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Bi-directional conversion in *Turritopsis nutricula* (Hydrozoa)*

GIORGIO BAVESTRELLO¹, CHRISTIAN SOMMER² and MICHELE SARÀ¹

¹Istituto di Zoologia dell'Università, Via Balbi 5 I-16126 Genova.

²Ruhr-Universitaet Bochum, Institut fuer Spezielle Zoologie & Parassitologie, D-W-4630 Bochum.
Germany.

SUMMARY: The transformation of degenerating young medusae of the clavid hydroid *Turritopsis nutricula* into polyps is described. Under laboratory conditions the medusae settled on the aquarium bottom and produced stolonal structures from which new polyps arose. This process differs from the more common asexual production of polyps from the free swimming medusae because the transformation involves the whole medusa. The conversion of the young *Turritopsis* medusa into polyp is one example of how the general succession from polyp to medusa stage in the life cycle of Hydrozoa can be reversed.

Key words: Developmental conversion, evolutionary biology, hydromedusa, life cycle.

INTRODUCTION

In the life cycle of hydroids, two alternative morphs are often present: a benthic, polypoid stage and a planktonic, medusoid. These two stages differ in morphology, behaviour, habitat, their types of somatic cells (SCHMID, 1974) and their method of reproduction.

The polyps and the medusae can be derived in ways different to the typical life-cycle, where the medusa arises asexually from a lateral bud of a polyp and the polyp is the product of sexual reproduction of medusae. Several free swimming medusae are able to bud new medusae or functional polyps that remain in connection with the medusa and which are able to bud new medusae (MILLS, 1987). In *Clytia mccradyi* (BROOKS, 1888) and *Eirene elliseana* (AGASSIZ and MAYER, 1902) gonothecae arise from the gonads of the medusae. In *Eirene exanemalis* a free swimming polyp buds a me-

dusa that develops while the polypoid structures are completely resorbed (BOUILLON, 1983). In all these cases it is possible to regard the relationships between the two morphs as adaptations to particular habitats. In particular the life-cycle adaptations to life in the open ocean have been discussed by MILLS (1987).

Studying medusae of *Eucheilota paradoxica* reared under different temperatures CARRÉ and CARRÉ (1990) demonstrated that at 15 °C one or two polyps arise from the radial canal. The development of these polyps is accompanied by a simultaneous regression of the medusa. This situation is the opposite to that described by BOUILLON (1983) in *Eirene exanemalis*.

VAN BENEDEN (1844) showed that, subsequent to the liberation of gametes, medusae of *Obelia* can settle on the bottom and transform into polyps. This observation was confirmed by MEREJKOWSKY (1883) but their accounts must be taken rather cautiously because the two authors did not describe the production of perisarc tubes that are typical of the polypoid stage.

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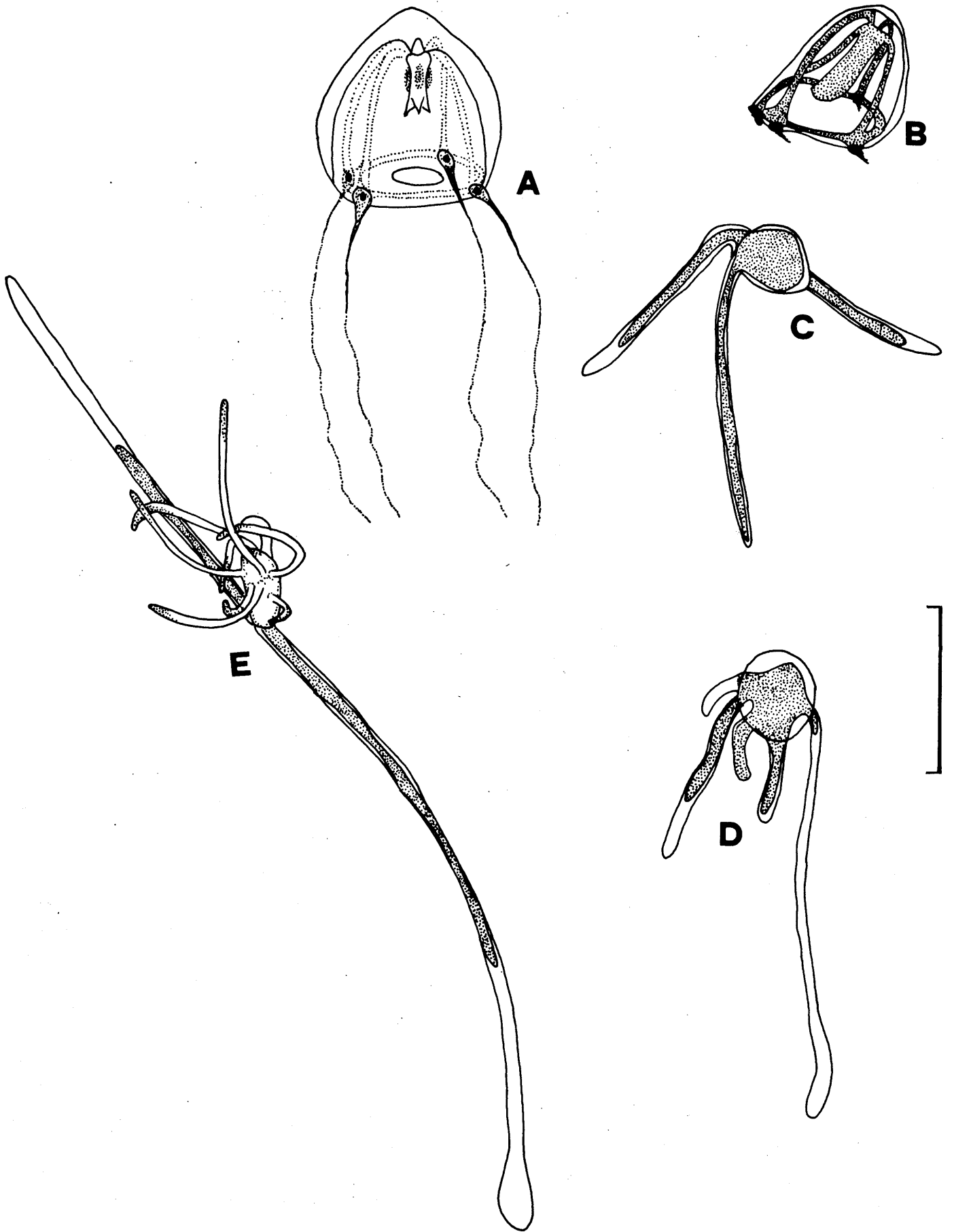


FIG. 1. — *Turritopsis nutricula* A) Newly liberated and B) degenerating medusa. C), D) Stolons arising from degenerated medusae and E) producing a new polyp. Scale bar = 1 mm.

SCHMID (1974) demonstrated that regressive transformation of isolated medusa buds of *Podocoryne carnea* into stolon and polyps was possible. This phenomenon is dependent on the developmental stage of the bud: the probability of bud regression drastically decreases at stage 8/9, when development is divided into ten stages (FREY, 1968). At this time a significant increase in the thickness of the mesoglea probably plays a role in stabilizing the medusoid form. SCHMID (1974) also demonstrated that following dissociation of medusan tissue, the fragments are able to reorganize and produce stolonial and polypoid structures.

This paper describes a case of transformation of medusae into polypoid structures observed in young free swimming medusae of the clavid *Turritopsis nutricula* McCrady. The evolutionary and ecological consequences of this phenomenon in the scenario of the relationships between the two hydrozoan morphs are also discussed.

MATERIAL AND METHODS

Hydroid colonies of *T. nutricula* were collected at 0-5 m depth from the Portofino Promontory (Eastern Ligurian Riviera) in September 1988. The colonies were maintained for several days in petri dishes and fed with nauplii of *Artemia salina*. The hydroids produced several medusae the development of which was observed.

RESULTS

The young medusae (Fig. 1A) swam for 1 or 2 days without taking *Artemia* nauplii and then settled on the bottom of the dish. The process of morphological reorganization started with the umbrella contracting around the manubrium and the tentacles were resorbed. During this process it was possible to observe intensive movements of gonadal cells on the manubrium, similar to those described by GOY (1970) in *Scolionema suvaense*.

After one day some hydrorhizae enclosed in perisarc tubes arose from the manubrium (Fig. 1C, D) and grew across the substratum with a rate of about 1 mm/day. Within a few days 3-5 hydrorhizae per medusa were produced. Occasionally during the growth of hydrorhizae the coenosarc was resorbed and new hydrorhizae produced while the old tubes remained empty (Fig. 1C, D).

In the following days, small polyps similar to those of the original colony, with 6-10 scattered filiform tentacles, arose from the hydrorhizae. Almost all the medusae of our rearing showed development of polyps but it was impossible to feed these polyps in order to study the subsequent development of the colonies.

DISCUSSION

The expression of alternative morphs in hydroids can be assimilated to the discrete plastic response of the phenotype. This was called developmental switch by LEVINS (1968) and associated with the environmental differences of the polyp and medusa (STEARNS, 1982). More recently the process has been discussed as developmental conversion (SMITH-GILL, 1983) with examples from many animal groups including the different morphs of female social insects, alternative modes of adult reproduction, sex changes, the different morphs of batesian mimics in butterflies, and the morphological differences due to cyclo-morphosis in the cladocerans. WEST-EBERARD (1986, 1989) discussed the evolutionary consequences of developmental conversion where the different morphs evolve semi-independently and BOERO and BOUILLON (1989) showed the importance of this phenomenon in the evolution of Hydrozoa.

The present observations on *T. nutricula*, like those of CARRÉ and CARRÉ (1990) on *Eucheilota paradoxica*, demonstrate that, at least in some species of Hydrozoa, the developmental conversion is possible in both directions.

Environmental stress may activate some blocks of genes that were de-activated during ontogeny. This may be true for morphological reorganization and the production of structures such as the perisarc tubes. The production of perisarc structures in medusae is uncommon and known only in the gonothecae of *Clytia mccradyi* (BROOKS, 1888) and *Eirene elliseana* (see AGASSIZ and MAYER, 1902).

Generally in developmental conversion, a critical period exists during which environmental factors may be able to direct subsequent morphogenetic processes in different directions via a genetic switch (SMITH-GILL, 1984). This period is normally short and the following phenotypic transformation irreversible. The expression of alternative morphs in Hydrozoa does not correspond to these aspects of the developmental conversion process. The data of SCHMID (1974) indicate that in *Podocoryne carnea* a long period exists

during which a morphogenetic reversion of medusa buds is possible. The present observations demonstrate that this reversion is also possible in free swimming medusae and that therefore, at least in some species a well defined critical period does not exist and any genetic switch may operate throughout the life cycle. For *Turritopsis*, however, it has to be shown up to what stage of medusa growth this reversal remain possible.

Producing distinct morphs has been interpreted as an adaptive strategy because the two morphs generally occupy two distinct niches and have different environmental requirements. This is relevant for polyps and medusae which also show different reproductive methods.

The occurrence of a free swimming morph may represent a survival chance for a benthic sessile organism (such as hydroid polyps) when environmental disturbances render its habitat unsuitable. Under stressed conditions an acceleration of the production of medusae by hydroid colonies has been described (STEBBING, 1980). In this way the genotype may survive longer. Up to now regressive transformation in Hydrozoa has been exclusively observed in laboratory rearing experiments. If, however, bidirectionality is a natural phenomenon, by avoiding sexual reproduction, it may represent a peculiar mechanism to asexual multiplication for the dispersal of the genotype.

The existence of bi-directional development poses the questions of what are the mechanism and structures which allow a so large phenotypic plasticity and, in this aim, research at the molecular level is required.

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