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VARIATIONS IN *STROMBUS PUGILIS ALATUS*

BY CALVIN GOODRICH

THE late Lucius L. Hubbard, Regent of the University of Michigan from 1911 to 1933, spent a series of winter seasons on the western or Gulf shores of Florida. The varied shapes, colors, and sculptural patterns of the marine gastropod *Strombus pugilis alatus* (Gmelin), appearing sometimes in numbers on the beaches, caught first his attention and then the collecting enthusiasm which seems to have been strong in him all his life. He brought together several hundred examples and these, shortly after his death in 1933, were presented to the Museum of Zoology by his daughter, Mrs. Harry F. Goodell, of Houghton. It has been thought possible to use at least part of the collection for a study of molluscan variability. To that end, eleven hundred specimens from a single locality, Sanibel Island, Lee County, were selected, all of them adults in good condition. In addition, young shells were available from the same station so that growth could be traced in steps from a stage immediately postembryo to that just preceding complete maturity. Sanibel Island, by designation, is the type locality of the subspecies.

Strombus pugilis of Linnaeus is a heavy, short-spined, spinose mollusk, which is surprisingly uniform of shape, color-

ation, and sculpture considering the fact that its colonies have become established "from southeastern Florida, through the West Indies, to Central America and south as far as southern Brazil" (Clench and Abbott). In comparison, the subspecies *alatus* gives no such impression of heaviness. In the environment around Sanibel Island, it is both short and long spired, and at every stage between these extremes. Sculpture ranges from feebly nodulous to stoutly spinose. Color is protean, uncorrelated with any other character so far as could be learned. In short, the striking feature of *alatus*, in contrast to typical *pugilis*, is the absence of uniformity. Distribution is from North Carolina to the shores of the Gulf of Mexico in Texas.

Information was asked of W. J. Clench as to environmental conditions at Sanibel. He answered:

I would gather that Hubbard limited his collecting of *Strombus pugilis alatus* to the open beach. It is quite rare on the "inside" of the island. A series of sand bars occur off the island. At the spring tides, two and sometimes three of these bars are exposed at low tide, especially towards the light-house or eastern end. *Strombus* occasionally occurs in considerable numbers on these bars, particularly during the summer months. Though no count was made, as many as 100 specimens per 100 running feet along the inner bar would not be a high average for at least two miles at the eastern end of the island. They are partially buried in the sand at high water, but during their period of exposure they work themselves out of the sand, and though they move about a little, they appear to be decidedly out of their element on the exposed sand.

Irregularities ignored, the shape of *alatus* is elliptical, and such variations that occur in it are simply differences in the proportions between the vertical and horizontal axes. The number of whorls observed by Clench and Abbott in their examples of the shell was nine or ten. This, like other features, proved to be variable among the eleven hundred adults examined. A few specimens have reached maturity with only eight whorls; one was of twelve volutions. Shells having a fraction more than ten whorls were not rare. Total size, it was learned, was not determined by numbers of whorls, but by the size that any two or three whorls might attain, the variation in the matter noticeable to the eye being in the last ones.

A characteristic common to most of the species of *Strombus* is an upward flaring of the body whorl, so that the point of the outer lip overtops maturing whorls and, in instances, the apex. In typical *pugilis* this tip is about on a plane with the suture above the periphery, as seen with the aperture facing the observer. Clench and Abbott directed attention to the fact that the crest of the outer lip commonly slopes downward, not up. The variation in the Hubbard examples may be tabulated as follows:

	Number of specimens	Percentage
Shoulder point sloping downward	1015	92.3
Shoulder point in the plane of the suture	72	6.5
Shoulder point elevated	13	1.2

The shells of the last two categories are those sculptured at the periphery with spines or nodules, in no case those in which the sculpture is obsolescent. A correlation between high spire and depressed shoulder point can be said to obtain only insofar as both are prevailing features. That less than 8 per cent of the Hubbard mollusks have the flaring aspect of true *pugilis* stresses the subspecific differentiation of *alatus*.

Near the base of the outer lip is a notch serving as an egress for the animal's siphon. It varies in conspicuousness mostly with age, though not always so. Thus, in specimens of an altitude as little as 26 mm. to 31 mm. it is absent. Thereafter, it becomes perceptible more and more. But even in fully adult specimens, the notch may be so little developed that it is represented solely by an interruption or deviation in the border of the outer lip and as a depression as seen in the aperture. The differences, a shallow or slight notch to a deep one, probably lack significance except as showing that during the deposit of shell material the siphon can exert a mechanical influence.

In measuring the shells, modifications had to be made in regard to both length and breadth. Variable erosion of the apices compelled assuming the length to be the distance between the base, that is, the point of the produced columella, and the undamaged last three whorls. Again, the irregular

development of spines and nodes, and their not infrequent absence, precluded the determination of the diameter at the widest expanse, which happens to be the sculptured area. Instead, the swelling immediately below the shoulder was measured for breadth. While the figures obtained are not the true dimensions, reliable comparisons have been permitted inasmuch as all the shells have been measured alike. What may be called the shell index was obtainable with this simple formula:

$$\frac{\text{Breadth} \times 100}{\text{Length}} = \text{Shell Index}$$

The mature specimens were examined in lots of a hundred each, the ten largest and the ten smallest of each group being the ones measured. This is to say that the sampling was of 20 per cent of the eleven hundred adult shells. In the following table are totals of the length and breadth of the ten largest and the ten smallest of every hundred mollusks, the shell index of each ten and that of the 110 largest and 110 smallest.

TABLE I
Measurements in millimeters

Large			Small		
Length	Breadth	Shell Index	Length	Breadth	Shell Index
785.8	528.0	67.2	657.0	440.2	67.0
742.7	523.9	70.5	627.6	430.7	68.6
788.2	522.0	66.2	632.1	420.5	66.5
778.6	513.4	65.9	654.6	429.4	65.6
789.3	527.3	66.8	667.4	429.4	64.3
799.7	511.8	64.0	665.1	434.9	65.4
828.4	540.6	65.3	670.3	443.8	66.2
828.8	539.0	65.0	660.6	427.2	64.7
788.2	528.2	67.0	667.9	441.9	66.2
826.2	551.7	66.8	636.8	426.1	66.9
787.3	500.6	63.6	630.7	421.3	66.8
Shell index of 110 large specimens				66.2	
Shell index of 110 small specimens				66.2	

That in spite of the diversity in size and, to the eye, in form, the shell indexes of the two groups proved to be exactly the

same appears to argue a mode of growth in which the ratio of length to breadth is held more or less strictly to a standard, symmetry being assured, in general, whether shells are large or small.

In Table II is shown the composition of the two series according to length and breadth. In each, it will be seen, is a normal curve of size distribution whichever dimension is considered.

TABLE II
Measurements in millimeters

Large				Small			
Length		Breadth		Length		Breadth	
70-73	6	47-48	3	60-61	14	38-39	9
74-77	26	49-50	22	62-63	19	40-41	14
78-81	50	51-52	37	64-65	29	42-43	52
82-85	25	53-54	29	66-67	29	44-45	26
86-88	3	55-57	19	68-69	19	46-47	9
Total	110		110		110		110

The nuclear whorls are smooth and vary between one and one-half and two. Postembryonic growth starts immediately with the development of axial ribs or plicae, very crowded and extending from suture to suture. As adolescence is approached, this sculpture becomes more widely spaced, more thickened and rounded, and, finally, the nodes or spines of maturity. Clench and Abbott speak of the axial plicae beginning to form subsutural spines from the fourth whorl onward. This is true only in a general sense, for this feature, the same as others, is subject to variation. Thus, among twenty-five specimens having a maximum length of 31 mm., ten showed no development of the kind. Similar modification appeared in shells somewhat older. A distinction between spines and nodes is perhaps vague since both are phases of the same feature, but spines may here be assumed to be the sculpture which is pointed and pronounced; nodes that which is low and rounded. Of the eleven hundred adult specimens

of *alatus*, only 204 or 18.5 per cent could be said to be spinose. Nodulous shells, 719 in all, were 65.3 per cent of the whole. Among the nearly two hundred remaining mollusks were individuals in which sculpture had nearly or entirely disappeared before growth had ceased and others in which the nodes, instead of standing out separately, were joined by ridges of shelly material, as though the glandular control of shell secretion was defective. The formation of double rows of nodules at the shoulder was found to occur in only five specimens, and in two of these were evidences of injury.

A secondary sculpture of revolving ridges begins on the upper part of the fifth whorl. It increases in strength as growth proceeds and before the beginning of the seventh whorl it has covered the whole disk of the shell. As adolescence is entered upon, these spiral costae tend to flatten out and to disappear from all parts of the body whorl except a small area of the parietal wall near the base. Variations among the eleven hundred adults may be summed up as follows:

	Specimens	Percentage
Spirals confined to an area just above the base	927	84.3
Spirals covering the body whorl	158	14.3
Spirals altogether absent	15	1.3

In about half of the shells in which the spirals persist the sculpture is delicate and nearly microscopic, as though the folds of the mantle which determine the ridges had all but smoothed out. Five of the individuals that have no costae show marks of injury.

Clench and Abbott described ground colors as ranging from "mottled salmon or orange brown to dark uniform brownish red." In this matter the Hubbard shells are to be considered of indifferent guidance since many of them have not only been subjected to desiccation on the beaches, but also have doubtless faded while in storage. These authors said further that "often an aluminum-like glass is superimposed on the parietal wall and outer lip." This was observed in the Hubbard specimens in only about a half-dozen specimens. It is probably a

character restricted to fresh material. It is improbable that alterations have taken place in the following mollusks:

	Specimens	Percentage
Mottled over nearly the whole disk	68	6.1
Having a zigzag pattern over most of the disk	83	7.5
Albino	22	2.0
Partly albino	64	5.8

The zigzag pattern is distinguished here from the mottled in being laid down with regularity. It is perhaps an ancient character now becoming obsolete since, according to Dall: "In the Miocene of Haiti and Jamaica the fossil *S. proxima* Sby. (*pugiloides* Guppy plus *ambiguus* Sowerby) shows the zigzags very plainly," and is absent apparently in the living *S. pugilis* typical. An increase in pigmentation is fairly frequent in shells in parts secreted after the body whorl has reached most of its development. On the other hand, a decrease at this stage is rare.

Specimens of six to eight whorls and about 30 mm. long are light, and about one-third of them could be pronounced albino or partly so. With increase in growth, a mottled effect resembling freckles appears, and after that the marked pigmentation.

A revolving band or stripe begins to appear on the shell surface between base and shoulder just about when the mollusk is passing out of the strictly juvenile stage. It may be hair-like or as much as 15 mm. in breadth, be dim or sharply defined, or irregularly mottled or marked with a pattern of zigzag pigmentation. Among young shells at hand, the band is present in 28 per cent of those which have reached a length of 31 mm., but in 94.7 per cent of the individuals of a length between 32 and 38 mm. The findings in the case of adults may be summed up as follows:

	Specimens	Percentage
Having one band only	999	90.8
Having two or more bands	51	4.6
Lacking bands	50	4.5

The shells having bands can thus be classified:

	Specimens	Percentage
Light band on a dark ground color	991	94.3
Dark band on a lighter ground color	59	5.6

In both these groups, the band instead of being uniformly pigmented may be mottled or show the pattern which is spoken of above as zigzag, the mottled effect occurring about three times as often as the other.

While *Strombus* is one of the distinctive molluscan groups, the steps through which its sculpture has gone are precisely those of scores of other genera, that is, the axial sculpture is the first to develop, and from it are formed the nodes and spines of adult life. The spiral sculpture emerges a little later, has what may be called an assertive period, and then rapidly diminishes in prominence until it is all but obsolete.

In defining acceleration as applied to mollusca, Grabau said that "some of the later, acquired, more specialized characteristics are pushed back into earlier stages, occurring side by side with characters of more primitive type." Possibly the early occurrence of the primitive axial sculpture and spiral ornamentation together in *S. pugilis alatus* can be considered such an instance. The still more "pushing" acceleration is that in which nepionic characteristics have been attained by the embryo shell. This has been observed by Grabau in the genus *Fusus* and remarked by Pilsbry in *Drymaeus*. It does not occur in *alatus*. In sculpture, gerontism is manifested by stunting or even complete disappearance after having been, earlier in shell life, of pronounced development. Individuals were found among the Hubbard specimens which could be called gerontic, using this definition, but they were relatively too few to indicate a racial trend in that direction. They are the "occasionally completely non-spinose specimens" of which Clench and Abbott took notice.

The pigmentation of the porcelaneous shell substance has its beginning in small, inconspicuous "islands" of reddish brown, the shell being in what may be termed an advanced juvenile stage. Clearly, the most active period of the pigment-secret-

ing glands of the mantle is at the age in which shell growth is being brought to its termination. Not only is there a variety of hues as between adults, but the body whorl of a single individual will sometimes show as many as three or four different color tones in addition to those color patterns mentioned as mottled and zigzag. What amounts to a reinforcement of pigmentation is a triangular field of dark brown on the parietal wall at the aperture. Colton found that *Thaias lapillus* was light-colored in exposed situations, darkest in sheltered areas. Experimenting with the same species, Moore was able to halt the laying down of revolving bands by taking snails from beds of *Mytilus*, on which the mollusks fed, to spots in which *Mytilus* was absent; and to bring about a restoration of the secretion by returning the shells to the original feeding grounds. The operative factors for all they seem simple may be complex. This may be suspected from the fact that color adaptations in certain crustacea have been discovered to have their sources in hormonal materials. There is sufficient parallelism in invertebrate physiology to warrant surmising the existence of a similar endocrine influence in the Gastropoda.

S. pugilis alatus has a discontinuous distribution on the North American littoral from North Carolina to Texas, and this indicates that the separate colonies are direct offshoots of *pugilis* typical rather than emigrants from some original stock of *alatus*. The modification appears in fact to be going on now in Lake Worth, Palm Beach County, Florida, the two forms occupying the same waters. The ecological controls which bring about the differentiation of subspecies from species are, of course, unknown at this time.

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