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## ASEXUAL REPRODUCTION IN SOLITARY SCLERACTINIA

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### ABSTRACT

A compilation and reorganization of asexual modes of reproduction in Scleractinia is presented and discussed, based on intratentacular and extratentacular budding, and transverse division. Eleven modes are recognized, including the relatively newly described processes of polyp bail-out, partial colony mortality, asexual planulae, and an elaboration of the anthoblast mode. Modes by which solitary Scleractinia produce clones are emphasized, which include: accidental and nonaccidental fragmentation, production of anthoblasts, and transverse division. Some of the modes of asexual reproduction employed by Scleractinia have analogs in the Actiniaria.

The possibility and extent of asexual reproduction in Scleractinia is of potential interest to the coral systematist, population biologist, and ecologist, since the sampling of potential clonemates would influence the results of an analysis based on the assumption of independent genotypes. Although not all modes of asexual reproduction are of supraspecific taxonomic value, some modes, such as transverse division, seem to represent key innovations that warrant the establishment of new genera, i.e., within Flabellum and Dendrophyllia.

### PREFACE

"The many modes by which this [asexual reproduction] is accomplished and the different conditions to which they lead are one of the most remarkable aspects of the Scleractinia; they have great systematic importance because the form of the colonies is largely determined by them." (Wells, 1956:347)

### INTRODUCTION

The various modes of sexual reproduction in Scleractinia have been reviewed recently (Fadlallah, 1983; Harrison, 1985) and discussed (Wallace & Szmant-Froelich, 1985), but the counterpart of asexual reproduction has not been comprehensively addressed since Wells (1956) discussed the three main modes consisting of intratentacular budding, extratentacular budding, and transverse division. Lang (1984:22) briefly reviewed various kinds of asexual reproduction pertaining to their use as systematic characters, and Rosen (1986:119-122) presented a review of many clonal strategies employed by corals. Since 1956 several different asexual reproduction processes have been discovered and many more examples of most modes have come to light. In this paper emphasis is given to the modes by which

solitary corals asexually reproduce clonemates (i.e., modes IB1-2, IID, III), however, all modes are reviewed including those of colonial corals. Although almost one-third of the scleractinian genera are exclusively solitary (Wells, 1956), asexual reproduction by solitaires leading to complete severance of connection of polyps clonopary, *sensu* Rosen 1986) is still considered to be rare and unusual (Fadlallah, 1982; Wells, 1956). Nonetheless, many more examples of clonopary are now known and discussed below.

Table 1 is a modification of Wells' (1956) discussion of asexual reproduction. It is difficult to determine and categorize the modes of asexual reproduction for all 846 valid genera of Scleractinia (Wells, 1956; Wells, 1986), the majority of which are exclusively fossil. Nonetheless, Table 1 is an attempt to list and organize the currently known modes. The term "method" refers to the four basic processes of asexual reproduction (main modes of Wells, 1956); "mode" refers to specific variation of a more general method.

### RESULTS

Intratentacular Budding.--Intratentacular zooidal budding resulting in physiologically associated polyps (i.e., clonoteny, *sensu* Rosen 1986, method IA) is a very common mode of asexual reproduction

Table 1.--Modes of Asexual Reproduction in Scleractinia.

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- I. Intratentacular Budding ("Fission")
    - A. Zooidal Budding within a Colony (Clonoteny)
    - B. Fragmentation/Regeneration
      - \*1. Accidental (Traumatic) Fragmentation
      - \*2. Nonaccidental Fragmentation (including Longitudinal Division and Parricidal Budding)
    - 3. Partial Colony Mortality
  - II. Extratentacular Budding
    - A. Zooidal Budding within a Colony (Clonoteny)
    - B. Fragmentation/Regeneration
      - 1. Accidental (Traumatic) Fragmentation
      - 2. Partial Colony Mortality (including Polyp Bail-Out)
    - C. Polyp Balls
    - \*D. Production of Anthoblasts (Bud Shedding)
  - \*III. Transverse Division ("Strobilation", Programmed Detachment)

### IV. Asexual Planulae

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\* Modes known to be employed by solitary corals

in reef corals and is well described and illustrated by Vaughan & Wells (1943), Wells (1956), and Rosen (1986). Some examples include species of Favia, Pavona, Merulina, Agaricia, Mycetophyllia, Goniastrea, and Psammocora, to mention only a few. According to Wijsman-Best (1977), corals that bud intratentacularly are, in general, better adapted to the reef environment than those that bud extratentacularly.

As noted earlier, Wells (1956) discussed three main modes (=methods) of asexual reproduction and one ancillary mode, regeneration, the latter of which has been redistributed into the methods of intra- and extratentacular budding. I therefore agree with Wells in not considering regeneration a main method of asexual reproduction but rather a possible consequence of fragmentation of an intratentacularly budding colony or solitary corallum (modes IBI-3) or of an extratentacularly budding colony (modes IIB1-2). Highsmith's (1982) excellent review of reproduction by fragmentation primarily addressed regeneration following accidental fragmentation (mode IBI) of reef corals (mostly colonial) and included Pavona as the only example of an intratentacularly budding coral. Willis & Ayre (1985) also discussed accidental fragmentation in Pavona cactus. Among the solitaries, fragments of species of Deltocyathus and Fungiacyathus often regenerate whole coralla. An unusual example of regeneration from accidental fragmentation is that of the cylindrical solitary Stenocyathus vermiformis (Pourtalès), which, when broken, will regenerate a calice on the broken proximal piece and another calice on the broken distal piece, thereby forming two coralla, the distal fragment with a calice on each end of the cylindrical corallum.

Regeneration as a consequence of nonaccidental fragmentation (mode IB2), including longitudinal division and parricidal budding, is found in a variety of solitary corals. Longitudinal division differs from accidental fragmentation in that the corallum is genetically programmed to fracture longitudinally, either at random intervals corresponding to weak intercostal spaces (e.g., Dasmosmilia, Tropidocyathus nascornatus Gardiner & Waugh, 1938) or along predetermined fracture lines, always dividing the corallum into six wedges (e.g., Schizocyathus). Following fracture, one or more polyps may bud from the exposed internal tissue. Because this tissue was once within the polyp, this process is considered to be a form of intratentacular budding. Other examples of longitudinal division are the carvophylliid genera Aulocyathus and Fragilocyathus; the Jurassic guyniid Microsmilia; the Jurassic amphistroid Polymorphastraea; the Diaseris form of Cycloseris; and the flabellids Flabellum laciniatum (Philippi) and F. macandrewi Gray, the latter of which is extremely rare as a complete corallum. Longitudinal fission is one of four methods of asexual reproduction known in Actiniaria (Chia, 1976) and one that is considered to be quick and efficient, allowing rapid and usually successful colonization with a minimum expenditure of energy. Parricidal budding is known in the solitary coral genus Asterosmilia, whereby one or two buds originate from the parent calice. Contrary to the implication of the name parricidal budding, the parent polyp does not die but, instead, is rejuvenated in the case of one bud, or subdivided

into two smaller corallites in the case of two buds.

A third mode of asexual reproduction resulting from fragmentation occurs by the partial mortality of a colony (mode IB3), wherein various corallites of a colony die, causing the segregation of the former colony into two or more genetically identical smaller colonies. Each subdivided colony may regenerate, subsequently fuse with the parent colony, die, or reproduce sexually or asexually. This phenomenon was first reported by Lewis (1974) for Agaricia agaricites (Linnaeus) and later elaborated upon by Hughes & Jackson (1980), Highsmith (1982), and Jackson & Hughes (1985). In addition to Agaricia, this mode is also known to occur in Leptoseris cucullata (Ellis and Solander), Pavona clavus (Dana), Meandrina meandrites (Linnaeus) (see Highsmith, 1982), and a variety of other extratentacularly budding corals (see mode IIB2). This is probably a very common phenomenon in massive colonial reef corals.

Extratentacular Budding.--Extratentacular zooidal budding resulting in physiologically associated polyps (clonoteny, mode IIA) is the most common form of asexual reproduction in Scleractinia. The many families and genera characterized by extratentacular zooidal budding from colonies include Acropora, Dendrophyllia, Goniopora, Montastraea, Montipora, Pocillopora, Porites, and Seriatopora, to name a few.

As a corollary to the previously described mode, regeneration from fragmentation of extratentacularly budding corals (mode IIB1) is also very common. In fact, Highsmith (1982) suggested that fragmentation may be the predominant mode of reproduction of the major reef-building corals. He listed and discussed species in the following genera that reproduce by fragmentation: Acropora, Goniopora, Montastraea, Pocillopora, and Porites; Tunnicliffe (1981) discussed in detail regeneration in Acropora cervicornis (Lamarck); and Jokiel, Hildemann, and Bigger (1983) discussed fragmentation in Montipora.

As in intratentacular budding, fragmentation also occurs by partial mortality (mode IIB2) of intervening coenosarc or entire polyps in the colony. Jackson & Hughes (1985) discussed and illustrated this phenomenon for Montastraea annularis (Ellis & Solander), and Highsmith (1982:217) reviewed examples in other reef corals, including Porites, two species of Acropora, and two species of Montipora. Wells (1956:248) also noted that corallites of certain rhizangiid genera with reptoid growth, such as Culicia, Rhizangia, Madracis and Astrangia, often become disassociated from one another, as does the dendrophylliid Rhizopsammia. Fadlallah (1982) documented this phenomenon in Astrangia lajollaensis, which proceeds through an initial phase called edge-zone reorganization prior to budding. The asexual process followed by rhizangiid corals is not unlike pedal laceration in Actiniaria, one of the four methods of asexual reproduction known in that order (Chia, 1976).

Another unusual variation of asexual reproduction by partial mortality of intervening coenosarc is that of polyp bail-out. According to Sammarco (1982a,b), under unfavorable conditions the coenosarc between adjacent corallites of Seriatopora

*hystrix* Dana has been observed to degenerate, isolating individual polyps, which subsequently detach from the corallum. The detached polyps are a form of reduction stage because they are not known to have tentacles in the free state. Detached polyps are adapted for dispersal under unfavorable conditions, some eventually settling and producing colonies. The process of polyp bail-out remains to be confirmed by experimentation.

A unique mode of extratentacular budding known only in *Goniopora stokesi* Milne Edwards & Haime, is by "polyp balls" (Scheer, 1960; Rosen & Taylor, 1969; mode IIC). Unlike the previous mode, a small spherical colony of 1-30 polyps originates from near the oral end of a polyp of the parent colony. This polyp ball has a calcified inclusion that is not continuous with the parent corallum. Eventually the polyp ball detaches from the parent and a separate, genetically identical clone is produced. A fairly close analog to this process occurs in the Actiniaria, called budding (Chia, 1976), in which tentacles autonomously and subsequently regenerate complete individuals.

A final mode of extratentacular budding that occurs in solitary or "quasicolonial" corals is by anthoblast production or bud shedding (see Zibrowius, 1985 for review) (mode IID). In this mode one or more asexual buds (anthoblasts) are produced on the theca of a solitary coral, they subsequently detach leaving a scar at the base, and finally either reproduce sexually and/or asexually by budding more anthoblasts. The process is similar to transverse division in that a solitary corallum is produced with a truncate base but there are significant differences (Figure

1). 1) The anthocaulus of transverse division is a result of sexual reproduction; the anthoblast is an asexually produced bud. 2) The anthocaulus is presumably sexually immature, producing one distally placed anthocyathus at a time; the anthoblast is sexually mature and may also produce numerous laterally placed anthoblasts simultaneously. 3) The anthocyathus cannot reproduce asexually, they simply grow to a progressively larger size; anthoblasts, as noted before, can reproduce asexually. 4) Whereas transverse division allows reproduction of potentially successful clonal genotypes *in seriatim*, the anthoblast mode allows for multiple cloning of genotypes, each of which has the potential for sexual or asexual reproduction. Transverse division thus allows for a gradual linear increase of clones, whereas the anthoblast mode allows for the exponential increase in clones. According to Zibrowius (1985), another possible advantage to the anthoblast method, and undoubtedly transverse division, is an adaptation to life on soft bottoms where solid substrates are rarely available for larval settlement.

The anthoblast mode is best described for the fungiids (Wells, 1966), most of which can actually reproduce by both transverse division and anthoblasts. In the Caryophylliina it occurs in *Blastotrochus nutrix* Milne Edwards and Haime, which produces a series of anthoblasts along its lateral edges, the anthoblasts eventually detaching from the parent colony and falling to the substrate. *Anomocora fecunda* (Pourtalès), and various species of recumbent *Dendrophyllia* (e.g., *D. cornucopia* Pourtalès, *D. oahensis* Vaughan, and *D. serpentina* Vaughan), *Balanophyllia* (see Zibrowius, 1985), and *Endopachys* also produce an-

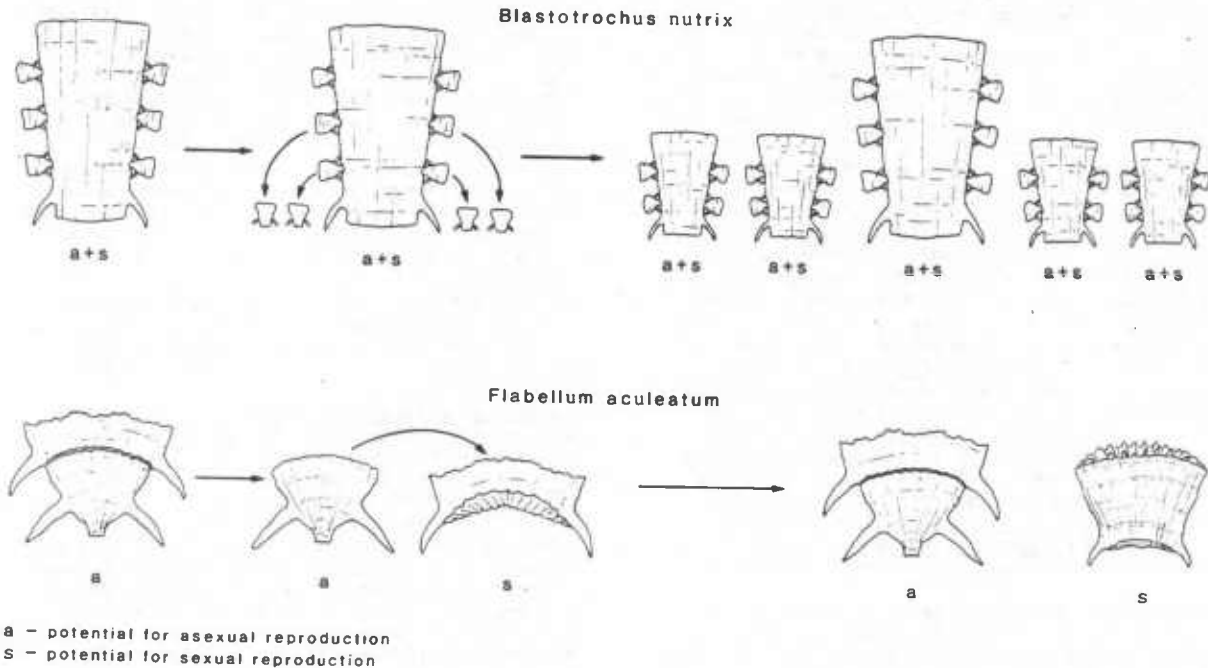


Figure 1. Comparison of Anthoblast Production (mode IID), exemplified by *Blastotrochus nutrix*, and Transverse Division (mode III), exemplified by *Flabellum aculeatum*.

thoblasts on their theca, some anthoblasts becoming quite large before detaching, leading to the term "quasicolonial" for some otherwise solitary species. The extratentacular offsets of Gywnia annulata Duncan described by Wells (1973) are included as a variant of the anthoblast mode as is the basal budding of Sphenotrochus andrewianus Milne Edwards & Haime described by Zibrowius (1980: pl. 56, figs. E, F, N, O; 1984).

Transverse division.--Transverse division (method III) was one of the three main modes of asexual reproduction discussed by Wells (1956), a mode restricted to certain solitary corals. Although it might appear to be a derivative of intratentacular budding, in that the distally budded individual appears to originate within the tentacular ring, until histology is done on various intermediate stages, transverse division is retained as a separate method. Although Milne Edwards & Haime (1848) described many species of Flabellum with a truncate base, it was not until 1872 that Semper pointed out that the corallum (anthocaulus) of F. aculeatum Milne Edwards & Haime forms a distally free anthocyathus by transverse asexual division from the still attached anthocaulus, the latter capable of asexually budding additional anthocyathi. Wells (1984) later referred to this process as "strobilation". It has also been referred to as "programmed detachment" (in part) by Highsmith (1982:211), because the division is genetically predetermined. Approximately 30 species of Flabellum follow this mode of asexual reproduction (Cairns, in prep.); these species were placed in the section "flabella truncata" of Flabellum by Milne Edwards & Haime (1848) and the "second group" of Flabellum by Zibrowius (1974). Also within the superfamily Flabellidae, all species of the genera Placotrochides, Placotrochus s. str., and an as-yet-undescribed guyniid genus from the Philippine Islands reproduce by transverse division. It is also common in the life cycles of many fungiids (see Wells, 1956, 1966 for a complete description). Other examples include the caryophylliid Bourneotrochus (see Wells, 1984), Trochocyathus (see Vaughan and Wells, 1943:47, text-fig. 20b), Dunocyathus (see Wells, 1958), and Peponocyathus folliculus (Pourtales); dendrophylliid genus Endopachys; Eocene astrangiid genus Pleuropodia (Dennant, 1903); and possibly the Cyclolitidae (see Wells, 1956). Occasionally the anthocyathi and anthocauli have been described separately, even attributed to different genera, analogous to the overnaming of hydromedusae and hydroids. For instance, Endopachys and Rhectop-sammia were names given to the anthocyathus and anthocaulus stages, respectively, of the same genus. Deltocyathus rotaeformis Woods, 1878 is the anthocyathus of the anthocaulus Dunocyathus parasiticus Woods, 1878 (see Wells, 1958), the latter name having page priority. And, Deltocyathus stellulatus Cairns, 1984 is the anthocyathus of Bourneotrochus veroni Wells, 1984, the former name having chronological priority.

Transverse division is one of four methods of asexual reproduction known in Actiniaria (Chia, 1976), shared by only three species in that order. It is also known in hydroids and Scyphozoa; in the latter case known as strobilation of scyphistoma larvae (Campbell, 1974). Transverse division is a form of clonopary (sensu Rosen, 1986) in that the

budded polyp becomes detached from the parent. Modes IB and IIB-D are also considered clonoparyous.

Asexual Planulae.--An entirely different method of asexual reproduction working at an earlier ontogenetic stage is that of asexual planulae (method IV), whereby genetically identical planulae are released from a colony asexually (Stoddart, 1983). The planulae of Pocillopora damicornis (see Stoddart, 1983, 1984), Tubastraea diaphana Dana, and T. coccinea Lesson (see Ayre & Resing, 1986) have been shown electrophoretically to be clones of their parent colony. It is unknown if the planulae are produced by a form of internal budding or parthenogenesis (Stoddart, 1983).

## DISCUSSION

Biological Advantages of Asexual Reproduction in Scleractinia.--Asexual reproduction in Scleractinia is often an integral and genetically determined process in the life history of the coral. It is not known to be the exclusive method of reproduction for any species but is often the predominant one, especially for species that employ modes IBI-2, IIB1, and IID.

The chief advantage of asexual reproduction is in the geographically local amplification of well-adapted genotypes, whereas sexual reproduction produces variation to adapt to a changing environment (Williams, 1975). The apparent disadvantages of asexual reproduction are the inability to adapt to a changing environment and a lesser dispersal ability, but with a proper combination of both modes an equilibrium should, in theory, be approached. Other advantages of asexual reproduction are that it can occur year round; it is often a faster process; and, because the bud is usually larger than a sexually produced propagule, the chance of survival is greater (Williams, 1975). Furthermore, the genotype of a large population of clonemates has a better chance of survival than individual colonies (Cook, 1978). Asexual reproduction also usually requires less energy and can be accomplished in environments where sexually reproducing units may be few and far between, such as the deep sea (Francis, 1979:678). The relative advantages of the eleven modes of asexual reproduction listed in Table 1 are not discussed here and would require much additional observation and experimentation to determine: such as the studies done by Semper (1872), Highsmith (1982), Sammarco (1982a), and Jackson & Hughes (1985).

Systematic Implications of Asexual Reproduction in Scleractinia.--There is a need to know the possibility and extent of asexual reproduction in Scleractinia by the systematist, population biologist, and ecological theorist (Williams, 1975). As Stoddart (1983:283) summarized, between-polyp morphological variation is used to estimate environmentally induced effects; between-colony morphological variation is usually assumed to represent environmental and genetic differences. But, if asexually produced clonemates are inadvertently compared to the between-colony distinction is confused and a morphometric analysis of variation would be less meaningful. Fortunately, electrophoretic and immunogenic evidence can detect asexual clonemates, distinguishing even

the rather subtle forms of asexual reproduction such as asexual planulae and fragmentation (Willis & Ayre, 1985). One of the purposes of this paper is to show the widespread and diverse nature of asexual reproduction in Scleractinia for the benefit of scientists working on potentially asexually reproducing species.

As the preface implies, mode of asexual reproduction with resultant corallum morphology is a potentially important taxonomic character, often significant above the species level (Wells, 1956:368), but not all modes listed in Table 1 define or are consistent for supraspecific taxa. For instance, accidental fragmentation and asexual planulae are simply adjunct reproductive methods to sexual reproduction, not necessarily of any taxonomic value. Likewise, most forms of partial colony mortality are environmental accidents, not taxonomically important. Rosen & Taylor (1969) suggested that polyp ball production may be important at the subspecies level. But some modes of asexual reproduction, specifically transverse division and production of anthoblasts, seem to represent "key innovations" (Bock, 1985), in the sense that these adjunct methods of asexual reproduction may allow the exploitation of a new habitat and/or are central to an adaptive radiation. The 30 species of truncate Flabellum (about 13% of the nominal species in the genus, Cairns, in prep.) that reproduce by transverse division are hypothesized to represent such a radiation. A possible adaptive advantage of this mode compared to the nontruncate Flabellum would be the potential of producing numerous large clonemates with relatively little energy expenditure, each of which would have the potential for sexual reproduction. Another possible advantage of transverse division is one already mentioned for anthoblast production: an adaptation to soft substrates. Based on these potential reproductive advantages and the associated morphological distinction of the truncate base, I conclude that these species should form a genus separate from Flabellum s. str. For the same reasons, the truncate guyniid should be described as a separate new genus. Blastotrochus nutrix Milne Edwards and Haime, also currently placed in Flabellum, asexually reproduces by anthoblast production, quite differently from the transverse division of the truncate flabellids, as previously discussed, with different population outcomes. To reiterate, transverse division allows for an efficient but gradual increase in clonemates; the anthoblast mode allows for an exponential increase. I would therefore suggest a resurrection of Blastotrochus to accommodate B. nutrix. And finally, the quasicolonial species of Dendrophyllia that reproduce asexually by anthoblast production should be removed from that genus, defined as having dendroid colonies (Wells, 1956), and made a separate genus. I hope to effect most of these taxonomic changes in a revision of the deep-water Scleractinia of the Philippine Islands (Cairns, in prep.).

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