Boll. Zool. 54: 147-153 (1987)

Aspidiophorus polystictos, a new marine species (Gastrotricha, Chaetonotida) and its life cycle

MARIA BALSAMO
MARY ANTONIO D. TODARO
Dipartimento di Biologia Animale, Università di Modena,
via Università 4, 41100 Modena (Italy)

ABSTRACT

Aspidiophorus polystictos, a new marine species of Gastrotricha Chaetonotida is described and compared with the species of the group *A. marinus* - *A. mediterraneus*. This species is characterized by the subrectangular shape of the scales. The life cycle of individuals reared under laboratory conditions is described for the first time in marine Chaetonotida. A parthenogenetic phase precedes a hermaphroditic phase as in several freshwater Chaetonotidae.

KEY WORDS: Marine gastrotrichs; Chaetonotida; Reproductive biology; Hermaphroditism; *Aspidiophorus polystictos* n. sp.

ACKNOWLEDGEMENTS

The authors are grateful to the referees for their helpful and critical revision of the manuscript.

The research was supportd by grants from the Italian Ministry for Education and from the National Research Council (Group «Biologia della riproduzione e del differenziamento»).

(Accepted 23 March 1987)

INTRODUCTION

The genus *Aspidiophorus* is mostly composed of freshwater species of which twenty are named and three unnamed. Only eight species of *Aspidiophorus* are marine of which three have been collected in the Mediterranean sea. Here we describe a new marine species, *A. polystictos*. Unlike most marine gastrotrichs, *A. polystictos* can be reared rather easily under laboratory conditions. It was thus possible to study relevant features of its reprodutive biology. At present, this study is particularly interesting since there is a growing interest in the sexuality and the reproductive biology of the Chaetonotidae. Numerous recent findings of hermaphroditic individuals among freshwater species, so far considered obligately parthenogenetic, provide growing support for the hypothesis of a more complex life history involving two distinct reproductive phases (Hummon, 1984, a, b, c; Kisielewska, 1981; Levy, 1984 a, b; Levy & Weiss, 1980; Weiss & Levy, 1978, 1979, 1980). This study also discusses the existence of a biphasic life cycle in marine Chaetonotidae.

MATERIAL AND METHODS

Numerous specimens of this new species were isolated from sediment samples collected in September 1984 from the sandy beach of Marina of Ginosa (Taranto, Ionian Sea, 40°25'48" N, 16°49'48" E).

Morphological analysis was performed on living specimens, some of which were anaesthesized according to a method previously described (Balsamo, 1977, 1980). Photographic documentation was obtained by phase contrast light microscopy, by differential interference contrast (Nomarski optics) and also by scanning electron microscopy (SEM), after critical point drying. Drawings were mainly based on SEM observations. Photographic negatives of the holotype and paratypes have been deposited in the «Museo Civico di Storia Naturale», Verona, Italy.

The study of the life cycle was carried out on animals hatched from single eggs and reared individually in 0.2 ml of artificial sea water [obtained by dissolving sea salt (Prodac Mare, Cittadella di Padova) in spring water], in the wells of microtest plates (Microtiter System, Greiner Co., P. B. I. Milano). The plates were placed in a moist chamber, incubated at constant temperature (20 ± 0.5 °C). A 12L:12D photoperiod was adopted. The culture medium was changed daily. Aliquots (0.02 ml) of humus infusion (Pourriot, 1957, with slight modifications) were added weekly as food.

RESULTS

Description

A diagrammatic representation of *A. polystictos* and of its main structures is provided in Figure 1, photomicrographs are shown in Figures 2 and 3, and measurements in Table I.

The body (113.7-150 μm long) appears to b divided into a head (20.5-33 μm wide) and neck region (15.5-26.2 μm wide) as well as a trunk (22-34.

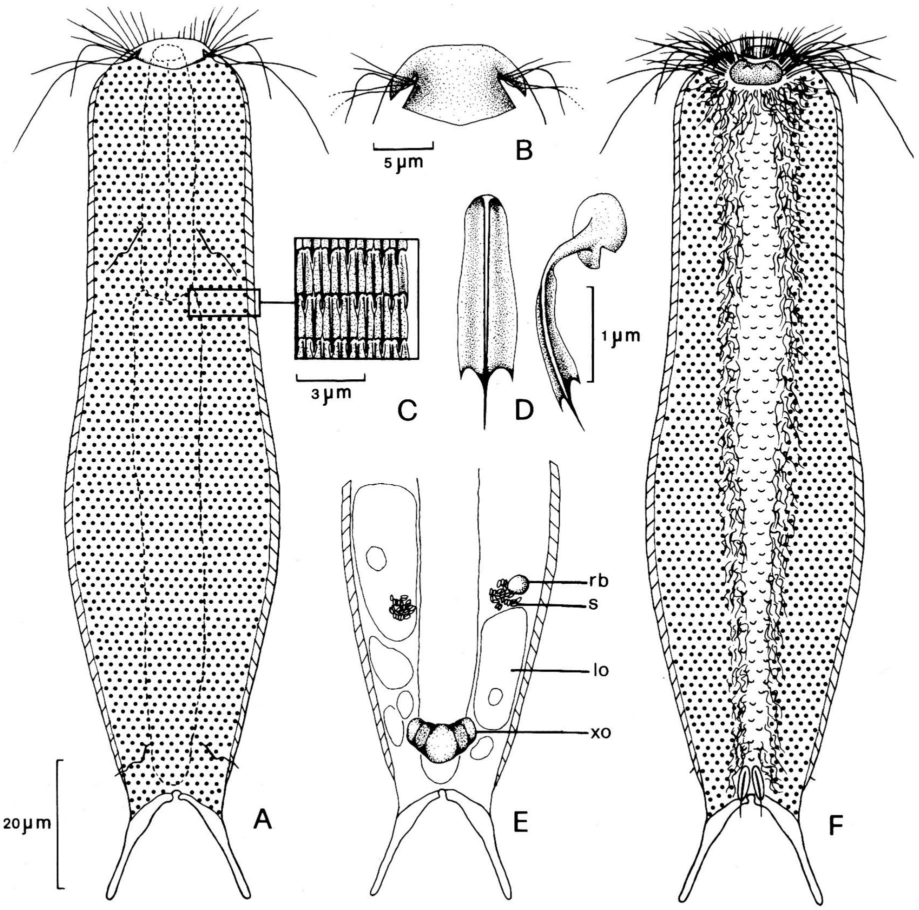

Fig. 1 - *Aspidiophorus polystictos* n. sp. A dorsal view of an adult specimen (spots indicate positions of scale peduncles); B. detail of the cephalion from the dorsal side (only dorsal tufts of cilia are shown and the longest cilia are only partly represented); C. detail of the scale covering; D. dorsal and lateral view of a scale; E. ventral view of a hermaphroditic adult, showing sperm clusters (s), residual body (rb), X-organ (xo) and «late» oocytes (lo); F. ventral view of an adult specimen.

µm wide) ending with a relatively short furca (13.4-19.5 µm long). The head shows a slightly trilobed outline and has a cephalion which extends on the dorsal side and fuses laterally with two very reduced epipleuria. Cephalic cilia are numerous and grouped into 4 tufts. The dorsolateral ones are inserted between the cephalion and the epipleuria. Each tuft includes five-six cilia ranging from 7 to 26 µm in length. The two ventrolateral tufts are implanted immediately below the epipleuria and each one is composed of at least eight-ten cilia 4.6-20.5 µm long. These cilia merge with the ventral locomotory ciliature. Other eight-ten shorter and more rigid cilia, 3-4 µm, surround the mouth. This is subterminal, 5-6 ▷m wide, and delimited on the ventral side by the trapezoidal hypostomion endowed with two conical protuberances (Fig. 2C). The terminal furca has a narrow base of 13-15 µm and its crura consist of a conical base and a long straight adhesive tube of 8.5-12 µm. 70-80 longitudinal columns of 40-45 scales extend to cover the furca base laterally. 38-42 rows are dorsal and lateral, 14-19 ventral per side.

Scales are supported by a peduncle of 1 µm which is inserted into a small round posteriorly concave platelet, 1-1.2 µm in diameter. Each scale has a rounded anterior end, a median keel ending in a thick spine of 0.5-0.7 µm and nearly parallel pointed edges. The scales increase slightly in size from 2.2-2.7 × 0.6-0.7 µm on the head to 2.3-3.5 × 0.6-0.8 µm on the trunk.

Two pairs of dorsal bristles arise from papillae located on the neck and close to the base of the furca. Each bristle, 6-11.7 µm, has a stiff basal part and a very

TABLE I – *Morphometric parmeters of* Aspidiophorus polystictos *n. sp.* *(The measurements are in μm).*

	range	$\bar{X}$	sd	n
Total body length	113.7 - 150.0	135.6	9.91	31
Furca length	13.4 - 19.5	16.4	1.44	31
Adhesive tube length	8.5 - 12.0	9.8	1.10	20
Head width	20.5 - 33.0	25.9	4.08	16
Neck width	15.5 - 26.2	20.3	3.59	9
Maximum trunk width	22.0 - 34.6	28.8	4.59	10
Furca base width	13.0 - 15.0	13.9	0.69	7
Pharynx length	32.0 - 41.0	36.2	6.64	29
Pharynx formula*	6.8 - 11.0	9.0	1.08	14
	5.0 - 11.0	7.4	1.61	12
	6.0 - 12.7	7.7	3.31	14
Mouth diameter	5.5 - 6.0	5.7	0.17	8
Total number of longitudinal columns of scales	70 - 80	78	2.61	22
Number of dorsal longitudinal columns of scales	38 - 42	40.5	1.90	22
Scale number in each longitudinal column	40 - 45	44	1.80	15
Head scale length	2.2 - 2.7	2.5	0.20	12
Head scale width	0.6 - 0.7	0.6	0.05	12
Trunk scale length	2.3 - 3.5	2.8	0.37	12
Trunk scale width	0.6 - 0.8	0.7	0.11	12
Dorsal bristles length	6.0 - 11.7	7.6	2.51	5
Ventral terminal scale length	5.3 - 6.5	5.9	0.54	4
Ventral terminal scale width	1.0 - 1.3	1.1	0.15	4
X-organ length	5.0 - 5.3	5.1	0.21	4
X-organ width	6.5 - 6.7	6.6	0.14	4
Sperm length	1.4 - 3.0	2.0	0.70	10
Sperm width	0.8 - 1.0	0.9	0.07	10
Egg length	49.2 - 56.7	53.4	2.49	12
Egg width	26.6 - 37.5	29.2	2.83	12

$\bar{X}$ = mean value
sd = standard deviation
n = number of specimens measured
* ratios of width of the anterior, central and posterior part of the pharynx to the pharynx length (according to Kisielewski, 1981).

flexible distal part. The two ventral ciliary bands merge together behind the hypostomion. They are wider at the head and neck region, where they are formed by transverse rows of seven-eight cilia, than on the trunk where they are closer and only have three-four cilia per row. Correspondingly, the area between the ciliary bands narrows from 9.5 to 5 μm. In this area a very fine ornamentation is present, consisting of slightly curved protruding processes visible only by SEM observation and disposed in 3-5 alternate longitudinal columns (Fig. 2D). These processes probably represent protruding posterior edges of very reduced scales. A pair of elliptic large keeled scales (5.3-6.2 × 1.1-1.5 μm) are present at the ventral posterior end.

The cylindrical pharynx is 32.5-41 μm long. A pair of protonephridia may be frequently observed lateral to the upper part of the intestine.

In the parthenogenetic adult it is possible to observe oocytes at different stages of development.

The egg, 49.2-56.7 × 26.6-37.5 μm, has a very thin shell covered by numerous small roundish protuberances (Fig. 2E). The postparthenogenetic hermaphroditic adult has a horse-shoe-shaped organ, probably identifiable with the X-organ (sometimes called «bursa seminalis») described in other chetonotids by Remane (1936), Hummon W. D. (1966, 1969), Renaud-Mornant (1968), Ruppert (1977), Kisielewska (1981) and Hummon M. R. (1984c). This organ surrounds ventrally the terminal portion of the intestine. One or two ventrolateral groups of at least 20 rod-like non flagellate and apparently immotile sperm (1.4-3 × 0.8-1 μm) appear laterally to the posterior half of the intestine. One or two refracting bodies may be associated with each sperm group (see next section) (Figs. 1E, 3D-G).

Diagnosis

Total body length of 135.6 ± 9.91 μm; furca length 16.4 ± 1.44 μm; pharynx length 35.6 ± 6.64 μm. Head slightly trilobed with cephalion, epipleuria and hypostomion. Cephalic cilia arranged in four tufts. Body covered with 70-80 longitudinal columns (38-42 of which are dorsal) of 40-45 pedunculated scales inserted on semicircular indented platelets. Subrectangular scales with a median keel and lateral edges ending in small spines. Two pairs of dorsal bristles arising from papillae. Two ventral ciliary bands running closer to each other on the posterior region of the trunk. Curved protruding processes arranged in three-five longitudinal columns between the ciliary bands. At the posterior end are two elliptical keeled scales with a short spine. Cylindrical pharynx. Protonephridia present. The hermaphroditic stage develops a median, lobed X-organ surrounding the terminal part of the intestine. Very small, rod-like, non-flagellate sperm grouped into one-two ventrolateral clusters. Egg-shell ornamented with small roundish protuberances.

Derivatio nominis: from the Greek terms «*πολύς*» = much and «*στικτός*» = dotted, to emphasize the heavily dotted appearance.

Life Cycle

The observations on the life cycle were carried out on specimens reared individually from the time of hatching under constant temperature and salinity conditions which were identical to those detected during sampling (i.e. 20±0.5 °C and 35‰ salinity). A time span of 11-51 days ($\bar{X}$ = 24.59 ± 12.83 days on 22 observed individuals) was necessary for *A. polystictos* to complete its life cycle that may be divided into four main phases: 1. embryonic ($\bar{X}$ = 2±0.92), 2. juvenile ($\bar{X}$ = 4.2 ± 2.37), 3. parthenogenetic ($\bar{X}$ = 8.6 ± 6.40) and 4. postparthenogenetic hermaphroditic ($\bar{X}$ = 9.7 ± 10.7).

1. The *embryonic* phase. Only one morphological type of egg is produced, as is usual for marine gastrotrichs.

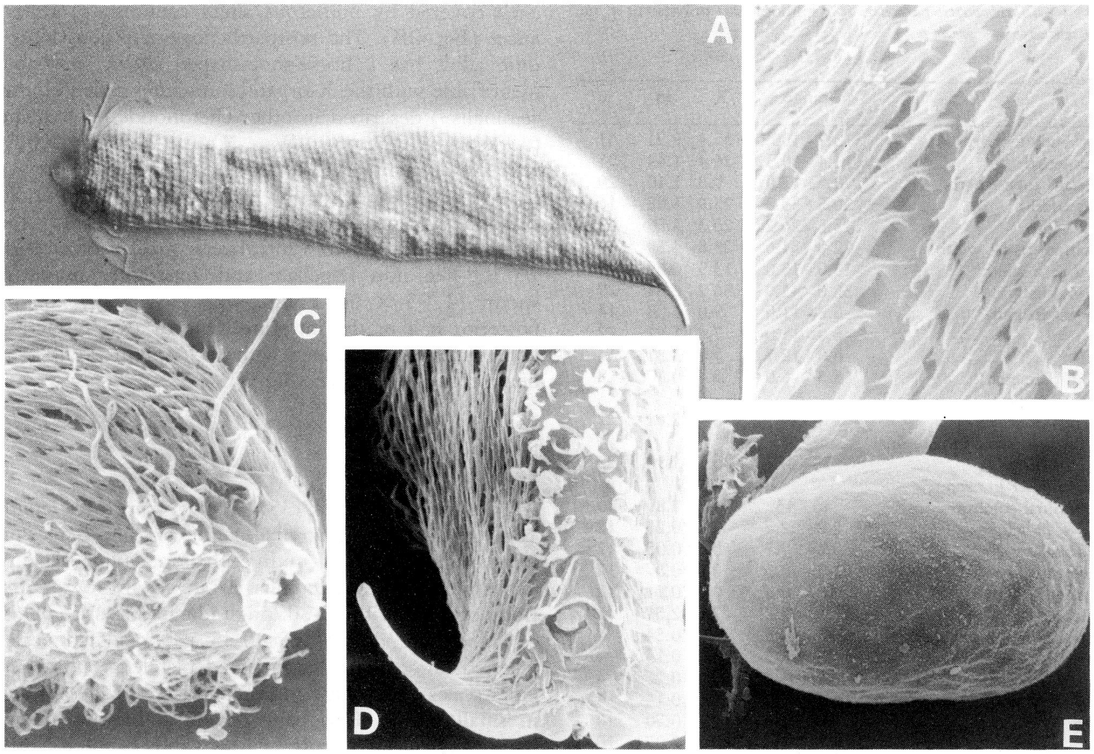

Fig. 2 - *Aspidiophorus polystictos* A. dorsolateral view of a parthenogenetic adult (Nomarski optics, × 800); B. detail of the scale covering, showing the peduncles and the basal platelets of the scales (SEM, × 5000); C. front-lateral view of the head (SEM, × 2500); D. ventral view of the posterior end (SEM, × 2500); E. an egg attached to the substratum (SEM, ×1250).

Cleavage begins within 0.5-1 h following the egg laying. A complete embryo can be seen through the shell 19-22 h later (Fig. 3A). At this stage it has muscular contractions which tend to increase in frequency and intensity. Several hours later ciliary movements can be seen. Apparently, vigorous muscular contractions facilitate the breaking of the egg shell.

2. The *juvenile* phase. The hatched individual is about two thirds of the dimension of the adult (see Table II and Fig. 3B). Within 5 days the individual reaches its final size and shape. At this time it also contains one-two mature parthenogenetic oocytes.

3. The *parthenogenetic* phase. This phase (Fig. 3C) coincides with the completed maturation of the parthenogenetic oocytes. They are released singly, in a number which varies from one to ten, more often (77% of observations) between three and six.

4. The *hermaphroditic (postparthenogenetic)* phase (Fig. 3D). The development of a X-organ and sperm characterizes this phase. The horsehoe shaped X-organ ventrally surrounding the terminal part of the intestine becomes clearly visible (Figs. 1E, 3G). As earlier described, the sperm gradually cluster into one group on each side of the body. Repeated observations of the same individuals by Nomarski optics allow the recognition of at least three distinct stages in sperm formation, corresponding to stages 2, 3, 4 described for *L. squammata* Dujardin (Hummon, 1984b). Initially the sperm are found in rather compact groups which are enclosed by a barely visible membrane (Fig. 3E); later the sperm appear more separated and strictly associated with one or two strongly refracting bodies reminiscent of the «androsphere» described as «a modified residual body» by Hummon (1984b, p. 623) (Fig. 3F). These bodies are then resorbed, while the sperm appear very scattered (Fig. 3G). Sperm release was never observed and the presence of sperm within the X-organ was not detectable at any stage. This is the main reason why we prefer to maintain the general name «X-organ» for this structure, the function of which is still to be proved. Oocytes at different stages of maturation, rich in refracting granulations, persist in this life phase (Figs. 3D, F). These «late» oocytes (following Levy's definition (1984a), for *L. squammata* Dujardin) were never observed to be laid, at least in isolation culture, even if hermaphroditic individuals were kept together with

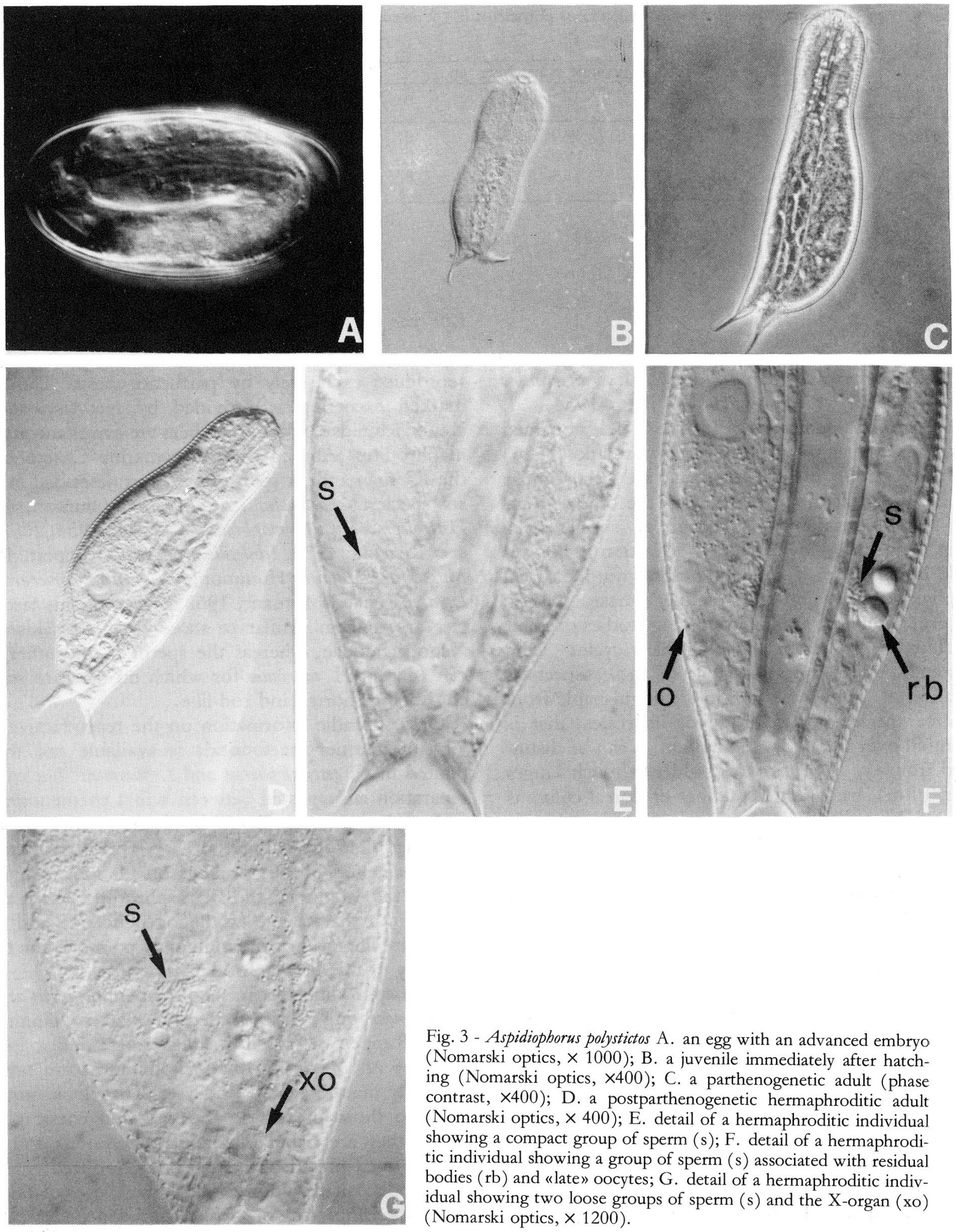

Fig. 3 - *Aspidiophorus polystictos* A. an egg with an advanced embryo (Nomarski optics, × 1000); B. a juvenile immediately after hatching (Nomarski optics, ×400); C. a parthenogenetic adult (phase contrast, ×400); D. a postparthenogenetic hermaphroditic adult (Nomarski optics, × 400); E. detail of a hermaphroditic individual showing a compact group of sperm (s); F. detail of a hermaphroditic individual showing a group of sperm (s) associated with residual bodies (rb) and «late» oocytes; G. detail of a hermaphroditic individual showing two loose groups of sperm (s) and the X-organ (xo) (Nomarski optics, × 1200).

other one-three hermaphroditic or parthenogenetic individuals. The «late» oocytes never showed the egg shell precursor granules, that are usually visible in the outer layer of parthenogenetic oocytes just before being laid. A gradual resorption of the left-over oocytes is evident in the late postparthenogenetic phase, while male structures still remain visible. This phase lasts markedly longer than the previous ones, constituting more than 40% of the entire life span of the observed specimens.

TABLE II – *Changes in body dimensions* (*μm*) *of* Aspidiophorus polystictos n. sp. during development. For other explanations see Table I.

	Juvenile at hatching				Adult			
	range	X̄	sd	n	range	X̄	sd	n
Total length	92.0 - 105.2	99.9	4.80	8	113.7 - 150.0	135.6	9.91	31
Furca length	14.5 - 19.0	16.0	1.70	8	13.4 - 19.5	16.2	1.44	30
Pharynx length	33.6 - 36.4	34.5	2.10	8	33.6 - 41.0	36.2	6.64	29

DISCUSSION

Morphology

Aspidiophorus marinus Remane, 1926, *A. mediterraneus* Remane, 1927, *A. tentaculatus* Wilke, 1954, *A. paramediterraneus* Hummon, 1974 and the unnamed *Aspidiophorus* species described by Swedmark (1956) constitute a group of species which are very similar and difficult to distinguish one from the other. Hummon (1974) considered this group of species as a «sibling complex». However, this definition is not applicable in this case. It denotes a close morphological and phylogenetic similarity among these species: however it should be applied following studies on their reproductive isolation, biological cycles and behaviours. As yet the knowledge of these aspects is too scanty. *A. polystictos* is clearly distinguishable from the above species by the shape of its scales, that is constant all over the body. In addition, it can be distinguished from: 1. *A. tentaculatus*, which is much longer (250-300 μm), has a larger number of dorsal columns of scales (about 60), and shows two rod-like cephalic tentacles; 2. *A. marinus*, which shows a lower number of columns of scales (20), two pseudocells, a smaller hypostomion and four ventral terminal spines; 3. *A. mediterraneus*, which has fewer columns of scales (about 40) and a cephalion with a protruding anterior edge; 4. *A. paramediterraneus*, which is longer (180-250 μm) and has a ventral locomotory ciliature arranged in a single band along the trunk region. The close similarity, if not identity (Hummon, 1974), of the unnamed species of *Aspidiophorus* described by Swedmark (1956) to both *A. tentaculatus* and *A. paramediterraneus* led us to exclude the attribution of *A. polystictos* to this species.

Sperm and a X-organ have never been described in marine species of the genus *Aspidiophorus*. These species can reproduce exclusively by parthenogenesis, as postulated by Rieger & Rieger (1980) and Hummon (1982). However it is also possible, that they have simply been regarded as parthenogenetic since no hermaphroditic individual has been collected: these are rarer in nature than the parthenogenetic ones. In this context it is not possible to carry out a comparison of the morphology of male structures, which might prove to be a valid diagnostic character.

Life cycle

The great majority of marine Chaetonotida seem to reproduce exclusively by parthenogenesis. The most marked exception is provided by Neodasyidae and Xenotrichulidae, whose members are simultaneous hermaphrodites. Among the other marine Chaetonotida, the X-organ and/or sperm have been described in only six species: ***Chaetonotus testiculophorus*** Hummon, 1966, ***Heterolepidoderma hermaphroditum*** Wilke, 1954, ***H. marinum*** Remane, 1926, ***Ichthydium hummoni*** Ruppert, 1977, ***Musellifer sublitoralis*** Hummon, 1969 and ***Polymerurus delamarei*** Renaud-Mornant, 1968. Sperm of this last species are filiform similar to those of Neodasyidae and Xenotrichulidae, whereas the sperm of the other species (except *H. marinum* for which no data are reported) appear shorter and rod-like.

Only sporadic information on the reproductive biology of marine Chaetonotida is available and this is limited to *C. testiculophorus* and *I. hummoni*. A clear-cut separation is suggested between a first parthenogenetic and a second hermaphroditic phase in the life cycle (Hummon, 1966; Ruppert, 1977). This observation is in agreement with our findings on *A. polystictos*. Moreover, the length of the hermaphroditic phase compared with that of the parthenogenetic one and with the entire life span of the individual points to the functionality of this hermaphroditism.

Hermaphroditic specimens of *C. testiculophorus* and of *I. hummoni* only have immature oocytes (Hummon, 1966; Ruppert, 1977). Instead, hermaphroditic individuals of *A. polystictos* contain both immature oocytes and fully mature («late») oocytes. They look quite similar to those present in the parthenogenetic phase, except they are richer in granular inclusions and lack the egg shell precursor granules. As fertilized eggs are usually deposited without delay, there cannot be evidence for either self- or cross-fertilization under experimental conditions. Also, we cannot exclude the possibility that rearing conditions could influence the normal course of the life cycle. Pairs of individuals with their posterior ends close to each other were observed in mass cultures: however, it was difficult to decide whether or not this behaviour involved effective mating.

The sperm of *A. polystictos* have a different shape from those of other marine hermaphroditic species. Following acetic orcein staining the sperm did not appear to be flagellate, which is consistent with the complete absence of motility both inside the animal and outside.

A biphasic life cycle similar to that described here for *A. polystictos* has recently been observed in at least three freshwater Chaetonotidae (Hummon, 1986; Levy, 1984 a, b). Many other freshwater species have a X-organ and sperm of various shapes (Remane, 1936; Kisielewska, 1981; Weiss & Levy, 1980; Weiss, 1984; Balsamo, unpublished data). Hermaphroditism has been described in only two freshwater species of *Aspidiophorus*: *A. oculifer* Kisielewski (1981) and one unnamed species studied by Levy (1984a). The life cycle of this one was carefully observed and by and large it corresponds to that of other freshwater Chaetonotida and also of *A. polystictos*. Differences in the life cycle of the freshwater *Aspidiophorus* species as compared to the marine *Aspidiophorus* include: 1. the production of «both resting and non-resting eggs» (Levy, 1984a, p. 75), as normally occurs in freshwater gastrotrichs and 2. the presence of only «unilateral and left-handed sperm-bearers» irrespective of their age (Levy, 1984a, pp. 75 and 83). The sperm of the *Aspidiophorus* described by Levy (1984a, p. 83, Fig. 64) are «straight rods, 5-6 μm long by 0.7 μm in diameter», and thus longer than those of *A. polystictos*.

CONCLUSIONS

To summarize, the length of the postparthenogenetic hermaphroditic phase, the presence of two successive generations of oocytes and the existence of sperm and of a X-organ are all aspects which support a functional hermaphroditism in *A. polystictos*, even though this has not yet been experimentally demonstrated. Freshwater and marine Chaetonotidae can no longer be considered obligate parthenogenetic organisms on the sole basis of a presumed absence of male structures. The biphasic life cycle demonstrated in three species of freshwater Chaetonotidae and implied in many other species is applicable to *A. polystictos* and probably it may also apply to other marine species of Chaetonotidae.

REFERENCES

Balsamo M., 1977 - Prime ricerche sui Gastrotrichi dulciacquicoli italiani. Atti Soc. tosc. Soc. nat., Mem., ser. B., *84*: 87-150.

Balsamo M., 1980 - Secondo contributo alla conoscenza dei Gastrotrichi delle acque dolci italiane. Atti Soc. tosc. Sc. nat., Mem., ser. B, *87*: 97-126.

Hummon M. R., 1984a - Reproduction and sexual development in a freshwater gastrotrich. 1. Oogenesis of parthenogenic eggs (Gastrotricha). Zoomorphology, *104*: 33-41.

Hummon M. R., 1984b - Reproduction and sexual development in a freshwater gastrotrich. 2. Kinetics and fine structure of postparthenogenic sperm formation. Cell Tissue Res., *236*: 619-628.

Hummon M. R., 1984c - Reproduction and sexual development in a freshwater gastrotrich. 3. Postparthenogenic development of primary oocytes and the X-body. Cell Tissue Res., *236*: 629-636.

Hummon M. R., 1986 - Reproduction and sexual development in a fresh-water gastrotrich. 4. Life history traits and the possibility of sexual reproduction. Trans. Am. Microsc. Soc., *105*: 97-109.

Hummon W. D., 1966 - Morphology, life history, and significance of the marine gastrotrich, *Chaetonotus testiculophorus* n. sp. Trans. Am. Microsc. Soc., *85*: 450-457.

Hummon W. D., 1969 - *Musellifer sublitoralis*, a new genus and species of Gastrotricha from the San Juan archipelago, Washington. Trans. Am. Microsc. Soc., *88* (2): 282-286.

Hummon W. D., 1974 - Gastrotricha from Beaufort, North Carolina, U.S.A. Cah. Biol. Mar., *15*: 431-446.

Hummon W. D., 1982 - Gastrotricha. In: S. P. Parker (ed.), Synopsis and classification ofliving organisms, Mc Graw-Hill, New York, Vol. 1, pp. 857-863.

Kisielewska G., 1981 - Hermaphroditism of freshwater gastrotrichs in natural conditions. Bull. Acad. Polon. Sci., Ser. Sci. Biol., Cl.II, *29*: 167-172.

Kisielewski J., 1981 - Gastrotricha from raised and transitional peat bogs in Poland. Monogr. Fauny Pol., Pol. Akad. Nauk, Krakow, *11*: 143 pp.

Levy D. P., 1984a - Obligate postparthenogenetic hermaphroditism and other evidence for sexuality in the life cycles of freshwater gastrotrichs. Ph. D. thesis, Rutgers University, New Brunswick (New Jersey): 257 pp.

Levy D. P., 1984b - Equivalent life cycles with obligate postparthenogenetic hermaphroditism in three genera of freshwater gastrotrichs. Am. Zool., *24*: 140 (abstract).

Levy D. P., Weiss M. J., 1980 - Sperm in the life cycle of the freshwater gastrotrich, *Lepidodermella squammata*. Am. Zool., *20*: 749 (abstract).

Pourriot R., 1957 - Sur la nutrition des Rotifères à partir des algues d'eau douce. Hydrobiologia, *9*: 50-59.

Remane A., 1926 - Marine Gastrotrichen aus der Ordnung der Chaetonotoidea. Zool. Anz., *66*: 243-252.

Remane A., 1927 - Gastrotricha. In: G. Grimpe (ed.), Die Tierwelt der Nord- und Ostsee, Akad. Verlag., Leipzig. Bd. X, Teil VII, 56 pp.

Remane A., 1936 - Gastrotricha. In: H. G. Bronn (ed.), Klassen und Ordnungen des Tierreichs, Akad. Verlag., Leipzig, Bd. 4, Abt. II, 1 (2), 242 pp.

Renaud-Mornant J., 1968 - Présence du genre *Polymerurus* en milieu marin, description de deux espèces nouvelles (Gastrotricha, Chaetonotoidae). Pubbl. Staz. zool. Napoli, *36*: 141-151.

Rieger G. E., Rieger R. R., 1980 - Fine structure and formation of eggshells in marine Gastrotricha. Zoomorphology, *96*: 215-229.

Ruppert E. E., 1977 - *Ichthydium hummoni* n. sp., a new marine Chaetonotid gastrotrich with a male reproductive system. Cah. Biol. Mar., *18*: 1-5.

Swedmark B., 1956 - Etude de la microfaune des sables marins de la région de Marseille. Arch. Zool. exp. gén., *93*: 70-95.

Weiss M. J., Levy D. P., 1978 - Existence of sperm in a freshwater gastrotrich. Am. Zool., *18*: 631 (abstract).

Weiss M. J., Levy D. P., 1979 - Sperm in «parthenogenetic» freshwater gastrotrichs. Science, *205*: 302-303.

Weiss M. J., Levy D. P., 1980 - Hermaphroditism and sperm diversity among freshwater Gastrotricha. Am. Zool., *20*: 749 (abstract).

Weiss M. J., 1984 - How widespread is hermaphroditism among freshwater gastrotrichs? Am. Zool., *24*: 140 (abstract).

Wilke U., 1954 - Mediterrane Gastrotrichen. Zool. Jb. Abt. Syst., *82*: 497-550.