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

by Jean E.A. GODEAUX

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, Doliopsioideae, Doliopsidae, Paradoliopsidae, Doliopsioideesatlanticum, Doliopsisbahamensis nov. sp., Paradoliopsis harbisoni.

Résumé
L’histoire des recherches successives menées sur l’Ordre des Doliolidae 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-clés: Familles Doliolidae, Doliopsioideae, Doliopsidae, Paradoliopsidae, Doliopsioideesatlanticum, 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 CHIAIE (D. papillosum and D. sulcatum) do not exist, as they only represent artefacts made by a crustacean parasitising a colony of Pyrosoma (P. atlanticum?). QUOY & GAIMARD (Astrolable Expedition 1826-1829) named Doliolum denticulum a kind of barrel (“barrillet denticulé”) first observed in Ambonina 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 loops 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 Ambonina roads QUOY & GAIMARD named Doliolum caudatum (“barrillet à queue”) a second species “Doliolum, corpore cylindrico, elongato, octonis circulis cincto, postice caudato, orbibus terminalibus, 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 scrutinizing the drawings and correction of the orientation of the body (Fig.1b), that doliolid seems to be an oozoooid 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 KOHN (1852) who gave the first correct position of the body of the animals and recognized their relationships with the Ascidiae. 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.
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), ULIJANIN (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. ULIJANIN (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 Doliolleta. 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...
considered as close to *Anchinia*, was successively named *Doliops is 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 *Doliops is savigniana* specimens mainly collected in the southern Atlantic Ocean. Numerous specimens mainly caught in the Bahamas seem to belong to another species, *Doliops is 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 doliolet species called *Doliopsoi des meteori* and collected in the southern Atlantic Ocean, mostly below 400m depth. The barrel-shaped body evokes that of the doliolium. Another species, *Doliopsideis horizonti* has been described from the eastern tropical Pacific Ocean by TOKIKA & BERNER (1958a,b). *Doliopsideis 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 *Paradoliopsideis h arbisoni* (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 (≥ 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 periphrayngeal 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.

- **Suborder Doliopsidina with two families:**
  a) Doliopsidae with one genus and two species.
  b) Paradoliopsidae with one genus and one species.

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

- **a) 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-
The pelagic stage appears soon (after two days at 18°C in _Doliolites 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 ganglionic cluster of cells, the future brain, while its ventral part and the anterior part of the medullar tube respectively become the so-called sub-ganglionic 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 respond 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 two 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 split slits opens on both sides of the oesophageal opening. The endostyle responds to the lower part of the embryopharyngeal 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 stomach 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 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 _Doliolosetta gegenbauri_ (PAFFENHOFER & GIBSON 1930). Growth of the different stages is very fast; a phorozooid (25 mm) can liberate 10 gonozooids a day during
The life cycle is complex and seems traced from that of the full-grown specimens. Red or yellow-red pigmented areas have been observed in missing. 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 arches, 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 digestive tube 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 & Bernar (1958 b) pleads for a possible metagenesis with three stages at least (Ooz, PZ and GZ).

The systematics of genus Doliopsis is founded on the position of the muscles, the number of gill slits and the form of the gonads.

**b) 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 siphon of the buccal siphon. It is followed by a 300 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 slightly 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

   - 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

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

   - 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

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. anuran 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) e. 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 Dolioleoides rarum (after ULJANIN 1884; size unknown).
a) **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 oozoids  

- 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  

- 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) **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. sigmoïdes. The species Doliolina undulata and D. obscura, only known as gonozoids, belong to the same subgenus. Subgenus Doliolinetta comprises the species Doliolinetta indica, D. intermedia and D. resistibilis. Species Doliolinetta separata, only known as gonozoid, belongs to the same subgenus (GODEAUX 1998c). All the blastozooids display a U-shaped (sometimes 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 - 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. Doliolitta Doliolitta gegenbauri (Fig. 5d)

11 - wide muscles with narrow interspaces  

- 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. Doliolitta Doliolitta 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. oozeoid of Doliolina muelleri (after GODEAUX 1957-58; scale bar 100 μm).  b. oozeoid of Doliooloides raren (after NEUMANN 1906; scale bar 500 μm).  c. oozeoid of Doliolum species (D. denticulatum and D. nationalis; scale bar 250 μm).  d. oozeoid of Dolioletta gegenbauri (scale bar 250 μm).

Fig. 6.  a. nurse of Doliolium 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 .................................................................

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

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)

15 - no wings ......................................................... *Dolioletta mirabilis*

**A3**

**Phorozoids and gonozoids**

Barrel-shaped animals provided with 8 complete parallel muscle hoops. Phorozoids with a lot of developing buds on their ventral stalk, gonozoids 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 between 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 1938a; scale bar 1 mm). g. gonozooid of Doliolina obscura (after Tokioka & Berner 1938b; 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 Dolioletta according to shape and disposal of the gonads.

- tubular testis extending horizontally, ovary in front of M VII ................................................................. s.g. Dolioletta 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, gonozoid .............................. 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 VII 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 ........................................... Dolioliinetta 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 ..................................................... Dolioliinetta intermedia (Fig.9b)

- endostyle M II 1/2 to M IV 1/2, arched branchial septum (M III - M VI 1/2), 30 to 40 gill slits, M VII complete ventrally, tubular testis swollen at the level of M III, ovary in front of M VII .................................................. Dolioliinetta 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 .................................................. Dolioliinetta 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, gonozoid .......................................................... 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, gonozoid .................................................. 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 resistentilis* (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).
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. Gegnbaur, 1856, p.303-304, pl.16, fig. 12 et 13 (oozoid according to Ulianin),
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 ULIJANIN 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.

Just behind M II, ovary under M VII.
End ostyle extending from M II close to M V, branchial or behind M V II, horizontal 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 indica NEUMANN 1906,
Doliolinetta indica (NEUMANN 1906) see GODEAUX 1998c.

Doliolum (Doliolina) indica NEUMANN 1906, p. 220-221, p.227, pl.23, fig.7 (branchiai septum), pl. 24 , fig. 5, pl. 28, fig. 5 (gonozooid),
Doliolum (Doliolina) indica NEUMANN 1913b, p.13,
Doliolum (Doliolina) indica SEWELL 1953, p.46-47, text-fig.13 (young gonozooid, Doliollette?),
Doliolinetta indica GODEAUX 1979, p. 162 (oozooid, nurse, phorozooid, gonozooid),
Doliolinetta indica GODEAUX 1982 (1984), p. 185-186 (nurse, phorozooid, gonozooid),
Doliolinetta indica GODEAUX 1986, p. 195 (oozooid, phorozooid, gonozooid),
Doliolinetta indica 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): PHORZOOID 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), slightly 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.

**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, gonozyoid).

**Doliolum (Doliolina) intermedium** Neumann 1906, p. 211-212, p. 227.

**Doliolum sp.** Farran 1906, p.7, fig.1 and distribution,

**Doliolum (Doliolina) intermediate** Ingle 1927, p. 21.

**Doliolina intermedium** Garstang 1933, fig. 4.

**Doliolum (Doliolina) intermedium** Hant & 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),

**Doliolina intermedium** Godeaux 1973, p. 63 (nurse, phorozooid, gonozyoid),

**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 (gonozooid), map 2 (distribution),

**Doliolinetta intermedia** Godeaux & Harbison (in press).

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

**NURSE:** barrel-shaped, stemonyomic, aclinoius, very slender muscles, separated by 10 times wider interspaces (Garstang 1933, Godeaux 1996, Godeaux & Harbison in press).

**Length:** → 25 mm.

**TROPHOOZOID:** large size, numerous gill slits (Godeaux 1998b, Godeaux & Harbison in press). Height: 7 mm.

**PHOROOZOID and GONOOZOID** 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; 3 phorozooids and 7 gonoozooids in 6 stations of the Antarctic 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 & Bernt 1958.

**Doliolinetta separata** (Tokioka & Bernt 1958) see Godeaux 1998c, p. 1761, fig. 2 h (gonozooid).

**Doliolina separata** Tokioka & Bernt 1958b, p. 319-320, fig. 2 (gonozooid),

**Doliolina separata** Godeaux 1998a, p.282-283, fig. 17.11 b (gonozooid).

**LARVA, OOOZOID, NURSE and TROPHOOZOID** unknown.

**PHOROOZOID and GONOOZOID** 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).

Subgenus Doliolina BORGER 1894. Five species.

Type species: Doliolina muelleri KROHN 1852

Doliolum muelleri KROHN 1852, pl.2, fig.44,
Doliolum nordmanni KROHN 1852, p. 59, pl.2, fig. 5-6-7 (metamorphosing larvae of Doliolum troschelli),
Doliolum sp. GEGENBAUR 1856, p. 303, 1.15, fig.8,
Doliolum Muelleri KEFFERSTEIN & EHLERS 1861 p. 66-68, pl. 10, fig 3 & 5 (larva, oozeoid, nurse), pl.21, fig. 21 (young oozeoid),
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, oozeoid and trophozooid),
Doliolum muelleri RITTER 1905, p. 95-97, fig. 29 (oozeoid),
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, nurse), p. 363, 364 & 368, text-fig. 280, 281 & 285 (larva, oozeoid),
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),
Doliolum muelleri TRÉGOUëOFF & ROSE 1957, p. 567, pl. 203, fig. 7 (phorozooid), pl. 304, fig. 2-3 (larvae),
Doliolum 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 (Doliolina) muelleri BRACONNOT 1970, p. 639-641, fig. a, b (larva), p. 650-661, p. 3 g (nurse), pl. 4 c, d (oozeoid, nurse), pl. 6 a, b (trophozooid),
Doliolum muelleri BRACONNOT 1971, p. 10-12, fig. 280-281, fig. 6 (larva), 7a (oozeoid), fig. 8a (nurse), fig. 9a (trophozooid), 10b (gonozooid),
Doliolina muelleri ESNAL et al. 1982a, p. 52-53 (map), fig. 3 d (phorozooid), fig. 4d (nurse),
Doliolina muelleri ESNAL et al. 1982b, tabl. 1, fig. 2 (distribution),
Doliolina muelleri FRASER 1982, p. 20-23,
Doliolina muelleri GODEAUX 1998a, p. 279-282, fig. 17.6 (larva), 17.7a (oozeoid), 17.8 (nurse), 17.9 (trophozooid), 17.10b (gonozooid),
Doliolina Godeaux 1998c, p. 1758, fig. 1 a-b (oozeoid, 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.

Oozeoid: 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.

Nut: widening muscle hoops at the time of disappearance of the viscera, narrow interspaces, M IV wider 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, slightly 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 HERDAN 1888.

Doliolina krohni BORGER 1894

Doliolina krohni HERDAN 1888, p. 49, pl. 3, fig. 1 (schema),
Doliolum krohni TRAUSTEDT 1889, p. 4, pl. 1, fig. 11,
Doliolina krohni BORGER 1894, p. 15, pl. 6, fig. 11 (gonozooid) and 13 (blastozooid),
Doliolina krohni BORGER 1896, p. 715,
Doliolina krohni BORGER 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 HELE 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) müelleri 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).

**DISTRIBUTION:**

The genus *Doliolina* comprises two closely related species: *Doliolum denticulatum* (Quoy & Gaimard 1835) and *Doliolum nationalis* Berg 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, tabular 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 IV, testis rarely overlapping M IV.

**LARVA, OOZOOID, NURSE, TROPHOZOOID unknown.**

Phorozooid similar: swollen barrel-shaped body, thin, and less sticky tunic. Slight differences 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 specimen?), 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

**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 in midway of M III and M IV, long endostyle extending from M II to M V, arched branchial septum (M IV/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 denticulatum* Quoy & Gaimard 1835

  The genus *Doliolum* comprises two closely related species: *Doliolum denticulatum* (Quoy & Gaimard 1835) and *Doliolum nationalis* Berg 1893.

  **Genus Doliolina var. *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.

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

*Doliolum denticulatum* QUY & 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 1853, p. 57-58, pl. 2, fig. 1-3, *Doliolum sp.* GEGENBAUR 1856, p. 297-300, pl. 16, fig. 4-5 (phorozooid), *Doliolum Ehrenbergii* KROHN 1853, p. 57-58, pl. 2, fig. 1-3, *Doliolum sp.* 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* HERDMAN 1888, p. 91-91 (oozooid), *Doliolum Ehrenbergii* KROHN 1853, p. 57-58, pl. 2, fig. 1-3, *Doliolum sp.* GEGENBAUR 1856, p. 284, Pl. 14, *Doliolum denticulatum* HERDMAN 1888, p. 101-111 (= *Doliolum tritonis*, HERDMAN 1888), *Doliolum denticulatum* FOL 1884, p. 150-153, pl. 8, fig. 2-3 (young), 4-5, *Doliolum Ehrenbergii* UJANIN 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 ehrenbergii* 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 (Doliolletta) 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-oozooid), p. 384-387, text-fig. 302-303 (trophozooid), p. 327, text-fig. 253 (gonozooid), *Doliolum denticulatum* RUSSEL & COLMAN 1935, p. 207-208, *Doliolum (Doliolletta) denticulatum (= D. ehrenbergii)*

**HARANT & VERNIÈRES 1938, p. 50, fig. 62, Doliolletta denticulatum** KRÜGER 1939, p. 132-133, map 78, *Doliolum denticulatum* 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 (Doliolletta) denticulatum* SEWELL 1953, p. 50-53, text-fig. 15 (gonozooid), *Doliolum denticulatum* TREGOUBOFF & 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, oozyoid, 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 Doliolletta 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 (oozyoid), 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:** Folicular fusiform envelope (→ 3mm), differentiated tail, precardial 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 oozyoid is set free at the length of 800 mm. Length > 800 μm.

**NURSE:** Holomyconic with M II to M VIII sold in a continuous sheet (cutrass), 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 V12 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: \( \rightarrow 4 \text{ mm} \).

**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 Challenger* HEDRMAN var. TRAUSTEDT 1893, p. 3-4, pl. 1, fig. 14,

*Doliolum nationalis* BORGERT 1893, p. 406-408, text-fig. p. 407 (gonozooid),

*Doliolum (Doliolleta) 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* IHELE 1910, p. 15,

*Doliolum nationalis* SIGL 1913, p. 279,

*Doliolum nationalis* NEUMANN 1913a, p. 21,

*Doliolum nationalis* NEUMANN 1913b, p. 18,

*Doliolum (Doliolleta) nationalis* IHELE 1927, p. 21,

*Doliolum nationalis* GARSTANG 1933, p. 221-224, text-fig. 8,

*Doliolum (Doliolleta) nationale* HARANT & VERNIÈRES 1938, p. 49, fig. 63,

*Doliolleta nationalis* KRÜGER 1939, p. 132 - 133, map 79,

*Doliolum nationalis* FRASER 1947, p. 2, text-fig. (gonozooid ?), p. 4 (distribution),

*Doliolum nationalis* (not Doliolleta 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* 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 OOOZOID:** similar to those of *Doliolum denticulatum* (BRACONNOT 1976).

**NURSE and TRPHOROZOOID:** 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 V12 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 \( \rightarrow 3 \text{ mm} \), length of the gonozooid \( \rightarrow 4 \text{ mm} \).

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 Doliolleta GARSTANG 1933.** Four species. (subgenus *Doliolleta* 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 tests.

Type species *Doliolella 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, 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 (gonozooid), 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 gonozooid, not *Doliolum denticulatum*),

*Doliolum (Doliolleta) gegenbauri* NEUMANN 1913b, p. 15-16,

*Doliolleta gegenbauri* GARSTANG 1933, p. 216-217, p. 229 text-fig. 5,

*Doliolleta gegenbauri* NEUMANN 1935, p. 369, text-fig. 369, text-fig. 286 (young gonozooid, not *Doliolum denticulatum*),

*Doliolleta gegenbauri* RUSSEL & COLMAN 1935, p. 208,

*Doliolleta gegenbauri* HARANT & VERNIÈRES 1938, p. 49,

*Doliolleta gegenbauri* KRÜGER 1939, p. 133, map 80,

*Doliolleta (Doliolleta) gegenbauri* FRASER 1947, p. 2, text-fig. 4 (gonozooid), p. 4 (distribution),

*Doliolleta gegenbauri* - *tritons* THOMPSON 1948, p. 91, pl. 30, fig. 1 (= gonozooid of *Doliolum nationalis* ??), pl. 31, fig. 2 (nurse),

*Doliolleta (Doliolleta) gegenbauri* BERRILL 1950, p. 285-286, fig. 103a (gonozooid),

*Doliolleta gegenbauri* SEWELL 1953, p. 47-50, text-fig. 14 (gonozooid of *D. tritons*?),

*Doliolleta gegenbauri* TRÉGOUFFBOFF & 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),

*Doliolleta gegenbauri* (not *Doliolum denticulatum*) GODEAUX 1957-1958, text-fig. 65, 66, 68, 70, 71, 72, 73, 80, 84 & 85 (larva, gonozooid),

*Doliolleta gegenbauri* BARNES 1961, p. 103, pl. 29 (distribution),

*Doliolleta gegenbauri* (not *Doliolum denticulatum*)
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.

**Dolioletta tritonis** HERDMAN 1888
**Doliolum 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 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 (Doliioletta) tritonis* IHLE 1927, p. 21-22, text-fig. 10 (gonozooid);
*Doliolum gegenbauri* RUSSEL & HASTINGS 1933, p. 635;
*Doliioletta tritonis* BERRILL 1935, p. 286 fig. 103 b (gonozooid), 103 c (trophozooid), fig. 103 d (phorozooid);
*Doliioletta (Doliioletta) tritonis* HARANT & VERNIÈRES 1938, p. 49;
*Doliioletta tritonis* KRÜGER 1939, p. 133, map 80;
*Doliioletta (Doliioletta gegenbauri) var tritonis* FRASER 1947, p. 2 text-fig. (larva, oozooid, nurse, phorozooid, gonozooid), p. 4 (distribution);
*Doliioletta gegenbauri-tritonis* THOMPSON 1948, p. 94-95, text-fig. 10, pl. 30, fig. 1 (gonozooid? schema), pl. 31, fig. 1 (gonozooid), fig. 2 (nurse);
*Doliioletta tritonis* VAN ZYL 1959, p. 20-24 (distribution), p. 31 (map);
*Doliioletta 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,
**Doliioletta tritonis** GODEAUX 1998 a, p. 282-283, fig. 17.12 b (gonozooid).

**LARVA, OOOZOID 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 *Doliioletta 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
**Doliioletta 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 (Doliioletta) mirabile** NEUMANN 1913 b, p. 17-18,
**Dolchinia mirabilis = Doliolum chuni** FEDELE 1923, p. 152-158,
**Doliioletta mirabile** GARSTANG 1933, p. 216, text-fig. 5, p. 230-221, text-fig. 6-7 (*Doliioletta mirabilis*: phorozooid, gonozooid),
**Doliolum (Doliioletta) mirabile** HARPAN & VERNIÈRES 1938, p. 49,
**Doliolum (Doliioletta) mirabilis** FRASER 1947, p. 2 text-fig. (gonozooid),
**Doliolum (Doliioletta) mirabilis** SEWELL 1953, p. 53-55, text-fig. 16-17 (phorozooid, gonozooid),
**Doliioletta mirabilis** TRÉGOUOFF & ROSE 1957, vol. I, p. 568, Vol.II, pl. 205, fig. 6,
**Doliioletta mirabile** GODEAUX & DAPONTE 1999, p. 1415, fig. 3.1 a,b (gonozooid), map 2 (distribution).

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

**LARVA, OOOZOID and NURSE:** unknown, but possibly similar to those of *Doliioletta gegenbauri* The pieces of the dorsal spur observed by KOROTNEFF (1891, 1904) attest of the great length of this appendice (→ 45 cm?).
Doliolum valdiviae KRÜGER 1939, p. 133, map 82,  
Doliolum valdiviae GODEAUX 1972, p. 268,  
Doliolum valdiviae GODEAUX 1998a, p. 282-283, fig. 17. 12  
d (gonozoid),  
Doliolum valdiviae ESNAL & DAPONTE 1999, p. 1415, fig. 3. 2  
(gonozoid), map 2 (distribution).

LARVA, OOZOOID, NURSE and TROPHOZOOID: probably similar to those of Doliolletta 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 DOLIOPSIDIIDAE. Three species.

- Genus Doliopsoides

Type species: Doliopsoides meteori KRÜGER 1939.

Only blastozoooids 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, cardiodipercardium 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, oozyoid unknown, blastozoooids developing on a lace.

Genus Doliopsoides ESNAL & DAPONTE 1999, p. 1916-1417, fig. 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 GODAEUX & HARBISON in press; scale bar 1 μm).

27 - M II and M II bound by a thin sub-endosty lar 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, periharyngeal 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\(^{10}\) to M IV\(^{16}\), 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 gonozoids 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
Doliopsideis 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-endostyral 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 pocket, 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 Doliopsideis 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.
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).


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 PARADOLOPSIDAE

- Genus *Paradoliopsis* GodeauX 1996.

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

Type species: *Paradoliopsis harbinsi* 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 broadly 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 endodermal fold along M III, M IV open ventrally, endodystyle running above a cloud of withish pigment, two clusters of white pigmented cells at its fore-end, peripheryrngeal 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 peripheryrngeal band, simplified endodystyle structure (as in Doliolidae), cardiopericardium at the rear of the endodystyle, 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. Gonophorozoid.

---

**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 harbinsi* (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).

**Literature cited**


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


TERRY, R.M., 1961. Investigations of inner continental shelf waters off lower Chesapeake Bay. III - the photozood stage of the Tunicate Doliolium nationalis Chesaapeke Science, 2: 60-64.


USSW, M., 1876. Beiträge zur Kenntniss der Organisation der Tunicaten, Magnow (cited by ULJANIN, 1884).


J.E.A. GODEAUX
Institut de Zoologie, Biologie marine
Université de Liège
Quai Édouard Van Beneden, 22
B-4020 Liège, Belgique