

Cloning and dispersal by buoyant autotomised hydranths of a Thecate hydroid (Cnidaria; Hydrozoa)*

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SUMMARY: *Zelounies estrumbordi* gen. nov. sp. nov. is a small stoloniferous thecate hydroid discovered in the coral reefs of La Reunion Island (Indian Ocean). In culture it released hydranths that were able to lead a free pelagic life before settling to develop a new benthic colony. The process passes through the following stages; 1) modification and broadening of the base of the hydranth, 2) detachment autotomy of the hydranth, 3) pelagic life, 4) settlement and attachment at the aboral end by epidermal secretions, 5) contraction of the hydranth, 6) expulsion of waste products, 7) disaggregation of oral end of the hydranth including the loss of tentacles and hypostome, 8) development into an adherent spherule, 9) growth of a hydrorhiza, 10) growth of a small hydranth, the first of the new colony. Stages 4 to 10 take about four days. The autotomy of hydranths, an unusual method of asexual reproduction and dispersal in thecate hydroids, is compared to that of athecates where the behaviour is more common. Implications concerning the biology and ecology of *Z. estrumbordi* are discussed. Observations on feeding and other behaviour are given, including the production of hydrorhizal propagules from fragments of the hydrorhiza of colonies kept in unsuitable conditions.

Key words: Hydroid, cloning, dispersal, autotomy, life cycle

INTRODUCTION

Cloning, under the name of asexual or vegetative reproduction, and dispersal are well known among hydroids (HYMAN, 1940; BOUILLON, 1968; CAMPBELL, 1974; MACKIE, 1974; CORNELIUS, 1981; JACKSON, 1985; HUGHES, 1987; HUGHES, 1989). In most cases cloning is associated with dispersal, when units separate from a parent (benthic or pelagic, polyp or medusa). Such separated units can be produced accidentally (fragmented colonies), by budding (planula-like buds, frustules, free hydranths, medusae), or by fission (frustules, stolonisation, autotomised hydranths, scissiparous medusae). In all these cases dispersal is achieved,

which is in addition to dispersal associated with sexual reproduction (gametes, planulae and medusae) and by rafting of hydroids on mobile substrates (eg. boats, *Sargassum*).

Cloning and dispersal by free hydranths is rare and, with one exception, all previously known examples were athecates. The exception is *Eirene hexanemalis*, which BOUILLON (1983) described as developing from the planula which never settles, but this is the product of sexual reproduction rather than asexual cloning. Free hydranths result from one of the following mechanisms; 1) temporary detachment of a solitary polyp from the substratum, 2) budding, 3) autotomy. Cloning is implicated only in budding. Hydroids of the genera *Climacodon*, *Myriothela* and *Pelagohydra* of the family Margelopsidae are not con-

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sidered here since their entire life-cycle is pelagic (MACKIE, 1974).

Specimens of an undescribed thecate hydroid were cultured with a view to determining the life-cycle of the species. This led to the observation of a mode of asexual reproduction and dispersal by the autotomy of hydranths. The processes are described and discussed in the context of cloning, dispersal and colonization. The description and diagnosis of the new genus and new species, named *Zelounies estrambordi* is in preparation (GRAVIER-BONNET, in prep.).

MATERIAL AND METHODS

Z. estrambordi was found in an aquarium which contained sand, algae and corals from the reef-flat of Saint-Gilles/La Saline on the west coast of the island of La Réunion (Indian Ocean). Two small fragments, bearing one and two hydranths respectively, were transferred to a separate aquarium containing natural unfiltered sea water. After three weeks the species had colonised new substrates by releasing hydranths some of which attached to Petri-dishes which could be removed for regular microscopic examination. The hydroids were observed discontinuously from November 1988 to January 1990. The temperature varied from 23° to 28° and the salinity from 35 ppt. to 40 ppt. according to the season.

Attempts to feed *Z. estrambordi* with *Artemia* nauplii failed as the hydranth died soon after ingestion. However, the hydroids flourished without artificial feeding by feeding on the microflora and fauna that developed in the aquarium (see below).

RESULTS

Z. estrambordi developed small colonies consisting of straight hydrorhizae that supported erect hydranths in short pedicellate hydrothecae (Fig. 1a). In the oldest colonies the growth of several successive pedicels from an original one may lead to the formation of small erect sympods supporting a single distal hydranth. The hydranth has a long column, a proboscoidal (non-conical) hypostome, and a ring of 6 or 7 filiform tentacles. The hydranths can reach 2 mm in length and although greatly contractile cannot retract inside the theca which is only approximately 0.15 mm wide and 0.10 mm long. The gonozoids grow on the pedicel and each produces a single medusa. Ten medusae were observed but only three, all male, reared

to maturity. The colonies derived from the original two fragments were all male.

Asexual reproduction and dispersal by hydranth autotomy.*

Some hydranths were distinguishable from the others because of their broadened base (Fig. 1b) (stage 1). These hydranths eventually detached from the colony immediately above where the hydranth was connected to the theca by desmocytes (stage 2). detachment was effected by either contraction of a tentacle that was temporarily attached to the substrate, or artificially by disturbing the water nearby. Following autotomy the hydrotheca remained empty and no subsequent regeneration of any hydranth was observed. The liberated hydranth entered a free-living pelagic phase (stage 3). The morphology of the hypostome, tentacles and distal column was similar to that of normal hydranths but at the aboral end of the column the gastric cavity was small and both the gastrodermis and epidermis were enlarged. In this region the epidermis contained glandular secretory cells and numerous nematocysts. The limits of individual cells in both layers were inconspicuous. The free hydranths were passively carried by the currents caused by the aeration system. The tentacles, which were up to three times the length of the column, were extended forming a sort of parachute beneath which was suspended the column (Fig. 1c, d). Free hydranths were capable of feeding on the microflora and microfauna in the water (see below, and Fig. 1e). No marking experiments were conducted and it is not known how long a hydranth spent, or may spend, in the pelagic phase. The pelagic phase ended with settlement and attachment. Some free hydranths crept over the substrate, usually by contractions of tentacles that became temporarily adhered to the substrate. The mouth may also become temporarily attached to the substrate when contraction of the hypostome can effect some movement of the hydranth (Fig. 1). Temporary attachment and creeping may occur immediately after detachment from the parent colony. Final attachment occurred at the aboral end of the hydranth by adhesive secretions from epidermal gland cells (stage 4). Immediately before attachment, or at the same time, the hydranths contracted to less than one-third of their original length (Fig. 1g, stage 5). One or more tentacles remained ex-

* Notice: Autotomy in the case of *Zelounies estrambordi* is intended here not as an auto-mutilation for the colony but as a process of self-detachment for hydranths that have been prepared to be separate.

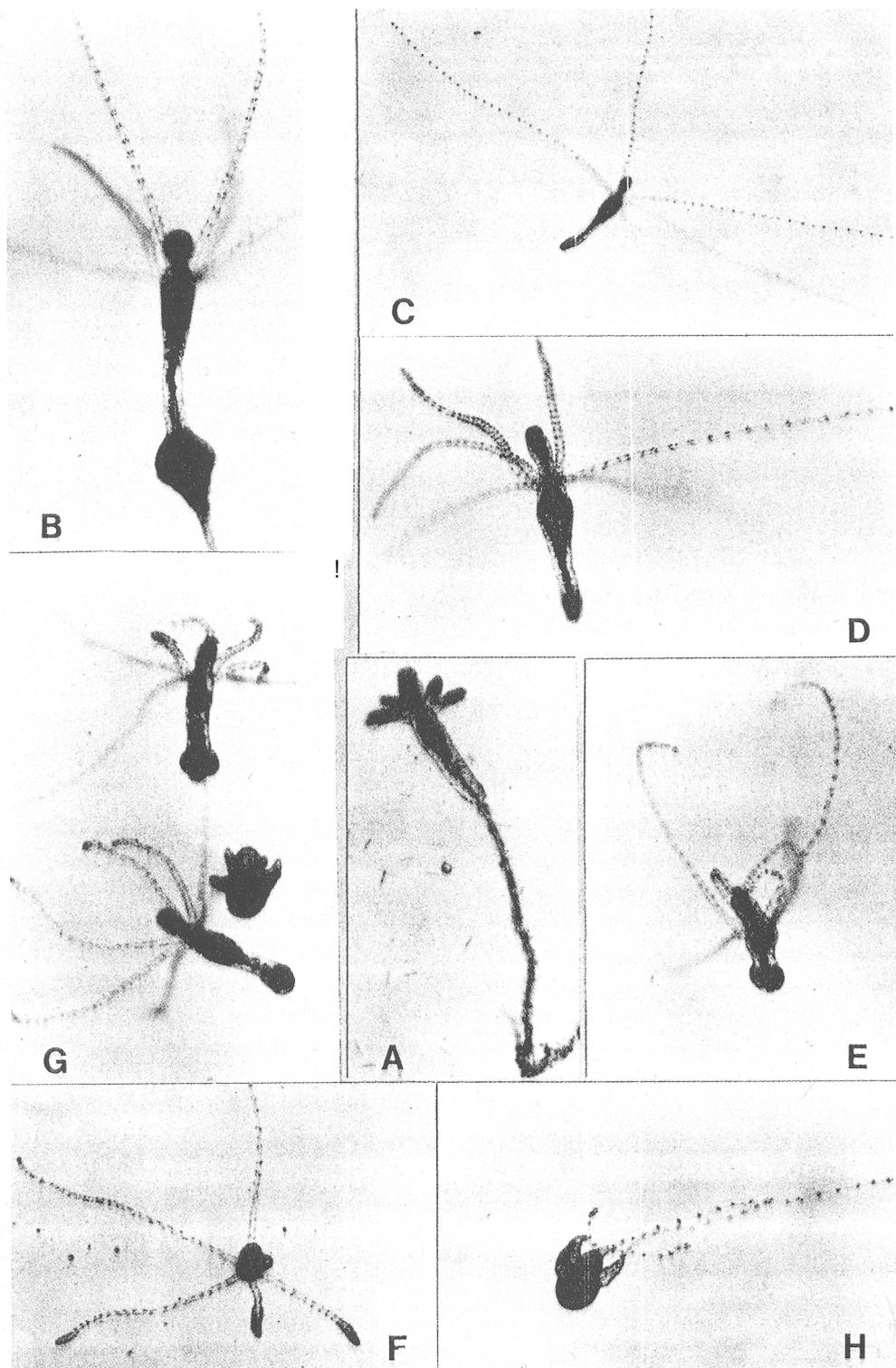


FIG. 1. — *Zelounies estrambordi*. A - Colonial hydranth (notice: the particularly long pedicel, the extended column in 2 parts — pedal proximal, gastric distal — the high hypostome and the fully contracted tentacles). B - Colonial hydranth prior to detachment (notice: the extended column in 3 parts — broadened basal, pedal intermediate, gastric distal — the rounded hypostome and the rings of nematocysts on the tentacles). C - A free hydranth floating (notice the fully extended tentacles and the so large hydroid span). D - Detail of a floating free hydranth (notice: the well developed gastric region, the high tubular hypostome, the two tentacles homogeneously semi-contracted). E - Feeding behaviour of a free hydranth during floating (notice the tentacles in the mouth, the contracted column with broadened base and the long curved tentacles). F - A free hydranth erected on the bottom during creeping, its mouth down (notice: the heterogeneous contraction of the tentacles from the tip; the size of hydranth body diameter compared with that of largely extended tentacles's span). G - Free hydranths lying on the bottom (notice the entire contraction and small size of one of them which is settling; the others are still moving). H - A free hydranth contracting and settling (notice the heterogeneous contraction of the tentacles from the base and the thinness of their tip).

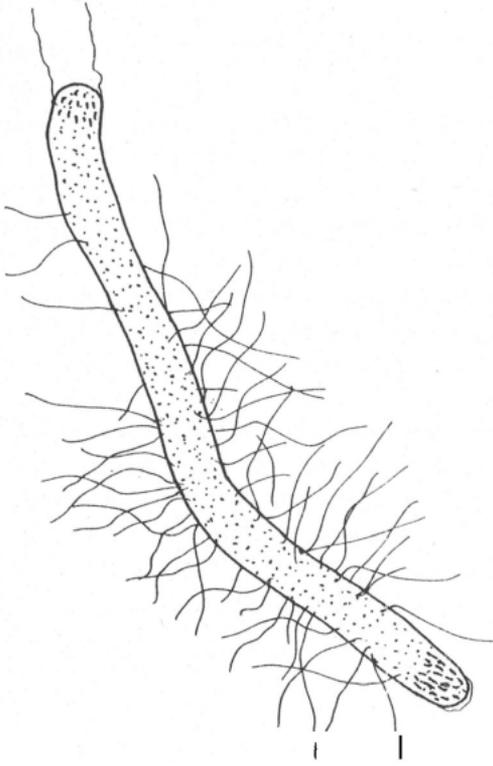


FIG. 2. — Schematic drawing of a frustule (semi-squashed under lamella).

tended or only partially contracted (Fig. 1h). Attachment and contraction was usually followed by the expulsion of waste products from the gastric cavity through the mouth (stage 6). The oral end of the hydranth began to disintegrate (stage 7). The tentacles, hypostome and mouth disappeared and the hydranth was reduced to a small spherical body adhered to the substrate (stage 8). One or two days after settlement a hydrorhiza developed from one side of the spherical body (stage 9) and three or four days after settlement the first new hydranth appeared a short distance along the new hydrorhiza (stage 10). The new hydranths were similar to, but smaller than, the hydranths of the parent colony. One week after settlement the new colonies were composed of a straight hydrorhiza, growing from both ends, supporting one or two functional hydranths. Colonies derived from free hydranths remained small with only a few hydranths. Hydrorhiza were approximately straight and rarely branched. The hydrorhizae did not grow over another nor fuse, despite being of the same clone. In the oldest colony several pedicels had been transformed into simple sympods by the successive growth of up to three hydranths. New hydranths did not regenerate in the theca of an autotomized hydranth but from a bud below the theca.

The influence of environment on development

When left in a dish with no circulation nor aeration of the water the colonies were relatively starved and perhaps lacked sufficient oxygen. In these conditions the hydranths were lost and the coenosarc within the hydrorhiza fragmented. The fragments of hydrorhiza developed into frustules* some of which detached from the colony. They were ovoid in shape with rounded tips and surrounded by a thin perisarc. The gastrodermis appeared to be laden with reserves and the epidermis contained many merotrichous nematocysts of the two main types. Almond shaped nematocysts were concentrated in the tips of the ovoid frustules and did not discharge under pressure. Croissant-shaped nematocysts were more abundant and discharged under pressure. The tubules of discharged nematocysts passed through the thin perisarc to give the frustules a bristled appearance (Fig. 2). After being isolated in Petri-dishes for 9-10 days some frustules developed into erected hydranths, the size of which was proportional to the size of the propagule. About four days later hydrorhizae developed from the base of the new hydranths (Fig. 3-3).

Feeding

Z. estrambordi fed conventionally by passive contact with benthic and pelagic prey. Benthic hydranths extended their tentacles across the substrate, or in the water just above it. When on the substrate the tentacles were indistinguishable among the benthic microorganisms because of their thinness and lack of colour. Benthic hydranths consumed benthic green algae, diatoms, ciliates, sessile protozoans (Actinozoarians?), foraminiferans, rotifers, nematodes and copepods. Pelagic hydranths fed with the tentacles extended as described above and in the aquaria ate principally microflora, but other prey included foraminiferans, nematodes (caught when brushing the bottom) and fragments of crustaceans. Two species of pennate diatom (one spindle-shaped and one box-shaped) were found in different states of digestion in the gastric cavity and inside digestive cells. 138 diatoms were found in one hydranth.

The method of ingestion was different according to the type of prey. Where prey were incapable of movement or of only slow movements (eg. diatoms)

* The frustule is a "larva-like propagule of certain hydroids, produced by budding" or by fission; the propagule is "any form of new individual arising from gametic or agametic reproduction, that will become reproductive itself" (see HUGHES, 1989).

the tentacle bent slowly toward the hypostome and either was wiped across the open mouth or was engulfed and withdrawn through the partially closed mouth. This process removed the prey which were retained in the hypostome. Capture of motile prey (eg. rotifers) caused the tentacle to bend rapidly toward the mouth. The tentacle was either engulfed (as described above) or remained near the mouth while the prey was transferred to the hypostome. The prey were apparently not paralysed and struggled throughout, even when in the gastric cavity.

The yellow pigment of diatoms was concentrated in inclusions of the digestive cells. Empty frustules were expelled but it seemed that they passed into gastrodermal cells first. Undigested fragments were expelled through the mouth after the hydranth had become swollen and the mouth and the hypostome distended.

DISCUSSION

The life-cycle (see Fig. 3).

It is presumed that the release of free hydranths noted in the aquaria is a natural behaviour since it occurred over several months when the colonies grew and multiplied and were apparently healthy. The life-cycle of *Z. estrambordi* includes at least two methods of asexual reproduction which lead to dispersal and clone formation. Gametic reproduction presumably is similar to other thecates with medusae.

The free hydranth of *Z. estrambordi* is unique among the thecates and differs from those of athecates in its mode of formation, detachment and subsequent development. *Z. estrambordi* hydranths undergo a series of tissue transformations after settlement and produce a new colony only after disaggregating into a spherical stage. No other species possessing free hydranths shows a similar behaviour, the formation of new structures occurring by budding from the settled hydranth, as in *Hydra* on *Vannuccia*. Among other thecates a free hydranth has been found only in the life-cycle of *Eirene hexanemalis* but as this is derived from the planula which never settles it is the result of sexual reproduction. Among the athecates life-cycles including free hydranths have been described by several authors. Solitary polyps may alternate free and sessile phases. In *Hydra* separation from the substrate may facilitate dispersal but this is a special behaviour rather than a part of the life-cycle.

Moerisia hydranths become detached and leave a "basal bulb" attached to the substrate which may bud a new hydranth (RITCHIE, 1915). In other capitate hydroids free hydranths are released because of simple separation after budding, for example *Coryne* and *Tricyclusa* (see REES, 1941), or fragmentation (or fission) at the base of hydranths, for example *Euphysa* (see BRINCKMANN-VOSS, 1967) and *Hypolytus* (see MURBACH, 1899). These are viable hydranths that bud after settlement. Free hydranths of *Tubularia* may occur after disintegration of the epithelia at their base. They die after about 30 days and do not resettle but may release sperm or actinula larvae (MACKIE 1966; RUNGGER, 1969). Whether these autotomisms hydranths are an integral part of the life-cycle has been doubted by HUGHES (1983).

The transformations observed in the proximal hydranth of *Z. estrambordi* before detachment may be interpreted as a preparation for the development of the new colony. The gastrodermis is laden with reserves and the epidermis contains many nematocysts, presumably for defence (and possibly for attachment). Epidermal gland cells appear that are not found elsewhere on the hydranth and whose secretions attach the hydranth. No other case of similar transformations before release are recorded, including the detailed study of autotomy of *Tubularia crocea* (RUNGGER, 1969). The development of a hydrorhiza from the spherical body is similar to a few unusual cases where the settled planula first produces a hydrorhiza rather than the more usual primary hydranth. This is the case for *Eutima mira* (BROOKS, 1984) *Eutonina indicans* and *Eucheilota maculata* (WERNER, 1968a, 1968b respectively).

Dispersal behaviour

The free hydranth of *Z. estrambordi* is composed of a long thin column crowned by a ring of extended tentacles, a similar shape to the pelagic hydranths of *Eirene hexanemalis* and to the "parachute" of wind dispersed seeds of the dandelion. This shape is stable in the fluid medium and increased drag facilitates transport (positive buoyancy). RUNGGER (1969) observed that the autotomised hydranths of *Tubularia crocea* were transported by currents in the aquaria with their proximal tentacles folded aborally with the peristome hanging downwards. These hydranths were negatively buoyant and only suspended in the water by drag in currents. This may also be the case in young hydranths of *Coryne tubulosa* which can occasionally be found in the plankton (REES, 1957).

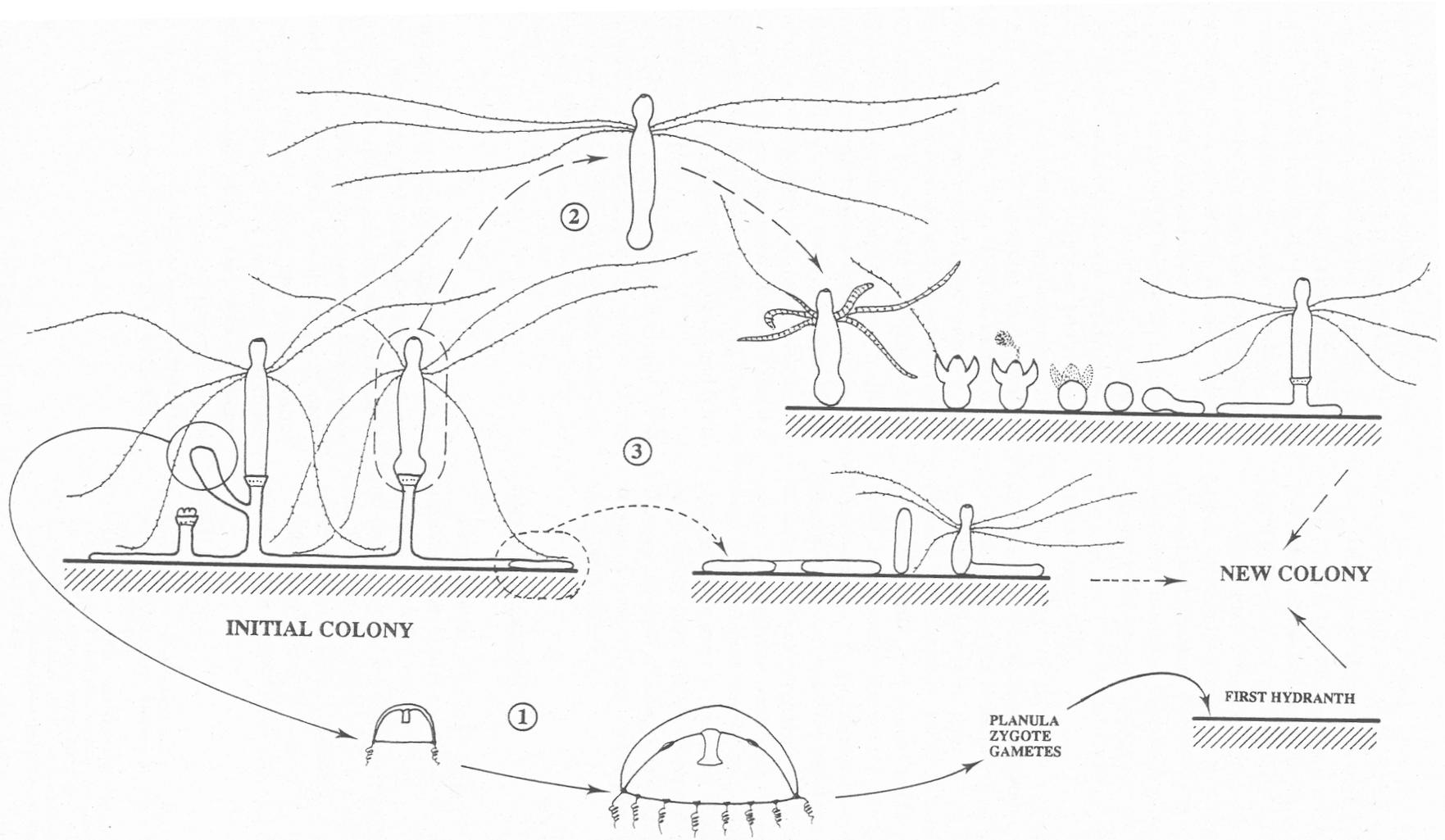


FIG. 3 — Schematic drawing of the life-cycle of *Zelounies estrambordi*: 1) gametic reproduction by medusae; 2) agametic reproduction by frons hydranths (stages 1 to 4 from left to right); 3) agametic reproduction by founder.

Z. estrambordi hydranths can change their shape by extension or contraction of different parts of the body. Of significance is the contraction of the hydranth which promotes sinking to the substrate prior to attachment. RITCHIE (1915) considered that the large vacuolar cells in the tentacles of *Annulella* may assist in buoyancy and similar cells occur in the tentacles and in the gastrodermis of the column of *Z. estrambordi*. RITCHIE's hypothesis needs to be tested experimentally.

Creeping of *Z. estrambordi* hydranths is reminiscent of that of *Hydra*, as described by MACKIE (1974). In *Hydra* nematocysts are involved in the temporary adherence of the tentacles and column to the substrate but this has not been examined in *Z. estrambordi*. Creeping of *Vannucciaforbesii* was described by BRINCKMANN-VOSS (1967). Liberated hydranths do not settle immediately but move around slowly until they affix themselves after some hours or even one or two days. REES (1941) cited observations on young budded hydranths of *Tricyclusa singularis* that use their tentacles to creep about. Besides hydranth creeping dispersal of the colony (genotype) may also occur by frustules that have settled. The frustule develops a tube of perisarc through which it displaces itself. The coenosarc moves from place to place while the perisarc grows from one tip and is left empty behind (see Fig. 2).

The frustules of *Z. estrambordi* temporarily lifted into the water by currents sank as soon as water movement was stopped. They have neither the capacity to float nor cilia with which to move actively the substratum.

Feeding

In contrast to the generally accepted view that hydroids are carnivores and consume small invertebrates caught with nematocysts, the hydranths of *Z. estrambordi* have shown an opportunistic omnivorous feeding behaviour involving a wide range of prey. They consumed diatoms, algae, and small invertebrates, depending on what was available, in both the planktonic and benthic phase. The "sucking" behaviour that occurs when small inactive prey are caught (diatoms, for example) is similar to that described for *Laomedea* that ate dinoflagellates (CORNELIUS and OSTMAN, 1987).

Dispersal

Z. estrambordi has at least four agents of dispersal, the free hydranth, the hydrorhizal propagule, the

medusa and the planula. The first three arise from asexual reproduction, and disperse the genotype (albeit in the case of the medusa perhaps for a relatively short period) and the planula from sexual reproduction. The medusa and the hydranths feed while in the water column while the frustules and planulae have to exist on their own reserves, apart from any utilisation of dissolved organic material. The free hydranths and medusae may therefore disperse further than either frustules or planulae. Usually the medusa will not produce new colonies by asexual reproduction (but see CARRÉ and CARRÉ, 1990 and BAVESTRELLO *et al.* 1992).

The strategy of autotomy and dispersal of hydranths, to produce clones elsewhere, may have several advantages. (For a discussion of the adaptive advantages of cloning in general see HUGHES, 1989; HUGHES and CANCELO, 1985). It would appear to be an opportunistic trait which enables colonization of small and perhaps temporary patches of available habitat, and rapid reproduction from young colonies. In culture *Z. estrambordi* existed for several months in spite of the development of algae over the substrate by occupying occasional temporary bare patches. In the shallow water biotopes of the coral reefs in La Réunion there is a summer algal bloom in areas of relatively calm water protected by the reef front. The opportunistic cloning behaviour of *Z. estrambordi* may therefore have a particular adaptive advantage in this situation.

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