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STAGING AND INDUCTION OF MEDUSA METAMORPHOSIS IN *CARYBDEA MARSUPIALIS* (CNIDARIA, CUBOZOA)

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CNIDARIA
CUBOZOA
CARYBDEA
METAMORPHOSIS
DEVELOPMENT
EVOLUTION
ECOLOGY

ABSTRACT. – The cubozoan life cycle is characterized by the transformation of a solitary benthic polyp into a pelagic medusa. We investigated the morphodynamics and kinetics of this metamorphosis in *Carybdea marsupialis*. Nine stages in metamorphosis are defined. Metamorphosis is induced by a stop of feeding and culturing polyps at temperatures > 28°C. Metamorphosis is inhibited by feeding, but stimulated in the presence of a metamorphosing polyp. The transformation of the polyp into the medusa is localized to the apical half of the polyp, which is reminiscent to metamorphosis in Stauromedusae. The relationship of cubozoan metamorphosis to other scyphozoan and hydrozoan medusa formation modes is discussed.

CNIDARIA
CUBOZOA
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MÉTAMORPHOSE
DÉVELOPPEMENT
ÉVOLUTION
ÉCOLOGIE

RÉSUMÉ. – Le cycle de vie d'un Cubozoaire est caractérisé par la transformation d'un polype benthique solitaire en une méduse pélagique. Nous avons étudié la dynamique morphogénétique de cette métamorphose chez *Carybdea marsupialis*. La métamorphose, que nous avons divisée en 9 étapes, est induite par une privation de nourriture ainsi que par une température > 28°C. Le phénomène est inhibé par l'ajout de nourriture dans le milieu, et est stimulé en présence de polypes en cours de métamorphose. La transformation en méduse se produit dans la partie apicale du polype. Ce processus est très similaire à la métamorphose des Stauroméduses. La métamorphose chez les Cubozoaires, ainsi que le mode de formation des méduses chez les Scyphozoaires et les Hydrozoaires sont discutés.

INTRODUCTION

An important question about the cnidarian life cycle is whether the polyp or the medusa represents the ancestral typ (Nielsen 2001). Some hydrozoans and scyphozoans lack a polyp stage and their life cycle has been interpreted as ancestral, and regarding the polyp stage, as a larval specialisation (Boero *et al.* 1998, Bouillon & Boero 2000, Brusca & Brusca 1990, Hyman 1940, Piraino *et al.* 1996). The contrary hypothesis holds that the ancestral cnidarian was a polyp and the medusa is considered to be a specialized sexual state (Collins & Valentine 2001, Nielsen 2001, Salvini-Plawen 1978, Werner 1984).

Phylogenetic analyses of Cnidaria have determined the relationship among the four main taxa that compose it, Anthozoa, Cubozoa, Hydrozoa, and Scyphozoa (Bridge *et al.* 1992, 1995, Brusca & Brusca 1990, Meglitsch & Schram 1991, Odoric & Miller 1997, Petersen & Eernisse 2001, Salvini-Plawen 1978, Schuchert 1993, Werner 1973). From these investigations, a framework has emerged that Anthozoa are the sister group of the remaining Cnidarians which are collectively referred to as Tesserazoa (Salvini-Plawen 1978) or Medusozoa (Petersen 1979). The interpretation of Anthozoa as a sister group of Medusozoa is also supported by a number of morphological characters (Nielsen 2001, Salvini-Plawen 1978) and by mitochondrial chromosome structure (Bridge *et al.* 1992).

Medusae are formed through different processes in the three medusa bearing classes. In cubozoans, the polyp goes through a metamorphosis and becomes a medusa, the tentacles of the polyp are reduced and become sense organs, and new medusa tentacles differentiate (Werner *et al.* 1971, Werner 1973, 1975, 1984). Cubozoans were orginally classified within the Scyphozoa (Cubomedusae) based on distinct morphological characters as rhopalia, gastric filaments, eyes and the tetraradial shape of the medusa (Berger 1898, 1900, Claus 1878, Conant 1897, 1898, Hyman 1940, Okada 1927,

Uchida 1929), these still represent synapomorphies between both classes (Salvini-Plawen 1987, Schuchert, 1993). In scyphozoans, medusae are formed through a process of transverse fission (strobilation) of the polyp below the tentacle disc or calyx. By comparison, in hydrozoans, the polyp typically forms lateral medusae buds, which detach as free-living medusae or remain attached as variously reduced medusoid reproductive units (for review see Bouillon 1981, 1985, Bouillon & Boero 2000, Brusca & Brusca 1990, Hyman 1940, Meglitsch & Schram 1991, Nielsen 2001, Salvini-Plawen 1978, Tardent 1978, Werner 1984). Thus, the evolutionary differentiation of medusae (Medusozoa, Medusogona) has been considered to be at least diphyletic (Salvini-Plawen 1987).

The cubozoan metamorphosis was detected by Werner *et al.* (1971) in *Tripedalia cystophora* and characterized as a complete transformation of the solitary radial symmetrical polyp into a tetraradial medusa. In a number of further studies histology and life cycle of *Tripedalia cystophora* and other cubopolyps has been described (Arneson & Cutress 1976, Chapman 1978, Cutress & Studebaker 1978, Werner 1975, 1983, 1984, Werner *et al.* 1976, Yamaguchi & Hartwick 1980, Yamasu & Yoshida 1976). Although these studies are nicely in accord with the classical concept that the medusa corresponds the (transformed) pelagic form of a solitary benthic polyp, it was less clear whether the entire polyp undergoes metamorphosis or only a part of it. In order to gain a better understanding of the kinetics and mechanisms of metamorphosis, we investigated the kinetics of metamorphosis in another cubozoan species, *Carybdea marsupialis*.

MATERIAL AND METHODS

Animals: Polyps of *Carybdea marsupialis* (Linné, 1758) were a kind gift of Dr J Jarms (Zoological Institute, University of Hamburg). The animals were the offspring of an original culture established by late Dr Bernhard Werner (Biologische Anstalt Helgoland, Hamburg) in 1978. Animals were kept in artificial seawater (Tropic Marin), pH 7.5-8.0 at 24 ± 0.3°C in the dark. They were grown on watch glass dishes as substrate and fed 4-5 times a week with freshly hatched brine shrimps (*Artemia salina*); the seawater was replaced about 8 hr after feeding. Mass cultures of the cubopolyps were kept in plastic dishes (500 ml, 5 cm depth, ~ 1000 polyps per dish), which were stored in an incubator allowing various temperatures between 10-30°C. For induction of metamorphosis adult polyps were carefully removed from the glass substrate and kept separately in 24 well microculture plates.

Microscopy: Polyps and medusae were analyzed by using a Wild MP5 stereomicroscope. For micrographs and fluorescence microscropy we used an Axiovert 100 (Zeiss) with neofluar optics and a MC 80 analog camera.

For DAPI-staining, animals were relaxed in Ca^{2+}-free sea water containing 0.2% $MgCl_2$ for 15 min and fixed with 4 % paraformaldehyde in seawater for 12 hr. DAPI staining of PBS (pH 7.2) washed specimens was performed using DAPI at a concentration of 15 µg/ml in PBS buffer (pH 7.2). Under these conditions not only the nuclei are stained, but also the gamma-polyglutamate matrix of differentiated nematocysts (Szczepanek *et al.* 2002). All experiments were carried out in the former laboratory of TW Holstein at the Zoological Institute of the JW Goethe-University at Frankfurt a. Main.

RESULTS AND DISCUSSION

Stages of Metamorphosis

In cubozoans the entire polyp goes through a metamorphosis and becomes a medusa (Werner 1975). To analyze this process quantitatively, we reanalyzed metamorphosis and subdivided it into nine characteristic developmental stages which can be easily distinguished by light microscopy (Fig. 1, 2). These stages define a continuous morphogenetic process which takes about two weeks; it can be reliably induced by a temperature shift from 20°C to 28° (see below).

Steady state polyps

The steady-state polyp, which is ready to undergo metamorphosis corresponds to Stage 0. This solitary polyp is of radial symmetry, has a size of about 1-3 mm and a uniform tube-shaped gastric cavity (Fig. 1A, 2). Three regions can be distinguished along the polyp's apico-basal axis: head region, gastric region, and foot region (Fig. 1A). The head region is comprised by a large, conus-shaped hypostom and a circle of capitate solid tentacles (n = 6-24) at the hypostomal base. On the ultrastructural level, the side of tentacle insertion is additionally characterized by a nerve-ring (Werner *et al.* 1976, Chapman 1978) located immediately apical to the tentacles ("supratentacular" region). Budding of new polyps occurs at the lower end of the gastric region at temperatures below 25°. At higher temperatures there was a significant shift of the budding region towards the apical end. Polyps undergoing metamorphosis can have buds initially, but they never begin to propagate asexually when metamorphosis was initiated. Throughout metamorphosis, the polyp is embedded with its foot region in a muccous-like peridermal cup, which attaches the polyp to the substratum.

Formation of the medusa anlage

During the first phase of metamorphosis (stage 1-4), several changes occur which are restricted to the

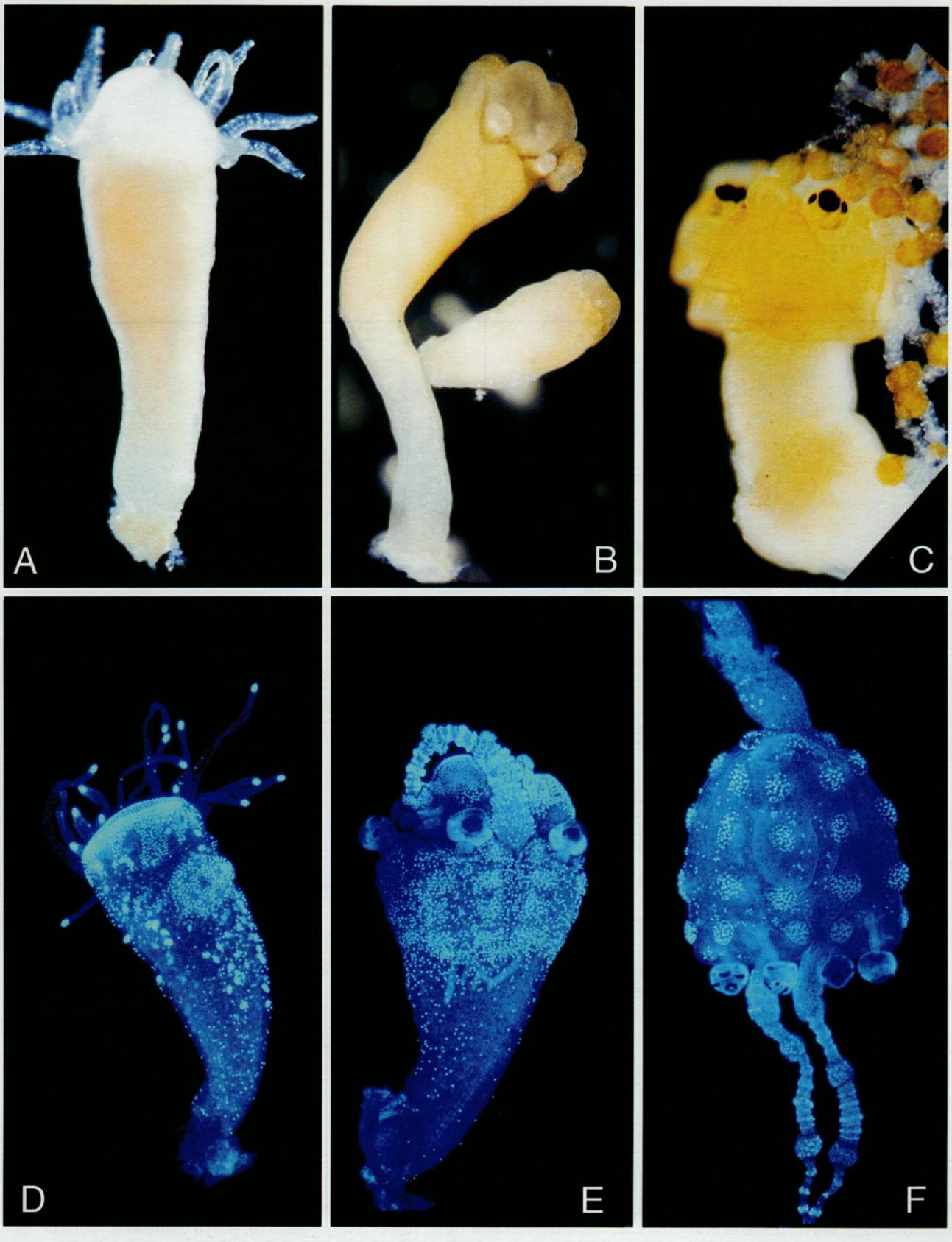

Fig. 1. – Metamorphosis of *Carybdea marsupialis*. A-C, macrographs show the transformation of a steady state cubopolyp (stage 0; A) into a medusa which occurs mainly at the oral end of the polyp; B, stage 5 and (C) stage 7 correspond to Fig. 2E, G, respectively. Note the polyp bud in (B) which also undergoes metamorphosis. D-F, Pattern of nematocysts as visualized by DAPI-staining in a stage 0 polyp (D), a polyp in the midth (stage 5; E) and a polyp at the end of metamorphosis (late stage 8; F). For clarity the stage 8 polyp (F) is inverted by 180°C which corresponds to the orientation of a detached medusa. Note the pseudostenoteles at the tip of the tentacles in (D) and the rudiment of the polyp's stalk at the top of the exumbrella in (F). Maginifications (A-C) X 47; (D-F) X 50.

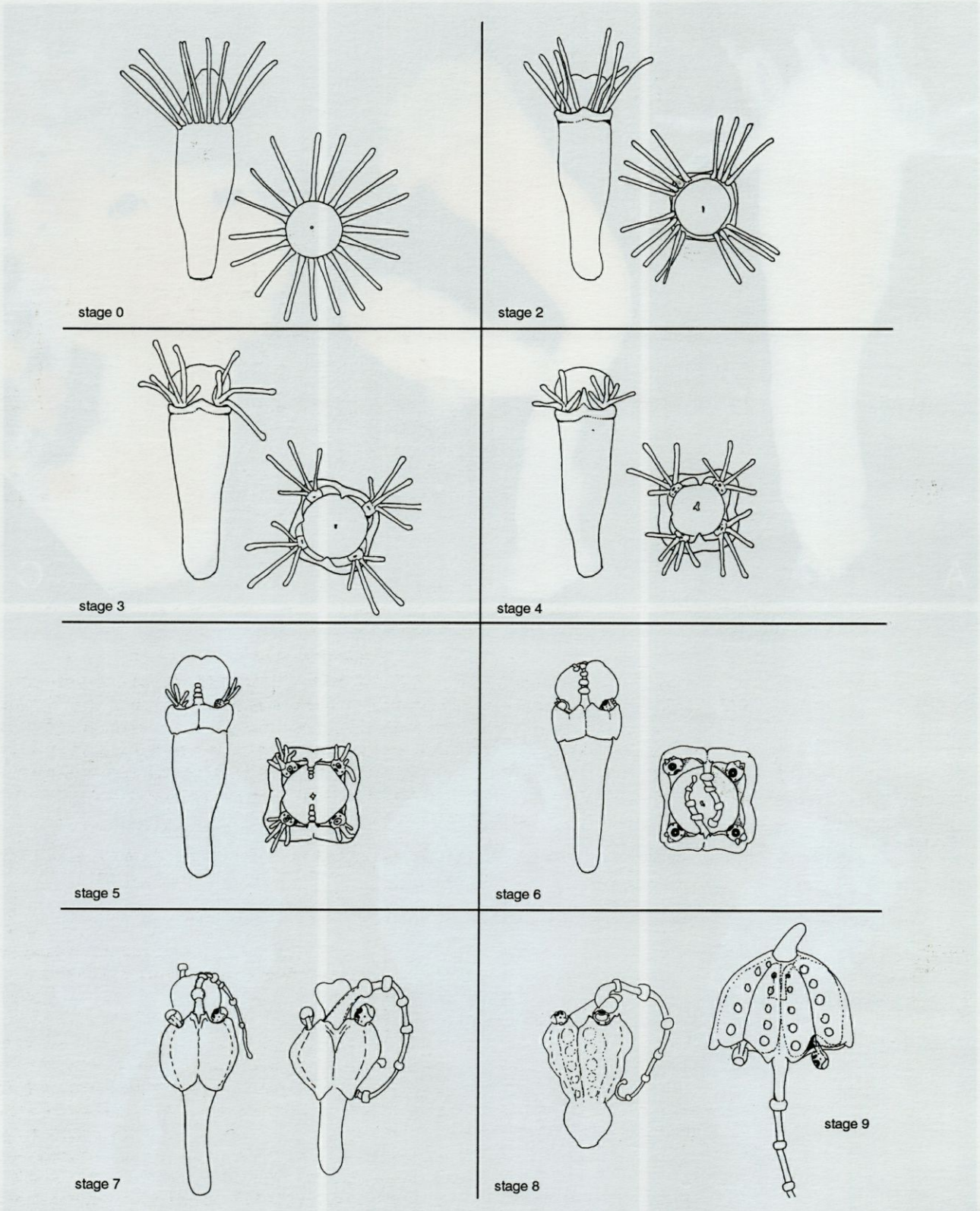

Fig. 2. – Schematic drawings of characteristic stages of cubozoan metamorphosis (*Carybdea marsupialis*). (Stage 0-6) for each stage the lateral and oral views are depicted left and right, respectively (stage 0), polyp exhibits a "perfect" radial symmetry; (stage 2), extension of the hypostomal region and concentration of the polyp's tentacles in four quadrants; (stage 3), fusion of the polyp's tentacle bases and appearance of pigmented eye spots; (stage 4), appearance of the medusa tentacles; (stage 5), fully differentiated eyes and rudiments of polyp' tentacles; (stage 6), disappearence of the polyp's tentacles, elongated medusa tentacles; (stage 7) lateral view of an early and late stage 7 polyp; (stage 8) late stage 8 polyp, the polyp's stalk region becomes reduced and the hypostomal region acquires a bell-like shape; (stage 9) early detached fully metamorphosed medusa with rudiment of the polyps stalk at the tip of the exumbrella (compare Fig. 1F).

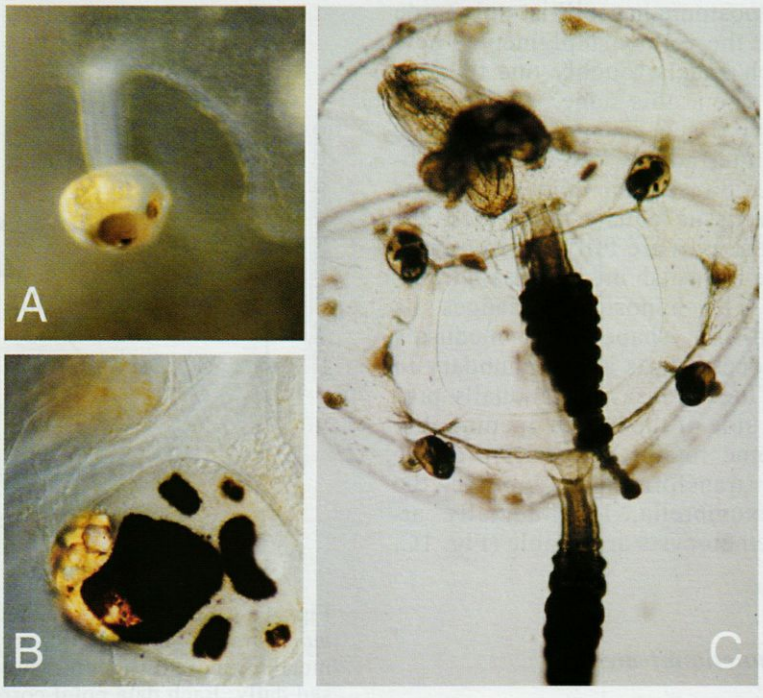

Fig. 3. – Detached, fully differentiated medusa of *Carybdea marsupialis*. (A-B) Rhopalium and lens eyes in a macroscopic (A) and microscopic view (B). Free swimming medusa exhibiting the velarium, two tentacles with thickened pedalia, the four rhopalia and the manubrium with gastral filaments inside (C). (A) X 100; (B) X 150; (C) X 45.

apical region of the polyp, i.e. to the hypostomal and subhypostomal region (Fig. 2). This tissue becomes gradually pigmented and aquires a tetraradial symmetry while the rest of the polyp retains its radial symmetry. During stage 1 (not shown in Fig. 2), a furrow forms in the basal hypostomal region at the boundary to the side of tentacle insertion, so that a disitinct bulge-like ring of subhypostomal tissue forms just below the tentacle base. This furrow progressively invaginates during metamorphosis and represents the shaping force for the formation of gastric cavities and subumbrellar space. During stage 2, the tentacles become displaced into four distinct groups with 4-6 tentacles, which is the first visible step in the transformation of the radial symmetry towards a tetraradial symmetry. Simultaneously, the hypostomal and subhypostomal region expand (Fig. 2, stage 2). In stage 3 a furrow (hypostomal furrow) forms at the base of the lower hypostome thereby separating the hypostomal region from the rest of the polyp (Fig. 2, stage 3). In each of the four tentacle groups, tentacle bases begin to merge and at their common base a pigmented spot appears. This pigmented tissue will finally differentiate into the lens eye of the medusa (Fig. 3A-B). Stage 4 is characterized by the emergence of the first anlage of the medusa tentacles, which differentiate interradially (Fig. 2, stage 4). Only one of the two tentacle pairs grows further during metamorphosis; the second pair completes differentiation not before the young medusa. Additionally, further pigmented spots appear in the eye anlage. Interestingly, also the entire ectodermal tissue of the presumptive medusa is acquiring a yellowish colour, which might reflect an increased tissue turnover or cell differentiation.

Setting up the medusa body plan

During the second phase of metamorphosis (stages 5-7) the redesign of the polyp continuously extends towards a basal direction (Fig. 1B-C). This process includes an invagination of the circular (hypostomal) furrow and the formation of four gastric pockets. By these changes the polyp acquires a tetraradial symmetry. During stage 5 the distal parts of the polyp's tentacles are progressively resorbed and the rhopalia further increase in size (Fig. 1B, Fig. 2, stage 5). Each rhopalium finally differentiates six eyes, and by invagination of the two large central pigment spots the lens eyes are formed. Apically, a statolith differentiates which is easily visible by its crystalline inclusions. The medusa tentacles elongate and form an increasing number of circular nematocyst battery cells. Thereafter (stage 6), the polyp's tentacles are completely absorbed and the eye stalk becomes visible (Fig. 2, stage 6). The medusa's tentacles contract, grow, and differentiate battery cells with mounted

nematocysts. The hypostome has still ist polypoide conus-like shape, but the yellowish pigmented new medusa tissue, which equals roughly one third of the polyp's original size at this stage, is contrasted from the whitish polyp tissue. The gastric filaments which differentiate interradially can be easily observed through the transparent body wall. At stage 7 the medusa tissue equals about half the original tissue, and the eyes are fully differentiated (Fig. 2, stage 7). The brownish medusa has a transparent appearance. The hypostome changes its shape into a bell-like shape, the medusa's manubrium. This process starts at the boundary to the gastric cavity of the medusa and gradually progresses to the apical side of the mouth opening, but notably the hypostome retains its position at the apical end of the transforming polyp. In the ectoderm of the exumbrella, longitudinally arranged clusters of nematocysts are visible (Fig. 1C, Fig. 2, stage 7).

Liberation of the functional medusa

During the final phase of metamorphosis the medusa attains its final shape and becomes functional. In stage 8 the hypostome (manubrium) becomes rapidly translocated into the interior of the medusa, and nematocytes are restricted to the squarelike opening of the manubrium (Fig. 2, stage 8). At the side of the exumbrella the longitudinally arranged nematocyste clusters are visible. Mostly the tentacles are retracted inwards to the subumbrellar cavity so that the velum is visible. The medusa begins to contract regularly, and at the final stage 9 the young, bell-shaped medusa detaches from the peridermal cup (Fig. 2, stage 9). Frequently, one can find at the tip of the exumbrella a pointed piece of the rest of the polyps basal end, which is absorbed within a few hours (Fig. 1F). The umbrella has a diameter of about 2.5 mm depending on the polyp's original size. The early detached medusa lacks pedalia and velar channels, but it can catch and digest prey.

In summary, about three weeks are required from the induction of metamorphosis until the detachment of the medusa. A quantitative analysis of the length of individual developmental stages on an absolute time scale (Fig. 4) revealed that each stage required about 36-42 hours. This progression was roughly linear with a mean variation of only 36 hr, indicating that we selected representative developmental stages for the staging scheme of metamorphosis.

Differentiation of a medusa-specific cnidom

The medusa of *Carybdea* possesses medusa-specific nematocysts (cnidom), which differ from

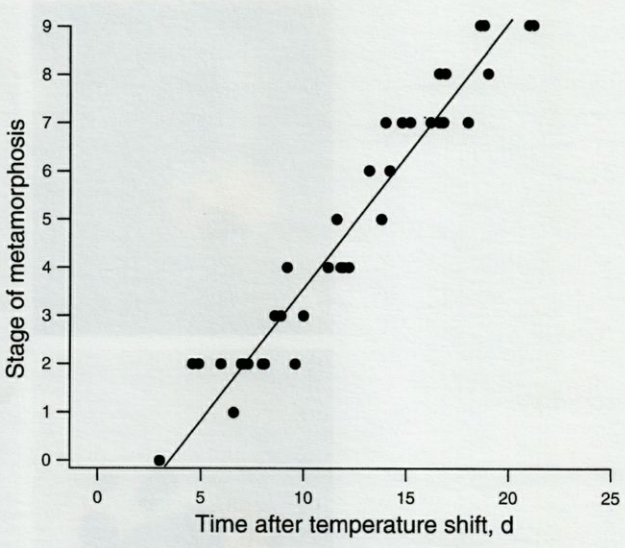

Fig. 4. – Time course of metamorphosis in *Carybdea marsupialis*. Cubopolyps were kept at 20°C, induced to metamorphose by a temperature shift to 28°C and analysed daily. Each data point corresponds to the average of five animals, and ordinate indicates time after temperature shift.

those of the polyp. The polyp has pseudo-stenoteles and microbasic euryteles while the medusa has heterotrichous microbasic euryteles and microbasic mastigophore, atrichous, basitrichous, and holotrichous isorhizas. The medusa-specific nematocysts begin to differentiate during early metamorphosis. Differentiation stages can be visualized by staining with the cationic dye DAPI which binds the polyanioc rich matrix (gamma-polyglutamate) of nematocysts tightly (Szczepanek *et al.* 2002) (Fig. 1D-F). During metamorphosis, the large, polyp-specific pseudo-stenoteles of the polyp (Fig. 1D) rapidly disappear and we presume that they undergo apoptosis. At stage 6 of metamorphosis large (13.3 ± 1.6 μm) and small haplonemes (5.4 ± 0.6 μm) begin to form a highly regular pattern which finally ends in eight bands of five clusters each on the surface of the presumptive exumbrellar ectoderm (compare Figs. 1E and 1F). These nematocyst bands extend from the apex of the presumptive medusa up to the region where tentacles and ropalia are inserted (Fig. 1F). Interestingly however, these nematocyst bands do not colocalize with the site of tentacle insertion, but they rather define the tissue located between the tentacles and rhopalia, i.e. the "interradii". During further growth of the exumbrella the distance between these clusters increases, but neither the number of clusters nor the number of bands increases until the medusa is fully differentiated. In the medusa tentacles ring-like batteries consisting of heterotrichous microbasic euyteles (15.9 μm ± 10.6 μm) and tentacle-specific isorhizas differentiate.

Induction of Metamorphosis

Cubozoan polyps of *Tripedalia cystophora* can spontaneously metamorphose into a medusa (Werner *et al.* 1971). To induce metamorphosis in *Carybdea marsupialis* we explored three environmental parameters: feeding, temperature and population density. We found that the polyps, which were cultured at temperatures varying from 18°C to 28°C, never underwent metamorphosis at temperatures lower than 23°C. However, higher temperatures seemed to be permissive, and sometimes the majority of polyps in a culture dish metamorphosed. We therefore analysed the effect of temperature on metamorphosis first. For that, daily fed polyps were selected. They had an average of 16-17 tentacles (Fig. 1A) and could propagate asexually by budding. These polyps were cultured for a period of two weeks at temperatures of either 20°C or 24°C. Thereafter, the polyps were kept at 28°C without further feeding. Figure 5A shows that both, at a sudden temperature shift from 20°C to 28°C (filled triangles) and a temperature shift from 24°C to 28°C (filled squares) reliably induced metamorphosis in all polyps. Under these conditions the first signs for metamorphosis, e.g. formation of the subhypostomal bulge (stage1) and displacement of the tentacles (stage 2), appeared after 5 and 7 days respectively, and metamorphosis was complete at about 20 days. By comparison, a temperature shift from 20°C to 24°C (filled circles) could also induce metamorphosis, but it was not sufficient for finishing metamorphosis. Metamorphosis was stopped at stage 2 to 3 in such polyps which continued to propagate asexually afterwards. This indicates that not a relative increase in temperature, but rather an increase over a critical threshold temperature of 24°C is required for metamorphosis in *Carybdea marsupialis*.

We also found that the population density had an effect on metamorphosis. When polyps were kept at a high density (1 polyp/ml), progression of metamorphosis was slowed down at late stages (Table I) compared to polyps cultured at low density (1 polyp/30 ml) which finished metamorphosis after 20 days. Interestingly, however, the presence of metamorphosing polyps also exerted a stimulatory effect on metamorphosis. Figure 5B shows a co-culture experiment where an already metamorphosing polyp was placed into a culture dish. In such a co-culture the fraction of polyps starting metamorphosis after a temperature shift from 20 to 24°C (filled circles) significantly increased. While in normal cultures only 40% of all polyps started metamorphosis, in the co-culture 75% started metamorphosis. More dramatically, about 8% of the co-culured polyps reached the medusa stage, while in normal cultures metamorphosis stopped at stage 2-3 (Fig. 5A). Even after a temperature shift to 28°C, which reliably induced metamorphosis (Fig. 5A), we found that the efficiency of metamorphosis was significantly higher as kinetics were shortened by about 2 days (Fig. 5B). This indicates that metamorphosing polyps release a factor stimulating and maintaining metamorphosis.

Table I. – Influence of population density on the induction metamorphosis in *Carybdea marsupialis*. Polyps were cultured at 20°C or 24°C and fed every second day. Metamorphosis was induced by a temperature shift as indicated. In the high density and low density experiment polyps were kept at a density of one polyp per 1 ml and 30 ml seawater, respectively. For the induction and feeding experiment we used high density conditions. The presence of an metamorphosing polyp stimulated metamorphosis (induction), while feeding completely inhibited metamorphosis.

	Stage 0 (polyp)	stages 1-2	stages 3-5	stages 6-8	stage 9 (medusa)
high density					
20°C → 25°C	54%	46%	0%	0%	0%
24°C → 28°C	8%	0%	17%	25%	50%
20°C → 28°C	0%	0%	0%	0%	100%
low density					
24°C → 28°C	0%	0%	0%	10%	90%
induction					
20°C → 25°C	25%	33%	33%	1%	8%
feeding					
20°C → 28°C	100%	0%	0%	0%	0%

Metamorphosis can be blocked by reducing the temperature again down to 20°C. This block is efficient up to metamorphosis stage 7, when polyp tentacles have been completely absorbed and the medusa eyes are already present. Under these conditions the medusa-specific organs regress. After about a week the polyp tentacles have regenerated. This indicates a considerable morphogenetic plasticity of *Carybdea* tissue, which is reminiscent to similar phenomena found in hydrozoans (Hauenschild 1956, Kakinuma 1969, Schmid 1972, 1992, Tardent 1965) and scyphozoans (Kakinuma & Sugiura 1980, Spangenberg 1965).

In a further experiment we tested the effect of feeding on metamorphosis (Table I). In mass cultures that were fed once a week at temperatures of 24°C metamorphosing polyps could be periodically found. However, in cultures which were fed daily over a period of 18 months, we never observed any metamorphosing polyps. Even after a temperature shift from 20°C to 28°C, which is the strongest inducing factor, no polyp started metamorphosis (Table I). This clearly shows that feeding is an efficient inhibitor of metamorphosis in *Carybdea marsupialis*.

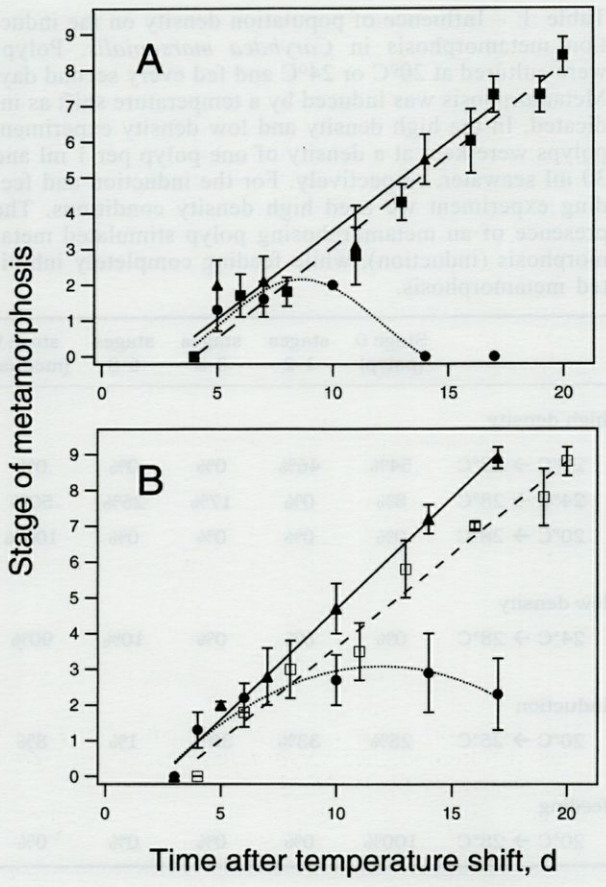

Fig. 5. – The induction and maintenance of metamorphosis requires a shift over a critical threshold temperature. (A) Animals were kept at 20°C or 24°C. At t_0 the temperature was shifted from 20°C to 24°C (filled circles) or to 28°C (filled triangles), and from 24°C to 28°C (filled squares). In animals shifted from 20°C to 24°C metamorphosis is initiated but stops at stage 2-3. (B) Stimulatory effect of a metamorphosing polyp. Animals were kept as in (A), except that a metamorphosing polyp was added to the culture (for details see text).

Medusae represent the gamete producing generation in the cubozoan life cycle. In other cnidarians, the production and release of gametes can be induced by very different external triggers. An increase of temperature can cause the Anthozoa *Anthopleura* to spawn rapidly under laboratory conditions (Siebert 1974), and in *Hydra vulgaris,* which lacks the medusa stage, polyps form gametes in response to starvation within 10-14 days (Hobmayer *et al.* 2001, Martin *et al.* 1997, Miller *et al.* 2000). By comparison light stimuli, which are an important factor for the synchronization of gamete release in hydrozoans (Ballard 1942, Müller 1961) and anthozoans (Baker 1936, Fritzenwanker & Technau 2002, Ryland 1997) have virtually no effects on medusa induction in *Carybdea.*

Medusa formation in Carybdea *is similar to the metamorphosis of the stauromedusa* Stylocoronella

The mode of medusa formation in *Carybdea* shares some similarities with the metamorphosis in Stauromedusae. Polyps of this group do not produce free-swimming medusae by strobilation, as it is typical for other scyphozoans, and adult stauromedusae live attached to the substrate by a stalk. Kikinger & Salvini-Plawen (1995) have shown that the juvenile polyp of *Stylocoronella* develops into a sessile medusa by metamorphosis. The apical half of the metamorphosed medusa bears a number of characters that are similar to adult medusae in other scyphozoans and cubuzoans, e.g. rhopalia, circular coronal muscles gonads and occeli, while the stalk region by comparison retains a polypoid characters such as gastric septa and four longitudinal muscles which are associated with the four peristomal pits surrounding the mouth. This form of metamorphosis is highly reminiscent to the metamorphosis we found in *Carybdea marsupialis*, where the transformation of the polyp was initially restricted to the oral end of the polyp. This is different to *Tripedalia*, where, as in detail described by Werner (1983), the entire polyp appears to undergo a metamorphosis, only leaving the periderm cup of the polyp.

It should be pointed out that in scyphozoans, i.e. in Coronatae, Semaeostomae and Rhizostomae juvenile medusae (ephyrae) are produced by strobilation, i.e. by transverse fission of the ephyra at the oral end of the polyp. While most scyphozoans are characterized by polydisc strobilation, in rhizostomae only a single ephyra develops at the oral end of the polyp. However, monodisc strobilation is different to the stauromedusan and cubozoan mode in medusa formation, since polyps always remain intact after transverse fission of the medusa and continue to propagate asexually.

It has been also proposed that the cubozoan metamorphosis shares some characteristics with medusa formation in the hydrozoan Narcomedusae (Bouillon 1987, Petersen 1979). Similar to Cubozoa the narcopolyps reproduce asexually and subsequently undergo metamorphosis into a single medusa. However, the parasitic narcopolyps are extremely different from other hydrozoan polyps (Bouillon 1987). Both groups are pelagic and have lost their polyp stage, only in some parasitic Narcomedusae a polyp is present, and probably represent a re-evolved polyp-like stage.

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