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# History and revised classification of the order Cyclomyaria (Tunicata, Thaliacea, Doliolida)

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**Abstract**

The history of the successive investigations done on the Order Doliolida is summarized and a revised classification of the Order is presented including all the species belonging or not to the family Doliolidae. New families are defined. Geographical distribution of the species is given.

**Key-words**: Families Doliolidae, Doliopsoidae, Doliopsidae, Paradoliopsidae, *Doliopsoidesatlanticum*, *Doliopsisbahamensis* nov. sp., *Paradoliopsis harbisoni.*

**Résumé**

L'historique des recherches successives menées sur l'Ordre des Doliolida est présenté avec une révision de sa classification incorporant toutes les espèces appartenant ou non à la famille des Doliolidae. De nouvelles familles ont été introduites. La distribution géographique des espèces est présentée.

**Mots-clefs**: Familles Doliolidae, Doliopsoidae, Doliopsidae, Paradoliopsidae, *Doliopsoidesatlanticum*, *Doliopsisbahamensis* nov. sp., *Paradoliopsis harbisoni.*

## Historical introduction

The phylum Tunicata LAMARCK 1816 is divided into three classes, the benthic Ascidiacea, and the pelagic Thaliacea and Appendicularia. The class Thaliacea consists of three Orders: Cyclomyaria, Pyrosomatida and Salpida, the affinities of which are still disputed (GODEAUX 1998).

The Order Cyclomyaria CLAUS 1862 (Doliolida DELAGE & HEROUARD 1898) is the last Thaliacean order to be identified, probably owing to the tiny size and the transparency (thinness) of the tissues of the animals. Up to now, that order comprises the single family Doliolidae (BRONN 1861) the systematics of which were established by GARSTANG in his classical memoir (1933). Although several genera and species have been described since that time, no real attempt was done to improve the systematics of the order until the paper by GODEAUX (1996).

The genus *Doliolum*, with the species *Doliolum mediterraneum*, was created in 1823 by A.W. OTTO who described a barrel-shaped structure inhabited by a female amphipod of the genus *Phronima*. That "species " and those created later (1830) by DELLE CHIAJE (*D. papillosum* and *D. sulcatum*) do not exist, as they only represent artefacts made by a crustacean parasiting a colony of *Pyrosoma* (*P. atlanticum*?).

QUOY & GAIMARD (Astrolable Expedition 1826-1829) named *Doliolum denticulum* a kind of barrel ("barrilet denticulé") first observed in Amboina roads (Indonesia) (1835, pl. 89, fig. 25-26) and later on off Vanikoro Island (Melanesia), and described as "*Doliolum corpore minimo, hyalino, cylindrico-ovato, subtruncato in utroque apice perforato, antice crenulata, circulis octonis salientibus*" (Length: 4.5 mm). The authors also emphasized the presence of a dorsal vessel (in fact the ventral endostyle), of the heart and of a gill composed of two sheets. The eight salient rings represent eight muscle hoops and expose the blastozooid. The description of the animal is correct, and genus and species (now named *Doliolum denticulatum* QUOY & GAIMARD 1835 after HUXLEY 1851b) are still accepted (Fig.1a). From Amboina roads QUOY & GAIMARD named *Doliolum caudatum* ("barrilet à queue") a second species "*Doliolum, corpore cylindrico, elongato, octonis circulis cincto, postice caudato, oribus terminalis*, length 18-22.5 mm" cylindrical, elongated, 4 to 5 times longer than the other species, bearing eight circles (muscles ?) and a tail (1835, pl.89, fig. 29-30). After scrutening the drawings and correction of the orientation of the body (Fig.1b), that doliolid seems to be an oozooid deprived of its viscera = nurse (the "ventral tail" being the dorsal spur); one may suggest that it belongs to the genus *Dolioletta*. QUOY & GAIMARD (*loc.cit.*) also stressed the relationships between *Doliolum* and salps.

Descriptions of the doliolid anatomy and of the life cycle were initiated by HUXLEY (1851b) and especially by KROHN (1852) who gave the first correct position of the body of the animals and recognized their relationships with the Ascidiacea. He also observed both the tailed larva and the gonozooid of *Doliolum denticulatum* and the oozooid and the gonozooid of a new species named *Doliolum muelleri.*

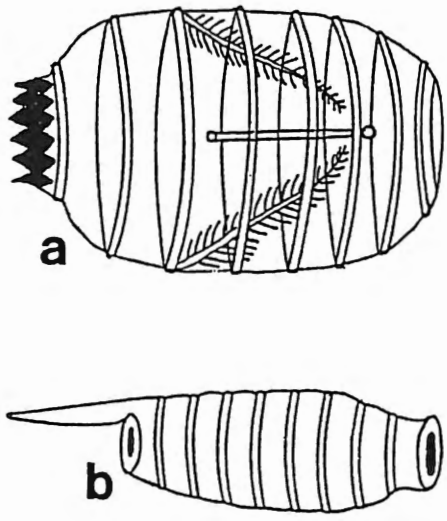


Fig. 1. **a**. blastozooid of *Doliolum denticulum* (now *D. denticulatum*) after QUOY & GAIMARD 1835. **b**. *Doliolum caudatum* (nurse of *Dolioletta* sp?, after QUOY & GAIMARD 1835).

KROHN concluded in favor of a simple alternation of generations (metagenesis) as already known in salps.
Further researches by GEGENBAUR (1855), KEFERSTEIN & EHLERS (1861), GROBBEN (1882), ULJANIN (1884) and NEUMANN (1906, 1913) progressively cleared up the complexity of the life cycle of the doliolum: the sterile oozooid buds thanks to its ventral stolon three successive generations of blastozooids, namely the sterile trophozooids (=gastrozooids) and phorozooids, and the hermaphroditie sexual gonozooids; the dorsal spur (cadophore) of the oozooid is just an organ carrying on the developing buds. ULJANIN (1884) and NEUMANN (1906, 1913) also proved that the gonozooids are not budded by the phorozooids but that they represent a third generation of buds resulting of the strobilization of a probud issued from the stolon of the oozooid and carried by the phorozooids. The phorozooid and gonozooid are fully similar as the sole difference is either the absence or the presence of the gonads. The same authors divided the genus *Doliolum* into two subgenera, *Doliolum* and *Dolioletta*.
Therefore the life cycle of a doliolum is especially complicated as the same species is represented by six successive stages: tadpole or larva (L), fullgrown oozooid (Ooz), degenerated (eviscerated) oozooid or nurse (N, Fig. 2 a), all three issued from the egg, and three blastozooids: trophozooid or gastrozooid (TZ), phorozooid (PZ) and gonozooid (GZ, Fig.2 b). That cycle has just been described in three species, especially thanks to rearing of eggs and larvae (BRACONNOT 1970 a,b). Moreover the oozooids and nurses of the different species of a genus are so similar that they cannot be separated (cryptic species as suggested by GODEAUX 1961). The current systematics (GARSTANG 1933) is based on the anatomical structure of the phorozooids and gonozooids and recognizes four genera and some twenty species.
Beside of the Doliolidae, several doliolum-like types have been progressively discovered and described.
In 1835, RATHKE, after papers left by ESCHSCHOLTZ, named

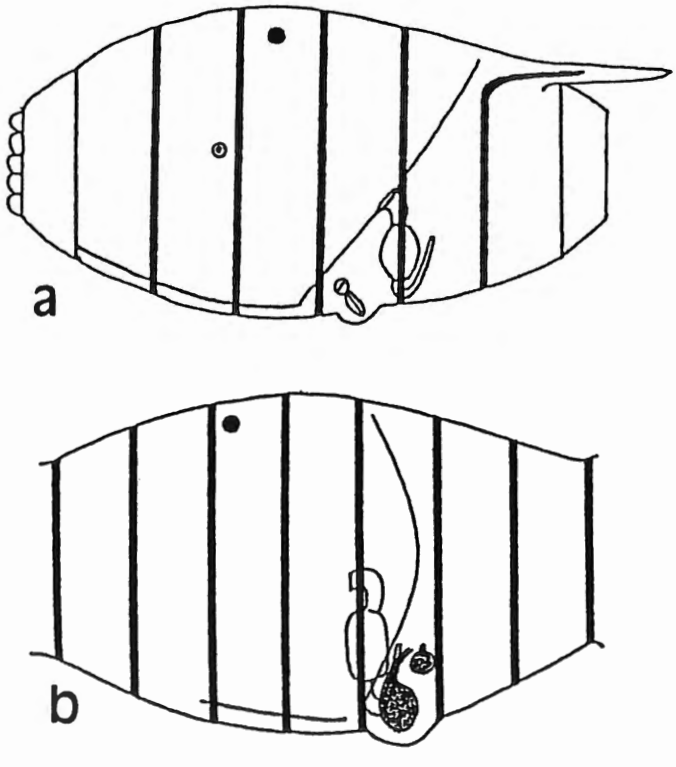


Fig. 2. *Doliolina muelleri*: **a**: oozooid, **b**: gonozooid.

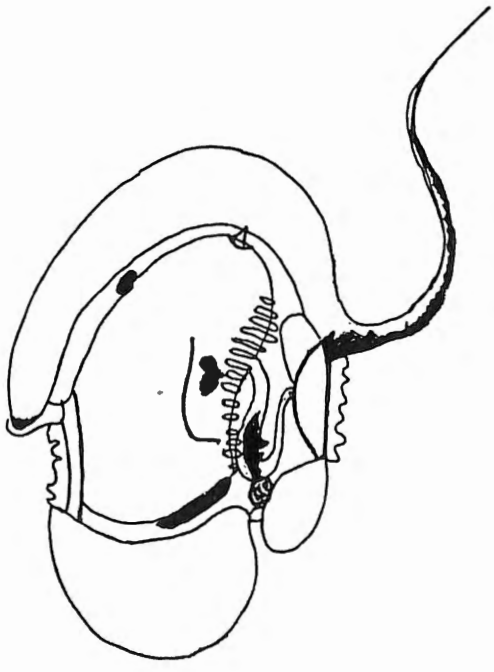

Fig. 3. *Doliopsis* sp.: gonozooid (after BARROIS 1885, modified).

*Anchinia savigniana* a second type of Doliolid discovered in the northern Atlantic Ocean (48° N-16° W). NEUMANN (1913b), after GEGENBAUR, GROBBEN and ULJANIN, considered that this species does not exist and is just a doliolum nurse with its dorsal spur. Later on a mediterranean species,

considered as close to *Anchinia*, was successively named *Doliopsis rubescens* (VOGT, 1852, Fig.3) and *Anchinia rubra* (VOGT 1854, KOWALEVSKY & BARROIS 1883, BARROIS 1885). GROBBEN (1882) recognized two species: *A. savigniana* and *A. rubra*, while KRÜGER (1939) called *Doliopsis savigniana* specimens mainly collected in the southern Atlantic Ocean. Numerous specimens mainly caught in the Bahamas seem to belong to another species, *Doliopsis bahamensis* (GODEAUX, 1996). The relationship with *Doliolum* has been early on suggested by HUXLEY (1851a), VOGT (1852), GROBBEN (1882) and NEUMANN (1913b). The life cycle of these animals remains practically unknown (see below). Metagenesis is probable, but only blastozooids have been described up to now.
In 1939, KRÜGER described a third type of doliolid species called *Doliopsoides meteori* and collected in the southern Atlantic Ocean, mostly below 400m depth. The barrel-shaped body evokes that of the doliolum. Another species, *Doliopsoides horizoni* has been described from the eastern tropical Pacific Ocean by TOKIOKA & BERNER (1958a,b). *Doliopsoides atlanticum* GODEAUX 1996 is a third species of the same genus from the north western Atlantic Ocean (GODEAUX 1996, GODEAUX & HARBISON in press). Nothing is known about their life cycle, although metagenesis seems probable.
In 1996, GODEAUX created the species *Paradoliopsis harbisoni* (GODEAUX & HARBISON in press) after two mature individuals and four developing buds still undescribed and caught at 740 m depth at two distant stations of the north-western Atlantic Ocean (Dry Tortugas and Bahamas). Metagenesis is probable.

## Diagnosis

### - Anatomical characters common to the different types of Doliolids

The close relationship between the four types of Doliolids is founded on a series of anatomical characters:
Marine, holoplanktonic, solitary, microphagous animals, often of a small size, sometimes locally pigmented. More or less elongated body (spherical to barrel-shaped), covered by a hyaline, less adhering, and more or less locally thick (depending of the species) tunic. Buccal and cloacal siphons located at both ends of the main axis, and generally provided with flaps. Complete or not, annular, parallel running muscle hoops. Nervous system reduced to a single dorsal ganglion (brain); neural gland absent in adult stage. Body cavity divided into a spacious anterior pharyngeal cavity and a reduced posterior atrial cavity separated by the transversal branchial septum; this septum bearing a single series ($\geq 4$) of horizontal ciliated gill slits on both sides of the opening of the oesophagus; slits or stigmata corresponding to a primitive single protostigma. Simplified endostyle (GODEAUX 1981, COMPERE & GODEAUX 1997) with two peripharyngeal ciliated bands emerging from its anterior end and forming the dorsal vibratile organ. Simplified digestive tube reduced to an oesophagus, a globulous stomachal pouch, an intestine and a pyloric gland; no differentiated digestive gland. Hermaphroditism of the gonozooids.

### - Differentiation of the four types

The four types of Doliolids can be distributed into four families thanks to diverse characters: length of the endostyle, shape of the digestive tube, number (5, 8 or 9) and disposition of the muscle hoops, position of the vibratile organ with regards to brain and M III, shape of the branchial septum, number of gill slits, position of the gonads, shape of the testis (in gonozooid), presence of pigmented areas.

## Subdivisions of the Order Doliolida (Cyclomyaria)

According to these different characters, a division of the order Doliolida in two suborders and four families is proposed:

Suborder Doliolidina with two families:

a) Doliolidae with four genera and about twenty species.

b) Doliopsoididae with one genus and three species.

The common characters are: barrel-shaped body, siphons at both ends of the main axis, thinness of the tunic, number of the muscle hoops (9 in oozooid and nurse, 8 in phorozooid and gonozooid), similar disposition of the organs, vibratile organ *in front* of brain and muscle III in blastozooids, testis on the left side of the animal.

Suborder Doliopsidina with two families:

a) Doliopsidae with one genus and two species.

b) Paradoliopsidae with one genus and one species.

The common characters are: more globulous shape of the body, siphons at both ends of the main axis, thickness of the tunic (at least locally), five muscle hoops, sigmoid incomplete lateral muscles III in symmetrical elements, vibratile organ *behind* brain and muscle III, U-shaped digestive tube, gonads close to the digestive tube, locally red, yellow or white pigmentations. Only blastozooids are known.

## Description of the four types and of their life cycle

### α) SUBORDER DOLIOLIDINA

a) The type Doliolum is by far the best known. The embryological development of the most common species has been described by ULJANIN (1884), NEUMANN (1906, 1913d), GODEAUX (1957-1958), and BRACONNOT (1964, 1968, 1970, 1971, 1974, 1977). The blastogenesis has been mainly investigated by NEUMANN (1906, 1935b).
- The egg is small-sized and loaded with little yolk. The segmentation is regular and similar to that of an oligolecithic ascidian egg. It seems possible that the same presumptive ar-

eas are present. The development (*Doliolina muelleri, Doliolum denticulatum*) leads to an ascidian-like tadpole; the body is composed of an anterior trunk (cephalenteron) and a posterior simplified tail devoid of nervous and digestive anlagen. Both parts of the body are preblastoporal (BRIEN 1948). Different organs will progressively develop inside the cephalenteron: nervous system, digestive apparatus, heart, muscles, peribranchial invaginations eventually fused into a median atrial cavity, branchial septum. The tail is a larval transient locomotive organ which disappears during metamorphosis, its sole organs being the axial chord (a file of some 40 swollen cells), and two lateral striated muscle layers bordered with mitochondria. Even these tissues remain embryonic in the tadpole of *Dolioletta gegenbauri* (anuran larva). The larvae are free in a follicular envelop (either fusiform in *Doliolum muelleri*, *Doliolum nationalis* and *Doliolum denticulatum*, or spherical in *Dolioletta gegenbauri*).

- The pelagic stage appears soon (after two days at 18° C in *Dolioletta gegenbauri*, BRACONNOT, 1970b). The body progressively swells and its epithelia flatten. The ectoblast becomes an epithelium covered by a thin and easily removed tunic. The tubular nervous anlage develops a dorsal ganglionary cluster of cells, the future brain, while its ventral part and the anterior part of the medullar tube respectively become the so-called sub-ganglionary neural gland and its canal opening into the pharyngeal cavity through a ciliary funnel. On the left side and in front of M III appears an ectodermal and more or less closed vesicle: the statocyst. The pharyngeal cavity grows hollow in the cephalenteron, while above the tail two dorsal ectodermal invaginations dive into the embryo and eventually fuse into the atrial cavity, the atrial siphon resulting of the fusion of the two primitive apertures. Simultaneously the tail is progressively pushed downwards, slowly shortens, and becomes an internal cluster of cells before complete disappearance. Nine muscle hoops develop from mesodermal anlagen, sliding between ectoderm and endoderm. M I and M IX become the buccal and atrial sphincters. M I to M IV are in front of the brain and responds to the muscles of an ascidian buccal sphincter. Similarly M VII to M IX respond to the muscles of an ascidian atrial sphincter. M VII is dorsally open and its free ends turn backwards to a dorsal ecto-mesodermal spur which appears and extends above the atrial siphon; later on the spur will carry the buds of trophozooids and phorozooids. The branchial septum results from uniting of the pharyngeal and of the atrial transversal walls; a series of four horizontal gill slits opens on both sides of the oesophageal opening. The endostyle responds to the lower part of the embryonary pharyngeal cavity. The digestive tube is located in a reduced abdomen and is of a variable shape according to the genus; it is composed of an oesophagus, a stomachal pouch and an intestine; a pyloric gland is always present. The cardiopericardium and stolon with its amoeboid phorocytes are located below the endostyle midway of M V and M VI.
- The developed oozooid escapes from its follicular envelope and swims. Its free life is short as it soon degenerates into a nurse deprived of endostyle, branchial septum and digestive tube. Just remain the brain, statocyst, cardiopericardium and actively budding stolon. Buds are carried on by the phorocytes to the spur. This displays two lateral series of developing trophozooids and two median series of developing phorozooids.

The systematics of nurses is founded on the width of the muscle hoops, on the presence or absence of the statocyst. Most of them are still unknown.

- The development of buds has been followed by NEUMANN, mainly on *Doliolum denticulatum.* The structure of the stolon which appears early, is especially complex (rosette organ): two processes from the pharynx (= epicardia), two from the atrial wall, and two from the mesoblast and cardiopericardium contribute to its structure. The bud is protected by an ectodermal sheet.
- The trophozooids (TZ) represent the first generation of blastozooids. Their anatomy is highly simplified. The body is spoon-shaped with asymmetrical gill slits series and muscles according to the position of the bud on the spur of the nurse (GROBBEN 1882). Below the endostyle stands the fixation stalk provided with a distal sole; it is supposed that fullgrown trophozooids feed the gut deprived nurse.

A broad, very high and sphincter-devoid buccal siphon opens in the spacious pharyngeal cavity. The endostyle occupies the ventral wall. A more or less high number of gill slits are visible on the hinder wall, slits directly opening to outside as the atrial cavity disappears during development (GROBBEN 1882, GODEAUX 1957-1958).The brain is located above the buccal siphon; five nerves radiate. The muscles are reduced to two groups, a dorsal one limited to three arches running downwards, a ventral one comprising the two muscles of the stalk and a transversal muscle running below the pharyngeal cavity.

The systematics of the few identified trophozooids is founded on the relative positions of the oesophageal funnel and anal aperture, the number of gill slits, the position of the rear end of the endostyle, the position of the anterior muscle of the stalk (GODEAUX 1998b).

- The phorozooids are the second generation of blastozooids. The phorozooid is barrel-shaped and similar to the oozooid, but with only 8 complete muscle hoops and no dorsal spur, stolon and statocyst. The fixation ventral stalk bears the developing gonozooids.

Length of the endostyle, shape of the branchial septum, number of branchial slits (≥ 5), shape of the digestive tube are systematic characters used for identification of some 20 species (GARSTANG 1933, GODEAUX 1998a,b).

- The gonozooids are the third generation of blastozooids. Their anatomy is quite similar to that of the phorozooids of the same species. The position, shape and length of the testis on the left side of the animal, position of the ovary are important classification characters.

The phorozooid is probably an abortive gonozooid as a cluster of cells is visible in young specimens at the level of the genital anlage of the gonozooid. Moreover gonophorozooids have been described in *Doliolum nationalis* (BRACONNOT & CASANOVA 1967, BRACONNOT 1967, 1974, 1977).

The mean length of the entire life cycle of a Doliolum is estimated 20.5 days in *Dolioletta gegenbauri* (PAFFENHOFER & GIBSON 1980). Growth of the different stages is very fast; a phorozooid (≥5 mm) can liberate 10 gonozooids a day during

8 to 18 days, what explains the sudden bursts of Doliolum at determined periods of the year (BRACONNOT 1995).

b) The genus *Doliopsoides* is known since 1939 (KRÜGER). The individual is barrel-shaped and similar to the phorozooid and gonozooid of a doliolum but its 8 muscles are arranged in a different pattern (Fig.12). The tunic and ectoderm are thin; the siphons are located at both ends of the main axis, with M I and M VIII as sphincters. The brain is dorsal and in front of M III. M I to M IV are complete hoops while M V and M VI open dorsally with their free extremities fusing into lateral archs, a configuration characteristic of the genus. M VI may be either complete or not ventrally. M VII is open ventrally and its branches cross those of M VI before ending in a ventral stalk (a single case known). A thin sub-endostylar muscle joins either M II - M III, either M III - M IV, and a thin lateral sigmoid muscle binds M IV and M V on both sides. The vibratile organ lies in front of the brain and behind M II. The branchial septum is transversal, arched, with numerous gill slits. The digestive tube is U-shaped, and above the gonads. The possible presence of pigment is unknown.
Nothing is known about the life cycle. A single phorozooid described by TOKIOKA & BERNER (1958 b) pleads for a possible metagenesis with three stages at least (Ooz, PZ and GZ).
The systematics of genus *Doliopsoides* is founded on the position of the muscles, the number of gill slits and the form of the gonads.

### β) SUBORDER DOLIOPSIDINA

a) The third genus is known since VOGT's descriptions of *Doliopsis rubescens* (1852). The individual is globulous, as high as long. The tunic is locally thick but easily removed. The ectoderm is a flattened epithelium. The siphons open at both ends of the horizontal axis (Fig.13).
The animal is provided with five muscles. M I and MV are the siphons sphincters. M II is complete and close to M I. M III is incomplete, short, sigmoid, limited to the flanks of the animal. M IV forms a complete ring at the level of the atrial cavity.
The spacious pharyngeal cavity is separated from the atrial cavity by the transversal branchial septum, pierced by two series of numerous gill slits.The endostyle lies on the ventral side. The peripharyngeal ciliated bands run behind M II and unit into the vibratile organ located far *behind* the brain, occupying the top of the body. Viscera are concentrated in the rear of the body. The digestive tube is U-shaped with the hermaphroditic gonads visible below it. A stolon is always missing.
Red or yellow-red pigmented areas have been observed in living specimens, with position differing according to the species. The fixation stalk is retracted into a tunical tube in fullgrown specimens.
The life cycle is complex and seems traced from that of the Doliolum.The oozooid remains unknown; it must produce a long whitish lace bearing three kinds of blastozooids, the two first sterile (= trophozooid and phorozooid?) and the last one hermaphroditic. Their developments were studied by KOWALEVSKY & BARROIS (1883), BARROIS (1885) and KOROTNEFF (1883, 1884).
The systematics of genus *Doliopsis* is founded on the pigmentation and diverse anatomical characters as position and shape of the gonads, number of gill slits, presence of oesophageal whorls.

b) The fourth genus is *Paradoliopsis* with a single species *Paradoliopsis harbisoni* GODEAUX 1996 observed up to now (Fig.14). Its rectangular body is longer than higher with the siphons at both ends of the main axis. The relatively thick (especially above the buccal siphon) tunic adheres loosely to the thin ectoderm. Five muscles are visible. M I is the sphincter of the buccal siphon. It is followed by a 500 mm-long vestibule limited in the rear by M II. This muscle also forms a complete ring. Muscles III are long, sigmoid, and extend from behind the dorsal brain (free ends not fusing, but overlapping) towards the middle part of the endostyle before forming a loop ending behind the branchial septum.The pharyngeal epithelium is folded along these muscles, creating a kind of internal crest. The role of these folds remains unclear but possibly they provide support for the walls of the spacious pharyngeal cavity. M IV stays at the level of the atrial cavity; it is open ventrally just before a ventro-posterior stalk carrying a developing bud. M V forms the sphincter of the atrial siphon.
The long ventral endostyle bears two anterior roughly rectangular clusters of white pigmented cells; a whitish cloud is also present below the organ. The peripharyngeal ciliated bands pass behind M II, then on the right of the brain and unit *behind* M III into the vibratile organ located in front of the branchial septum and *on the right side* of the animal, a position never observed till now in Doliolida.
The branchial septum bears two series of horizontal gill slits, divided into dorsal and ventral parts. The U-shaped digestive tube is sligthly inclined forwards.The testis comprises four caeca, two running along the descending intestine, two directed downwards. The ovary is close to the genital pore.
Buds are visible on the ventral stalk, but a stolon cannot be observed. The animal is thus a kind of gonophorozooid.

## DICHOTOMOUS KEYS OF THE CYCLOMYARIA

The different species, particularly the Doliolidae, will be considered under the successive stages of their life cycle.

Just a few larvae of Doliolidae have been identified up to now. In every genus, larvae are possibly identical as it is the case for the oozooids and nurses, and therefore could not be separated (cryptic species), except with rearing from the egg or a possible genetic analysis.

1 - larva free in its follicular envelope, body composed of a dense trunk and a tail ..... **2**

- barrel-shaped individual, completely developed, free swimming, an open siphon at both extremities, no tail ..... **4**

- spoon-shaped individual, tied on the dorsal spur of a barrel-shaped animal, buccal siphon widely open ..... trophozooid (A2) **13**
Doliolidae

**Larvae**

2 - elongated, mobile larva, with a well differentiated active tail, fusiform follicular envelope, anterior rostrum ..... **3**

- larva with a dense body, undifferentiated tail, spherical follicular envelope, no rostrum ..... g. *Dolioletta*
*Dolioletta gegenbauri* (Fig.4 a,b )

3 - larva with the trunk separated from the tail by a hyaline vesicle (x) ..... g. *Doliolina*
*Doliolina muelleri* (Fig.4 c,d)

- no caudal hyaline vesicle ..... g. *Doliolum*
*Doliolum denticulatum* (Fig.4 e,f)
*Doliolum nationalis* (xx)

REM.: (x) Possibly the larva of *Dolioloides rarum* (Fig.4 g) could also be provided with a caudal vesicle (ULJANIN 1884, pl.5, fig.1). (xx) Larvae of these two species are identical (BRACONNOT 1974, 1977).

**SUBORDERS AND FAMILIES**

4 - barrel-shaped individual, body longer than higher, 9 (M I to M IX) or 8 (M I to M VIII) muscle hoops, complete or open, viscera present or not, vibratile organ *in front* of the brain ..... s/o Doliolidina **5**

- globulous individual, body as high as long, 5 (M I to M V) muscles, M III incomplete and S-shaped, the other muscles annular, viscera always present, vibratile organ *behind* the brain ..... s/o Doliopsidina **6**

5 - individual provided with 9 muscles, VII open dorsally with free ends curved backwards to the posterior processus (spur) carrying buds, brain *in front* of M V, viscera present or missing ..... Doliolidae
**(A1) 7**
(oozooids and nurses)

- individual provided with 8 complete and parallel muscle hoops, no dorsal spur, viscera always present, brain *in front* of M IV, no statocyst ..... Doliolidae
**(A3) 16**
(phoro = and gonozooids)

- individual provided with 8 muscle hoops, some incomplete or fused, viscera always present, brain *in front* of M III ..... Doliopsoididae
**(B) 27**

6 - individual with body as high as long, M III short, S-shaped, no buccal vestibule, vibratile organ apical, *behind* the brain ..... Doliopsidae
**(C) 29**

- individual longer than higher, M III S-shaped, long, open dorsally, buccal vestibule present, two clusters of white pigmented cells at the anterior end of endostyle, vibratile organ located on *the right side* and *behind* the brain ..... Paradoliopsidae
**(D) 32**

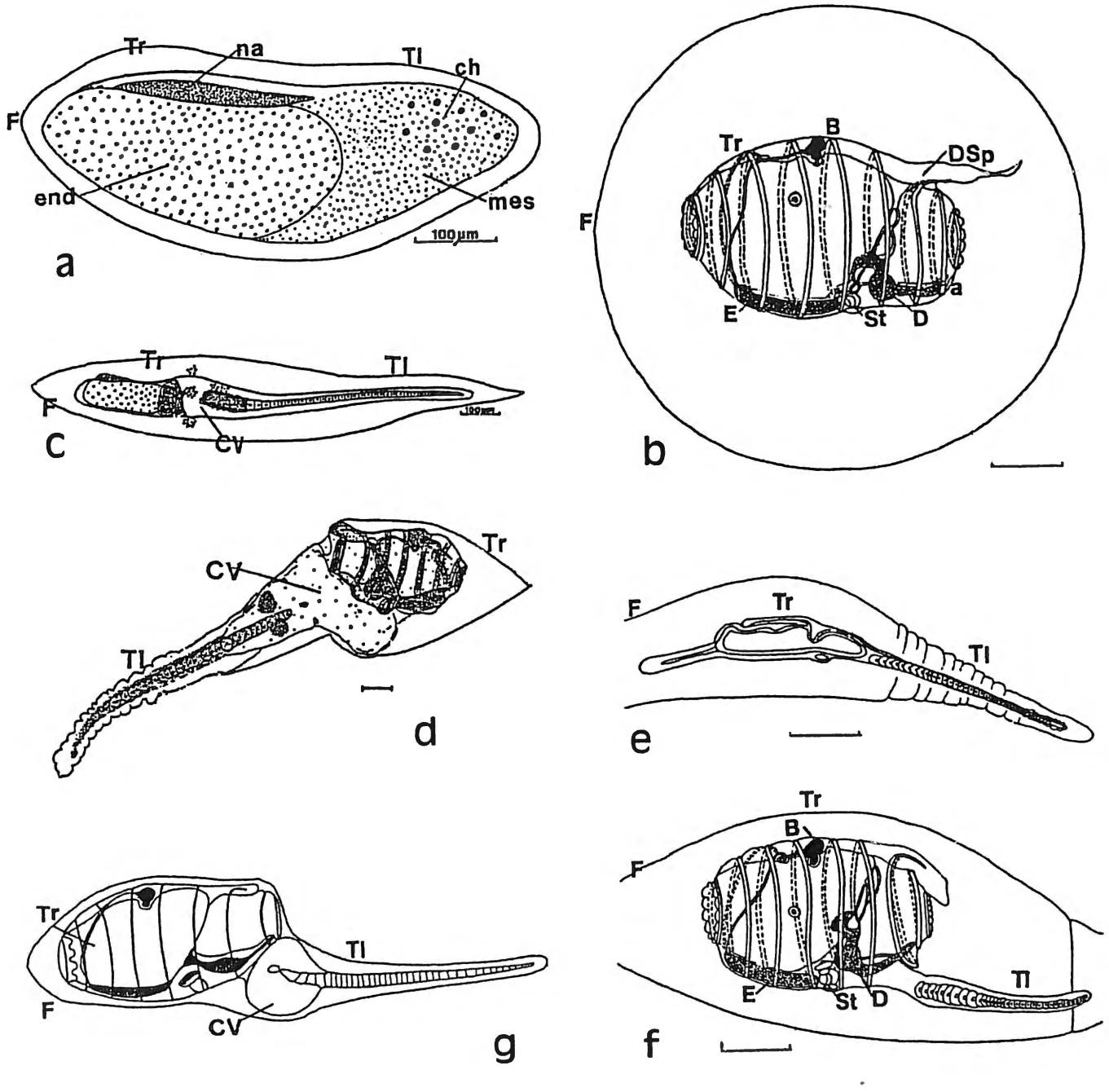


Fig. 4. **a**. anouran larva of *Dolioletta gegenbauri* (after GODEAUX 1957-58; scale bar 100 µm). **b**. metamorphosed larva of *Dolioletta gegenbauri* still inside its envelope (after NEUMANN 1906; scale bar 500 µm) **c**. larva of *Doliolina muelleri* (late neurula, after GODEAUX 1957-58; scale bar 100 µm). **d**. metamorphosing larva of *Doliolina muelleri* (after GODEAUX 1957-58; scale bar 100 µm). **e**. larva of *Doliolum denticulatum* (neurula after NEUMANN 1906; scale bar 300 µm). **f**. metamorphosing larva of *Doliolum denticulatum* (after NEUMANN 1906; scale bar 300 µm). **g**. metamorphosing larva of *Dolioloides rarum* (after ULJANIN 1884 ; size unknown).

### α) Suborder Doliolidina

The different stages will be successively considered

### A) Family Doliolidae

**A1**
**Oozooid and nurses**

**7** - barrel-shaped individual bearing 9 muscle hoops, M VII dorsally open, free ends curved backwards to the dorsal spur, first buds present, viscera always present, gonads always missing, a ventral stolon, a series of 4 gill slits on each side of the oesophagus ..... fullgrown oozooids **8**

- barrel-shaped individual bearing 9 muscle hoops, M VII open dorsally, free ends curved backwards, dorsal spur with numerous buds, gill slits, viscera and gonads always absent, a ventral stolon ..... nurses **11**

**8** - straight digestive tube ..... **9**

- U-shaped digestive tube, long endostyle extending from midway between M III and M IV to M V ..... g. *Doliolina*
*Doliolina muelleri* (Fig.5a)[x]

x) Rem.: The oozooids of the other species of the genus have not yet been identified.
The former genus *Doliolina* Garstang 1933 is now divided in two subgenera: a) subgenus *Doliolina* (Borgert 1894) nurses of which are provided with 9 muscle hoops separated by narrow interspaces and b) subgenus *Doliolinetta*, close to the preceding one, but with nurses provided with slender muscle hoops separated by 10 times wider interspaces (Godeaux 1998c). The subgenus *Doliolina* comprises the species *Doliolina muelleri*, *D. krohni* and possibly *D. sigmoides*. The species *Doliolina undulata* and *D. obscura*, only known as gonozooids, belong to the same subgenus. Subgenus *Doliolinetta* comprises the species *Doliolinetta indica*, *D. intermedia* and *D. resistibilis*. Species *Doliolinetta separata*, only known as gonozooid, belongs to the same subgenus (Godeaux 1998c ). All the blastozooids display a U-shaped (sometime V-shaped) digestive tube as *Doliolina muelleri*. Garstang considers this type of gut as primitive; it is in fact similar to the gut of the ascidians and of a lot of sessile animals. It is possibly the remain of a former sessile life of the doliolum ancestors.

**9** - long oesophagus, concavity upwards, stomachal pouch in front of M VII, endostyle M II close to M V, slender muscles ..... *Dolioloides rarum* (Fig.5b)

- oesophagus concavity downwards, stomachal pouchpouch at the level of M VI ..... **10**

**10** - endostyle extending from M II to M V ..... g. *Doliolum*
*Doliolum denticulatum* (Fig.5c)
Doliolum nationalis

- endostyle extending from M III to M IV ..... g. *Dolioletta*
*Dolioletta gegenbauri* (Fig. 5d)

**11** - wide muscles with narrow interspaces ..... **12**

- M II to M VIII fused in a continuous sheet (cuirass), statocyst below M III ..... g. *Doliolum*
*Doliolum denticulatum* ( Fig.6a)

**12** - M III wider or at least equal to M IV, not contracted appearance, statocyst always present in front of M III ..... g. *Dolioletta*
*Dolioletta gegenbauri* (Fig. 6b)

- M IV wider than M III, statocyst missing, contracted appearance, small size ..... s.g. *Doliolina*
*Doliolina muelleri* (Fig.6c)

- all muscles very narrow, wide interspaces ..... s.g. *Doliolinetta*
*Doliolinetta intermedia* (Fig.6d)

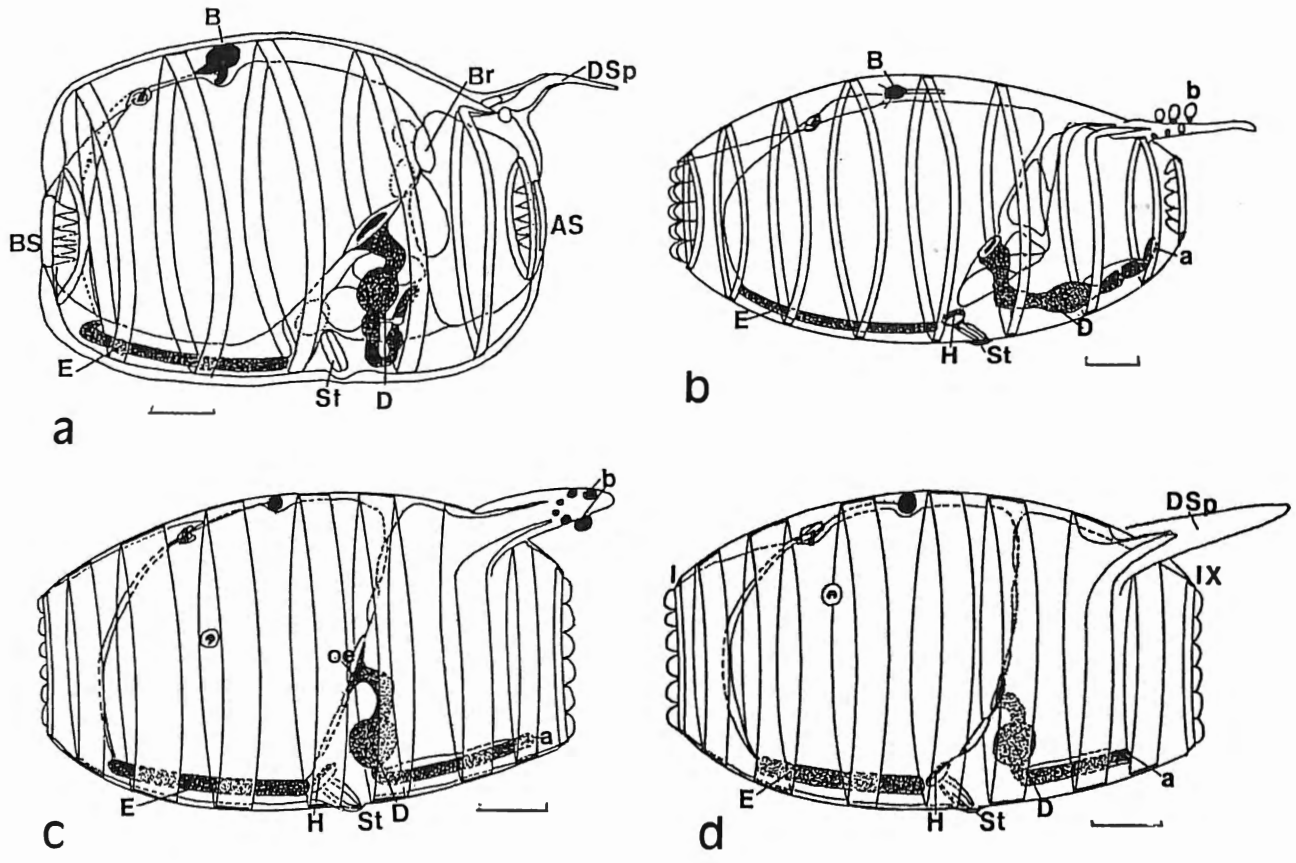


Fig. 5. **a**. oozooid of *Doliolina muelleri* (after GODEAUX 1957-58; scale bar 100 µm). **b**. oozooid of *Dolioloides rarum* (after NEUMANN 1906; scale bar 500 µm). **c**. oozooid of Doliolum species (*D. denticulatum* and *D. nationalis*; scale bar 250 µm). **d**. oozooid of *Dolioletta gegenbauri* (scale bar 250 µm).

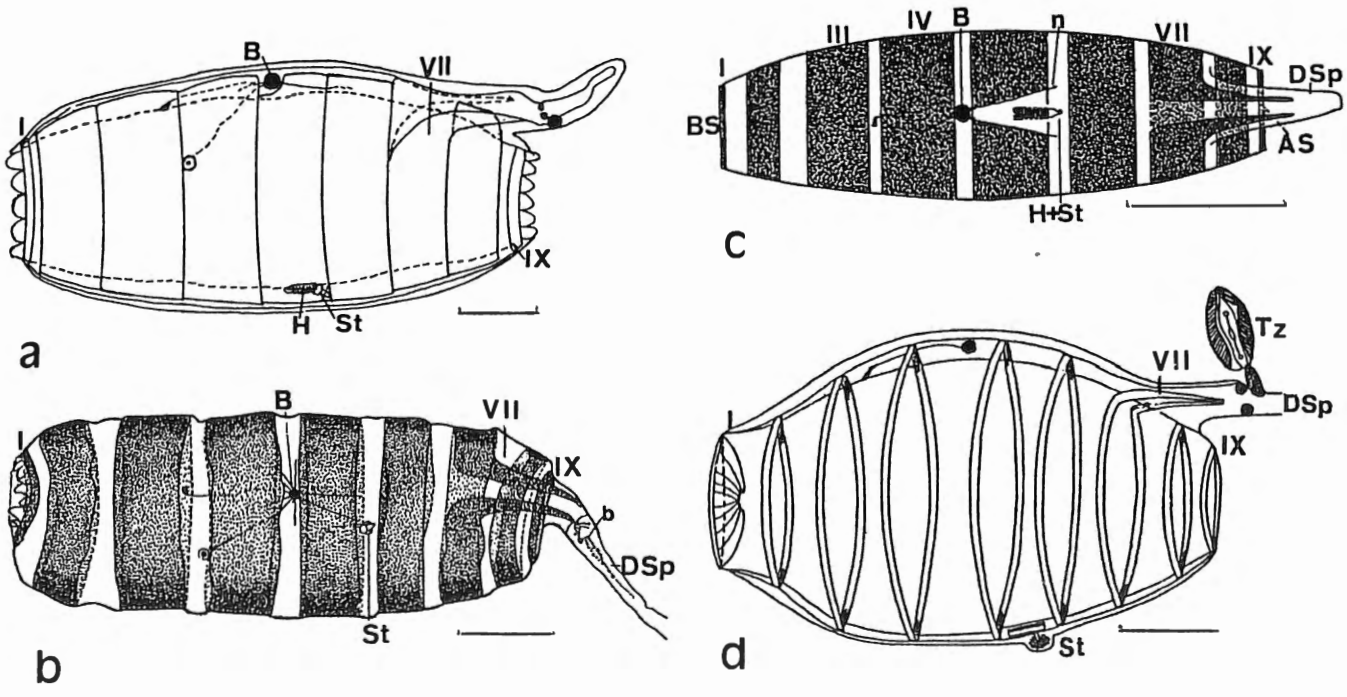


Fig. 6. **a**. nurse of *Doliolum denticulatum* (after GROBBEN 1882; scale bar 1.2 mm). **b**. nurse of *Dolioletta gegenbauri*; scale bar 500 µm). **c**. nurse of *Doliolina muelleri*; scale bar 500 µm). **d**. nurse of *Doliolinetta intermedia* (after GODEAUX & HARBISON in press; scale bar 500 µm).

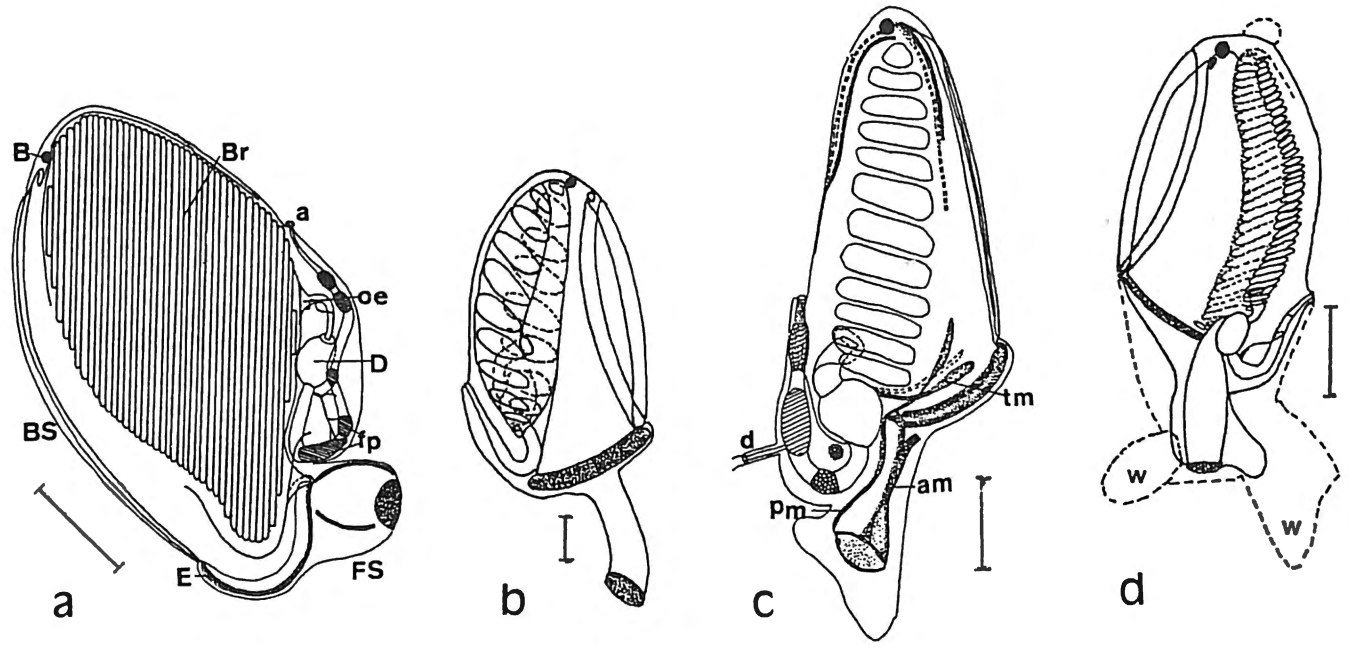


Fig. 7. **a**. trophozooid of *Doliolinetta intermedia* (after GODEAUX & HARBISON in press; scale bar 250 µm). **b**. trophozooid of *Doliolina muelleri* (after BRACONNOT 1970b; scale bar 350 µm). **c**. trophozooid of *Doliolum denticulatum* (after GODEAUX 1998; scale bar 1 mm). **d**. trophozooid of *Dolioletta gegenbauri* (after BRACONNOT 1970b; scale bar 1 mm).

**A2**
**Trophozooids:** all are similar with the possibility of a single form for each genus or subgenus.

**13** - spoon-shaped individual, spacious pharyngeal cavity, atrial cavity always missing, U-shaped digestive tube, thin muscles in two dorsal and ventral separated groups, a ventral fixation stalk, endostyle ending in front of the stomachal pouch ..... **14**

- similar individual, endostyle ending at the level of the intestinal loop, anal aperture above the pharyngeal opening ..... **15**

**14** - numerous gill slits, anal aperture above the oesophageal opening ..... *Doliolinetta intermedia* (Fig.7a)

- gill slits less numerous (up to 10), anal aperture below the oesophageal opening ..... *Doliolina muelleri* (Fig.7b)

- 15 - 12 to 13 gill slits..... *Doliolum denticulatum* (Fig.7c)

- 20 to 50 gill slits, ventral stalk bearing wings ..... *Dolioletta gegenbauri* (Fig.7 d)
no wings ..... *Dolioletta mirabilis*

**A3)**
**Phorozooids and gonozooids**

Barrel-shaped animals provided with 8 complete parallel muscle hoops. Phorozooids with a lot of developing buds on their ventral stalk, gonozooids hermaphroditic, testis always on the left side.

**16** - U-shaped or V-shaped digestive tube, small size, branchial septum of variable shape,variable number of gill slits (always ≥ 5), length of endostyle variable, testis club-shaped or extending along the left side of the animal ..... g. *Doliolina* **17**

- elongated digestive tube, oesophagus concavity upwards, endostyle M II $^{1/4}$ to close M V, five gill slits, testis extending beween M II and M VI, ovary under M VI ..... *Dolioloides rarum* (Fig.8a)

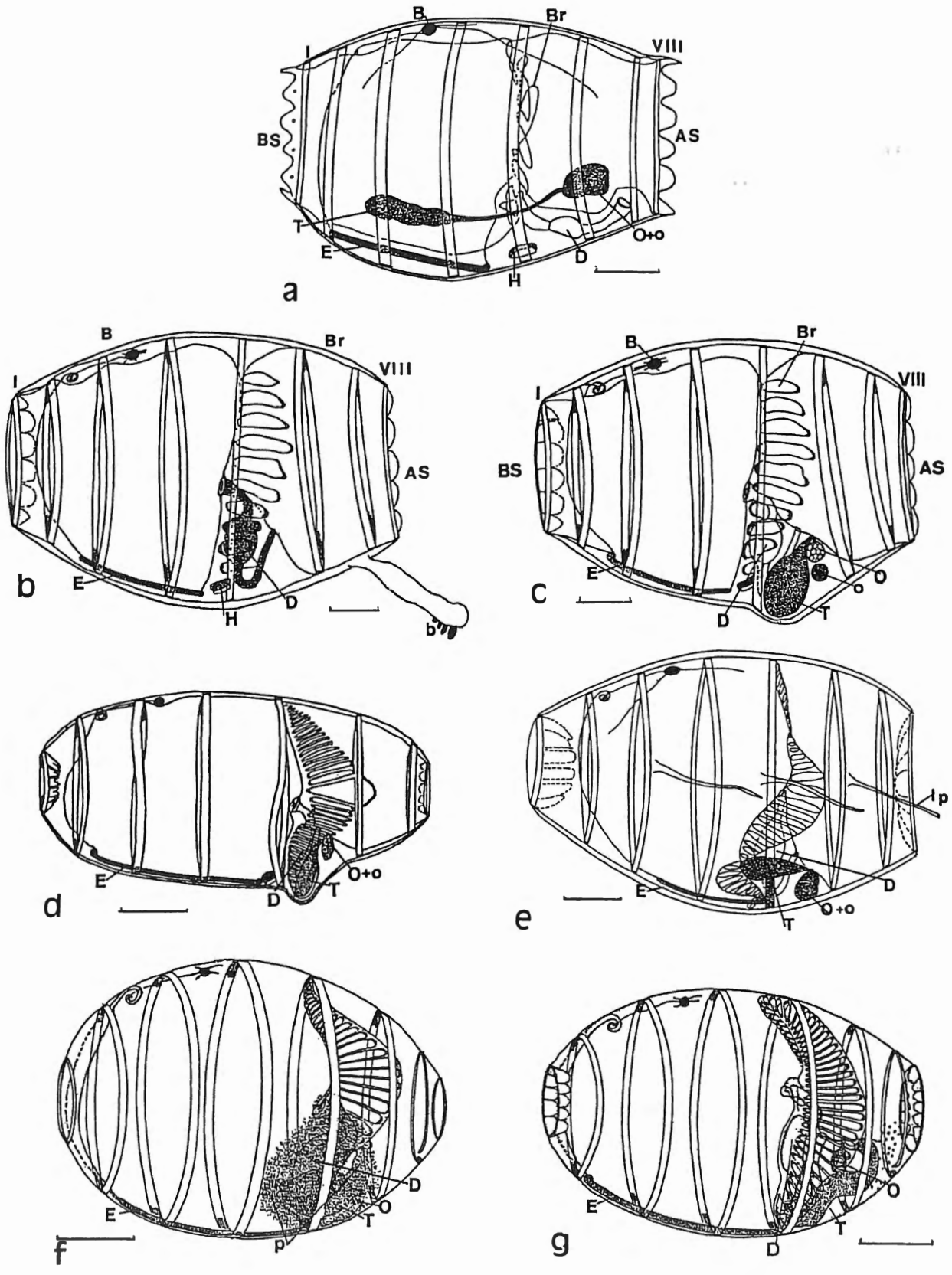


Fig. 8. **a**. gonozooid of *Dolioloides rarum* (after GARSTANG 1933; scale bar 500 µm). **b**. phorozooid of *Doliolina muelleri* (after GROBBEN 1882; scale bar 500 µm). **c**. gonozooid of *Doliolina muelleri* (after GROBBEN 1882; scale bar 500 µm). **d**. gonozooid of *Doliolina krohni* (after BORGERT 1894; scale bar 1 mm). **e**. gonozooid of *Doliolina sigmoides* (after NEUMANN 1906 ; scale bar 1 mm). **f**. gonozooid of *Doliolina undulata* (after TOKIOKA & BERNER 1958a; scale bar 1 mm). **g**. gonozooid of *Doliolina obscura* (after TOKIOKA & BERNER 1958b; scale bar 1 mm).

- dextral arched digestive tube, anus on the right side, endostyle M II to M IV, brain in front of M IV, branchial septum vertically curved, testis extending along the left side of the animal ..... g. *Doliolum* **20**

- coiled digestive tube, variable length of endostyle, brain behind M III, branchial septum extending between M II and M IV, tubular testis of various shapes ..... g. *Dolioletta* **21**

**17** - pear-shaped testis close to the digestive tube, ovary in front of M VI ..... s.g. *Doliolina* **18**

REM.: TOKIOKA & BERNER (1958) proposed to separate the diverse species of genus *Doliolina* in *Doliolina perfecta* and *Doliolina imperfecta* depending whether M VII is ventrally complete or open. Their division does not coincide with our own proposal of distinguishing two subgenera *Doliolina* and *Doliolinetta* according to shape and disposal of the gonads.

- tubular testis extending horizontally, ovary in front of M VII ..... s.g. *Doliolinetta* **19**

**18** - endostyle from before M III to before M V, arched branchial septum behind M V , 10 to 14 gill slits,
- gonads missing, ventral stalk with buds, phorozooid ..... *Doliolina muelleri* (Fig.8b)
- vertical club-shaped testis, protruding ventrally, ovary in front of M VI, gonozooid ..... *Doliolina muelleri* (Fig.8c)

- endostyle M II to M V, arched branchial septum between M V and M VI, 12 to 45 gill slits, M VII complete ventrally, pear-shaped testis, protruding ventrally, ovary in front of M VI ..... *Doliolina krohni* (Fig.8d)

- endostyle M II to M V, S-shaped branchial septum (M V - M VI to M IV - M V), M VII complete ventrally, three pairs of epidermal tentacle-like processes, short horizontal testis, from M $IV^{1/2}$ to M $VI^{1/2}$, ovary in front of M VI ..... *Doliolina sigmoides* (Fig.8e)

- endostyle M II to M V, S-shaped branchial septum (M V - M VI - M V), 40 gill slits, M VII open ventrally, pigmented cells concealing intestinal loop and gonads, globular testis at the level of M V, ovary in front of M VI ..... *Doliolina obscura* (Fig.8f)

- endostyle M II to M V, V-shaped branchial septum (M $IV^{1/2}$ - M VI - M V), 30 to 40 gill slits, M VII open ventrally, testis sausage-shaped, oblique, between M V and M VI, ovary in front of M VI ..... *Doliolina undulata* (Fig.8g)

**19** - endostyle M II to M V, branchial septum oblique (M VI to M V), 5 gill slits, clusters of black pigment around the gut, M VII complete ventrally, tubular horizontal testis, swollen at the level of M IV, ovary in front of M VII..... *Doliolinetta indica* (Fig.9a)

- endostyle from before M II to before M V, incurved branchial septum (M IV - M VII - M V), 30 to 50 gill slits, M VII complete ventrally, tubular testis, swollen at the level of M II, ovary in front of M VII..... *Doliolinetta intermedia* (Fig.9b)

- endostyle M $II^{1/2}$ to M $IV^{1/2}$, arched branchial septum (M III- M $VI^{1/3}$), 30 to 40 gill slits, M VII complete ventrally, tubular testis swollen at the level of M III, ovary in front of M VII ..... *Doliolinetta resistibilis* (Fig.9c)

- endostyle M II to M V, oblique branchial septum (M VI to M V), 10 gill slits, M VII open ventrally, tubular testis swollen between M II to M III, ovary in front of M VII ..... *Doliolinetta separata* (Fig.9d)

**20** - endostyle M II to M IV, brain in front of M IV, branchial septum (M II - M VI - M III), numerous branchial slits (→ 100), long tubular testis, swollen at the level of M II - M III, and over, ovary behind M V I, gonozooid ..... *Doliolum denticulatum* (Fig.10a,c)

- endostyle M II to M IV, brain in front of M IV, branchial septum M II - M VI to in front of M V, ventral stalk with buds, phorozooid ..... *Doliolum nationalis* (Fig.10b)
- short tubular testis swollen behind M IV, ovary behind M VI, gonozooid ..... *Doliolum nationalis* (Fig. 10d)

REM.: gonophorozooids of *D. nationalis* were observed by BRACONNOT & CASANOVA (1967) and BRACONNOT (1974, 1977).

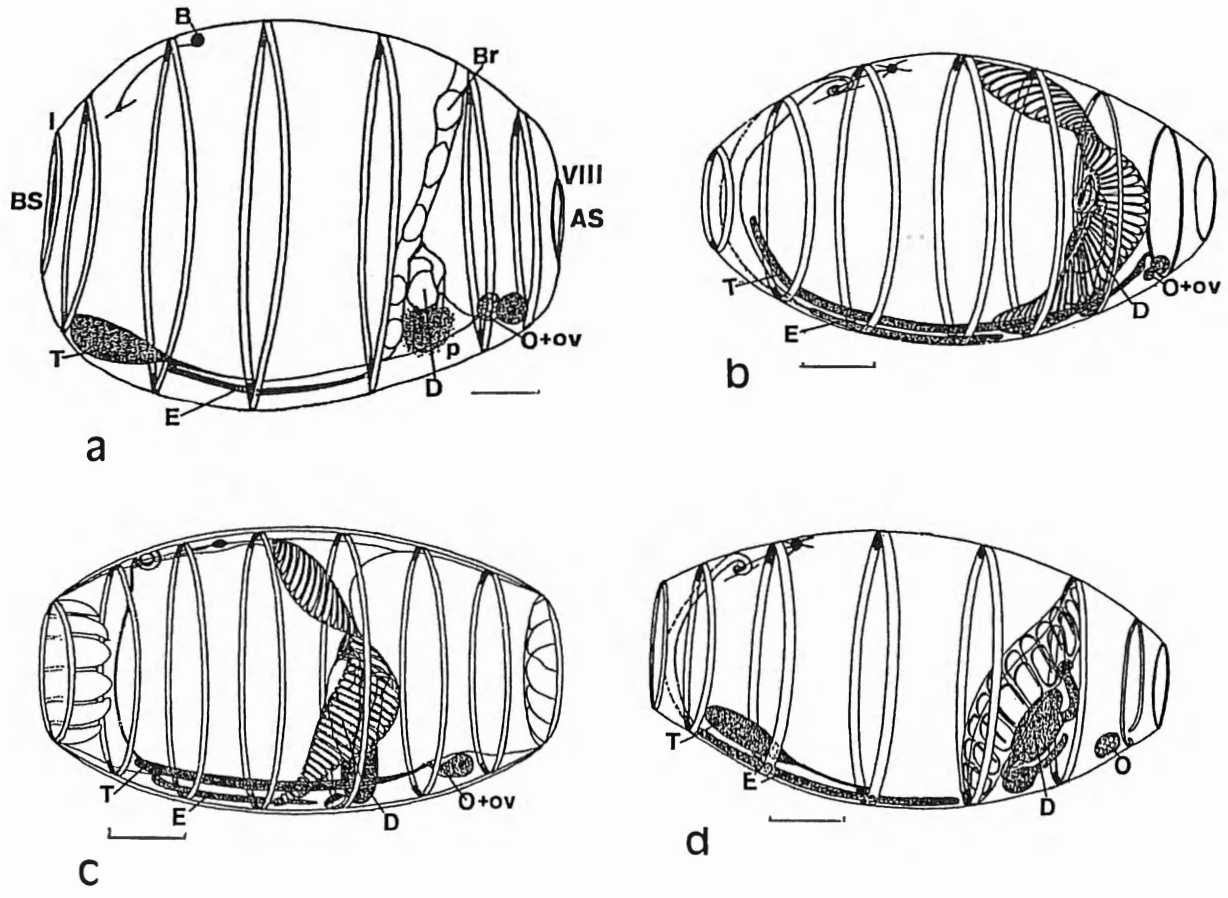


Fig. 9. **a**. gonozooid of *Doliolinetta indica* (after GODEAUX 1998c; scale bar 500 µm). **b**. gonozooid of *Doliolinetta intermedia* (after NEUMANN 1906; scale bar 150 µm). **c**. gonozooid of *Doliolinetta resistibilis* (after NEUMANN 1913; scale bar 150 µm). **d**. gonozooid of *Doliolinetta separata* (after TOKIOKA & BERNER 1958b; scale bar 500 µm).

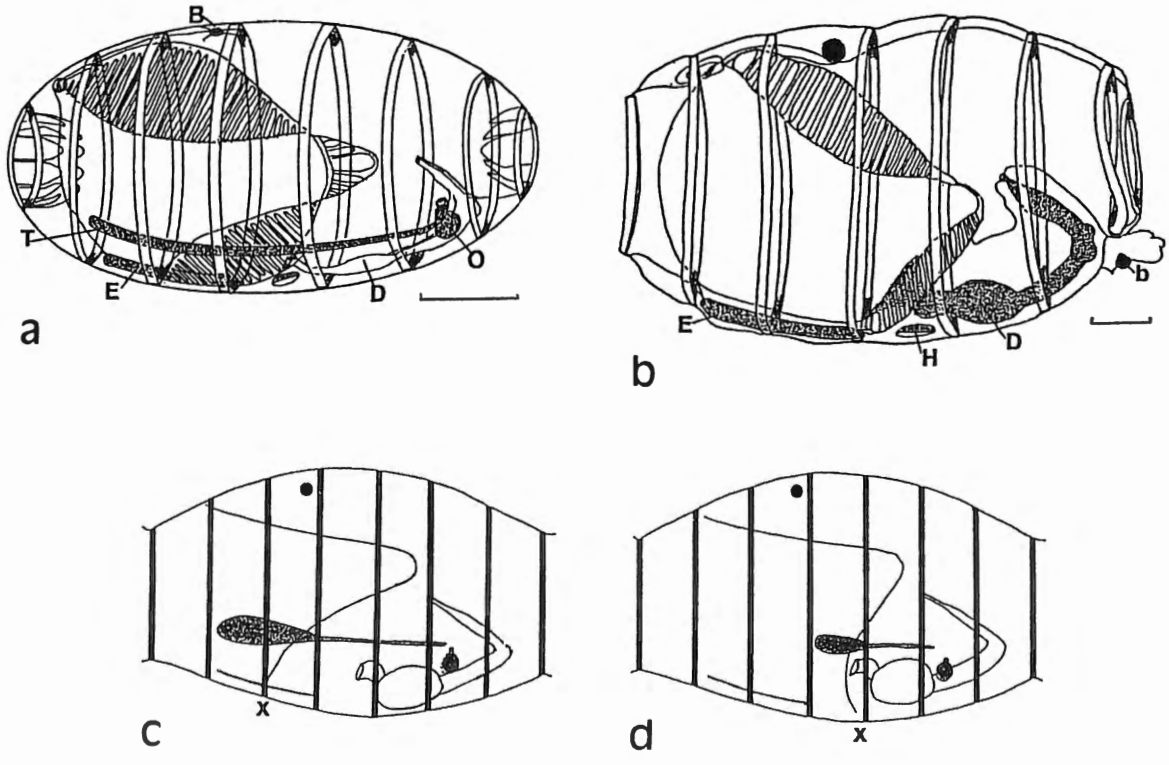


Fig. 10. **a**. gonozooid of *Doliolum denticulatum* (after NEUMANN 1906; scale bar 1 mm). **b**. phorozooid of *Doliolum nationalis* (scale bar 250 µm). **c-d**. schematic comparison of the gonozooids of *Doliolum denticulatum* (c) and *D. nationalis* (d).

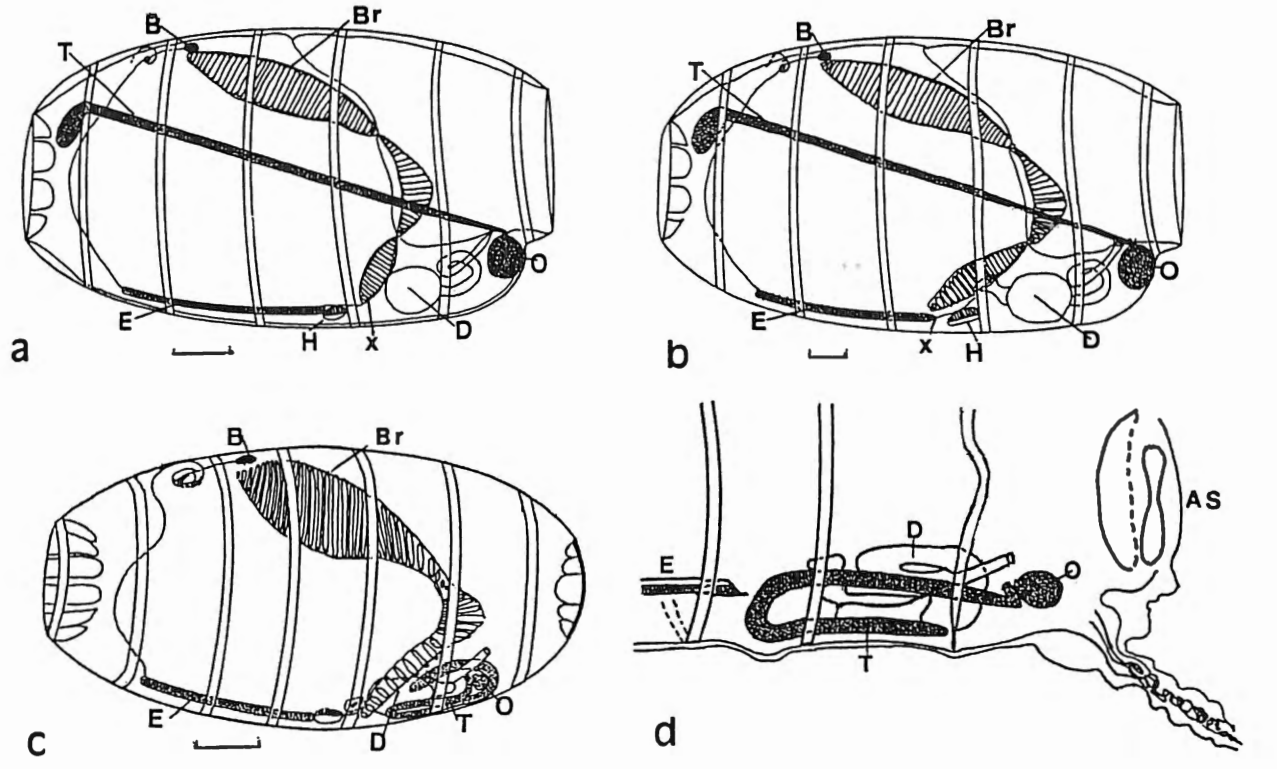


Fig. 11. **a**. gonozooid of *Dolioletta gegenbauri* (after ULJANIN 1884; scale bar 1 mm). **b**. gonozooid of *Dolioletta tritonis* (after RITTER 1905; scale bar 1mm). **c**. gonozooid of *Dolioletta valdiviae* (after NEUMANN 1906; scale bar 500 µm). **d**. viscera of *Dolioletta mirabilis* (*chuni*) (after KOROTNEFF 1891).

**21** - strongly arched branchial septum, not overlapping M V in the rear, up to 70 gill slits ..... **22**

- strongly arched branchial septum overlapping M VI in the rear, up to 70 gill slits ..... **23**

**22** - endostyle M $II^{1/2}$ to M $IV^{1/2}$ , branchial septum (M III - MVI - M V), tubular testis running obliquely, sometimes overlapping M II ..... *Dolioletta gegenbauri* (Fig.11a)

- endostyle M $II^{3/4}$ to M $IV^{1/2}$ , branchial septum (M III -MVI - M $IV^{1/2}$), tubular testis, running obliquely, sometimes overlapping M II ..... *Dolioletta tritonis* (Fig.11b)

**23** - long endostyle M $II^{1/5}$ to M V, branchial septum (M III - M VI - M V), tubular testis coiled between M IV and M VI around the gut, ovary in front of M VII ..... *Dolioletta valdiviae* (Fig.11c)

- short endostyle M $II^{4/5}$ to M $IV^{1/2}$, M VI thin or open ventrally, branchial septum (M II -M $VI^{1/2}$- M IV), tubular testis coiled between M IV and M VII on the left of the gut, ovary in front of M VII ..... *Dolioletta mirabilis (chuni?)* (Fig.11d)

## DESCRIPTION AND DISTRIBUTION OF THE SPECIES

### A) Family Doliolidae

(Maps with the distribution of the species of this family were published by DEIBEL 1998).
Type species: *Doliolum denticulatum* (QUOY & GAIMARD 1835)

The family is actually divided into four genera and two subgenera.

- Genus *Dolioloides* GARSTANG 1933. A single species.

***Dolioloides rarum*** (GROBBEN 1882)

*Doliolum* n.sp. GEGENBAUR, 1856, p.303-304, pl.16, fig. 12 et 13 (oozooid according to ULJANIN),

*Doliolum muelleri* (not KROHN) KEFERSTEIN & EHLERS, 1861, p.65, pl.9, fig. 5-6 (gonozooid) and fig.7 (oozooid),
*Doliolum rarum* GROBBEN 1882 *n.sp.*, p. 265-267 (oozooid), pl.18, fig.6 (gonozooid),
*Doliolum rarum* ULJANIN 1884, p. 130-132, fig.10, pl.5, fig.1 (*ehrenbergii*, larva), pl.8, fig. 11-12 (gonozooid),
*Doliolum rarum* BORGERT 1894, p.14, 16 and 17, pl.6, fig.14-15,
*Doliolum rarum* GRAEFFE 1905, p. 111-112,
*Doliolum rarum* NEUMANN 1906, p. 208-210, fig.18 (gonozooid - testis), pl.14, fig.4 (oozooid),
*Doliolum rarum* SIGL 1912, p.489-490 (oozooid, gonozooid), 1913, p.277-278,
*Doliolum rarum* NEUMANN 1913 a, p. 8 (gonozooid),
*Doliolum (Doliolina) rarum* NEUMANN 1913b, p.9, 12 and 13, fig. 10 (oozooid),
*Dolioloides rarum* GARSTANG 1933, p. 201, fig. 1, p.210, fig.3 (gonozooid),
*Doliolum rarum* NEUMANN 1935, p.328, fig. 255 (oozooid),
*Doliolum (Doliolina) rarum* HARANT & VERNIÈRES 1938, p.47,
*Doliolina rarum* KRÜGER 1939, p.136, map 82,
*Doliolum rarum* BRIEN 1948, p.790, fig. 255 (oozooid),
*Dolioloides rarum* TRÉGOUBOFF & ROSE 1957, p. 566-567, pl. 203, fig.1 (oozooid),
*Dolioloides rarum* GODEAUX 1998 a, p. 280-282, fig. 17, 6d (larva), 17,7 b (oozooid) 17,10 a (gonozooid),
*Dolioloides rarum* ESNAL & DAPONTE 1999, p. 1416, fig. 3.6, map. 2.

LARVA still unknown. Nevertheless an old developed larva showing an oozooid body, named *D.ehrenbergi* (= *Doliolum denticulatum*) by ULJANIN, could be really the larva of *Dolioloides rarum* according to the stretched digestive tube, with a long oesophagus with concavity upwards, anus behind M VIII, endostyle extending from M II to M V, and with the presence of a caudal ampulla (Fig.4g).

OOZOOID fully developed; was observed by NEUMANN (1913b) and corresponds to fig.3, pl.5 of ULJANIN. Thin tunic, body very fragile, 12 flaps at both siphons, brain between M IV and M V, very narrow but progressively widening muscle hoops, endostyle extending from M II close M V, digestive tube stretched in the sagittal plane, long oesophagus with concavity upwards, anus in front of M VIII, dorsal spur. Length → 5 mm.

NURSE unknown. According to GARSTANG (1933, p. 210), after GROBBEN (1882, p. 265), its viscera do not completely disappear as in the other species.

TROPHOZOOID and PHOROZOOID unknown. Most probably, phorozooid similar to gonozooid.

GONOZOOID very fragile body, thin tunic, 10 flaps at the buccal siphon, brain between M III and M IV, slender muscles, endostyle extending from M II close to M V, branchial septum behind M V, digestive tube stretched in the sagittal plane, long oesophagus with concavity upwards, anus below or behind M VII, horizontal tubular testis, swollen as a club just behind M II, ovary under M VII. Length → 3 mm.

DISTRIBUTION: species recorded, always in a small number of specimens, from Messina (GEGENBAUR 1856, KEFERSTEIN & EHLERS 1861, GROBBEN 1882), from the Bay of Naples (ULJANIN 1884, LO BIANCO 1904), from Adria (GRAEFFE 1905, SIGL 1912), from Atlantic and Indian Oceans (NEUMANN 1906, 1913a, KRÜGER 1939, ESNAL & DAPONTE 1999).
Recent record completely missing.

- Genus *Doliolina* GARSTANG 1933.

Current characters: small individuals, U or S - shaped digestive tube,
Differential characters: shape of testis and position of ovary.

- α) Subgenus *Doliolinetta* GODEAUX 1998. Four species

***Doliolum indicum*** NEUMANN 1906,
***Doliolinetta indica*** (NEUMANN 1906) see GODEAUX 1998c.

*Doliolum (Doliolina) indicum* NEUMANN 1906, p. 220-221, p.227, pl.23, fig.7 (branchial septum), pl. 24 , fig. 5, pl. 28, fig. 5 (gonozooid),
*Doliolum (Doliolina) indicum* NEUMANN 1913b, p.13,
*Doliolum (Doliolina) indicum* SEWELL 1953, p.46-47, text-fig.13 (young gonozooid, *Dolioletta*?),
*Doliolina indicum* GODEAUX 1979, p. 162 (oozooid, nurse, phorozooid, gonozooid),
*Doliolina indica* GODEAUX 1982 (1984), p. 185-186 (nurse, phorozooid, gonozooid),
*Doliolina indicum* GODEAUX 1986, p. 195 (oozooid, phorozooid, gonozooid),
*Doliolina indicum* GODEAUX 1998a, p. 282, fig. 17.10d (gonozooid),
*Doliolinetta indica* GODEAUX 1998c, fig. 2E.

LARVA, OOZOOID and TROPHOZOOID still unknown.

NURSE: specimens collected in the Red Sea, deprived of viscera and characterized by very slender muscle hoops, separated by 10 times wider interspaces, were attributed to the species *Doliolinetta indica* as phorozooids and gonozooids were also present (GODEAUX 1982).

PHOROZOOID and GONOZOOID similar. Small and very fragile animals, thin tunic liming foreign bodies, thin ectoderm, slender muscles, brain behind M III, endostyle extending from behind M II to M V, U-shaped digestive tube surrounded by clusters of black pigmented cells (especially in the gonozooid), slighly arched branchial septum, oblique between M V and M VI, 5 gill slits. In phorozooid, a thin and long postero-ventral stalk; in gonozooid, a horizontal testis swollen at the level of M IV, ovary in front of M VII.
Length > 1 mm.

DISTRIBUTION: tropical Indian Ocean, Gulf of Aden, Red Sea, Gulf of 'Aqaba, Arabian Sea (NEUMANN 1906, SEWELL 1953, GODEAUX 1979, 1982, 1986, 1987, 1989a,b), but unknown from the Arabian Gulf (GODEAUX 1987 and unpublished ).

***Doliolum intermedium*** NEUMANN 1906
***Doliolinetta intermedia*** (NEUMANN 1906) see GODEAUX 1998a,c.

*Doliolum* sp. BORGERT 1894, p.17, fig. 16,
*Doliolum* sp. BORGERT 1901, p. 2, fig. 2 (gonozooid),
*Doliolum* sp. FOWLER 1905, p. 90-91 (phorozooid, gonozooid),
*Doliolum (Doliolina) intermedium* NEUMANN 1906, p. 211-212, p. 227,
*Doliolum* sp. FARRAN 1906, p.7, fig.1 and distribution,
*Doliolum (Doliolina) intermedium* IHLE 1927, p. 21,
*Doliolina intermedium* GARSTANG 1933, fig. 4,
*Doliolum (Doliolina ) intermedium* HARANT & VERNIÈRES 1938, p. 47,
*Doliolina intermedium* KRÜGER 1939, p.136-138, maps 85, 94,
*Doliolum (Doliolina) intermedium* FRASER 1947, p. 2 (gonozooid), p. 4 (distribution),
*Doliolum intermedium* GODEAUX 1973, p. 63 (nurse, phorozooid, gonozooid),
*Doliolina intermedium* GODEAUX 1998a, p. 282, fig. 17.10 f (gonozooid),
*Doliolinetta intermedia* GODEAUX 1998c, fig. 10 (nurse), fig. 2 f (gonozooid),
*Doliolina intermedia* ESNAL & DAPONTE 1999, p. 1415, fig. 3.3 (gonozooid), map 2 (distribution),
*Doliolinetta intermedia* GODEAUX & HARBISON (in press).

LARVA and OOZOOID unknown, but possibly similar to those of *Doliolina muelleri.*

NURSE: barrel-shaped, stenomyonic, aclinous, very slender muscles, separated by 10 times wider interspaces (GARSTANG 1933, GODEAUX 1996, GODEAUX & HARBISON in press).
Length: → 25 mm.

TROPHOZOOID: large size, numerous gill slits (GODEAUX 1998b, GODEAUX & HARBISON in press). Height: 7 mm.

PHOROZOOID and GONOZOOID: similar, thin tunic and ectoderm, slender muscles, brain behind M III, endostyle extending from before M II to before M V, slightly bent branchial septum, from close to M IV dorsally to M VII in the rear and before M V ventrally, numerous gill slits (up to 45), U-shaped digestive tube, horizontal testis approaching M II, anteriorly swollen, ovary in front of M VII. Length → 6mm.

DISTRIBUTION: species from cold waters, known from the Atlantic Ocean, from 50° S (KRÜGER 1939, > 400 m depth, GODEAUX 1973) to 60° N (IHLE 1927), Eastern Mediterranean (GODEAUX 1988b), with a single record from the Red Sea (NEUMANN 1906).

***Doliolum resistibile*** NEUMANN 1913
***Doliolinetta resistibilis*** (NEUMANN 1913) see GODEAUX 1998c, fig. 2g .

*Doliolum resistibile* NEUMANN 1913a, p. 18-20, pl.1, fig. 5 (gonozooid),
*Doliolum (Doliolina) resistibile* NEUMANN 1913b, p. 7, fig. 8,
*Doliolina resistibile* GARSTANG 1933, fig. 4, p. 211,
*Doliolina resistibile* KRÜGER 1939, p. 136, maps 83, 84 & 94.
*Doliolina resistibile* (not *intermedium*) TOKIOKA & BERNER 1958a, fig. 3 (gonozooid),
*Doliolina resistibile* GODEAUX 1998a, p. 281, fig. 17.10 (gonozooid),
*Doliolinetta resistibilis* GODEAUX 1998c, p. 1764, fig. 2 g (gonozooid).

REM.: According to GARSTANG (1933), *Doliolinetta intermedia* and *D. resistibilis* are a single species, *D. resistibilis* being just a subspecies only recorded from the Antarctic waters. NEUMANN (1913b) considers them as distinct species as both species display anatomical differences in phorozooid and gonozooid (possibly vicarious species?).

LARVA and OOZOOID unknown.

NURSE: barrel-shaped, stenomyonic, aclinous, similar to that of *D. intermedia*, thin and sticky tunic, brain in front of M V, statocyst missing, slender muscle hoops, wide interspaces. Length → 15 mm.

PHOROZOOID and GONOZOOID similar, thin muscle hoops, brain behind M III, short endostyle beginning at M II $^{1/2}$ and ending in the 4th intermuscular space, branchial septum from behind M IV, bent to M V$^{1/2}$ to behind M IV, up to 40 gill slits, U-shaped digestive tube, horizontal tubular testis extending to M II, ovary in front of M VII. Length → 9 mm.

DISTRIBUTION: species from cold waters: 3 phorozooids and 7 gonozooids in 6 stations of theAntarctic Ocean, close to ice pack ( > 64° S, NEUMANN 1913a), 2 large nurses (15 mm) in the Pacific Ocean (67° S - 177° W, GARSTANG 1933, p. 213 and 249-250), 21 specimens below 500 m in the southern Atlantic Ocean (KRÜGER).

***Doliolina separata*** TOKIOKA & BERNER 1958.
***Doliolinetta separata*** (TOKOKIA & BERNER 1958) see GODEAUX 1998c, p. 1761,.fig. 2 h (gonozooid).

*Doliolina separata* TOKIOKA & BERNER 1958b, p. 319-320, fig.2 (gonozooid),
*Doliolina separata* GODEAUX 1998a, p.282-283, fig. 17.11 b (gonozooid).

LARVA, OOZOOID, NURSE and TROPHOZOOID unknown.

PHOROZOOID and GONOZOOID similar: small-sized animals, brain behind M III, slender widely separated muscle hoops, M VII open ventrally (its free ends entering a protuberance (= stalk of a phorozooid?), endostyle long, extending from M II to M V, branchial septum inclined between M V ventrally to M VI dorsally, 10 gill slits, S-shaped digestive tube, tubular testis along the left side, swollen between M II and M III, ovary in front of M VII. Length: 1.7 mm.

DISTRIBUTION: equatorial Eastern Pacific Ocean (Shellback Expedition, 1952).

β) Subgenus *Doliolina* BORGERT 1894. Five species.

Type species: ***Doliolina muelleri*** KROHN1852.

*Doliolum muelleri* KROHN 1852, pl.2, fig.44,
*Doliolum nordmanni* KROHN 1852, p. 59, pl.2, fig. 5-6-7 (metamorphosing larvae *of Doliolum troschellii*),
*Doliolum* sp. GEGENBAUR 1856, p. 303, l.15, fig.8,
*Doliolum Muellerii* KEFERSTEIN & EHLERS 1861 p. 66-68, pl. 10, fig 3 & 5 (larva, oozooid), non *Doliolum Muellerii* KEFERSTEIN & ELHERS 1861, pl. 9, fig.5, 6 (gonozooid of *Dolioloides rarum*),
*Doliolum Muelleri* GROBBEN 1882, p .255-265, pl.19, fig. 9-10 (trophozooid and larva), pl. 20, fig. 14-8 (gonozooid, phorozooid, nurse), pl.21, fig. 21 (young gonozooid),
*Doliolum Muelleri* ULJANIN 1884, pl. 2, fig. 1 - 8, pl.2, fig. 1-10, pl.3, fig. 1-7, pl.4, fig. 4-1, pl. 10, fig. 1-6, 9 (development of egg, larva, oozooid and trophozooid),
*Doliolum muelleri* RITTER 1905, p. 95-97, fig. 29 (oozooid),
*Doliolum Muelleri* NEUMANN 1906, p. 212-213,
*Doliolina muelleri* SIGL 1913, p. 272-275,
*Doliolum muelleri* NEUMANN 1913a, p. 20,
*Doliolum (Doliolina) muelleri* NEUMANN 1913b, fig.1 (nurse), fig. 3 (phorozooid), fig. 4 (gonozooid), p. 4, fig .6 (gonozooid),
*Doliolina muelleri* GARSTANG 1933, fig. p. 211,
*Doliolum muelleri* NEUMANN 1935, p. 326, 328, text-fig. 252, 254 (gonozooid, phorozooid), p. 363, 364 & 368, text-fig. 280, 281 & 285 (larva, oozooid),
*Doliolum (Doliolina) muelleri* HARANT & VERNIÈRES, 1938, p. 47,
*Doliolina muelleri* KRÜGER 1939, p. 133, map 82,
*Doliolina muelleri* FRASER 1947, p. 2, text-fig. (gonozooid), p. 4 (distribution),
*Doliolina muelleri* TRÉGOUBOFF & ROSE 1957, p. 567, pl. 203, fig. 7 (phorozooid), pl. 304, fig. 2-3 (larvae),
*Doliolum muelleri* GODEAUX 1957-1958, fig. 60, 62 a-h, 63, 64, 64 bis, 74, 77, 78, 82, 83,
*Doliolina muelleri* BARNES 1961, p. 103, pl. 29,
*Doliolina muelleri* FRASER 1961, p. 18,
*Doliolum muelleri* BRACONNOT 1970, p. 639-641, fig. a, b (larva), p. 650- 661, pl. 3 g (nurse), pl. 4 c, d (oozooid, nurse), pl. 6 a, b (trophozooid),
*Doliolum muelleri* BRACONNOT 1971, p. 10-12 , fig. 280-281, fig. 6 (larva), 7a (oozooid), fig. 8a (nurse), fig. 9a (trophozooid), 10b (gonozooid),
*Doliolina mulleri* ESNAL *et al.* 1982a, p. 52-53 (map), fig. 3 d (phorozooid), fig. 4d (nurse),
*Doliolina mulleri* ESNAL *et al.* 1982b, tabl. 1, fig. 2 (distribution),
*Doliolina muelleri* FRASER 1982, p. 20-23,
*Doliolina mülleri* ESNAL *et al.* 1990 (1993), p. 41-48, p. 43 tabl. (distribution),
*Doliolina muelleri* GODEAUX 1998a, p. 279-282, fig 17.6 (larva), 17.7a (oozooid), 17.8 (nurse), 17.9 (trophozooid), 17.10b (gonozooid),
*Doliolina muelleri* GODEAUX 1998c, p. 1758, fig. 1 a-b (oozooid, nurse), p. 1761, fig. 2a (gonozooid),
*Doliolina muelleri* ESNAL & DAPONTE 1999, p.1409, p. 1412, fig. 2 (map), p. 1415, p. 1417, fig. 3.4 (larva) and b (nurse).

LARVA: fusiform follicular envelope, differentiated tail, actively swimming, hyaline caudal vesicle. Length: ≥ 1 mm.

OOZOOID: small-sized animal, thin tunic and ectoderm, slender muscle hoops in young animal, progressively widening with ageing, brain between M IV and M V, statocyst as an ectodermic cupule below the tunic, in front of M V, long endostyle extending from midway between M II and M III to M V, branchial septum as a vertical arch between and M VI, 4 gill slits, U-shaped digestive tube. Length → 2.5 mm.

NURSE: widening muscle hoops at the time of disappearance of the viscera, narrow interspaces, M IV widener than M III, statocyst usually missing. Length < 10 mm.

TROPHOZOOID: small number of gill slits (up to 10), endostyle ending in front of the intestinal loop, anal opening below the oesophageal opening. Height → 1 mm.

PHOROZOOID and GONOZOOID: small-sized similar animals, slender muscle hoops, brain behind M III, endostyle short, beginning in front of M III and ending in front of M V, slighly arched branchial septum at the level of M V, 12 - 14 gill slits, U-shaped digestive tube below M V, ventral prominent stalk in the phorozooid, pear-shaped testis protruding ventrally into the fifth interspace, below the intestine loop, ovary in front of M VI.
Length → 1.5 mm.

DISTRIBUTION: cosmopolitan species in warm and temperate waters.

***Doliolina krohni*** HERDMAN 1888.
***Doliolina krohni*** BORGERT 1894

*Doliolina krohni* HERDMAN 1888, p. 49, pl. 3, fig. 1 (schema),
*Doliolum krohni* TRAUSTEDT 1889, p. 4, pl. 1, fig. 11,
*Doliolina krohni* BORGERT 1894, p. 15, pl. 6, fig. 11 (gonozooid) and 13 (blastozooid),
*Doliolina krohni* BORGERT 1896, p. 715,
*Doliolina krohni* BORGERT 1901, p. 1, pl. 1,
*Doliolina Krohni* FOWLER 1905, p. 90, 97,
*Doliolum Krohni* NEUMANN 1906, p. 214-216, pl. 14, fig. 6 - 7 (gonozooid),
*Doliolina krohni* SIGL 1913, p. 278-279,
*Doliolum (Doliolina) krohni* NEUMANN 1913b, p. 15,
*Doliolum (Doliolina) krohni* IHLE 1927, p. 21,
*Doliolina krohni* GARSTANG 1933, fig. 4, p. 211,
*Doliolum (Doliolina) krohni* HARANT & VERNIÈRES 1938, p. 49,
*Doliolina krohni* KRÜGER 1939, p. 133, map 81,
*Doliolum (Doliolina) mülleri* var. *krohni* FRASER 1947, p. 2, text-fig. (gonozooid), p. 4 (distribution),

*Doliolum muelleri* FRASER 1961 (distribution),
*Doliolina muelleri* var *krohni* ESNAL *et al.* 1990 (1993), p. 41-48, p. 43 tabl. (distribution),
*Doliolina krohni* GODEAUX 1998a, p. 282, fig. 17.10 c (gonozooid),
*Doliolina krohni* GODEAUX 1998c, p. 1761, fig. 2 c (gonozooid),
*Doliolina muelleri* var. *krohni* ESNAL & DAPONTE 1999, p. 1417, fig. 3.4 c (gonozooid).

LARVA, OOZOOID, NURSE probably similar to those of *Doliolina muelleri.*

TROPHOZOOID: unknown.

PHOROZOOID and GONOZOOID similar. Tunic sticking foreign bodies, slender muscle hoops,brain behind M III, endostyle extending from M II to M V, branchial septum, strongly arched or not, between M V above, M VI in the rear and M V below, up to 45 gill slits, U-shaped digestive tube, pear-shaped testis ventrally protruding below the intestinal loop, ovary behind testis. Length → 2.5 mm.

DISTRIBUTION: cosmopolitan species, mainly in warm waters, but supporting various temperatures.

***Doliolina sigmoides*** GARSTANG 1933.

Non *Doliolum krohni* NEUMANN 1906, p. 214-216, pl. 14, fig. 6, 7 (gonozooid),
*Doliolina sigmoides* GARSTANG 1933, p. 211, text-fig. 4, p. 214-215,
*Doliolina sigmoides* GODEAUX 1998a, fig. 17.11 (gonozooid),
*Doliolina sigmoides* GODEAUX 1998c, p. 1760 and 1762,
*Doliolina sigmoides* ESNAL & DAPONTE,1999, p. 1416, map 2, fig. 3.5.

LARVA, OOZOOID, NURSE and TROPHOZOOID unknown.

PHOROZOOID and GONOZOOID similar. Brain behind M III, long endostyle extending from M II to M V, S-shaped branchial septum, bulged forwards in front of the U-shaped digestive tube, then bulged backwards between M V and M VI, up to 45 gill slits, three pairs of lateral tentacle-like processes, short and swollen testis below M V, ovary in front of M VI.
Length → 7 mm.

DISTRIBUTION: very rare species, only known from 4 stations in the Guinea Current in the tropical Atlantic Ocean and from the Indian Ocean (NEUMANN 1906). No recent records.

***Doliolina obscura*** TOKIOKA & BERNER 1958

*Doliolina obscura* TOKIOKA & BERNER 1958b, p. 317- 20, fig.1 (gonozooid),
*Doliolina obscura* GODEAUX 1988a, p. 282, fig. 17.11a (gonozooid),
*Doliolina obscura* GODEAUX 1998c, p. 1762, fig. 2 c.

LARVA, OOZOOID, NURSE, TROPHOZOOID unknown

PHOROZOOID and GONOZOOID similar: swollen barrel-shaped body, thin and less sticky tunic, slender muscles separated by wide interspaces, M VII open ventrally, its free ends entering the long ventral stalk of the phorozooid, endostyle long, extending from behind M II to MV, brain in midway between M II and M IV, S-shaped branchial septum, bound to M V, about 40 gill slits, digestive tube covered with a cloud of pigmented cells (red-orange in living specimens?), less dense in the phorozooid, sausage-shaped testis swollen at the level of M IV, on the left side of the digestive tube, ovary in front of M VI. Length < 5 mm.

DISTRIBUTION: tropical Eastern Pacific Ocean (Shellback Expedition 1952).

***Doliolina undulata*** TOKIOKA & BERNER 1958

*Doliolina undulata* TOKIOKA & BERNER 1958a, p. 137-138, fig. 22, 1958b, p. 521-522, fig. 4,
*Doliolina undulata* GODEAUX 1998a, p. 282-283, fig. 17.11 (gonozooid),
*Doliolina undulata* GODEAUX 1998c, p. 1762, fig. 2 d.

LARVA, OOZOOID, NURSE, TROPHOZOOID unknown.

PHOROZOOID unknown, but probably similar to gonozooid.

GONOZOOID: thin, easily removed tunic, slender muscle hoops, M VII open ventrally, brain imidway of M III and M IV, long endostyle extending from M II to M V, arched branchial septum (M $IV^{1/2}$ - M VI - MV), sausage-shaped testis on the left side of the digestive tube between M V and M VI, ovary in front of M VI. Length → 4.6 mm.

DISTRIBUTION: tropical Eastern Pacific Ocean (Shellback Expedition 1952).

- Genus *Doliolum* QUOY & GAIMARD 1835. Two species
(Subgenus *Dolioletta* BORGERT 1894)

Type species: *Doliolum denticulum* QUOY & GAIMARD 1835
*Doliolum denticulatum* HUXLEY 1851b.

The genus *Doliolum* comprises two closely related species: *Doliolum denticulatum* (QUOY & GAIMARD 1835) and *Doliolum nationalis* BORGERT 1893.

Common characters of the blastozooids of both species: thin and less sticky tunic, extended branchial septum attached dorsally in front of M II, numerous gill slits, short endostyle, digestive tube curved to the right, anus behind M VI, tubular horizontal testis running on the left side, ovary behind M VI.

Differential characters: In *Doliolum denticulatum*, branchial septum ventrally attached at the level of M III, testis extending to and over M II; in *Doliolum nationalis*, branchial septum ventrally attached at the level of M V, testis rarely overlapping M IV.

***Doliolum denticulatum*** (QUOY & GAIMARD 1835).

*Doliolum denticulum* QUOY & GAIMARD 1835, p. 599, pl. 89, fig. 25-28,
*Doliolum denticulatum* HUXLEY 1851b, p. 600, pl. 18, fig. 5-9,
*Doliolum denticulatum* + *Doliolum Ehrenbergii* KROHN 1852, p. 57-58, pl. 2. fig. 1-3,
*Doliolum* sp. GEGENBAUR 1856, p. 297-300, pl. 16, fig. 4-5 (phorozooid),
not *Doliolum Troschellii* GEGENBAUR 1856, p. 284, Pl. 14, fig. 1-3 ,pl. 15, fig. 7, 9, 10, pl. 16, fig. 12, 15 (larva, nurse, trophozooid, phorozooid) (= *Doliolum gegenbauri*),
*Doliolum denticulatum* KEFERSTEIN & EHLERS 1861, p. 65, pl. 9, fig. 1-4 (gonozooid) and fig. 8 (phorozooid),
*Doliolum* generations 2B & 4B KEFERSTEIN & EHLERS 1861, p. 68, pl. 9, fig. 7, pl. 10, fig. 2-4 (oozooid),
Doliolum denticulatum GROBBEN 1882, p. 206-223, text-fig. p. 213 (gonozooid), p. 274 (cycle), pl. 18, fig. 1-5, pl. 19, fig. 7-8, pl. 21, fig. 19-20 (complete life cycle),
not *Doliolum denticulatum* HERDMAN 1883, p. 101-111 (= *Doliolum tritonis*, HERDMAN 1888),
*Doliolum denticulatum* FOL 1884, p. 150-153, pl. 8, fig. 2-3 (young), 4-5,
*Doliolum Ehrenbergii* ULJANIN 1884, p. 45-71 pl. 5, fig. 1 (larva?) - 2, pl. 12, fig. 8 (oozooid), not *Doliolum denticulatum* HERDMAN 1888, p. 101, pl. 18-20 (= *Doliolum tritonis*),
*Doliolum ehrenbergi* HERDMAN 1886, p. 46, pl. 3, fig. 5-7,
*Doliolum denticulatum* HERDMAN 1888, p. 44-46,
not *Doliolum Challengeri* HERDMAN 1888, p. 44, 48, pl. 3, fig. 4 (= *Doliolum tritonis*),
*Doliolum Challengeri* TRAUSTEDT 1893, p. 4 & 10, pl. 1, fig. 12-14 (gonozooid),
*Doliolum denticulatum* BORGERT 1893, p. 402-408,
*Doliolum denticulatum* BORGERT 1894, p. 7, text-fig.1 (trophozooid), p. 22-25,
*Doliolum denticulatum* BORGERT 1896, p. 716,
*Doliolum ehrenbergii* RITTER 1905, p. 91-94, text-fig. 27-28 (oozooid, nurse),
*Doliolum denticulatum* NEUMANN 1906, p. 222-224, pl. 24, fig. 1 (gonozooid),
*Doliolum denticulatum* IHLE 1910, pars 56 d, p. 15,
*Doliolum denticulatum* SIGL 1912, p. 496, fig. 14,
*Doliolum denticulatum* SIGL 1913, p. 275-277,
*Doliolum ehrenbergii* SIGL 1913, p. 279,
*Doliolum denticulatum* NEUMANN 1913a, p. 22,
*Doliolum (Dolioletta) denticulatum* NEUMANN 1913b, p. 18-19, fig. 9, 11-13 (larva, nurse, trophozooid),
*Doliolum denticulatum* GARSTANG 1933, p. 224-226, p. 229, text fig. 8 (gonozooid),
*Doliolum ehrenbergii* GARSTANG 1933, p. 224, text-fig. 8 (gonozooid),
*Doliolum denticulatum* NEUMANN 1935, p. 364-365, text-fig. 281-282 (larva), p. 367-369, text-fig. 283-286 (oozooid), p. 283, text-fig. 300 (phoro-gonozooid), p. 384-387, text-fig. 302-303 (trophozooid), p. 327, text-fig. 253 (gonozooid),
*Doliolum denticulatum* RUSSEL & COLMAN 1935, p. 207-208,
*Doliolum (Dolioletta) denticulatum* (= *D. ehrenbergii*) HARANT & VERNIÈRES 1938, p. 50, fig. 62,
*Dolioletta denticulatum* KRÜGER 1939, p. 132-133, map 78,
*Doliolum denticulum* FRASER 1947, p. 2 (gonozooid), p. 4 (distribution),
*Doliolum denticulatum* THOMPSON 1948, p. 97, text-fig. 12 (gonozooid), pl. 30, fig. 2-3,
*Doliolum ehrenbergii* THOMPSON 1948, p. 97, text-fig. 12 (gonozooid),
*Doliolum denticulatum* BRIEN 1948, p. 805-807, text-fig. 268-271 (gonozooid), p. 208, text-fig. 273, p. 810, text-fig. 275 (trophozooid), p. 814, text-fig. 280 (larva),
*Doliolum denticulatum* BERRILL 1950, p. 278, text-fig. H, p. 280, text-fig. a, b, c, d, p. 284, text-fig. B-D,
*Doliolum (Dolioletta) denticulatum* SEWELL 1953, p. 50-53, text-fig. 15 (gonozooid),
*Doliolum denticulatum* TRÉGOUBOFF & ROSE 1957, p. 568, pl. 203 fig. 8 (gonozooid), fig. 4, (trophozooid), fig. 5 (nurse), pl. 204, fig.1 (gonozooid), fig. 4 (oozooid),
*Doliolum denticulatum* GODEAUX 1957-1958, p. 249, fig. 103 (phorozooid),
*Doliolum denticulatum* VAN ZYL 1959, p. 16-17 (distribution), p. 31 (map),
*Doliolum denticulatum* BRACONNOT 1964, p. 4361-4363 (larva),
*Doliolum denticulatum* BRACONNOT 1970, p. 629-668 (larva, oozooid, nurse, trophozooid),
*Doliolum denticulatum* BRACONNOT 1971, p. 13-21, fig. c-g (phorozooid, gonozooid),
*Doliolum denticulatum* ESNAL *et al.* 1982a, p. 53, fig. 2 (map), fig. 3 e-g (phorozooid), fig.3 f-h (gonozooid), fig. 4 a (nurse, not *Dolioletta gegenbauri*), fig. 4 f-g (gonozooid),
*Doliolum denticulatum* ESNAL *et al.* 1982b, p. 64-66, fig. 1-2 (distribution),
*Doliolum denticulatum* ESNAL *et al.* 1990 (1993), p. 43 tabl., p. 48 (distribution),
*Doliolum denticulatum* GODEAUX 1998a, p. 280-283, fig.17.6 (larva), 17.7 (oozooid), 17.8 b (nurse), 17.11 d (gonozooid),
*Doliolum denticulatum* GODEAUX 1998b, fig 1-2 (trophozooid),
*Doliolum denticulatum* ESNAL & DAPONTE 1999, p. 1416, fig. 3.7, map 2.

LARVA: Follicular fusiform envelope (→ 3mm), differentiated tail, precaudal vesicle missing. Length of the body → 600 µm.

OOZOOID: firm tunic adhering to ectoderm, muscles and interspaces equal, brain in front of M IV, closed statocyst in front of M IV, endostyle extending from M II to M V, digestive tube straight sagittally, oesophagus concavity downwards, anus at the level of M VIII. The oozooid is set free at the length of 800 mm. Length > 800 µm.

NURSE: holomyonic with M II to M VIII sold in a continuous sheet (cuirass), interspaces disappeared, statocyst below M III - M IV junction. Stolon protruding ventrally.
Length → 10 mm.

TROPHOZOOID: 12 to 13 gill slits, endostyle ending in front

of the stomachal pouch, a single tunical process behind the ascending intestine, anal aperture above the opening of the oesophagus. Height: 7 mm.

PHOROZOOID and GONOZOOID: similar, thin sticky easily removed tunic, brain in front of M IV, short endostyle extending from behind M II to before M IV, digestive tube turning to the right, anus at the level of M VI, branchial septum elongated from M I dorsally to M $V^{1/2}$ in the rear and to M III ventrally, more than 50 gill slits, horizontal testis extending to M II and over, phorozooid with a short and broad stalk bearing numerous buds. Length: → 4 mm.

DISTRIBUTION: open sea species, common in the tropical and temperate waters of the three Oceans, rare in shallow waters (e.g. present in the Red Sea and the Gulf of 'Aqaba, rare in the Gulf of Suez).

REM.: *Doliolum ehrenbergii* is a dwarf form of *D. denticulatum* with less gill slits and testis not overlapping M IV (NEUMANN, 1906, p. 224). This subspecies does not exist according to BRACONNOT (1971, p. 20 - 21, unimodal curve).

***Doliolum nationalis*** BORGERT 1893

*Doliolum Challengeri* HERDMAN var. TRAUSTEDT 1893, p. 3-4, pl. 1, fig. 14,
*Doliolum nationalis* BORGERT 1893, p. 406-408, text-fig. p. 407 (gonozooid),
*Doliolum (Dolioletta) nationalis* BORGERT 1894,
*Doliolum nationalis* BORGERT 1896, p. 716,
*Doliolum nationalis* FOWLER 1898, p. 583,
*Doliolum nationalis* BORGERT 1901, p. 4, text-fig. 4,
*Doliolum Nationalis* FOWLER 1905, p. 90 (gonozooid?),
*Doliolum nationalis* NEUMANN 1906, p. 222,
*Doliolum nationalis* IHLE 1910, p. 15,
*Doliolum nationalis* SIGL 1913, p. 279,
*Doliolum nationalis* NEUMANN 1913a, p. 21,
*Doliolum nationalis* NEUMANN 1913b, p. 18,
*Doliolum (Dolioletta) nationalis* IHLE 1927, p. 21,
*Doliolum nationalis* GARSTANG 1933, p. 221-224, text-fig. 8,
*Doliolum (Dolioletta) nationale* HARANT & VERNIÈRES 1938, p. 49, fig. 63,
*Dolioletta nationalis* KRÜGER 1939, p. 132 - 133, map 79,
*Doliolum nationalis* FRASER 1947, p. 2, text-fig. (gonozooid ??), p. 4 (distribution),
*Doliolum nationalis* (not *Dolioletta gegenbauri*) THOMPSON 1948, p. 97, fig. 12 (gonozooid),
*Doliolum nationalis* BERRILL 1950, p. 282-284, pl. 100, fig. h, pl. 102, fig. A,a,
*Doliolum nationalis* TRÉGOUBOFF & ROSE 1957, p. 568, pl. 205, fig. 9 (gonozooid),
*Doliolum nationalis* VAN ZYL 1959, p. 18-20 (distribution), p. 31 (map),
*Doliolum nationalis* BARNES 1961, p. 103, pl. 29 (distribution),
*Doliolum nationalis* FRASER 1961, p. 18 (distribution),
*Doliolum nationalis* GODEAUX 1961, p. 8; text-fig. 3 (phorozooid),
*Doliolum nationalis* BRACONNOT & CASANOVA 1967, p. 393-402 (gonophorozooid),
*Doliolum nationalis* TAVARES 1967, pl. 1 a-b (oozooid & gonozooid),
*Doliolum nationalis* BRACONNOT 1971, pl. 4, fig. a, b (gonophorozooid),
*Doliolum nationalis* BRACONNOT 1974, p. 1759-1760 (larva),
*Doliolum nationalis* BRACONNOT 1977, p. 836-837 (oozooid),
*Doliolum nationalis* ESNAL *et al.* 1982a, p. 53, fig. 2, fig. 3 i-j (phorozooid), fig. 3 k-l-m (gonozooid), fig.4 c (gonozooid), fig. 4 h (phorozooid),
*Doliolum nationalis* ESNAL *et al.* 1982b, p. 66, tabl. 1, fig. 2 (distribution),
*Doliolum nationalis* ESNAL *et al* 1990 (1993), p. 41-48 (distribution),
*Doliolum nationalis* LINDLEY *et al.*, 1990, p. 679-682 (distribution),
*Doliolum nationalis* GODEAUX 1998a, p. 282- 83, fig. 17.11e (gonozooid),
*Doliolum nationalis* EDWARDS *et al.* 1999, p. 737-739 (distribution),
*Doliolum nationalis* ESNAL & DAPONTE 1999, p. 1416, fig. 3.8, map 2.

LARVA and OOZOOID: similar to those of *Doliolum denticulatum* ( BRACONNOT 1976).

NURSE and TROPHOZOOID: unknown, but probably similar to those of *D. denticulatum.*

PHOROZOOID and GONOZOOID: similar; thin, less sticky tunic, brain in front of M IV, endostyle extending from behind M II to before MV, arched branchial septum extending from M II dorsally to M $V^{1/2}$ in the rear and to midway between M IV to M V ventrally, 25 gill slits, testis short and club-shaped, swollen close to M IV, ventral stalk short and thick in the phorozooid. Length of the phorozooid → 3 mm , length of the gonozooid → 4 mm.
The real gonozooid is rarely observed (BORGERT 1893, BRACONNOT 1971, GODEAUX unpublished), while the buds carried on by the phorozooid give secondary asexual phorozooids.

COMPOSITE ANIMALS: (phorozooid + gonozooid = gonophorozooid) are known from the western Mediterranean, mainly in the Gulf of Lions (BRACONNOT & CASANOVA 1967, BRACONNOT 1971).

DISTRIBUTION: neritic species, very common, eurytherm, cosmopolitan, swarms often observed (Villefranche sur Mer, Gulf of Suez), may occasionally reach the German Bight (LINDLEY *et al.* 1990, EDWARDS *et al.* 1999).

- Genus *Dolioletta* GARSTANG 1933. Four species.
(subgenus *Dolioletta* BORGERT 1894)

Common characters to the blastozooids of the different species of the genus: brain behind M III, branchial septum

dorsally close to M II or M III, strongly curved backwards over M V, ventrally between M III and M IV according to the species, numerous gill slits, coiled digestive tube, oesophagus concavity downwards, voluminous stomachal pouch, anal aperture at the level of M VI, ovary in front of M VI.

Differential characters: variable extension of the endostyle and branchial septum, position and shape of the testis.

Type species ***Dolioletta gegenbauri*** ULJANIN 1884

*Doliolum Troschelii* (not KROHN 1852) GEGENBAUR 1856, pl. 284, pl. 14, fig. 1-3, pl. 15, fig. 7, 9, 11 (nurse and trophozooid),
*Doliolum* nov.sp. FOL 1872, p. 452, fig. 4 (*D. gegenbauri* according to NEUMANN 1913a),
*Doliolum denticulatum* (not QUOY & GAIMARD) GROBBEN 1882, vol. 4, p. 238,
*Doliolum Gegenbauri* ULJANIN 1884, p. 134, pl. 5, fig. 10 (larva?), pl. 7, fig. 5 (gonozooid),
*Doliolum Ehrenbergii* (not KROHN 1852) ULJANIN 1884, p. 88, p. 133, pl. 5, fig. 1, 3 (larva?), pl. 10, fig. 1 (gonozooid), pl. 11, fig. 5 (trophozooid),
*Doliolum Ehrenbergii* RITTER 1905, p. 91-94, text-fig. 27 (oozooid), text-fig. 28 ( nurse),
*Doliolum Gegenbauri* NEUMANN 1906, p. 216-219,
*Doliolum gegenbauri* SIGL 1912, p. 49-54, text-fig. 13,
*Doliolum gegenbauri* SIGL 1913, p. 277,
*Doliolum gegenbauri* NEUMANN 1913a, p. 21, p. 23, text-fig. 3 - 4 (young oozooid, not *Doliolum denticulatum*),
*Doliolum (Dolioletta) gegenbauri* NEUMANN 1913b, p. 15-16,
*Dolioletta gegenbauri* GARSTANG 1933, p. 216-217, p. 229 text-fig. 5,
*Doliolum gegenbauri* NEUMANN 1935, p. 369, text-fig. 369, text-fig. 286 ( young oozooid, not *Doliolum denticulatum*),
*Doliolum gegenbauri* RUSSEL & COLMAN 1935, p. 208,
*Doliolum (Dolioletta) gegenbauri* HARANT & VERNIÈRES 1938, p. 49,
*Dolioletta gegenbauri* KRÜGER 1939, p. 133, map 80,
*Doliolum (Dolioletta) gegenbauri* FRASER 1947, p. 2 , text-fig (gonozooid), p. 4 (distribution),
*Doliolum gegenbauri - tritonis* THOMPSON 1948, p. 91, pl. 30, fig. 1 (= gonozooid of *Doliolum* nationalis ??), pl. 31, fig. 2 (nurse),
*Doliolum (Dolioletta) gegenbauri* BERRILL 1950, p. 285-286, fig. 103a (gonozooid),
*Dolioletta gegenbauri* SEWELL 1953, p. 47-50, text-fig. 14 (gonozooid of *D. tritonis*?),
*Dolioletta gegenbauri* TRÉGOUBOFF & ROSE 1957; p. 567-568, pl. 203, fig. 2 (dorsal spur of a nurse), fig. 3 (trophozooid and phorozooid buds on the spur), fig. 5 (nurse), fig. 6 (gonozooid buds on the stalk of a phorozooid), fig. 8 (young gonozooid),
*Dolioletta gegenbauri* (not *Doliolum denticulatum*) GODEAUX 1957-1958, text-fig. 65, 66, 68, 70, 71, 72, 73, 80, 84 & 85 (larva, oozooid),
*Dolioletta gegenbauri* BARNES 1961, p. 103, pl. 29 (distribution),
*Dolioletta gegenbauri* (not *Doliolum denticulatum*) GODEAUX 1961, p. 7 text-fig. 1 - 2,
*Dolioletta gegenbauri* TAVARES 1967, pl. l, fig. c-d (phorozooid and gonozooid), fig. e-f (oozooid and nurse),
*Dolioletta gegenbauri* GODEAUX 1967, p. 535-536,
*Doliolum (Dolioletta) gegenbauri* BRACONNOT 1970, p. 641-662, pl. 2, fig. g-h (larva), pl. 3, fig. e-f (oozooid), pl. 4, fig. e-f (nurse), pl. 5 fig. e-f (trophozooid), fig. b (nurse),
*Dolioletta gegenbauri* BRACONNOT 1971, p. 12-13, pl. 2, fig. a-e (phorozooid), pl. 3 (gonozooid),
*Dolioletta gegenbauri* HARPER 1972, p. 49-50 (distribution),
*Dolioletta gegenbauri* ESNAL *et al.* 1982a, p. 53, fig. 2 (distribution), fig. 3a (gonozooid), fig. 3b-c (phorozooid),
*Dolioletta gegenbauri* ESNAL *et al.* 1982b, p. 64, p. 66, tabl.1, fig. 2 (distribution),
*Dolioletta gegenbauri* TEBEAU & MADIN 1994, p. 1076, text-fig. 1 (nurse with its spur bearing buds of trophozooids and phorozooids),
*Dolioletta gegenbauri* FRASER 1982, p. 20-22.
*Dolioletta gegenbauri* LINDLEY *et al.* 1990, p. 681 (map),
*Dolioletta gegenbauri* ESNAL *et al.* 1990 (1993), p. 41-48, p. 43 tabl., (distribution),
*Dolioletta gegenbauri* GODEAUX 1998a, p. 280-283, fig. 17.6 c (larva), 17.7 d (oozooid), 17.8 c (nurse),17.9 b (trophozooid), 17.12 a (gonozooid),
*Dolioletta gegenbauri* PAFFENHOFER & GIBSON, 1999, p. 1183-1189 (length and characteristics of the life cycle ),
*Dolioletta gegenbauri* EDWARDS 1999 *et al.*, p. 737-739, fig.1, tabl. 1 (distribution),
*Dolioletta gegenbauri* ESNAL & DAPONTE 1999, p. 1414-1415, fig. 1, 3.1, 3.2, map 2.

LARVA: dumpy anuran animal in spherical follicular envelope ($\Theta$ >1.5 mm), limited development of the tail, muscles and chorda cells remaining undifferentiated. Length ≥ 350 µm.

OOZOOID: short endostyle extending from M III to M IV, brain in front of M IV, digestive tube stretched, oesophagus concavity downwards, stomachal pouch below M VI, anal aperture in front of M VIII. Length ≥ 2 mm.

NURSE: solid and less flexible appearance, muscles broadening at the time of viscera disappearance, narrow interspaces (less of the half muscle width), M III wider than M IV, closed statocyst visible between M III and M IV, dorsal spur reaching a great length (up to 15 cm), with numerous more or less developed buds (BRACONNOT 1970, TEBEAU & MADIN 1994). Length ≥ 30 mm.

TROPHOZOOID: great number of gill slits (up to 30 and more), endostyle ending in front of the stomachal pouch, thick stalk muscle not forked below endostyle, stalk provided with two wings at its free end. Height: 2.5 mm.

PHOROZOOID and GONOZOOID: similar, solid tunic, individual often flattened, slender muscles separated by wide interspaces, endostyle extending from M $II^{1/2}$ to M V, V-shaped branchial septum, extending dorsally from M II, close to M VI in the rear, and ending ventrally at the level of M V, up to 70 gill slits, testis rising obliquely on the left side

of the animal, up to M II, sometimes overlapping and twisted, ovary in front of M VII, red-orange pigment on the branchial axis and in front of the endostyle (destroyed by fixatives), short ventral stalk in phorozooid, gonads development starting early in gonozooids still bound to the phorozooid stalk. Length of phorozooid → 20 mm, length of gonozooid → 20 mm.

DISTRIBUTION: cosmopolitan species common in the three oceans, in Mediterranean, reaching north of British Islands (even the northern North Sea, HARPER, LINDLEY *et al.*, EDWARDS *et al.*) thanks to the warm summer transgression. Also observed along the western border of the Gulstream (TEBEAU & MADIN), possibly associated with frontal eddies (DEIBEL).

***Doliolum tritonis*** HERDMAN 1888
***Dolioletta tritonis*** (HERDMAN 1888).

This species is easily confused with *Dolioletta gegenbauri* on not very well preserved specimens and is considered by some authors as a simple sub-species.

*Doliolum denticulatum* HERDMAN 1883, p. 101-113, pl. 18–20;
*Doliolum tritonis* HERDMAN 1888, p. 47, pl. 3, fig. 3 (schema),
*Doliolum tritonis* HERDMAN 1888, p. 50, pl. 3, fig. 9 (nurse type *Dolioletta gegenbauri = tritonis*?),
*Doliolum tritonis* TRAUSTEDT 1893, p. 4, pl. 1, fig. 10,
*Doliolum tritonis* 1894, p. 19-20, pl. 3, fig. 17-18,
*Doliolum tritonis* BORGERT 1896, p. 715 (phorozooid, gonozooid),
*Doliolum Tritonis* FOWLER 1898, p. 580,
*Doliolum tritonis* BORGERT 1901, text-fig. 3, p. 3 (gonozooid),
*Doliolum tritonis* RITTER 1905, p. 85-91, text-fig. 24-26 (gonozooid, phorozooid, trophozooid),
*Doliolum Tritonis* FOWLER 1905, p. 89 (gonozooid), p. 91(phorozooid), p. 93, pl. 8, fig. 1 (oozooid) p. 97, fig. 2-3 (trophozooid),
*Doliolum tritonis* FARRAN 1906, p. 1-7 (distribution),
*Doliolum (Dolioletta) tritonis* IHLE 1927, p. 21-22, text-fig. 10 (gonozooid),
*Doliolum gegenbauri* RUSSEL & HASTINGS 1933, p. 635,
*Dolioletta tritonis* BERRILL 1935, p. 286 fig. 103 b (gonozooid), 103 c (trophozooid), fig. 103 d (phorozooid),
*Doliolum (Dolioletta) tritonis* HARANT & VERNIÈRES 1938, p. 49,
*Dolioletta tritonis* KRÜGER 1939, p. 133, map 80,
*Doliolum (Dolioletta gegenbauri)* var. *tritonis* FRASER 1947, p. 2 text-fig. (larva, oozooid, nurse, phorozooid, gonozooid), p. 4 (distribution),
*Dolioletta gegenbauri-tritonis* THOMPSON 1948, p. 94-95, text-fig. 10, pl. 30, fig. 1 (gonozooid? schema), pl. 31, fig. 1 (gonozooid), fig. 2 (nurse),
*Dolioletta tritonis* VAN ZYL 1959, p. 20-24 (distribution), p. 31 (map),
*Dolioletta gegenbauri*, var. *tritonis* GODEAUX 1960, p. 13, fig. 4 (gonozooid buds),
*Dolioletta tritonis* BARNES 1961, p. 103 (distribution),
*Dolioletta tritonis* FRASER 1961, p. 18 (distribution),
*Dolioletta tritonis* FRASER 1982, p. 20 - 22,
*Dolioletta tritonis* GODEAUX 1998 a, p. 282-283, fig. 17.12 b (gonozooid).

LARVA, OOZOOID AND NURSE: similar to those of *Dolioletta gegenbauri* (FOWLER 1905).Length of oozooid: 13 mm, length of nurse: 17 mm.

TROPHOZOOID: broad stalk with relatively strong muscles, with flattened extremities, up to 25 gill slits. Height: 3 mm.

PHOROZOOID and GONOZOOID: similar, the sole difference from *Dolioletta gegenbauri* is the branchial septum ventrally attached between M IV and M V.
Length of phorozooid → 8 mm, length of gonozooid → 15 mm.

DISTRIBUTION: species known from the three oceans but seems to prefer warmer waters than *D. gegenbauri*, sometimes in warm summers up to Faroe and North Sea, missing in the Mediterranean, present in the Gulf of 'Aqaba.

***Dolchinia mirabilis*** KOROTNEFF 1891
***Dolioletta mirabilis*** (KOROTNEFF 1891)

*Dolchinia mirabilis* KOROTNEFF 1891, p. 187, pl. 12, fig. 1 (phorozooid),
*Dolchinia mirabilis* KOROTNEFF 1904, p. 480, pl. 19, fig. 1 (trophozooid),
*Doliolum (Dolioletta) mirabile* NEUMANN 1913 b, p. 17-18,
*Dolchinia mirabilis = Doliolum chuni* FEDELE 1923, p. 152-158,
*Dolioletta mirabile* GARSTANG 1933, p. 216, text-fig. 5, p. 230-221, text-fig. 6-7 (*Dolioletta mirabilis*: phorozooid, gonozooid),
*Doliolum (Dolioletta) mirabile* HARANT & VERNIÈRES 1938, p. 49,
*Doliolum (Dolioletta) mirabilis* FRASER 1947, p. 2 text-fig. (gonozooid),
*Doliolum (Dolioletta) mirabilis* SEWELL 1953, p. 53-55, text-fig. 16-17 (phorozooid, gonozooid),
*Dolioletta mirabilis* TRÉGOUBOFF & ROSE 1957, vol. I, p. 568 , Vol.II, pl. 205, fig. 6,
*Dolioletta mirabile* GODEAUX 1972 (phorozooid, gonozooid),
*Dolioletta mirabilis (chuni?)* GODEAUX 1998 a, p. 282-283 (gonozooid),
*Dolioletta mirabilis* ESNAL & DAPONTE 1999, p. 1415, fig. 3.1 a,b (gonozooid), map 2 (distribution).

REM.: According to FEDELE (1923), *Dolioletta chuni* and *D. mirabilis* are a single species.

LARVA, OOZOOID and NURSE: unknown, but possibly similar to those of *Dolioletta gegenbauri* The pieces of the dorsal spur observed by KOROTNEFF (1891, 1904) attest of the great length of this appendice (→ 45 cm?).

TROPHOZOOID: similar to the trophozooid of *Dolioletta gegenbauri*; numerous gill slits (up to 42 , KOROTNEFF), no wings on the stalk. Height: 8 mm.

PHOROZOOID and GONOZOOID : similar, thin tunic, slender muscles widely separated, M VI open or very narrow ventrally, brain behind M III, short endostyle extending from short before M III to midway between M IV and M V, V-shaped branchial septum starting from M II dorsally, trespassing M VI in the rear and ending close to M II ventrally, up to 70 gill slits, testis coiled on the left side of the digestive tube, between M IV and M VI, ovary in front of M VII, very long and thick stalk in phorozooid. Length → 8 mm.

DISTRIBUTION: species present in Naples, tropical Atlantic Ocean, Indian Ocean, south of the Arabian Sea, southern Pacific Ocean (north of New Zealand). No recent records.

***Dolioletta chuni*** NEUMANN 1906

*Doliolum Chuni* NEUMANN 1906, p. 221, pl. 14, fig. 3 (gonozooid),
*Doliolum (Dolioletta) chuni* NEUMANN 1913 b, p. 17,
*Dolchinia mirabilis* = *Dolioletta chuni* FEDELE 1923, p. 152-158,
*Dolioletta chuni* = *Dolioletta mirabile* GARSTANG 1933, p. 219-220, fig. 5,
*Dolioletta chuni* = *Dolioletta mirabilis* TRÉGOUBOFF & ROSE 1957, Vol. I, p. 568, Vol. II, pl. 205, fig.6.

LARVA, OOZOOID, NURSE and TROPHOZOOID: unknown but possibly similar to those of *Dolioletta gegenbauri.*

PHOROZOOID and GONOZOOID: similar, thin but firm tunic, slender muscles, brain behind M III, endostyle extending from before M III to the midway between M IV and M V, branchial septum strongly curved from behind M III to behind M VI in the rear and to the midway between M IV and MV ventrally, up to 90 gill slits, tubular testis bent close to the left ventral side of the digestive tube, short and broad ventral stalk in phorozooid. Length of gonozooid: → 7 mm.

DISTRIBUTION: species rarely observed in the Atlantic and Indian Oceans (NEUMANN 1906, 1913).

***Doliolum valdiviae*** NEUMANN 1906,
***Dolioletta valdiviae*** (NEUMANN 1906).

*Doliolum valdiviae* NEUMANN 1906, p. 219-220, pl. 24, fig. 2 (gonozooid),
*Doliolum (Dolioletta) valdiviae* NEUMANN, 1913b, p. 17,
*Dolioletta valdiviae* GARSTANG 1933, p. 219, text-fig. 5 (gonozooid),
*Doliolum valdiviae* NEUMANN 1935, p. 324, text-fig. 251 (gonozooid),
*Dolioletta valdiviae* KRÜGER 1939, p. 133, map 82,
*Dolioletta valdiviae* GODEAUX 1972, p. 268,
*Dolioletta valdiviae* GODEAUX 1998a, p. 282-283, fig. 17. 12 d (gonozooid),
*Dolioletta valdiviae* ESNAL & DAPONTE 1999, p. 1415, fig. 3. 2 (gonozooid), map 2 (distribution).

LARVA, OOZOOID, NURSE and TROPHOZOOID: probably similar to those of *Dolioletta gegenbauri.*

PHOROZOOID and GONOZOOID: similar, less developed tunic, slender and widely separated muscles, brain behind M III, endostyle extending from just behind M II to before M V, V-shaped branchial septum from M III dorsally, to M VI in the rear and M V ventrally, up to 75 gill slits, sausage-shaped closely coiled testis, ovary in front of M VII, phorozooid stalk short and broad. Length → 6 mm.

DISTRIBUTION: species observed in great numbers in the southern Atlantic Ocean, westwards of Cape Town (NEUMANN, KRÜGER) and also in the Mozambique Channel (GODEAUX & MEURICE).

**B) FAMILY DOLIOPSOIDIDAE.** Three species.

- Genus *Doliopsoides*

Type species: *Doliopsoides meteori* KRÜGER 1939.

Only blastozooids are known.

Description of the genus: barrel-shaped body, thin tunic, flattened ectoderm, siphons at both ends of the main axis, buccal siphon provided with flaps, M I, M II, M III and M VIII as complete hoops, M V ventrally open, and dorsally united with M VI in a characteristic dorso-lateral arch, M VI and M VII crossing ventrally; a longitudinal sub-endostylar thin muscle, a thin muscle laterally uniting M IV and M V, five nervous roots and an anterior thread ending at the ciliated funnel, ample pharyngeal cavity, endostyle extending from M II to M V, peripharyngeal bands running behind M II, and dorsally uniting into a vibratile organ in front of the brain, cardiopericardium close to the rear of endostyle, transversal twisted branchial septum with a series of horizontal gill slits on both sides of the oesophagus, U-shaped and bent forwards digestive tube comprising oesophagus, stomachal pouch, intestine and pyloric gland, anal aperture in front of atrial siphon, hermaphroditic gonads below the digestive tube, no stolon.
Life cycle probably metagenetic, oozooid unknown, blastozooids developing on a lace.

Genus *Doliopsoides* ESNAL & DAPONTE 1999, p. 1916-1417, f ig. 3.9, map 2.

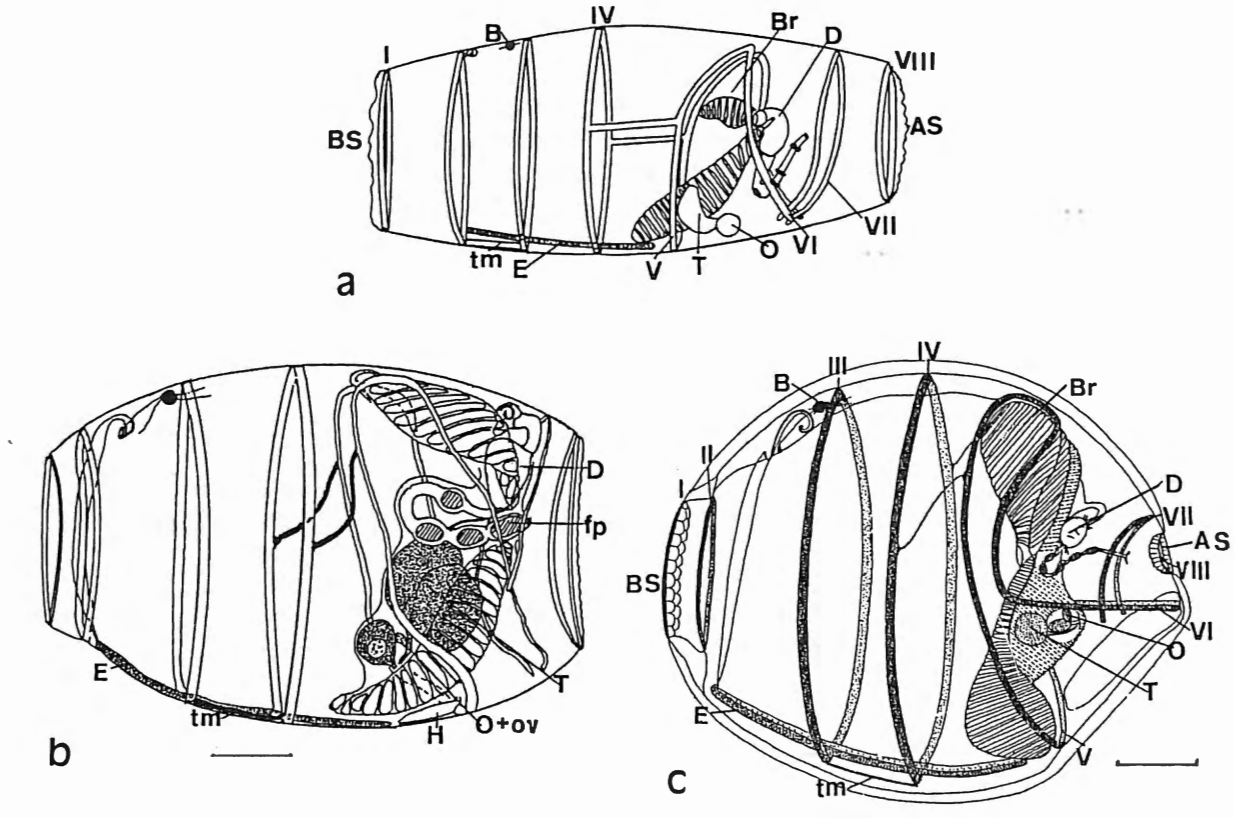


Fig. 12. **a**. gonozooid of *Doliopsoides meteori* (after KRÜGER 1939; size unknown). **b**. gonozooid of *Doliopsoides horizoni* (after TOKIOKA & BERNER 1958a; scale bar 500 µm). **c**. gonozooid of *Doliopsoides atlanticum* (after GODEAUX & HARBISON in press; scale bar 1 µm).

**27** - M II and M II bound by
a thin sub-endostylar muscle ..... *Doliopsoides meteori* (Fig.12a)

M III and M IV bound by a thin
sub-endostylar muscle, stomachal caeca..... 28

**28** - siphons devoid of lobes, testis behind and above ovary, M VII overlapping M VI ..... *Doliopsoides horizoni* (Fig.12b)

siphons provided with lobes, testis in front of ovary, M VII passing below M VI ..... *Doliopsoides atlanticum* (Fig.12c)

***Doliopsoides meteori*** KRÜGER 1939

The drawing is not very good and gives little details of the anatomy; it responds to the genus description.
Brain in front of M III, peripharyngeal bands united behind M III, thin sub-endostylar muscle uniting M II and M III, straight lateral muscle uniting M IV and M V, M VI complete ventrally, M VII open ventrally; endostyle extending from M $II^{3/4}$ to M $IV^{1/6}$, branchial septum divided into two parts, with 10 dorsal gill slits and 20 ventral gill slits on each side, digestive tube in the 6th muscular interspace, pyloric gland absent ?, pear-shaped testis in front of the ovary.

DISTRIBUTION: 12 gonozooids collected with closing nets in 11 stations in the Atlantic Ocean (one in front of Cape Verde, the others between 28 and 42° S), mostly below 400 m depth (KRÜGER).

***Doliopsoides horizoni*** TOKIOKA & BERNER 1958

Siphons deprived of flaps, thin sub-endostylar muscle uniting M III and M IV, thin lateral sigmoid muscle uniting M IV and M V, M VI open ventrally, M VII passing *above* M VI and its free extremities projecting in the ventral stalk of the sole known phorozooid, endostyle extending from M II to M

V, large branchial septum in two parts, 30 to 40 gill slits, digestive tube bent forwards, stomachal pouch provided with caeca, bilobated testis behind and below the ovary. Length → 5.2 mm

DISTRIBUTION: several gonozooids and a single phorozooid collected in eastern tropical Pacific Ocean (Shellback Expedition 1952). Depth of catches and water temperature not given.

***Doliopsoides atlanticum*** GODEAUX 1996

Buccal siphon with 18 - 20 flaps, atrial siphon with 20 elongated flaps, slender muscles (maximum 14 fibres), M VI open ventrally and ending under the atrial siphon, M VII passing below M VI, thin sub-endostylar muscle with an exchange of 2 fibres between M III and M IV, thin lateral sigmoid muscle uniting M IV and M V with exchange of 2 fibres, vibratile organ dorsal, straight endostyle extending from behind M II to before M V, branchial septum twisted with 20 and 30 gill slits on each side, oesophagus provided with a spiral fold ending at the stomachal pouch, stomachal pouch provided with numerous scattered caeca, pyloric gland of variable form, bilobate testis in front of ovary, common genital pore behind ovary, protogyny? Length → 8mm.

DISTRIBUTION: Three gonozooids in excellent condition, collected *in situ* at three close stations in the north-western Atlantic Ocean in the Bahamas at ≥700 m depth, temperature ≥ 10° C (Johnson Sea Link, Woods Hole, date: 1984).

REM.: a sole gonozooid observed in the Indian Ocean (38°S), similar to *Doliopsoides atlanticum* (GODEAUX & MEURICE 1978).

## β) SUBORDER DOLIOPSIDINA

### DESCRIPTION AND DISTRIBUTION OF THE SPECIES

### C) FAMILY DOLIOPSIDAE

- Genus *Anchinia* ESCHSCHOLZ 1835
  *Doliopsis* VOGT 1854

Type species: *Doliopsis rubescens* VOGT 1852.
A single genus with three species. Only blastozooids are known.

Description of the genus: globulous body, higher than longer, tunic less adhering, especially thick ventrally, with widespread starlike cells, thin ectoderm, five muscles M I, M II, M IV and M V as complete hoops, short, sigmoid M III, narrow lobated siphons at both ends of the horizontal axis, brain antero-dorsal, vibratile organ *behind* the brain and M III, occupying the top of the animal, U-shaped digestive tube, gonads below the digestive tube, remains of the fixative stalk retracted inside the tunic in old specimens, pigmented spots present or not on living specimens.

**29** - M I = buccal sphincter, M II a little behind, both annular hoops, M III incomplete, sigmoid on the flanks, M IV at the level of the atrial cavity, M V = atrial sphincter, annular hoop, gonads missing ..... 30

- similar appearance, gonads close to the digestive tube ..... 31

**30** - short endostyle, pigmented papilla above the buccal sphincter, starlike red spot in front of the branchial septum, long pigmented process above the atrial siphon, gonads missing (abortive?) ..... "phorozooid" of *Doliopsis rubescens* (Fig.13a)

similar appearance, long endostyle, no process above the atrial siphon, large cluster of red pigment below the digestive tube, gonads missing ..... "trophozooid" of *Doliopsis rubescens* (Fig.13b)

**31** - long endostyle, pigmented papilla above the buccal siphon, starlike red spot in front the branchial septum, long pigmented process above the atrial siphon, hand-like testis against the intestine, ovary below the digestive tube ..... gonozooid of *Doliopsis rubescens* (Fig.13c)

- endodermic fold along M III, spiral whorl along the oesophagus, no process above the atrial siphon, red-orange pigment on the digestive tube, no starlike red spot in front of the branchial septum, 1 to 5 tubular testis caeca along the ascending intestine, ovary below the digestive tube ..... gonozooid of *Doliopsis bahamensis* (Fig.13d)
bud tied to stolon (Fig.13e)

DISTRIBUTION: *Doliopsis rubescens* was discovered in Villefranche sur Mer (Nice). Later on diverse names were given : *Anchinia savigniana* HUXLEY 1851a, *Doliopsis rubescens* VOGT 1852, *Anchinia rubra* VOGT 1854, GEGENBAUR 1856, *Doliopsis rubra* GROBBEN 1882, *Anchinia rubra* KOWALEVSKY & BARROIS 1883, *Anchinia* sp. KOROTNEFF 1883, 1884, *Doliolum (Anchinia) savignianum* ULJANIN 1884, *Anchinia rubra* WAGNER 1884, 1885, *Anchinia rubra* BARROIS 1885, *Doliopsis rubescens* BRIEN 1948.
Same names were given to specimens collected out of the Mediterranean: e.g. *Anchinia rubra* BEDOT 1909 (roads of

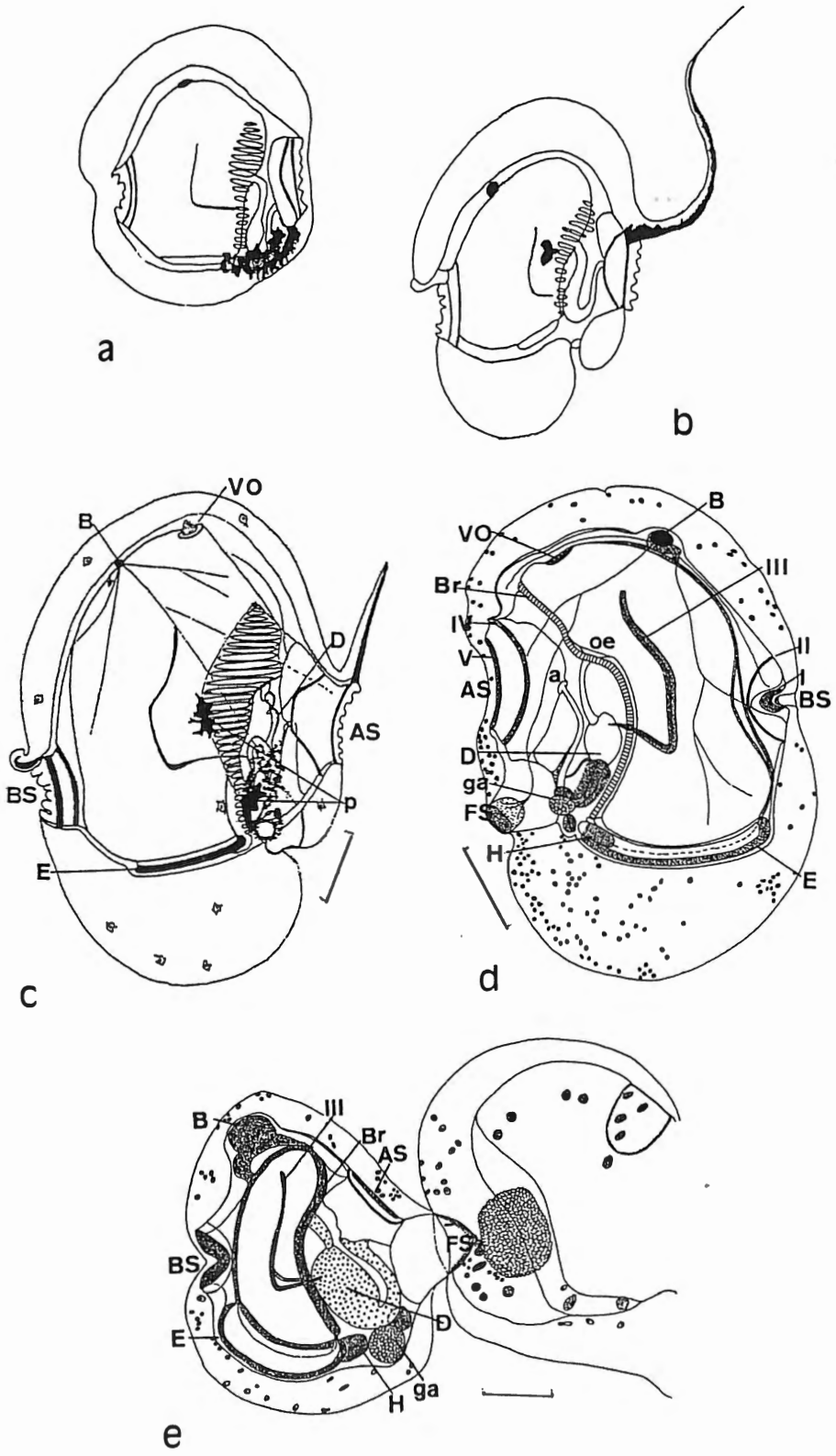


Fig. 13. **a**. "phorozooid" of *Doliopsis rubescens* (after BARROIS 1885 modified). **b**. "trophozooid" of *Doliopsis rubescens* (after BARROIS 1885 modified). **c**. gonozooid of *Doliopsis rubescens* (after KOWALEVSKY & BARROIS 1883; scale bar 1 mm). **d**. gonozooid of *Doliopsis bahamensis* (after GODEAUX & HARBISON in press; scale bar 500 µm). **e**. bud of a young gonozooid of *Doliopsis bahamensis* still attached to the stolon (scale bar 10 µm).

Amboina, Indonesia), *Anchinia rubra* IHLE 1910 (off Island of Celebes), *Anchinia savigniana* NEUMANN 1913a,b (South Atlantic Ocean), *Doliopsis savigniana* KRÜGER 1939 (South Atlantic Ocean), *Doliopsis rubescens* VAN SOEST 1975 (Bermudas), *Doliopsis rubescens* ESNAL & DAPONTE 1999 (South Atlantic Ocean).
The species seems to live preferably in depth but may be caught near the surface.

REM.: the " phorozooid " of *Doliopsis rubescens* could just be an abortive gonozooid as in Doliolidae.

D) FAMILY PARADOLIOPSIDAE

- Genus *Paradoliopsis* GODEAUX 1996.

A single genus with a single species known up to now.

Type species: *Paradoliopsis harbisoni* GODEAUX 1996.

Description of the genus: rectangular body, thick tunic, especially above the buccal siphon, less adhering to the thin ectoderm, siphons at both ends of the main axis, buccal siphon bnoadly open, provided with 24 tunical lobes, brain dorsal with four pairs of nervous roots, five muscles, M I, M II and M V complete hoops, M I and M II at both ends of the buccal vestibule, M III long, sigmoid, open at both ends with dorsal extremities overlapping behind the brain, a longitudinal endodermic fold along M III, M IV open ventrally, endostyle running above a cloud of withish pigment, two clusters of white pigmented cells at its fore-end, peripharyngeal bands running behind M II, and uniting in an vibratile organ *behind brain* and *M III,* and *shifted on the right side* of the body (as in all the few specimens collected), ciliated funnel tied to the left peripharyngeal band, simplified endostyle structure (as in Doliolidae), cardiopericardium at the rear of the endostyle, twisted branchial septum, more than 60 gill slits in a series disrupted at midway by a narrow epithelial zone, U-shaped digestive tube, reddish pigment on the oesophagus provided of two spiral whorls, yellow-gold pigment at the end of the organ, on stomachal pouch and descending intestine, hermaphoditic animal, 4 slender testicular caeca, two stretching upwards along the digestive tube, two running downwards uniting at the genital pore close to the ovary (protogyny?), ventral stalk in the rear of the free ends of M IV, and bearing a developed bud, younger buds present on the stalk, stolon missing. Gonophorozooid.

**32** -Type species: rectangular body, 2.2 x 1.9 cm, thick tunic, M I and M II at both ends of a buccal vestibule, M III on the flank, long, sigmoid , M IV at the level of the atrial cavity, M V as atrial sphincter, ovary, 4 less developed testicular caeca, no stolon ..... *Paradoliopsis harbisoni* (Fig 14a)

Paratype specimen: slightly different: 2.5 x 2.3 mm., four testicular caeca well developed (Fig.14 b), two running along the digestive tube, two running downwards, uniting at the genital pore, ovary missing, ventral stalk bearing a S-shaped series of young buds (maximum size 400 µm).

Three other isolated and well identifiable buds (Fig.14c) were also collected, probably detached from the adults during handling.

DISTRIBUTION: Two adult specimens and four developing buds were caught at two widely separated locations, the first individual with two buds near George's Bank, the second one also with two buds near the Dry Tortugas, in the Gulf of Mexico, at similar depths (700m) and in cold waters (5.7 and 4.8° C). Then the distribution reveals extended (Johnson-Sea-Link, Woods Hole, date: Aug.1987).

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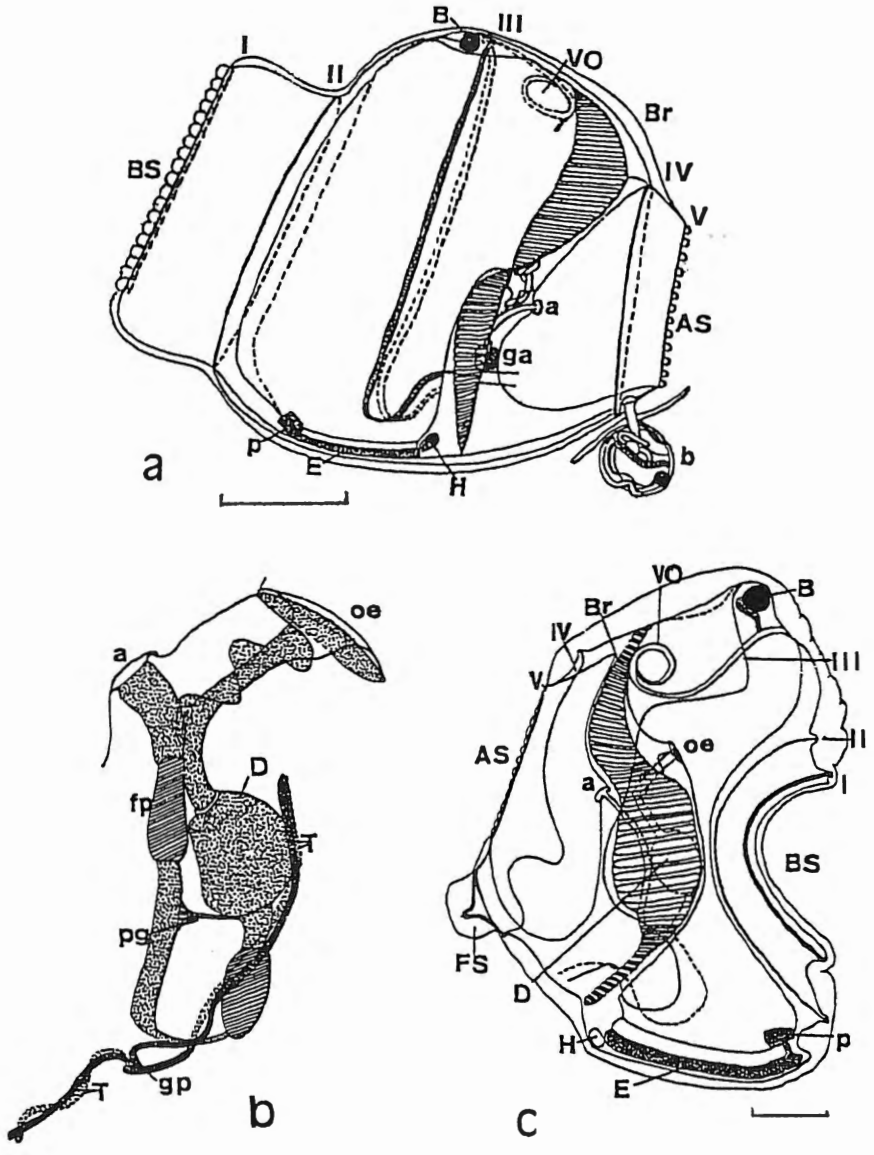


Fig. 14. **a**. left side of a gonophorozooid of *Paradoliopsis harbisoni* with weakly developed gonads (after GODEAUX 1996; scale bar 5 mm). **b**. follicular testis of a gonophorozooid of *Paradoliopsis harbisoni*, right side (after GODEAUX & HARBISON in press). **c**. right side of a bud of *Paradoliopsis harbisoni* (after GODEAUX & HARBISON in press; scale bar 10 μm).

Abbreviations: I-V, I-VIII, and I-IX: muscle hoops, a: anal aperture, am: anterior muscle, A.S.: atrial siphon, B: brain (nervous ganglion), b: bud, Br: branchial septum (gills), B.S: buccal siphon, ch: chord, C.V: caudal vesicle, D: digestive tube, d: diverticulum, D.Sp: dorsal spur, E: endostyle, end.: endoblast, F: follicular envelope, fp.: faecal pellets, F.S.: fixation stalk, ga: gonad anlage, gp: genital pore, H: heart, mes.: mesoblast, na: neural anlage, oe: oesophageal opening, p: pigment clusters, pg: pyloric gland, pm: posterior muscle, St: stolon, T: testis, Tl: tail, tm: transverse muscle, Tr: trunk, Tz: trophozooid, V.O.: vibratile organ, w: wings, x: ventral attachment of the branchial septum.

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