THE GIANT PSAMMOPHILOUS CILIATE *AVELIA MARTINICENSIS* (CILIOPHORA, PROTOHETEROTRICHIDA) IN GUANABARA BAY, BRAZIL, WITH TAXONOMIC AND NOMENCLATURAL NOTES

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ABSTRACT

Avelia martinicensis (Nouzarède, 1975), endemic to the Caribbean island of Martinique, is recorded from Guanabara Bay, Rio de Janeiro, Brazil, extending its range over more than 35 degrees of latitude. The organisms were studied by optical (protargol staining) and both scanning and transmission electronic microscopy. The general morphology and the ultrastructure of the nuclear apparatus and the somatic and peribuccal systems of myonemes are in accordance with the original description. Several nomenclatural emendations and changes are made. The specimens have been found in samples of fine sand with high content of organic matter, in an area which shows great variations in temperature and salinity.

KEYWORDS. Karyorelictophora, systematics, *Avelia,* nomenclature, distribution.

INTRODUCTION

Giant psammophilous ciliates form part of the interstitial fauna inhabiting the capillary spaces between sand particles in the superficial layers of marine littorals. They are microporal fauna (FAURÉ-FREMIET, 1950) and have several common adaptive characteristics, such as a strong thigmotactism, a slender sharp body and a system of microfilaments — the myonemes — which render them capable of remarkable cell contraction. Most studies on this group deal with European, North American or African specimens (DRAGESCO & DRAGESCO-KERNÉIS, 1986; HARTWIG, 1980). Reports on South American specimens are very scarce (KATTAR, 1970).

The systematic position of *Avelia* has undergone change and remains rather controversial. There are also some nomenclatural difficulties, which are discussed in this paper.

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Avelia martinicensis (Nouzarède, 1975) has hitherto been regarded as endemic to Martinique. This paper refers to its discovery 35° of latitude further south, in Guanabara Bay, Rio de Janeiro, Brazil (22° 53'S, 47° 17'W).

The study area. The beach where the samples were collected supports strong evaporation due to insolation, especially during summer, producing an increase in salinity. The abundant rainfall and the large volume of freshwater flowing out from rivers cause abrupt reductions in the level of salinity. PARANHOS & MAYR (1993) studied the seasonal temperature and salinity variations in Guanabara Bay; our collection site is near sampling point 7 of that paper. There is a great influx of organic matter in Guanabara Bay, originating in the mangrove areas and caused by anthropogenic activity, including the spread of untreated sewage. HAGLER & MENDONÇA-HAGLER (1981) and HAGLER **et al.** (1986) informed on organic pollution and microbial indicators in Rio de Janeiro; our collection site is between the sampling points 5 and 6 of these studies. The sand in the samples was partially darkened, reduced, with a hydrosulphuric smell which is characteristic of the environments inhabited by the giant psammophilous ciliates (NOUZARÈDE, 1975).

MATERIAL AND METHODS

Samples were gathered from an unnamed sandy beach on the north coast of the "Ilha do Fundão", in the neighbourhood of the "Instituto de Microbiologia, Universidade Federal do Rio de Janeiro", during low tide, which occurred between 8 AM and 4 PM from mid-summer to the end of autumn 1989 (February to September).

The sand was collected by dragging manual dredges with a capacity of 250ml over a small area down to a depth of 5cm within the sediment. The living samples were kept in the laboratory at room temperature and the ciliates were sorted by hand picking with micropipettes.

These ciliates contract rapidly in the face of mechanical or chemical stimuli. It was thus necessary to apply a pretreatment with an anaesthetic solution to avoid excessive contraction during fixation. The ciliates were left in a solution of 20 mM EGTA and 3 mM $MgSO_4$ in sea water for approximately 10 minutes, until they had reached a similar size to that shown when they were active. EGTA is a chelating agent of Ca^{++}, which is the ion producing the myoneme contraction when liberated as a response to stimuli; Mg^{++} contributes to the relaxation (HUANG & PITELKA, 1973; SLEIGH & PITELKA, 1974; HALLER, 1977). Afterwards, the anaesthetic solution was replaced by the fixing solution. This pretreatment was used for both optical and electronic microscopy. Optical microscopy: the protargol staining technique was employed (TUFFRAU, 1967), using glutaraldehyde 12.5% (V/V) in a sodium cacodylate buffer as a first fixing solution. Electronic microscopy: fixation was carried out using glutaraldehyde 12.5% (V/V) and osmium tetroxide 1% (W/V) during 30 minutes at room temperature. The specimens were then washed three times in a sodium cacodylate buffer and preembedded in agar blocks, which were dehydrated by an ethanol series of increasing concentration. Embedding was carried out using EPON 812; polymerization ran for 48 hours at 60° C. The specimens were sectioned with a diamond knife in a LKB 2088 Ultratome V ultramicrotome, and contrasted with uranile acetate in alcohol solution and lead citrate. A Philips EM 301 transmission electron microscope and a JEOL 25SII scanning electron microscope were used for the observations and photomicrographs.

SEM stubs and TEM material were deposited at the "Laboratório de Microscopia Eletrônica, Instituto de Microbiologia, Universidade Federal do Rio de Janeiro", Brazil. Protargol stained slides are housed at the "Laboratorio de Ecología Acuática, Departamento de Biología, Universidad Nacional del Sur", Argentina.

RESULTS

Subphylum KARYORELICTOPHORA Puytorac, Grain, Legendre & Dévaux, 1984.
Class PROTOHETEROTRICHEA Puytorac, Grain & Mignot, 1987.
Order PROTOHETEROTRICHIDA Nouzarède, 1977.
Family AVELIIDAE Puytorac, Grain & Mignot, 1987.

Avelia Nouzarède, 1977

Avela NOUZARÈDE, 1975: 625-627. Type species by original designation *Avela martinicense* Nouzarède, 1975.
Avelia NOUZARÈDE, 1977: 4. Replacement name for *Avela*, preoccupied in the Lepidoptera by Walker, 1856. The gender of generic name is feminine (genus dedicated to Prof. Avel with the addition of the suffix-**ia**).

Avelia martinicensis (Nouzarède, 1975)

(Figs. 1-12)

Avela martinicense NOUZARÈDE, 1975: 627. Incorrect specific spelling due to incorrectness of the adjectival termination.
Avelia martinicense NOUZARÈDE, 1977: 39-40; SMALL & LYNN, 1985: 427; DRAGESCO & DRAGESCO-KERNÉIS, 1986: 215.

Description. A typical psammophilous ciliate, nematomorph, of great size, more than 2mm long when fully extended, dark brown in colour, extremely contractile (figs. 1, 2).

The sharp anterior region is differentiated from the rest of the cell; fore ending like a curved bill. Small buccal aperture, 0.025-0.030mm long, lying ventrally in this anterior region (fig. 3). The wider medial region bears the nuclear apparatus formed by a single, oval to triangular micronucleus between two semispherical to broadly reniform macronuclear masses (figs. 5, 6). Acute posterior region (fig. 4).

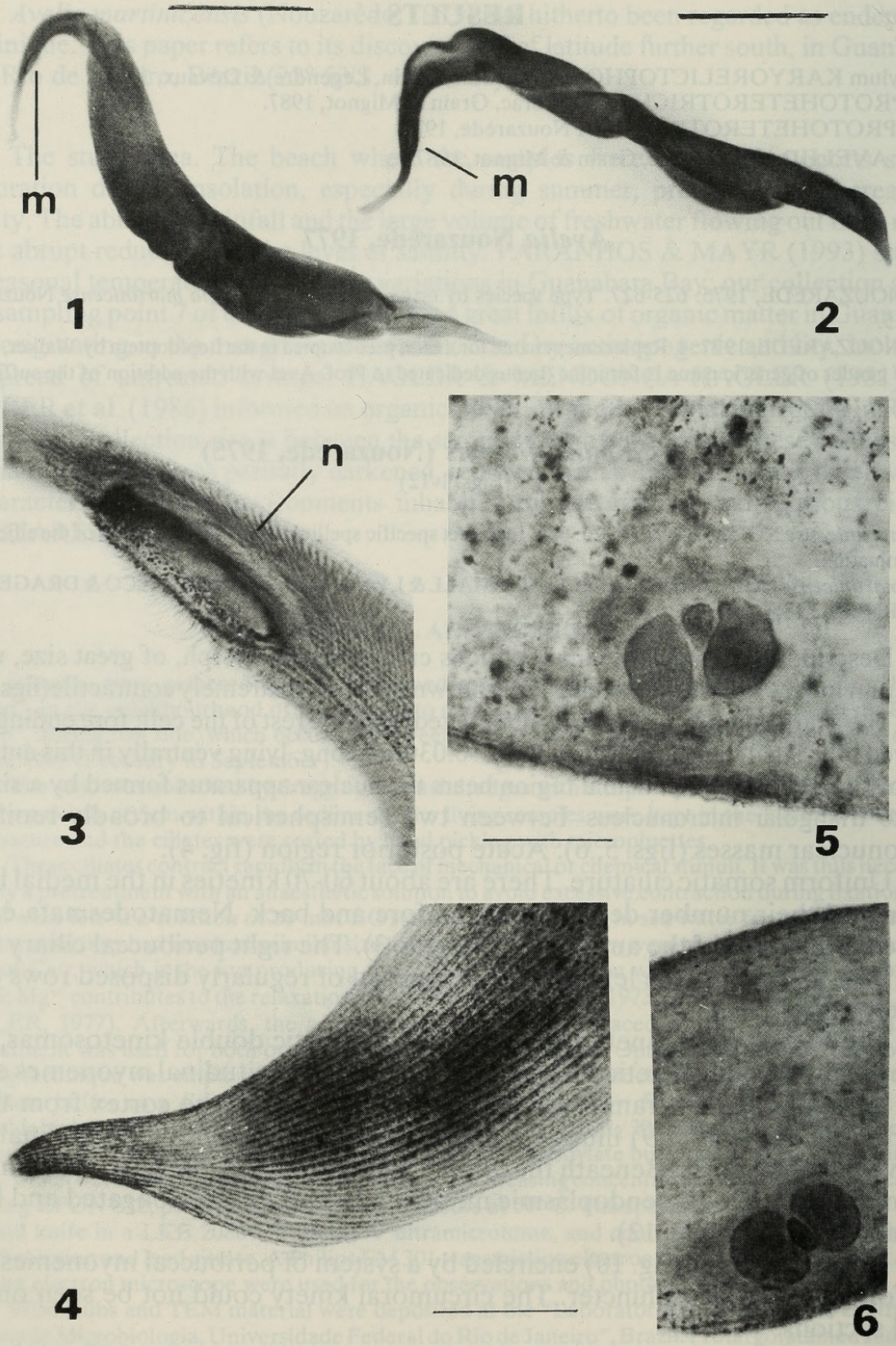
Uniform somatic ciliature. There are about 60-70 kineties in the medial body region and their number decreases to the fore and back. Nematodesmata easily visible on the sides of the anterior region (fig. 3). The right peribuccal ciliary field more developed than the left one and composed of regularly disposed rows of 6-7 kinetosomas.

The longitudinal kineties show the characteristic double kinetosomas, and are separated by interkinetic ridges containing 2 or 3 longitudinal myonemes each. They are underlaid by transversal myonemes. Sections of the cortex from three different planes (figs. 7-9) illustrate the relative position of the longitudinal and transversal myonemes. Beneath the latter a large number of subcortical, round to oval mitochondria. The endoplasmic mitochondria are more elongated and have acuminate endings (fig. 12).

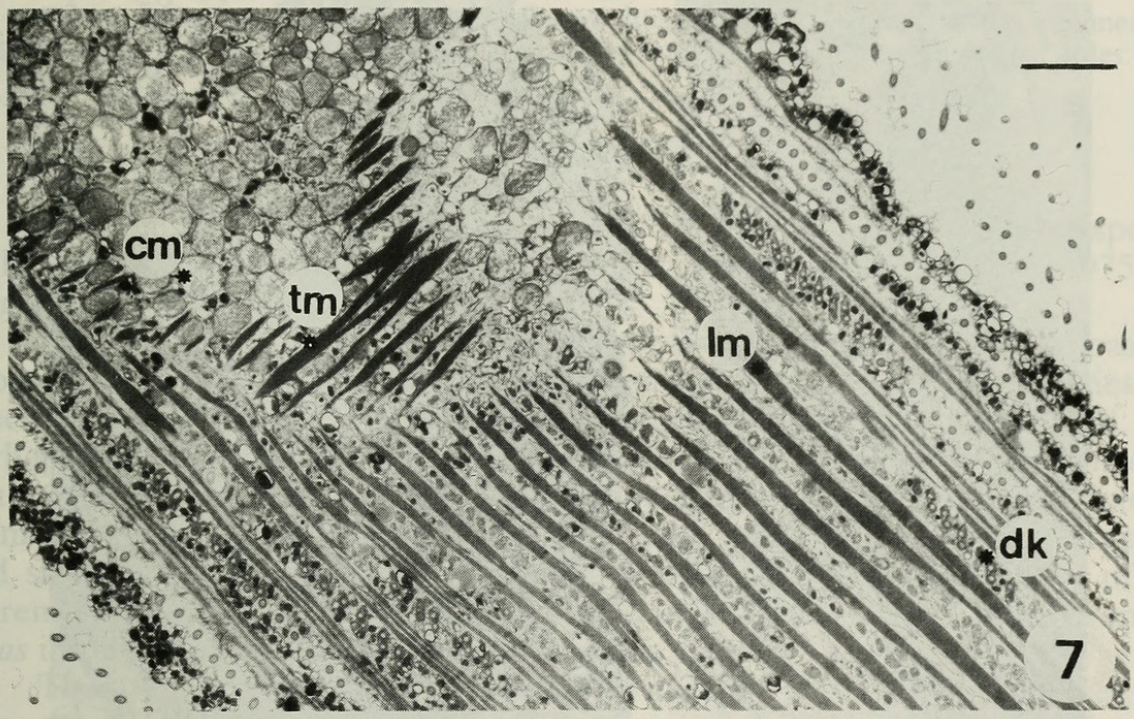
Buccal aperture (fig. 10) encircled by a system of peribuccal myonemes (fig. 11), forming a strong sphincter. The circumoral kinety could not be seen on our TEM sections.

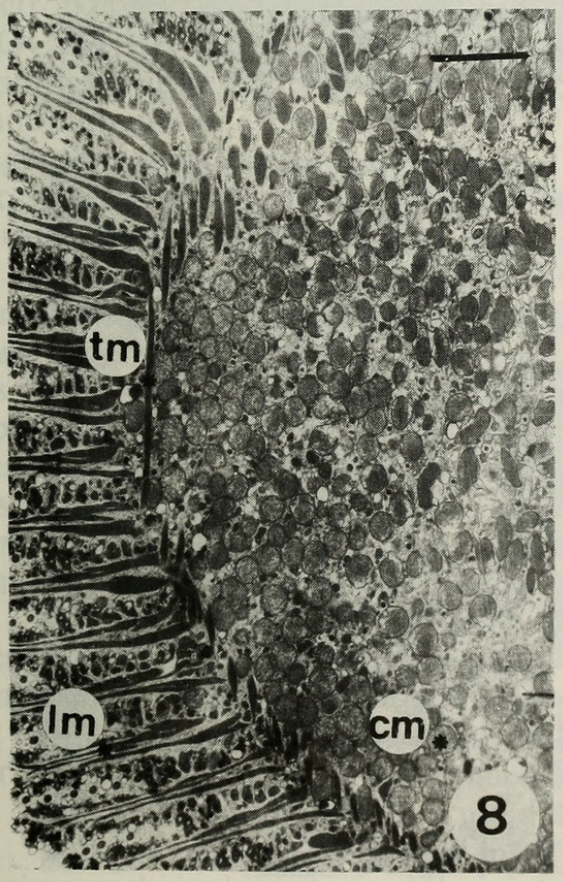
Micronucleus long and oval, lying between the macronuclei (fig. 12). The latter contain a macronuclear spherule, and are surrounded by a thickened coat.

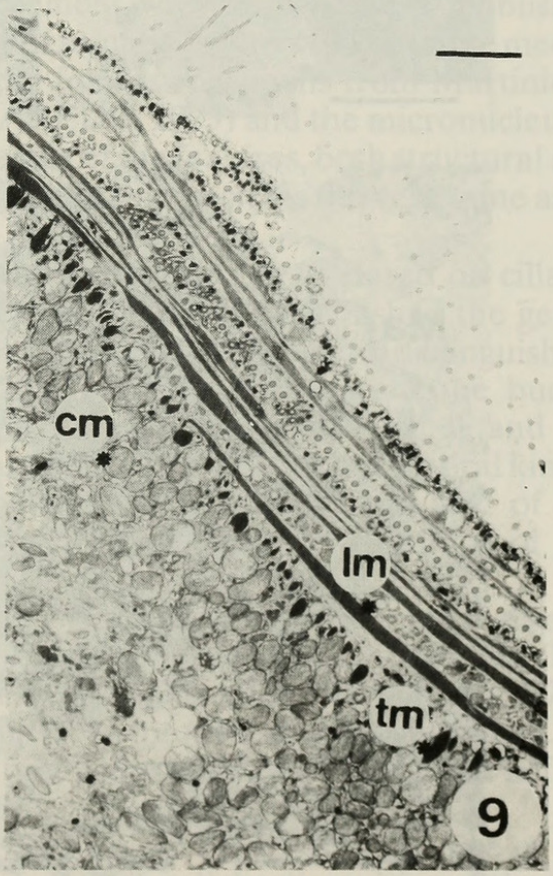
Previously known distribution. Martinique, West Indies.



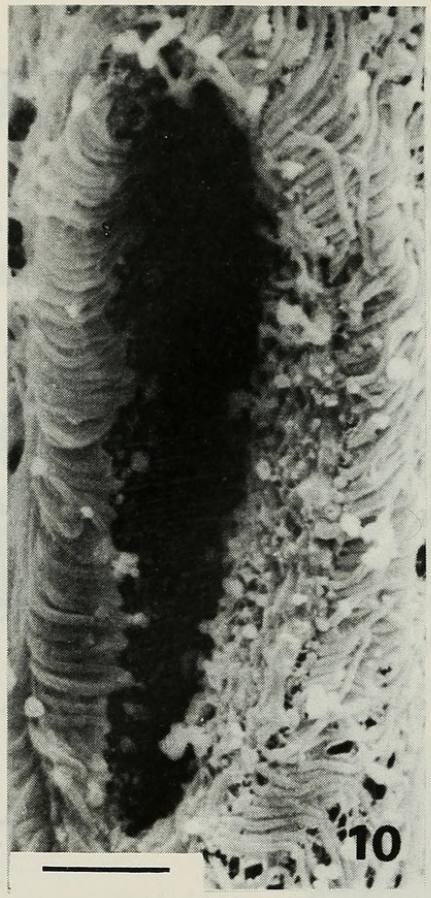
Figs. 1-6. *Avelia martinicensis* (Nouzarède, 1975) from Guanabara Bay, Brazil. 1, 2, general appearance; 3, detail of the mouth in the anterior part; 4, somatic kineties in the posterior end; 5, 6, nuclear apparatus. (m, mouth; n, nematodesmata). Bars: 1,2 = 200 µm; 3-6 = 20 µm.

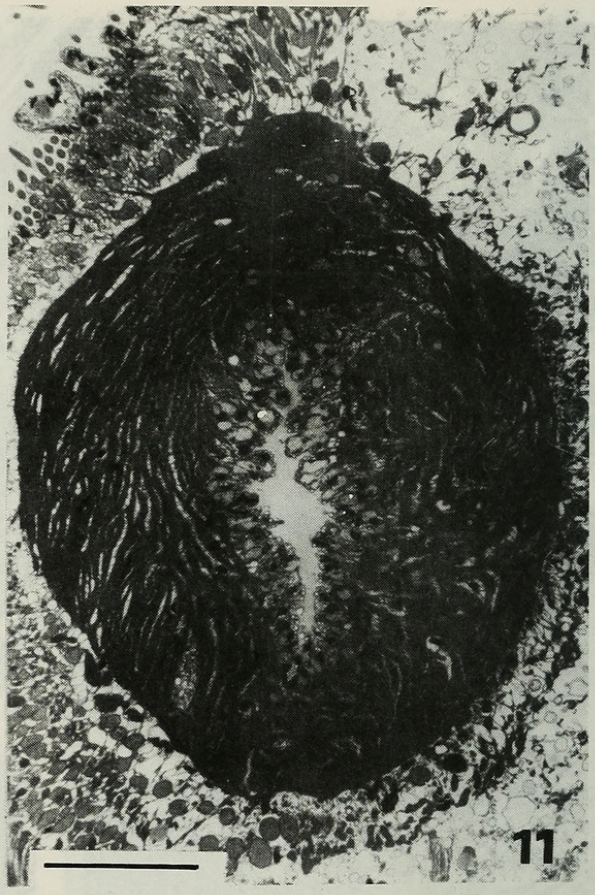


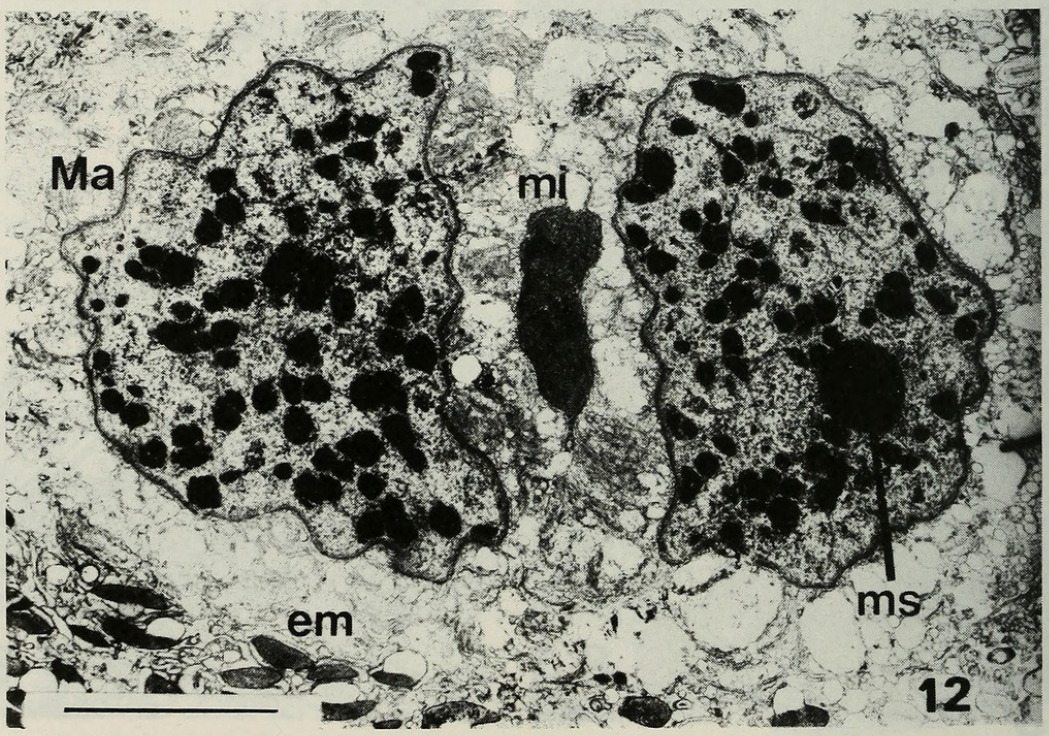




Figs. 7-9. *Avelia martinicensis* (Nouzarède, 1975) from Guanabara Bay, Brazil. 7, tangential and slightly oblique section of the cortex; 8, transveral section of the cortex; 9, sagittal section of the cortex. (cm, cortical mitochondria; dk, series of double kinetosomas in the basis of a kinety between the longitudinal myonemes; lm, longitudinal myonemes running along interkinetic ridges; tm, transversal myonemes). Bars = 3 μm.







Figs. 10-12. *Avelia martinicensis* (Nouzarède, 1975) from Guanabara Bay, Brazil. 10, SEM photomicrograph of the mouth; 11, frontal section of the peribuccal myoneme sphincter (TEM photomicrograph); 12, TEM photomicrograph of the nuclear apparatus. (em, endoplasmic mitochondria; Ma, macronucleus; mi, micronucleus; ms, macronuclear spherule). Bars = 5 µm.

Examined material. BRAZIL. **Rio de Janeiro**: Ilha do Fundão. About 60 living specimens, II-IX.1989, of which 20 are in TEM cut grides; 10 in SEM stubs, and 15 in protargol stained slides.

DISCUSSION

The nominal species of *Avelia*. NOUZARÈDE (1975) recognized three species within the genus: *A. martinicensis* Nouz., 1975, *A. arcachonensis* Nouz., 1975 and *A. gigas* (Dragesco, 1960).

A. martinicensis is differentiated from *A. arcachonensis* only on the basis of geographic location and their general external appearance. The latter species was described as "apparently very rare", its anterior part is more cylindrical, and perhaps it is somewhat smaller. NOUZARÈDE (1975, 1977) stated *A. martinicensis* can reach 3mm long when completely extended, and *A. arcachonensis* can exceed 2mm in lenght: the size difference does not appear to be significant. Overall aspect and size may be considered imprecise and subjective criteria, in view of the extremely contractile nature of these forms. Both species clearly differ from *A. gigas* in the structure of the nuclear apparatus.

The specimens from Guanabara Bay do not show significant differences with respect to previous descriptions of *A. martinicensis*. Our protargol slides and electron micrographs are in general agreement with those already published (NOUZARÈDE, 1975, 1977). The number of somatic kineties (60-70 in the medial region) is a little higher than that indicated for the specimens from Martinique ("une cinquantaine" according to NOUZARÈDE, 1975) and the micronucleus is longer than that illustrated previously. The rest of the features, both structural and ultrastructural, are identical and convince us that the species is the very same as *A. martinicensis*.

Taxonomic history and systematic position of the genus. Based on ciliates from France and the West Indies, NOUZARÈDE (1975) established the genus *Avela* as pertaining to family Geleiidae Kahl, 1933. The characteristics distinguishing this genus from *Geleia* Kahl, 1933 are the form and structure of the buccal apparatus, which lies in the anterior region and is proportionally small, and the presence of peribuccal myonemes, which are absent in *Geleia*. A circumoral kinety was also described. The peribuccal sphincter prevents the anterior part of the animal from transforming into a "fisherman's basket", which is typical of the behaviour of *Geleia* (NOUZARÈDE, 1975).

Two years later, NOUZARÈDE (1977) changed the generic name to *Avelia*, because *Avela* fell in homonymy with *Avela* Walker, 1856 (Lepidoptera). The significant Nouzarède's monograph appeared in a publication "for the year 1976," but in actuality it was not available in print until into the next year, 1977 (J. O. Corliss, **in littera**). Legally and nomenclaturally, the work cannot be cited before the date at which it really was printed-and-distributed.

The genus *Geleia* is divided into two groups, on the basis of the size of the specimens, their ability to twist themselves, and above all the disposition of the two peribuccal ciliary fields: the *G. orbis* group shows a main regular peribuccal ciliary field on the right, and an anarchical smaller ciliary field on the left; whereas the *G. fossata* group has the main regular field on the left (NOUZARÈDE, 1977). The

genus *Avelia* has the main peribuccal ciliary field on the right, as in the first group.

A new order was proposed for the Geleiidae (NOUZARÈDE, 1977): Protoheterotrichida, within the subphylum Polyhymenophora, but there is by no means consensus regarding the systematic position of *Avelia* and *Geleia*. CORLISS (1979) did not accept the order Protoheterotrichida, considering it to be a junior synonym of the order Karyorelictida Corliss, 1974, in which he includes the Geleiidae.

On the basis of the study of the cortical fibrillar structures, SMALL & LYNN (1981, 1985) consider this group as a new class, Karyorelictea Corliss, 1974, within the subphylum Postciliodesmatophora Gerassimova & Seravin, 1976.

In the phenetic classification of PUYTORAC **et al.** (1984), the Geleiidae are included within subphylum Hymenophora, class Spirotrichea, order Heterotrichida, suborder Protoheterotrichina, thus placing them far removed from the Karyorelicta, which they consider a class within a new subphylum, Karyorelictophora Corliss, 1974.

DRAGESCO & DRAGESCO-KERNÉIS (1986) recognize the validity of the genera *Geleia* and *Avelia* but do not agree with NOUZARÈDE's (1975, 1977) diagnostic characteristics. They do not regard the peribuccal sphincter of myonemes as a generic difference but emphasize the position of the main ciliary field, redefining *Avelia* as having the main peribuccal ciliary field on the right and *Geleia* as being its mirror image. Consequently they transfer *Geleia orbis* Fauré-Fremiet, 1950 to *Avelia* and suggest that the same should be done with the other species of the *orbis* group. DRAGESCO & DRAGESCO-KERNÉIS (1986) classify the Geleiidae with the order Karyorelictida as an **incertae sedis** group, and stress the need for further studies on the infraciliature in view of the lack of this information in most taxa.

PUYTORAC **et al.** (1987) also include *Avelia* and *Geleia* with the Karyorelicta (as a subphylum assigned to "Corliss, 1974") in the class Protoheterotricha that they attribute to NOUZARÈDE (1977), on the basis of the order Protoheterotrichida Nouzarède. However, they now differentiate between two monotypic families: the Geleidae [**sic**] Kahl, 1933 and the Avelidae [**sic**] Nouzarède, 1977 (**erratum pro** PUYTORAC **et al.**, 1987).

In the diagnosis of *Avelia*, PUYTORAC **et al.** (1987) note the presence of the peribuccal myoneme sphincter and the position of the main peribuccal ciliary field on the right, formed by numerous segments of juxtaposed kineties, the left ciliary field being "relatively anarchical" and formed by short segments of 2-4 kinetosomes. We agree with the importance of the peribuccal sphincter in defining the genus. It is a constant and well-defined structure and, as stressed by NOUZARÈDE (1975), gives rise to special etho-ecological consequences affecting the feeding strategy of *Avelia*. The latter is not therefore a mere mirror image of *Geleia*, as attempted by DRAGESCO & DRAGESCO-KERNÉIS (1986). We are not aware to the transference of *G. orbis* to the genus *Avelia*, since in this species there are none of the peribuccal myonemes (NOUZARÈDE, 1977) so typical in our specimens. The mouth of *G. orbis* is longer than that of any *Avelia* species, even if the contraction of the material (DRAGESCO & DRAGESCO-KERNÉIS, 1986) is taken into account.

We tentatively adopt here the classification accorded by PUYTORAC **et al.** (1987), until such time as a more stable classification is arrived at.

Notes on authorship and nomenclature. It is common practice in the changing systematics of the Ciliophora to propose assigning authorship of new suprafamiliar taxa to the person who proposed a taxon of lower rank. Though controversial, this procedure is made possible by the fact that only infraordinal names come under the jurisdiction of the International Code. We agree with CORLISS'(1979) remarks on the need for caution in adopting this procedure, because if a taxon is shifted to an entirely different level [as in the case of the order Karyorelictina Corliss, 1974, which is regarded as a class by SMALL & LYNN (1981, 1985), or a subphylum by PUYTORAC **et al.** (1987), but still retaining the authorship of Corliss], the change becomes not only nomenclatural but taxonomical, and the concept of the original author is completely distorted. We conclude that if the most recent classifications are accepted — and we tentatively do accept them — then it would be highly convenient to adopt the following combinations for the higher taxa, using the proper authorships and dates: Subphylum Karyorelictophora Puytorac **et al.**, 1984, Class Protoheterotrichea Puytorac **et al.**, 1987, Order Protoheterotrichida Nouzarède, 1977.

In the Aveliidae the monotypic nature of the new family in no way makes it permissible to attribute its name to the genus' author, especially since NOUZARÈDE (1975, 1977) expressly stated that *Avelia* pertains to the Geleiidae. Within the family group it is imperative that authorship be respected; the only circumstance under which a taxon can be attributed to another author is that foreseen in the Principle of Coordination (articles 36 and 37 of INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (1985). The only correct combination for the family name is therefore: Aveliidae Puytorac **et al.**, 1987.

The nomenclatural act of replacing the generic name *Avela* by *Avelia* (NOUZARÈDE, 1977) was not emendation, but a proposal to provide a replacement name (**nomen novum**) due to homonymy (article 60a of the Code). For this reason the new name has its own author and date — *Avelia* Nouzarède, 1977 —, and parentheses are to be used when the author's name of *Avelia martinicensis* (Nouz., 1975) and *A. arcachonensis* (Nouz., 1975) are cited. NOUZARÈDE (1977) himself overlooked this and omitted the parentheses. DRAGESCO & DRAGESCO-KERNÉIS (1986) wrongly attributed the name *Avelia* to NOUZARÈDE (1975).

As for specific names, *Geleia* and *Avelia* are feminine names under article 30b of the International Code, but Nouzarède used some neuter names that are incorrect original spellings (articles 31b and 32c). In order to achieve harmony as regards gender they should be corrected (article 32d[ii]) as follows: *Geleia arcachonensis* Nouzarède, 1965, *Avelia arcachonensis* (Nouzarède, 1975), *Geleia martinicensis* (Nouzarède, 1977) and *Avelia martinicensis* (Nouzarède, 1975).

It is worth noting that if the suggested transferring of the *Geleia orbis* group to the genus *Avelia* (DRAGESCO & DRAGESCO-KERNÉIS, 1986) were to be accepted, which is not the case in this paper, then the two pairs of specific names mentioned in the previous paragraph would become secondary homonyms (articles 53c and 57c of the Code), making it necessary to propose replacement names for

A. arcachonensis (Nouz., 1975) and *G. martinicensis* (Nouz., 1977). Recommendation 5a in Appendix D of the Code is precisely intended to avoid this kind of nomenclatural problems.

The need to undertake so many nomenclatural changes and emendations, from the subphylum to the specific level, is indicative of the need to pay more attention to internationally adopted principles in order to achieve a greater stability and universality of scientific names. Nomenclature is a serious tool dealing with the names of an astonishing world of biodiversity, and is still the best way of communicating dynamic ideas on the classification and relationships of living things.

Biogeography. As mentioned previously, the main argument for the validity of *A. arcachonensis* seems to be a biogeographical one.

Free-living phagotrophic protists are usually believed to have a cosmopolitan distribution. This viewpoint has been controverted and, in the case of the species dealt with here, NOUZARÈDE (1977) stated that *A. martinicensis* counts among those species restricted to certain geographical areas, viz. endemic to Martinique. The finding of *A. martinicensis* in Guanabara Bay contradicts the hypothesis of its endemism in Martinique. The species shows a remarkable morphological uniformity over more than 35 degrees of latitude and appears to be a very conservative form.

The subtle differences between *A. martinicensis* and *A. arcachonensis* lead one to the conclusion that there are no significant difference between the *Avelia* specimens from Arcachon and Martinique, and either they are conspecific, or they are vicariant remnants of a very conservative taxon which was widely distributed along the Pangaean coasts. Though ciliates have many means of dispersing over great distances, *Avelia's* littoral distribution, and their remarkable thigmotactism and adherence to sand advocate against a transoceanic dispersalistic explanation for their present distribution.

Avelia martinicensis was present in Guanabara Bay throughout the sampling period (February-September 1989), although in less density during the coldest months. The beaches where our samples were gathered are characterized by strong temperature and salinity variations, abundant influx of organic matter and reduced sediments with formation of sulphur. These conditions are favourable to the development of Geleiidae populations and in particular to *Geleia* and *Avelia* populations in Arcachon and Martinique (NOUZARÈDE, 1975, 1977). Our findings on *Avelia martinicensis* agree with the hypothesis that protozoan species in coastal seas are widely distributed, and that the same or sibling species occur in similar habitats everywhere (FENCHEL, 1987).

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