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Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod

[risk/phenotypic plasticity/morphological defense/trade-off/*Thais* (or *Nucella*) *lamellosa*]

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ABSTRACT **Individuals of the morphologically variable, rocky intertidal gastropod *Thais* (or *Nucella*) *lamellosa* developed larger apertural teeth when held in the presence of the predatory crab *Cancer productus* than when held in its absence, regardless of whether snails were fed or not. In addition, among fed snails larger apertural teeth were produced in the presence of crabs fed conspecific snails than in the presence of crabs fed frozen fish. Because all snails were held in containers through which water flowed from physically separated aquaria holding the crabs, these results indicate that water-soluble chemical cues released by this predatory crab and by damaged conspecifics induced *T. lamellosa* to improve the defense effectiveness of their shells. Finally, when allowed access to food, snails exposed to these stimuli ate fewer barnacles and grew less than those in the controls.**

Although documented several times in plants (refs. 1–4; but see ref. 5), and colonial (6–8) and clonal (9–14) invertebrates, examples of predator-induced defensive adaptations in solitary organisms [*sensu* Jackson (15)] are rare [but see Lively (16)]. The apparent rarity of this phenomenon in solitary organisms is thought to result from their low probability of surviving nonfatal encounters with predators (6). For example, consumers of plants and colonial invertebrates usually only remove part of the plant or colony; hence, the remainder may respond by mobilizing defensive chemicals or structures. In an analogous manner, clonal planktonic organisms may benefit from such flexibility because members of a single genotype may respond phenotypically to temporal variation in the risk of predation within a single clonal generation. Although gastropods sometimes bear shells exhibiting repaired injuries (17, 18), there is little evidence that previously attacked individuals produce more defense-effective shells (19).

Species of shallow-water marine gastropods in the family Thaididae (Muricacea) are notorious for their variable shells (20–26). *Thais* (or *Nucella*) *lamellosa*, from rocky shores of the northeastern Pacific, is among the most variable; its shell varies in pigmentation (27) and morphology [overall shape (28), thickness (29), and degree of development of axial and spiral sculpture and of apertural teeth (25)]. Like other species of thaidid gastropods (26, 30–33), thicker-shelled *T. lamellosa* with more well-developed apertural teeth generally are found in quieter water habitats (25) where crabs like *Cancer productus* are more common intertidally (34). Although variation in pigmentation and spiral sculpture appears to be largely under genetic control (29, 35–37), variation in such traits as shell thickness, shell shape, and development of apertural teeth appears to have a strong environmental component: the shells of animals raised in the laboratory often differ substantially from those of their parents who matured in the field (28, 38). The causes of these differences in laboratory-raised animals are largely unknown, but they appear to depend upon rate of growth (39, 40). We report here evidence for two environmental cues that have a marked effect upon the rate of growth and upon shell form: effluents from predatory crabs and from damaged conspecific snails.

METHODS

Collection and Measurement. To determine if the responses to experimental treatments were influenced by initial size or by initial shell form, we collected *T. lamellosa* in two size categories (larger or smaller than 20 mm shell length) from each of two populations having different shell forms (initially thin- or initially thick-shelled, Table 1; see also Fig. 2). Snails were collected in Barkley Sound, on the west coast of Vancouver Island, Canada: thin-shelled, from a site in the Ross Islets of intermediate wave exposure (48°52′24″N, 125°37′38″W), and thick shelled, from a quiet water habitat in Grappler Inlet (48°50′00″N, 125°06′49″W). Shell length was measured from the apex to the tip of the siphonal canal. Body wet weight and shell dry weight were estimated by using a nondestructive procedure whereby individual snails were weighed suspended in seawater to estimate shell dry weight and then weighed again in air after removing the extravisceral water to obtain total weight in air; subtracting estimated shell dry weight from total weight yielded estimated body wet weight (41).

Although apertural teeth were noted as present or absent, their height was not measured at the beginning of the experiments because so few animals exhibited teeth (Table 1). Final apertural tooth height was obtained to the nearest 0.01 mm as the difference between two apertural width measurements taken perpendicular to the long axis of the aperture with inside-measuring dial calipers: one jaw of the caliper was held at a fixed point on the columella and the second was used to record first the distance to the top of the posterior-most tooth on the lip and then the distance to the lip at the gap between this and the adjacent tooth.

Experimental Protocol. Three predator treatments were established by using *C. productus* collected in the vicinity of the Bamfield Marine Station (Fig. 1). Each predator treatment consisted of an individual 40-liter glass aquarium supplied with running seawater (≈11°C) that either (*i*) held no crab and served as a control for the effect of laboratory conditions ("no crab" treatment), (*ii*) contained a single crab that was fed pieces of frozen fish every 2–4 days ("fish-crab"), or (*iii*) contained a single crab that was allowed continuous access to live, adult, thin-shelled *T. lamellosa* collected near the Ross Islets site ("snail-crab"). Each of these three treatments was replicated twice. Maximum carapace widths of the crabs used in the experiments were

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Abbreviation: ANOVA, analysis of variance.

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Table 1. Initial shell lengths, estimated body weights and shell dry weights, and initial frequencies of occurrence of apertural teeth in the *T. lamellosa* used in the experiments

Initial size	Initial phenotype	*n*	Shell length, mm	Body wet weight, g	Shell dry weight, g	No. showing apertural teeth
Large	Thin-shelled	180	26.5 ± 0.24 (21.2–32.2)	0.49 ± 0.015 (0.22–1.00)	1.66 ± 0.053 (0.62–3.43)	4
Large	Thick-shelled	180	26.9 ± 0.17 (22.6–32.2)	0.46 ± 0.010 (0.22–0.87)	3.31 ± 0.062 (1.62–5.76)	41
Small	Thin-shelled	180	17.5 ± 0.11 (14.9–20.1)	0.13 ± 0.003 (0.067–0.21)	0.44 ± 0.008 (0.21–0.80)	1
Small	Thick-shelled	180	17.5 ± 0.14 (13.5–21.5)	0.12 ± 0.003 (0.045–0.25)	0.87 ± 0.023 (0.35–1.63)	2

Values are expressed as mean ± SEM with the range in parentheses.

fish-crab = 97.7 and 113.6 mm and snail-crab = 109.2 and 115.0 mm for replicates 1 and 2, respectively. Over the duration of the experiments (76 days), crabs in the snail-crab treatment consumed 21 and 52 snails in replicates 1 and 2, respectively.

To separate the potentially confounding influence of growth rate on shell form, snails of both initial phenotypes were held under three different feeding regimes (Fig. 1): (*i*) starved, (*ii*) fed 33% (fed 2, starved 4 days), or (*iii*) fed 67% (fed 4, starved 2 days). Their preferred prey, the barnacle [*Balanus glandula* (42)], was provided attached to small stones; barnacles were added and removed according to the appropriate feeding schedule and replaced with fresh barnacles when necessary. When stones were replaced, eaten barnacles were measured and counted.

From each predator-treatment aquarium (a total of six), seawater siphoned separately through three elongate plastic freezer containers (12 × 12 × 35 cm), each of which contained snails held at only one of the three feeding frequencies (Fig. 1). Each freezer container was divided into four compartments delineated by plastic mesh that held 10 snails of a single type: large, thin-; small, thin-; large, thick-; or small, thick-shelled. To provide more uniform water flow, seawater flowed up through a false bottom in the freezer container and drained out through one end (average = 0.9 liter/min); no air was allowed in the cages; thus, the snails were held continuously immersed. To minimize disturbance to the crabs, the seawater tables in which the experiments were conducted were surrounded with black plastic for the duration of the experiments: a total of 76 days (May 25–Aug. 8, 1985).

Data Analysis. Analysis of variance (ANOVA) was conducted upon the final mean values for each compartment in the experiment (a mean of 10 snails) rather than upon the raw data for three reasons: (*i*) variances were heteroscedastic, (*ii*) variation among individuals within some cages was skewed, and (*iii*) small, but statistically significant, differences existed between some replicates. The use of means limits the statistical power of the ANOVA, but it renders our conclusions conservative with respect to type I error (43). The starved treatments were analyzed separately from the fed treatments because we anticipated *a priori* that the pattern of response of starved snails would differ from fed ones and we did not wish to confound the interpretation of differences in final shell form between starved and fed snails. A total of 12 snails were lost or died over the course of the experiments and were not included in the analyses (4 of 360 initially thin- and 8 of 360 initially thick-shelled).

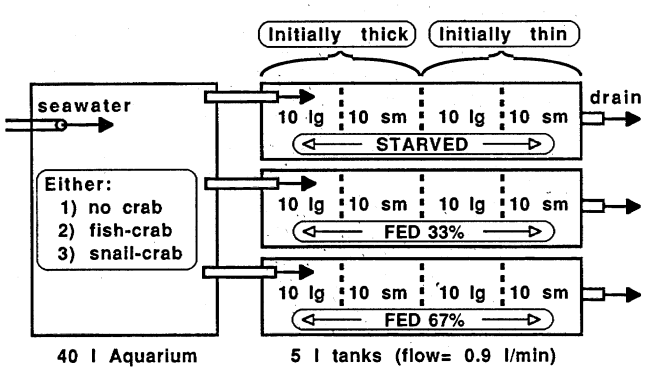

FIG. 1. Configuration of manipulated factors for a single replicate of the experimental design. Solid arrows indicate pattern of seawater flow. Vertical dashed lines indicate mesh partitions between compartments. lg, Initially "large"; sm, initially "small."

RESULTS

For starved and fed *T. lamellosa*, the three remaining manipulated factors (predator treatment, initial morphology, and initial size) had highly significant overall effects on the development of apertural teeth ($P \leq 0.001$; P, I, S, Table 2; Figs. 2 and 3). Although the pattern of response was virtually the same for large and small snails of each phenotype, it differed somewhat between the fed and starved groups. Among fed snails, the rank order of response across predator

Table 2. Results from a factorial ANOVA on final apertural tooth height in *T. lamellosa*

Source of variation*	Fed snails only df	Fed snails only MS (×10³)	Fed snails only *P*	Starved snails only df	Starved snails only MS (× 10³)	Starved snails only *P*
Main effect						
P	2	104.51	<0.001	2	15.31	0.001
I	1	49.67	0.001	1	51.80	<0.001
S	1	149.19	<0.001	1	118.58	<0.001
F	1	0.65	0.68	—	—	—
Interaction						
PI	2	2.11	0.58	2	2.68	0.16
PS	2	10.95	0.074	2	0.83	0.53
PF	2	0.42	0.89	—	—	—
IS	1	20.75	0.028	1	3.15	0.14
IF	1	3.92	0.32	—	—	—
SF	1	0.10	0.87	—	—	—
PSF	2	0.09	0.98	—	—	—
PIF	2	0.42	0.89	—	—	—
PIS	2	1.53	0.67	2	4.03	0.074
ISF	1	1.24	0.57	—	—	—
PISF	2	0.015	0.99	—	—	—
Error	24	3.772		12	1.235	

Analyses were conducted upon the means for each replicate rather than upon the raw data. df, Degrees of freedom; MS, mean squares; *P*, exact probability; dashes indicate not applicable.
*P, predator treatment; I, initial phenotype; S, initial size; F, feeding frequency.

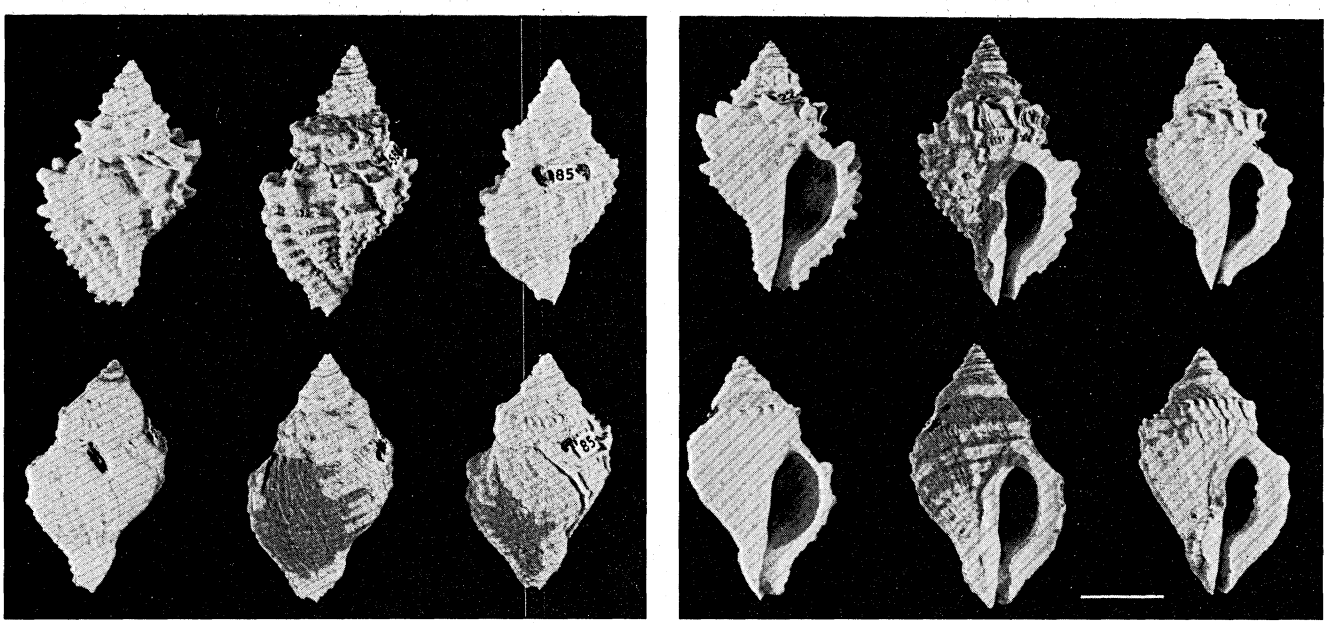

FIG. 2. Abapertural (*Left*) and apertural (*Right*) views of *T. lamellosa* following 76 days of exposure to water-borne stimuli from three different experimental conditions in the laboratory; no crab, crabs fed fish, and crabs fed live conspecific snails (first, second, and third shell in each row, respectively). The upper row in *Left* and *Right* illustrates initially thin-shelled snails and the lower row indicates initially thick-shelled snails. All snails were from the fed 67% treatment and were selected to be as near the median tooth response within each treatment as possible. (Bar = 10 mm).

treatments was invariant: snail-crab > fish-crab > no crab. The actual magnitude of response, however, depended at least in part upon initial size: larger snails tended to produce larger teeth ($P = 0.074$; PS in Table 2). The effect of initial size, in turn, also depended upon initial phenotype: initially thick-shelled snails produced consistently larger teeth than initially thin-shelled ones when large, but the differences were less pronounced for small snails ($P = 0.028$; IS in Table 2). Finally, feeding frequency (33% or 67%) had no significant effect on tooth development in fed snails.

The response of starved *T. lamellosa* also varied significantly among predator treatments ($P = 0.001$; P in Table 2), although the rank order differed somewhat from the fed treatments: fish-crab ≥ snail-crab > no crab. Significantly, starved snails on average produced larger teeth in the presence than in the absence of crab effluent (38% and 52% larger for initially large and initially small snails, respectively). In addition, tooth development was greater for initially thick- than initially thin-shelled snails (42% and 207% for large and small groups, respectively; $P < 0.001$; I in Table

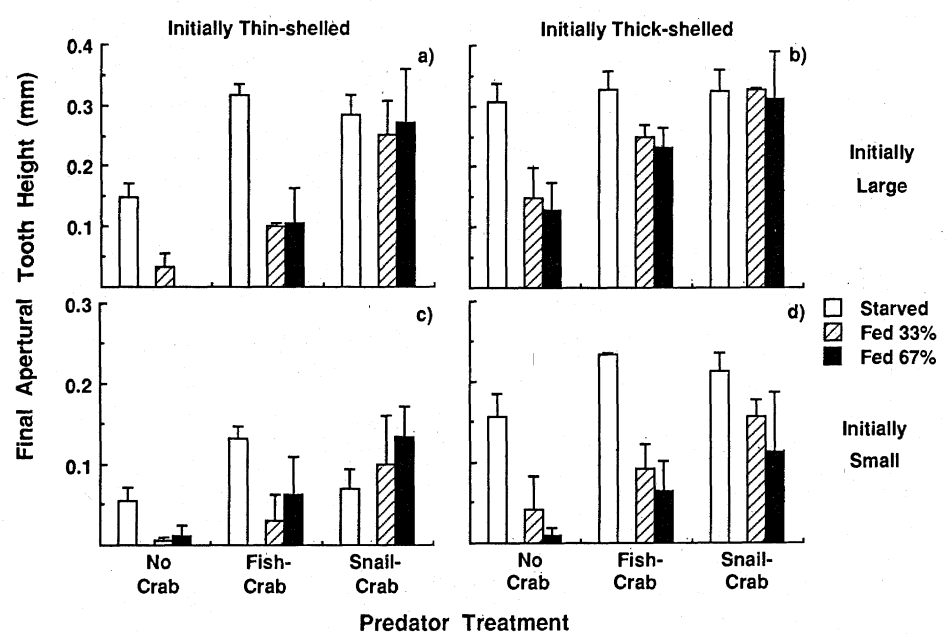

FIG. 3. Final apertural tooth height (mm; mean ± SE) of *T. lamellosa* following 76 days under different conditions in the laboratory (n = 2 replicate compartments for each bar). Groups of individuals of the same initial body size (large or small), but of two different initial morphologies (initially thin- or initially thick-shelled), were held under three different feeding regimes (starved, fed 2 of each 6 days, or fed 4 of each 6 days) while exposed to water flowing from one of three predator treatments. No Crab, a control for laboratory conditions; Fish-Crab, crabs fed frozen fish; and Snail-Crab, crabs fed live *T. lamellosa*. (*a*) Large, initially thin-shelled. (*b*) Large, initially thick-shelled. (*c*) Small, initially thin-shelled. (*d*) Small, initially thick-shelled.

2). We are unsure why tooth development in starved snails was somewhat less in the snail-crab than the fish-crab treatment, but we suspect increased metabolic activity exhausted the snail's energy reserves more quickly.

Finally, among fed snails, crab effluent and the scent of damaged conspecifics had a marked effect on the rates of feeding and growth by *T. lamellosa*. On average, animals in the snail-crab and fish-crab treatments consumed only 58% and 91% as many barnacles and grew only 15% and 78% as much, respectively, compared to the no crab treatment (Table 3). As a consequence, among the fed treatments, final apertural tooth height was negatively correlated with growth rate ($r = -0.84$, $n = 12$, $P < 0.001$; compare Fig. 3 with Table 3).

DISCUSSION

Adaptive Value and Mechanism of Transduction. The adaptive value of apertural tooth induction seems clear. Although we did not test it directly in *T. lamellosa*, in other marine gastropods apertural teeth function primarily as a predator deterrent by thickening the apertural lip, which reduces vulnerability to shell-peeling predators (44), and by decreasing the area of the aperture through which crabs may insert their claws (45, 46). Since apertural teeth thicken the outer lip of the aperture, however, producing them almost continuously would require the deposition of more total shell material per unit of habitable shell volume. This would not only cost more energetically but it could also limit the maximal rate of growth by way of constraints on the maximal rate of calcification (47). The conditional development of apertural teeth over the life-span of an individual snail thus avoids the costs of enhanced morphological defense when risk of predation is low at a particular place or time.

Starvation has been suggested as the principal proximate cue inducing apertural teeth in European *Nucella lapillus* (48), and starvation alone did stimulate tooth development in *T. lamellosa* (no crab treatments, Fig. 3). As a consequence, had we only examined the response of *fed* snails exposed to the various predator treatments, we would have been unable to separate a direct predator induction of apertural teeth from an indirect stimulation of tooth production due to suppressed growth. The consistent development of larger apertural teeth in starved snails exposed to crab effluent, however, provides unambiguous evidence of a direct, predator-induced amplification of tooth development.

Table 3. Average numbers of barnacles eaten and average body weight gain per snail over 76 days by *T. lamellosa* held in the laboratory under different experimental conditions

Feeding frequency, %	Initial shell phenotype	Predator treatment	Mean no. of barnacles eaten per snail ($n = 4$)	Mean body wet weight gain per snail, mg ($n = 40$)
33	Thin	No crab	27.1	228.4
		Fish-crab	27.3	164.1
		Snail-crab	16.3	1.3
33	Thick	No crab	20.4	114.1
		Fish-crab	18.6	72.8
		Snail-crab	13.6	15.8
67	Thin	No crab	44.0	388.6
		Fish-crab	38.6	335.9
		Snail-crab	24.6	83.8
67	Thick	No crab	29.6	214.4
		Fish-crab	25.3	165.3
		Snail-crab	15.6	42.3

Tabled values represent the mean of four compartments (two replicates containing 10 large and two containing 10 small snails each). Fortuitously, because of similar barnacle size distributions among cages, the mean number of barnacles eaten per snail (x) was related to the mean kcal (1 kcal = 4.18 kJ) consumed per snail (x) as follows: $x = 0.045y - 0.066$ ($r = 0.999$, $n = 12$). The gain per snail in body wet weight was obtained by averaging across both initial size classes of snails; hence, these data are presented for qualitative comparison only. A detailed analysis will be presented elsewhere.

Given that *T. lamellosa* can recognize directly the increased risk of predation implied by the presence of crab effluent or the scent of damaged conspecifics, why do apertural teeth still develop in the absence of such cues when snails are starved? Earlier studies have offered no adaptive explanation for this phenomenon (48, 49). We suggest they develop because, when snails are no longer growing, the cost of producing teeth is presumably slight (little shell material is involved) and the potential defensive value is high. Consistent with this suggestion is the observation that in *T. lamellosa*, as well as in the closely related *N. lapillus* (48, 49), apertural teeth occur most commonly in mature individuals that have ceased or nearly ceased to grow (see also Table 1).

Our experiments demonstrate that exposure to the scent of crabs or damaged conspecifics ultimately results in a greater development of apertural teeth (Fig. 3). Two pathways, however, appear to contribute to the transduction of perceived risk into more defense-effective shells: (*i*) inhibition of feeding and growth (Table 3), which, in turn, stimulates the development of teeth, and (*ii*) direct amplification of tooth development. Regardless of the pathway, the ultimate advantage is the same.

Interpopulation Differences in Plasticity. Our results also suggest the rather intriguing possibility that the norm of reaction (50) for apertural tooth development varies among local populations: although grown under identical conditions in the laboratory and initially of very similar shell lengths and body weights (Table 1), initially thick-shelled individuals developed larger apertural teeth overall than did initially thin-shelled ones ($P < 0.001$, I in Table 3; Fig. 3). These data imply that in the quiet-water habitat, natural selection has favored the retention of phenotypic plasticity, but in the more wave-exposed habitat where predatory crabs are less common, *T. lamellosa* have lost some of this flexibility. Presumably, the persistence of greater phenotypic plasticity reflects a greater temporal fluctuation in the intensity of predation by crabs or in the availability of food to the snails.

Implications for Interpreting Morphological Change. Our results are relevant to several studies of temporal changes in which the observed morphological differences in the shells of gastropods were assumed to have a genetic basis. Williamson (51, 52) interpreted "rapid" [5000–50,000 yr (52)] morphological change in a variety of freshwater gastropod lineages as evidence of genetical change associated with speciation. Seeley (53) concluded that intense natural selection, which requires genetical change by definition (54), was responsible for the rapid (50–100 yr) change in shell thickness and shape observed in the periwinkle *Littorina obtusata* following range expansion by the introduced predatory crab *Carcinus maenas*. Vermeij (55), observing similar changes in the shells of *N. lapillus*, concluded only that this snail had "adapted phenotypically" to the introduction of *Carcinus*; he attributed this capacity to adapt phenotypically, however, to reduced gene flow and, hence, presumably greater opportunity for genetic divergence in *Nucella* when reconciling these data with those for the widely dispersing *Littorina littorea*, which exhibited no significant morphological change over the same timer period (56). Although some shell variation does have a genetic basis (ref. 37 and references therein), the results reported here add to the growing list of examples of rather extensive ecophenotypic variation in the shells of marine gastropods (28, 38, 40, 57, 58). The implication seems clear: for the same reasons that geographic variation cannot be assumed to reflect genetic differences because of ecophe-

notypic effects, temporal variation in morphology may also have a strong ecophenotypic component. To conclude with much confidence that observed temporal variation in morphology reflects genetic change, the variation in time must exceed that known to be possible ecophenotypically.

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