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# Jeremy Jackson, Bryozoa, and the Punctuated Equilibrium Debate

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## 1. Introduction

In *The Adventures of Punctuated Equilibria, A Struggle for Authority in the Evolutionary Sciences*, sociologist Andrew Grimshaw (2001) attributed a share of the responsibility for the lengthy debate following Niles Eldredge and Steve Gould's (1972) introduction of their theory to "the poor quality of communication" between its proponents (mainly paleontologists) and its opponents (chiefly biologists). He further suggested that one way in which conflicting views could be reconciled is through collaborative efforts between members of the two groups, going on to say, "Indeed there is only one example of a sustained research programme between a paleontologist and biologist attempting to address the macroevolution-microevolution divide—the joint projects of paleontologist Alan Cheetham of the Smithsonian Institution and biologist Jeremy Jackson of the Scripps Institution of Oceanography in California" (Grimshaw, 2001, p. 164). Many of the respondents to the questionnaires that he used to supplement his analysis of the punctuated equilibrium literature admitted that this was a type of long-term effort to which few scientists would be willing to commit.

Just how did it come about that Jeremy, a marine biologist/reef ecologist, committed to a 20-year-long collaboration with a paleontologist/bryozoan taxonomist on such an undertaking? It began formally in 1986 when the Smithsonian Institution funded our proposal entitled "Are skeletons enough to tell species apart? A test using cheilostome Bryozoa." However, its roots go back at least 10 years before that, to the time shortly after

Jeremy's arrival at Johns Hopkins when he began spending time in my lab in Washington identifying bryozoans from his experiments with the cryptic reef communities in Jamaica. From that work, Jeremy and one of his students, Leo Buss, developed the notion of non-transitive competitive networks ("A beats B, B beats C, but C beats A") among encrusting organisms (Jackson, 1979; Buss and Jackson, 1979), an idea that proved useful to subsequent workers investigating the contrasting fates of major bryozoan clades from the Mesozoic into the Cenozoic (McKinney, 1995). Then, in 1981, as though anticipating our future collaboration, Jeremy spent some of his own grant money, when travel funds had been frozen by the incoming federal administration, to allow me to attend his symposium in New Haven on the biology of clonal organisms (Jackson et al., 1985). Moreover, I was not the only bryozoan paleontologist with whom Jeremy was collaborating in 1986; he was also working on a book on bryozoan evolution with Ken McKinney (McKinney and Jackson, 1989).

## 2. A Question and a Challenge

One day late in 1983 or early in 1984, seeing me struggle to fit more than a dozen morphologically distinct groups, or morphotypes, of the cheilostome bryozoan *Metrarabdotos* from Miocene and Pliocene deposits in the Dominican Republic into what I was convinced could be no more than four species, Jeremy asked a simple question: "Have you considered the possibility that your 'morphotypes' could all be species?"

Both of us were quite aware of the results that the biologist Frank Mauro (1973) had obtained from an experiment with two morphotypes, long considered conspecific, of another cheilostome, *Parasmittina*. By rearing larvae of known maternal morphotype, but unknown paternity, he expected, as he put it in the oral presentation of his results two years earlier at a meeting of the International Bryozoology Association, to become the "Mendel of Bryozoa." Both morphotypes, however, bred true; they also show consistent, although small, morphological differences strongly supporting the conclusion that they are different species (Mauro, 1973).

My reluctance to accept a similar conclusion for the *Metrarabdotos* morphotypes stemmed from their greater variability and significant overlap with each other, in addition to the fact that the genus is not very closely related to *Parasmittina*. In an oral presentation in 1983 of preliminary results with the Dominican Republic material (Cheetham, 1985), I interpreted most of the morphotypes as "intermediates" between various pairs of the four inferred species. However, the fact remained that the distinctiveness of all the morphotypes was based on high levels of significance in statistical tests that considered simultaneously all of more than 40 morphological characters. With some misgivings because of the looseness of the analogy to the species on which Mauro's (1973) genetic results were obtained, I accepted a statistical cutoff level that made 13 of the Dominican Republic *Metrarabdotos* morphotypes species. In doing so, I also had to accept that most of the resulting species had stratigraphic durations overlapping by millions of years in the Dominican Republic sections. That, together with the close spacing of occurrences

through the sections, made it obvious that here was a good example on which to test evolutionary tempo with a variety of statistical methods. As one of the many paleontologists who were skeptical about accepting the punctuated equilibrium model, I formulated the tests to make it as difficult as possible to reject gradualism and thus accept punctuation (Cheetham, 1986).

The results (Cheetham, 1986, 1987) all supported the punctuated equilibrium model. By the time the first paper was published, however, Jeremy reawakened my hesitation about accepting the *Metrarabdotos* morphotypes as species. As he put it to Richard Kerr (1995) of *Science* magazine, “Clearly, the strength of any discovery of punctuated equilibrium—a model of speciation—depends on our ability to recognize species. So I challenged him [Cheetham] to submit his methods to biological examination.” Thus we embarked in 1986 on the project to test whether “cheilostome bryozoan skeletons are enough to tell species apart.”

### 3. The Test

Our project consisted of three parts, each of which required a feat of collecting—of both specimens and biological data—on Jeremy’s part. The first collection, of specimens from both coasts of Panama, would provide the material with which I would apply the morphometric/statistical methods used in the *Metrarabdotos* study to discriminate a series of morphospecies based on measurements and other characters of their skeletons; these results would form the framework for the “biological examination” to follow. Unfortunately, *Metrarabdotos* itself would not be part of the test; unlike their fossil congeners, surviving species are few and uncommon. Pat Cook (1973) had grown colonies of one species (*M. cookae*) in West Africa, but it includes just a single morphotype refractory to further division, even in the latest morphometric/statistical analysis (Cheetham et al., 2007).

Instead, we settled on three distantly related cheilostome genera of quite different morphology, including the one that had been the subject of Maturo’s (1973) experiment on inheritance. All of them were common on one or both of the Panamanian coasts, and each showed significant evidence of variation in morphotype. In the anascan genus *Steginoporella*, we distinguished three morphospecies and in the ascophorans *Stylopoma* and *Parasmittina* four and 16, respectively. Thus, the generality of the results Maturo obtained with just two morphotypes of a single genus could be tested; if the results were sufficiently consistent, they would strengthen the analogy for *Metrarabdotos*.

The maternal colonies for the second part of our project, the experiment on heritability of species identity, were all collected on the Caribbean coast of Panama from different water depths at sites as much as 110 km apart; they included two species of *Steginoporella*, two of *Stylopoma*, and three of *Parasmittina*. The offspring of the 131 colonies were all grown in a common environment at the field station of the Smithsonian Tropical Research Institute in the San Blas, an environment that was different from those in which any of the maternal colonies were collected. The morphospecies identities of both the maternal and

offspring colonies remained uncertain until the end of the experiment. Then, skeletal measurements from both sets of colonies were incorporated into the morphometric/statistical analyses (one for each genus) on which the first part of the project was based. All but nine of 450 offspring (two percent) were assigned by the analyses to the same morphospecies as their maternal parent (paternity was unknown); this slight difference from the results obtained by Maturo (1973) could have been the result of a mix-up in returning fallen colonies to their positions after a storm (Jackson and Cheetham, 1990).

For the third part of the test—analysis of enzyme variation by electrophoresis—Jeremy collected another 402 colonies, all from Panama’s Caribbean coast. He sorted them into morphospecies by visual inspection, three species each of *Steginoporella* and *Stylopoma* and two of *Parasmittina*. Subsequent morphometric/statistical analysis of voucher portions (remaining after sampling for electrophoresis) of 10-20% of the specimens confirmed the visual assignments. Between each of the pairs of morphospecies within each genus, he found diagnostic alleles at one or more of seven loci, and no diagnostic alleles between colonies of the same species from different localities, showing that the morphospecies are unambiguously distinct genetically.

By December 1988, the second part of the test had been completed, and I was dispatched to the annual meeting of the American Society of Zoologists to present the results (Cheetham and Jackson, 1988) in a symposium on “Species and Evolution in Clonal Organisms” (Budd and Mischler, 1990). In the fall of the next year, Jeremy presented the results of the whole project at the annual meeting of the Geological Society of America (Jackson and Cheetham, 1989), and in 1990, the complete study was published (Jackson and Cheetham, 1990).

While accepting the principal conclusion of our test—the correspondence between skeletal morphology and genetics—Jeffrey Levinton (1991), one of the most outspoken critics of the punctuated equilibrium model, questioned whether any of the species we used were sufficiently closely related to each other to provide an analogy for the punctuated pattern of morphological change in *Metrarabdotos* that we inferred to be a record of speciation. The genetic distances (Nei’s unbiased D) that we reported for *Steginoporella* and *Stylopoma*, ranging from 0.34 to 2.12 (mean 1.2), “cannot be distinguished from distances between fairly distantly related nonsibling species” (Levinton, 1991), and the single distance for *Parasmittina* was even greater. The morphological distances (square root of Mahalanobis’  $D^2$ ) we had obtained were also much greater than those among most species of *Metrarabdotos*, averaging 77, 41, and 58 in *Steginoporella*, *Stylopoma*, and *Parasmittina*, respectively, with a total range of 14 to 103 (Jackson and Cheetham, 1990), compared to 26 in *Metrarabdotos*, with a total range of 5.5 to 46 (Cheetham et al., 2007).

In 1992, the Smithsonian funded our second grant—“Does morphologic stasis of fossils reflect biologic evolution at the species level?”—that enabled us to enlarge the dataset in order to address some of these deficiencies. Morphological and genetic data were collected from a wider range of geographic localities, and morphological data were obtained from fossil bryozoans as well as the living ones. For logistic reasons, including

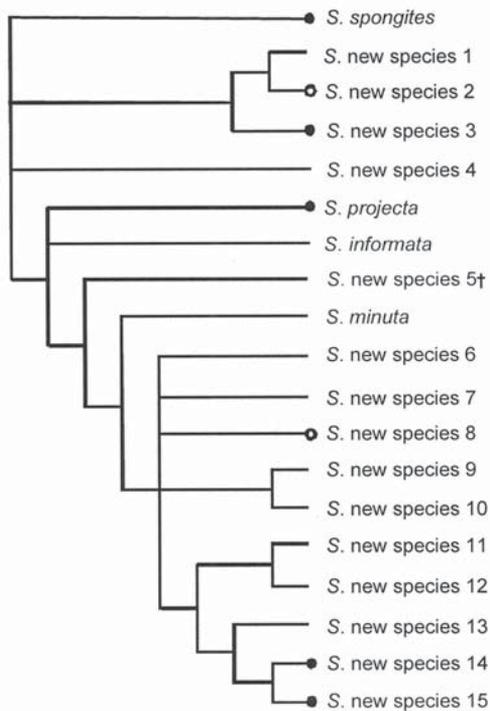


Figure 1. Cladogram for tropical American species of *Stylopoma*, redrawn from Jackson and Cheetham (1994, fig. 5). Circles mark species analyzed electrophoretically, solid circles for species from Panama, open ones for those from Curacao. Cross (†) marks apparently extinct species.

the readiness with which specimens could be recognized in collecting by scuba, we focused the new study on *Stylopoma*. Jeremy made new collections from Curacao, more than 1000 km from Panama, and submitted replicate specimens from 11 local populations to electrophoresis. Morphological measurements from these and more than 100 suitable fossil and recent museum specimens (including type specimens of three named species of *Stylopoma*) from the Caribbean, Gulf of Mexico, and southeastern United States were added to those from our first study. Then, the morphological analysis was completely redone.

The new analysis yielded 19 *Stylopoma* species. The three species from Caribbean Panama in the original study split into five (Fig. 1; Jackson and Cheetham, 1994). *Stylopoma* species 1 of Jackson and Cheetham (1990) separated into *S. spongites* (which included all of the *S. species 1* specimens from the maternal inheritance experiment) and *S. new species 3*; *S. species 2* remained distinct but now included the holotype of *S. projecta* from the Panamanian Pleistocene; *S. species 3* was resolved into *S. new species 14* and *S. new species 15*; and the new material from Curacao yielded two species, *S. new species 2* and *S. new species 8*, neither of which occurs in Panama. Only three of the 19 species in total, including *S. new species 15* from Panama and *S. new species 8* from Curacao, lack fossil records. One of the 19 species, *S. new species 5*, is known only from fossils. Thus, the strategy of broadening the scope of the dataset appeared to achieve the objective of making the results more comparable to the *Metrarabdotos* record.

The morphological distances between species in *Stylopoma* became more comparable

Table 1. Genetic (Nei's D) and morphological (square root of Mahalanobis D<sup>2</sup>) distances between pairs of *Stylopoma* species analyzed electrophoretically (Panamanian species in boldface). These data were the source for figure 4a in Jackson and Cheetham (1994).

Species pair	Nei's D	Mahalanobis D
<i>S. spongites</i> - <i>S. new species 2</i>	0.479	3.37
<i>S. spongites</i> - <b><i>S. new species 3</i></b>	0.050	3.88
<i>S. spongites</i> - <b><i>S. projecta</i></b>	0.963	4.18
<i>S. spongites</i> - <i>S. new species 8</i>	0.817	3.37
<i>S. spongites</i> - <b><i>S. new species 14</i></b>	1.438	7.06
<i>S. spongites</i> - <b><i>S. new species 15</i></b>	1.505	10.97
<i>S. new species 2</i> - <b><i>S. new species 3</i></b>	0.601	4.58
<i>S. new species 2</i> - <b><i>S. projecta</i></b>	1.606	4.93
<i>S. new species 2</i> - <i>S. new species 8</i>	1.566	6.41
<i>S. new species 2</i> - <b><i>S. new species 14</i></b>	2.526	7.55
<i>S. new species 2</i> - <b><i>S. new species 15</i></b>	2.616	11.46
<b><i>S. new species 3</i></b> - <b><i>S. projecta</i></b>	1.161	5.87
<b><i>S. new species 3</i></b> - <i>S. new species 8</i>	1.035	5.90
<b><i>S. new species 3</i></b> - <b><i>S. new species 14</i></b>	2.300	6.10
<b><i>S. new species 3</i></b> - <b><i>S. new species 15</i></b>	2.273	10.18
<b><i>S. projecta</i></b> - <i>S. new species 8</i>	0.632	5.26
<b><i>S. projecta</i></b> - <b><i>S. new species 14</i></b>	2.337	7.39
<b><i>S. projecta</i></b> - <b><i>S. new species 15</i></b>	3.836	11.22
<i>S. new species 8</i> - <b><i>S. new species 14</i></b>	1.298	4.18
<i>S. new species 8</i> - <b><i>S. new species 15</i></b>	1.385	8.67
<b><i>S. new species 14</i></b> - <b><i>S. new species 15</i></b>	0.004	5.79
Mean		

to those in *Metrarabdotos* also (Table 1; Jackson and Cheetham, 1994), with mean morphological distance (6.6) only slightly greater than the smallest distance in *Metrarabdotos* (5.5). Moreover, although the mean genetic distance between the 21 pairs of *Stylopoma* species (1.45) was greater than that between the three pairs in the original study (0.86), distances between species of two pairs (0.05 and 0.004, Table 1) were well below the level (0.34) that Levinton (1991) had pointed to as indicating "fairly distantly related non-sibling species." Finally, as additional evidence of the correspondence between morphology and genetics, the correlation between Nei's D and Mahalanobis D for the 21 species pairs is highly significant ( $r_s = 0.739$ ,  $p < 0.001$ , with 19 degrees of freedom; Jackson and Cheetham, 1994, table 3).

#### 4. Implications for the Tempo of Speciation

The results of the test of correspondence between morphology and genetics not only provided justification for interpreting the punctuated pattern of morphological change in *Metrarabdotos* as a record of speciation, but they also suggested a similar tempo of change in *Stylopoma*. The stratigraphic record of *Stylopoma* species in tropical America is less dense than that of *Metrarabdotos* (Cheetham and Jackson, 1994), making the statistical approach used to establish the static morphologies of species in the latter genus less appropriate. However, of the 18 extant species of *Stylopoma*, eight persisted for millions of years from Late Miocene or Pliocene time with probabilities exceeding 0.9 (and five of the eight with  $p > 0.99$ ) (Jackson and Cheetham, 1994, fig. 5b). “Moreover,” Jeremy wrote, “11 of the species originate fully formed at  $p > 0.9$ , with no evidence of morphologically intermediate forms, and all ancestral species but one survived unchanged along with their descendants, as required by Levinton’s (1988) persistence criterion” (Jackson and Cheetham, 1994, p. 420).

The criticisms of Levinton (1991) and of Bob Anstey (quoted in Grimshaw, 2001, p. 165) that the “relatedness” of species in our analyses was “clouded” by our reliance on phenetic rather than cladistic methods was blunted by our inclusion of cladograms for both *Stylopoma* (Fig. 1; Jackson and Cheetham, 1994, fig. 6) and *Metrarabdotos* (Jackson and Cheetham, 1994, fig. 7). Although we found that none of the *Metrarabdotos* cladograms

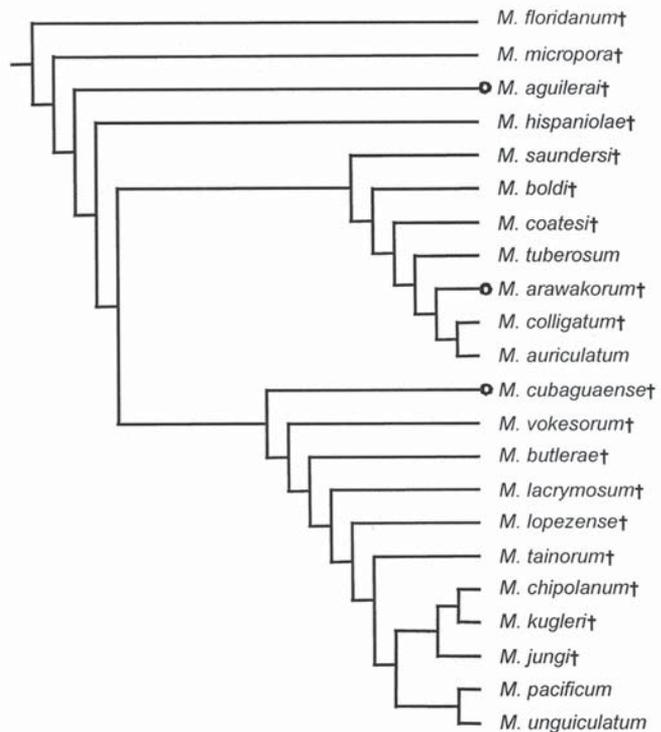


Figure 2. Cladogram for tropical American species of *Metrarabdotos*, redrawn from Cheetham et al. (2007, fig. 8). Three Venezuelan species showing significant evidence of clonal propagation are marked with open circles. Crosses (†) mark extinct species.

in 1994 was closely consistent with stratigraphic ranges, we produced a new, more congruent cladogram in our later, complete re-analysis of *Metrarabdotos* (Fig. 2; Cheetham et al. 2007, fig. 8); it resulted in no change in our conclusions regarding within-species morphological stasis and the persistence of putative ancestors after cladogenesis (Cheetham et al., 2007, p. 18-20, fig. 10). Moreover, our results in *Stylopoma* showed that genetic distances between species were at least as highly correlated with morphological distances ( $r_s = 0.739$ ) as they were with cladistic distances ( $r_s = 0.730$ ),  $p < 0.001$  with 19 degrees of freedom in both cases (Jackson and Cheetham, 1994, table 3).

In concluding the 1994 paper, Jeremy wrote (Jackson and Cheetham, 1994, p. 421):

“[T]he tight correlation between phenetic, cladistic, and genetic distances among *Stylopoma* species suggests little or no conflict between molecular and morphological approaches to phylogeny reconstruction in cheilostomes, unlike that found in some other taxa ... Moreover, changes in all measures of interspecific difference may have occurred together during speciation, as predicted by the punctuated equilibrium model. Morphological stasis and an episodic pace of speciation thus may imply an episodic pattern of molecular evolution, rather than a constantly evolving molecular clock. This would suggest that calculations of the timing of cheilostome speciation based on allozyme data may be erroneous, and phylogenies based on allozymes should be no better or worse than those based on morphology, assuming equal analytical rigor.”

To estimate how prevalent punctuated speciation may have been beyond these two cheilostome bryozoans is a difficult undertaking. In their 1995 book, *New Approaches to Speciation in the Fossil Record*, Doug Erwin and Bob Anstey tabulated 58 cases from the paleontological literature under three headings, “gradualism,” “gradualism with stasis,” and “punctuation with stasis” (Erwin and Anstey, 1995, table 1.1). Gradualism (with or without stasis), accounted for 32, or 55%, of the cases, and punctuation (with stasis) for 26 cases, or 45%. Thus, they concluded, no single pattern is prevalent, although “they concede that many of these studies have their weaknesses” (Kerr, 1995).

In order to test whether or not a case in the fossil record supports punctuated equilibrium theory, Jeremy laid out a rigorous set of requirements (Jackson and Cheetham, 1999, p. 72-73):

“[S]upport for punctuated equilibria requires that changes in morphology within a species are so small and unsustained in direction that they cannot account for morphological differences between ancestors and descendants. This in turn requires rigorous taxonomy, sampling, stratigraphy and phylogenetic analysis.

“To compare the morphology of populations in space and time quantitatively, taxonomic resolution must be sufficient to discriminate species with confidence. Consequently, good preservation of abundant, morphologically complex fossils is necessary to obtain enough specimens and characters for biometrical discrimination of morphospecies (species defined on the basis of morphology). These requirements largely limit studies to marine shelly invertebrates.

Likewise, genetic support for morphospecies is necessary to have confidence in their equivalence to recent biological species. Genetic calibration effectively limits studies to the past 25 million years (Neogene and Quaternary), when most modern clades originated.

“To resolve biogeographic and stratigraphic ranges with confidence, the density and distribution of sampling must be sufficient. These sampling requirements also limit studies to shelly clades that are common throughout most of their history. Biogeographic resolution is necessary to distinguish ecophenotypic change or biogeographic replacement from evolution. Stratigraphic precision is required to constrain phylogenies that are routinely plagued by extreme problems of convergent evolution when species of disparate geological age are combined in cladistic analyses. Well determined ages of first and last occurrence are critical because well resolved phylogenies are necessary to establish ancestor-descendant pairs of species with high confidence. Resolving these relationships depends at least as much on the quality of the taxonomy and sampling as the method of phylogenetic analysis.”

Use of these criteria to evaluate cases in the paleontological literature—which eliminated on stratigraphic grounds alone more than half of the cases tabulated by Erwin and Anstey (1995)—led to the conclusion that 29 out of 31 species (94%) of Neogene benthic invertebrates “exhibited punctuated change at cladogenesis that is consistent with the theory of punctuated equilibria” (Jackson and Cheetham, 1999, p. 75). Even though the evidence was tilted more in the direction of anagenesis for the 16-18 Neogene planktonic species (only six of which showed cladogenesis), “most but not all cases of speciation in the sea are punctuated” (Jackson and Cheetham, 1999, p. 75).

## 5. The Speciation Process and the Red Herring of Bryozoan Clonality

In concluding the 1999 paper, Jeremy wrote, “Most cases of speciation in the sea over the past 25 My show prolonged morphological stasis punctuated by geologically sudden morphological shifts at cladogenesis ... Prolonged stasis requires stabilizing selection but causes of punctuated speciation are unresolved. We cannot reject genetic drift for cheilostomes, so if directional selection is important for speciation in these animals it must act extremely fast” (Jackson and Cheetham, 1999, p. 76).

The data that enabled us to reach this conclusion are from the maternal inheritance experiment on which the second part of our original project was based (Jackson and Cheetham, 1990). The original purpose of the experiment was simply to test the “heritability of morphospecies identity by raising offspring of colonies from different populations in a common garden ... through two generations of offspring” (Jackson and Cheetham, 1990, p. 580). However, the morphospecies themselves were delineated by data on individual morphological characters, which, with standard methods of quantitative genetics, could provide estimates of the heritable variation in each character and the correlations, genetic as well as phenotypic, between pairs of characters. These values then were the raw material for calculations of putative selection forces and divergence rates in the morphological differentiation of a pair of species.

To make these calculations, large numbers of parent and offspring colonies of each of two species were required for reliable estimates of genetic parameters. Of the three genera in the breeding experiment, only *Stylopoma* measured up to this requirement (Jackson and Cheetham, 1990, table 2). Thus, we could estimate values from two species (*S. species 1* and *S. species 2*, or *S. spongites* and *S. projecta*, in the nomenclature of Jackson and Cheetham, 1994) independently, rather than following the questionable practice of extrapolating values from one species to another. The heritabilities we calculated for the two species (Table 2; Cheetham et al., 1993, table 5) justified this concern. For example, heritabilities of eight of 10 characters are significant in *S. spongites*, whereas only five of 10 are so in *S. projecta*, even though their mean heritabilities are very nearly equal (0.3395 and 0.3404, respectively).

Using the genetic parameters estimated for the two species of *Stylopoma*, methods developed by quantitative geneticists, especially Russell Lande (1977, 1979) and Michael Lynch (1988, 1990), and the assumption that rates of mutation in these bryozoans are in the vicinity of those in many other groups of organisms, we calculated that mutation alone could be sufficient to account for the observed morphological differences between *S. spongites* and *S. projecta* in as few as tens of thousands of years (Cheetham et al., 1993). This geologically very brief time scale, well within the limits of stratigraphic resolution

Table 2. Heritabilities (estimated from parents and two generations of offspring) and among-colonies variance components (estimated by single-classification ANOVA of parental colonies) for 10 morphological characters in two species of *Stylopoma* (modified from Cheetham et al., 1993, tables 1, 2, and 5). Nomenclature has been changed from *S. species 1* and *S. species 2* to conform to that in Jackson and Cheetham (1994). Significance of heritabilities: \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

Morphological character	<i>Stylopoma spongites</i>		<i>Stylopoma projecta</i>	
	Heritability	Variance component	Heritability	Variance component
Zooid length	0.3056**	0.5683	0.1516	0.4492
Zooid width	0.2269*	0.3732	0.1948***	0.4334
Frontal pore density	0.2438*	0.4704	0.5818***	0.3064
Orifice length	0.7719***	0.5011	0.2818	0.3308
Orifice width	0.3402*	0.4269	0.7050***	0.4284
Oral sinus length	0.1968	0.3961	0.4191**	0.3604
Oral sinus width	0.1635	0.3778	0.1934	0.3376
Avicularium length	0.3053*	0.3066	0.8178***	0.5336
Avicularium position	0.4158***	0.4020	0.2134	0.2854
Avicularium orientation	0.4254***	0.2130	-0.1549	0.0642
Mean	0.3395	0.4035	0.3404	0.3529

for the best sampled species of *Metrarabdotos* (Cheetham, 1986), is especially instructive given that these two species of *Stylopoma* are probably not nearest relatives (Fig. 1) and *S. spongites* is more similar morphologically and genetically to *S.* new species 2 and *S.* new species 3 than to *S. projecta* (Table 1). On shorter time scales of course, species divergence would require the intervention of directional selection, but our calculations also showed that directional selection acting alone would require unrealistically high levels of minimum selective mortality throughout the interval of divergence. Conversely, their divergence on time scales of millions of years would require stabilizing selection to mitigate the effects of mutational pressure, even if they did not exhibit the morphological stasis so typical of *Metrarabdotos* species. Thus we concluded that the results obtained for *Stylopoma* "... are consistent with theoretical models in which phenotypic evolution is mediated by interaction between mutation, random genetic drift, and stabilizing selection" (Cheetham et al., 1993, p. 1536).

The maternal inheritance data for *Stylopoma* also gave us a more direct way of gaining access to the genetic basis for morphological divergence and stasis in fossil bryozoans such as *Metrarabdotos*, rather than having to rely on analogy between fossil and living bryozoans. To do so, we made use of the modular morphology of bryozoans in which asexually budded modules (zooids) remain physically connected to form a colony, thus genetically a clone. The phenotypic variation in zooidal morphology in populations of colonies can be partitioned statistically into within-colony and among-colonies components, the latter corresponding to a measure termed clonal repeatability in quantitative genetics. Clonal repeatability in general sets an upper limit to heritability, but in the two species of *Stylopoma* (Table 2), the correspondence between mean heritability and mean repeatability is close, within the limits of sampling error in *S. projecta*, perhaps because within-colony variance includes a small, but significant heritable component itself (Cheetham et al., 1995). For individual characters, however, the correlation between heritability and repeatability (Table 2) is much less close ( $r_s = 0.684$ ,  $p < 0.05$  in *S. projecta*;  $r_s = 0.166$ , not significant in *S. spongites*; with eight degrees of freedom in each case). Nevertheless, by substituting clonal repeatabilities for heritabilities and similarly estimated phenotypic values for genetic correlations in the calculations we had made in *Stylopoma* for divergence times and selection forces, we obtained results that were inconsequentially different from those based on the actual genetic values (Cheetham et al., 1993).

With the good fit between calculations with genetic and phenotypic values in *Stylopoma* as justification, we went on to make similar calculations for six pairs of fossil species of *Metrarabdotos*, with results generally similar to those obtained for the single pair of species of *Stylopoma* (Cheetham et al., 1994; Cheetham and Jackson, 1995). In concluding the 1994 paper, we wrote:

"In general, these results support genetic models of speciation involving relatively sudden shifts between multiple adaptive peaks on which phenotypes remain more or less static through long-term stabilizing selection ... Models based on shifting balance among local demes (Wright, 1982) and isolation on the peripheries of large distributions (Mayr, 1954, 1963) are both

plausible for *Metrarabdotos* and other cheilostomes, based on their Neogene to Holocene distribution patterns in tropical America (Cheetham and Jackson, 1994). Random processes may be sufficient to explain phenotypic differentiation at speciation in these models, or directional selection may be required [depending on divergence time]. In either case, the agents of speciation are different from the pervasive stabilizing selection required to explain phenotypic stasis within species. In this sense, the results presented here are consistent with the ‘stronger’ version of punctuated equilibria theory decoupling speciation from forces acting within species (Maynard Smith, 1988).”

It was the last sentence in this passage that led Jeremy to write (Jackson and Cheetham, 1999, p. 76), “Finally, granted the prevalence of punctuated equilibria, macroevolutionary trends must arise through differential rates of origination and extinction, and not by adaptive evolution within single species,” i.e., by sorting or selection at the level of species rather than individuals, thus putting us squarely in the camp of the punctuated equilibrium model’s strongest proponents. Evolutionary biologists for the most part have continued to follow John Maynard Smith in regarding higher level selection as ultimately reducible to selection acting on individuals in populations and thus unnecessary as a concept (Grimshaw, 2001, p. 178). On the other hand, paleontologists have been receptive to the need for such a concept to explain macroevolutionary trends (Grimshaw, 2001, p. 172), albeit with some reservations about whether differential rates of species origination and extinction require traits “emergent” at the species level. Thus, Grimshaw (2001, p. 172) found that species selection or sorting is the aspect of punctuated equilibrium theory most likely to be a stumbling block to communication between the paleontologists and biologists.

The methods that we used to reconstruct genetic parameters in *Metrarabdotos* also enabled us to dispel the notion that, because Bryozoa are often characterized as clonal animals (e.g., Eldredge et al., 2005, p. 135), the principles governing their speciation might differ from those in exclusively sexually reproducing organisms. At the 1988 symposium “Species and Evolution in Clonal Organisms” in which we presented the first results of our research (Cheetham and Jackson, 1988), much of the roundtable discussion centered on whether the biological species concept has any meaning for clonal organisms at all (Budd and Mischler, 1990), because cloning decreases or eliminates the opportunity for genetic recombination (thus compromising the model of genetic cohesion on which the biological species concept is based) and reduces the pool of genetic variation from which new species may arise.

Bryozoa do have the potential to propagate clonally, given their growth as colonies of physically connected, genetically identical modules. Colonies originating by accidental or programmed fragmentation of other colonies are abundant in some species of groups such as the free-living cupuladriids, but we had seen little to indicate clonal propagation in either *Stylopoma* or *Metrarabdotos*. The maternal inheritance experiment of Jackson and Cheetham (1990), like that of Maturo (1973), was based on rearing sexually produced larvae. Even when grown in isolation for a year, colonies of *Stylopoma spongites* and *S. projecta* produce viable offspring sexually by self-fertilization, as Jeremy and his

colleague Amalia Herrera-Cubilla demonstrated (Jackson and Herrera, 1995).

An opportunity to investigate the effect of clonal propagation—in no less pertinent a group than *Metrarabdotos* itself—came unexpectedly one morning in 1999 when Jeremy appeared in my lab in Washington with fossil bryozoans he had collected from three different formations of Miocene and Pliocene age from two regions in Venezuela. These collections were part of the Panama Paleontology Project, begun by Jeremy and Tony Coates in 1986 at the Smithsonian Tropical Institute, which by the 1990s had burgeoned into a collaboration involving dozens of specialists in numerous marine taxa (Collins, 2009).

The Venezuelan material yielded three new species of *Metrarabdotos* (Cheetham et al., 2001), *M. aguilerai*, *M. arawakorum*, and *M. cubaguense* in the nomenclature of

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*Table 3. Mean among-colonies variance components (heritability estimates) for 15 morphological characters in two groups of tropical American species of Metrarabdotos (based on Cheetham et al., 2001, table 2). “Clonal” species are the three from Venezuela with half their colonies originating from pre-existing fragments; “aclonal” species are the 16 remaining species with few or no such colonies. Characters left blank are invariant in all species of that group.*

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Morphological Character	Mean among-colonies variance component	
	“Clonal” species	“Aclonal” species
Zooid length	0.6192	0.5612
Zooid width	0.3125	0.5257
Number of frontal areolae	0.4259	0.4858
Orifice length	0.5459	0.5862
Orifice width	0.6001	0.3994
Number of denticles		0.1278
Distance between lateral denticles	0.6136	0.4960
Length of smaller avicularium	0.4028	0.2520
Position of smaller avicularium	0.3903	0.1720
Lateral-medial orientation of smaller avicularium	0.3482	0.1753
Distal-proximal orientation of smaller avicularium	-0.0526	0.1253
Length of larger avicularium	0.5170	0.3273
Position of larger avicularium	0.3690	0.2109
Lateral-medial orientation of larger avicularium	0.2368	0.1143
Distal-proximal orientation of larger avicularium		0.4058
Mean	0.4099	0.3310

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Cheetham et al. (2007); approximately half of the colonies in each species originated asexually. However, genetic variation in their zooidal characters (estimated from among-colonies variance components) is no less than in *Metrarabdotos* species showing no or negligible evidence of asexual propagation (Table 3). The three “clonal” species proved not to be closely related (Fig. 2), suggesting separate but similar responses to an environmental condition, such as elevated nutrient levels in a region of coastal upwelling, that promoted vegetative growth without reducing their sexual productivity (Cheetham et al., 2001). A similar situation occurs among the European and African species of *Metrarabdotos*, where one (*M. thomseni*) of the six species in Cheetham et al. (2007) shows significant evidence of clonal propagation, but apparently unreduced levels of heritable variation in zooidal morphology (Cheetham, 2002).

## 6. After Words

In summarizing the results of the quantitative genetic tests, Jeremy attempted to communicate directly with evolutionary biologists dismissive of punctuated equilibrium theory when he wrote, “The genetic analyses help clarify two important misunderstandings about punctuation and stasis. First, stasis does not imply lack of morphological evolution, but lack of net morphological change. Stabilizing selection *is* evolution [emphasis added]. Second, punctuation is not about absolute time required for species to originate, rather it is about the time required for a species to originate relative to how long the species persists with no new morphological change before it becomes extinct” (Jackson and Cheetham, 1999, p. 76).

There is evidence that this attempt has been at least partly successful. In several chapters of his new evolutionary biology textbook, *Evolution*, Doug Futuyma (2005) discusses punctuated equilibrium, both as pattern and process (including the macroevolutionary importance of species selection and sorting). This stands in contrast to the brief, perfunctory discussions in biology textbooks at the time of Grimshaw’s (2001) analysis. However, acceptance of the importance of punctuated equilibrium remains stronger among paleontologists, as indicated by the extensive coverage of these topics in the new edition of the widely used textbook *Principles of Paleontology* (Foote and Miller, 2007).

Continuing research by Jeremy and his associates at the Smithsonian Tropical Research Institute on the cupuladriids *Cupuladria* and *Discoporella*, with similar morphometric methods and more advanced molecular techniques than we used in *Stylopoma*, has confirmed and expanded upon the relationship between morphology and genetics in cheilostomes (Dick et al., 2003; Herrera-Cubilla et al. 2005, 2008). Both cupuladriid genera have dense and abundant fossil records in the tropical American Neogene similar to that of *Metrarabdotos* (Cheetham et al., 1999; Cheetham and Jackson, 2000), and thus the potential for yielding patterns of speciation just as pertinent to the punctuated equilibrium debate. Moreover, abundant and diverse living cupuladriid faunas on both coasts of Panama provide the opportunity to relate life histories to evolutionary

patterns (O’Dea and Jackson, 2002; O’Dea et al., 2004), as well as to study the genetics of both genera directly. Although such opportunity was barred for *Metrarabdotos* by the extinction of most of its species (Fig. 2), our interpretation of its fossil record as a history of speciation stands as a monument to Jeremy’s willingness to devote years of effort to acquiring the genetic data to back it up.

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## References

- Budd, A.F. and Mischler, B.D. 1990. Species and evolution in clonal organisms—summary and discussion. *Systematic Botany* **15**, 166-171.
- Buss, L.W. and Jackson, J.B.C. 1979. Competitive networks: non-transitive competitive relationships in cryptic coral reef environments. *American Naturalist* **113**, 223-234.
- Cheetham, A.H. 1985. Patterns of morphologic change in late Tertiary cheilostome bryozoans from the Dominican Republic: *Metrarabdotos* revisited, p. 65-66. In C. Nielsen and G. P. Larwood (eds), *Bryozoa: Ordovician to Recent*. Fredensborg, Denmark: Olsen and Olsen.
- Cheetham, A.H. 1986. Tempo of evolution in a Neogene bryozoan: Rates of morphologic change within and across species boundaries. *Paleobiology* **12**, 190-202.
- Cheetham, A.H. 1987. Tempo of evolution in a Neogene bryozoan: Are trends in single morphologic characters misleading? *Paleobiology* **13**, 286-296.
- Cheetham, A.H. 2002. Asexual propagation in the cheilostomes *Metrarabdotos* and *Coscinopleura*: Effects on genetic variation and larval productivity, p. 73-80. In P.N. Wyse Jackson, C.J. Buttler and M.E. Spencer Jones (eds), *Bryozoan Studies 2001, Proceedings of the Twelfth International Bryozoology Association Conference*. Lisse/ Abingdon/ Exton (PA)/ Tokyo: A.A. Balkema Publishers.
- Cheetham, A.H. and Jackson, J.B.C. 1988. Morphologic versus genetic distinctions between species of living Bryozoa. American Society of Zoologists, 1988 Annual Meeting.
- Cheetham, A.H. and Jackson, J.B.C. 1994. Speciation, extinction, and the decline of arborescent growth in Neogene and Quaternary cheilostome Bryozoa of tropical America, p. 205-233. In J.B.C. Jackson, A.F. Budd and A.G. Coates (eds), *Evolution and Environment in Tropical America*. Chicago and London: University of Chicago Press.
- Cheetham, A.H. and Jackson, J.B.C. 2000. Neogene history of cheilostome Bryozoa in tropical America, p. 1-16. In A. Herrera and J.B.C. Jackson (eds), *Proceedings of the*

- 11<sup>th</sup> International Bryozoology Association Conference. Lawrence, KS: Allen Press.
- Cheetham, A.H. and Jackson, J.B.C. 1995. Process from pattern: Tests for selection versus random change in punctuated bryozoan speciation, p. 184-207. In D.H. Erwin and R.L. Anstey (eds), *New Approaches to Speciation in the Fossil Record*. New York: Columbia University Press.
- Cheetham, A.H., Jackson, J.B.C. and Hayek, L.C. 1993. Quantitative genetics of bryozoan phenotypic evolution. I. Rate tests for random change versus selection in differentiation of living species. *Evolution* **47**, 1526-1538.
- Cheetham, A.H., Jackson, J.B.C. and Hayek, L.C. 1994. Quantitative genetics of bryozoan phenotypic evolution. II. Analysis of selection and random change in fossil species using reconstructed genetic parameters. *Evolution* **48**, 360-375.
- Cheetham, A.H., Jackson, J.B.C. and Hayek, L.C. 1995. Quantitative genetics of bryozoan phenotypic evolution. III. Phenotypic plasticity and the maintenance of genetic variation. *Evolution* **49**, 290-296.
- Cheetham, A.H., Jackson, J.B.C. and Sanner, J. 2001. Evolutionary significance of sexual and asexual modes of propagation in Neogene species of the bryozoan *Metrarabdotos* in tropical America. *Journal of Paleontology* **75**, 564-577.
- Cheetham, A.H., Jackson, J.B.C., Sanner, J. and Ventocilla, Y. 1999. Neogene cheilostome Bryozoa of tropical America: Comparison and contrast between the Central American Isthmus (Panama, Costa Rica) and the north-central Caribbean (Dominican Republic). *Bulletins of American Paleontology* **357**, 159-192.
- Cheetham, A.H., Sanner, J. and Jackson, J.B.C. 2007. *Metrarabdotos* and related genera (Bryozoa: Cheilostomata) in the late Paleogene and Neogene of tropical America. *Paleontological Society Memoir* 67, *Journal of Paleontology* **81**: supplement to no. 1.
- Collins, L. 2009. About the Panama Paleontology Project. <[www.fiu.edu/~collins/pppabout.html](http://www.fiu.edu/~collins/pppabout.html)>
- Cook, P.L. 1973. Settlement and early colony development in some Cheilostomata, p. 65-71. In G. P. Larwood (ed.), *Living and Fossil Bryozoa, Recent Advances in Research*. London and New York: Academic Press.
- Dick, M.H., Herrera-Cubilla, A. and Jackson, J.B.C. 2003. Molecular phylogeny and phylogeography of free-living Bryozoa (Cupuladriidae) from both sides of the Isthmus of Panama. *Molecular Phylogenetics and Evolution* **27**, 355-371.
- Eldredge, N. and Gould, S.J. 1972. Punctuated equilibria: an alternative to phyletic gradualism, p. 82-115. In T.J.M. Schopf (ed.), *Models in Paleobiology*. San Francisco: Freeman, Cooper.
- Eldredge, N., Thompson, J.N., Brakefield, P.M., Gavrillets, S., Jablonski, D., Jackson, J.B.C., Lenski, R.E., Lieberman, B.S., McPeck, M.A. and Miller, W. III. 2005. The dynamics of evolutionary stasis, p. 133-145. In E.S. Vrba and N. Eldredge (eds), *Macroevolution, Disparity, Contingency, Essays in Honor of Stephen Jay Gould*. *Paleobiology*, Supplement to Volume 31(2).
- Erwin, D.H. and R.L. Anstey (eds). 1995. *New Approaches to Speciation in the Fossil Record*. New York: Columbia University Press.

- Erwin, D.H. and R.L. Anstey. 1995. Speciation in the fossil record, p. 11-38. In D.H. Erwin and R.L. Anstey (eds), *New Approaches to Speciation in the Fossil Record*. New York: Columbia University Press.
- Foote, M. and Miller, A.I. 2007. *Principles of Paleontology* (Third Edition). New York: W. H. Freeman and Company.
- Futuyma, D.J. 2005. *Evolution*. Sunderland, MA: Sinauer Associates.
- Grimshaw, A.J. 2001. *The Adventures of Punctuated Equilibria. A Struggle for Authority in the Evolutionary Sciences*. <<http://tux.lib.deakin.edu.au/adt-VDU/public/adt-VDU20051110.141422/>>
- Herrera-Cubilla, A., Dick, M.H., Sanner, J. and Jackson, J.B.C. 2005. Neogene Cupuladriidae of tropical America. I. Taxonomy of recent *Cupuladria* from opposite sides of the Isthmus of Panama. *Journal of Paleontology* **80**, 245-263.
- Herrera-Cubilla, A., Dick, M.H., Sanner, J. and Jackson, J.B.C. 2008. Neogene Cupuladriidae of tropical America. II. Taxonomy of recent *Discoporella* from opposite sides of the Isthmus of Panama. *Journal of Paleontology* **82**, 279-298.
- Jackson, J.B.C. 1979. Overgrowth competition between encrusting cheilostome ectoprocts in a Jamaican cryptic reef environment. *Journal of Animal Ecology* **48**, 805-823.
- Jackson, J.B.C., Buss, L.W. and Cook, R.E. (eds). 1985. *Population Biology and Evolution of Clonal Organisms*. New Haven: Yale University Press.
- Jackson, J.B.C. and Cheetham, A.H. 1989. Are skeletons enough to tell species apart? a test using cheilostome Bryozoa. Geological Society of America, 1989 Annual Meeting.
- Jackson, J.B.C. and Cheetham, A.H. 1990. Evolutionary significance of morphospecies: A test with cheilostome Bryozoa. *Science* **248**, 579-583.
- Jackson, J.B.C. and Cheetham, A.H. 1994. Phylogeny reconstruction and the tempo of speciation in cheilostome Bryozoa. *Paleobiology* **20**, 407-423.
- Jackson, J.B.C. and Cheetham, A.H. 1999. Tempo and mode of speciation in the sea. *Trends in Ecology and Evolution* **14**, 72-77.
- Jackson, J.B.C. and Herrera, A. 1995. Sex and selfing in *Stylopoma*. International Bryozoology Association, 10<sup>th</sup> International Conference, Wellington, New Zealand.
- Kerr, R. A. 1995. Did Darwin get it all right? *Science* **267**, 1421-1422.
- Lande, R. 1977. Statistical tests for natural selection on quantitative characters. *Evolution* **31**, 442-444.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* **33**, 402-416.
- Levinton, J. 1988. *Genetics, Paleontology and Macroevolution*. Cambridge, United Kingdom: Cambridge University Press.
- Levinton, J. 1991. Bryozoan morphological and genetic correspondence: What does it prove? *Science* **251**, 318-319.
- Lynch, M. 1988. The rate of polygenic mutation. *Genetical Research Cambridge* **51**, 137-148.
- Lynch, M. 1990. The rate of morphological evolution in mammals from the standpoint of neutral expectation. *American Naturalist* **136**, 727-741.

- Maturo, F.J.S., Jr. 1973. Offspring variation from known maternal stocks of *Parasmittina nitida* (Verrill), p. 577-584. In G.P. Larwood (ed.), *Living and Fossil Bryozoa, Recent Advances in Research*. London and New York: Academic Press.
- Maynard Smith, J. 1988. *Games, Sex and Evolution*. Hemel-Hempstead, UK: Harvester-Wheatsheaf.
- Mayr, E. 1954. Geographic speciation in tropical echinoids. *Evolution* **8**, 1-18.
- Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, MA: Harvard University Press.
- McKinney, F.K. and Jackson, J.B.C. 1989. *Bryozoan Evolution*. London: Unwin.
- McKinney, F.K. 1995. One hundred million years of competitive interactions between bryozoan clades: Asymmetrical but not escalating. *Biological Journal of the Linnean Society* **56**, 465-481.
- O'Dea A. and Jackson, J.B.C. 2002. Bryozoan growth mirrors contrasting seasonal regimes across the Isthmus of Panama. *Palaeogeography, Palaeoclimatology, Palaeoecology* **185**, 77-94.
- O'Dea, A., Herrera-Cubilla, A., Fortunato, H. and Jackson, J.B.C. 2004. Life history variation in cupuladriid bryozoans from either side of the Isthmus of Panama. *Marine Ecology – Progress Series* **280**, 145-161.
- Wright, S. 1982. Character change, speciation, and the higher taxa. *Evolution* **36**, 427-443.