n = 5$, one large metacentric chromosome; the smallest chromosome is about ⅓ the length of the largest.

Karyotype formula: 19.1 µm; 7; I: 30.09, 45.43 (m); II: 22.33, 34.88 (sm); III: 18.80, 13.76 (st); IV: 16.44, 12.34 (t); V: 12.31, 7.09 (t).

Discussion of the genus Calviria

The species of the genus *Calviria* are recognizable on the basis of the hard structures and the karyotype. While *C. solaris* is obviously distinct, the differences among the other two species are more subtle and based on differences in size and shape of the spines (see identification key and Fig. 25). However, these are constant in the specimens examined; the karyotype also confirms that two species are concerned.

The three species of the genus *Calviria* show

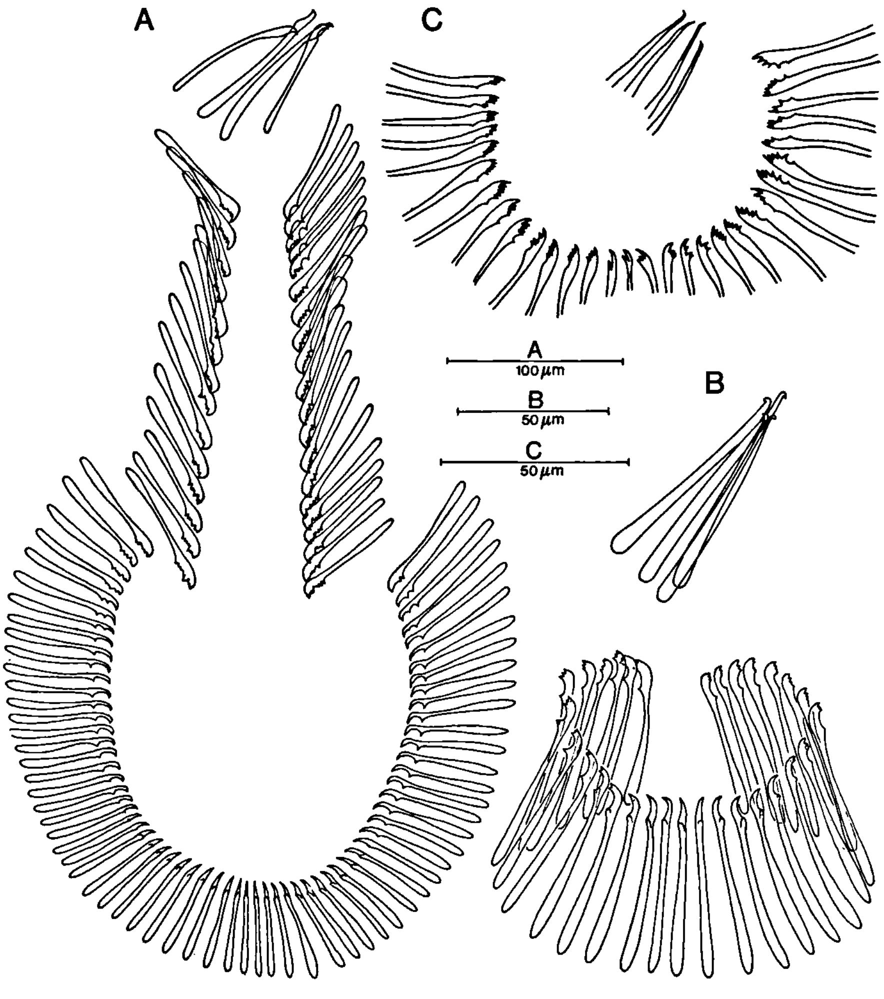

Fig. 25. Calviria solaris sp. n., spines and accessory spines; B, *C. sublittoralis* sp. n., spines and accessory spines; C, *C. banyulensis* sp. n., spines and accessory spines.

characters which are not present in any other member of the Archimonocelididae, such as the subepidermal vesicles, the prepenial glandular complex, and the accessory glandular organ which is separated from the male atrium. These three characters can be considered as autapomorphies for the genus (see phylogenetic analysis).

C. solaris and *C. sublittoralis* share a common character in their karyotype, i.e. chromosome 1 is distinctly longer than chromosome 2. This can be explained by a translocation from the latter to the former. *C. sublittoralis* has undergone also several pericentric inversions, resulting in chromosomes 2–6 being acrocentric. *C. banyulensis* and *C. sublittoralis* have the same fundamental number and comparable absolute length of the haploid genome. From these observations and from comparing the relative lengths of their sets, the karyotype of *C. banyulensis* can be derived easily from a karyotype similar to that of *C. sublittoralis* through one fusion (possibly involving chromosomes 4 and 6). From the hypothesis above, we can conclude that the basic karyotype of the genus *Calviria* is derived from the basic set of the Paramonocelida (Martens et al., 1989) through the above-suggested translocation. Within the genus, the basic karyotype evolved, as a result of several pericentric inversions, into a karyotype at the basis of both *C. sublittoralis*

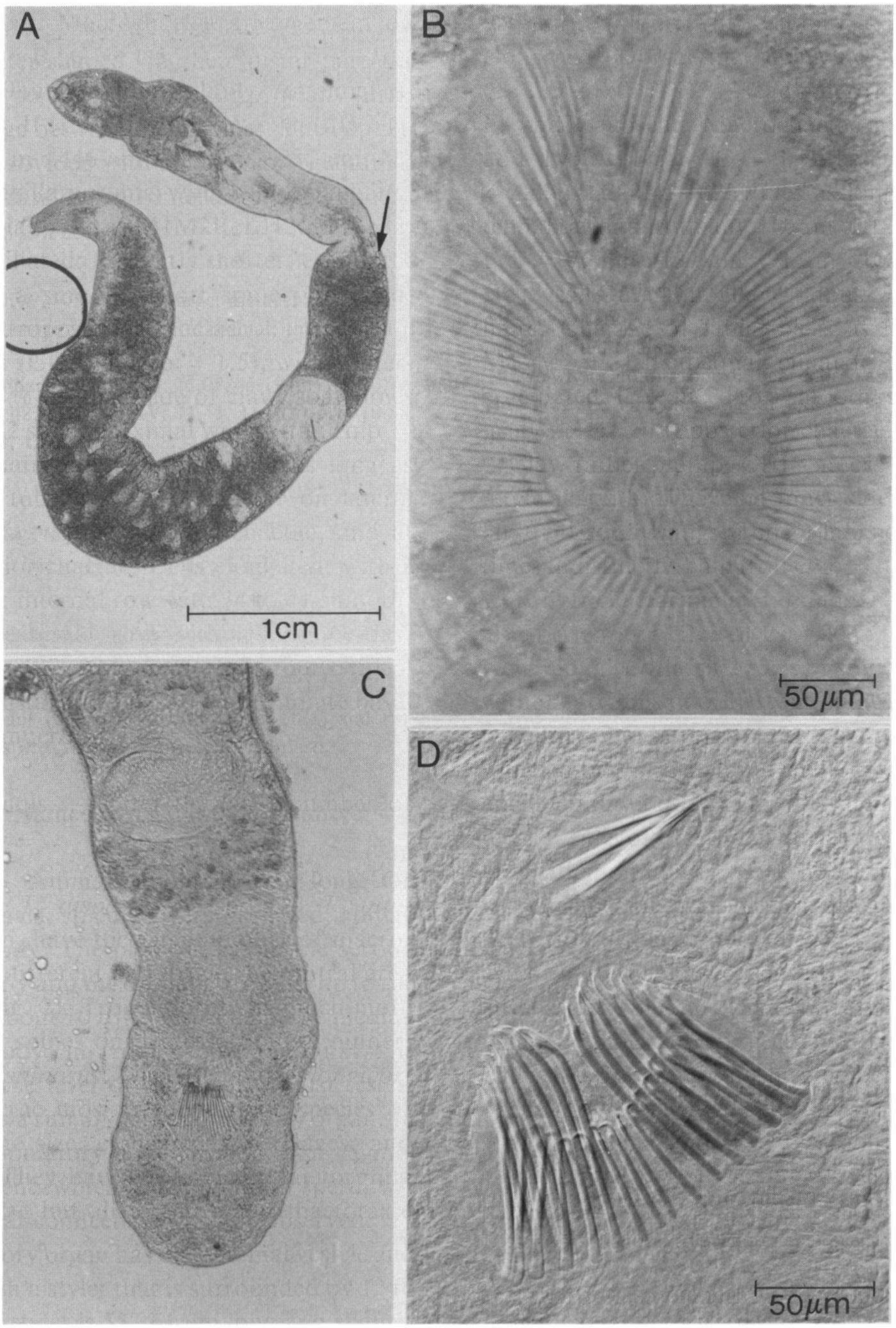

Fig. 26. A–B, *Calviria solaris*: A, habitus; B, copulatory organ. C–D, *Calviria sublittoralis*: C, caudal end; D, copulatory organ.

and *C. banyulensis*. From this karyotype, through one fusion, the karyotype of *C. banyulensis* originated. The karyological evolution within the genus is given schematically in Fig. 27.

The genus is so far known only from the central Mediterranean, with species occurring littorally as well as sublittorally but always in dynamic conditions.

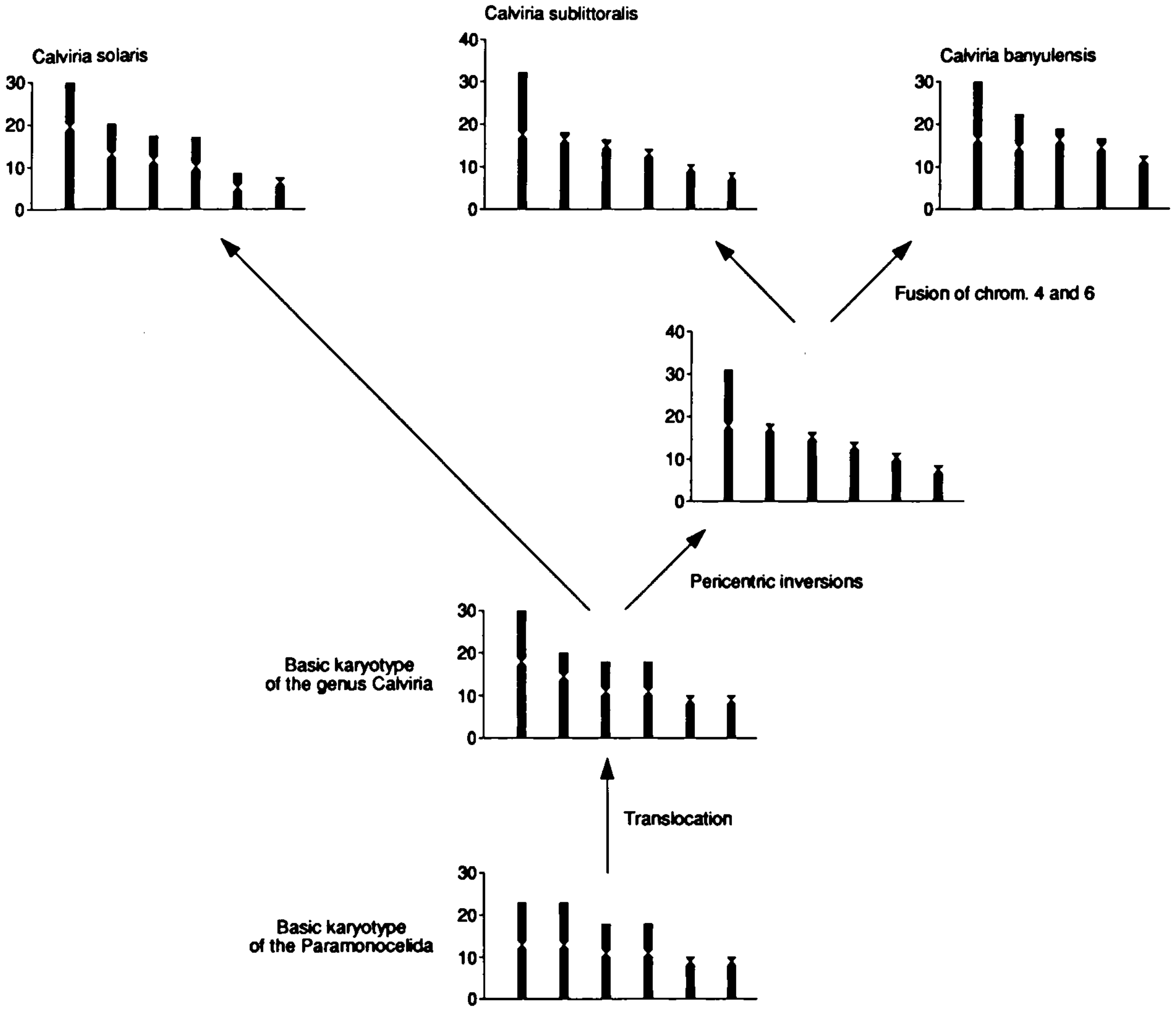

Fig. 27. Idiograms of the three *Calviria* species, based on karyometric data reported in the species descriptions and hypothesized karyological evolution of the genus (see text).

Genus *Asilomaria* Karling, 1966

Diagnosis. – Calviriinae with paired seminal vesicles, without prostate vesicle, and with a simple penis papilla.

Accessory glandular organ with a bilobated glandular complex which ends into a bulbus and is surrounded by several spines. With a large ventral, postpenial invagination.

Type species: *Asilomaria ampullata* Karling, 1966.

Asilomaria ampullata Karling, 1966
(Fig. 28)

Distribution and material. – Pacific, North America, Bodega Bay, shell gravel (type locality).

One serially sectioned animal (holotype) (SMNH).

Description and discussion. – For the general morphology, see Karling's (1966a) description. The pharynx is similar in general shape and morphology to *Calviria*. A prepharyngeal septum with a dorsal sphincter through which the gut penetrates is also present. In the original description, Karling men-

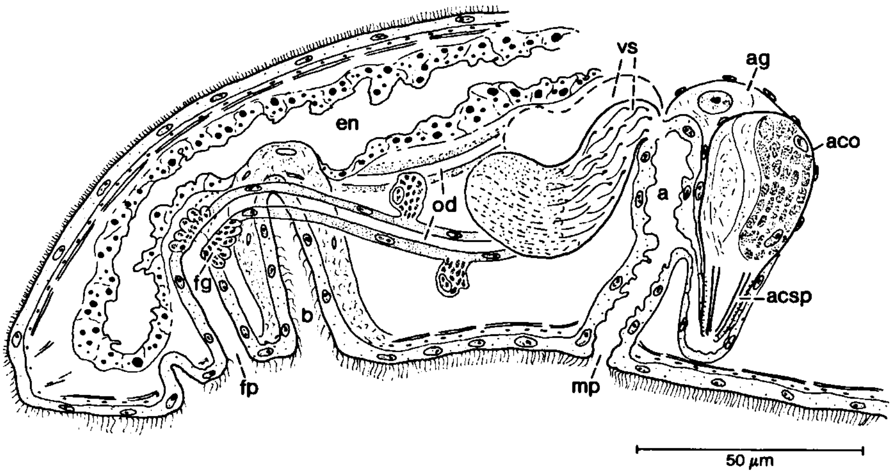

Fig. 28. Asilomaria ampullata Karling, 1966. Reconstruction of the copulatory organs from serial sagittal sections.

tioned that the two seminal vesicles are connected with the prostate glands. From the analysis of the type material (see Fig. 28) no evidence for such a connection was found. It seems that the two seminal vesicles fuse and open into the male atrium, without forming a differentiated penis. This male atrium is not provided with hard structures. In front of this rudimentary copulatory organ there is an accessory glandular organ. This is constituted by two large glandular globules, surrounded by a tunica (these globules, according to Karling, constitute the prostate glands). The two globules fuse and form the bulbus of the accessory organ. This bulbus opens into an atrium and its surrounded by 12 spines, which are embedded in the epithelium, thus indicating their intracellular origin. The atrium of the accessory organ is connected with the male atrium through a small canal.

Character analysis and phylogeny

The hypothesized phylogenetic relationships are shown in Fig. 30.

Epidermis

In the Archimonocelididae, the epidermis is totally ciliated, with intraepithelial nuclei. This is the plesiomorphic condition for the Proseriata. The Archimonocelididae differ in this character from the Monocelididae, in which the nuclei are mostly insunk and the caudal region is without ciliation. Within the Archimonocelididae, a reduction of ciliation is found only in *Archimonocelis glabrodorsata*, in which dorsal ciliation is absent. Another secondary modification is found in two North Atlantic species (*Archimonocelis koinocystis* and *A. bathycola*) in which the nuclei are insunk (see Karling, 1966a).

Cnidosacs

Cnidosacs (see Karling, 1966b) are epidermal or subepidermal structures containing cnidocysts (originating from food) and supporting cells. In the Platyhelminthes, cnidosacs are present in several taxa (see Karling, 1966b). Within the Seriata, they are present in two families: the Archimonocelididae (within the genus *Archimonocelis*) and the Nematoplanidae (within the genera *Nematoplana* and *Ezoplana*). In the Nematoplanidae, cnidosacs are always arranged in two or more rows (see Curini-Galletti & Martens, 1992), while in *Archimonocelis* there is one median dorsal row. We consider a single row of cnidosacs as an autapomorphy for the genus *Archimonocelis* (4 in Fig. 30).

Subepidermal vesicles

These are only found in species of the genus *Calviria*. They probably consist of one single cell, lying subepidermally, with a large vacuole (see species description). There seem to be some similarities with paracnids present in other groups of Proseriata, like in the Coelogynoporidae and in *Notocaryoplanella glandulosa* and *Notocaryoturbella bigermaria* (Otoplanidae) (see Ax & Ax, 1967; Karling, 1966b; Lanfranchi, 1969).

Due to the existence of other autapomorphies for the genus *Calviria*, and since subepidermal vesicles are not present in any other member of the Archimonocelididae, and as a consequence of the phylogenetical system here proposed, these vesicles have to be taken as a synapomorphy for the species of the genus (13 in Fig. 30).

Anal pore

This structure, within the family Archimonocelididae, is present only in species of the genus *Archimonocelis*. It is considered as a functional anus by Karling (1966c), open only at the moment of defecation. A pore has been observed in *A. bathycola*, *A. semicircularis*, *A. coronata*, and *A. itoi*. In all the other *Archimonocelis* species of which sectioned material has been studied, the gastrodermis at the terminal tip was reduced, resulting in contact between the lumen of the gut and the epidermis, thus suggesting that a temporary opening to the outside may exist. Karling (1966c) suggests a correlation between the presence of the anal pore and an elongated muscular pharynx, through which defecation is difficult.

A functional anus is also known in other taxa which have a long body (*Haplopharynx*, *Tabaota*, and *Polystyliphora*) (Ax & Ax, 1974; Karling, 1965, 1966c; Marcus, 1950) or a large volume (Polycladida, Digenea) (Ehlers, 1985; Hyman, 1951). The presence of an anus is considered as a secondary feature which is developed in many taxa independently by parallel evolution (see Ehlers, 1985). The reduction of the gastrodermis at the rear end of the body and the presence of a temporary pore can, however, be considered as an autapomorphy for the genus *Archimonocelis* (5 in Fig. 30).

Postpharyngeal septum

The gut can be interrupted behind the pharynx by a transverse septum, with a central diaphragm. This postpharyngeal septum is widely distributed within the Platyhelminthes. It is present in many Monocelididae and in the genus *Ezona* (Coelogynoporidae), and in the genera *Myozona* and *Myozonaria* (Macrostomida) (see Ax, 1956b; Marcus, 1951; Rieger, 1971). Karling (1966c) correlated the presence of this structure to the anal pore and considered both structures together as a "defecation apparatus". Rieger (1986) considered this diaphragm as a relict of the asexual reproduction by paratomy, thus regarding these diaphragms as homologous.

Within the family Archimonocelididae, a septum is present in most, maybe all species of the genus *Archimonocelis*, though it is not always visible in live animals and can be overlooked easily in sectioned material. In all species we have sectioned, a postpharyngeal septum was present. Because of the wide distribution of this character, it could be considered as an underlying synapomorphy at least for all Platyhelminthes.

Pharynx

Within the Archimonocelididae the pharynx is of the plicatus type (see Ax, 1963). The tubiform pharynx is a synapomorphy for the Seriata (Karling, 1974; Sopott-Ehlers, 1985). Within the Archimonocelididae, a tubiform pharynx is present in the genera *Archimonocelis*, *Calviria*, and *Asilomaria*. In the genus *Meidiama* the pharynx is short and ventrally oriented: an autapomorphy for the genus (7 in Fig. 30).

The lumen of the tubular pharynx is normally provided with a ciliated epithelium with insunk nuclei. The proximal epithelium of the pharynx lumen is not ciliated, provided with intraepithelial nuclei, and sometimes with glands. This part is called the oesophagus. A short oesophagus is present in many Monocelididae, Coelogynoporidae, and Otoplanidae (see Ax, 1956a; Tajika, 1982). The presence of a short oesophagus is a plesiomorphy for the Proseriata. Within the Archimonocelididae, the pharynx of the *Archimonocelis* species is extremely long, and only the distal part of the epithelium of the pharynx is ciliated; half or more than half of the pharynx is provided with a nonciliated glandular epithelium with intraepithelial nuclei, which can be considered as the oesopha-

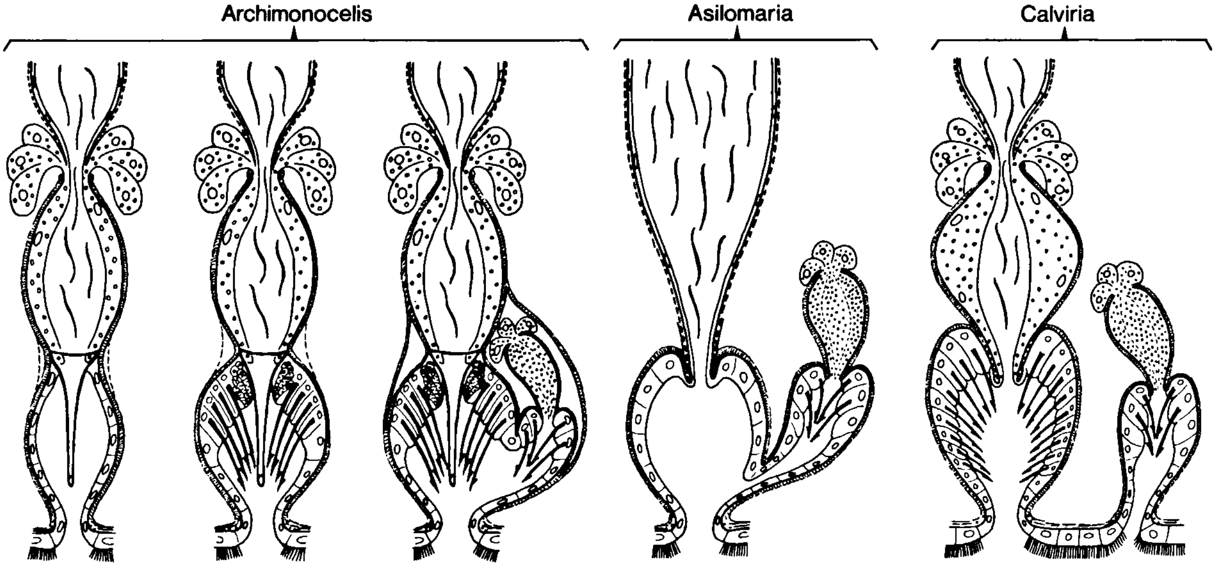

Fig. 29. Schematical reconstruction of the different copulatory organs in the Archimonocelididae.

gus (see Fig. 3). An extremely long pharynx with reduction of ciliation and with extended oesophagus is an autapomorphy for the genus *Archimonocelis* (6 in Fig. 30).

Prepharyngeal septum
In the genera *Asilomaria* (see Karling, 1966a) and *Calviria*, a prepharyngeal muscular septum is present, lying at the base of the pharynx, connected with the internal pharynx musculature. The gut penetrates this septum dorsally through a sphincter (for description of the septum, see *Calviria solaris* and Fig. 21). The prepharyngeal septum is not connected with the outer pharyngeal muscles and the pharyngeal tissue is still connected to the parenchyma and gastrodermis (cf. septum of the pharynx of the bulbosus type; Ax, 1963).

This prepharyngeal septum is not the same as the pharyngeal retractor muscles of the Coelogynoporidae (Tajika, 1982) and of the Otoplanidae (Ax, 1956a), which lie ventrally to the pharynx and are connected with outer pharyngeal longitudinal muscles. The prepharyngeal septum, connected with internal pharyngeal muscles, is a synapomorphy for the genera *Calviria* and *Asilomaria*, i.e. for the Calviriinae subfam. n (10 in Fig. 30).

Male copulatory organ (see Fig. 29)
In *Archimonocelis* and *Meidiama* the copulatory organ consists of one or two seminal vesicles and a prostate vesicle separated from each other, a character which is also found in the Otoplanidae, Coelogynoporidae, Unguiphora, and many other Platyhelminth taxa, thus constituting a plesiomorphic condition for the Proseriata. In both *Meidiama* species the prostate vesicles are anteriorly oriented, a synapomorphy for both species (9 in Fig. 30). In *Archimonocelis* and *Meidiama*, the ductus ejaculatorius ends in a stylet which lies in the male atrium and is surrounded by numerous spines. These hard structures are intracellular in origin.

Within the Paramonocelida (Martens & Schockaert, 1988) a stylet is present in the Archimonocelididae, Unguiphora, Otoplanidae, and in some Coelogynoporidae. Atrial spines are found in Archimonocelididae, Coelogynoporidae, and Otoplanidae. We therefore consider the presence of the stylet and of the atrial spines as the plesiomorphic condition within the Paramonocelida. Within the Archimonocelididae, the stylet is absent in the Calviriinae subfam. n., an autapomorphy for this taxon (11 in Fig. 30). The absence of a real prostatic bulbus in *Asilomaria* (15 in Fig. 30) and in *Calviria solaris* are secondary reductions. The spines are

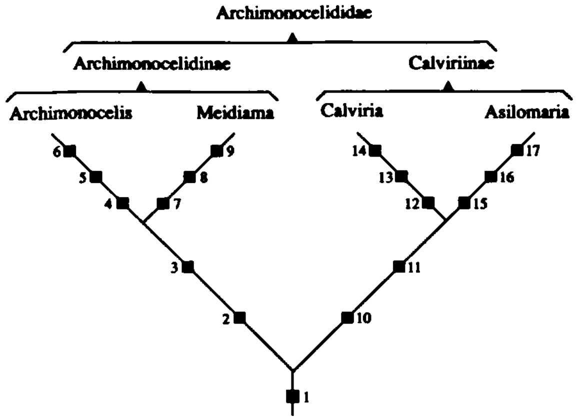

Fig. 30. Phylogenetic relationships within the Archimonocelididae: 1, accessory glandular organ; 2, ovaria in front of the vitellaria; 3, long female duct; 4, cnidosacs; 5, gastrodermis reduced at the rear end, temporary anal pore; 6, pharynx extremely long with reduced ciliation and extended oesophagus; 7, pharynx short and oriented ventrally; 8, accessory glandular organ lost; 9, prostate vesicles oriented anteriorly; 10, prepharyngeal septum; 11, loss of stylet; 12, prepenial glandular complex; 13, subepidermal vesicles; 14, accessory glandular organ not connected with the male atrium; 15, prostatic bulb absent; 16, no spines in the male atrium; 17, postpenial invagination.

secondarily lost in *Asilomaria* (16 in Fig. 30) and some *Archimonocelis* species. In *Asilomaria* there is a postpenial invagination (17 in Fig. 30).

Accessory glandular organ (see Fig. 29)
In *Asilomaria*, *Calviria*, and some *Archimonocelis* species, an accessory glandular organ (prostatoid) is present. It is constituted by a number of glandular cells, the necks of which are surrounded by a muscular bulb. The opening of this bulb is encircled by some spines. The accessory glandular organ is remarkably similar in the three genera; accessory structures with this morphology have not been found in any other member of the Proseriata. The topology of the phylogenetic tree proposed (Fig. 30) suggests that it is an autapomorphy for the Archimonocelididae (1 in Fig. 30) and that the absence of this character in some species of the genus *Archimonocelis* and in *Meidiama* results from secondary loss which, for the genus *Meidiama*, can be considered as an autapomorphy (8 in Fig. 30).

In *Archimonocelis* species, the accessory glandular organ is included in the copulatory bulb (see Fig. 29) and the accessory spines are formed within the epithelial cells of the atrium, similarly to the spines of the male copulatory organ. In some *Archimonocelis* species (e.g. *A. semicircularis*) it is even very difficult to see differences between spines and accessory spines. Also in *Asilomaria*, the accessory organ is connected with the male atrium. These observations suggest that the connection of the accessory glandular organ with the male atrium is the plesiomorphic condition for the Archimonocelididae. In *Calviria*, the accessory glandular organ has no connection with the male atrium, and is probably connected with the precopulatory glandular complex (for morphology of this structure, see description of *Calviria solaris*). Both the loss of connections with the male atrium (14 in Fig. 30) and the presence of the prepenial glandular complex (12 in Fig. 30) are autapomorphies for the genus *Calviria*.

Ovaria and vitellaria
Ovaria among the vitellaria, and located just in front of the pharynx, can be considered as the plesiomorphic condition for the Proseriata. This character is present in all families of the Proseriata, although it can be subject to secondary modification. Within the Archimonocelididae, the ovaria lie in front of the vitellaria in the genera *Archimonocelis* and *Meidiama* (synapomorphy for the two genera) (2 in Fig. 30).

Oviducts
Within the subfamily Archimonocelidinae, the two oviducts fuse at the level of the last vitellaria, always in front of the copulatory organ. The common female duct is long and can be widened prepenially into a bursa, which may be provided with a vagina. This is similar to the situation found in many Monocelididae. In the subfamily Calviriinae, the two oviducts fuse behind the copulatory organ, forming a short common female duct. This is the situation found mostly in Tricladida, Coelogynoporidae, Otoplanidae, and Unguiphora. From the distribution of the character, a short female duct can be taken as the plesiomorphic condition for the Seriata. From the proposed phylogeny (cf. Martens & Schockaert, 1988), similarities between the Archimonocelidinae and the Monocelidi-

dae have to be considered as homoplasous. The long female duct is then a synapomorphy for *Archimonocelis* and *Meidiama* (3 in Fig. 30).

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