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COLOR PATTERN VARIATION AMONG SNAILS
OF THE
GENUS LIGUUS ON THE FLORIDA KEYS

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COLOR PATTERN VARIATION AMONG SNAILS OF THE GENUS *LIGUUS* ON THE FLORIDA KEYS

FRANK N. YOUNG¹

SYNOPSIS: The basic color patterns of Florida tree snails of the genus *Liguus* (Mollusca: Gastropoda, Bulimulidae) show little correlation with environmental conditions. The occurrence of distinctive variants in "pure colonies" suggests that the basic pattern and pigments are directly controlled by a relatively few genes. The segregation of various elements of the basic patterns among the colonies of the Lower Florida Keys and mainland can be used as the basis for an hypothesis concerning the genetic control of axial coloration, banding, pigmentation, and other characters. A new form from Little Torch Key, *Liguus fasciatus vonpaulseni* new subspecies, combining many of the color pattern elements previously known from the Florida Keys is described and figured. This form is presumably close to the ancestral form that migrated to Florida from Cuba. A key to the described forms of *Liguus* from the Florida Keys illustrates the known combinations of color pattern elements.

Clench's description of *Liguus fasciatus osmenti* (1942) suggests the possibility that the color forms of *Liguus* occurring on the Lower Florida Keys represent segregates derived from some ancestral form with a complex color pattern. This supposed ancestor may have come to Florida from Cuba directly or have been produced by the combination of a number of forms coming to the islands separately and interbreeding. In the early days of settlement, the large colonies on the Lower Keys apparently contained a number of different color forms. Key West, for example, supported three or more, including *L. f. solidus*, *solidulus*, and *pictus*. Big Pine Key supported several mixed colonies which, in addition to the forms known from Key West, included *L. f. crassus*, *graphicus*, and possibly others now lost. Other colonies on the Lower Keys were also mixed, and the rarity of certain color patterns suggests that they appeared only as chance homozygotes in large panmictic populations.

Since these tree snails can live only in the tropical jungle hammock vegetational association, they were always segregated into separate

¹ Frank Young completed his doctoral work at the University of Florida in 1942. His principal contributions have been on aquatic beetles, but he has maintained a steady interest in the distribution, genetics, and evolution of the tree snails of Florida. The present paper is based on detailed studies of material in the Charles Torrey Simpson collection at the University of Miami, the material in the University of Michigan Museum of Zoology, and specimens and notes from the active group of collectors in southern Florida. It represents contribution No. 683 from the Zoological Laboratories of Indiana University, Bloomington, Indiana. Manuscript submitted 4 May 1960.

colonies. The great destruction of the hammocks in recent years by burning and clearing has increased the isolation of the colonies, and today, most of the known colonies on the Pine Islands of the Lower Keys are each composed of a single variant. Such colonies may be essentially pure clones produced from single snails which possibly reproduced parthenogenetically.² The resulting genetic screening against lethal and detrimental genes together with the intense selective action of the environment may account for the success of the Lower Key colonies under apparently hopeless conditions of drought, burning, and human intervention.

If the colonies of *Liguus* composed of single variants on the Keys and the Florida mainland represent the segregates of the characters of an original stock plus accumulated mutations in pure form, we may make certain assumptions about the genetics of the color pattern of these snails. The following seem to be unit characters: (1) colored apex and columella, (2) peripheral banding, (3) sutural banding, (4) yellow pigments, (5) dark pigments, (6) brown or brownish-red peripheral or sutural lines or both, (7) periostracal green lines on periphery of whorls. Each of these characters may be due to the action of only a single gene or the result of combined action of several genes, but the way in which they segregate in different colonies suggests that single genes or very small groups of genes are involved. Each of these positive characters is matched by a negative character. The latter may be assumed to be recessive, but there are certainly exceptions. Many other elements of the color pattern must also be genetically controlled, but cannot be distinguished from environmental effects under field conditions.

On the Lower Keys pure colonies showing the combinations 1-2-0-4-5-6-0 (*L. f. graphicus*), 1-2-3-4-5-6-0 (*pictus*), 1-2-0-0-5-6-7 (*osmentii*), and 0-3-4-0-0-7 (*solidulus*) survive today or have been preserved by

² Dr. W. J. Clench of the Museum of Comparative Zoology does not believe that parthenogenesis in *Liguus* is probable. It is true that *Liguus* like other pulmonates is hermaphroditic, but if the reproductive behavior is comparable to that in *Cepaea* and other land snails which have been studied in detail in this regard self-fertilization is very rare. Observations on *Liguus* in captivity suggest, in fact, that mutual fertilization does not normally occur. Snails may be alternately male in one mating and female in another. If these observations hold generally and *Liguus* has devices to prevent self-fertilization, such as those in *Cepaea*, parthenogenesis in isolated individuals is as probable as self-fertilization. Self-fertilization alone would not insure a "pure" colony except in the case of homozygous individuals.

transfer to the Everglades National Park area.³ The combination 1-2-0-4-0-0-0 (*dryas*) occurs on Little Pine Key in a nearly pure colony, but there is an area in which it occurs with *graphicus*. Other combinations appear in pure colonies on the mainland, including 1-2-3-4-5-6-7 and 0-0-0-0-0-0-0. Certain combinations are rare, however, suggesting, as might be expected, linkage and crossing over and other genetic complications. For example, colored apex, colored columella, and peripheral banding frequently occur together. Banded forms with white tips are rare as are washed forms (combining peripheral and sutural banding) with pink tips. In some cases where the latter condition occurs as in *pictus* and some *ornatus* (Simpson, 1929) the apex is colored but not the columella suggesting that translocation may have occurred.

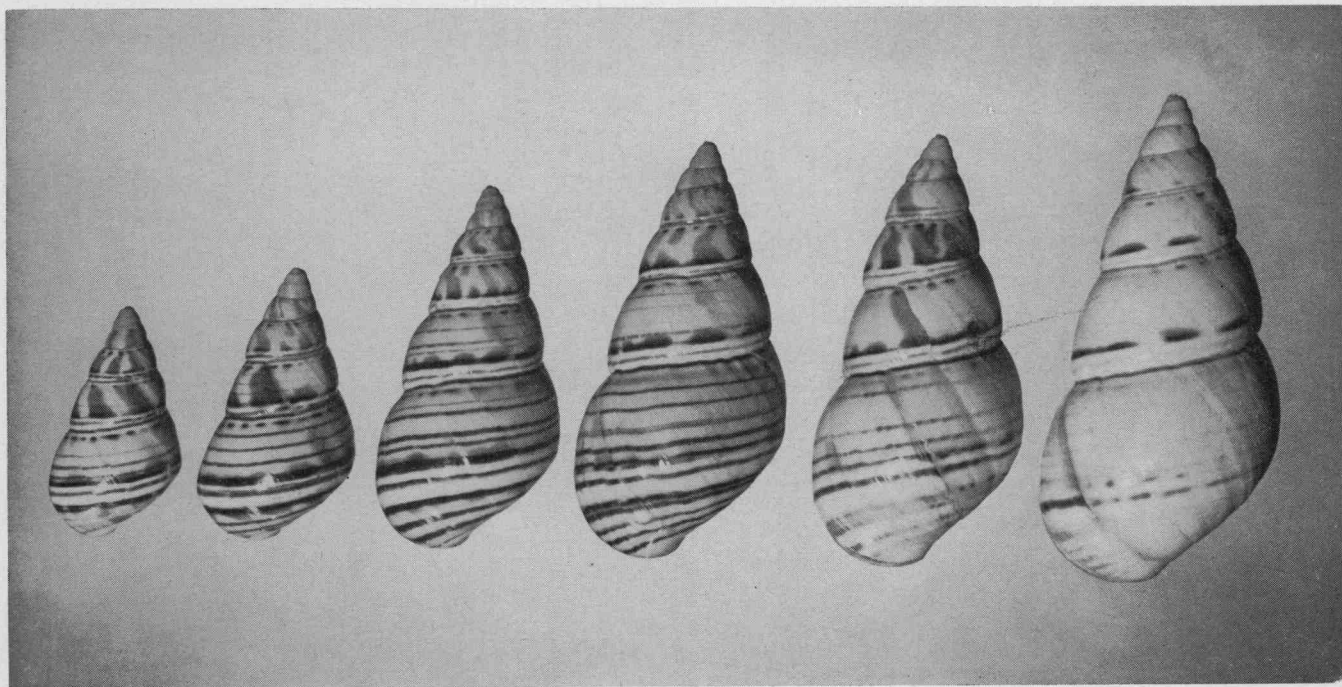
Erwin Winte of the Everglades National Park staff made some interesting artificial crosses of snails from the Lower Keys with some of the mainland forms. Unfortunately, exact data could not be preserved under the conditions of the experiment, but the progeny of the cross that were retrieved suggest that the first generation shows only characters of the Lower Key parent while the second shows segregation. Modification of the shell shape and texture in the hybrids also indicates genetic influences.

Recently, C. C. Von Paulsen, William Osment, and Erwin Winte have discovered an interesting colony on Little Torch Key, one of the Pine Islands, in which all the shells are 1-2-0-4-5-6-7. These snails which are associated with *Orthalicus floridensis* (Pilsbry) in a small, dry hammock represent a distinctive color form. I wish to thank Erwin Winte and Archie L. Jones for calling this discovery to my attention, and with the permission of the discoverers I take pleasure in naming it:

Liguus fasciatus vonpaulseni new subspecies

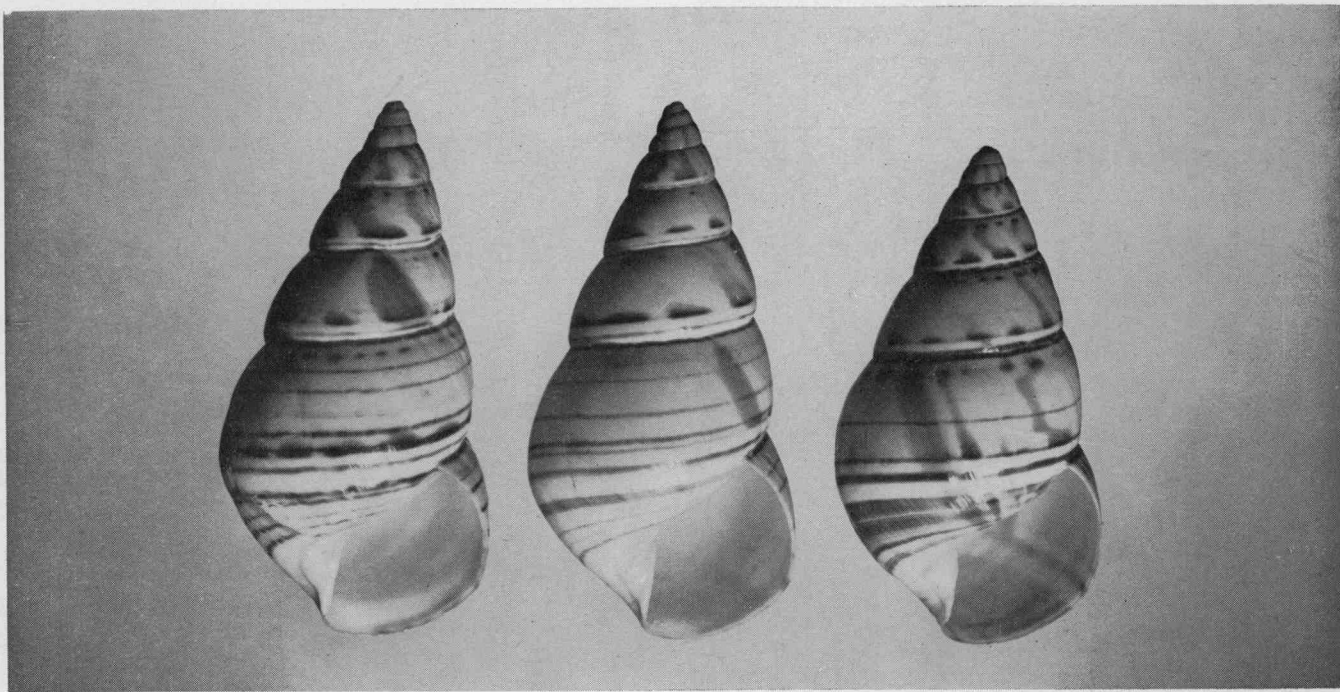
DIAGNOSIS: Similiar to *Liguus fasciatus graphicus*, but differing in the presence on the periphery of numerous periostracal green lines

³The project of transferring and preserving the Lower Key snails is being conducted by Ralph Humes, Archie L. Jones, C. C. Von Paulsen of Miami, and Erwin Winte of the National Park Service with cooperation of the Everglades National Park authorities. Snails are being colonized in formerly barren hammocks, and the results to date are most gratifying. It is hoped that all of the surviving pure colonies of Florida *Liguus* can be preserved and thus be available for future research. A number of experimental crosses to test genetic assumptions have already been made in other separated hammocks, but the result of these will not be known for some time.



Photograph by DELLENBACK

Figure 1. Holotype (fourth from left) and series of paratypes showing appearance of *Liguus fasciatus conpaulseni* at various stages of growth. Shell at left 30 mm. in length; shell at right about 65 mm.; type 55 mm.



Photograph by DELLENBACK

Figure 2. Holotype of *Liguus fasciatus vonpaulseni* (left) compared with forms *osmenti* (center) and *ligumvitae* (right) to show development of lip.

and in having the lip of the shell crenate at the juncture of the periostracal green lines. The distinction of the subspecies *vonpaulseni* from the other forms now found or formerly occurring on the Lower Keys is given in the key following the description.

DESCRIPTION: Shell—Moderately elongate, heavy in texture, varying from shining in younger examples to dull in older specimens; whorls not inflated, slightly flattened; columella straight; outer lip crenate at juncture of periostracal green lines even in old specimens, but not crenate at juncture of sutural or peripheral brown-red lines; lip moderately thickened internally. Color—In younger specimens, including the type, richly banded with yellow as in the subspecies *graphicus*; apex and columella pink; peripheral and sutural brown-red lines well developed; dark pigments in form of blotches on peripheral bands of upper whorls and as small spots along upper border, and as elongate streaks along the lower border of the bands on the intermediate and lower whorls; in very young shells these elongate streaks form nearly continuous lines, but in older specimens the streaks separate into elongate spots of varying lengths; old specimens fade until there is a superficial resemblance to the form *L. f. osmenti*, but yellow pigment and the periostracal green lines are retained in the bands on at least the last two whorls even in the largest shells seen, and the outer lip is crenate at the juncture of the periostracal green lines; periostracal green lines well developed, up to six reaching the lip above the brown-red peripheral line.

TYPE MATERIAL: Holotype, University of Florida Collections (UF) 18865. Collected on Little Torch Key, Monroe County, Florida, by C. C. Von Paulsen, William Osment, and Edwin Winte, during the summer 1959. The type is a mature shell with eight visible whorls in dorsal view. Length 55 mm., greatest width 27 mm., distance from suture to tip of columella 21 mm. Smallest shell seen, 30 x 18 x 12 mm.; largest seen, 65 x 32 x 24 mm. Paratypes, 70 in all are distributed as follows: University of Florida Collections (UF) 18866 (5), Museum of Comparative Zoology (4), University of Michigan Museum of Zoology (4), and the private collections of Captain Von Paulsen, and Messrs. Winte, Humes, Osment, and Jones (56).

The form *L. f. vonpaulseni* falls in the Clench and Fairchild classification of Florida *Liguus* (1939) under *Liguus fasciatus solidus* (Say). As indicated in the following key it should be placed next to *graphicus*.

Three aberrant shells collected by William Osment are not designated as paratypes. One of these is abnormally elongate with the suture deeply indented. Otherwise it seems to be typical. Another

shell shows most of the characteristics but has the green periostracal lines reduced or fused. The third shows the green lines only at the base of the shell on the new growth, although the yellow pigment is not at all bleached as it is in older shells.

A KEY TO THE DESCRIBED FORMS OF *Liguus fasciatus* (Müller)
FROM THE LOWER FLORIDA KEYS

1. Apex of shell and usually the columella pink 2
 Apex of shell and columella colorless or white 7
2. Yellow pigment present in bands or whorls or as a general wash
 over the shell 3
 Yellow pigment lacking; periostracal green lines present, but lip of shell
 not or only feebly crenate at their juncture; shell relatively heavy;
 dark pigment in blotches on upper whorls, and in elongate streaks
 along brown-red peripheral lines on lower whorls; peripheral and
 sutural brown-red lines present, usually strongly developed even in
 old shells *osmenti* Clench
3. Blotches of dark pigments on upper whorls and as elongate streaks or
 squarish blotches along the peripheral brown lines 4
 Dark pigment lacking or greatly reduced; yellow pigment intense, often
 appearing orange in fresh specimens, confined to regular bands from
 near the apex to the lip; peripheral and sutural brown lines lacking
 *dryas* Pilsbry
4. Yellow pigment present in definitely restricted peripheral bands on the
 whorls; both apex and columella usually pink; dark pigment seldom,
 if ever, in the form of squarish blotches along the peripheral brown
 lines, if so within these lines not crossing them 5
 Yellow pigment present as a wash over shell; columella pale pink or white,
 usually white; dark pigment present as blotches on upper whorls and
 as squarish blotches along peripheral brown lines to lip, the blotches
 crossing peripheral lines or above and below them rather than con-
 fined to area between them on each whorl as in *graphicus* . . *pictus* (Reeve)
5. Shell thin, translucent, resembling form *lignumvitae* Pilsbry from Lower
 Matecumbe and adjacent keys; periostracal green lines developed on
 lower whorls at least; lip not crenate; dark pigment in blotches on
 upper whorls, but intensely dark elongate streaks on lower whorls
 reduced; extinct form from No Name Key *innominatus* Pilsbry
 Shell relatively thick, not translucent; elongate dark streaks along periph-
 eral brown lines often intense 6
6. Periostracal green lines fully developed as in typical *fasciatus*, up to six
 reaching the lip of shell between the peripheral brown-red lines in
 unfaded examples and some green lines evident even in old shells,
 although in the latter the yellow pigments fade so that they resemble
 osmenti; lip of shell crenate at juncture of periostracal green lines

(but not at juncture of brown-red peripheral lines) in young specimens, moderately crenate on new growth in old shells; shell shape and columellar form similar to *graphicus*; body of snail lighter brown than in *graphicus* *vonpaulseni* new subspecies

Periostracal green lines lacking; lip of shell not crenate; size sometimes very large, up to 72 mm. in length *graphicus* Pilsbry

7. Yellow pigment absent; shell heavy, inflated, ground color ivory white with bronzy peripheral line (or lines) present or absent; presumably extinct, known only from figure of type from Big Pine Key and a doubtful specimen from Ramrod Key (heavy ridge inside lip of type and Ramrod Key specimen of doubtful significance) . . . *crassus* Simpson

Ground color of shell white, cream, or straw yellow; yellow pigment present, either as a general wash over shell or in restricted bands . . . 8

8. Shell with a broad basal and suprapерipheral pale yellow band (probably with periostracal green lines in young specimens); presumably extinct, but once widely distributed over the Lower Keys . . . *solidus* (Say)

Shell with two narrow yellow peripheral bands and one at the suture, presenting essentially a photographic-type negative of *solidus*; young shells with periostracal green lines *solidulus* Pilsbry

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