Predation and parallel evolution: recurrent parietal plate reduction in balanomorph barnacles

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Abstract.—Field and laboratory data indicate that all four species of *Thais* (Gastropoda, Muricacea) from rocky shores of the northeastern Pacific selectively attack barnacles at the margins of parietal (lateral) and opercular plates. Attacks are also more likely to be successful at plate margins. Such preferential attack and differential attack success may account for the evolutionary reduction in the number of parietal plates exhibited within seven of the eight families of balanomorph barnacles. Additional evidence suggests that predation by drilling gastropods may have also favored the evolution of strong external ribbing on these plates within some balanomorph lineages.

Radiation and plate reduction in the Balanomorpha occurred in concert with extensive radiation in muricacean gastropods, starting in the Late Cretaceous. Of the three skeletal conformations exhibited by open-surface dwelling barnacles (8, 6 and 4 parietal plates), only genera of the four-plated form have become proportionally more common in the Recent. Further, in a rather striking evolutionary experiment, a lineage of barnacles evolving free from gastropod predation retained primitive skeletal features. This supports the interpretation that predation by drilling gastropods has been an important selective force behind the widespread, parallel evolutionary tendency towards plate reduction in the Balanomorpha; a trend recognized by Darwin (1854), but for which he offered no explanation.

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Introduction

Vermeij (1977) has documented a pervasive morphological revolution among marine assemblages of both hard and soft bottoms that began towards the end of the Mesozoic. One consequence of this revolution was widespread diversification among invertebrates with predator-resistant skeletons. He attributed this diversification to the concurrent evolution of a host of skeleton-destroying predators, primarily teleost fishes and decapod crustaceans. Two important recent groups that appeared during this revolution were the balanomorph barnacles (Newman et al. 1969) and the muricacean gastropods (Sohl 1969). These two groups appear to have been involved in an evolutionary skirmish of their own.

The widely successful, wholly enclosed balanomorph, or acorn, barnacles first appeared approximately 95 Myr BP in the Late Cretaceous and were clearly derived from a fleshy-stalked, scalpellid ancestor (Darwin 1854). They represented one of three early experiments in sessility within the Cirripedia, the others of which have either gone extinct (Brachylepado-

morpha) or have given rise to a limited number of species and are largely restricted to the deep sea (Verrucomorpha, Newman et al. 1969). The primitive balanomorphs (e.g. *Catophragmus*) were characterized by the loss of the fleshy stalk and by a skeleton having eight primary parietal (lateral wall) plates and numerous smaller accessory plates. All the wall plates at this stage were solid.

Following their initial radiation, a persistent trend towards reduction in the number of parietal plates became apparent, a trend later accompanied by the appearance of parietal plate tubes (Newman et al. 1969). Darwin (1854), in his monograph on the Cirripedia, recognized the near universality of plate reduction within independent lineages but offered no causal mechanism. With one exception (Gruvel 1903), subsequent systematicists recognized the same independent evolutionary tendency towards fewer plates (Kruger 1940; Newman et al. 1969; Newman and Ross 1976; Pilsbry 1916; Withers 1953). The only hypotheses advanced to explain plate reduction have been that it represents 1) an adaptation to intertidal existence (Newman

1967), or 2) an adaptation for commensal living in corals (Newman and Ladd 1974). I report here new evidence from a study of feeding in thaidid gastropods (Palmer 1980, submitted) which suggests that predation by drilling gastropods could have been the predominant selective force behind plate reduction in the noncommensal balanomorphs and perhaps also behind the evolution of strong external ribbing. I further suggest it may have favored the evolution of tubiferous wall plates (see also Newman and Ross 1971).

Many prey of muricacean gastropods are encased to a greater or lesser extent in a calcium carbonate skeleton (Taylor et al. 1980), and hence only accessible via drilling. For example, the *Thais* species discussed here consume barnacles (see below), mussels (*Mytilus californianus* and *M. edulis*), and occasionally other gastropods (*Littorina scutulata, L. sitkana* and some acmaeid limpets) (Palmer 1980). The repeated two-step process used to penetrate calcareous shells has been thoroughly documented by Carriker and VanZandt (1972). It involves the alternating applications of an accessory boring organ to partially dissolve the intercrystalline matrix and then the radula to rasp off exposed crystals. This process may be repeated more or less continually for periods as long as 48 to 60 h (Butler 1953; Carriker 1959; Menge 1974; Palmer 1980). The duration of the process, coupled with the positioning precision required to avoid drilling through more shell material than necessary suggests that selection of drill sites may be of considerable importance to drilling gastropods. Drill-site locations have been documented for a number of recent (Barnett 1979; Berg and Porter 1974; Black 1978; Chapmann 1955; Edwards and Huebner 1977; Luckens 1975; Menge 1974; Morgan 1972a; Negus 1975; Radwin and Wells 1968; Tanaka 1950; Vermeij 1980a,b) and fossil (Adegoke and Tevesz 1974; Berg and Nishenko 1975; Carriker and Yochelson 1968; Dudley and Vermeij 1978; Reyment 1967; Sohl 1969; Thomas 1976) gastropods. Further, Paine's (1966) interpretation that labial spines have evolved in muricacean gastropods to improve their purchase while drilling hard-shelled prey provides further support for the importance of maintaining a fixed position for the duration of the drilling process.

In addition to drilling, thaidid gastropods have long been suspected of producing a narcotizing toxin to facilitate prey consumption (Connell 1970; Dubois 1909; Emlen 1966; Moore 1938; Spight 1972). Such a toxin has been described from *Thais haemastoma* by Huang (1971, 1972). Its use appears to reduce the amount of drilling required to attack a barnacle successfully (see discussion below). Toxic salivary secretions have also been noted for other non-toxoglossan gastropods (Cornman 1963; Day 1969; Eaton 1971; Hourbrick and Fretter 1969; Taylor et al. 1980).

Methods

During a study of the feeding ecology of *Thais*, a genus of predatory, rocky intertidal gastropods (Palmer 1980), I collected feeding observations for all four species that occur along the Pacific Northwest coast of North America: *T. canaliculata* (Duclos), *T. emarginata* (Deshayes), *T. lamellosa* (Gmelin), and *T. lima* (Gmelin). These included feeding observations on four barnacle species, *Semibalanus cariosus* (Pallas), *Balanus glandula* (Darwin), *B. nubilus* (Darwin) and *Chthamalus dalli* (Pilsbry), although there are only sufficent data to consider attack locations on the first two species. Feeding observations were obtained both from animals in the field during low tides and from animals used in feeding experiments (Palmer 1980). Upon locating a snail that was still in the feeding position in the field, drill sites were recognized either as distinct holes or, most commonly, as circular or subcircular cavities of recently exposed shell immediately in front of the anterior portion of the snail's foot. Even when snails had eaten a barnacle successfully, drill holes were often incomplete, particularly when located at plate margins; thus I did not distinguish between complete or incomplete boreholes in these field compilations. Also, many snails were interrupted while still drilling.

Laboratory data on drill-site selection were obtained from *Semibalanus cariosus* removed from cages containing *Thais* (Palmer 1980). These barnacles were scored as eaten or not eaten and carefully inspected for drill-site locations. All observed drill sites were noted whether the barnacle had been eaten or not.

TABLE 1. Frequencies with which *Thais lamellosa, T. canaliculata, T. emarginata* and *T. lima* drill *Balanus glandula* at various positions on the skeleton.

Region	Site	T. lam.	T. can.	T. em.	T. lima
Opercular plates	Not at suture	14	3	19	20
	At suture	4	1	89	45
	Total opercular	18	4	109	65
Middle of wall plates	Not at suture	4	1	3	5
	At suture	29	18	10	18
	Total at middle	33	19	13	23
Base of wall plates	Not at suture	14	2	11	13
	At suture	9	4	5	7
	Total at base	23	6	16	20
	Total observations	74	29	137	108

Results

To expedite an analysis of drill-site selection, observations were categorized into three distinct 'regions' within which there were two or more attack 'sites' (Tables 1 and 2). These regions included: 1) the 'opercular region,' including any attack immediately associated with the opercular plates, 2) the 'middle region,' which included all drill sites on or between parietal plates except those occurring at the base of these plates, and 3) the 'basal region,' or all drill sites that fell on or immediately adjacent to the junction between a parietal plate and the basal margin or the calcareous basis. Although the specific attack site was noted in all cases, these observations were summarized as falling into one of two 'site' categories within each 'region'; drill sites were tallied as falling either: 1) directly on a skeletal plate ('not at suture') or 2) at the junction between skeletal plates ('at su-

ture'). Within the basal region, an attack falling on a suture refers to an attack at the basal margin of a plate that also occurred at the junction between parietal plates.

Drill-site differences among Thais *species.*— There were significant differences among the four *Thais* in their choice of the region in which to attack *B. glandula* ("snail spp. vs. region: all snail spp.," Table 3). *Thais lamellosa* and *T. canaliculata* both attacked *B. glandula* more frequently in the middle or basal region of the skeleton than did *T. emarginata* or *T. lima*, both of which attacked in the opercular region most frequently (Table 1). In addition, *T. emarginata* attacked *B. glandula* more frequently in the opercular region than did *T. lima* ("snail spp. vs. region: *T. em.* and *T. lima* only," Table 3). Both *T. emarginata* and *T. lima* drilled *B. glandula* more frequently at opercular plate margins than *T. lamellosa* or *T. canaliculata*

TABLE 2. Frequencies with which *Thais lamellosa, T. canaliculata, T. emarginata* and *T. lima* drill *Semibalanus cariosus* at various positions on the skeleton.

Region	Site	T. lam.	T. can.	T. em.	T. lima
Opercular plates	Not at suture	1	0	1	0
	At suture	2	0	3	1
	Total opercular	3	0	4	1
Middle of wall plates	Not at suture	25	12	5	0
	At suture	23	38	3	1
	Total at middle	48	50	8	1
Base of wall plates	Not at suture	23	8	0	0
	At suture	9	6	0	0
	Total at base	32	14	0	0
	Total observations	83	64	12	2

TABLE 3. Results from contingency table analyses of drill-site selection on *Balanus glandula* by all snail species. Entries in the 'comparison' column indicate the particular snail species or attack region for which the factors in column one are being considered. χ—Chi square value. df—degrees of freedom. P—exact probability. Sign.—significance. Abbreviations are as in Tables 1 and 2. In tables 3–8: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Factors considered	Comparison	χ	df	P	Sign.
Snail spp. vs. Region	All snail species	88.98	6	< 0.001	***
Snail spp. vs. Region	*T. em. + T. lima* only	10.63	2	0.005	**
Snail spp. vs. Region	*T. lam. + T. can.* only	3.69	2	0.158	
Snail spp. vs. Site	Opercular region only	32.01	3	< 0.001	***
Snail spp. vs. Site	Mid region only	3.15	3	0.37	
Snail spp. vs. Site	Basal region only	2.47	3	0.48	

which more frequently drilled directly through rather than between opercular plates. The modes of attack in *T. emarginata* and *T. lima* are thus more similar to *Thais* (=*Nucella*) *lapillus* of European shores (Barnett 1979).

There was also a significant difference among the four *Thais* species in their region of attack on *S. cariosus* (Table 4), due largely to the greater attack frequency by *T. canaliculata* in the middle region than by *T. lamellosa*. In addition, there was a significant difference among snail species in their site of attack within the middle region ("snail spp. vs. site: mid region," Table 4), primarily because of the higher frequency of attack at sutures by *T. canaliculata* and *T. lamellosa*. There are thus significant differences among all the *Thais* species in their site of attack on both barnacle species.

Drill-site differences between barnacle species. —Except for *T. lima*, all the *Thais* exhibited significant differences in the region of attack on the two barnacle species; *S. cariosus* was rarely drilled in the opercular region, while *B. glandula* was often drilled there ("region vs. barnacle spp.: both barnacle spp.," Tables 5 to 7; the low number of observations for *S. cariosus* precludes such a comparison for *T. lima*). Within the mid region, all species attacked be-

tween parietal plates of *B. glandula* much more frequently than through them (Table 1), indicating that positioning of drill sites in this region was not random. If drilling were random, there should have been a *less* frequent occurrence of drill sites between parietal plates since overlap zones at plate margins form only a fraction (<15%) of the total outer surface of the parietal plates.

In this context it is interesting to compare selectivity within the middle region to selectivity in the basal region, since by drilling at the base of the parietal plates the snail is already positioned at a plate edge and the positioning relative to margins between parietal plates should be less important. Drilling occurred more frequently at vertical sutures in the middle than the basal region for all species on *B. glandula* except *T. canaliculata* for which there were only six attacks recorded in the basal region ("site vs. region: mid and base only, *B. glandula*," Tables 5 to 8). The same pattern was evident for *T. lamellosa* and *T. canaliculata* on *S. cariosus*, though only significantly so at the 5% level for *T. canaliculata* (there were too few observations to make these comparisons for *T. emarginata* and *T. lima*).

TABLE 4. Results from contingency table analyses of drill-site selection on *Semibalanus cariosus* by all snail species. Entries in the 'comparison' column indicate the particular snail species or attack region for which the factors in column one are being considered. χ—Chi square value. df—degrees of freedom. P—exact probability. Sign.—significance. Abbreviations are as in Table 1 and 2. [1] Except *T. canaliculata*. [2] Except *T. emarginata* and *T. lima*.

Factors considered	Comparison	χ	df	P	Sign.
Snail spp. vs. Region	All snail species	41.30	6	< 0.001	***
Snail spp. vs. Region	*T. em. + T. lima* only	—	—	—	
Snail spp. vs. Region	*T. lam. + T. can.* only	7.76	2	0.021	*
Snail spp. vs. Site	Opercular region only[1]	0.44	2	0.80	
Snail spp. vs. Site	Mid region only	10.65	3	0.014	*
Snail spp. vs. Site	Basal region only[2]	0.96	1	0.33	

TABLE 5. Results from contingency table analyses of drill-site selection by *Thais lamellosa* on both barnacle species. Entries in the 'comparison' column indicate the particular barnacle species or attack region for which the factors in column one are being considered. χ—Chi square value. df—degrees of freedom. *P*—exact probability. Sign.—significance.

Factors considered	Comparison	χ	df	P	Sign.
Region vs. Barnacle spp.	Both barnacle spp.	14.50	2	< 0.001	***
Site vs. Barnacle spp.	Opercular only	2.49	1	0.11	
Site vs. Barnacle spp.	Mid region only	13.59	1	< 0.001	***
Site vs. Barnacle spp.	Basal region only	0.74	1	0.39	
Site vs. Region	Mid and base only (*B. glandula*)	14.77	1	< 0.001	***
Site vs. Region	Mid and base only (*S. cariosus*)	3.13	1	0.077	

Discussion

Significance of drill-site specificity for Thais.—The above observations imply that some benefit accrues from penetrating barnacles between, rather than through, lateral plates. The likely benefit of such a behavior is that snails need not drill completely through to the central chamber of the skeleton to consume a barnacle successfully. At sutures, lateral extensions (radii and alae) of adjacent parietal plates overlap each other (in an adult *B. glandula*, 12–14 mm basal diameter, this overlap is approximately 1 mm wide), and the total thickness at sutures is comparable to, though somewhat less than, the thickness of individual plates at their centers (see cross-sections of whole barnacle skeletons in Barnes et al. 1970, figs. 3–6). In this zone of overlap, however, there is a slight space between the apposed faces of the adjacent plates within which tissue resides that is presumably involved in plate growth. Because *Thais* are equipped with a powerful toxin (Huang 1971, 1972), they need only penetrate a barnacle far enough to reach a space that communicates with the rest of the body. The toxin may be injected into the space between the radii and alae at a suture, thus circumventing a need to penetrate through to the central lumen where the main body resides. When relaxed, the barnacle may be consumed between the opercular plates since these plates will no longer be held closed. Also, when drilling through a plate, if a toxin is injected to relax the barnacle, the snail need not enlarge the final hole to permit entry of the buccal mass. In 99.6% of all observations pooled ($N = 762$), prey drilled elsewhere were being consumed between the gaping opercular plates. This contrasts with numerous other studies of thaidid gastropods preying on barnacles (Barnett 1979; Carefoot 1977; Fischer-Piette 1935; Galtsoff et al. 1937; Largen 1967; Moore 1938; Morgan 1972a,b; Wood 1968) where snails were claimed to have 'forced apart' the opercular plates, presumably because the proboscis was rarely observed extended through a drill hole or it was found inserted between the opercular plates in the absence of a completed borehole.

Further support for the importance of drilling between rather than through parietal plates de-

TABLE 6. Results from contingency table analyses of drill-site selection by *Thais canaliculata* on both barnacle species. Entries in the 'comparison' column indicate the particular barnacle species or attack region for which the factors in column one are being considered. χ—Chi square value. df—degrees of freedom. *P*—exact probability. Sign.—significance.

Factors considered	Comparison	χ	df	P	Sign.
Region vs. Barnacle spp.	Both barnacle spp.	9.27	2	0.010	**
Site vs. Barnacle spp.	Opercular only	—	—	—	
Site vs. Barnacle spp.	Mid region only	3.16	1	0.075	
Site vs. Barnacle spp.	Basal region only	0.95	1	0.33	
Site vs. Region	Mid and base only (*B. glandula*)	3.40	1	0.065	
Site vs. Region	Mid and base only (*S. cariosus*)	5.59	1	0.018	*

TABLE 7. Results from contingency table analyses of drill-site selection by *Thais emarginata* on both barnacle species. Entries in the 'comparison' column indicate the particular barnacle species or attack region for which the factors in column one are being considered. χ—Chi square value. df—degrees of freedom. *P*—exact probability. Sign.—significance.

Factor considered	Comparison	χ	df	*P*	Sign.
Region vs. Barnacle spp.	Both barnacle spp.	30.30	2	< 0.001	***
Site vs. Barnacle spp.	Opercular only	0.14	1	0.71	
Site vs. Barnacle spp.	Mid region only	3.26	1	0.071	
Site vs. Barnacle spp.	Basal region only	—	—	—	
Site vs. Region	Mid and base only (*B. glandula*)	5.99	1	0.014	*
Site vs. Region	Mid and base only (*S. cariosus*)	—	—	—	

rives from some preliminary growth experiments with *Thais* (Palmer 1980), in which relatively large (mean opercular diameter = 8.5 ± 2.42 mm), eaten and uneaten, *S. cariosus* were examined for drill-site locations (Table 9). A significant difference exists in the relative success at drilling *S. cariosus* as a function of attack site (Table 10): all three *Thais* species were consistently more successful when they attacked *S. cariosus* at a suture (mean success = 41.0%) than when they attempted to drill through a parietal plate (mean success = 12.2%, Table 9). Thus, when drilling larger barnacles, not only may handling time be reduced by drilling barnacles at plate margins but the probability of successful penetration appears to be higher as well.

Although it is possible to explain differences in *Thais* behavior when attacking the two barnacle species (see next section), it is somewhat more difficult to account for site-selection differences among snail species. If there is an advantage to attacking a given barnacle in a given manner, why do all species not attack in the same way? One possible explanation is that

these behaviors are learned; with more experience a snail may be more likely to learn the attack mode requiring the least time. This could account for why *T. emarginata* and *T. lima* are more similar to each other when attacking *B. glandula* than to either *T. canaliculata* or *T. lamellosa*, since both former species feed extensively in the upper and middle intertidal on *Balanus glandula* (Palmer 1980). It would not account for why *T. canaliculata* and *T. lamellosa* differ in their attack of *S. cariosus* (Tables 2 and 4).

Another possible explanation is that attack-mode differences among the *Thais* species may be related to trade-offs between decreased handling time and increased risk of dislodgement. If attacking *B. glandula* between the opercular plates requires less drilling time, snails higher in the intertidal such as *T. emarginata* and *T. lima* (Palmer 1980) may derive a greater benefit from this behavior because handling time constraints are more important. However, if the drilling position of the snail when attacking the opercular plates increases the likelihood of its being dislodged, either by raising it further off

TABLE 8. Results from contingency table analyses of drill-site selection by *Thais lima* on both barnacle species. Entries in the 'comparison' column indicate the particular barnacle species or attack region for which the factors in column one are being considered. χ—Chi square value. df—degrees of freedom. *P*—exact probability. Sign.—significance.

Factors considered	Comparison	χ	df	*P*	Sign.
Region vs. Barnacle spp.	Both barnacle spp.	1.15	2	0.56	
Site vs. Barnacle spp.	Opercular only	0.44	1	0.51	
Site vs. Barnacle spp.	Mid region only	0.27	1	0.50	
Site vs. Barnacle spp.	Basal region only	—	—	—	
Site vs. Region	Mid and base only (*B. glandula*)	8.23	1	0.004	**
Site vs. Region	Mid and base only (*S. cariosus*)	—	—	—	

TABLE 9. Percentage of successful drilling attacks on *Semibalanus cariosus* as a function of drill-site location for three species of *Thais*. Numbers in parentheses indicate sample sizes; some barnacles were attacked more than once but all attacks were counted separately.

Snail species	Location of attack	
	At suture	Not at suture
T. lamellosa	52.4% (21)	22.2% (9)
T. canaliculata	44.6% (92)	23.5% (17)
T. emarginata	22.6% (31)	7.8% (64)
All species pooled	41.0% (144)	12.2% (90)

TABLE 10. Two way, model II analysis of variance without replication of the arcsine transformed proportions of successful drilling attacks from Table 9. The two factors considered are snail species and drill-site location. SS—sums of squares. df—degrees of freedom. *F*—*F* value. *P*—exact probability. Sign.—significance.

Variance component	SS	df	F	P	Sign.
Snail species	206.33	2	24.05	0.040	*
Drill site	311.47	1	56.25	0.017	*
Remainder	11.07	2			
Total	588.88				

the bottom or providing a less stable foothold (e.g. see Menge 1974), the advantage to decreased handling time may not be sufficient to outweigh this risk lower on the shore.

Barnacle morphological evolution.—Drilling gastropods are common predators of balanomorph barnacles (Barnett 1979; Carefoot 1977; Connell 1961a,b, 1970; Dayton 1971; Fischer-Piette 1935; Galtsoff et al. 1937; Largen 1967; Luckens 1975; Menge 1974; Moore 1938; Morgan 1972b; Taylor et al. 1980; Wood 1968). Because they are an important source of mortality, skeletal attributes reducing the vulnerability of barnacles to drilling should be selected. Three skeletal features may have evolved in response to this selective pressure: 1) tubes within parietal plates, 2) strong external sculpture on parietal plates, and 3) a reduced number of plates.

Tubular wall plates in the Balanidae and Tetraclitidae may have evolved since tubes would increase the distance, but not the amount of material, to be drilled (see also Newman and Ross 1971). Drilling gastropods use the radula and the accessory boring organ (ABO) to penetrate calcareous skeletons (Carriker and VanZandt 1972). While the radula is at the tip of the proboscis and thus may be inserted to any depth, the ABO is a muscular, secretory pad located on the leading edge of the foot in muricacean gastropods. Because the ABO is surrounded by foot musculature, it is possible that the depth to which a gastropod may drill may be limited by the depth to which it can extend the ABO (Radwin and Wells 1968). Parietal plate tubes would permit construction of a thicker skeletal wall with the same amount of shell material.

This interpretation differs in emphasis from

the one advanced by Stanley and Newman (1980), who suggested that porous wall plates were primarily an 'adaptive breakthrough' permitting increased competitive ability. They argued that porous plates permitted more rapid growth because less energy or time was invested in producing shell material. However, since mortality due to predation is significantly greater for most barnacles than mortality due to competitive interactions (Connell 1961a,b, 1970), antipredatory morphological adaptations should be more conspicuous (Vermeij 1978). The ontogenetic filling of parietal plate tubes, yielding solid plates in larger individuals of *Balanus balanoides, B. glandula* and many species of *Tetraclita* would tend to further reduce their vulnerability to drilling because in addition to a thicker wall, there would also be more skeletal material that would have to be removed. Since the rate of skeleton production may set an upper limit to the rate of body growth independent of food supply (Palmer 1981), porous wall plates would be favored in rapidly growing juveniles because they permit a greater level of defense for the same amount of skeletal material. Larger barnacles, for which the selective pressure for further rapid growth will be less, may fill the parietal plate tubes and experience less of an impact on growth rate. Rapid growth is associated with thinner or more porous carbonate skeletons in many marine invertebrates (Palmer 1981), and for species that can achieve a size refuge from predation (Paine 1976), the advantages to rapid growth when small are obvious.

Another skeletal attribute that may reduce the susceptibility of barnacles to drilling gastropods is strong external sculpture. Barnacles are more vulnerable at the margins between lateral plates (Table 9) and such sculpture may make
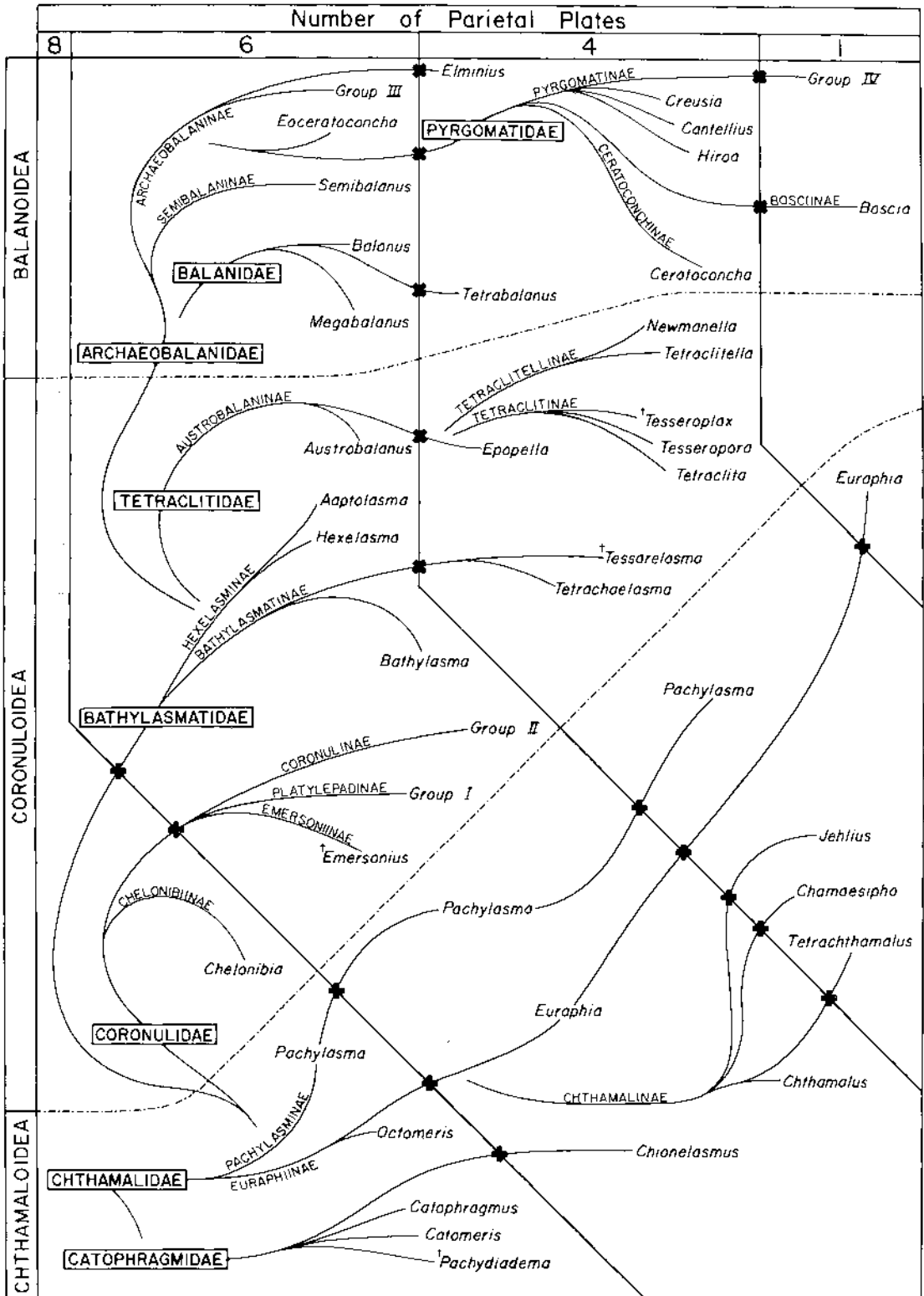
FIGURE 1.   A phylogeny of the Balanomorpha illustrating the numerous independent lineages exhibiting reduction in the number of parietal plates (modified from Newman and Ross 1976). The number of plates in a genus is represented by the

BARNACLE PLATE REDUCTIONthese margins more difficult to locate. The evidence supporting this interpretation is that all snail species for which there are sufficient data are more successful at recognizing sutures on the relatively smooth *B. glandula* than on the heavily 'thatched' *S. cariosus* ("site vs. barnacle species: mid region," Tables 5–8). This comparison is significant at the 0.05 level only for *Thais lamellosa*, but for both *T. canaliculata* and *T. emarginata* the probabilities that differences in site selectivity are due to chance alone are less than 0.08 (Tables 7 and 8). These texturally camouflaged sutures may thus be less apparent to the rugosensory propodium of a predatory gastropod. Additional evidence supporting this interpretation is that strong sculpture is often more common on lower shore barnacles. The pattern of the lower shore, generally larger barnacle, exhibiting thatched or strongly tubular wall plates is true not only along the coast of the northeastern Pacific (Kozloff 1974; Dayton 1971; Palmer 1980, submitted; Ricketts et al. 1968) but also along the coast of California (*B. glandula* and *Chthamalus fissus* high, and *Tetraclita squamosa rubescens* thatched and low in the intertidal) and Brazil (*Chthamalus bisinuatus* unthatched and higher on the shore, and *Tetraclita stalactifera* thatched and lower on the shore) (personal observations). These patterns suggest that external sculpture may be a morphological defense against drilling gastropods, since predation will be a more important source of mortality lower on the shore (Connell 1961a, 1970). Similar patterns occur among Australian and South African barnacles (Stephenson and Stephenson 1972) as well as in southern Chile (R. T. Paine, pers. comm.).

Finally, the widespread evolutionary reduction in the number of parietal plates may also be explained as a response to predation by drilling gastropods in many balanomorph lineages. Figure 1 illustrates the phylogeny of balanomorph barnacles as interpreted by Newman

and Ross (1976). Plate reduction is a conspicuous trend apparent within many lineages regardless of suprafamilial grouping. Five lineages have made the transition from 8 to 6 plates, ten lineages from 6 to 4 plates and three lineages from 4 to a single concrescent parietal wall. Plate reduction in the Pyrgomatidae (Fig. 1), species of which may exhibit a single fused wall, is most likely due to the specialized growth pattern required to live commensally within growing corals (Newman and Ladd 1974). However, with one exception (the genus *Euraphia*, Fig. 1), plate reduction has not proceeded beyond a minimum of four plates in open-surface dwelling barnacles because of the constraints this would place on growth. Four parietal plates is the minimum number of plates at which barnacles can continue to expand the size of the aperture with increasing growth (Newman and Ladd 1974). Species of *Euraphia* have six lateral plates when young and rapidly growing, but these fuse into a solid wall in older individuals (Darwin 1854).

Two points are of interest with respect to patterns of plate reduction in open-surface dwelling barnacles. First, changes in the number of wall plates were all in the direction of fewer plates (Fig. 1). Second, although all lineages exhibited a reduction in plate number, this was accomplished by the fusion or loss of different plates in different lineages (Fig. 2). Thus, it appears that it was not the loss of particular plates that was favored evolutionarily but rather a nonspecific reduction in the overall number of plates.

Three hypotheses could account for these parallel reductions in the number of wall plates in open-surface dwelling barnacles. First, Newman (1967) has noted that the reduction from six to four parietal plates is most common in intertidal barnacles. He suggested such skeletal reorganization in *Tetrachthamalus* was an adaptation to intertidal existence *per se*. Fewer sutures could reduce the rate of water loss, but

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position of the generic name (e.g. although the lineage leading to *Elminius* had six plates, the genus presently has only four plates as illustrated). Each independent reduction is indicated by an 'X.' Note that no lineages show an increase in the number of parietal plates. Genera contained in the groups include: Group I—*Stephanolepas, Cylindrolepas, Stomatolepas, Platylepas*; Group II—*Xenobalanus, Tubicinella, Cryptolepas, Cetolepas* (extinct), *Cetopirus, Coronula*; Group III—*Armatobalanus, Notobalanus, Solidobalanus, Chirona, Kathpalmeria* (extinct), *Actinobalanus* (extinct), *Archaeobalanus* (extinct), *Pseudacasta, Acasta, Membranobalanus, Conopea*; Group IV—*Hoekia, Pyrgopsella, Pyrgoma, Nobia, Savignium*. Genera accompanied by a cross are extinct.
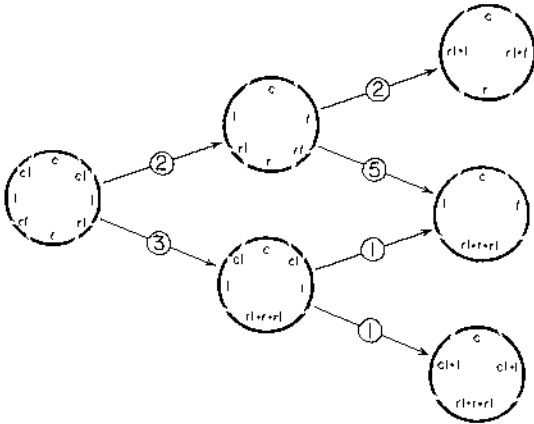
FIGURE 2. Evolutionary changes in skeletal conformation of balanomorph barnacles via deletion or fusion of parietal plates. Arrows indicate the direction of change and numbers within the arrows indicate the number of lineages exhibiting the illustrated reduction. Plate abbreviations: c—carinal, cl—carinolateral, l—lateral, rl—rostrolateral, r—rostral. Compiled from Newman and Ross (1976).
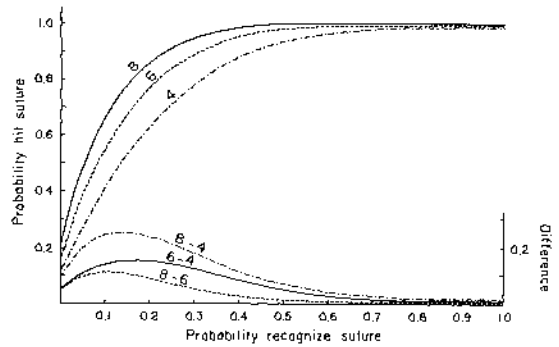

FIGURE 3. Probability of drilling at (=hitting) any suture on eight-, six- and four-plated barnacles as a function of the probability that gastropods can detect sutures. The function used to predict the probability of drilling at a suture is $D = [1 - (1 - R)^N] + A(1 - R)^N$, where D = the probability of hitting any suture, A = the probability of hitting any suture at random (=the proportion of total wall area corresponding to combined suture overlap zones, approximately 0.21, 0.16 and 0.11 for eight-, six- and four-plated barnacles respectively assuming 1 mm wide overlap zones on a 12 mm basal diameter barnacle), R = the probability a gastropod recognizes any one suture, N = number of sutures. The model assumes: snails initiate searching at a point randomly located with respect to sutures, a given suture is encountered no more than once, all sutures are equally recognizable, and if all sutures are missed, the snail drills at the point where searching was initiated (i.e. snails search around a barnacle no more than once). If snails searched more than once around the periphery of a barnacle, the curves would become more closely spaced, however, if they searched less than 0.2 of the perimeter, or if snails abandoned a barnacle after not detecting any sutures on a transit of the periphery, these curves would be more widely spaced, particularly at the asymptotes, and plate reduction would be more advantageous.

The differences between the probability of hitting a suture on barnacles with a higher vs. a lower number of plates are plotted in the lower portion of the figure; the greater this difference the greater the advantage to reducing the number of wall plates.

two observations suggest that this was not important evolutionarily: a) water loss appears to be much more dependent on morphological attributes other than plate number since *Chthamalus* lose water at a much slower rate than *Balanus* on the same shore (Foster 1971a,b), yet both have six parietal plates, and b) all of the living balanomorph genera that retain the condition of eight fully articulated parietal plates (Fig. 1) live in the mid and upper intertidal (Stanley and Newman 1980) and thus occur above many six-plated species. The retention of eight plates does not appear to have been an important factor influencing their survival in the upper intertidal.

Predation by decapod crustaceans could also have favored the reduction in plate number. Since sutures between parietal plates are the points at which barnacle skeletons are most likely to fail on impact (Barnes et al. 1970), it is possible that reduction in the number of sutures could reduce vulnerability to being crushed. Although there are some exceptions (e.g. the crabs *Acanthocyclus* in coastal Chile and *Eriphea* in Panama, personal observation) muricacean gastropods appear to be a more important source of mortality for intertidal, balanomorph barnacles, particularly on temperate shores (Connell 1961a,b, 1970; Dayton 1971; Luckens 1975).

A final hypothesis, and the one favored here, is that recurrent parietal plate reduction has been selected because it reduces vulnerability to predation by drilling gastropods. A reduction in the number of plates would decrease the number of sutures where barnacles are most vulnerable to attack (Tables 9 and 10). Further, up to a point, as gastropods become more likely to detect sutures, the relative advantage to decreasing the number of sutures increases (Fig. 3). For example, if drilling were at random, the probability of hitting a suture (D) of a 12 mm basal diameter barnacle with 1 mm wide suture zones would be higher by approximately 0.1 for
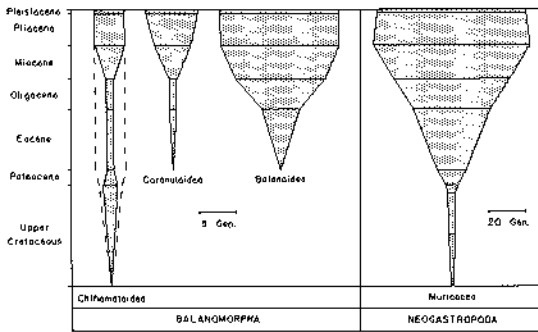
FIGURE 4. Concurrent radiations in number of genera within three superfamilies of balanomorph barnacles (as compiled from Newman and Ross 1976) and within the muricacean gastropods (modified from Sohl 1969) over the interval from the Late Cretaceous to the end of the Pleistocene. Note the different scales used for barnacles and gastropods. Dashed lines in the Chthamaloidea indicate suspected number of genera.
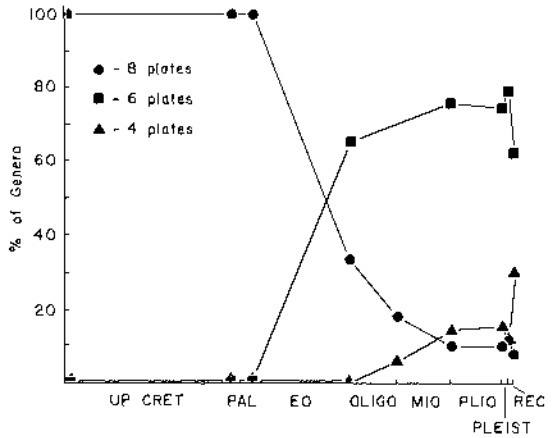

FIGURE 5. Changes over time in the percent of balanomorph genera exhibiting an eight-, six- or four-plated skeletal conformation. Genera in the commensal Pyrgomatidae and Coronulidae have not been included. Data compiled from Newman and Ross (1976).

an eight-plated barnacle compared to a four-plated one (Fig. 3). On the other hand, if gastropods recognize a suture one out of five times they encounter one ($R = 0.2$), the probability of drilling at a suture for an eight-plated barnacle will be higher than a four-plated one by approximately 0.24. Clearly, if gastropods were always successful at locating sutures ($R = 1.0$), reduction in the number of plates to anything less than a single, fused wall would not be favored. However, gastropods do not always drill at sutures (Tables 1, 2 and 9), and although they are more likely than not to do so, their lack of consistency provides the selective force favoring reduction in the number of wall plates. The strength of this force will depend on the relative vulnerability of barnacles at sutures vs. wall plates and the ability of gastropods to detect sutures.

Concurrent radiation in barnacles and drilling gastropods.—A necessary condition for the last hypothesis is that drilling gastropods evolved prior to or concurrently with balanomorph barnacles. Muricacean gastropods and balanomorph barnacles both first appeared in the Cretaceous (Fig. 4). By the Eocene there were approximately 40 genera of drilling gastropods (Sohl 1969) while only seven genera of balanomorphs are known from this time (Newman and Ross 1976). In contrast, although the number of muricacean genera less than doubled from the Eocene to the Plio-Pleistocene (42 to 76), the

number of balanomorph genera expanded by nearly fourfold to 27. Thus much of the radiation within the Muricacea appears to have occurred prior to the widespread radiation in the Balanomorpha. The evolutionary history of the Thaididae, a family of muricacean gastropods which includes most of the modern barnacle predators, is very poorly known. However, based on the tropical American record, it may be a more recent group not extending much beyond the Miocene (G. J. Vermeij, pers. comm.). Prior to this time, the muricids may have been the only potential barnacle predators.

Not only does the pattern of generic radiation in barnacles follow that of drilling gastropods but so do the patterns of change in the proportions of barnacle genera with a reduced number of wall plates (Fig. 5). Notably, the only skeletal conformation to become proportionally more abundant in the Recent is the four-plated conformation.

An evolutionary experiment.—I have suggested above that strong external sculpture, reduced number of parietal plates and perhaps tubes within parietal plates have evolved in response to predation by drilling gastropods. An obvious evolutionary experiment to test these hypotheses would be to establish a lineage of barnacles in an environment free of gastropod predators but not so different as to require radical departure from the basic balanomorph de-

sign. Such an experiment has been performed within the oldest living genus of the commensal Coronulidae, or turtle and whale barnacles (Newman and Ross 1976).

Chelonibia, a modern genus known also from the Miocene, lives attached to the integument of pelagic marine reptiles, primarily turtles and snakes, although it is also found on manatees, xiphosurans, and certain decapod crustaceans (Ross and Newman 1967). As a consequence, it would rarely, if ever, fall prey to drilling gastropods. As expected, in the absence of gastropod predation, species of *Chelonibia* have relatively unsculptured external surfaces on the parietal plates; the parietal plates are solid; and, most importantly, they retain distinct evidence of the primitive, eight-plated skeletal configuration (Newman and Ross 1976). Although species of *Chelonibia* are not the only barnacles among the more advanced Coronuloidea and Balanoidea that do not exhibit strong external sculpture or porous wall plates, they are the only ones that retain morphological evidence of the primitive configuration of eight wall plates in the adult. The rostrum is actually tripartite with the three elements narrowly fused along their outer edges. Traces of the plate margins are still apparent on the outer surface of the rostrum and there are deep internal grooves corresponding to the original plate margins; both attributes would have rendered these barnacles as vulnerable to drilling at these sites as a barnacle with unfused plates. Of additional interest, the Coronulidae is the only family of balanomorph barnacles within which no four-plated species have evolved, as would also be expected in the absence of drilling gastropods.

Another morphological trait indicating lower levels of drilling predation on coronulid barnacles is small opercular plates. Nearly all species of the almost entirely commensal Coronulidae are conspicuously different from other balanomorphs in having dramatically reduced opercular plates surrounded by opercular membranes (Newman et al. 1969). Such an arrangement would render these barnacles easy prey, since they could be attacked by drilling gastropods without having to penetrate the skeleton.

Predation by drilling gastropods thus appears to provide a simple, mechanistic explanation for the repeated, parallel evolutionary reduction from eight to six or four parietal plates in most lineages of balanomorph barnacles. Such predation may also have favored the evolution of strong external sculpture as textural camouflage for plate margins and the evolution of tubular wall plates.

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