

MODES OF REPRODUCTION IN RECENT AND FOSSIL CUPULADRIID BRYOZOANS

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Abstract: Cupuladriid cheilostome bryozoans can make new colonies both sexually and asexually. Sexual (aclonal) colonies are derived from larvae while asexual (clonal) colonies result from the fragmentation or division of larger colonies. A number of specialised morphologies exist which either enhance or discourage clonality, and cupuladriids preserve these in their skeletons, meaning that it is possible to count the abundances of individual modes of reproduction in fossil assemblages, and thus measure the mode and tempo of evolution of life histories using fossil colonies. In this paper we categorise, illustrate and describe the various clonal and aclonal methods of propagation in cupuladriids through the Cenozoic. Sexual reproduction is the only aclonal method of propagation, while four clonal methods are described comprising: (1) mechanical fragmentation, (2) autofragmentation, (3) colonial budding and (4) peripheral fragmentation. The processes involved

in each are discussed and we explain how their prevalence can be measured in the fossil record using preservable morphologies. Compiling a record of the occurrence and distribution of the various modes of propagation through time and space we discover a general trend of evolution towards more complex modes in all three cupuladriid genera, but a geologically recent extinction of some modes of propagation that has left the present-day assemblage relatively depauperate. We see striking similarities in the general timing of expansion of modes of reproduction between the two most important genera, *Cupuladria* and *Discoporella*, although it is clear that *Discoporella* evolved a much wider range of special morphologies either to enhance or to discourage clonality than did *Cupuladria*.

Key words: bryozoa, Cupuladriidae, clonal, aclonal, fragmentation, life history, evolution

ONE of the many advantages of a colonial over a solitary (unitary) lifestyle is the ease with which clonal (asexual) dispersal can take place (Hughes and Jackson 1985; Jackson and Coates 1986). Solitary organisms usually require complex processes to clone (including parthenogenesis), while the modular construction of colonies facilitates clonality because their modules (e.g. zooids, polyps) are often able to survive individually or in small groups. Thus, all that is required is for the colony to divide, either by itself or through breakage, and then regenerate from each separated part (ramet). The ability to clone provides a species with a distinct method of dispersal that avoids a number of risks associated with sexual reproduction (Jackson 1977), including increased size-dependent mortality and reliance upon gamete production. All major groups of extinct and extant colonial organisms have at some time employed clonal methods for dispersal, and clonal propagation has been important in the evolutionary success of many clades (Highsmith 1982; Jackson and

Coates 1986; Urbanek and Uchmanski 1990), particularly for reef framework builders.

Measuring the relative proportion of clonal vs. aclonal individuals in a population of a colonial animal can be problematic. Molecular approaches, such as those employed by Foster *et al.* (2007), provide highly informative data but become extraordinarily laborious as the numbers of individuals incorporated increases. Normally, using morphology is no less challenging as the reproductive origin of individuals for the majority of colonial animals is irretrievable because the founding part of the colony is often not visible (Hughes and Jackson 1980, 1985; Hughes 1984). Because of this very fact, the fossil record has added little to our understanding of the evolutionary dynamics of clonal and aclonal propagation (but see Thomsen and Håkansson 1995; Cheetham *et al.* 2001; Håkansson and Thomsen 2001).

Cupuladriid bryozoans unambiguously preserve the reproductive origin in the calcified skeletons of both

living and fossil colonies (O'Dea *et al.* 2004). Colonies from a sexually recruited larva show orderly radial budding from a central origin, while clonal colonies tend to have slightly asymmetrical forms and include the fragment from which they regenerated (Text-fig. 1). Cupuladriids have a rich Palaeogene and Neogene fossil record and are common in tropical seas today (Cook and Chimonides 1983); as such, cupuladriids are valuable tools for exploring the consequences of clonality through evolutionary time.

Recent advances in the understanding of the life histories of living cupuladriids (Håkansson and Thomsen 2001; O'Dea 2006) have revealed that clonal propagation can occur in many different ways, each with their own morphological signature that is preserved in the fossil record. It is necessary to describe these various modes of propagation and their preservable morphological features before using cupuladriids as a model evolutionary system.

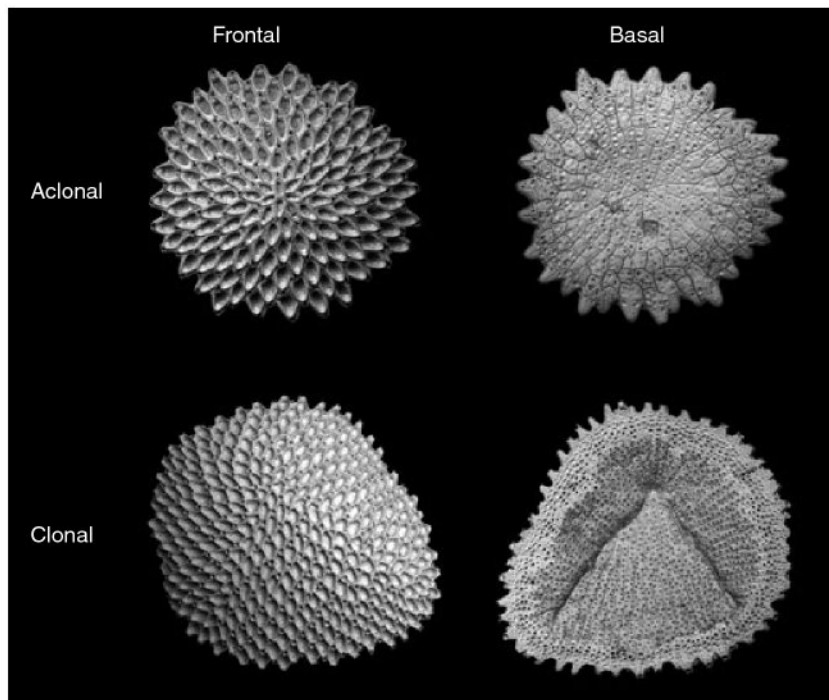
Accordingly, this paper reviews and clarifies the currently known modes of propagation in cupuladriids, introduces and describes previously undescribed modes of propagation, compiles and figures all known modes of propagation for future classification, and discusses their potential ecological and evolutionary significance. The paper focuses principally on the Neogene and Recent of the Caribbean and eastern tropical Pacific because this is currently the most intensively studied region and is potentially the most valuable for evolutionary studies because of the exhaustive record of Neogene cupuladriids that exists owing to the collections of the Panama Paleon-

tology Project (PPP) (Collins and Coates 1999; Cheetham and Jackson 2000).

LIFE HISTORY STRATEGIES AMONG CUPULADRIIDS

The family Cupuladriidae comprises three genera, *Cupuladria* Canu and Bassler, 1919, *Discoporella* d'Orbigny, 1852 and *Reussirella* Baluk and Radwanski, 1984; each of which adopts a semi-mobile, free-living life habit (Cook 1965; Baluk and Radwanski 1984; Cook and Chimonides 1994; Rosso 1996). Unlike most other bryozoans that live attached to rocks, shells or macroalgae, cupuladriids are unattached and rest on or within the sea-floor sediment. Colonies possess polymorphic zooids called vibracula with long setae that can be used to aid in the removal of sediment from the colony surface, movement up through sediment if buried, and even walking.

The oldest fossil record of the family is from the early part of the Palaeogene in Senegal (Gorodiski and Balavoine 1962). The group then seems to have spread into Asia in the Eocene, subsequently followed by a rapid widening of their range in the Miocene to Australia and the Americas (Lagaaij 1963; Rosso 1996). However, the evolutionary origins of the family remain enigmatic (Cook and Chimonides 1983), and an Asian origin of the family cannot be ruled out given the dearth of collections from the region. The distribution of both fossil and Recent species is tropical to subtropical and they are almost always associated



TEXT-FIG. 1. Aclonal colonies (top) of cupuladriids have an unmistakable radial budding pattern and produce ancestrular zooids that originate from the metamorphosis of a sexually produced larvae, while clonal colonies (bottom) have no ancestral region but possess evidence of fragmentation or separation and the ensuing regenerative growth; $\times 7$.

with sandy or silty sea-floors, often in great abundance (Winston 1988; Rosso 1996).

Present-day tropical American cupuladriids exhibit a wide range of life history strategies. Some species propagate entirely clonally whereas others make all new colonies entirely aconally. Many other species have a roughly equal mix of clonal and aconal colonies, and are clearly able to interchange between the two modes from generation to generation (O'Dea *et al.* 2004). Although the mechanisms are not understood, there is a strong positive correlation between the prevalence of clonality and the levels of food available both among and within species (O'Dea *et al.* 2004; O'Dea 2006). It appears that higher food levels are more beneficial for clonal propagation because cloning requires 'vegetative' growth of the colony and growth rates increase with increasing food levels, and also because higher food levels may be necessary for the successful regeneration of a fragment.

Morphological features, such as the degree of calcification and shape of colonies, also correlate strongly with the prevalence of clonality (Håkansson and Thomsen 2001; O'Dea *et al.* 2004). Essentially, species that produce large, indeterminately growing colonies are lightly calcified, which helps promote fragmentation and, thus, their populations tend to be clonal. On the other hand, species that produce small, determinately growing colonies and are more heavily calcified tend to be aconal as they are more resistant to fragmentation (Winston 1988; Håkansson and Thomsen 2001; O'Dea *et al.* 2004). If clonal propagation of new colonies is the result of external forces causing the breakage of colonies, cupuladriid morphology can either promote or inhibit fragmentation. As such, strength and size of colonies may, therefore, be adaptive features that control reproductive life history strategy. The preservable features of fossils can thus be used to explore detailed evolutionary changes in life histories.

When clonal propagation in cupuladriids was first studied, the fragmentation of colonies was attributed either to high energy currents or waves (Dartevelle 1935), or to the breakage of colonies during grazing by other animals (Greeley 1967). Combined, these modes of cloning are termed mechanical fragmentation because they require external forces to break the colony (O'Dea 2006). Some cupuladriids, however, do not rely on chance to fragment and clone, but are able to control when, where and how fragmentation takes place using a variety of special morphologies. Colonies of *Cupuladria exfragminis* from the Pacific coast of Panama are able to autofragment, i.e. separate their colonies into parts without the need for external force (O'Dea 2006), and appear to do so in synchrony when conditions are favourable. Fossil colonies of the Miocene *Ruessirella haidingeri* were probably able to detach colony buds by removal of an uncalci-

fied connection between bud and parent colony (Håkansson and Thomsen 2001).

Basic discrimination between clonal and aconal colonies is straightforward based on simple morphological differences (Cook 1965), which are normally so striking that colonies can be distinguished with the naked eye despite their small size (Text-fig. 1). Discriminating the variety of different modes of clonal propagation, however, requires more attention to detail. Although the resulting colonies from each clonal mode are somewhat morphologically similar, and discriminating between some of the modes is often difficult, it is still possible to categorise the majority of clonal colonies using detailed features that are preserved in the skeleton.

The following section describes five modes of propagation in cupuladriids. For each mode we (1) illustrate the life cycle, (2) figure a range of examples, (3) describe the process of propagation and (4) list the preservable (hard skeleton) morphologies that can be used to distinguish them in fossil material.

CLASSIFICATION OF MODES OF PROPAGATION

Mode I. Aconal propagation by sexual reproduction (Text-figs 2–3)

Process. Sexual reproduction in cupuladriids is not dissimilar from that of other cheilostome bryozoans that brood internally within the zooid rather than in ovicells (McKinney and Jackson 1989) (Text-figs 2–3). Cupuladriid colonies are hermaphroditic. They do not produce polymorphic male or female zooids, unlike some other free living bryozoans such as Selenariidae (Cook and Chimonides 1987). Embryos are brooded in ovisacs within normal feeding zooids (Cook and Chimonides 1994) and, when mature, are released as lecithotrophic larvae into the water, swimming for a short time to search for a suitable substratum upon which to metamorphose (Driscoll *et al.* 1971) (Text-fig. 2). The substrates most often used are sand and silt grains, small stones or fragments of shell material, less often the tests of foraminifera or plant fragments. The chosen substrate normally remains attached to the colony throughout its life, and can often be easily observed in the basal parts of fossil colonies (Text-fig. 3).

Metamorphosis of the larva on a substrate initially produces a triad of three small but complete zooids (Text-figs 2–3) (Håkansson 1973), normally within 24 h of settlement (Cook and Chimonides 1994). Zooids are budded radially from this ancestrular triad, as illustrated in detail by Cook (1965). As the colony expands it grows over the edge of the substratum (if the substrate area is small) and, owing to an expanding basal coelom that

produces secondary calcification on the underside of the colony, is able to support itself and live freely on the sediment (Cook and Chimonides 1994; Håkansson and Thomsen 2001). Colony size increases by the budding of marginal zooids, initially through a zone of astogenetic change characterised by a progressive increase in zooid size, and subsequently into a zone of astogenetic repetition comprising zooids of full size (Cook and Chimonides 1994; O'Dea and Jackson 2002). Sexually produced colonies, therefore, typically grow in an almost perfectly radially symmetrical pattern (Text-fig. 3A), unless a part of the colony fails to bud new zooids through localized mortality or breakage. If growth is impeded, zooids lateral to the affected region normally bud relatively rapidly to fill the space and quickly regain the circular shape of the colony. Another fairly common cause of irregular-shaped, sexually derived (aclonal) colonies in both fossil and Recent assemblages occurs when colonies fuse with other colonies during their early development, usually when larvae of the two colonies metamorphose on the same substratum (Text-fig. 3E). Interestingly, although fusion occurs frequently when abundance is high, fused individuals rarely build very large colonies.

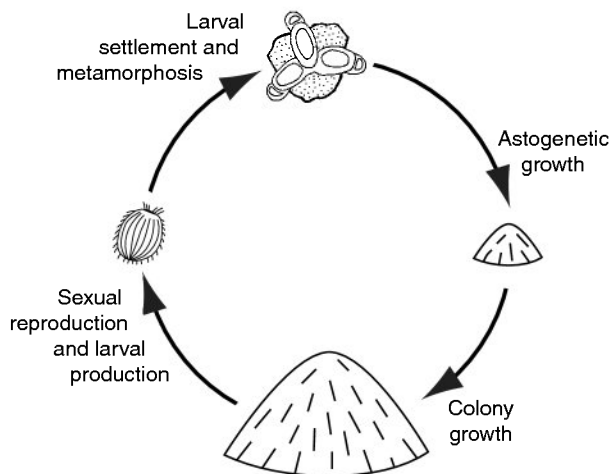
In most species, larvae are selective of type and size of substratum (Lagaaij 1963; Driscoll *et al.* 1971; Winston 1988; Håkansson and Thomsen 2001). For example, *D. triangula* seems to be particularly selective in its choice of substratum. Although the species inhabits areas of silt and sand, colonies use relatively large, spherical sediment grains 2 or 3 mm in diameter, which are rare in the sediment in which the species is found (O'Dea, unpublished data). The reason for this selectivity becomes apparent when the morphology and life history of *D. triangula* are considered. The species rarely, if ever, propagates clonally, and produces squat colonies with an extremely calcified base (Text-fig. 3G). The inclusion of the round sediment

grain confers to add greater strength to the colony without requiring excessive production of skeleton. Other species seem to be considerably less discerning and their selection of sediment types as substrata sometimes seems simply to reflect the availability of sediment on the sea-floor (Text-fig. 3H).

Preservable morphology. Sexually produced colonies exhibit a wide range of morphological types (Text-fig. 3A–H) but are easily recognized by the presence of one or more of the following characteristics: (1) ancestrular triad of zooids that originated from larval metamorphosis; (2) entire zone of astogenetic change characterized by distally increasing zooid sizes; (3) presence of an attached substratum in the central basal region; (4) radially symmetrical growth.

It should be noted, however, that the ancestrular region and zone of astogenetic change are sometimes eroded, some species do not need a substratum on which to metamorphose, and the substratum can be lost during colony growth or obscured by basal calcification.

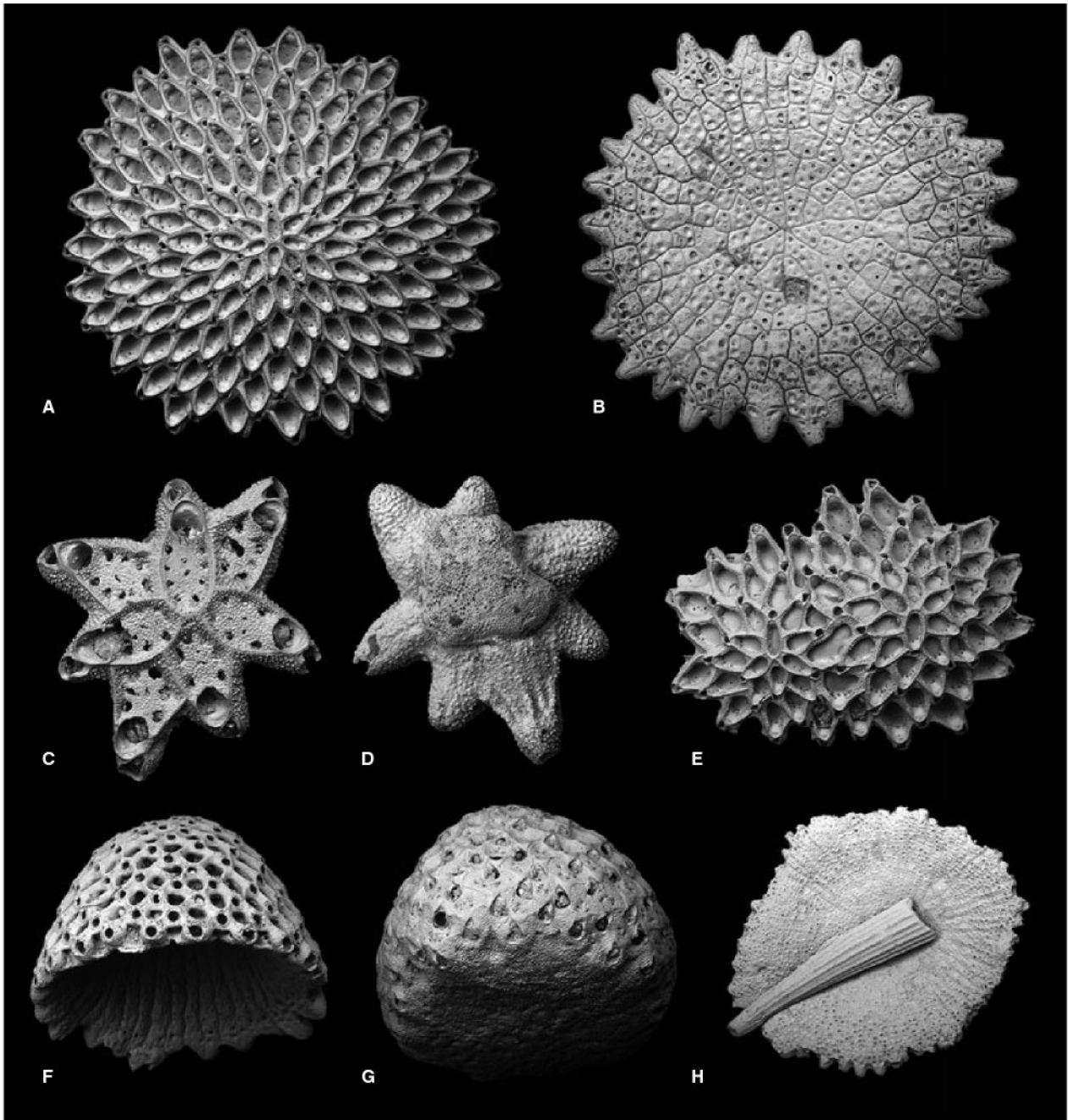
A number of cupuladriid species have fairly specialised morphologies that should inhibit fragmentation and thus prevent clonal propagation. Determinate growth into small, squat colonies is one way species may avoid fragmentation; another is by creating stronger colonies. Species of *Cupuladria* increase colony strength by the addition of a basal layer of kenozooids, an increase in kenozooidal density and an increase in the thickness of calcification of the kenozooids. Thus, *Cupuladria* species that rarely fragment often have numerous layers of tightly packed, thick kenozooids (e.g. Herrera-Cubilla *et al.* 2006, figs 4.5, 5.5). In species of *Discoporella* that lack kenozooids, colony strength can be increased simply by increasing the thickness of basal calcification.



TEXT-FIG. 2. Cycle of asexual propagation by sexual reproduction in cupuladriid bryozoans.

Mode II. Clonal propagation by mechanical fragmentation (Text-figs 4–5)

Process. Fragmentation by mechanical means can be caused by abiotic or biotic processes (Text-figs 4–5). Although Darteville (1933), Brown (1952) and Marcus and Marcus (1962) believed that agitation caused by currents and waves was the most important source of fragmentation, there is actually very little evidence to support this inference. Winston (1988) did present a case for wave-induced fragmentation of cupuladriid colonies in a shallow, high-energy, sand environment (Capron Shoals, Florida), and our studies suggest that a similarly high energy and shallow environment (Isla San Jose, Gulf of Panama) may also cause fragmentation of colonies of *C. exfragminis* (O'Dea 2006). However, not only has current- or wave-induced fragmentation never been observed or recreated in the laboratory, it is unlikely to be an impor-



TEXT-FIG. 3. Range of morphologies produced during asexual propagation by sexual reproduction. A–B, frontal and basal views of a radially symmetrical, sexually produced colony of *Cupuladria biporosa*, Bocas del Toro, Recent Caribbean; $\times 14$. C–D, frontal and basal view of ancestrular region of unidentifiable *Discoporella* colony showing foraminifera substratum; $\times 40$. E, fused ancestrulate colonies of *Cupuladria surinamensis*, Golfo de los Mosquitos, Caribbean, Recent; $\times 20$. F, *Cupuladria panamensis*, Nicaragua, Caribbean, Recent; $\times 20$. G, *Discoporella triangula*, Swan Cay, Bocas del Toro, Plio-Pleistocene; $\times 20$. H, basal view of colony of *Cupuladria biporosa* with a scaphopod substratum, Caribbean, Nicaragua, Recent; $\times 7$.

tant factor in the fragmentation of colonies that inhabit deeper, low-energy environments. Because the majority of cupuladriids live below the surf, and inhabit silty sediments, we agree with Lagaaij (1963), Cadée (1975) and Baluk and Radwanski (1977) that mechanical fragmenta-

tion by waves or currents is on the whole insignificant and that the actions of other organisms play a much more important role in mechanical fragmentation of cupuladriids. Biotic interactions that could be the cause of fragmentation can be divided into (1) predation on the

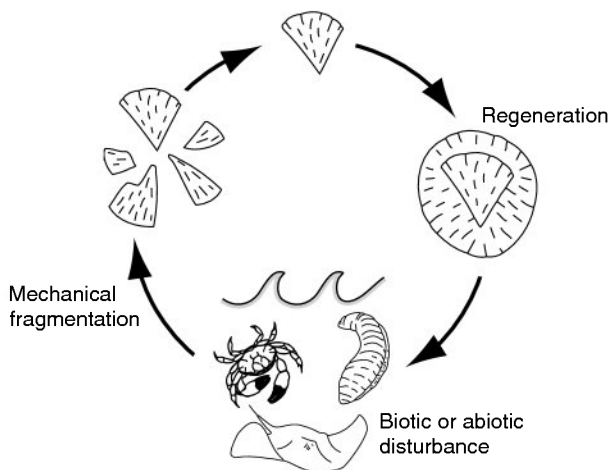
cupuladriids themselves, (2) predation on the animals and plants that use cupuladriid colonies as a substratum, and (3) inadvertent breakage.

Cupuladriids have been found in the gut contents of holothurians (Lagaaij 1963) and echinoids (Silén 1942). Such ingestion would undoubtedly result in fragmentation of cupuladriid colonies, and both holothurians and echinoids are often found in high abundance where cupuladriids occur. Yet it remains unknown if such animals are predators of cupuladriids, are consuming the epibionts that live on colonies, or are merely accidentally ingesting them during the course of feeding on other organisms. Neither is it known if cupuladriid colonies are able to survive ingestion by holothurians, although a variety of other organisms can pass through holothurian guts alive (Goldbeck *et al.* 2005).

A range of vertebrate deposit feeders, especially fishes, are well known to be important bioturbators in soft-bottom habitats typical of cupuladriids. These animals indiscriminately disturb and rework large amounts of sediment while feeding, which may indirectly cause cupuladriids to fragment.

Observations have shown that crabs interact with cupuladriids in at least two ways that may lead to fragmentation. Firstly, they have been observed to graze upon the epibiotic communities that often use cupuladriid colonies as substrata (Greeley 1967). In another instance, immediately following a dredge along the Pacific coast of Costa Rica, a crab of the family Xanthidae was observed to take a colony of *C. exfragminis* in both claws and bite the edge of the colony repeatedly while rotating it (F. Rodriguez, pers. obs. 2005).

Preservable morphology. Although little is understood about the relative importance of biotic or abiotic factors in mechanical fragmentation, it is clear that a variety of



TEXT-FIG. 4. Cycle of clonal propagation by mechanical fragmentation in cupuladriid bryozoans.

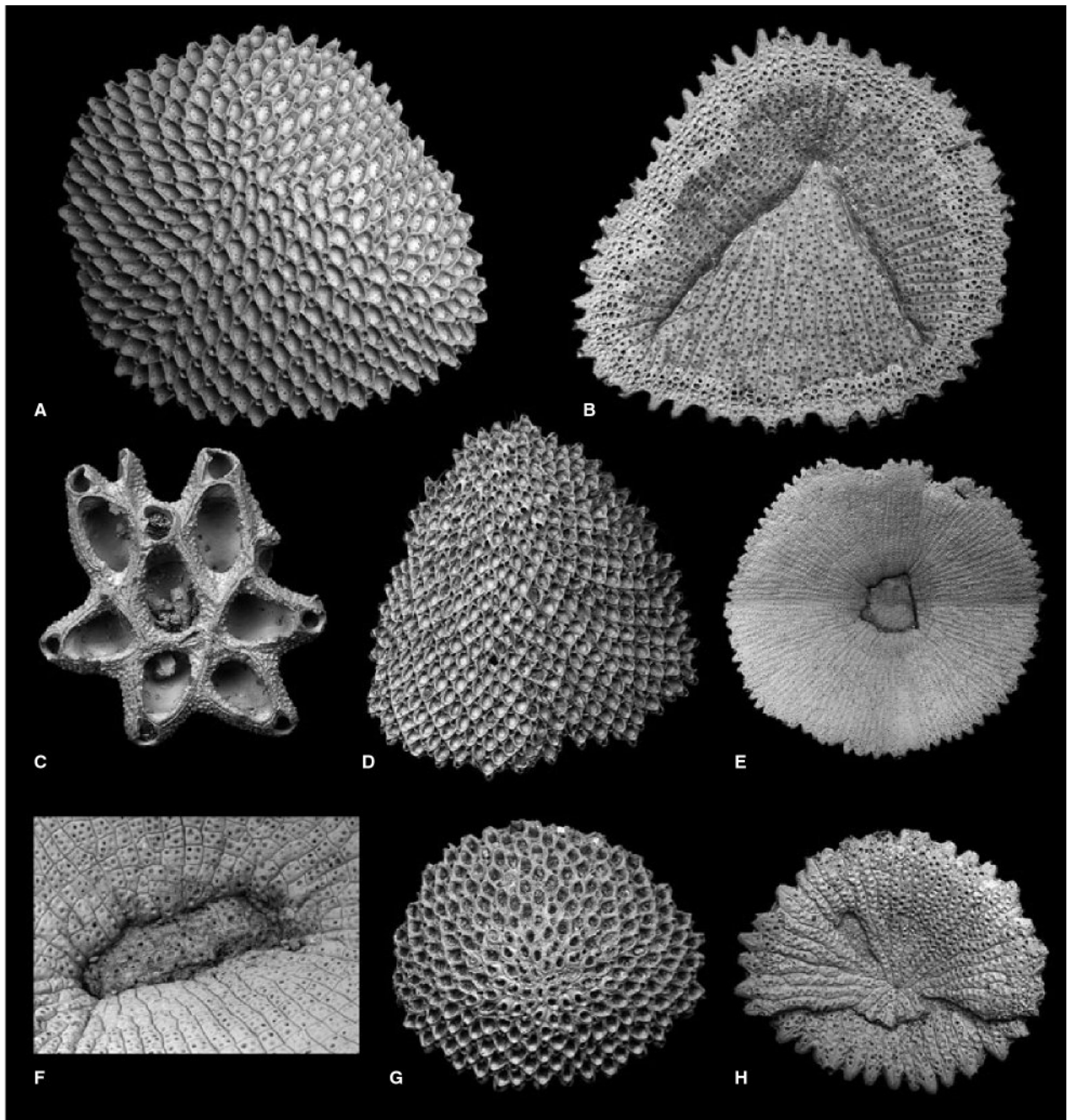
shapes and sizes are produced (Cook and Chimonides 1994). This variation is dependent on the morphology of the original colony and the type of process causing fragmentation. Fragments that are able to regenerate to produce new colonies vary from triangular and very large (Text-fig. 5A–B, D) to small and square (Text-fig. 5E) or rectangular (Text-fig. 5F). They can also be almost entire colonies (Text-fig. 5G–H) or just one or two zooids (Text-fig. 5C; and detailed in Baluk and Radwanski 1984).

To understand more about the processes of fragmentation, we broke cupuladriid colonies by hand in different ways and the resulting morphology was noted. If the species had lightly calcified colonies, and pressure was placed upon the whole colony, as if it were being compressed from all sides as can be imagined during ingestion, the resulting fragments were very often triangular in shape (e.g. Text-fig. 5A–B, D) because the colonies split radially from the centre. If a force was placed at the edge of a colony, as if being roughly manipulated by crabs or bitten, small square fragments broke away from the colony margin (e.g. Text-fig. 5E). Both triangular and square fragments can be commonly observed forming the centres of regenerative growth in both Recent and fossil assemblages of cupuladriid species. We also shook colonies vigorously in a jar with sand and water to replicate conditions during a storm or strong wave activity. Remarkably, this high energy test only rarely resulted in fragmentation, even in very lightly calcified species, again supporting the idea that current and wave action play insignificant roles in the clonal reproduction of cupuladriids.

Mode III. Clonal propagation by autofragmentation (Text-fig. 6)

Process. Autofragmentation, the self-separation of colonies into viable fragments, was first observed under culture conditions, and inferred from morphological evidence in natural populations of the eastern Tropical Pacific *Cupuladria exfragminis* (O’Dea 2006) (Text-fig. 6). Colonies create uncalcified regions (Text-fig. 7A–B) along which splitting into parts can occur without the aid of mechanical force (O’Dea 2006). A similar morphology has also been observed in the Atlantic *C. biporosa*, although it remains unclear if this species is able to autofragment *per se*, or if the lines of reduced calcification are produced simply to aid mechanical fragmentation.

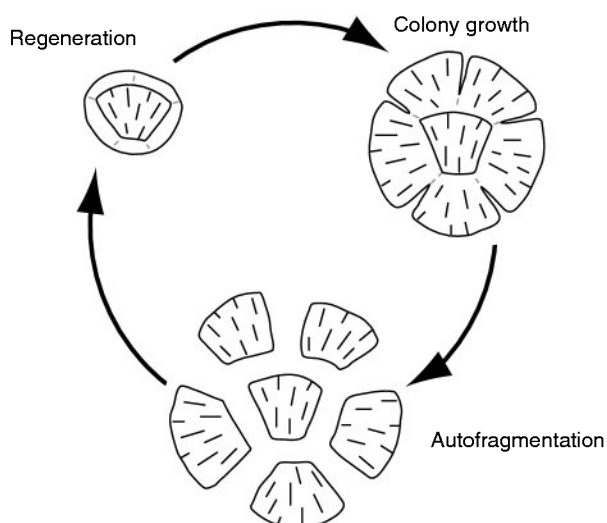
Text-figure 6 illustrates the process of autofragmentation. As the colony begins regeneration from a fragment, the lateral connections between zooids at a number of locations around the colony margin do not calcify normally. Adjacent zooids become entirely spatially separated with further radial growth. This results in the formation



TEXT-FIG. 5. Range of morphologies produced during clonal propagation by mechanical fragmentation. A–B, frontal and basal views of clonally produced colony of *Cupuladria biporosa* showing original fragment, Bocas del Toro, Caribbean, Recent; $\times 10$. C, clonal colony of *Cupuladria biporosa* regenerated from three zooids, Dominican Republic, Miocene; $\times 50$. D, colony showing regeneration from a large triangular fragment in *Cupuladria exfragminis*, Gulf of Panama, tropical eastern Pacific, Recent; $\times 7$. E, basal view of colony founded from small square fragment in *Cupuladria exfragminis*, Gulf of Panama, tropical eastern Pacific, Recent; $\times 4$. F, basal view of colony founded from rectangular fragment in *Cupuladria exfragminis*, Gulf of Panama, tropical eastern Pacific, Recent; $\times 20$. G–H, frontal and basal views of an aclonal colony of *Cupuladria incognita* with reparative, clonal regeneration, Pliocene, Escudo de Veraguas Formation, Bocas del Toro, Panama; $\times 10$.

of characteristic deep notches at the margin of the colony (Text-fig. 7A). At this stage the colony is undoubtedly prone to mechanical fragmentation.

Sometimes notches appear not to extend fully into the central part of the colony, and although zooids appear to be in contact, close inspection reveals an uncalcified lat-



TEXT-FIG. 6. Cycle of clonal propagation by auto-fragmentation in cupuladriid bryozoans.

eral connection (Text-fig. 7B). The separation of adjacent fragments occurs between zooids on the frontal side and between basal sectors on the basal side, thereby leaving the zooids (autozooids and kenozooids) intact. Presumably, the connection between the original central fragment and the new growth either fails to calcify fully from the outset of regenerative growth or the calcified connection is eliminated prior to fragmentation. We did not, however, dissect autofragmenting colonies to determine levels of calcification along lines of fragmentation at different stages of growth.

Each fragment resulting from autofragmentation is potentially able to regenerate and form a new colony. Although survivorship of fragments is not 100 per cent, it is considerably higher than in mechanically fragmented colonies of the same species (O'Dea 2006). The original central fragment can also regenerate and, therefore, has the capability to act as a continual source of new colonies.

Preservable morphology. Autofragmentation usually results in the production of 3–5 new fragments that normally have a truncated-triangular shape (Text-fig. 6). Central fragments can be a variety of shapes, but colonies derived from them can almost always be recognised because they themselves derive mostly from clonal rather than aclonal colonies, and the line of fracture can often be observed.

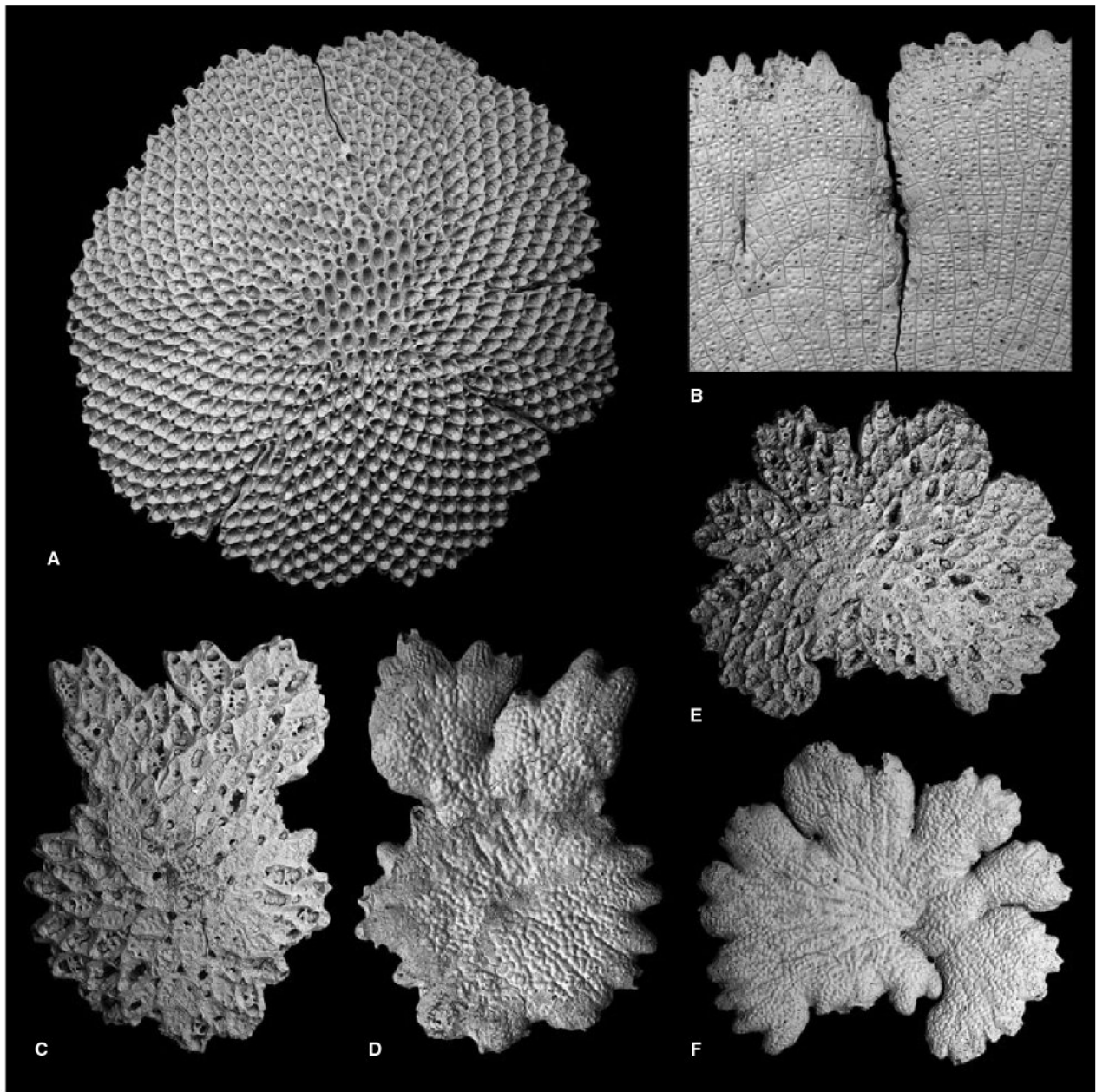
Using gross morphology to distinguish between fragments produced by autofragmentation and those produced by mechanical fragmentation is impracticable in the fossil record because fragments of both modes are similar in shape and the characteristic notched margins of colonies preparing to autofragment have an inherently low preservational potential. A better approach is to examine morphological clues at the zooidal level. O'Dea

(2006) noted that in *C. exfragminis*, fragments produced by autofragmentation had entire unbroken marginal zooids, while the zooids of those produced by mechanical fragmentation were often split and broken. We tested if it was possible to discriminate between auto- and mechanically fragmented colonies based upon the proportion of entire and partial zooids resulting from fragmentation. Three species were analysed, chosen because of their general morphological similarities but very different prevalence of autofragmentation. *Cupuladria exfragminis* readily autofragments in natural populations (O'Dea 2006), *C. biporosa* produces some of the characteristic morphologies of autofragmentation (but less frequently than *C. exfragminis*), and *C. surinamensis* has never been observed to autofragment even after many years of observation in aquaria, nor does it produce morphologies typical of autofragmentation. *Cupuladria exfragminis* and *C. biporosa* are sister species, most probably separated during the formation of the Isthmus of Panama (Dick *et al.* 2003).

We collected living and dead colonies of *C. exfragminis* from the Gulf of Panama, eastern Tropical Pacific, and *C. biporosa* and *C. surinamensis* from Bocas del Toro, southwestern Caribbean, by dredging. For each species, 100 asexually produced colonies were randomly chosen for study. In each colony, the line of fragmentation was followed, starting at the most proximal point in relation to the growth of the original fragmented colony. Along the line, a maximum of 30 sequential zooids located within the original fragment were counted as either entire (e.g. Text-fig. 8A) or partial (e.g. Text-fig. 8B). If the colony did not have 30 sequential zooids along the line of fragmentation, all the available zooids were counted and discriminated. For each colony, the proportion of entire to partial zooids was calculated. The difference in the proportion of entire zooids resulting from fragmentation between the three species was assessed using a one-way ANOVA. Data were arcsine square-root transformed prior to analysis to adjust for non-normality. Frequency histograms of the proportion of entire to broken zooids were compiled for each species.

Results reveal that each of the three species has a very different morphological response to fragmentation (Text-fig. 9). In *C. exfragminis* the mean proportion of entire zooids was 0.94 (SD, 0.07), in *C. biporosa* 0.81 (SD, 0.09), and in *C. surinamensis* 0.39 (SD, 0.22). The means of each were significantly different (F, 355.63, $P < 0.001$) from each other (confirmed using Fisher's Individual Error Rate).

In *C. exfragminis*, in which autofragmentation is widespread, half of the colonies had all of their zooids intact and none had more than half of their zooids broken. In *C. biporosa*, which is presumed to autofragment at a lower rate than *C. exfragminis*, only 1 per cent of colonies

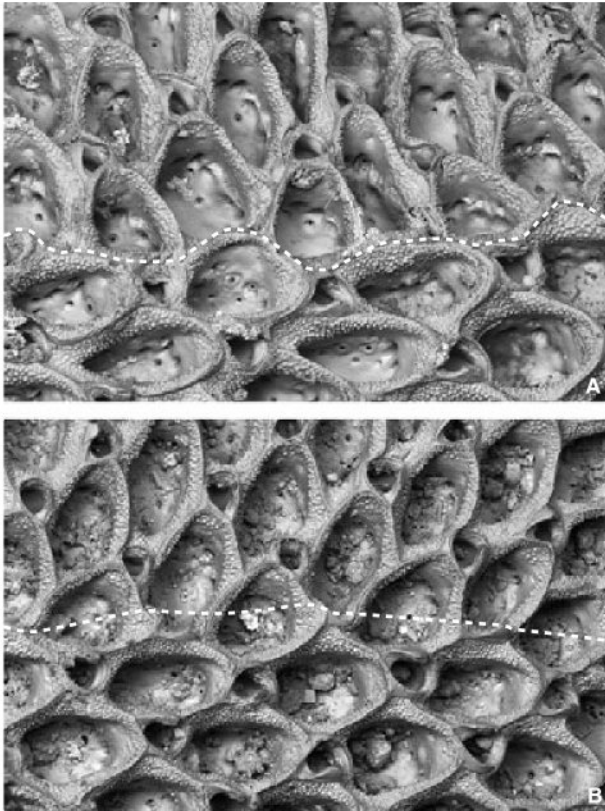


TEXT-FIG. 7. Autofragmentation and colonial budding. A, large colony of *Cupuladria exfragminis* undergoing autofragmentation, Gulf of Panama, tropical eastern Pacific, Recent; $\times 9$. B, marginal notches in *Cupuladria exfragminis* undergoing autofragmentation, Gulf of Panama, tropical eastern Pacific, Recent; $\times 25$. C–D, frontal and basal views of *Discoporella* sp. nov. 20 undergoing colonial budding, Gulf of Chiriqui, tropical eastern Pacific, Recent; $\times 14$. E–F, frontal and basal views of *Discoporella* sp. nov. 20, Gulf of Chiriqui, tropical eastern Pacific, Recent; $\times 10$.

had all their zooids intact but the majority of zooids were left intact. The majority of *C. surinamensis* colonies had a large proportion of broken zooids, consistent with the fact that this species has never been observed to autofragment or produce morphologies suggestive of autofragmentation, and also tends to avoid fragmentation by constructing thicker and stronger colonies than either *C. exfragminis* or *C. biporosa* (O'Dea et al. 2004). Thus, the

proportion of entire zooids created during natural fragmentation appears to correlate with the mode of fragmentation.

This approach cannot be used unequivocally to determine mode of fragmentation in individual colonies because mechanical fragmentation could leave all zooids intact and an autofragmented colony could have some of its zooids broken by mechanical factors following auto-

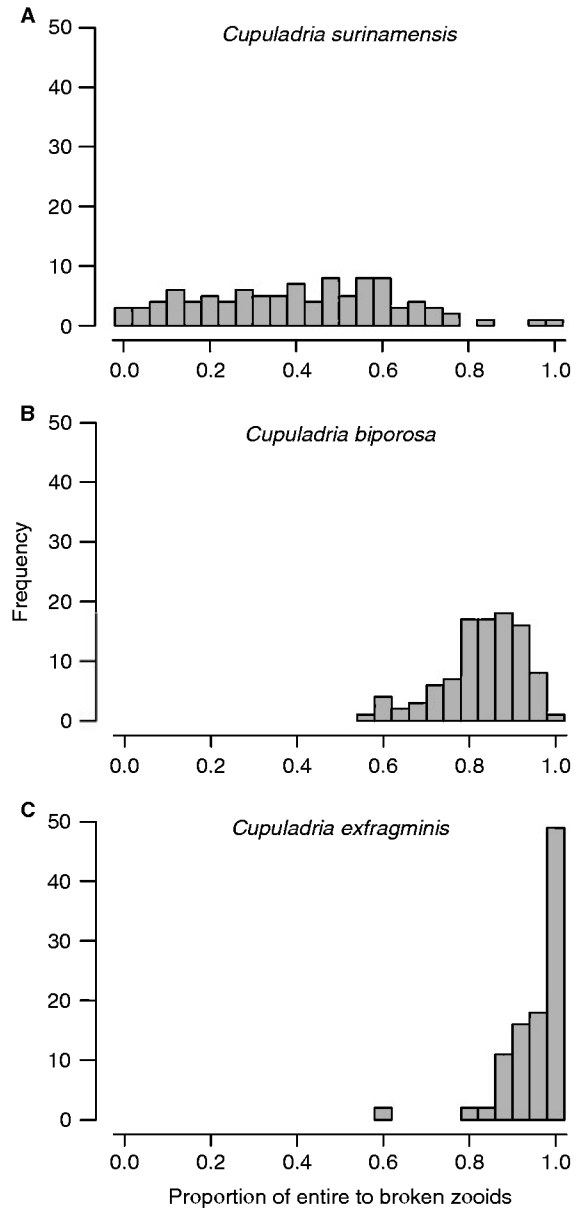


TEXT-FIG. 8. Morphological differences in the colony fracture and regeneration from A, autofragmentation, and B, mechanical fragmentation; $\times 100$. In both, original pre-fragmentation growth is at bottom with a direction from left to right, and lateral regeneration growth at top perpendicular to original growth. Dotted white line delineates line of fragmentation. A, *Cupuladria exfragminis*, Gulf of Panama, tropical eastern Pacific, showing entire zooids along line of fracture typical of autofragmentation. B, *Cupuladria biporosa*, Bocas del Toro, Caribbean, showing broken zooids along line of fracture typical of mechanically fragmented colonies.

fragmentation. The differences between auto and non-autofragmenting species or populations should, however, be recognizable through the analysis of many colonies, the construction of frequency histograms and comparison of mean proportions of entire to broken zooids, as shown here for these three species.

Mode IV. Clonal propagation by colonial budding
(Text-fig. 10)

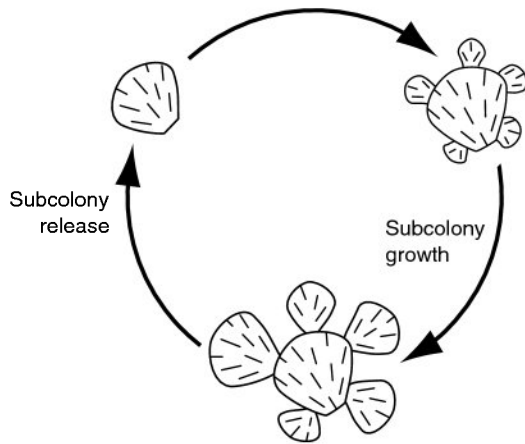
Process. Colonial buds develop through the distal extension of one or a group of new zooids at the growing edge of the colony, which then continue budding distal and distolateral zooids (Text-fig. 10). Zooids situated lateral to the extended group refrain from joining this growth, resulting in the expansion of a fan-shaped subcolony from



TEXT-FIG. 9. Frequency histograms of the proportion of entire to broken zooids along lines of fracture in three cupuladriid species. A, *Cupuladria surinamensis*. B, *Cupuladria biporosa*. C, *Cupuladria exfragminis*.

the colony margin (Text-figs 7C–F, 10) (Håkansson in press).

The manner in which subcolonies are attached to the ‘parent’ colony varies between species. In *Discoporella umbellata* from the Brazilian Atlantic coast, subcolonies are attached by only one or two zooids and the connection is not heavily calcified but held together only by a strong cuticle, which aids in the eventual separation of the subcolony (Marcus and Marcus 1962, pl. 4, fig. 15). Colonies of *Discoporella* sp. nov. 20 from Tropical America appear somewhat similar in appearance to those of *D. umbellata*,



TEXT-FIG. 10. Cycle of clonal propagation by colonial budding in cupuladriid bryozoans.

but the connection between the subcolonies and the parent colony is composed of up to five zooids and seems to remain calcified (Text-fig. 7C–F). Because of this calcified connection, colonial budding in *D. sp. nov. 20* is also preserved in fossil Miocene and Pliocene colonies from Panama and Costa Rica. Håkansson and Thomsen (2001) reported colonial budding in *D. 'umbellata'* from Venezuela. However, unlike the *D. umbellata* colonies from Brazil, the authors reported that the subcolonies maintained a calcified connection with the parent colony, and the material they figured suggests that subcolonies are connected to the parent colony by several zooids, much in the same way as Pacific *D. sp. nov. 20*.

In addition, Håkansson and Thomsen (2001) and Håkansson (in press) described colonial budding in the extinct species *Reussirella haidingeri* from the Miocene of northern Europe. This species did not have a calcified connection between the parent and subcolonies but, like *D. umbellata* from Brazil, the connection was non-calcified. Separation occurred when the non-calcified section broke, leaving the most proximal zooid of the subcolony bisected. As the subcolony developed into a new independent colony, the bisected zooid regenerated either with the original or the reversed polarity, just as occurs in present day *D. umbellata* (Marcus and Marcus 1962).

Non-calcified connections between parent and subcolony may allow colonies to have some control over when subcolonies are released. However, there are no studies testing how the detachment of colonial buds takes place. Presumably, the species that retain a calcified connection require mechanical breakage, because of, for example, predation, inadvertent fragmentation or current action. The likelihood of this happening almost certainly increases with subcolony size.

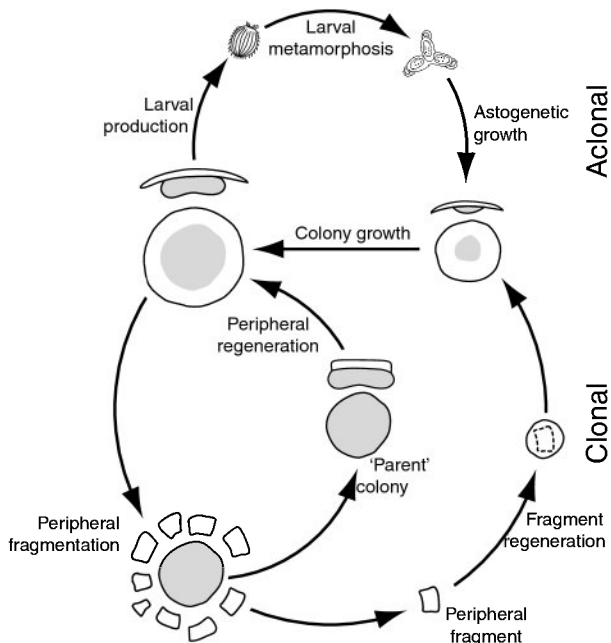
Preservable morphology. Colonial budding can be somewhat difficult to recognize in fossil assemblages. In species

that maintain a calcified connection between parent and subcolonies, colonial budding is likely to be preserved if colonies are abundant enough to ensure that detection and taphonomic disturbance is low enough to prevent post-mortem detachment of subcolonies. However, if parent and subcolonies employ uncalcified connections, the evidence for colonial budding itself will not be preserved except in extremely fortuitous circumstances (e.g. Håkansson and Thomsen 2001, fig. 11.8). Also, a colony produced by colonial budding is superficially very similar to a sexually produced colony because, unlike fragmentation and regeneration, colonial budding produces remarkably symmetrical colonies, and lines of fragmentation are normally obscured because growth is not interrupted. Indeed, the initial zooid of a colonial bud of *D. umbellata* was termed a pseudoancestrula by Marcus and Marcus (1962). Nonetheless, distinction between the two modes can be made by close inspection of the central region of the colony. The ancestrula of a sexually produced cupuladriid colony invariably has a characteristic morphology with a central triad of small zooids followed by a zone of astogenetic change where zooids become larger in size distally (McKinney and Jackson 1989). A colony formed by colonial budding, on the other hand, originates from normal-sized autozooids and, therefore, has neither ancestrula nor a true zone of astogenetic increase in zooid size (see Håkansson and Thomsen 2001).

Mode V. Peripheral fragmentation (Text-fig. 11)

Process. Peripheral fragmentation is a previously undescribed and highly distinct type of propagation (Text-fig. 11). Colonies have an unusual shape with an extremely well-calcified central region but a lightly calcified margin. This morphology has so far only been observed in one fossil species of *Discoporella* from the south-western Caribbean. *Discoporella sp. nov. 3* occurs in Upper Pliocene rocks of the Cayo Agua and Isla Solarte formations of Bocas del Toro, Panama, and in the Rio Banano Formation of Limon, Costa Rica (Collins and Coates 1999). The extinction of the species at the end of the Pliocene means that the reproductive cycle has not been observed in living populations but is inferred from morphological evidence in fossil colonies.

Text-figure 11 illustrates inferred cycles of reproduction in species using peripheral fragmentation. Colonies founded from larvae develop normally, but through time thicken their basal calcification in the central part of the colony. This produces a very prominent bulbous and eventually globular protuberance (Text-fig. 12A–B, D, G). In the meantime, zooidal budding continues at the colony margin so that in section the colony eventually becomes mushroom shaped (Text-fig. 12F). Lacking any significant



TEXT-FIG. 11. Cycle of clonal propagation by peripheral fragmentation in cupuladriid bryozoans.

basal calcification, the zooids that overhang the region of basal thickening are vulnerable to being broken-off. They break away from the 'parent' colony in small squares of c. 30 zooids (Text-fig. 12E) that then create new colonies through regeneration. This life-cycle hypothesis is strongly supported by the observation that almost all clonal colonies originated from such small squares of zooids (Text-fig. 12C). The strongly calcified 'parent' colony is, therefore, able to act as a source of repeated peripheral growth, 'seeding' the area with clonal offspring when conditions permit.

Clonal propagation was dominant among populations of *D. sp. nov. 3*, although sexual reproduction remained important. In 601 colonies of *D. sp. nov. 3* from Cayo Agua we found that 190 (31.6 per cent) of the colonies were sexually produced while 411 (68.4 per cent) had originated from clonal propagation.

Peripheral fragmentation in *D. sp. nov. 3* almost certainly occurred mechanically rather than through autofragmentation because the mean proportion of entire to broken zooids in a sample of 100 colonies from Cayo Agua was low (0.42, SD, 0.22), and the histogram of the proportion of entire to broken zooids (Text-fig. 13) most similar to the non-autofragmenting *C. surinamensis* (see Text-fig. 9A). Because the thinly calcified marginal growth would have been prone to fragmentation from the 'parent' colony, *D. sp. nov. 3* would not have required autofragmentation to maintain high levels of clonal propagation.

Preservable morphology. Colonies using peripheral fragmentation are unmistakable (Text-fig. 12). The greatly thickened calcified basal section that the colony develops is highly characteristic, preservation of whole colonies is excellent, and the small square fragments that are produced by peripheral fragmentation are easily identified.

DISCUSSION

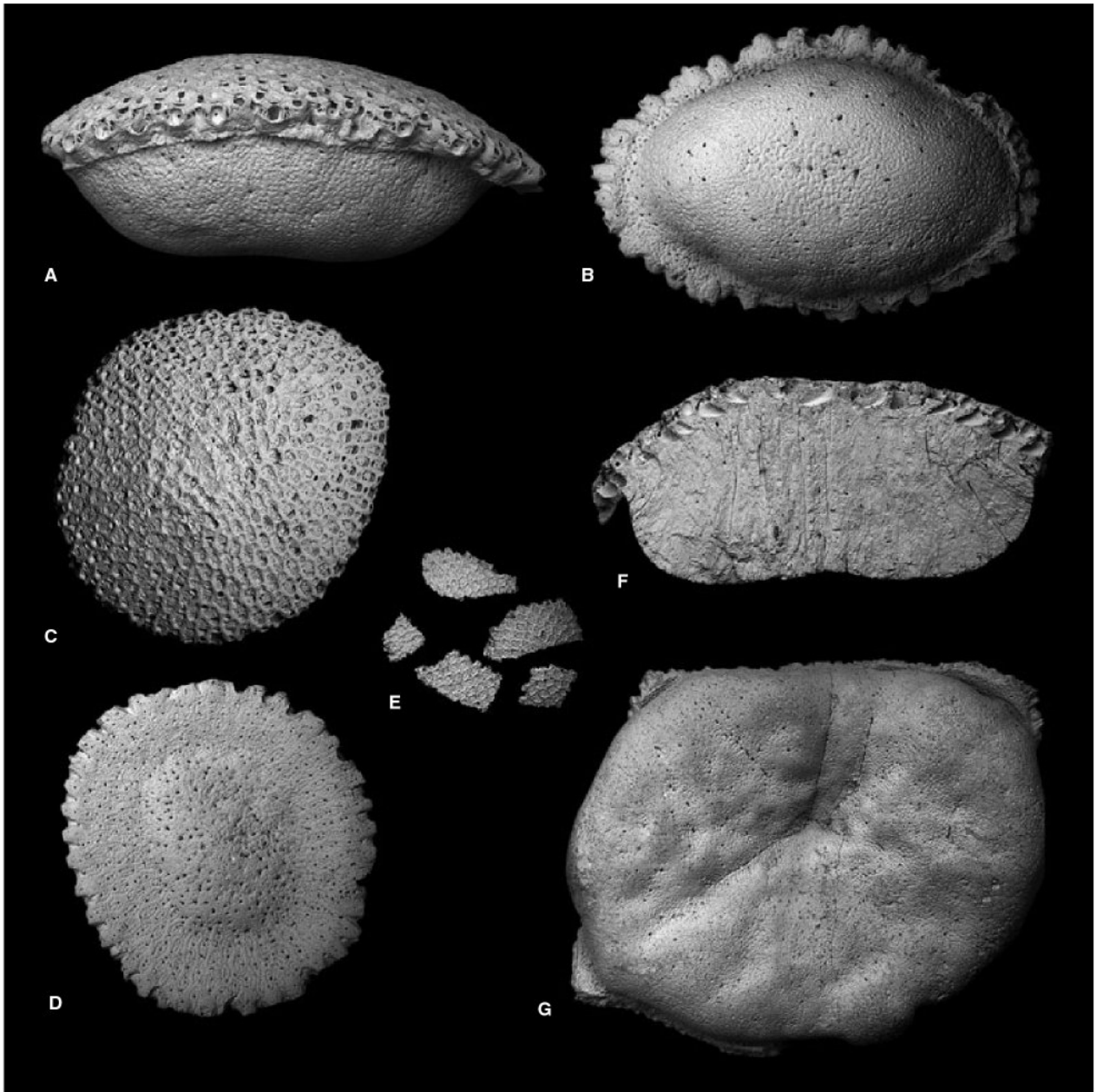
Occurrence and distribution of modes of propagation in cupuladriids

Currently known occurrences and distributions of the different modes of propagation in cupuladriids in space and time are summarised in Table 1. Data have been gathered from both published and unpublished works as well as our continuing studies.

Although clonal propagation is the dominant form of propagation in a number of species (e.g. *C. exfragminis*), no species propagates exclusively clonally; our review shows that all species produce aclonal colonies and, therefore, must reproduce sexually at some time. Unfortunately, however, there is currently no method of measuring variations in fecundity or investment in sexual reproduction between species without counting egg abundance in living colonies, because, unlike many cheilostome species, cupuladriids do not produce ovicells for embryonic brooding (Håkansson and Thomsen 2001).

Not all cupuladriids regularly propagate clonally; some species never do so (e.g. *D. triangula*) while a number clone very rarely (e.g. *D. peltifera*). For the latter, it is likely that the rare incidences of clonality are simply accidents, as all of these species possess morphologies designed to prevent fragmentation (O'Dea *et al.* 2004). Species that do not rely upon cloning to maintain populations are classified as 'specialised aclonal' even though they maintain the ability to propagate clonally and sometimes do (Table 2). All other cupuladriids can be grouped into either the 'clonal and aclonal' group, which is made up of those species that deliberately use mechanical fragmentation to clone and whose populations normally have a mix of clonal and aclonal colonies, or the 'specialised clonal' group, which is made up of species that have dedicated structures or a special type of growth-enhancing clonal propagation and whose populations are normally dominated by clones (Table 2).

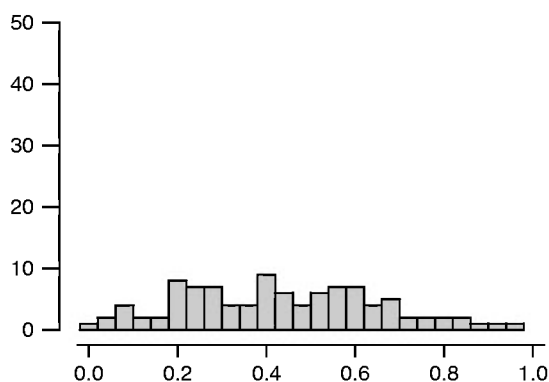
Although the fossil record of cupuladriids is good, it is on the whole poorly studied. It does appear, however, that the earliest species had no specialised morphologies for aclonal or clonal propagation (Gorodiski and Balavoine 1962). By the Miocene, however, both 'specialised clonal' and 'specialised aclonal' morphologies had appeared, and this correlates with a time of global expansion and



TEXT-FIG. 12. Peripheral fragmentation in *Discoporella* sp. nov. 3 from the Pliocene Cayo Agua Formation, Bocas del Toro, Panama. A, lateral, and B, basal views of a typical colony; $\times 10$. C, frontal, and D, basal views of a young colony with developing basal protudence; $\times 8$. E, typical size and shape of fragments produced during peripheral fragmentation; $\times 5$. F, cross section of well-developed colony showing solid calcification of basal protudence; $\times 10$. G, basal view of a huge, and presumably very old colony, showing massive basal development; $\times 6$.

diversification of cupuladriids (Cook and Chimonides 1983). It also appears that this combined phyletic and morphological radiation occurred simultaneously in both the *Cupuladria* and *Discoporella*. Whether such parallel evolution towards similar types of morphological divergence also occurred in other free-living bryozoan groups such as *Mammillopora* and *Selenaria* remains unknown.

Nonetheless, it does suggest the possibility of an important change in the benthic environment that allowed such a radiation to occur in both clades. A potential cause is the well-known middle Miocene ocean-climate transition, which saw major evolutionary changes in benthic assemblages resulting from a global drop in deep-water temperature, enhanced upwelling into coastal waters and



TEXT-FIG. 13. Frequency histogram of the proportion of entire to broken zooids along lines of fracture in *Discoporella* sp. nov. 3.

increased oxygenation of deep waters (Flower and Kennett 1993). Clearly, these speculations require testing, with the accumulation of further occurrence data and analyses of life histories and morphologies through geological time.

It is clear that *Discoporella* has a much wider range of special morphologies for propagation than *Cupuladria*, at least in the Americas (Table 1). For example, the aclonal species of *Cupuladria* and *Discoporella* are both small and dome-shaped with heavier calcification that will prevent fragmentation, but some *Discoporella* species have extreme calcification to the extent of producing completely infilled bases (compare Text-fig. 3F and G). Likewise, although clonality is promoted in *Cupuladria* species through indeterminate growth and very lightly calcified colonies, the only special mode of cloning is autofragmentation, while *Discoporella* species have evolved both peripheral fragmentation and at least two types of colonial budding (Table 1).

The importance of regeneration

Clonal propagation in bryozoans undoubtedly originated from the ability of colonies to make reparative regeneration following colony damage. Such repair is widespread among bryozoans, with examples recorded from both encrusting (e.g. Jackson and Palumbi 1979; Taylor 1985) and erect (Thomsen and Håkansson 1995; Cheetham *et al.* 2001) colony morphotypes. If the damage in question causes separation, and the separated parts are able to regenerate into individual entities, then clonal propagation has occurred. In encrusting colonies this can happen through partial mortality of the colony or fragmentation of the underlying substratum (Hughes and Jackson 1985). The free-living habit of cupuladriids permits relatively easy cloning via fragmentation, and many species

have evolved to use this as their principal means of propagation.

If colonies are unable to regenerate following fragmentation, mortality will affect not only the local abundance of a species but also the relative proportion of clonal to aclonal propagation in a species assemblage. In a previous study, O'Dea *et al.* (2004) suggested that following fragmentation a cupuladriid will have a smaller reserve of energy dedicated to colony growth than an unfragmented colony while correspondingly a relatively large area requiring regenerative growth, and thus may not survive. They also speculated that the rupture of soft tissues that often occurs during mechanical fragmentation may increase chances of infection, leading to reduced growth or mortality during fragmentation. Both of these effects were presented as potential factors in determining levels of clonal propagation within species assemblages. However, these ideas were rejected when the study found no clear relationship between the rate of regeneration and prevalence of clonality in species.

In spite of this, O'Dea (2006) presented both experimental and observational evidence that the ability to regenerate is extremely important in controlling levels of both abundance and relative prevalence of modes of propagation in populations of *C. exfragminis*. Mechanically broken fragments perished when placed under stressed (low food) conditions whereas unbroken colonies tended to survive (O'Dea 2006). Moreover, mechanically-fragmented colonies of *C. exfragminis* had a much higher mortality rate and a significantly lower rate of regenerative growth than autofragmented colonies (O'Dea 2006). Because colonies that experience autofragmentation spend considerable amounts of time in preparation to fragment [almost certainly over a year in many cases, given the growth rate of cupuladriids (O'Dea and Jackson 2002) and the depth of marginal notches; Text-fig. 7B], one may propose that the colony prepares itself by reserving energies for regeneration. This would help to explain why mechanically fragmented colonies fare so badly in culture. Additionally, species that prepare to autofragment may have a greater capacity to mobilise energy across the colony. If this is the case then the capacity to regenerate is of exceptional importance to cupuladriids, and will be a crucial factor in determining the proportion of clonal colonies within an assemblage.

Colonies of *C. exfragminis* from the Gulf of Panama were shown to undergo autofragmentation in synchrony with increased levels of primary productivity (O'Dea 2006). It may be that regeneration of colonies is easier when food levels are elevated, and *C. exfragminis* opts to autofragment when its chances of survival are higher. This may explain in part why prevalence of clonality in species and genera is higher in areas of higher productivity (O'Dea *et al.* 2004; O'Dea 2006) and why the number of species that regularly

TABLE 1. Occurrence, gross distribution and prevalence of different modes of aclonal and clonal propagation in fossil and Recent cupuladriids based on counts of individual colonies in assemblages of each species if data are available, or based upon field observations or prevalence in figured material if not. Distribution based on fossil and Recent occurrences of taxa.

Taxon	Distribution	Age	Clonal					Ref.
			Aclonal	Sex	Mech.	Auto.	Bud.	
<i>Cupuladria</i>	Tropical and subtropical	Palaeogene–Recent	••	••	•	×	×	
<i>C. aff. biporosa</i>	Europe	Miocene	••	••	×	×	×	1
<i>C. biporosa</i>	West Africa, Atlantic, Caribbean	Miocene–Recent	••	••	•	×	×	2
<i>C. canariensis</i>	Eastern Atlantic, Mediterranean	Recent	•••	••	×	×	×	1,2,3
<i>C. cavernosa</i>	Europe	Miocene–Pliocene	○	○	×	×	×	2
<i>C. cheethami</i>	Caribbean	Pliocene–Recent	••	••	×	×	×	
<i>C. doma</i>	Western and eastern Atlantic	Recent	•••	•	×	×	×	4,5
<i>C. eocaenica</i>	Africa	Palaeogene	○	○				6
<i>C. exfragminis</i>	Eastern Pacific and Caribbean	Miocene–Recent	•	•	•••	×	×	
<i>C. guineensis</i>	Indo–West Pacific	Recent	○	○	×	×	×	7
<i>C. incognita</i>	Caribbean	Pliocene–Recent	•••	•	×	×	×	
<i>C. multesima</i>	Caribbean	Pliocene–Recent	•••	•	×	×	×	
<i>C. sp. nov. 6.</i>	Caribbean	Miocene–Pleistocene	••	••	×	×	×	
<i>C. sp. nov. 'biporosa B'</i>	Caribbean	Miocene–Recent	••	••	×	×	×	
<i>C. sp. nov. 'gigante'</i>	Caribbean	Recent	•	•••	×	×	×	
<i>C. ovalis</i>	Africa	Palaeogene	○	○				6
<i>C. panamensis</i>	Caribbean	Miocene–Recent	•••	•	×	×	×	
<i>C. surinamensis</i>	Caribbean, western Atlantic	Miocene–Recent	••	••	×	×	×	
<i>C. vindobonensis</i>	Europe	Miocene	○	○	×	×	×	8
<i>Discoporella</i>	Tropical and subtropical	Paleocene–Recent	•••	•	×	•	•	
<i>D. bocasdeltoroensis</i>	Caribbean	Miocene–Recent	•••	•	×	×	×	
<i>D. cookae</i>	Eastern Pacific and Caribbean	Miocene–Recent	••	••	×	×	×	
<i>D. marcusorum</i>	Eastern Pacific and Caribbean	Miocene–Recent	•••	•	×	×	×	
<i>D. sp. nov. 3</i>	Caribbean	Pliocene	•	×	×	×	••	
<i>D. sp. nov. 20</i>	Eastern Pacific and Caribbean	Miocene–Recent	•	•	×	•••	×	
<i>D. sp. nov. P1</i>	Eastern Pacific	Recent	••••	×	×	×	×	
<i>D. peltifera</i>	Caribbean	Pliocene–Recent	•••	•	×	×	×	
<i>D. scutella</i>	Caribbean	Miocene–Recent	•••	•	×	×	×	
<i>D. terminata</i>	Caribbean	Pliocene–Recent	•••	•	×	×	×	
<i>D. triangula</i>	Caribbean	Pliocene–Recent	••••	×	×	×	×	
<i>D. umbellata</i>	East and west Atlantic, Caribbean	Miocene–Recent	•	•	×	•••	×	1,3
<i>D. umbellata depressa</i>	Western Atlantic	Recent	••	••	×	×	×	4
<i>Reussirella</i>	Tethys, Mediterranean	Miocene–Recent	••	•	×	•	×	
<i>R. haidingeri</i>	Tethys	Miocene	•	•	×	••	×	1
<i>R. multispinata</i>	Gulf of Tunisia	Recent	○	○	×	○	×	9

••••, all (100%); •••, frequent (>70%); ••, common (30–70%); •, infrequent (<30%); ○, known to occur but prevalence not measured; ×, never; empty cells, not known. References represent source of information in distribution, age and/or mode of reproduction; if no reference is given, data were collated from specimens: 1, Håkansson and Thomsen (2001); 2, Cook and Chimonides (1994); 3, Marcus and Marcus (1962); 4, Winston (1988); 5, Cook (1965); 6, Gorodiski and Balavoine (1962); 7, Canu (1916, p. 322); 8, Baluk and Radwanski (1984); 9, Paul D. Taylor and Rakia Ayari (unpublished 2006).

use clonality to propagate is relatively lower in more oligotrophic areas (O'Dea *et al.* 2004). Another explanation that could apply to species relying on mechanical fragmentation to clone is that an increase in productivity, and thus higher food levels, could lead to faster zooidal budding, resulting in more brittle and thinly calcified colonies if biomineralization rate remains constant.

Divergent evolution: the trade-offs of clonal vs. aclonal propagation in cupuladriids

Both sexual reproduction and clonal propagation require energy from food, and although the energetic requirements of these modes of reproduction remain unknown, a number of issues are worth discussing.

TABLE 2. Broad scale discrimination of types of propagation in species of cupuladriid Bryozoa.

Type	Description	Typical morphologies	Characteristic species
Specialised aclonal	Large majority of colonies aclonal. Special morphological traits to avoid fragmentation although may maintain ability to clone if fragmented.	Heavy calcification; small and squat colonies; determinate growth	<i>D. peltifera</i> <i>D. sp. nov. P1</i> <i>D. triangula</i>
Non specialised clonal and aclonal	A mix of clonal and aclonal colonies. Relies upon mechanical fragmentation to clone.	Moderate to lightly calcified colonies; may have indeterminate growth	<i>C. surinamensis</i> <i>C. panamensis</i> <i>D. bocasdeltoroensis</i>
Specialised clonal	Large majority of colonies clonal. Special morphological traits to enhance fragmentation or clonal propagation.	Weakly calcified colonies (except peripheral fragmentation), autofragmentation or budding; indeterminate growth.	<i>C. cheethami</i> <i>C. exfragminis</i> <i>D. sp. nov. 20</i> <i>D. sp. nov. 3</i>

Growth is the fundamental basis of clonal propagation (Håkansson and Thomsen 2001), and this is the case irrespective of which mode of cloning is used because growth is required to create material to fragment and to regenerate fragments. A potential disadvantage of relying upon happenstance to break colonies mechanically is that control is lost over the timing of fragmentation. Sexual reproduction presumably enables organisms to delay reproduction and dispersal by accruing energy and initiating reproduction when conditions (environmental or biotic) are most suitable (Harvell and Grosberg 1988; Hall and Hughes 1996). The same is almost certainly true for clonal propagation when the colony has control over when fragmentation takes place (O'Dea 2006), and the benefits of such control justifies the additional expenses incurred by the creation of special modes of clonal propagation, such as autofragmentation, colonial budding and peripheral fragmentation. Indeed, control of timing of propagation (both clonal and aclonal) may explain why the extreme divergences of life histories, from excessive protection against fragmentation in aclonal species to special modes to propagate in clonal species, have become so successful.

One advantage clonal propagation has over sexual reproduction is that of potentially increased dispersal success under certain circumstances. Clonality bypasses the hazards of larval predation, which may severely reduce larval densities (Gaines and Roughgarden 1987), especially in the yolk-rich lecithotrophic larvae of bryozoans, although it appears likely that cupuladriid larvae settle very soon after spawning (Winston 1988). Size dependent mortality rates may be a more important factor in promoting clonal propagation. Fragmentation of a colony almost always results in the production of new colonies that are substantially larger than young colonies formed from newly metamorphosed larvae, and thus, size-dependent predation may be reduced.

Likewise, clonal propagation may reduce mortality rates because the likelihood of being smothered during sedi-

mentation is probably less for the larger colonies produced during fragmentation than those produced through sexual reproduction (Jackson and Coates 1986). Although the advantages of having movable setae, which occur in large numbers in cupuladriids, have yet to be quantified, their presence is clearly of great importance to the ecological and evolutionary success of cupuladriids in soft sediments. A small colony from a fragment has longer and, therefore, presumably stronger setae than a colony that has been produced sexually because the setae-bearing vibraculae produced in early astogeny are relatively small. Thus, a fragment may be better prepared to function in a situation where mobility is required for survival, especially under processes where mortality rates are size-dependent.

On the other hand, the advantages of investing energy in extra calcification to reduce the chances of fragmentation may be related to the high mortalities that occur during fragmentation (O'Dea 2006). It is currently not known if clonal cupuladriid species invest less energy in the production of gametes, although such a relationship has been previously shown for other bryozoan groups (Cheetham *et al.* 2001; Håkansson and Thomsen 2001). Nonetheless, it is conceivable that if the fitness gained by investing energies into repair and regeneration is less than that achieved by investing energies in sexual reproduction, then morphological strategies that aid aclonal propagation should be favoured.

The evolution of a special method to reproduce clonally does not necessarily mean that a species has abandoned sexual reproduction. Indeed, all species that employ special methods to clone do propagate aclonally at some time (Table 1). The use of sex and a specialised clonal method of propagation may serve to increase the types of environmental conditions under which a population can successfully disperse. One example can be found in species that use peripheral fragmentation; if food is scarce, the use of clonality may become ineffective because of insufficient

energies for the regeneration of fragments. In this case, the heavily thickened 'parent' colony may be able to cease peripheral growth and instead invest in the slow maturation of gametes for sex and asexual propagation. If food levels are high, the colony could invest more in peripheral growth for the successful propagation of clones.

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