

The life cycles of *Octotiarra russelli* and *Stomotoca atra* (Cnidaria, Anthomedusae, Pandeidae)

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The previously unknown life cycles of *Octotiarra russelli* and *Stomotoca atra* are described. Both species present differentiated hydroids and medusae. From the morphology of the newly liberated medusae both species are referred to the Pandeidae and, from the presence of a manubrial peduncle, to the subfamily Stomotocinae, together with *Timoides*. Some aspects of feeding and gonad growth are described and discussed.

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Introduction

The family Pandeidae is defined merely on medusa morphology, but many different hydroid forms can produce 'pandeid' medusae. Moreover, the hydroid stage is unknown in the majority of the species (see Bouillon 1985, for family and generic diagnoses). Arai & Brinckmann-Voss (1980) recently concurred with previous authors (e.g. Russell 1953; Uchida 1964; Millard 1975) in remarking that the Pandeidae comprises a vast array of hydroid and medusa forms and that it might be wise to split it into several families or at least, as they did, into subfamilies (see also Bouillon 1985).

It is presently difficult to refer an infertile hydroid lacking the crucial reproductive characters to this family rather than, for instance, to the Bougainvillidae, the Clavidae or to certain specialized families comprising the parasitic forms. As a consequence the Pandeidae is the only large family of hydromedusae to which no species with a suppressed medusa stage is ascribed. This dishomogeneity of the hydroid stage is counterbalanced by the uniform morphology of the newly released medusae, so that it is almost always possible to tell a young pandeid from any other medusa. The distinguishing features are: two opposite perradial tentacles, two small perradial bulbs without tentacles, four radial canals, manubrium shorter than subumbrellar cavity, mouth with four simple lips, a rounded exumbrella. This 'archetype' possibly indicates a common ancestry for all pandeids.

One of the recognized subfamilies of the Pandeidae is the Stomotocinae, comprising the genera *Octotiarra*, *Stomotoca* and *Timoides*.

Octotiarra is a monotypic genus comprising *O. russelli* Kramp, and constitutes an exception in the Pandeidae in having eight instead of four radial canals. The hydroid

was unknown and so also was the development of the medusa.

Stomotoca is a well known medusa-based genus, represented by two species: *S. atra* L. Agassiz and *S. pterophylla* Haeckel. Larson (1982) linked *Stomotoca pterophylla* with the parasitic hydroid *Hydrichthys* and, since many nominal species have been referred to this last genus, there might be other medusae to be discovered (see Bouillon 1985).

Timoides is a monotypic genus represented by *T. agassizi* Bigelow, a rare species based on adult medusa morphology, the hydroid being unknown. Bouillon (1980) has shown that *T. agassizi* is not a leptomedusa, as previously thought, but is instead a pandeid, with great affinities with *Stomotoca* and *Octotiarra*. *Timoides* is thus referable to the Stomotocinae, all genera of this subfamily having a distinct manubrial peduncle.

The hydroid stages of *Octotiarra russelli* and *Stomotoca atra* were collected in July and August 1986, by diving between 10 and 20 m depth on the coral reefs encircling Laing Island, a small coralline island off Papua New Guinea (see Bouillon *et al.* 1986 for a general description of the main features of the area). Fertile colonies were isolated and cultured in finger bowls. After medusa release the hydroids were preserved. The medusae were kept in finger bowls and fed daily with *Artemia* nauplii; the water (28°C) was changed after feeding.

Plankton samplings carried out in the same locality provided additional developmental stages, which were compared with cultured material. Fertile colonies of *Octotiarra* were also collected in February 1987 at Wuvulu Island, Bismarck Sea.

Results

Octotiarra russelli (Figs. 1–3, 4A)

Hydroid. Hydroid colony symbiotic with the bryozoan *Steginoporella mandibulata* Harmer (Fig. 1A) growing on

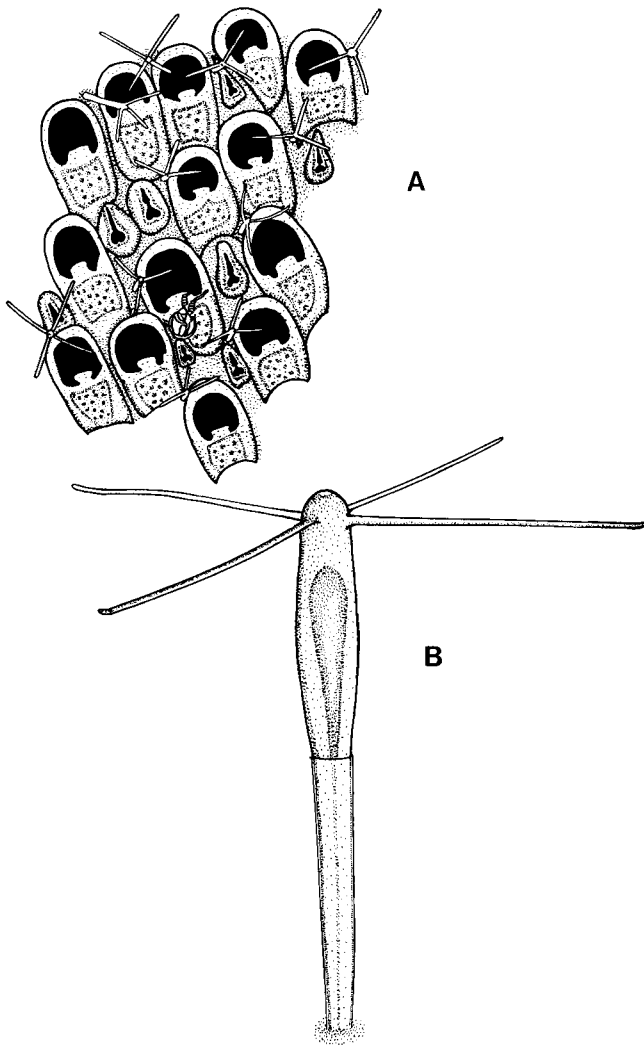


Fig. 1. *Octotiarra russelli*.—A. Colony with medusa bud, growing on the bryozoan *Steginoporella mandibulata*.—B. Hydranth.

the undersides of dead and living corals (*Acropora*), stolonial, hydrorhiza growing under the skeleton of the bryozoan. Hydranths (Fig. 1B) rising among zoeciae, about 0.5 mm high, with single row of 3 or 4 filiform tentacles, white rounded hypostome, reddish column; hydrocaulus short, covered by thin perisarc. Medusa buds isolated, on hydrorhiza, dark green, with 2 large and 2 small tentacular bulbs.

Medusa. Newly-released medusa (Fig. 2A) roundish to quadratic, about 0.5–0.7 mm in diameter, exumbrella green, manubrium reddish, cylindrical, reaching $\frac{2}{3}$ of height of subumbrellar cavity, mouth with 4 simple lips; 2 long opposite marginal tentacles originating from triangular–elongate perradial tentacular bulbs, 2 small atentaculate perradial bulbs, 4 smaller interradial bulbs. All bulbs reddish. Small apical projection present in some specimens.

The growth of medusa cannot be divided into separate stages, changes being gradual and affecting different structures in different periods.

Five-day-old medusa (Fig. 2B) with a rounded apical projection, manubrium cruciform. Lips of unfed specimens of any observed age invisible, contracted towards centre of mouth.

Nine-day-old medusa (Fig. 2C) about 2 mm in diameter, apical projection blunt, almost indistinct, base of manubrium wide, manubrium cruciform, with 4 ridges corresponding to the lips. Lips white. Radial canals ribbon-like. Four additional radial canals originating from base of manubrium, narrower than the main ones, reaching only $\frac{1}{5}$ of subumbrellar cavity. Perradial tentacular bulbs triangular, but less elongated than in younger stages.

Fifteen-day-old medusa (Fig. 2D) of nearly the same size as the nine-day-old one, but with 4 perradial tentacles, 4 interradial and 8 adradial tentacular bulbs. Supplementary radial canals reaching $\frac{1}{2}$ of height of subumbrellar cavity.

Twenty-day-old medusa (Fig. 3A) much flatter, with rounded apical projection, manubrium protruding outside velar opening, cruciform distally but with 8 proximal ridges, corresponding to the 8 radial canals. A peduncle starts to form. The additional 4 radial canals originate from the sides of only 2 opposite perradial radial canals, possibly the two with tentacles since the beginning of development. No trace of gonads.

This stage of growth was abundant around Laing Island during the period in which the specimens were cultured. Successive growth stages could be found in the plankton, up to the mature adult, corresponding to the description of Kramp (1953). In the adult stages the manubrium shows eight ridges, each starting proximally at the insertion of the radial canals in the manubrium itself and terminating distally in a lip. Each ridge, in the proximal part of the manubrium, shows a series of simple or bifid folds within which the gametes are produced (Figs. 3B and 4A).

Remarks. The hydroid of *O. russelli* was previously unknown. It is not referable to any hydroid described so far. Its strict association with a bryozoan is not an exception in hydroids. *Zanclaea* (Zanclaeidae), *Halocoryne* (Halocorynidae), *Perarella* (Cytaeidae), *Hydranthea* (Haleciidae) and other still undescribed genera (Boero & Bouillon unpublished observations) also have species with this type of symbiosis.

The development of the medusa of *O. russelli* is slow, and the cultured specimens did not increase much in size during the first period of life. The metamorphosis from a simple young pandeid medusa to the highly differentiated adult is gradual, though a noticeable modification occurs between 15 and 20 days (Figs. 2D, 3A), when the exumbrella becomes flatter and the manubrium protrudes from the exumbrellar cavity. The additional radial canals can originate one by one, at different stages of development. The tentacles, though 5–7 times the length of the exumbrella, could not catch *Artemia* nauplii and the cultured specimens were fed by forceps. Possibly their diet does not consist of crustaceans and their nematocysts (microbasic euryteles) are not adapted to such a food source as *Artemia* nauplii.

Stomatoca atra (Figs. 4B, 5, 6)

Hydroid. Colony stolonial (Fig. 5), growing on algae, sponges and bryozoans, typically with unbranched stems,

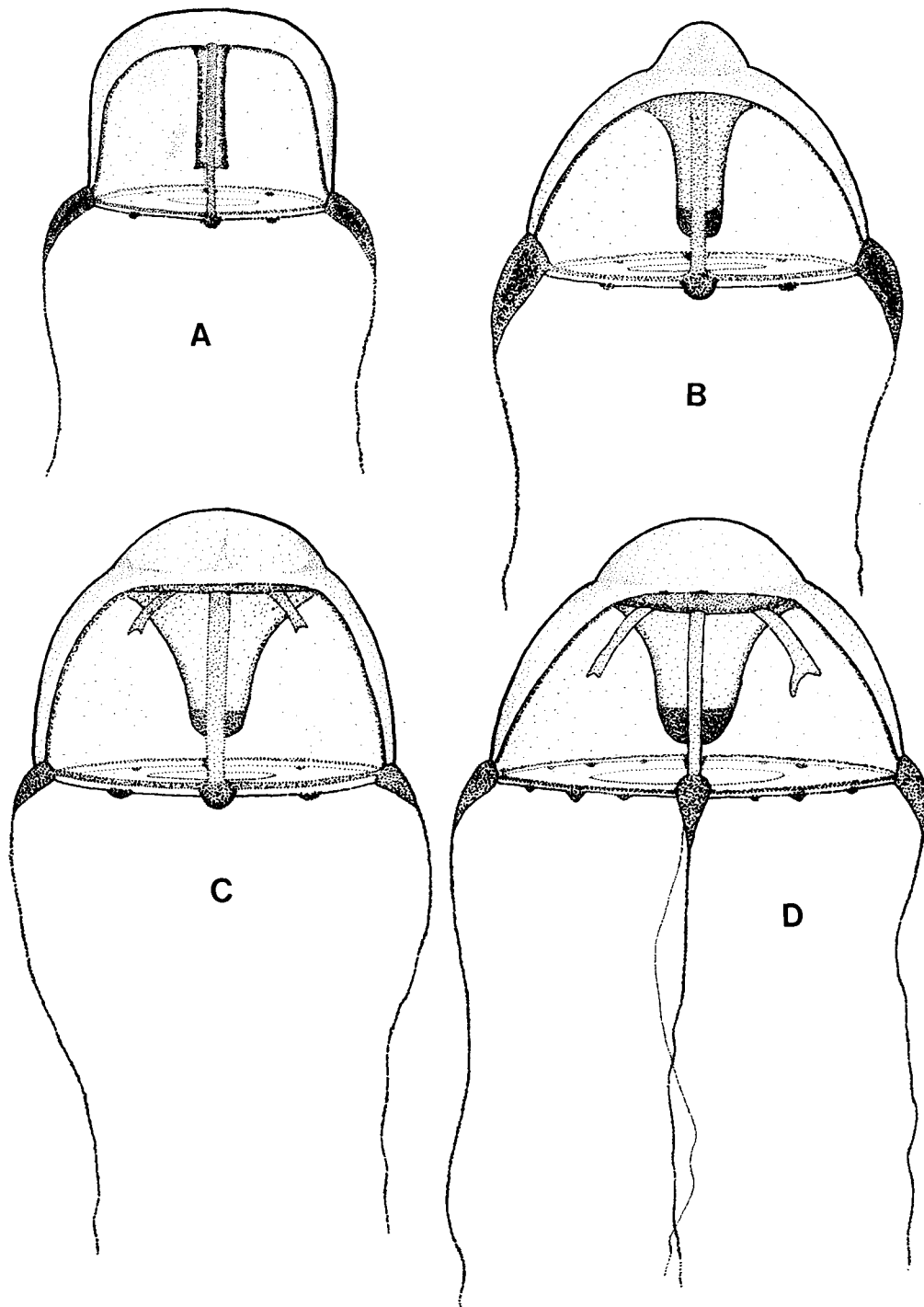


Fig. 2. *Octotiarra russelli*.—A. Newly released medusa.—B. Five-day-old medusa.—C. Nine-day-old medusa.—D. Fifteen-day-old medusa.

rarely with 2 hydranths per stem. Stem about 1 mm high, covered with perisarc encrusted with microalgae and silt. Hydranth about 1 mm high, with white hypostome and three rows of tentacles, which may merge into a single one in contracted specimens or fixed material. Oral whorl with 6–7 tentacles held upwards, middle aboral whorl with about 6 tentacles perpendicular to hydranth column, proximal aboral whorl with about 6 tentacles held downwards. Medusa buds solitary, on hydrorhiza, occasionally on stem, shortly pedicellate, with 2 large and 2 small, red tentacular bulbs, 4 radial canals.

Medusa. Newly-released medusa (Fig. 6A) about 1 mm in diameter, rounded, with 2 large perradial tentacular bulbs with tentacles and 2 small perradial bulbs without

tentacles. Four radial canals. Manubrium cylindrical, reaching $\frac{3}{4}$ of height of subumbrellar cavity, mouth with 4 small lips. Manubrium and bulbs red.

Two-day-old medusa (Fig. 6B) with a small apical projection and 4 small interradial tentacular bulbs.

Eight-day-old medusa (Fig. 6C) with larger apical projection, manubrium cruciform, almost reaching velar opening, radial canals with small diverticula.

Twelve-day-old medusa (Fig. 6D) 3.5–4 mm high, with large, round apical projection, manubrium protruding outside bell cavity, cruciform, with 4 distinct lips, 2 tentacles in length $5\times$ height of umbrella, with large, triangular bulbs. Non-tentaculate perradial bulbs small. Four non-tentaculate bulbs per quadrant, triangular, small. Radial canals somewhat wavy, with small

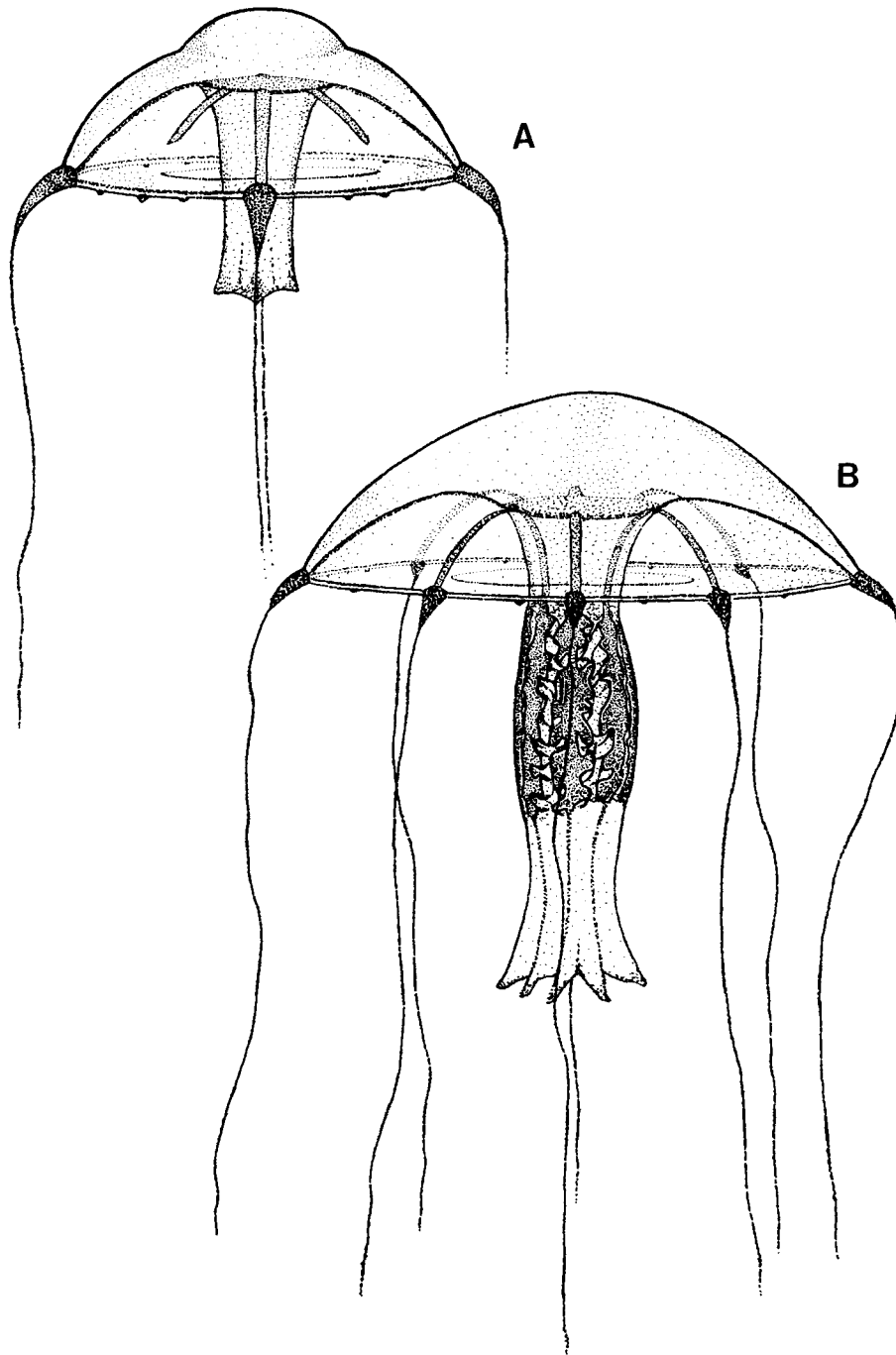


Fig. 3. *Octotiarra russelli*.—A. Twenty-day-old medusa.—B. Adult medusa collected from the plankton.

diverticula. Four reddish perradial gonads, developing at base of manubrium, with 4 transversal folds each and growing on ridges of cruciform manubrium. Each ridge terminating in a lip which can be curved upwards or held straight. Velum narrow, delimiting a smaller part of umbrellar opening than in young specimens.

Sixteen-day-old medusa constant in shape, manubrium longer, gonads reaching level of velum. Five non-tentaculate bulbs per quadrant. Tentacles always contracted.

Twenty-day-old medusa (Fig. 6E) 4.5 mm from apex to mouth, dome-shaped, with a large apical projection, $\frac{2}{3}$ of manubrium protruding from subumbrellar cavity, a wide peduncle present, radial canals bending towards the base of manubrium. Four gonads, each formed by 2 series of folds, reaching level of velar opening.

Twenty-four-day-old medusa of same general aspect as twenty-day-old one, but with mature eggs in proximal part of the gonad, immature eggs in distal part (Fig. 4B). Eggs enclosed by the folds forming the gonad.

Mature medusae, collected in the field, with long peduncle, manubrium being completely outside the subumbrellar chamber (Fig. 6F).

Remarks. The hydroid of *S. atra* resembles a clavid, owing to tentacle disposition in three rows. Its behaviour, and also that of *Octotiarra russelli*, is similar to that of *Amphinema* (Pandeidae), in having the ability of rapidly bending to one side if stimulated, whereas clavids tend to contract uniformly (Boero, unpublished).

The study of feeding and growth of the medusa allowed a series of observations which could be of general interest.

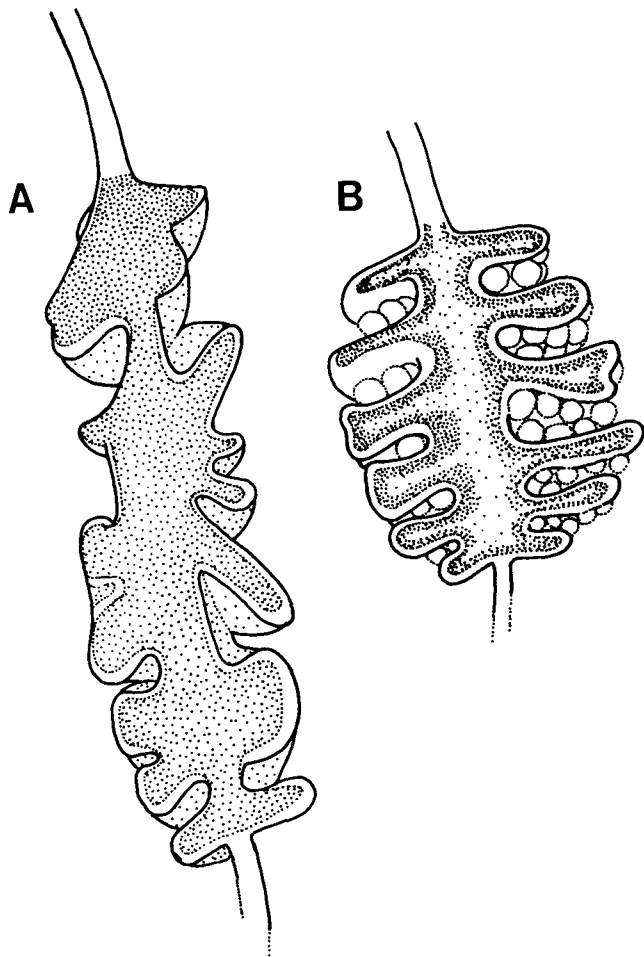


Fig. 4.—A. Gonad of *Octotiarra russelli*.—B. Gonad of *Stomotoca atra*.

Feeding. The medusae of *S. atra*, like those of *Octotiarra russelli*, do not catch *Artemia* nauplii with their tentacles; those of *S. atra*, however, are able to catch their prey with the lips. They usually remained on the bottom of the finger bowl, pulsating so as to crawl around; the two large tentacular bulbs preventing the medusa from rolling. A similar behaviour has been described by Larson (1982) in *Stomotoca pterophylla*. Mills (1981), however, described *S. atra* as an active swimmer, mainly feeding on other medusae.

No matter how much food is ingested, the part of the manubrium deprived of gonad remains empty, all the food passing into the part with the gonad. The manubrium, then, can be divided into a non-digestive pharynx and a digestive stomach. The tentacular bulbs become larger during digestion, being filled throughout the radial canals by the nourishing mixture deriving from the digestion of the prey. Their size, then, can be variable according to the amount of ingested food. The same phenomenon has been observed by Boero in *Phialella* spp. (1987) and in *Sarsia* spp. (unpublished) and is possibly generalizable to all hydromedusae.

Development of gonads. The so-called gonads of the Pandeidae we have studied are nothing other than folds in the manubrial wall. The development of the gonad of *Stomotoca* shows that on both sides of each arm of the cruciform manubrium a series of folds is formed, quite indistinct in the beginning, but becoming increasingly more evident. The gametes are produced in the grooves

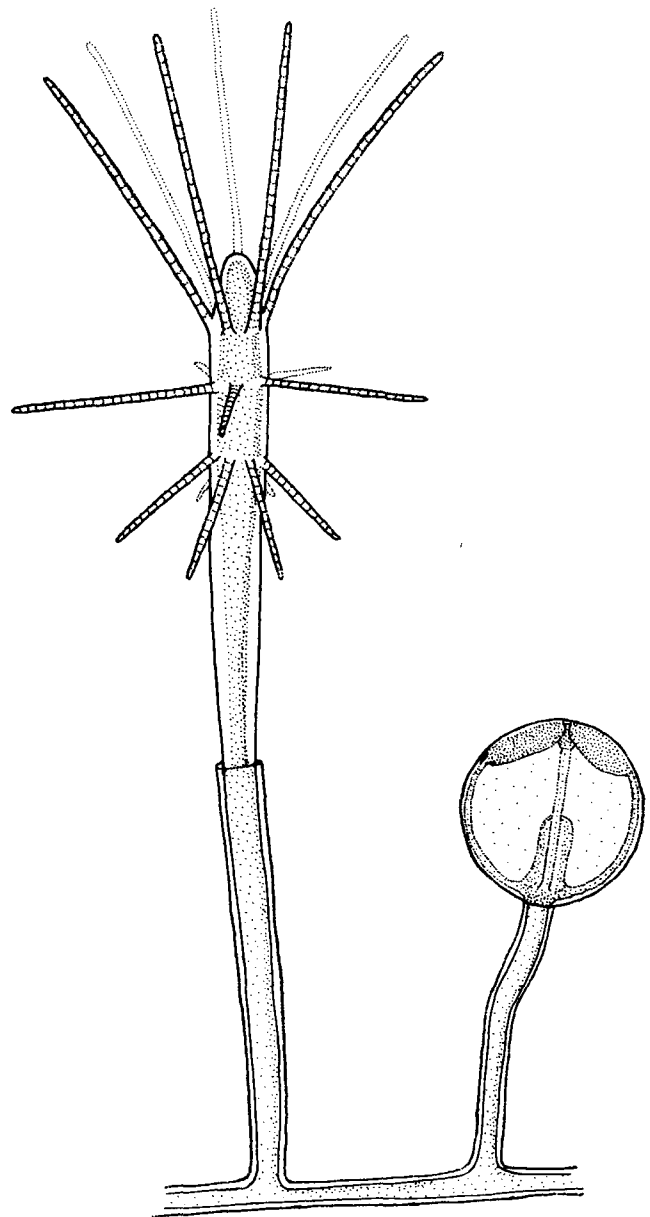


Fig. 5. *Stomotoca atra*. Hydroid and medusa bud.

of the folds. This architecture of pandeid 'gonads' increases the surface of the manubrium so that more gametes may be produced, but the sexual products are formed on the manubrial wall just as in simpler anthomedusae such as the Corynidae. As a matter of fact, the hydromedusae do not have specialized organs (gonads) for production of gametes. In the pandeids it is not the gonad which is particularly complicated, but simply the manubrial wall. The sexual products need a great quantity of nutrients for their development and one of the best positions for them is right on the other side of the digestive part of the manubrium, where energy transfer occurs over a very short distance. In hydromedusae, as well as in hydranths, a definite correlation exists between the development of zones of cell proliferation (budding zone, sexual zone, cnidogenous zone, etc.) and the accentuation of the assimilatory function (see Bouillon 1956, 1968). The increase in surface of the manubrial wall, via the folds, is not only a way to produce more gametes, but also to have a higher ability of assimilation. The two phenomena are strictly linked.

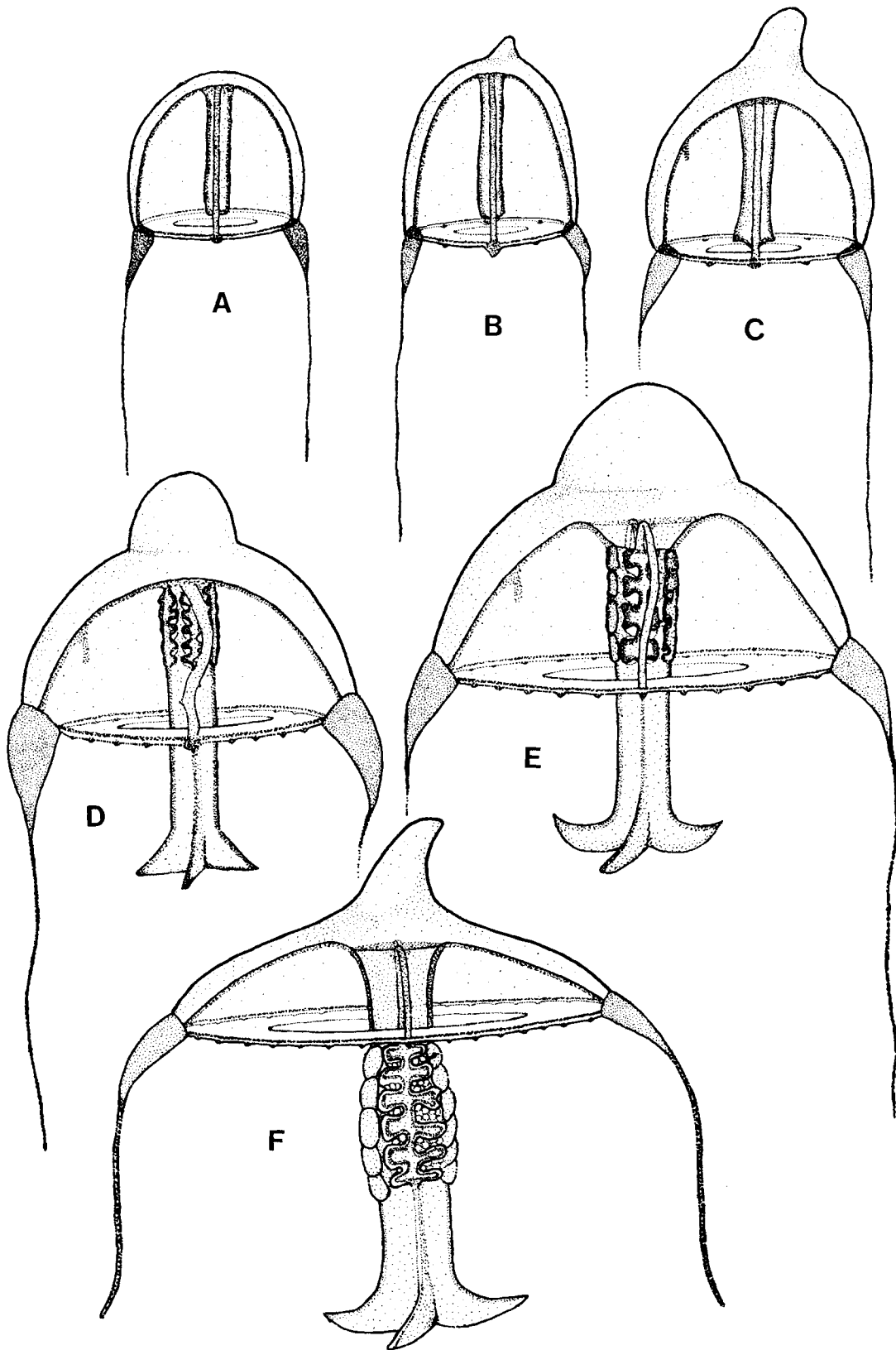


Fig. 6. *Stomatoca atra*.—A. Newly released medusa.—B. Two-day-old medusa.—C. Eight-day-old medusa.—D. Twelve-day-old medusa.—E. Twenty-day-old medusa.—F. Adult medusa collected from the plankton.

The maturation and liberation of the sexual products are not simultaneous, so that the release of gametes by an individual is protracted in time and, presumably, also in space. We could not establish whether a specimen can become mature only once or whether the gonad can go through a series of maturations, as happens, for instance, in *Phialella zappai* Boero (Boero 1987).

Discussion

The two species described here are very different in both the hydroid and medusa stages. As remarked in the Introduction, however, in these species the newly released medusae are typically pandeids and this feature possibly allows the assignment of both species to the

Pandeidae. However, the erection of subfamilies, as proposed by Arai & Brinckmann (1980) and Petersen (1979), seems appropriate.

Stomotoca is an outstanding example of how the hydroid and the medusa stage of a given genus can undergo divergent evolution, so that in some species the hydroids are diverging, in others the medusae (see Boero & Bouillon 1987; Boero & Sarà 1987 for detailed discussions). In the case of *Stomotoca* there is one species, *S. atra*, with 'normal' hydroids, and *S. pterophylla* with parasitic hydroids, formerly referred to the genus *Hydrichthys* (see Larson 1982). The medusae of the two species can be easily confused, due to their great similarity, whereas without knowledge of the life cycles their hydroids might be referred to separate families. Adaptation to parasitic life has evidently played a major role in the evolution of the hydroid stage of some species of *Stomotoca*, but the morphology of the medusa allows retention of both parasitic and free-living forms in the same genus.

The hydroid of *Octotiarra*, if compared with other hydroids known to be symbiotic with bryozoans, shows that adaptation to a particular microhabitat can be in various ways. An almost constant feature of hydroids symbiotic with bryozoans is the presence of a specialized hydrorhiza which, in many of the species, can grow under the skeleton of the bryozoan (Osman & Haugsness 1981; Riestedt & Schuhmacher 1985). In some species, however, it grows on the bryozoan (as in *Perarella*), whereas in *Hydranthea margarica* (Hincks), the only thecate hydroid known to be associated with bryozoans, the hydrorhiza is loose on the surface of the bryozoan, being anchored to the skeleton of the host by specialized perisarcal projections (Boero & Sarà 1987). The hydranths of hydroid species symbiotic with bryozoans are of different morphology, ranging from species with many scattered tentacles (*Zanclaea*) to polymorphic species, deprived of tentacles (*Halocoryne*). *Octotiarra*, if compared with *Perarella schneideri* (Motz-Kossowska), the only other filiferan known to be associated with bryozoans, shows oligomerization of the tentacles. Decrease in number of tentacles and in size seem to be common features characterizing the different evolutionary trends leading to specialized associations of hydroids with bryozoans. This is possibly due to the utilization by the hydroid of the feeding currents generated by the lophophores, with a passage from macrophagy to microphagy.

Conclusion

Too many life cycles of the Pandeidae have still to be studied to propose a possible phylogeny of the family at the generic level. It is evident, from the present results, that both stages have to be taken into consideration, even if, at least in the Pandeidae, the medusa generation is far more constant in general morphology and development than the hydroid; thus exactly the opposite happens in this family as compared to some Campanulinidae *s.l.*, in which it is the hydroid stage that is uniform and the medusa that is varied.

The great variation in morphology and biology of these

hydromedusae provides a unique opportunity to study phenomena of adaptation, convergence and divergence in a single group. The simplicity of the organization plan of cnidarians, furthermore, allows an easier comparative analysis of the different forms, so that evolutionary trends can be constructed relatively easily, owing to the lack of redundancy in characters. Cnidarians provide an outstanding 'model' for researches in experimental biology and will possibly prove to be a useful 'model' for studying the basic rules of evolution.

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