Evolution, 39(3), 1985, pp. 699–705

QUANTUM CHANGES IN GASTROPOD SHELL MORPHOLOGY NEED NOT REFLECT SPECIATION

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Received April 30, 1984. Accepted January 29, 1985

Considerable disagreement currently exists over the prevailing mechanisms responsible for morphological change in the fossil record. For example, Gould and Eldredge (1977 and references therein), Stanley (1979), and others have argued that the supposedly widespread pattern of "punctuated" morphological change cannot be accounted for by conventional genetic mechanisms: morphological stasis is claimed to reflect developmental constraints, and long-term morphological trends are thought to require species selection. Yet, as Levinton (1983) emphasizes in his review of macroevolution, the virtual absence of information about the genetic mechanisms underlying variation in most fossilizable traits "makes much of the debate about punctuative change rather sterile." Other reviews echo this sentiment regarding punctuational change and emphasize further that change during speciation does not appear to be a fundamentally different process from change within lineages, since genetic differences among modern species are in general not qualitatively different from those among either populations or individuals within species (Charlesworth et al., 1982; Maynard Smith, 1983; Turner, 1983). Hence, a prerequisite for the evaluation of alternative hypotheses about modes of evolutionary change in specific fossil taxa is an understanding of the genetic basis of fossilizable variation in these taxa.

One of the most discussed examples of punctuational change (Lewin, 1981) is that in Cenozoic molluscs from the Turkana Basin (Williamson, 1981). Although the punctuational pattern exhibited by these mollusc lineages has largely been accepted (but see Cohen and Schwartz, 1983), the claim that this punctuational change corresponds to speciation has been widely criticized (Arthur, 1982; Boucot, 1982; Mayr, 1982; Kat and Davis, 1983; Kemp and Bertness, 1984). An inspection of the "simultaneous speciation events in all lineages" at the two stratigraphic levels emphasized by Williamson (1981; base of the Lower and top of the Upper Member of the Koobi Fora Formation, his fig. 4) reveals that cladogenesis was not observed in any of the six events in gastropods or the eight events in bivalves: daughter species were not contemporaneous with the parental form. In the absence of direct evidence for lineage splitting, the possibility that these punctuational events represent either ecophenotypic change or minor gene frequency changes within lineages cannot be rejected.

The question at issue regarding the mechanisms underlying seemingly rapid change in the fossil record is: based on our knowledge of the genetics of morphological variation and speciation in modern species, does punctuational change require that speciation took place? The consensus among neontologists appears to be that it does not (Charlesworth et al., 1982; Levinton, 1983; Maynard Smith, 1983). I present additional evidence below supporting this view: 1) a major component of variation in the rather conspicuous spiral scupture of the rocky intertidal gastropod *Thais* (or *Nucella*) *emarginata* (Prosobranchia, Mucicacea) is inherited in a Mendelian fashion, with sculpture dominant to lack of sculpture and 2) the phenotypic effect of the gene or genes controlling this sculpture can be modified by environmental conditions. Both of these results draw attention to the difficulty of inferring speciation from changes in shell morphology; in particular, they indicate that certain "quantum" changes in lineages of fossil gastropods could result from gene frequency changes at one or a few loci and hence need not reflect a "genetic revolution" associated with speciation.

MATERIALS AND METHODS

Immature *Thais emarginata* (<15 mm shell length) were collected from Wizard Rock (48°53'N, 125°09'W) near the Bamfield Marine Station (Bamfield, Vancouver Island, British Columbia, Canada) and were grown to maturity on a steady supply of one of their preferred prey, the barnacle *Balanus glandula* (Palmer, 1983). Throughout this time the molluscs were held continuously immersed in running seawater in plastic freezer containers with plastic mesh sides. To interpret the inheritance of shell sculpture, both wild-caught parents and F_1 progeny were sexed and paired prior to reaching maturity. The methods for hatching and rearing *T. emarginata* are detailed in Palmer (1984). To ensure paternity of backcrosses to mature females, only clutches produced more than 7 months after initiation of the cross were scored (sperm from prior matings declines to approximately 5% of original levels in less than 6 months; Palmer, unpubl.). The impact of growth environment on expression of

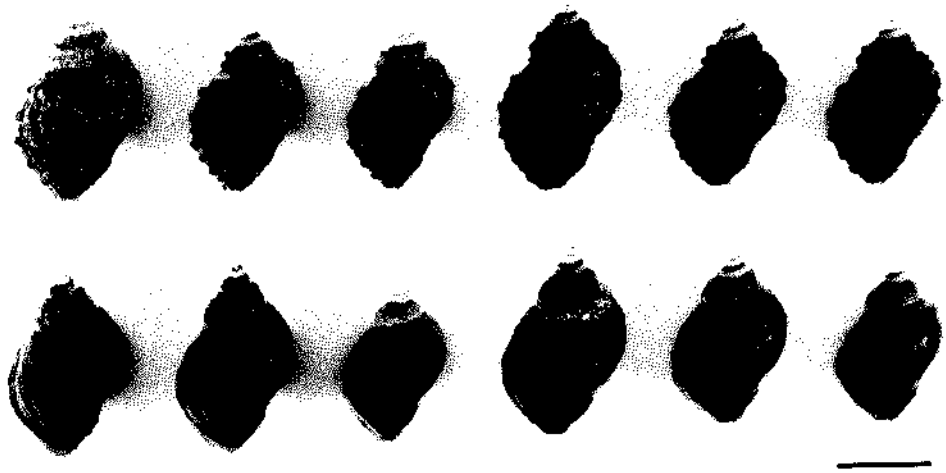

FIG. 1. Shell sculpture dimorphism in laboratory raised *Thais* (or *Nucella*) *emarginata* (Deshayes, 1839) from clutch 80-18-2-A6A (cross between sculptured F_1 male and sculptured F_1 female). In each row, the three left-most shells are predominantly orange, the three right-most, black. Only the three largest individuals of each phenotype combination were photographed. Approximate age of snails was eight months. Scale bar = 10 mm.

shell sculpture was assessed by collecting 47 juvenile *T. emarginata* (mean shell length = 14.4 ± 1.07 mm) from Wizard Rock and growing them one full whorl on average (to mean shell length = 21.9 ± 1.44 mm) on a diet of *B. glandula* in the laboratory.

Height of spiral ribs was measured using a video digitizer (Dithertizer®, Computer Station Inc., St. Louis, MO) connected to a Wild M7S microscope and operated by an Apple II Plus microcomputer. A video-digitized, silhouette image of the body whorl near the lip of the aperture was frozen on a video monitor (280 × 192 bit resolution) so that the ribs and grooves of the shell appeared as peaks and valleys (Wilson, 1983). Rib height was then calculated as the distance from the tip of the rib, perpendicularly to a line connecting the bases of the immediately adjacent grooves; these positions were identified and recorded using a single-bit cursor. Three spiral ribs were measured and averaged for each shell: the rib closest to the suture and the next two "major" spiral ribs anteriorly (the "minor" ribs between ribs 1 and 2 and between ribs 2 and 3 [see Fig. 1] were not measured). Repeat measurements of average rib height from different video images of a single shell varied by less than 10% from the final mean (mean error = 5.5 ± 2.79%, $N = 10$). Because absolute rib height increased with shell length among individuals with strong sculpture (≥0.35 mm; $Y = 0.0188X + 0.0753$, $r^2 = 0.506$, $P = 0.003$, $N = 15$; F_1 individuals from cross 80-18-1), rib heights in these figures were scaled to their equivalent size for an average length snail in this sample, 22.3 mm. Non-zero values for rib height on "smooth" shells reflect almost entirely the axial curvature of the shell perimeter where the three spiral ribs would have been.

RESULTS

Two generations of breeding have yielded two significant results. First, when raised under nearly constant conditions in the laboratory, variation in the seemingly complex morphological trait of spiral shell sculpture was inherited in a Mendelian fashion (Table 1). Although the sculpture of both parents of cross 80-18-1 was intermediate in degree of development, the F_1 progeny were clearly dimorphic (Fig. 2a), with approximately a 1:1 ratio sculptured : smooth ($\chi^2 = 0.31$, $P = 0.578$; both sexes pooled). All crosses with F_1 individuals (80-18-2-A4B to -A12A) and the backcross to a smooth, field-collected individual (81-80-1A) yielded phenotype frequencies consistent with a di-allelic, single-locus control of spiral shell sculpture with sculpture dominant. Backcrosses to the original parents (80-18-B2-MA, 80-18-B2-FE) revealed their genotypes: male-heterozygous, female-homozygous recessive (Table 1). In a second lineage, both parents were smooth and their F_1 progeny (80-17-1), as well as all F_2 progeny (80-17-2-pool), were smooth indicating that these parents were homozygous recessive for sculpture. Backcrosses of these F_1 progeny to both parents (80-17-B2-MA, 80-17-B2-FB) and to smooth individuals from the field (81-81-1A, 81-82-1A) yielded only smooth individuals (Table 1).

Finally, crosses between sculptured (presumably heterozygous) F_1 offspring from lineage 80-18 and smooth (presumably homozygous recessive) F_1 progeny from lineage 80-17 (81-78-1A, 81-79-1A) yielded close to the expected 1:1 ratio sculptured : smooth (Table 1).

The second result of significance was that the growth environment experienced by juveniles also appeared to influence adult shell phenotype. The sample of immature, wild-caught individuals raised to maturity in the laboratory exhibited a less well-defined bimodality in spiral shell sculpture than did entirely lab-raised offspring, with many shells exhibiting ribs of intermediate height, 0.2–0.3 mm high (Fig. 2b). Of snails raised in this manner, genotypes were known only for seven individuals: the original parents of 80-17-1, both of which were smooth (rib heights of 0.05 and 0.15 mm for the male and female respectively) and genetically homozygous recessive; the original parents of 80-18-1, both of which exhibited intermediate sculpture (Fig. 2a) even though the female was genetically homozygous recessive (cross 80-18-B2-FE, Table 1); and three field-collected males used in backcrosses (81-80-1A rib height = 0.20 mm; 81-81-1A rib height = 0.19 mm; 81-82-1A rib height = 0.13 mm) which were all homozygous recessive. Thus, the adult shell phenotypes of some individuals (e.g., the parents of lineage 80-18 and of the wild-caught animals exhibiting intermediate spiral sculpture [0.2–0.3 mm, Fig. 2b]) appear to have been influenced by environmental conditions early in life.

Discussion

Shells of living gastropods can vary substantially both within and among populations (Kincaid, 1957, 1964; Spight, 1973; Hamilton, 1980; Bowman, 1981), and shell differences are used to delineate species in the fossil record (Cox, 1960; Williamson, 1981; Jablonski and Lutz, 1983). In marine gastropods, intraspecific shell variation often correlates with variation in environmental conditions on both small (ca. 1 m [Reimchen, 1981]) and large (several km [Phillips et al., 1973; Kitching, 1976; Dudley, 1980; Smith, 1981; Crothers, 1982 and references therein; Currey and Hughes, 1982; Vermeij, 1982*a*]) geographic scales as well as over time (Vermeij, 1978, 1982*b*; Williamson, 1981). What few experimental data exist reveal that intraspecific variation in shell thickness or shape is often adaptive (Kitching et al., 1966; Kitching and Lockwood, 1974; Palmer, 1979; Wellington and Kuris, 1983; Palmer, 1985).

In spite of the conspicuous and widespread nature of this variation, and in contrast to the situation for color and size variation (Murray and Clarke, 1966, 1968; Jones, 1973 and references therein; Cole, 1975; Murray, 1975; Janson, 1982), the genetic basis of such fossilizable variation as shell sculpture, thickness, or shape has been examined in only a few instances (Warwick, 1944; Struhsaker, 1968; Largen, 1971; Newkirk and Doyle, 1975). All of these studies documented a heritable component to this variation; however, in none of these was paternity known with certainty nor was breeding continued for more than a single generation. Thus the details of this genetic control remain uncertain. Further, two recent studies (Arthur, 1982; Kemp and Bertness, 1984) suggest that shell shape in gastropods may be very sensitive to environmental influence.

Thais (or *Nucella*) *emarginata* is a common inhabitant of the upper intertidal of wave-exposed, rocky shores from the Bering Sea to California (Abbott, 1974; Morris et al., 1980) (differences in internal anatomy and in egg-capsule shape and a lack of interbreeding in the lab suggest that southern California populations belong to a separate species [Palmer and Kool, unpubl.]). They exhibit conspicuous variation in shell color, banding, sculpture, thickness, and shape (Kincaid, 1964; Abbott, 1974; Kitching, 1976; Morris et al., 1980; Palmer, 1984). When hatched and raised in the laboratory, they are strikingly dimorphic for shell sculpture (Figs. 1 and 2a). Rather remarkably, the sculpture phenotypes in laboratory-raised animals were inherited in a Mendelian fashion (Table 1).

Although discretely dimorphic when raised in the lab, juveniles collected from the field and raised to maturity in the laboratory sometimes exhibited intermediate sculpture (Fig. 1b). Thus, the conditions experienced as a juvenile appear to determine in part the phenotype of the adult, a pattern also observed for keel development in the shell of *Potamopyrgus jenkinsi* (Warwick, 1944). Although the reduced expression of sculpture in a heterozygous individual from the field (e.g., 80-18-1 male) does not seem unusual, the induction of sculpture in the "homozygous recessive" female of 80-18-1 (Fig. 2a) is surprising. This suggests that an individual "homozygous recessive" for spiral sculpture still retains the genetic information required to produce at least intermediate sculpture. Transplants (back to the field) involving juveniles of known genotype will be required to determine the full extent of the phenotypic plasticity of all three sculpture genotypes.

Several interpretations of the genetic mechanism underlying these results are possible. First, spiral sculpture could be controlled predominantly by a single locus, with secondary loci that: 1) modify the degree of expression of this locus and 2) are sensitive to environmental conditions. This seems rather unlikely given the nearly total absence of sculpture in lab-raised offspring recessive for this trait (Figs. 1, 2a). Second, spiral sculpture could be controlled by a block of tightly linked genes, some of which respond to environmental cues. Finally, a higher-level gene may regulate the expression of a block of genes coding for sculpture directly: a recessive allele could suppress the expression of the coding genes in phenotypically smooth individuals, yet its effectiveness at suppressing the coding genes could be influenced by environmental conditions. These hypotheses cannot be distinguished with the present data.

TABLE 1. Sex, origin, phenotypes, and inferred genotypes of parents and offspring of crosses with *Thais emarginata*. Entries under Source: field = collected as immature animals from the field; prog = progeny of specified cross; par = original parent of specified cross. Pheno. = observed phenotype of parents or offspring. Geno. = inferred genotype(s) of parents or offspring (*S* = dominant allele for "sculptured"; *s* = recessive allele for "smooth"). χ^2 = Chi square value from comparing observed phenotype frequencies with those expected from a single locus, two allele polymorphism. *P* = exact probability.

	Parents				Progeny						
						Sculpt		Smooth			
Cross label	Sex	Source	Pheno.	Geno.	Sex	*N*	Geno.	*N*	Geno.	χ^2	*P*
F_1											
80-17-1	m	field	smooth	*ss*	m	—	—	27	*ss*	0.00	1.00
	f	field	smooth	*ss*	f	—	—	27	*ss*		
80-18-1	m	field	int[1]	*Ss*	m	5	*Ss*	6	*ss*	2.86	0.44
	f	field	int[1]	*ss*	f	11	*Ss*	7	*ss*		
F_2											
80-17-2-pool[2]	m	prog 80-17-1	smooth	*ss*	—	—	—	749[2]	*ss*	—	—
	f	prog 80-17-1	smooth	*ss*							
80-18-2-A4B	m	prog 80-18-1	sculpt	*Ss*	—	81	*SS*, *Ss*	23	*ss*	0.46	0.50
	f	prog 80-18-1	sculpt	*Ss*							
80-18-2-A5A	m	prog 80-18-1	smooth	*ss*	—	—	—	72	*ss*	—	—
	f	prog 80-18-1	smooth	*ss*							
80-18-2-A6A	m	prog 80-18-1	sculpt	*Ss*	—	59	*SS*, *Ss*	20	*ss*	0.004	0.95
	f	prog 80-18-1	sculpt	*Ss*							
80-18-2-A11A	m	prog 80-18-1	sculpt	*Ss*	—	99	*SS*, *Ss*	32	*ss*	0.02	0.89
	f	prog 80-18-1	sculpt	*Ss*							
80-18-2-A12A	m	prog 80-18-1	smooth	*ss*	—	9	*Ss*	11	*ss*	0.20	0.65
	f	prog 80-18-1	sculpt	*Ss*							
81-78-1A	m	prog 80-17-1	smooth	*ss*	—	32	*Ss*	33	*ss*	0.015	0.90
	f	prog 80-18-1	sculpt	*Ss*							
81-79-1A	m	prog 80-17-1	smooth	*ss*	—	26	*Ss*	24	*ss*	0.08	0.78
	f	prog 80-18-1	sculpt	*ss*							
Backcrosses											
80-17-B2-MA	m	par 80-17-1	smooth	*ss*	—	—	—	62	*ss*	—	—
	f	prog 80-17-1	smooth	*ss*							
80-17-B2-FB	m	prog 80-17-1	smooth	*ss*	—	—	—	30	*ss*	—	—
	f	par 80-17-1	smooth	*ss*							

TABLE 1. Continued.

Cross label	Parents Sex	Source	Pheno.	Geno.	Progeny Sex	Sculpt N	Sculpt Geno.	Smooth N	Smooth Geno.	χ^2	P
80-18-B2-MA	m	par 80-18-1	int[1]	*Ss*	—	27	*Ss*	24	*ss*	0.17	0.67
	f	prog 80-18-1	smooth	*ss*							
80-18-B2-FE	m	prog 80-18-1	smooth	*ss*	—	—	—	35	*ss*	—	—
	f	par 80-18-1	int[1]	*ss*							
81-80-1A	m	field	smooth	*ss*	—	62	*Ss*	63	*ss*	0.008	0.93
	f	prog 80-18-1	sculpt	*Ss*							
81-81-1A	m	field	smooth	*ss*	—	—	—	38	*ss*	—	—
	f	prog 80-17-1	smooth	*ss*							
81-82-1A	m	field	smooth	*ss*	—	—	—	37	*ss*	—	—
	f	prog 80-17-1	smooth	*ss*							

[1] Phenotype intermediate between sculptured and smooth (see Fig. 2a).
[2] Pooled offspring from 12 separate crosses.

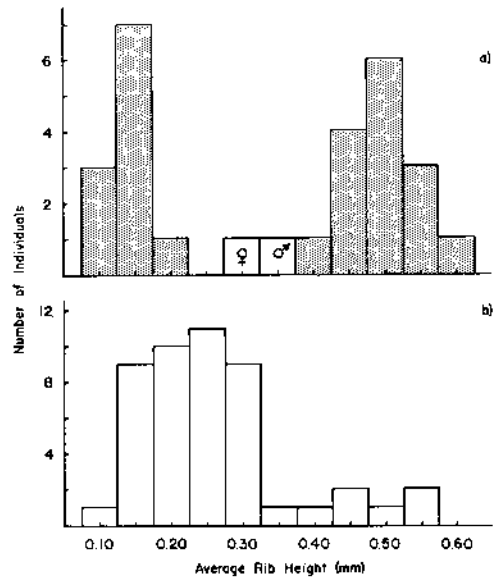

FIG. 2. Frequency distributions of spiral rib height for groups of *Thais emarginata* raised either partially or completely in the laboratory. a) rib heights of both the parents (open bars) and F_1 progeny (stippled bars) of cross 80-18-1. b) rib heights of 47 individuals collected as juveniles from the field and raised to maturity in the laboratory.

The above results are relevant to the interpretation of punctuational change in lineages of Turkana Basin gastropods (Williamson, 1981). To infer that punctuational change in the morphology of a fossil lineage reflects speciation when contemporaneity of the derived sister species is not directly observed requires that at least three alternative explanations be rejected: 1) that the pattern of change was not a rapid shift in phenotype from one fitness peak to another due to selection on a polygenically-controlled trait, as demonstrated theoretically by Kirkpatrick (1982); 2) that the pattern of change was not an ecophenotypic response, since such responses in gastropods can be quite marked (Arthur, 1982; Kemp and Bertness, 1984; Palmer, unpubl.); and 3) that the pattern of change was not due to changes in gene frequency at one or a few loci having major phenotypic effects, as demonstrated above for *Thais emarginata* (see also Maynard Smith, 1983; Turner, 1983). Due to a lack of genetic data, these alternatives cannot be rejected with confidence for Turkana Basin gastropods or, for that matter, for most instances of punctuational change where derived sister species are not observed to be contemporaneous following the punctuation event. Thus, the claim that such change within lineages is most likely a product of the "genetic revolution" thought to occur during speciation (Gould and Eldredge, 1977; Stanley, 1979; Williamson, 1981;

other references in Charlesworth et al., 1982; Levinton, 1983) seems tenuous at best.

ACKNOWLEDGMENTS

I thank the director and staff of the Bamfield Marine Station for their help and cooperation, and R. R. Strathmann and C. Strobeck for constructive comments on the manuscript. I am also particularly grateful to R. Boal for her dedicated maintenance of the breeding program and to the National Sciences and Engineering Research Council of Canada and the Central Research Fund of the University of Alberta for their generous support of this long-term study (grants A7245 and 55-48393 respectively).

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Corresponding Editor: R. H. Crozier

Evolution, 39(3), 1985, pp. 705–707

SIZE-DISASSORTATIVE MATING IN THE CHRYSOMELID BEETLE *CHRYSOLINA AURICHALCEA* (COLEOPTERA: CHRYSOMELIDAE)

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Received September 27, 1984. Accepted November 12, 1984

Size-assortative mating, in which large males mate with large females, is the most common reported form of assortative mating (Partridge and Halliday, 1984). This has also been reported for some species of insects (e.g., Johnson, 1983).

However, disassortative mating has been reported only rarely (Partridge and Halliday, 1984), and size-disassortative mating, in which there is a negative correlation between size of female and her mating partner, has not been reported so far in insects. Research on assortative mating and disassortative mating is important in studies of sexual selection (Partridge and Halliday, 1984; Thornhill and Alcock, 1983) and speciation (Lande, 1981). Here, I describe a case of size-disassortative mating in the chrysomelid beetle *Chrysolina aurichalcea*.

C. aurichalcea is a univoltine species, which mates in autumn. This beetle (Suzuki, 1978) feeds on *Artemisia* spp. A population of this beetle feeding on *A. princeps* on the campus of Niigata University at Ikarasi was sampled on October 10, 1983. This population consisted of 51 copulating pairs, 25 uncopulating males and 24 uncopulating females. The weight of the beetles was measured with a micro-