WALKERANA

Transactions of the POETS Society

Vol. 4

No. 12

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> Ann Arbor, Michigan 1990

WALKERANA, Vol. 4

Transactions of the POETS Society

No. 12

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Walkerana, 1990, 4(12): 237-270

THE GENUS *ELIMIA (=GONIOBASIS)* IN FLORIDA AND ADJOINING DRAINAGE BASINS (PROSOBRANCHIA: PLEUROCERIDAE)

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ABSTRACT. – Shell Characters identified in earlier electrophoretic and chromosomal studies were employed in a reexamination of the pleurocerid (Mesogastropoda) genus Elimia (=Goniobasis) found in Florida and river drainages flowing into Florida from Georgia (Chattahoochee and Flint river systems) and Alabama (Chattahoochee, Choctawhatchee, and Chipola river systems). Four species are recognized: Elimia floridensis, E. dickinsoni, E. boykiniana, and E. curvicostata. Earlier treatments recognized 10 species in this area. The major taxonomic changes proposed in this study concern E. floridensis and E. boykiniana. These two species are redescribed, and synonymies are presented for all four recognized species. Lectotypes are designated for E. boykiniana and 14 junior synonyms of either E. boykiniana or E. floridensis, and type localities are restricted for six junior synonyms.

KEY WORDS – Systematics, synonymies, lectotypes, Goniobasis, Elimia, E. boykiniana, E. curvicostata, E. dickinsoni, E. floridensis, Alabama, Florida, Georgia.

INTRODUCTION

Snails of the genus *Elimia* H. & A. Adams 1854, commonly referred to *Goniobasis* Lea 1862, are a diverse element of the extraordinarily diverse pleurocerid snail fauna of eastern North America. Isaac Lea alone described over 175 "species" in his genus *Goniobasis* (Scudder, 1885). Tryon (1873) recognized 255 *Goniobasis* species in his treatment of the family Strepomatidae, now known by the name Pleuroceridae. Basing his treatment on the works of Goodrich, Burch (1982b) recognized 83 species of North American *Elimia* and listed subspecies for some of those species.

The present report is concerned with the *Elimia* of Florida and drainage basins in Alabama and Georgia that flow into Florida. Most named species in this area were described by Lea, who named 18 species, during the last century. Pilsbry (1891) subsequently identified some synonyms among the Florida species. Goodrich described two additional species (1921, 1924) and discussed variation within some species (1935). Goodrich later (1942) recognized seven species in this area in his general review of Atlantic Coastal Plain species of the genus. Burch (1982b), mostly following the work of Goodrich, recognized ten species of *Elimia* in the area of concern here.

Clench & Turner's (1956) monograph on the freshwater mollusks of Florida and adjacent areas of Georgia and Alabama included the first treatment of the *Elimia* (=*Goniobasis*) of the area to be based upon extensive, first-hand field work. They recognized 10 species, including two that they newly described. Thompson (1984) generally followed their classification in his identification manual of Florida freshwater snails. A particularly significant observation by Clench & Turner was their discovery of three species of the genus occurring together in the Chipola River, Florida. Even more significant for the present understanding of the group was their discrimination here of two conchologically very similar species: *Goniobasis athearni*, which they described, and *G. floridensis*. Discussions later in the present paper will demonstrate that much of the variation in the genus in some areas can be explained by the sympatric occurrence of two, conchologically similar species.

Studies of electrophoretic and chromosomal variation in the Florida Elimia (Chambers, 1978, 1980, 1982a, 1982b) have provided new insights into evolutionary divergence among these snails. The electrophoretic studies were primarily of *E. floridensis* populations, but included samples of *E. dickinsoni, E. curvicostata*, and two synonyms (*E. albanyensis* and *E. athearni*) of Elimia boykiniana. Electrophoretic studies led to the detection of a sibling species (here recognized as a population of *E. boykiniana*) occurring with *E. floridensis* in the Ichetucknee River, Florida (Chambers, 1978). An additional finding was that three major groups were discernable in the fauna: (1) a group of which *E. floridensis* is the most widespread; (2) a group that included species here recognized as *E. boykiniana* and its synonyms; and (3) *E. curvicostata*. General findings of those studies were that certain shell sculptural features can give a misleading view of interspecific boundaries and relationships.

The sibling species of "Goniobasis" floridensis in the Ichetucknee River, Florida, and forms then known as Goniobasis albanyensis and G. athearni form a group that is electrophoretic-ally distant from G. floridensis (Chambers, 1978). That finding led to the discovery that the named species in that group share characters that separate them from the G. floridensis group. Those characters are the shape of the outer lip of the aperture and the relative stoutness of the shell. These characters have been used to separate members of these two groups and make possible the classification presented in this revision.

Another finding of the electrophoretic studies was that relatively little divergence exists among samples of *Elimia floridensis* within drainages as compared to among drainages (Chambers, 1980). In other words, there are genetic discontinuities between populations in adjacent drainages. This pattern was also seen in chromosomal variation in *E. floridensis* in three different drainage systems (Chambers, 1982a). That karyotypic study also provided evidence that shell sculptural features have been reduced or lost independently by populations in the headwaters of two adjacent drainage systems, which further demonstrated the unreliability of the presence or absence of certain shell sculptural characters for discriminating species in this group.

MATERIALS AND METHODS

Lots were examined in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), Museum of Comparative Zoology of Harvard University (MCZ), Florida State Museum (UF), The Ohio State University Museum of Zoology (OSUM), the Academy of Natural Sciences of Philadelphia (ANSP), and, to a much lesser degree, the University of Michigan Museum of Zoology (UMMZ). A few lots were located and loaned by the British Museum (Natural History) (BMNH) in response to my request for Reeve's type material. Material examined at UF in December 1982 included a large number of uncataloged lots. Although all UF lots were examined

and considered in the preparation of this revision, only the cataloged lots are recorded here in the species accounts. Type material was examined for nearly all names, the most notable exceptions being a few described by Reeve that could not be located. All original descriptions and illustrations were examined and compared with likely types.

All type lots examined and referred to consist of shells and, rarely, opercula. Numbers in parentheses following syntype or paralectotype catalog numbers indicate the number of shells in the lot. Some "holotypes" referred to by Clench & Turner (1956) were actually syntypes. Although designation of lectotypes of junior synonyms was not a major objective of this study, when a specimen that was figured with the original description could be identified in a type lot, that specimen was designated a lectotype. Many of the lectotypes were separated from their original lots and placed in the type collection of the USNM Division of Mollusks by J.P.E. Morrison, late curator in that division. Although each was labelled "holotype," they have not been formally designated as lectotypes until now.

Linear measurements of shell features were made to the nearest 0.1 mm with dial calipers. Spire apical angle is the apical angle as defined by Cox (1960). This angle was measured with reference to the first two remaining whorls, because the early one to four whorls are nearly always eroded away in all but the youngest individuals. Shells with more nearly complete spires were selected for measurement. Where measurements are given for two shells in a lot, individuals were selected with the intent to represent the extremes of variation in the characters measured. Measurements are presented in Table 1.

Localities given in the species accounts are in Florida unless other-wise indicated. Mixed lots of more than one species are indicated by "[part]" following the museum catalog number. Locality data are summarized in Fig. 1.

These studies centered on *Elimia floridensis*, *E. dickinsoni*, and *E. boykiniana*. *Elimia curvicostata* was studied less intensively, although type material of its synonyms was carefully examined, and special attention was given to characters that separate it from other *Elimia* in the area. *E. dickinsoni* and *E. curvicostata* are not redescribed because Clench & Turner's (1956) concepts of these species have not been changed by findings of the present study and their descriptions remain sufficient.

Although electrophoretic data (Chambers, 1978, 1980) led to the identification of shell characters used to separate *Elimia boykiniana* and *E. floridensis*, synonyms were ultimately determined by examining those characters in shells in type lots and other museum material. Electrophoretic data are available from populations formerly attributed to synonyms in a few cases that are identified in the remarks following the synonymies.

SYSTEMATICS

Elimia H. & A. Adams 1854

Elimia is the earliest available name (Pilsbry & Rhoads, 1896; Baker, 1963; Burch, 1982a,b) for the genus that includes the Florida pleurocerid species and is here used in place of *Goniobasis*. Walker (1918) recognized the priority of *Elimia* but rejected it in favor of *Goniobasis* on the basis of Pilsbry's view (apparently unpublished) that H. & A. Adams' *Elimia* was a composite group. Pilsbry & Rhoads' (1896) designation of *Elimia acutocarinata* (Lea, 1841), which is definitely within the group usually referred to as *Goniobasis*, as the type species of *Elimia* defines the group sufficiently so that Walker's objection can be rejected. Although it is regretful that the long-used name *Goniobasis* is to be replaced, it is unlikely that application to suppress *Elimia* would be successful in light of its

The Pleurocerid Genus Elimia

TABLE 1. Shell characteristics of *Elimia floridensis* and *E. boykiniana*. Identification numbers are USNM unless otherwise indicated. Measurement procedures are described under Materials and Methods. Abbreviations: AL=Alabama, FL=Florida, GA= Georgia, R=River, Sp=Spring(s), Cr=Creek, h=holotype, l=lectotype, p=paralectotype, s=syntype, t=topotype.

Source lot	Shell height (mm)	Spire angle (deg)	Aperture length/shell height
Elimia floridensis:			
Juniper Cr:782356	21.3	40	0.40
1	19.7	39	0.39
Lithia Sp:515830	16.6	39	0.41
	16.9	42	0.35
Rainbow R:782346	20.4	44	0.41
	21.1	50	0.45
Withlacoochee R, GA:665465	20.9	38	0.37
C1: 1 D 700050	21.8	43 35	0.35 0.38
Chipola R:782352	20.9	35 34	0.38
Dive Upla S-1782251	20.6 22.8	34 42	0.38
Blue Hole Sp:782351	19.6	42	0.43
Spring Cr:782344	20.0	36	0.42
oping on our of	23.8	29	0.38
Choctawhatchee R, AL:668077	19.4	35	0.44
	17.3	35	0.41
M. hallenbeckii:1	29.0	40	0.40
M. hallenbeckii:p	28.8	41	0.39
	22.8	34	0.51
:p:BMNH	21.8	40	0.42
M. etowahensis Lea, 1861:s:BMNH	13.0	36	0.44
G. inclinans:1	17.7	31	0.33
G. canbyi:l	17.8	33 34	0.37 0.36
G. couperii:1 G. downieana:1	15.0 16.5	34 40	0.36
	10.5	40	0.45
Elimia boykiniana:			
Ichetucknee R:862596	15.5	49	0.50
	16.1	50	0.48
Apalachicola R:809636	13.9	51	0.50
Chi-ala D:524197	15.7 15.0	45 48	0.45 0.52
Chipola R:524187	13.0	52	0.49
Flint R tributary:MCZ 98170	20.8	49	0.45
Think K thoulary. MCZ 50170	21.0	49	0.45
Chattahoochee R:MCZ 218147	20.7	54	0.49
	19.9	54	0.48
M. boykiniana:p	22.7	47	0.48
M. boykiniana:p	26.0	49	0.42
2 A	21.8	51	0.50
M. catenoides:s	17.8	44	0.48
M. modesta:h	14.9	44	0.52
M. papillosa:1:BMNH	14.0	57	0.48
:p:BMNH	11.4	55	0.53
G. viridostriatis:1	14.1	41	0.52
G. gesnerii:h	19.0	52	0.51
Range of above E. floridensis		29-50	.3351
Range of above E. boykiniana		41-57	.4253

[Table 1, continued]

	Shell height/ No. whorls	No. of spiral cords relative periphery	
* ²	(mm)	Above	Below
	4.3	3	7
	3.9	4	6
	3.3	3	7
	2.4	3	6
	3.4	3 3 4	9
	3.5	3	8
	3.0	3 3 3 2 2 3 0 3 3 3 2 3 2 3 3 2 3 4	8 8 7 6
	3.1	3	7
	4.0	3	6
	3.5	2	8
	3.3	2	4
	3.4	3	7
	2.9	0	7 3 6
	4.0	3	6
	3.9	3	4
	3.5	3	4 5 5 5 7 6
	4.8	2	5
	4.8	3	5
	3.8	2	5
	4.4	2	7
	3.7	3	6
	2.5	3	4
	3.0	2	5
	2.5	3	7
	3.3	4	7
	3.9	3	8
	4.0	3	7
	3.5	6	6
	3.9	7	7
	5.0	2	5
	4.7	3	5
	5.0	ž	6
	3.5	3 3 7 2 3 3 4	6
	4.1	5	4 5 7 7 8 7 6 7 5 5 6 6 7 8 9 7 8 9 7 8 6
	5.0	5 4	8
	5.7	4	9
	6.5	4	7
	4.4	5	8
	4.0	5	6
	3.7	4	õ
	3.5	3	7
	3.3	3 3	0 7 7
	3.5	3	6
	3.8	1	6
	2.4-4.8	0-4	3-9
	3.5-6.5	2-7	5-9

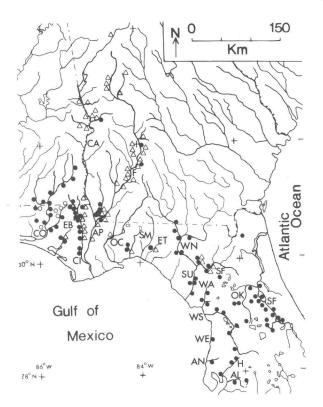


FIG. 1. Localities of three species of *Elimia* in Florida, Alabama, and Georgia. Closed circles: *E. floridensis*. Open circles: *E. dickinsoni*. Triangles: *E. boykiniana*. A single symbol may represent more than one closely-spaced locality. Abbreviations: CO - Choctawhatchee R.; EB - Econfina R., Bay Co.; CI - Chipola R.; AP - Apalachicola R.; CA - Chattahoochee R.; F - Flint R.; OC - Ochlockonee R.; SM - St. Marks River; ET - Econfina R., Taylor Co.; WN - Withlacoochee R., Suwannee R. drainage; SU - Suwannee R.; SF - Santa Fe R.; WA - Waccasasa R.; AN - Anclote R.; H - Hillsborough R.; AL - Alafia R.; OK - Oklawaha R.; SJ - St. Johns R.

occasional use in the past (Maury, 1916; Stewart, 1927; Henderson, 1935, 1936; Taylor, 1966) and the likely influence of its use in recent identification manuals (Burch & Tottenham, 1980; Burch, 1982a, b; Thompson, 1984).

Generic groupings and names within the Pleuroceridae have been intensively debated for many years. The Florida forms belong in the group including the genera recognized by Tryon (1873) and Walker (1918) as *Pleurocera* Rafinesque 1818 (with *Pleurocera acuta* Rafinesque 1831 designated the type species by Walker) and *Goniobasis* Lea 1862. Morrison (1954) argued that most species traditionally placed in these two genera are actually congeneric, and that genus should take the name *Oxytrema* Rafinesque, 1819, because the true type species of

Pleurocera is *Pleurocera verrucosa* Rafinesque 1820, which belongs in the genus *Lithasia* Haldeman 1840 as recognized by Walker (1918). *Pleurocera* should, according to priority (Hannibal, 1912; Morrison, 1954; Stein, 1976), be the name applied to the genus usually known as *Lithasia*. The International Commission on Zoological Nomenclature has recently (Melville, 1981) published an opinion that, in order to preserve stability in nomenclature and avoid a transfer of names between genera, *Pleurocerus acutus* Rafinesque *in* Blainville 1824 be designated the type species of *Pleurocera*. This opinion sets aside *Pleurocera verrucosa* as the type species of *Pleurocera* and preserves the usage of Tryon (1873) and Walker (1918).

Merging the genera *Pleurocera* and *Goniobasis* would be under the older name *Pleurocera*. These two groups are defined by shell characters, but the distinction is not precise (Burch, 1982a,b). The appropriateness of such a combination is supported by Dazo's (1965) finding little difference in the soft anatomy of *Pleurocera acuta* and *Goniobasis livescens* (Menke 1830). A full consideration of the distinctiveness of these two groups is not within the scope of the present study. The traditional placement of the Florida species in a genus other than *Pleurocera* will be followed, while acknowledging the merits of combining the two genera.

Elimia floridensis (Reeve) Figs. 2, 3A, B

- Melania floridensis Reeve 1860: pl. 45, species 334 [type, in Cuming Collection (now mainly at BMNH) according to Reeve, not found; type-locality: Florida]. - Brot, 1862: 34.
- Melania hallenbeckii Lea ms. Reeve 1860: pl. 45, species 332 [lectotype, here selected and figured (Fig. 2D) is probably not the shell figured by Reeve, but it comes closest of the type material and is the specimen figured by Lea (1862b, pl. 38, fig. 203): USNM 118406; paralectotypes are USNM 873100 (13), USNM 873101 (5), and BMNH, no number, (1) (Fig 3A); five shells in MCZ 186748 (Fig. 7) labeled as paratypes of *Goniobasis hallenbeckii* Lea are all *Elimia boykiniana* Lea; type-locality: United States, here restricted to Randall['s] Creek [Muscogee Co.], near Columbus, Georgia, which is the locality given by Lea (1862a)].
- Melania etowahensis Lea ms. Reeve 1861: pl. 55, species 426 [possible syntypes: BMNH, no number (1) (Fig. 3B), and MCZ 51334 (2) (figured specimen, according to Reeve in the Anthony collection, not found); type-locality: Georgia (doubtful - see Geographic Distribution and Variation section for Elimia floridensis); (not Goniobasis etowahensis Lea, 1862b: 229, pl. 37, fig. 133]; 1863: 121, pl., 37 fig. 133). - Brot, 1862: 34.
- Goniobasis inclinans Lea 1862a: 267 [lectotype here designated and figured (Fig. 2E) is Lea's figured specimen: USNM 118420; paralectotypes: USNM 873107 (24); type-locality: here restricted to near Albany, Georgia, which is indicated on the labels of the type material and is one of Lea's (1862a) localities along with "Etowah" and "Tuscambia, Alabama" (see Geographic Distribution and Variation section for *Elimia floridensis*)]; 1862b: 318, pl. 37, fig. 165; 1863: 140, pl. 37, fig. 165. Tryon, 1864: 26; 1873: 153, fig. 293.
- *Goniobasis hallenbeckii* (Lea ms. Reeve). Lea, 1862a: 271; 1862b: 339, pl. 38, fig. 203; 1863: 161, pl., 38 fig, 203. Tryon, 1864: 26; 1873: 149, fig. 281, but probably not 282.

- Goniobasis canbyi Lea 1862a: 271 [lectotype, here designated and figured (Fig. 2A), is specimen figured by Lea (1863): USNM 118415; paralectotypes: USNM 873103 (6) and USNM 873104 (1); type-locality here restricted to Lake Monroe, Volusia Co., Florida, which is the locality on the labels of the type material and which Lea (1862a) gave as a locality along with Etowah and Tennessee rivers (see Geographic Distribution and Variation section for *Elimia floridensis*); not Goniobasis canbyi Lea 1864: 3 footnote, not of Tryon, 1873: 260 (this name was transferred by Lea (1864: 3) to Goniobasis etowahensis Lea, 1862 to replace the name preoccupied by *Melania etowahensis* Lea ms. Reeve 1861)]. 1862b; 340, pl. 38, fig. 204; 1863: 162, pl. 38, fig. 204.
- Goniobasis couperii Lea 1862a: 271 [lectotype, here designated and figured (Fig. 2B) is the shell figured by Lea (1862b): USNM 118416; paralectotype: USNM 873105; type-locality: "Etowah River" (doubtful see Geographic Distribution and Variation section for *Elimia floridensis*)]. 1862b: 341, pl. 38, fig. 205; 1863: 163, pl. 38, fig. 205. Tryon, 1864: 26; 1873: 153, fig. 292.
- Goniobasis downieana Lea 1862a: 272 [lectotype, here designated and figured (Fig. 2C), is Lea's (1862b) figured specimen: USNM 118412; paralectotype: USNM 873116; type-locality: "Etowah River, Georgia" (doubtful see Geographic Distribution and Variation section for *Elimia floridensis*)]. Lea, 1862b: 341, pl. 38, fig. 206; 1863: 163, pl. 38, fig. 206.
- Goniobasis etowahensis (Lea ms. Reeve). Tryon, 1864: 26; 1873: 148, fig. 280. Dall, 1885: 258, pl. 17 fig. 7.
- Goniobasis floridensis (Reeve). Tryon, 1873: 147, figs. 274-275). Clench & Turner, 1956: 127, pl. 2, figs. 7-8. Chambers, 1978: 157, fig. 2C-D; 1980: 65, figs. 1A, F, 5, 6C-K, 7C-D; 1982a: 113, fig. 1E-H.
- Goniobasis vanhyningiana Goodrich 1921: 2 [holotype: UMMZ 133336; paratypes: UMMZ 10586 (not seen, referred to in Goodrich, 1921) and MCZ 93755; type-locality: creek below Seminole Springs, Lake County, Florida]. -Clench & Turner, 1956: 130, pl. 3, Fig. 7. - Chambers, 1980: 64, figs. 1B, 4.
- Goniobasis clenchi Goodrich 1924: 46, figs. 1-4 [holotype (not seen): UMMZ 31618; paratypes: ANSP 133512, 176482; MCZ 51282; and USNM 361587 (4) (Fig. 2F); type-locality: Choctawahatchee River, Newton, Dale County, Alabama]. Goodrich, 1942: 4. Clench & Turner, 1956: 140, pl. 3, figs. 4-5.
- Goniobasis effosa Smith 1938: 91, pl. 6 figs. 4a, b [holotype not found Maxwell Smith donated much of his collection to the University of Alabama, which has recently transferred its mollusk holdings, perhaps including the holotype, to the Florida State Museum; paratypes: ANSP 13329; type-locality reported as "Tertiary, Belle Glade, Florida"].
- Goniobasis catenaria inclinans Lea. Goodrich, 1942: 3.
- Goniobasis catenaria cancellata, Goodrich, 1942: 3. Not Melania cancellata Say, 1829 (see Clench, 1955).
- Goniobasis catenaria vanhyningiana Goodrich. Goodrich 1942: 3.
- Goniobasis catenaria effosa (Smith). Pilsbry, 1953: 445, pl. 65, fig. 3.

Elimia catenaria effosa (Smith). - Taylor, 1966: 110.

Oxytrema clenchi (Goodrich). - Stein, 1976: 34.

- *Elimia clenchi* (Goodrich). Burch & Tottenham, 1980: 131, fig. 330. Burch, 1982a: 32, fig. 330. Thompson, 1984: 30, fig. 54.
- Elimia catenaria inclinans (Lea). Burch & Tottenham, 1980: 132. Burch, 1982a: 33.
- *Elimia catenaria vanhyningiana* (Goodrich). Burch & Tottenham, 1980: 132, fig. 338. Burch, 1982a: 33, fig. 338.
- *Elimia floridensis* (Reeve). Burch & Tottenham, 1980: 134. Burch, 1982a: 34. Thompson, 1984: 29, fig. 53.
- Elimia vanhyningiana (Goodrich). Thompson, 1984: 27, fig. 50.

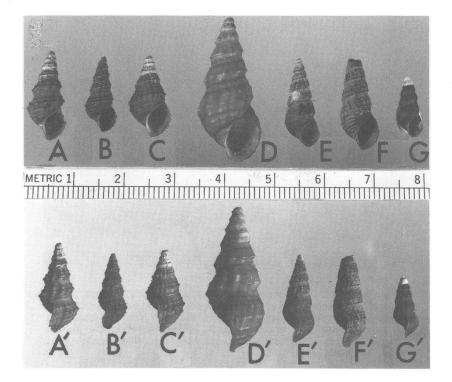


FIG. 2. Elimia floridensis - apertural (normal letters) and side (primed letters) of the same shells: A, Goniobasis canbyi Lea 1862, lectotype; B, G. couperii Lea 1862, lectotype; C, G. downieana Lea 1862, lectotype; D, Melania hallenbeckii, lectotype; E, G. inclinans, lectotype; F, G. clenchi, paratype (USNM 361587); G, G. vanhyningiana, topotype (USNM 341775). Scale is numbered in cm.

DESCRIPTION. Shell elongate, reaching 25 mm in length and 10 mm in width in most populations, although occasional older individuals may reach 34 mm in length and 13 mm in width, turriculate, thin, nonumbilicate, apical angle of spire ranging 29° to 40°, occasionally up to 50°, and consisting of up to 7 whorls, not counting apical whorls, which are nearly always eroded away in adults. Whorls flat-sided to uniformly convex or slightly swollen to almost carinate just above suture, forming an angled periphery. Growth lines opisthocline to opisthocyrt, parallel to or sometimes crossing axial sculpture, which consists of weak to strong costae having tubercles where intersected by spiral cords, which are sometimes absent. Tubercles increase in height towards periphery. Base of last whorl slightly to definitely convex. Costae on last whorl extend weakly below periphery or not at all. Spiral cords, when present, number 1-5 above and 3-9 below periphery of last whorl, often absent altogether or becoming weaker in later whorls, especially in some headwater populations. Early whorls with carinate

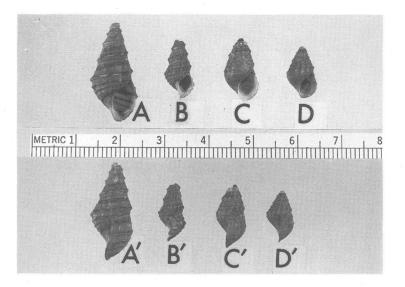


FIG. 3. Some *Melania* material of Reeve in the British Museum (Natural History). Apertural (normal letters) and side (primed letters) of the same shells: A and B are *Elimia floridensis*, and C and D are *Elimia boykiniana*. A, *Melania hallenbeckii*, paralectotype; B, *Melania etowahensis*, possible syntype; C, *Melania papillosa*, lectotype; D, *Melania papillosa*, paralectotype. Scale is numbered in cm.

nate periphery, even in individuals lacking spiral sculpture on later whorls. Suture indistinct to distinctly impressed. Aperture subquadrate, length 0.33 to 0.51 of entire shell. Inner surface of last whorl, including thin parietal callus, glossy and clear to chalky and opaque in dry shells. Outer lip of aperture sinuous, thin, and easily damaged. Color of periostracum light brown to black. Operculum chitinous and paucispiral.

REMARKS ON THE SYNONYMY. Clench & Turner's (1956) synonymy, which largely follows Goodrich's (1942) synonymy for "Goniobasis catenaria cancellata," for this species remains the foundation for defining Elimia floridensis, and is incorporated, except for Melania papillosa, into the present somewhat more inclusive synonymy. New synonyms include M. hallenbeckii, G. vanhyningiana, and G. clenchi.

Melania hallenbeckii Lea was first described in Reeve (1860), who credited a manuscript of Lea. Because Lea was undoubtedly the source of Reeve's material, Lea's locality is recognized as the restricted type locality. The description of *M. hallenbeckii* in Reeve (1860) appears earlier on the same page as that of Reeve's *Melania floridensis*, but the priority of the latter, well-established name is retained here. The broadly stated type-locality and lack of type material for *M. floridensis* do not present difficulties given the current understanding of the taxon; these factors could, however, become an issue if future evidence favors recognition of more than one species within the current *Elimia floridensis* and it becomes necessary to restrict the type-locality of *E. floridensis*. Proper restriction of the

type-locality of *E. floridensis* would require either the discovery of appropriate type material or the somewhat arbitrary designation of a neotype.

The most uncertain part of this synonymy is the inclusion of *Goniobasis* inclinans, which Clench & Turner considered a synonym of *Goniobasis* curvicostata. The finely tuberculated sculpture on this small, slender shell is the basis for its inclusion here as a synonym of *Elimia floridensis*. This is consistent with the treatment of Goodrich, who applied the name as a subspecies of *Goniobasis* catenaria (Say, 1822), the name he applied to most Florida populations now considered *Elimia floridensis*.

Forms referred to Goniobasis vanhyningiana by Goodrich (1942) and Clench & Turner (1956) appear to intergrade with highly sculptured forms that they referred to *Elimia floridensis* (Chambers, 1980). Goodrich (1935) was not entirely convinced of the taxonomic distinctness of G. vanhyningiana, referring to it as a "subspecies (or form)" of his G. cancellata (the name Goodrich used for E. floridensis) based on the geographic proximity of smooth and sculptured populations. Smooth and highly sculptured forms in Juniper Creek, Marion County, Florida, show no detectable differences at 18 isoenzyme loci (Chambers, 1980). Electrophoretic data are not available for snails from the type locality for G. vanhyningiana. A population in nearby Rock Springs that was considered to be G. vanhyningiana by Clench & Turner (1956) has been electrophoretically studied (Chambers, 1980). Shells from Rock Springs are somewhat larger but otherwise indistinguishable from shells from the type locality. The Rock Springs electrophoretic sample has a very high genetic identity with forms attributed by Clench & Turner (1956) to G. floridensis. Values for I_N , the genetic identity index of Nei (1972), between Rock Springs and E. floridensis populations from Juniper Creek and Rainbow River are 0.994 and 0.891, respectively, and alleles are shared by Rock Springs "G. vanhyningiana" and Rainbow River E. floridensis at all but one locus (Chambers, 1980). Electrophoretic evidence and the intergradation in shell features do not indicate species-level differences between populations formerly referred to G. vanhyningiana and E. floridensis.

Goniobasis clenchi is included as a synonym of Elimia floridensis for reasons discussed previously (Chambers, 1982b) and based on the existence of a population in the Econfina River, Bay County, Florida, that is intermediate in shell features between Clench & Turner's descriptions of G. floridensis and G. clenchi. E. clenchi has been distinguished from E. floridensis by its lack of a pronounced peripheral cord, which also gives the whorls a straighter outline and makes the sutures less distinct than in E. floridensis (Clench & Turner, 1956; Thompson, 1984). Both conditions and intergrades between them are found in the highly variable population of Elimia in Holmes Creek (Choctawhatchee River drainage) at Vernon, Florida. The Econfina River population is less variable, but shells with peripheral cords intermediate in expression between G. floridensis and G. clenchi as described by Clench & Turner (1956) are common. Those shells that I have examined in Goodrich's type lots of G. clenchi are the most distinctive of the shells that Clench & Turner (1956) included under that name, in that they are more attenuate and have more convex whorls (Fig. 2F) than the straight-sided forms illustrated by Clench & Turner (1956) and Thompson (1984). One population attributed to G. clenchi by Clench & Turner (1956) has been studied electrophoretically (Chambers, 1980). That sample has high genetic identities ($I_N>0.9$) and shares all major alleles with *G. floridensis* populations from the adjacent Chipola River drainage, which is comparable to the genetic distances observed between adjacent drainages among *E. floridensis* populations recognized by Clench & Turner (1956) and Thompson (1984).

COMPARATIVE REMARKS. *Elimia floridensis* can be readily distinguished from *Elimia boykiniana* by the shape of the outer lip of the aperture when viewed from the side of the shell. The outer lip is sinuous in *E. floridensis* and straight or slightly concave in *E. boykiniana*. Identification of individual shells of these species may be very difficult with shells having the outer lip broken or deformed by a disturbance during shell growth. *Elimia floridensis* is usually distinguished from *E. boykiniana* in such material by its sharper spire angle, which is usually 44° or less (23 of 24 shells in Table 1), whereas that of *E. boykiniana* is usually 44° or greater (18 of 19 shells in Table 1). *E. floridensis* usually has an aperture length to shell length ratio of 0.45 or less (23 of 24 shells in Table 1), while the relatively longer aperture of *E. boykiniana* gives a ratio of 0.45 or more (18 of 19 shells in Table 1) for that species. The shells reported in Table 1 were selected to represent extremes of variation within lots; actual overlap in characters between random samples of these two species is likely to be even less.

Both Elimia floridensis and E. boykiniana display substantial geographic variation. The following additional distinguishing characters apply only within the stated portion of these species' coincidental ranges. Shells of E. boykiniana in the Ichetuckee River and surrounding areas in the Suwannee River drainage have what appear to be costae studded with tubercles. On closer inspection the rows of tubercles that often produce the effect of costae can be seen to lack axial sculptural connections between the tubercles. Axial sculpture is always present on E. floridensis shells here and elsewhere. Perhaps the most difficult shells to identify are the very large shells collected during the last century in the Chattahoochee River and its tributaries, including some shells in the type lots of Melania hallenbeckii. In this material, shells of E. floridensis have two or less spiral cords above the periphery of the largest whorls, while shells of E. boykiniana have three or more.

The smooth-shelled headwater forms of *Elimia floridensis* in the Chipola River drainage are very similar to *E. dickinsoni*, which does not occur here, but can usually be distinguished by their relatively stronger axial sculpture and the persistence of a carina and spinal cords in later whorls than seen in *E. dickinsoni*.

Smooth forms of *E. floridensis* can be distinguished from *Elimia curvicostata* by the flatter-sided whorls, less rounded base of the body whorl, and more strongly sinuous outer lip of the aperture of the former species.

GEOGRAPHIC DISTRIBUTION AND VARIATION. Reeve (1861) cited material in the Anthony Collection as the basis for his description and figure of *Melania etowahensis*. The only specimen found under that name at BMNH is labeled Alabama rather than Georgia, the locality cited by Reeve, and does not appear to be the shell figured by him. The shell is very similar in its brown color and delicate sculpture to certain *Elimia floridensis* of the upper St. Johns drainage, such as shells from Lake George and Lea's type material for his original *Goniobasis canbyi* Lea, 1862, which is from Lake Monroe on the St. Johns River. Lea (1864) acknowledged the identity of his original *G. canbyi* with Reeve's *M. etowahensis*. Florida. It is likely that both Lea's and Reeve's material for these names came from the St. Johns drainage, Florida.

Localities recorded in the Tennessee and Etowah rivers, Georgia, for some of Lea's original material of Goniobasis inclinans, G. canbyi Lea 1862, G. couperii, and G. downieana are probably also erroneous. Pleurocerids reported from near the Etowah River (e.g., van der Schalie & Parmalee, 1960) would not be confused with these specimens, which also resemble in their brown color and fine sculptural features many populations from the St. Johns River drainage, Florida, Lea received this material (all but possibly G. inclinans collected by Couper) through James Postell. It is likely that these shells are from the St. Johns drainage, which is more closely and probably was more conveniently located to Couper's residence near Darien, Georgia, and Postell's on St. Simons Island, Georgia (Tryon 1873: 153-155) than the Etowah River of northern Georgia. Another factor that may have caused confusion on the source of this material is that the word "etowah," which is derived from Creek words meaning fallen trees, or snags, in a stream (Simpson, 1956: 53), and has been applied to at least one creek in the St. Johns River drainage of Florida and may have been widely applied, at least informally, by Creek-speaking inhabitants of peninsular Florida during the 19th century.

Clench & Turner (1956) noted that, although individual populations of Goniobasis floridensis were relatively uniform, there was a great range of variation within this species. Exceptions could be cited to uniformity within populations (Blue Hole Spring, Spring Creek, and a segment of Juniper Creek), but Clench & Turner's statement generally applies within the somewhat expanded concept of the species presented here. Genetic studies on isoenzyme loci (Chambers, 1980) and chromosomes (Chambers, 1982a) generally revealed that most variation was among rather than within drainage systems. Gene flow between drainages is apparently a rare event. Although genetic and morphological discontinuities between drainages are usually abrupt, they do not in themselves indicate reproductive isolation and therefore species-level divergence. It is possible that future studies may demonstrate reproductive isolation and therefore that the concept of *Elimia floridensis* presented here represents more than one species. Such divisions between species would most likely be along the land divisions between drainages. The present synonymy for *E. floridensis* contains names that are available for resurrection for many of these potential species.

Studies of chromosomes (Chambers, 1982a) have revealed a different characteristic karyotype in the *Elimia floridensis* samples from each of three drainage systems sampled (Suwannee River, Chipola River, and Holmes Creek). These populations may be considered as belonging to a Rassenkreis (Rensch, 1959) consisting of at least three chromosomal races of *E. floridensis*. (Note that the term "Rassenkreis" is comparable to "species complex" and, when used correctly, does not imply a circular pattern of geographic distribution [Huxley, 1943; Gould, 1982].) The karyotypic differences between the adjacent Holmes Creek and Chipola River drainages in western Florida are relatively small and neither justify nor preclude species level divergence between their *Elimia* populations. The difference between these populations and that at Ichetucknee River is far more substantial and is therefore more likely to be indicative of species differences, although comparable levels of variation have been found within some populations of the marine prosobranch *Nucella lapillus* (Linnaeus, 1758) by Staiger (1954) and Bantock & Cockayne (1975). The observed interspecific karyotypic variation within the single species Nucella lapillus plus the possibility that karyotypically intermediate populations may exist between the Ichetucknee River and the Chipola River justify treatment of all these chromosomal races as E. *floridensis* at this time. Breeding experiments involving individuals from different drainage systems could lead to confirmation or rejection of the conspecific status of these populations. Pleurocerids, however, have been found to be difficult to rear in aquaria and have relatively long generation times (Dazo, 1965; Chambers, 1980). The only breeding data relevant to inter-drainage relationships in Florida *Elimia* are limited a single successful mating between individuals from the Withlacoochee and Suwannee river drainages (Chambers, 1980).

Electrophoretic evidence bearing on the synonymy is available for populations attributed by Clench & Turner (1956) to Goniobasis clenchi and G. vanhyningiana. Those data were discussed earlier. Several other populations of Clench & Turner's (1956) G. floridensis have been electrophoretically studied (Chambers, 1978, 1980). Genetic identities (I_N) between these samples range from 0.740 to 0.933. Identities between adjacent or nearly adjacent drainages, however, tend to be in the higher portion of this range. The largest gap is between Florida panhandle and peninsular populations, although future samples from intervening drainages (Econfina River, Taylor Co., and St. Marks drainage) may genetically bridge that gap. Although discontinuities occur between drainages, and there are loci with large allelic differences, the genetic identities observed between adjacent drainages are not alarmingly low for conspecific populations. In light of the electrophoretic variation seen within and among populations recognized as G. floridensis by Clench & Turner (1956) and Thompson (1984), the divergences demonstrated by populations formerly attributed to G. vanhyningiana and G. clenchi are trivial.

Elimia floridensis ranges from the Choctawhatchee River drainage to the St. Johns River drainage. I have seen nothing west of the Choctawhatchee drainage that appears related to this species. In the Atlantic coastal drainages, sculptural forms north of the St. Johns River are more likely to be related to *E. boykiniana*, as discussed later under that species.

MATERIAL EXAMINED

ST. JOHNS RIVER SYSTEM, Florida:

St. Johns River, Volusia Co. (ANSP 346028); "Mc Greggs" [=Mc Girts?] Creek, Duval Co. (MCZ 46353); Glen Springs, Alachua Co. (ANSP 170668).

Oklawaha River Drainage: Blue Spring, Juliette, Marion Co. (ANSP 155259); Silver Creek, Marion Co. (ANSP 69037, 69509; USNM 128609, 465782); Silver Springs, Marion Co. (ANSP 69439, 149577, 180093, 219066, 316534, 343414; OSUM 36; USNM 321814, 321827, 420194, 468435, 487624); Lake Griffin, Lake Co. (UF 26714).

Beecher Run, Putnam Co. (OSUM 8235); Silver Glen Springs, Marion Co. (ANSP 197771, USNM 599865); Juniper Creek, Marion Co. (ANSP 327470, OSUM 1731; USNM 120902, 782356); Juniper Springs, Marion Co. (ANSP 159142, USNM 782354); Lake George, Volusia Co. (ANSP 142483, USNM 253601); Mt. Taylor, Volusia Co. (ANSP 71114); Tick Island, Volusia Co. (ANSP 327460); Lake Monroe, Volusia Co. (USNM 118415, 873103, 873104); Alexander Spring Creek, Lake Co. (OSUM 281, 869); Alexander Springs, Lake Co. (ANSP 27526, 43558, 162015); Seminole Creek, Lake Co. (ANSP 130136; MCZ 93755; USNM 341775, 359348); Creek below Seminole Springs, Lake Co. (MCZ 93755, UMMZ 133336); Seminole Springs, Lake Co.

(ANSP 131803); Wekiva River, Seminole Co. (ANSP 44943, OSUM 354, USNM 424353), Orange Co. (USNM 123178); mound near Enterprise, Volusia Co. (ANSP 122601); Lake Monroe, Volusia Co. (USNM 37507, 118414).

ALAFIA RIVER SYSTEM, Florida:

Alafia River, Polk Co. (ANSP 27527); Lithia Springs, Hillsborough Co. (ANSP 183909, 189080, 324596; USNM 484838, 484845, 515830, 596702-596707, 596709).

HILLSBOROUGH RIVER SYSTEM, Florida:

Hillsborough River, Hillsborough Co. (ANSP 118012, OSUM 7974), Pasco Co. (OSUM 11062); Magby Spring, Hillsborough Co. (ANSP 183908); Crystal Springs, Pasco Co. (ANSP 155265).

ANCLOTE RIVER SYSTEM, Florida:

Anclote River, Pasco Co. (OSUM 11076).

WEEKIWACHEE RIVER SYSTEM, Florida: Weekiwachee Spring, Hernando Co. (ANSP 149832, 155271).

WITHLACOOCHEE RIVER SYSTEM, Florida:

Withlacoochee River, Sumter Co. (OSUM 367), Marion Co. (USNM 466363, 466369), Pasco Co. (ANSP 155267); Blue Run (=Rainbow River), Marion Co. (USNM 782346); Rainbow Springs, Marion Co. (USNM 599866).

WACCASASSA RIVER SYSTEM, Levy Co., Florida:

Waccasassa River (USNM 782350); Wekiva River (USNM 61243, 782349); Blue Springs (USNM 862575-862581); Gunntown (ANSP 155270).

SUWANNEE RIVER SYSTEM, Florida:

Suwannee River, Dixie Co. (OSUM 262, 813), Suwannee Co. (OSUM 228, 8222); Manatee Spring, Levy Co. (UF 26876, OSUM 8477); Fannin Spring, Levy Co. (ANSP 155263, 155264); Hart Springs, Gilchrist Co. (UF 29508).

Santa Fe River Drainage, Florida: Santa Fe River, Columbia Co. (UF 30680); Ichetucknee River, Columbia Co. (ANSP 155269, UF 24884, OSUM 335); Ginny Spring, Gilchrist Co. (USNM 862568); Blue Spring, Gilchrist Co. (USNM 862567); Poe Springs, Alachua Co. (ANSP 155272); Columbia Springs, Columbia Co. (ANSP 155273; UF 4313, 4355, 4356).

Allen Mill Pond Spring, Lafayette Co. (UF 30673); Thomas Spring, Suwannee Co. (UF 30676).

Withlacoochee River Drainage: Withlacoochee River, Madison Co. (OSUM 253, 12391), Lowndes Co., Georgia (USNM 665465); Blue Spring, Madison Co. (USNM 782348).

ECONFINA RIVER SYSTEM, Florida:

Econfina River, Taylor Co. (ANSP 48427, 267623 [part]).

ST. MARKS RIVER SYSTEM, Wakulla Co., Florida:

Wakulla River (ANSP 267623 [part], MCZ 235041, OSUM 368); Wakulla Spring (MCZ 216232).

APALACHICOLA RIVER SYSTEM:

Flint River Drainage, Georgia: "near Albany," (USNM 118420, 873102); Spring Creek, Decatur Co. (MCZ 191551), Seminole Co. (MCZ 191547; Sealey's Spring, Decatur Co. (MCZ 191545); Shackleford Spring, Decatur Co. (MCZ 191546); Blue Spring, Decatur Co. (MCZ 189601, 190417); Paul Clark Spring, Decatur Co. (MCZ 191552).

Chattahoochee River Drainage. Georgia: Randall Creek, Muscogee Co. (ANSP 219014; USNM 118406, 188406 [part], 119330, 873100, 873101).

Chipola River Drainage: Chipola River, Calhoun Co. (ANSP 189823, 194656; UF 1049, 1986 [part], 4947 [part]; MCZ 190418, 190428; OSUM 304, 306, 8001, 13789-

13795; USNM 127038, 597406), Jackson Co. (ANSP 154984, 154986, 155261; UF 4948, 29435; MCZ 190419; OSUM 267, 268, 317, 12386; USNM 331806, 782352); Creek 3 miles NNW Sink Creek, Jackson Co. (UF 4946); Rocky Creek, Jackson Co. (UF 28348, 28353); Spring Creek, 2 miles SE of Marianna (ANSP 353846, 354765; UF 30095 [part]; OSUM 12399); Merritts Mill Pond (ANSP 7885, 218983; UF 1590 [part]; MCZ 191550, OSUM 5019; USNM 590392 [part], 592399 [part]); Blue Hole Spring, Jackson Co. (USNM 782351); Blue Spring Lake, Jackson, Co. (USNM 189877); Blue Springs, Jackson Co. (ANSP 155260); Blue Springs Branch, Jackson Co. (USNM 341682); Chipola River tributary 5 miles NE of Marianna, Jackson Co. (ANSP 160434; MCZ 53293, 92429); Reedy Creek, Jackson Co. (ANSP 194639 [part]; UF 1990; MCZ 99885, 190421); Big Creek, Jackson Co. (ANSP 194658 [part], MCZ 190420); Big Creek, Houston Co., Alabama (MCZ 41985). Spring Creek N of Campbellton, Jackson Co. (ANSP 151505, 346282; MCZ 91723; USNM 405611, 782344).

CHOCTAWHATCHEE RIVER SYSTEM:

Choctawhatchee River, Walton Co (UF 4341), Washington Co. (ANSP 162297, 183472; UF 1983; MCZ 191752; USNM 782347), Holmes Co. (ANSP 194625, MCZ 190499), Geneva Co., Alabama (MCZ 190500), Dale Co., Alabama (ANSP 133512, 176482, 267634; MCZ 51282, 91724, 189825; OSUM 13553; USNM 361587); Sandy Creek, Walton Co. (ANSP 162299); Holmes Creek, Washington Co. (ANSP 183472, OSUM 355), Geneva Co., Alabama (MCZ 1606).

Pea River drainage: Pea River, Geneva Co., Alabama (MCZ 191751); Limestone Creek, Walton Co. (ANSP 162296 [part], UF 4336 [part]); Flat Creek, Geneva Co., Alabama (MCZ 39979).

West Fork Choctawhatchee River, Dale Co., Alabama (MCZ 98159, 234057; OSUM 369; USNM 668077).

ECONFINA RIVER SYSTEM:

Econfina River, Bay Co. (OSUM 364, USNM 862554).

Elimia dickinsoni (Lea) Fig. 4A

Goniobasis dickinsoni Clench & Turner 1956: 141, pl. 2, fig. 10; [holotype: MCZ 191771; paratypes: MCZ 91771, USNM 673353 (15) (Fig. 4A); UMMZ and UF paratypes referred to by Clench and Turner (1956) not seen; type locality: Holmes Creek, 1 mile west of Graceville, Florida]. - Chambers, 1980: 65, figs. 1G, 6A-B (not 6C-D), 7A-B; 1982a: 113, fig. 1A-D (not C-D).
Elimia dickinsoni (Clench & Turner). - Burch & Tottenham, 1980: 136, fig. 359.

- Burch, 1982a: 35, fig. 359. - Thompson, 1984: 24, figs. 46-47.

REMARKS. Clench & Turner's (1956) description of this species remains sufficient and is not repeated here.

Within the Florida *Elimia*, smaller shells of *E. dickinsoni* can be difficult to distinguish from *E. curvicostata*. The outer lip of the shell aperture is usually more strongly sinuous in *E. dickinsoni*, and the base of the last whorl is less rounded, usually with some indication of an angle or carina. The base of the last whorl in larger shells of *E. curvicostata* is rounded with no hint of angulation.

Elimia dickinsoni can be distinguished from smooth forms of E. floridensis, which are allopatric, by the absence or reduced expression of spiral sculpture, which is more prominent and extends into relatively later whorls of the latter species.

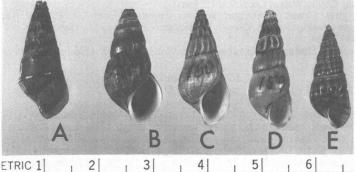


FIG. 4. Elimia dickinsoni (A) and Elimia curvicostata (B-E). A, E. dickinsoni, paratype (USNM 673353); B, Goniobasis elliotti; C, G. viennaensis, lectotype; D, G. doolyensis, lectotype; E, G. induta, lectotype. Scale is numbered in cm.

Elimia boykiniana has not been found sympatric with *E. dickinsoni*, although the two species are easily distinguished where they occur close to geographic contact by the presence of tubercles on the shells of *E. boykiniana*, which are absent in *E. dickinsoni*.

Elimia dickinsoni appears to be a distinct species, although chromosomal and isozyme evidence support a very close relationship with *E. floridensis*. The populations in the headwaters of the Chipola River that were attributed to *E. dickinsoni* by Clench & Turner (1956) are here considered to be *E. floridensis* based on their intergradation with highly sculptured forms of that species. *E. dickinsoni* is therefore confined to the headwater tributaries of the Choctawhatchee River. A very few shells (UF 1449) have small tubercles on earlier whorls that may represent introgression from *E. floridensis*. In the absence of stronger evidence for geographic intergradation with *E. floridensis*, the specific status of *E. dickinsoni* is retained. It cannot be ruled out that the populations of *E. dickinsoni*, as recognized here, in the Holmes Creek and Wrights Creek drainages are independently derived from *E. floridensis*.

Elimia dickinsoni has a high genetic identity $(I_N>0.9)$ with *E. floridensis* samples from the Chipola and Choctawhatchee River drainages (Chambers, 1980) and is karyotypically indistinguishable from *E. floridensis* from the Choctawhatchee drainage. This high genetic similarity indicates that if *E. dickinsoni* deserves specific status, its derivation from *E. floridensis* was relatively recent. Detailed genetic and morphological analysis of *Elimia* in the area of potential contact between these two species would be appropriate.

MATERIAL EXAMINED

CHOCTAWHATCHEE RIVER SYSTEM, Florida:

Holmes Creek Drainage: Holmes Creek, Washington Co. (UF 1451, USNM 745624), Jackson Co. (MCZ 191771, 94098; OSUM 14211 [part]; USNM 673353, 782345), Holmes Co. (MCZ 191773; OSUM 607, 12411).

Sandy Creek, Walton Co. (UF 4337 [part]);

Wrights Creek Drainage: Wrights Creek, Holmes Co. (USNM 782353); Hurricane Creek (=Tenmile Creek), Washington Co. (UF 1971), Holmes Co. (UF 1971, MCZ 191774).

Pea River Drainage: Limestone Creek, Walton Co. (UF 4336 [part], 4338 [part]).

Elimia boykiniana (Lea) Figs. 3C-D, 5-8

Melania boykiniana Lea 1840: 289 [lectotype, here designated and figured (Fig. 5), is not Lea's (1842a) figured specimen, which has a damaged outer lip: USNM 118428; paralectotypes (including Lea's probable figured specimen [Fig. 6A]): USNM 873106 (33); type-locality: Chattahoochee River, Columbus, Georgia]. - Lea, 1842a: 228, pl. 6, fig. 59; 1842b: 66, pl. 6, fig. 59. Brot 1862: 34.

Melania catenaria Lea 1840: 289. Preoccupied by Melania catenaria Say 1822.

- Melania catenoides Lea 1842a: 228, pl. 6, fig. 60 [syntypes: USNM 118429 (type collection) (Fig. 6C), USNM 118429 (5), USNM 118432 (17); type-locality: Chattahoochee River, Columbus Georgia; new name for Melania catenaria Lea, 1840]. 1842b: 66, pl. 6, fig. 60. Brot, 1862: 34.
- Melania modesta Lea 1845: 166 [holotype: USNM 119189 (type collection) (Fig. 6E); type-locality: Chattahoochee River, Columbus, Georgia]. Lea, 1848: 86, pl. 9, fig. 34. Reeve, 1860, pl. 41, species 297. Brot, 1862: 36.
- Elimia boykiniana (Lea). Chenu, 1859: 290, fig. 1978.

Elimia catenoides (Lea). - Chenu, 1859: 290, fig. 1982.

- Melania papillosa Anthony ms. Reeve 1861: pl. 59, species 467 [lectotype (shell and operculum), here selected and figured (Fig. 3C) is Reeve's figured specimen: BMNH, no number, Cuming Collection; paralectotype: BMNH, no number, (Fig. 3D), Cuming Collection; type-locality: Florida, but not Wekiva River, Enterprise (Clench & Turner, 1956) (see Remarks on the Synonymy); not Goniobasis papillosa 'Anthony,' Clench & Turner, 1956; MCZ 50233, labeled "cotypes" (Turner, 1946) are Elimia floridensis]. - Brot, 1862: 34.
- Goniobasis catenoides (Lea). Tryon, 1864: 26; 1873: 148, figs. 276-279. Clench & Turner, 1956: 134, pl. 3, fig. 8.
- Goniobasis boykiniana (Lea). Tryon, 1864: 26, 1873: 150, figs. 283-285. Clench & Turner, 1956: 132, not pl. 5, figs. 5-6, which are *Elimia floridensis*. Goodrich, 1935: 4; 1942: 3.
- Goniobasis papillosa (Anthony ms. Reeve). Tryon, 1864: 26; 1873: 151, figs. 287, 288, and (probably) 290, but not figs. 287a, 289, and 291.

Goniobasis modesta (Lea). - Tryon, 1864: 38.

- Goniobasis albanyensis Lea 1864: 4 [possible syntypes: USNM 118875 (3) (Fig. 6G) (see Remarks); type-locality: near Albany and Blue Springs, Baker Co., Georgia]; 1866: 140, pl. 23 fig. 49; 1867: 97, pl. 23, fig. 49. Clench & Turner, 1956: 139, pl. 3, fig. 6. Chambers, 1978: 158, figs. 3G-H; 1980: 65, fig. 1E.
- Goniobasis viridostriatis Lea 1864: 4 [lectotype, here designated and figured (Fig. 6H) is Lea's figured specimen: USNM 118413; paralectotypes: USNM 873107 (21): type-locality: Flint River, Georgia]. 1866: 140, pl. 23, fig. 48; 1967: 96, pl. 23, fig. 48.
- Goniobasis gesnerii Lea, 1868a: 151 [holotype: USNM 119134 (Fig. 6B); typelocality: Uchee River [Creek], Alabama]; 1868b: 330, pl. 54, fig. 5; 1869: 90, pl. 54 fig. 5.

Goniobasis boykiniana albanyensis (Lea). Goodrich, 1935: 4; 1942: 4.



FIG. 5. Two views of the lectotype of Elimia boykiniana.

Goniobasis athearni Clench & Turner 1956: 131, pl. 2 fig. 6 [holotype: MCZ 190102; paratypes: UF 1989 and MCZ 19076; type-locality: Chipola River, 2.5 miles south of Chason, Calhoun County, Florida]. - Chambers 1978: 158, fig. 3E-F; 1980: 65, fig. 1C.

Goniobasis sp. - Chambers, 1978: 158, figs. 2A-B, 3A-D.

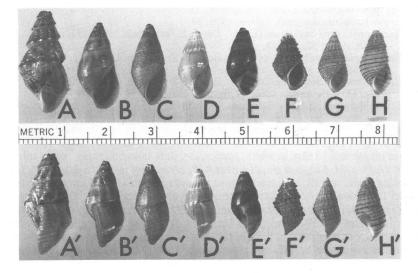


FIG. 6. Elimia boykiniana - apertural (normal letters) and side (primed letters) views of the same shells: A, Melania boykiniana, paralectotype and probably the shell figured by Lea; B, Goniobasis gesnerii, holotype; C, G. catenoides, syntype; D, E. boykiniana, labeled "Goniobasis viennaensis" (MCZ 98170); E, Melania modesta Lea 1845, holotype (outer lip damaged); F, G. athearni (USNM 524187); G, G. albanyensis, possible syntype; H, G. viridostriatis, lectotype (outer lip damaged). Scale is numbered in cm.

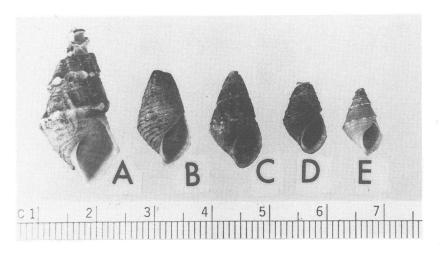


FIG. 7. Various forms of *Elimia boykiniana* in USNM lot 12090 from "Flint River, Georgia."

Oxytrema albanyensis (Lea). - Stein, 1976: 33. Oxytrema boykiniana (Lea). - Stein, 1976: 33. Oxytrema catenoides (Lea). - Stein, 1976: 34. Elimia boykiniana boykiniana (Lea). - Burch & Tottenham, 1980: 131, fig. 328.

- Burch, 1982a: 32, fig. 328. Burch, 1982a: J., Fig. 328.

Elimia boykiniana albanyensis (Lea). - Burch & Tottenham, 1980: 131. - Burch, 1982a: 32.

Elimia athearni (Clench and Turner). - Burch & Tottenham, 1980: 132. - Burch, 1982a: 33. - Thompson, 1984: 28, fig. 52.

Elimia albanyensis (Lea). - Thompson, 1984: 28, fig. 51.

DESCRIPTION. Shell elongate, reaching 15 mm in length and 10 mm in width in most populations, although occasionally very old individuals reach 27 mm in length and 13 mm in width, turriculate, thin, nonumbiculate, spire apical angle ranging 41-57°, but usually over 45°, consisting of up to 6 whorls, not counting apical whorls, which are almost always eroded away. Whorls above last whorl flat-sided to very slightly convex, with angled periphery. Growth lines opisthocyrt and crossing costae, when latter present. Axial sculpture of costae with tubercles where spiral cords intersect costae, or appearance of costae simulated by axially parallel lines of tubercles not actually connected by costae. Tubercles increase in height toward periphery. Base of last whorl straight to very slightly convex. Spiral cords of last whorl faint to strong, number 2-7 above periphery and 3-9 below periphery. Early whorls slightly convex or straightsided, with carinate periphery. Suture smooth to moderately impressed. Aperture ovate to elongate-ovate, length 0.42-0.53 of entire shell. Inner surface of last whorl, including parietal callus, glossy and clear to white and opaque. Outer lip of aperture straight to slightly concave. Color of periostracum yellow, green, or brown. Operculum chitinous and paucispiral.

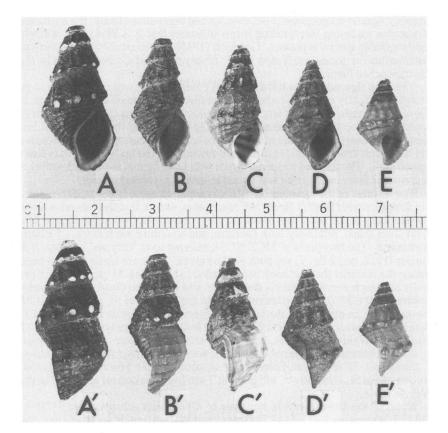


FIG. 8. Elimia boykiniana incorrectly labeled as "paratypes" of Goniobasis hallenbeckii (MCZ 186748); apertural (normal letters) and side (primed letters) views of the same shells. Scale is numbered in cm.

REMARKS ON THE SYNONYMY. Goodrich (1942) recognized many of the above synonyms as either synonyms or subspecies of *Goniobasis boykiniana*, although he also included names that are here referred to synonymies of other species. *Goniobasis athearni* and *Melania papillosa* represent the only new synonyms of *Elimia boykiniana* proposed here.

Elimia boykiniana exhibits extreme inter- and intrapopulation variation. The identification of synonyms of *E. boykiniana* is mainly based on two findings: (1) the constancy of the shape of the outer lip of the aperture in separating this species from *E. floridensis*, and (2) old MCZ and USNM lots, such as the type lot of *Melania boykiniana* and USNM 12090 (Fig. 7) that consist of shells exhibiting a range of variation that includes Clench & Turner's *Goniobasis boykiniana*, *G. albanyensis*, *G. athearni*, *G. catenoides*, and forms intermediate between them. Although the extremes in color and shell sculpture are striking and there is

probably significant geographic isolation among populations today, the existence of samples including intergrading forms indicates that it is likely that a single highly variable species is present. Goodrich (1935) also noted complex patterns of distribution for forms attributed to *G. albanyensis* and *G. boykiniana* in the Chattahoochee River.

The shell figured by Lea has a damaged outer lip. Growth lines appear to be straight or slightly concave, rather than the distinctly sigmoid condition seen in *Elimia floridensis*. To avoid any question about the state of this character in *E. boykiniana*, a lectotype was selected from the six shells of the type lot that had complete or nearly complete outer lips. The selected lectotype is more elongate and has much less-pronounced sculptural features on the body whorl than Lea's figured shell. The selected lectotype agrees with Lea's figured shell and description in sculptural features of earlier whorls and in having impressed sutures.

The features of the lectotype of Melania papillosa agree in color, dimensions, and sculpture with Reeve's figure and description, except that the tubercles along the periphery of the last whorl are slightly less prominent than in the figure. The souat shell shape, relatively long aperture, and sculpture are features of *Elimia* boykiniana. The two shells of MCZ 50234, referred to as "cotypes" by Clench & Turner (1956, pl., 2 fig. 9) are both E. floridensis. They are likely to have been among the material that Anthony had intended to be named M. papillosa, but the shells on which Reeve based his description and figure are clearly not the same species. Dall (1885) was also uncertain about the identity of *M. papillosa* and *M.* etowahensis Lea ms. Reeve, the latter being recognized here as a synonym of E. floridensis. Clench & Turner's (1956, p. 128) restriction of the type-locality of M. papillosa to Wekiva River [a St. Johns River tributary], Enterprise, Florida, must be rejected because the material on which it was based belongs to another species, E. floridensis. In any event, Enterprise is situated on Lake Monroe, an expanded portion of the St. Johns River, and is about 7 km from the nearest approach of the Wekiva River.

None of the three possible syntypes of Goniobasis albanyensis in USNM 118875 resembles Lea's (1875) figure, and all are much smaller than the dimensions given by him, although they might otherwise fit his brief description. These are the only lots collected by White (cited by Lea as the collector of the original material) found with the Lea Collection at USNM that could possibly be type material. Lea's figure portrays a larger shell with whorls that are more rounded than the possible syntypes and other material recognized under this name by Clench & Turner and subsequent workers. Lea also stated that the aperture is about two-thirds the length of the shell, while that proportion in the figure is less than one-half. The possible syntypes closely resemble shells figured in recent literature as examples of *Elimia albanyensis* (Clench & Turner, 1956; Chambers, 1978, 1980; Thompson, 1984). They also closely resemble the type material of G. viridostriatis. Given the uncertain status of Lea's figured specimen of G. albanyensis, those continuing to recognize taxonomic standing for these yellowish forms might consider using G. viridostriatis as the source of a name. Goodrich (1942) recognized the species-level identity of G. boykiniana, G. albanyensis, and G. viridostriatis by placing G. viridostriatis as a synonym of his G. boykiniana albanvensis.

Goniobasis gesnerii was recognized as a synonym of G. curvicostata by Clench & Turner (1956), but has been treated here as a synonym of Elimia boykiniana.

Although it is devoid of sculpture, as are most E. curvicostata, its spire angle, straight apertural lip, and relative aperture length place it with E. boykiniana. The type locality is described only as "Uchee River, Alabama." Uchee Creek has its source in Lee County, Alabama, and then flows through Russell County, Alabama.

COMPARATIVE REMARKS. *Elimia boykiniana* can be most easily distinguished from its sympatric congeners by its overall more squat shape and straight apertural lip. Characters that distinguish *E. boykiniana* and *E. floridensis* were discussed in detail in the remarks on the latter species.

Elimia boykiniana can usually be distinguished from *E. curvicostata* by the presence of spiral shell sculpture and the straight outer lip of the aperture (Figs. 3C'-D', 5-8). The latter species generally lacks tubercles and has a sinuous outer lip. *E. boykiniana* in the Flint River tributaries may be almost devoid of sculpture but can still be distinguished from *E. curvicostata* by the larger size of the aperture in relation to shell length.

Although *Elimia boykiniana* and *E. dickinsoni* have not been found in sympatry, they can most often be distinguished by the presence (in *E. boykiniana*) or absence (in *E. dickinsoni*) of spiral sculpture. Smooth forms of *E. boykiniana* can also be distinguish-ed from *E. dickinsoni* because *E. dickinsoni* is much like *E. floridensis* in the shell form and measurements that distinguish the latter species from *E. boykiniana*.

A major difficulty in understanding *Elimia boykiniana* has been its confusion with *Melania hallenbeckii*, here considered a synonym of *E. floridensis*. *Melania* (or *Goniobasis*) hallenbeckii has been considered a synonym of *Goniobasis* boykiniana by authorities from Brot (1862) and Tryon (1873) to Clench & Turner (1956). The confusion is understandable given the past emphasis on particular shell sculptural features that are similar in many *E. boykiniana* and *E. floridensis*. MCZ 186748 consists of 5 shells labelled "paratypes" of "*Goniobasis* hallenbeckii" are actually *E. boykiniana* (Fig. 8), which explains Clench & Turner's placement of the former species as a junior synonym of the latter.

GEOGRAPHIC DISTRIBUTION AND VARIATION. - *Elimia boykiniana* may be divided by geography and shell characters into the four major geographic divisions described below. Populations in each of these four major divisions are themselves variable and often geographically fragmented, but exhibit characteristics common to other members of their respective divisions.

(1) The Santa Fe River drainage populations formerly referred to *Goniobasis* athearni by Chambers (1980) and Thompson (1982a), plus snails from the Econfina (Taylor Co.), Wakulla, and the Ochlockonee river systems. The population of *Elimia boykiniana* in the Santa Fe River drainage, including the Ichetucknee River, has been referred to as *Goniobasis* sp. (Chambers, 1978), but was later provisionally referred to *Goniobasis athearni* (Chambers, 1980). The Santa Fe River drainage and Chipola River divisions share the same dark brown color, but the Chipola shells lack axial sculpture connecting their rows of tubercles, while costae are sometimes found on the Santa Fe River drainage shells. Although shells from the Santa Fe River drainage tend to have much sharper cords than the Chipola forms, they lack the extremely prominent peripheral cord of some of the Chipola shells.

(2) The upper Flint River tributary populations, formerly referred to Goniobasis viennaensis by Clench & Turner (1956) or *G. catenaria viennaensis* by

Goodrich (1942). The Flint River tributary forms appear much smoother than the others owing to their weaker shell sculpture.

(3) The Apalachicola, Chattahoochee, and lower Flint river populations formerly attributed to *Goniobasis boykiniana*, *G. albanyensis*, and *G. catenoides* by Clench & Turner. Some darker-colored shells from populations in this division resemble certain shells from the complex in the Chipola and Santa Fe River drainages. The finely-pointed tubercles and yellowish color of many of the Apalachicola-Chattahoochee River shells are lacking in the other divisions.

(4) The Chipola River drainage population, described by Clench & Turner (1956) and recognized by Chambers (1980) as *Goniobasis athearni*, plus a population in the Econfina River (Bay Co.).

Geographic gaps between the divisions (2-4) occupying the greater Apalachicola River drainage are difficult to interpret. They may be longstanding river segments of unsuitable habitat that formed natural barriers to gene flow, or they may be the result of more recently (approximately the last 150 years) degraded habitat that resulted from land clearing for agriculture and timber harvest (Clench & Turner, 1956). If these are artificial gaps, *Elimia* may have formerly existed in these gaps, but were uncommon or extirpated by the time that the earliest surviving collections were made.

The relative degrees of relationship among these divisions cannot be ascertained with the available data. For the present they are recognized as four groups of equal rank. If future work were to establish the specific or subspecific distinctness of any group included under *Elimia boykiniana*, it would most likely coincide with one or more of the gaps dividing these four divisions. Detailed electrophoretic study of populations within and among these divisions would be helpful in resolving relationships within this complex.

Thompson's (1982a, 1984) suggestion that the Santa Fe River drainage population is derived from an historical introduction of "Goniobasis athearni," presumably from the Chipola River, now seems less likely because Elimia boykiniana material from the Econfina (Taylor Co.), St. Marks, and Ochlockonee river systems reported here reduces the biogeographical and eliminates any morphological gap between samples from the Apalachicola and Suwannee river systems.

Electrophoretic data (Chambers 1978, 1980) are available for two populations formerly (Clench & Turner, 1956; Thompson, 1984) attributed to synonyms: *Goniobasis albanyensis* from the Apalachicola River and *G. athearni* from the Chipola River. In addition, the population of *Elimia boykiniana* from the Ichetucknee River, Suwannee River drainage, has been electrophoretically characterized. Genetic identities (I_N) range from 0.860 to 0.901 between these three samples, which averages greater than the average identities (range 0.716 to 0.770) between *E. floridensis* samples over the same geographic range from the Suwannee to the Chipola River. From this genetic comparison it is clear that, despite the greater distinctness of "forms" represented by *G. albanyensis* and *G. athearni*, these forms of *E. boykiniana* are less genetically divergent than populations of *Elimia floridensis*, as recognized by Clench & Turner (1956) and Thompson (1984), over the same geographic range.

Elimia boykiniana ranges from the Econfina River, Bay Co., Florida, to the Suwannee River drainage. To the west, somewhat smooth forms of *Elimia* in the Alabama River drainage may be related to this species. To the north, *Elimia* with

similar shells occur in the Altamaha river drainage on the Atlantic coast of Georgia. R.T. Dillon has sent me shells of *Elimia catenaria* Say from South Carolina and suggested that my *E. boykiniana* may be a synonym of *E. catenaria*. Although there is considerable merit in this suggestion, I decline to combine these Georgia and South Carolina populations with *E. boykiniana* at this time because they occur in major drainages for which genetic data are not available. The relationship between *E. catenaria* and *E. boykiniana* is probably close and would be a highly appropriate subject for detailed analysis of shell characters and genetic analysis.

Although the present synonymy may seem somewhat extreme to anyone who has used the classification recognized for the last 30 years, the present treatment of *Elimia boykiniana* is consistent with the general treatment accorded *E. floridensis* and *Elimia curvicostata* by Clench & Turner (1956) and in the present revision. Each case represents a relatively widespread, highly variable species that each comprises allopatric populations that differ in some degree from neighboring populations.

MATERIAL EXAMINED

SUWANNEE RIVER SYSTEM, Florida:

Santa Fe River Drainage: Santa Fe River, Columbia Co. (UF 28202); Ichetucknee River, Columbia Co. (UF 24885: OSUM 336, 337, 11713).

ECONFINA RIVER SYSTEM, Taylor Co., Florida: Econfina River (ANSP 7886, 267623 [part]).

ST. MARKS RIVER SYSTEM, Wakulla Co., Florida: Wakulla River (ANSP 267623 [part]).

OCHLOCKONEE RIVER SYSTEM, Gadsen Co., Florida: Ochlockonee River (UF 4349).

APALACHICOLA RIVER SYSTEM:

Apalachicola River, Florida: Libert Co. (OSUM 1387), Gadsen Co. (ANSP 353844; UF 4307, 24886; MCZ 186723, 190405, 191567; USNM 809636).

Chipola River Drainage, Florida: Chipola River, Calhoun Co. (UF 1049 [part], 1986 [part], 1989, 4947 [part]; MCZ 19076, 190076, 190102, 190423; OSUM 8002); Chipola River, Jackson Co. (ANSP 151264, 154985; UF 4290, 24887; MCZ 190076, 91721, 19721, 190075, 190077, 190423, 190424, 190102, 190423, 190424, 191571; OSUM 269, 318, 12387; USNM 524187); Creek, 2.5 miles NNW Sink Creek, Jackson Co. (MCZ 190074); Spring Creek, Jackson Co. (ANSP 151503, 219068, 319711; UF 30094, 30095 [part]; MCZ 289485; OSUM 12400; USNM 405610 [part], 809635); Merrits Mill Pond, Jackson Co. (UF 1590 [part], 1976); Big Creek, Jackson Co. (ANSP 194658 [part]).

Flint River Drainage, Georgia: Flint River (USNM 118413, 873107); Flint River, Decatur Co. (UF 228, 1993), Baker Co. (ANSP 177076, 91731), Dougherty Co. (ANSP 151276, 219175 [part]; UF 29619, 31268; MCZ 66720, 91727-91731; USNM 158668), Pike Co. (OSUM 255, 288, 370), "Georgia" (USNM 12090, 118413); Spring Creek, Seminole Co. (UF 227; MCZ 190067, 191570; USNM 656577 [part]); near Albany and Blue Springs, Baker Co. (USNM 118875); Chickasawhatchee River, Baker Co. (UF 29617, 31237); Spring Creek, Decatur Co. (UF 217a [part]); Abrams Creek, Worth Co. (ANSP 163064; MCZ 98155); Mill Creek, Worth Co. (ANSP 163064; MCZ 98155); Lee's Creek, Lee Co. (ANSP 151510; UF 9141; USNM 405536); Swift Creek, Crisp Co. (ANSP 151509; MCZ 91761; USNM 405537); Cedar

Creek, Crisp Co. (ANSP 151526; MCZ 91759); tributary 1 mile E of De Soto, Sumter Co. (USNM 603988); North Fork Pennahatchee Creek, Dooly Co. (ANSP 151274; MCZ 91760); Potato Creek, Upson Co. (OSUM 374); "Flint River tributary" (MCZ 98170).

Chattahoochee River Drainage: Chattahoochee River, Muscogee Co., Georgia (MCZ 1465, 87977, 103606, 103608, 186747-186749; OSUM 371-373; USNM 118428), Troup Co., Georgia (MCZ 218147), Cobb Co., Georgia (OSUM 1002); Howard Creek, Houston Co., Alabama (UF 204, 29618); Uchee Creek, Russell Co., Alabama (MCZ 91732, 218126; USNM 56991, 119134); Little Uchee Creek, Russell Co., Alabama (USNM 56990, 118403, 118405, 119819); Randall Creek, Muscogee Co., Georgia (MCZ 186748, USNM 118406 [part]); Ossahatchie Creek, Mulberry Creek drainage, Harris Co., Georgia (OSUM 302); Flat Shoal Creek, Harris Co., Georgia (UF 25467); "Columbus, Georgia" (USNM 12089 [part], 118428, 118429, 118430, 118432, 119139, 119330, 873106); "Chattahoochee River, Georgia" (USNM 59025, 59128, 118427).

ECONFINA RIVER SYSTEM:

Econfina River, Bay Co. (UF 29438; USNM 862599).

Elimia curvicostata (Reeve) Figs. 4B-E

- Melania curvicostata Anthony ms. Reeve 1861: pl. 58, species 462 [type, in Cuming Collection according to Reeve, not found; type-locality: Florida]. -Brot, 1862: 35.
- Melania densicostata Reeve 1861: pl. 58, species 465 [type, in Cuming Collection according to Reeve, not found; type-locality: Florida].

Melania densecostata [sic] Reeve. - Brot, 1862: 35.

- Goniobasis etowahensis Lea 1862a: 264 (not Melania etowahensis Lea ms. Reeve 1861; renamed Goniobasis canbyi Lea, 1864 - see entry for that name below); 1862b: 299, pl. 37, fig. 133; 1863: 121, pl. 37, fig. 133.
- Goniobasis doolyensis Lea 1862a: 266 [lectotype, here designated and figured (Fig. 4D), is the shell figured by Lea: USNM 119121; paralectotypes: USNM 873108 (32), USNM 873109 (15); type-locality: here restricted to near Vienna, Dooly Co., Georgia, in a small tributary of the Flint River, which is the locality of the lectotype and which along with "Tennessee" was given by Lea (1862a) as the source of his material]; 1862b: 315, pl. 37, fig. 159; 1863: 137, pl. 37, fig. 159. Tryon, 1864: 32; 1873: 187, figs. 366-367.
- Goniobasis viennaensis Lea 1862a: 267 [lectotype, here designated and figured (Fig. 4C), is the shell figured by Lea: USNM 118743; paralectotypes: USNM 873110 (2); type-locality: small stream tributary to the Flint River, Dooly Co., Georgia, here restricted to Pennahatchee Creek near Vienna, Dooly Co., Georgia (Clench & Turner's 1956 restriction of the type locality was based on *E. boykiniana* material from Pennahatchee Creek, possibly the same locality].
 Lea, 1862b: 315, pl. 37, fig. 160; 1863: 137, pl. 37, fig. 160. Tryon 1864: 31; 1873: 184, fig. 359. Clench & Turner, 1956: 135, not pl. 5, figs. 7-8.
- Goniobasis induta Lea 1862a: 267 [lectotype, here designated and figured (Fig. 4E), is the shell figured by Lea: USNM 119174; paralectotypes: USNM 873111 (41); type-locality: near Vienna, Dooly County, Georgia]; 1862b: 319, pl. 37 fig. 166; 1863: 141, pl. 37, fig. 166. Tryon 1864: 30. Goodrich, 1942: 5.
- Goniobasis ucheensis Lea 1862a: 270 [lectotype, here designated is the shell figured by Lea: USNM 119259; paralectotypes: USNM 873114 (26); type-

locality: Little Uchee River [Creek], Alabama, near Columbus, Georgia]; 1862b: 334, pl. 38, fig. 194; 1863: 156, pl. 38, fig. 194. - Goodrich, 1942: 4.

- Goniobasis inosculata Lea 1862a: 270 [lectotype, here designated, is the shell figured by Lea: USNM 119177; paralectotypes: USNM 873115 (7); type-locality: Little Uchee River [Creek], Alabama, near Columbus, Georgia]; 1862b: 334, pl. 38, fig. 195; 1863: 156, pl. 38, fig. 195. Tryon, 1873: 266 (treated as a synonym of Goniobasis pallescens [Lea, 1845], but later [p. 302] mistakenly discussed Goniobasis osculata Lea, 1862 under this same name).
- Goniobasis elliotti Lea 1862a: 271 [lectotype, here designated and figured (Fig. 4B), is the shell figured by Lea: USNM 119122; paralectotypes: USNM 873112 (4), USNM 873113 (10); type-locality: here restricted to Little Uchee River [Creek], Alabama, the locality on the label of the lectotype]; 1862b: 338, pl. 38, fig. 201; 1863: 160, pl. 38, fig. 201. Tryon, 1873: 265, fig. 509.
- Goniobasis canbyi Lea 1864: 3 footnote [holotype is Lea's (1863) figured specimen for his original Goniobasis etowahensis Lea, 1862 (see Remarks): USNM 121479; type-locality: Etowah River, Georgia; not Goniobasis canbyi Lea, 1862a: 271, not of Tryon, 1873: 260]; 1862b: 299, pl. 37, fig. 133 (as Goniobasis etowahensis Lea, 1862); 1863: 121, pl. 37, fig. 133 (as Goniobasis etowahensis Lea, 1862). - Tryon, 1873: 260, fig. 500.
- Goniobasis curvicostata (Reeve). Tryon, 1864: 34; 1873: 202, figs. 396-397. -Goodrich, 1935: 4; 1942: 4. - Clench & Turner, 1956: 136, pl. 2, figs. 4-5. -Chambers, 1980: 65, fig. 1D.
- Goniobasis boykiniana viennaensis (Lea). Goodrich, 1935: 4; 1942: 4.
- Elimia ucheensis (Lea). Burch & Tottenham, 1980: 131, fig. 346. Burch, 1982a: 32, fig. 346.
- *Elimia curvicostata* (Reeve). Burch & Tottenham, 1980: 136, fig. 358. Burch 1982a: 35, fig. 358. Thompson, 1984: 26, figs. 48-49.
- Elimia induta (Lea). Burch & Tottenham, 1980: 136. Burch, 1982a: 35.

REMARKS. Despite some changes from Clench & Turner's synonymy for this species, their concept of the species has not been altered by subsequent work. Their description remains sufficient and is not repeated here.

Elimia curvicostata generally has a more slender-spired shell than its sympatric congeners. It lacks the tubercled shell sculpture found in most *E. floridensis* and *E. boykiniana*, although some populations include individuals with a peripheral carina. *Elimia curvicostata* has more deeply rounded whorls, especially the base of the body whorl, than *E. floridensis*, *E. dickinsoni*, or *E. boykiniana*.

New synonyms for *Elimia curvicostata* include *Goniobasis etowahensis* Lea 1862, *Goniobasis inosculata* Lea, *Goniobasis viennaensis* Lea (accorded species rank by Clench & Turner [1956]), and *Goniobasis canbyi* Lea 1864 (considered a synonym of *Goniobasis floridensis* by Clench & Turner [1956]).

Two of Clench & Turner's (1956) synonyms for their Goniobasis curvicostata are here treated as synonyms of other species: Goniobasis inclinans Lea and Goniobasis gesnerii Lea are now synonyms of Elimia floridensis and E. boykiniana, respectively.

I examined lots (MCZ 91754, 91755, 91759-91761, 98170) identified by Clench & Turner (1956) as *Goniobasis viennaensis* and on that basis had been prepared to recognize that name as a synonym of *G. boykiniana*. However, the smooth shells, sigmoid apertural lips, and relatively short apertures of shells in the type lot (USNM 118743) of *G. viennaensis* place it with *Elimia curvicostata*. Clench & Turner's MCZ material is different and is here recognized as E. boykiniana.

Lea (1864: 3) transferred the name *canbyi* to his *Goniobasis etowahensis* Lea 1862 because the latter name was preoccupied by Reeve (1861), and he considered his original *canbyi* and Reeve's *etowahensis* to be identical. The latter two names are here treated as synonyms of *Elimia floridensis*.

The Etowah River type locality of *Goniobasis canbyi* may be in error because, as discussed earlier under *Elimia floridensis*, Postell is cited as the source of Lea's material.

Electrophoretic data (Chambers, 1980) indicate that *Elimia curvicostata* is genetically closer to *E. floridensis* (I_N ranges 0.380 to 0.575) than to *E. boykiniana* (I_N ranges 0.263 to 0.367), but is greatly divergent from both.

The eastern limit of this species is the Apalachicola River drainage, and no Florida forms east of that limit appear to be closely related. The western limit is the Escambia River. The relationship of *Elimia curvicostata* to *Elimia* with similarly smooth shells in the Alabama River drainage deserves investigation.

DISTRIBUTION. The Apalachicola, Choctawhatchee, Yellow, and Escambia river systems of Alabama, Georgia, and Florida. Detailed geographical records are given by Clench and Turner (1956).

DISCUSSION

Apparent convergent or parallel evolution in shell sculpture in Florida *Elimia*, along with extensive sympatry (Fig. 1) and great intraspecific variation, has caused the long-standing confusion of forms here attributed to *Elimia boykiniana* and *Elimia floridensis*. The confusion has been especially great over populations in the Chattahoochee River drainage, where both species exhibit extreme degrees of intraspecific variation. A particularly demonstrative indication of the degree to which these taxa may be considered sibling species is the presence of shells of both species in the previously recognized type material of *Melania hallenbeckii* Lea, a synonym of *E. floridensis*. Complete shells of these two species can now be separated by the shape of the apertural lip and, usually, by shell dimensions. Particular shell sculptural characters are of importance in distinguishing the species only within certain portions of their common ranges.

Comparisons of the present classification with that of Clench & Turner (1956), which was substantially followed by Thompson (1984), and with Burch's (1982a) modification of Goodrich's (1942) classification are presented in Tables 2 and 3. The present study recognizes four species, while Burch (1982a) and Clench & Turner (1956) each recognized 10. As discussed in the remarks on *Elimia boykiniana* and *E. floridensis*, each of these two species, as recognized here, may be a composite of more than one species, but current evidence does not support recognizion of more species. The equivalence of names recognized here to those recognized in two previous treatments is presented in Table 2.

The groupings of related species according to the views of Burch (1982a) and Clench & Turner (1956) are compared in Table 3. The Burch classification is the more similar to the present classification. Both of the previous classifications place elements of *Elimia floridensis* and *E. boykiniana* in more than one group. Burch's *E. boykiniana* group encompasses many of the names here recognized

TABLE 2. Equivalence of names applied to Florida *Elimia* populations in past classifications to the four species recognized in this paper. The Burch classification is that of Goodrich (1942) as modified by Burch (1982a). The Clench & Turner (1956) classification is followed by Thompson (1984). Exact equivalence of names between the Burch and the Clench & Turner classifications is not implied.

Burch (1982a)	Present	Clench & Turner (1956)
Elimia floridensis E. catenaria vanhyningiana E. catenaria inclinans	Elimia floridensis	Goniobasis floridensis G. vanhyningiana G. clenchi
E. dickinsoni	E. dickinsoni	E. dickinsoni
E. boykiniana boykiniana E. boykiniana albanyensis E. boykiniana viennaensis E. clenchi E. athearni	E. boykiniana	G. boykiniana G. albanyensis G. catenoides G. athearni
E. curvicostata E. ucheensis E. induta	E. curvicostata	G. curvicostata G. viennaensis

TABLE 3. Relationships of Florida *Elimia* taxa recognized in the classification of Goodrich (1942) as modified by Burch (1982a) and Clench & Turner (1956). Capital letters refer to species groupings recognized in the present paper: F= group including *E. floridensis* and *E. dickinsoni*; B= *E. boykiniana*; C= *E. curvicostata*.

Burch (1982)	Clench & Turner (1956) Group 1:	
E. boykiniana group:		
E. boykiniana boykiniana: B	G. boykiniana: B	
E. boykiniana albanyensis: B	G. athearni: B	
E. boykiniana viennaensis. C	G. floridensis: F	
E. ucheensis: C	G. vanhyningiana: F	
E. clenchi: F	, ₀	
	Group 2:	
E. catenaria group:	G. curvicostata: C	
E. athearni: B	G. viennaensis: C	
E. catenaria inclinans: F	G. catenoides: B	
E. catenaria vanhyningiana: F	G. albanyensis: B	
E. floridensis: F	G. clenchi: F	
	G. dickinsoni: F	
E. carinocostata group:		
E. curvicostata: C		
E. induta: C		
E. dickinsoni: F		

under *E. boykiniana*, although it contains *E. clenchi*, which is only distantly related, and *E. ucheensis*. *Elimia ucheensis* is treated here, with some uncertainty, as a synonym of *E. curvicostata*. Burch's *E. catenaria* group, except for *E. athearni*, corresponds to the present *E. floridensis*. Burch's *E. curvicostata* group corresponds to *E. curvicostata* recognized here, except that *E. dickinsoni* belongs with *E. floridensis*.

The groups attributed to Clench & Turner (1956) in Table 3 were inferred from an examination of their discussions of individual species. Except for *Goniobasis vanhyningiana*, their classification appears to be based mainly on the presence (group 1) or absence (group 2) of spiral sculpture. Axial sculpture is found in both groups. Group 1 contains elements of both *Elimia floridensis* and *E. boykiniana*, while group 2 contains members of all three groups recognized in the present classification.

Several taxa included in the present revision have been mentioned as likely to be extinct or require recognition as species needing conservation efforts. Goniobasis boykiniana and G. catenoides were considered likely to be extinct by Clench & Turner (1956), a conclusion accepted by Stein (1976) and (for G. catenoides) Opler (1977). These names are here considered synonyms under Elimia boykiniana, along with other names that have been applied to extant populations. Applying the expanded view of *Elimia boykiniana* presented here, this species is not extinct, although it has declined and the entire species should still be given consideration for possible protective status. These include populations until now known as "Goniobasis viennaensis," which has been suggested as a candidate for protection by Thompson (1974), in the Flint River. Thompson (1974) and Stein (1976) suggested that Goniobasis albanyensis receive protection, and that taxon has been included by the U.S. Fish and Wildlife Service in its review of invertebrate wildlife (1984) as a species that may qualify for protective status under the Endangered Species Act of 1973, as amended. It remains to be demonstrated that the phenotypes formerly associated with the names G. viennaensis and G. albanyensis are distinct enough throughout their ranges to deserve recognition as subspecies; Goodrich's (1935) concerns about their distinctiveness remain unresolved.

Gonibasis clenchi (here considered a synonym of Elimia floridensis) has been identified as a species of special concern in Florida (Thompson, 1982b). The relationships between the types and populations characterized by shells with flush sutures (Chambers, 1982b) must be determined before subspecific rank can be considered for populations formerly recognized as *G. clenchi*.

Although it may seem lamentable that taxa suggested for protective status have been reduced to synonymy, resolution of certain questions concerning their taxonomy would have been necessary in any case before the need for protective status could be determined. Biologically-based taxonomy will, in the long run, contribute to preservation of biological diversity by either clearly identifying taxa deserving protection or by providing a solid framework that can help identify the crucial investigations required for the naming and geographic restriction of taxa.

The implications of recognizing subspecies in the above cases should be very carefully considered. If subspecies are recognized in these cases, consistent treatment of equally distinct forms elsewhere would result in a number of additional recognized subspecies of both *Elimia floridensis* and *E. boykiniana*. Some of these subspecies would require the introduction of new names. Although

one may be tempted to retain such familiar names as *Elimia clenchi, E. athearni*, and *E. albanyensis* by applying them to subspecies, there is not enough information on variation within and among such presumptive taxa to support their recognition at this time. Proponents of subspecific taxa will need to describe this variation, evaluate and define boundaries between subspecies, which may involve zones of intergradation between forms, and in particular cases address the significance of intergradation between forms evident in old lots (*e.g.*, those portrayed in Fig. 7).

The present classification appears to be the most consistent with the available data. Its most satisfying feature is the application to *Elimia boykiniana* of the same inclusive species concept that has been previously used (Clench & Turner, 1956; Thompson, 1984) to unite highly variable forms in both *Elimia floridensis* and *Elimia curvicosta*. The taxonomic treatment of the populations attributed to these three species in the same general geographic area is now consistent. It is hoped that the simplified structure of this classification will not inhibit continuing investigation of variation within the recognized species, which are more likely to be found to be too inclusive rather than not inclusive enough.

ACKNOWLEDGEMENTS

I thank the following curators and their staffs for access to the collections under their supervision: J. Rosewater (National Museum of Natural History), K. Boss (MCZ), F.G. Thompson (UF), J.B. Burch (UMMZ), and G.M. Davis (ANSP). I am very grateful to Dr. N.J. Evans for his efforts to locate Reeve's types at the BMNH and thank him and BMNH for the loan of material. I also thank K. Boss for advice on some specific nomenclatural problems and for the loan of MCZ material. I have benefited greatly from discussions of molluscan nomenclature, particularly that of Isaac Lea, with James D. Williams and the late Joseph Rosewater. Comments from R.T. Dillon and anonymous reviewers were of considerable value in the preparation of the final manuscript.

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Walkerana, 1990, 4(12): 271-277

A STRATIGRAPHIC STUDY OF MOLLUSKS IN LAKE MANITOBA SEDIMENT

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ABSTRACT: Two sediment cores, spanning 12,000 and 2500 yr B.P., respectively, were obtained from the south basin of Lake Manitoba. Mollusc remains were present throughout most of the long core, although in the section representing 12,000-9,000 yr B.P. shells were sparse and represented few species. Periods of low water levels in Lake Manitoba were characterized by increased abundance of fossil lymnaeids. *Pseudosuccinea columella*, once common in the sediments, now no longer occurs in central Canada. During the last 4500 yr molluscan assemblages in the sediments have been similar to modern death assemblages in the lake.

KEY WORDS - Freshwater molluscs, Lake Manitoba, sediment cores.

INTRODUCTION

Present day Lake Manitoba, located in central Canada, has a surface area of 4700 km² and is the 13th largest lake in North America (Last, 1984). The lake is a remnant of glacial Lake Agassiz, a large deep water body whose sediments are distributed over a 950,000 km area (Teller *et al.*, 1983). The sediments were deposited as the Wisconsinan glacier retreated to the north, impounding meltwater between itself and the elevated lands to the south. By some time after 12,000 yr B.P., the glacier had uncovered the south basin of Lake Manitoba (Teller & Last, 1981). Subsequently, the water level fluctuated extensively due to climatic variation, differential isostatic rebound and the blockage and opening of various outlets; however in early stages the water level was almost 200 m higher than the present level of Lake Manitoba (Elson, 1967). The postglacial history of Lake Manitoba has been described in detail by Teller & Last (1981).

Today the south basin of Lake Manitoba covers an area of 3250 km² but has mean and maximum depths of only 4.5 and 6.3 m respectively. The lake is eutrophic with a high total dissolved solid content (up to 3200 mg/1) (Last, 1984) and supports a highly diverse molluscan fauna (Table 1).

The fluctuations in size, water chemistry and thermal regimes of the lake over time bring into question the nature of the aquatic communities at different times of the lake's history. Molluscan remains offer useful evidence, even though they are admittedly highly biased in favor of smaller shells and their abundance and species composition is dependent on a variety of taphonomic factors (Pip, 1988). Aside from an assemblage at a single level in southern Manitoba reported by Teller (1989), stratigraphic studies of molluscs have not been carried out in Manitoba, although data are available for the southern part of Lake Agassiz in Minnesota (Ashworth *et al.*, 1972) and Ontario (Zoltai, 1969) and basins to the east (Lake Superior (Zoltai & Herrington, 1966; Teller & Mahnic, 1988), Lake Huron (Miller *et al.*, 1979; 1985), and Gatineau and Ottawa Valleys (Bickel, 1970)).

TABLE 1. Species which presently occur in Lake Manitoba.

Valvata tricarinata (Say 1817) Amnicola limosa (Say 1817) Probythinella lacustris (Baker 1928) Lymnaea stagnalis Linné 1758 Stagnicola elodes (Say 1821) Stagnicola catascopium (Say 1817) Fossaria modicella (Say 1825) Fossaria decampi (Streng, 1896) Helisoma trivolvis (Say 1816) Helisoma anceps (Menke 1830) Gyraulus parvus (Say 1817) Planorbula armigera (Say 1821) Promenetus exacuous (Say 1821) Armiger crista (Linné 1758) Physa gyrina Say 1821 Aplexa hypnorum (Linné 1758) Ferrissia rivularis (Say 1817) Sphaerium striatinum (Lamarck 1818) Pisidium casertanum (Poli 1795) Pisidium compressum Prime 1852 Pisidium lilljeborgi Clessin 1886 Pisidium variabile Prime 1852 Anodonta grandis Say 1829 Lampsilis radiata siliquoidea (Barnes 1823)

During the winters of 1978 and 1979, Teller & Last (1981) collected cores from the south basin of Lake Manitoba and described their physical,mineralogical and chemical characteristics (Teller & Last, 1981, 1982; Last & Teller, 1983). A palynological study of selected cores was conducted by Nambudiri & Shay (1986). However only a single core (D1), 13.5 m long and taken from the center of the south basin, represents a continuous sequence from glacial time to the present. Shells have been well preserved throughout the core, partly due to the fine textured sediments (silty clay and clayey silt) and the large amounts of carbonate minerals (up to >50%), which resulted in reduced dissolution and abrasion rates of shell material.

MATERIALS AND METHODS

Core D1 was collected in the center of the south basin of Lake Manitoba using a hollow-stem augering system mounted on a Bombardier on winter ice (Teller & Last, 1981). This system yielded a continuous core 13.5 m long and 7.3 cm in diameter. The core was bisected longitudinally and sections of one of these halves were removed at 42 intervals along the core (Table 2). The other half was reserved for the mineralogical and palynological studies cited above. An additional core 1.3 m long was obtained using a modified Livingstone piston corer (Teller & Last, 1981). The samples were wet-sieved through a 0.5 mm mesh screen and shells and shell fragments were retained for study.

Molluscs in Lake Manitoba Sediment

TABLE 2. Species found in core D-1.

Sampl no.	le Depth (cm.)	Age (yr. B.P.)	Valvata tricarinata	Probythinella lacustris	Amnicola limosa	Fossaria modicella	Stagnicola elodes	Lymnaea stagnalis	Pseudosuccinea columella	Gyraulus circumstriatus	Sphaerium striatinum	Pisidium spp.
1	19-30		+	+	_	+	+	_			+	+
2	30-39		+	+	-	+	+	+	-	_	-	+
3	. 39-47		+	+	-	+	-	-	-	_		+
4	67-82	2200	+	+	+	+	+	-				+
5	109-116	2200	+	+	+	+				-		+
6	122-132	2500	+	+		+		-			-	
7	152-162	2500	ст -	+	Ē	т -	-	-	-	-		+
8	210-220		-	+	-	-		-	-	-	+	+
9	220-229			- -	-	-			-	-	-	-
10	264-272		-		-	-	-	-	-	-	-	+
11	289-295		-	+	+	-	-	-	-	-	-	+
12	300-313	4500		-	-	-	+	-	-	-	-	+
12	333-351	4300	+	-	-	-	-	-	-	-	+	+
13	381-400		-	+	-	-	-	-	-	-	-	-
14	404-423		-	+	+	-	-	-	-	-	+	-
			-	-	-	-	-	-	-		+	-
16	442-453		-	+	+	-	-		-	-	-	+
17	468-485		+	-	+	-	-	-	-	-	+	-
18	503-510	-	+	-	-	-	-		-	-	-	+
19	534-549	7000	-	-	-	-	100	-	-	-	$(-1)^{-1}$	-
20	580-590		-	-	-	-		-	-	-	-	-
21	608-619		-	-	-	-	-	-	-1	-	-	-
22	630-647		-	- 1	-	-	-	-	\sim	-	-	+
23	663-670		-	-	-	-	-	-	-	-	-	+
24	688-698	8000	-	-	-	-	-	-	-	-	-	+
25	737-744		-	-	-	+	+	-	-	+	-	-
26	747-758		-	-	-	+	-	-	-	-	-	+
27	786-804	9000	-	-	-	+	-	-	+	-	-	-
28	869-881		-		-	+	-	-	-	-	-	-
29	902-913		-	-	-	-	-	-	-	-	-	-
30	918-926		-	-	-	-	-	-	-	-	-	-
31	948-958	10,000	-	-	-	-	-	-	-	-	-	-
32	974-988		-	-	-	-	-	-	-	-	-	-
33	1001-1009	11,000	-	-	-	-	-	-	-	-	-	+
34	1029-1036	,	-	-	-	-	-	-	-	-	_	-
35	1052-1063		-	-	-	-	-					+
36	1079-1089		-	-								+
37	1116-1132						÷.					+
38	1154-1165				1		-	-			-	- -
39	1234-1242		_				-	-	-	_	-	+
40	1270-1282		+	63 7 .	-	-	-	-	-	-	-	т
40	1295-1308*		Ŧ	-	-	-	-	-	-	-	+	-
41	1330-1340	12,000										
42	1550-1540	12,000	-	-	-	-	-	-	-	-	-	-
							_					

* small shell fragments only

Radiocarbon dates for selected sections of the cores (Teller & Last, 1981) were corrected according to the technique of Nambudiri *et al.* (1980).

Voucher specimens are in the National Museum of Natural Sciences, Ottawa, Canada.

RESULTS AND DISCUSSION

The results from core D-1 are shown in Table 2. The core spanned approximately 12,000 years. As expected from differential attrition rates of modern shells in Lake Manitoba (Pip, 1988), small species and juveniles of larger forms were preferentially preserved. *Pisidium* spp. were grouped as a single unit, since in many cases shells were sparse and not intact, precluding specific determination. Where shells were intact, these were primarily *P. casertanum*, but *P. compressum*, *P. lilljeborgi* and *P. variabile* were seen as well.

Mollusc shells were substantially more abundant in the upper third of the core, although zones rich in remains occurred in other portions, notably at 7-8 m. While some of the increased shell densities undoubtedly reflected higher community productivity, the temptation toward quantitative comparisons was avoided in view of other factors, such as differential attrition and variable water chemistry at different times, different depositional conditions as water depth and distance from shore varied at the specific location in question, and the problem of shell fragments which represented an unknown number of individuals in a given sample.

Small fragments of shells were already present at the 13 m level (sample 41), even though at this time Lake Agassiz was cold and turbid, as high sedimentation rates resulted from material brought by rivers from the newly deglaciated prairies to the west (Teller and Last, 1981). By about 11,000 yr B.P., as the Late Wisconsinian ice continued to retreat, water levels dropped as much of Lake Agassiz drained into Lake Superior when a series of outlets emerged to the east (Teller & Mahnic, 1988), but about 9900 yr ago the lake rose again to more than 80 m over the Lake Manitoba basin (Teller & Last, 1981). During the period represented by much of the first 3000 yr shells were sparse in the sediment core and were composed almost entirely of sphaeriids, except for a single *Valvata tricarinata* at the 12.7-12.8 m level. However in the southern part of Lake Agassiz in northwestern Minnesota, which had been uncovered by glaciers about 1500 yr earlier than the Lake Manitoba basin, during 11,000-9900 B.P. a variety of other, shallow water species was also present in addition to the above taxa (Ashworth *et al.*, 1972).

The occurrence of Valvata tricarinata as well as certain other species in many early postglacial sediments has prompted their interpretation by some workers as indicators of cooler climate. However Ouellet (1975) has shown that no correlations exist between stratigraphic distributions of V. tricarinata and pollen profiles, and Pip (in press) has shown that at present this species does not frequent waters of mean monthly temperatures that are significantly different from those of other species in central Canada.

By approximately 9200 yr ago, eastern outlets into Lake Superior caused Lake Agassiz to disappear from southern Manitoba, and low water levels are believed to have prevailed throughout much of the south basin of Lake Manitoba (Teller & Last, 1981). The pollen record suggests that at this time the climate became increasingly warm and dry (Nambudiri & Shay, 1986). These observations are supported by the appearance in the core of the lymnaeids *Fossaria modicella*,

Molluscs in Lake Manitoba Sediment

Stagnicola elodes and Pseudosuccinea columella, and also Gyraulus circumstriatus, all of these species being indicative of shallow-water conditions and abundant aquatic vegetation. The core also contained numerous Carex seeds (Cyperaceae) at just > 8000 yr B.P. (sample 25), coinciding with peaks in Cyperaceae and Typha pollen abundance reported from this region of core D1 by Nambudiri & Shay (1986).

Pseudosuccinea columella has been previously reported from a lagoonal environment behind the west beach of Lake Agassiz from material dated at ca. 9500 yr B.P., together with Valvata sincera helicoidea, Helisoma anceps, Gyraulus circumstriatus, Fossaria exigua, Succinea avara, Anodonta grandis and Pisidium nitidum (see Teller, 1989). It is interesting that at this time P. columella was present in the Lake Agassiz basin; it is now considered extinct in Manitoba (Pip, 1985) and was not found in a survey of the Canadian Interior Basin by Clarke (1973), although it has been reported from a number of postglacial sediments in North America (see La Rocque, 1968). Valvata sincera has been also reported from Lake Agassiz sediments 11,000-9900 yr B.P. in Minnesota (Ashworth et al., 1972) and Ontario (Zoltai, 1969; Nielsen et al., 1982), as well as in Great Lakes

Sample no.	Depth (cm.)	Valvata tricarinata	Probythinella lacustris	Amnicola limosa	Marstonia gelida	Fossaria modicella	Stagnicola elodes	Sphaerium striatinum	Pisidium casertanum	Pisidium compressum
1	0-8.5	+	_	-	-	+	-	-	+	-
1 2 3 4 5 6 7 8	8.5-16.9	+	-	+	-	+	+	-	+	+
3	25.0-30.5	+	-	+	-	-	+		+	-
4	30.5-33.9	+	-	-	-	+	+	-	+	+
5	33.9-39.0	+	+	-	-	+	+	_	+	-
6	39.0-45.8	+	+	+	-	+	+	-	+	-
7	45.8-50.8	+	-	-	-	-	+	-	+	-
8	50.8-59.3	+	+	+	+	-	+	+	+	-
9	59.3-64.4	+	+	+	-	+	+	-	+	-
10	64.4-72.9	+	+	-	-	-	+	-	+	-
11	72.9-81.4	-	-	-	-	-	-	-	+	-
12	81.4-91.5	+	-	$\sim -\infty$	-	-	+	-	+	+
13	91.5-98.3	+	-	-	-	-	+	-	+	-
14	98.3-105.1	-	-	-	-	-	+	-	+	-
15	105.1-111.9	+	+	+	-	-	+	-	+	+
16	111.0-116.9	+	+	+	1.0	+	+	-	+	-
17	116.9-123.7	+	+	+	-	-	+	-	+	-
18	123.7-128.8	+	+	+	-	+	+	_	+	-

TABLE 3. Species found in the short core (0-2500 yr B.P.).

assemblages to the east (Zoltai & Herrington, 1966; Miller *et al.*, 1985), but this species does not now occur in Lake Manitoba and is very rare in southern Manitoba, where it survives only as a few small isolated populations.

The period until about 4500 yr B.P. was characterized by warmth and dryness, during which time the water levels and chemical conditions in the basin fluctuated, organic productivity in the lake increased, with increased amounts of organic matter deposition in the sediments, and water temperatures were warmer (Teller & Last, 1981). No molluscs were found in the core in samples examined between 5.3-6.2 m (ca. 7000 yr B.P.), possibly reflecting a change in local depositional conditions. At 4.7-4.9 m (sample 17), the first amnicolids were seen in the core, and by 3.8-4.0 m, these were abundant in the sediment and remained prominent in most of the later samples until the present day. Abundance of mollusc remains increased from sample 17 onwards, paralleling similar increases at this time (ca. 6000 yr B.P.) in the Lake Superior basin to the east (Bajc, 1986). However, *Amnicola limosa* had been present in more southerly parts of Lake Agassiz as early as 11,000-9900 yr B.P. (Ashworth *et al.*, 1972).

About 4500 yr B.P., the Assiniboine River was diverted into Lake Manitoba, raising the lake to present levels by 3500 yr B.P. (Last & Teller, 1983). At the same time the climate became cooler and wetter. By ca. 2000 yr ago, the Assiniboine River had abandoned its flow into the lake. The mollusc record during this last 4500 yr period shows an increasing prominence of lymnaeids and is similar in character to modern dead assemblages in Lake Manitoba (Pip, 1988). Detailed examination of the short core, which represented the last 2500 years (Table 3) also indicated little change in the mollusc communities of the lake during this period.

ACKNOWLEDGEMENTS

I wish to thank Drs. J.T. Teller and W.M. Last for generous access to their Lake Manitoba cores.

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Walkerana, 1990, 4(12): 279-306

THOMAS SAY'S GLOSSARY FOR CONCHOLOGY*

J. B. Burch

In reviewing the publications and species described by America's first conchologist/malacologist, Thomas Say (1787-1834), I came across his publication, A Glossary to Say's Conchology, printed in 1832 in New Harmony, Indiana. This 25-page pamphlet, although published separately, was associated with Say's (1830-34) American Conchology, with which it seems occasionally to have been bound.

On cover page 4 of Part 5 of Say's *American Conchology*, dated August 1832, is an announcement about Say's glossary:

* * * With this Number we send gratis to those who have paid for the preceding Nos., a copy of a work which we have recently printed, entitled "Glossary to the American Conchology," explanatory of the terms made use of in the science of Conchology. A copy will also be presented to each subscriber who shall transmit by mail, free of postage, his respective sum now due, within one month after having received this number. We hope at a future day to be able to present our subscribers with an "Introduction to the science of Conchology with plates," on the same terms.

As observed by Wheeler (1938a, p. 92), the glossary "was not a coordinate part of the American Conchology, but used as an inducement to subscribers [of American Conchology] to bring up their arrears."

Because of the rarity of Say's American Conchology, H.E. Wheeler (1937-38a) published a brief article which recounted its history, described its contents, and included information on the location of copies known to him. This article also included information about the glossary, of which only five copies were then known. Wheeler's paper stimulated the printing of other notices of additional copies of American Conchology unknown to him in 1937 (see Rodeck, 1938; Wheeler, 1938b; Baker, 1939; Hanna, 1939), and two additional copies of the glossary were located. As far as I know, only these seven copies of the glossary are now in existence.

Subsequent to Say's glossary, other authors have presented glossaries for descriptive conchology or malacology, but this one by Say is not only the first one in this country, it is still among the best. Also, it is especially illuminating because it has many of the words that furnish the roots of the descriptive adjectives used by Say (and other contemporary and later authors) in making names for newly discovered species. Also, the glossary explains the descriptive terms used in that formative period of American conchology/malacology, and, more importantly, defines the technical terms that Say, one of our foremost malacologists, himself used in descriptive mollusks. (Several of the terms are no longer used in descriptive malacology, and a few (which I have mentioned in the end notes) now are defined differently.)

^{*}This article was prepared while the author was a Regents Fellow at the Smithsonian Institution, Washington, D.C., U.S.A.

In Say's species descriptions, the clarity with which he wrote is clearly evident. As observed by George W. Tryon, Jr. (1862, p. 162), "With a quick eye for distinguishing differences, and a remarkably sound judgement of their proper values, most of his descriptions are models of accuracy combined with brevity. Very few of his species have been set aside. Mr. Say has also the merit of appending to most of his descriptions of species, their prominent distinctive characters from nearly allied forms – a very important part of a natural history description, too generally neglected." Unfortunately, some of Say's contemporaries, and many who followed, did not emulate his clarity, accuracy and brevity of expression.

Because of the rarity of Say's glossary, its historical significance in early American conchology, and its obvious continuing value in taxonomic and descriptive conchology, I am reproducing Say's glossary in the section which follows.

Say's glossary (pp. 1-24, plus title page) was followed by "General rules relative to diminutive compounds" (pp. 24-25), and by "Rules for the pronunciation of the Linnean names" (p. 25). I am including these in this reprinting.

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A GLOSSARY TO SAY'S CONCHOLOGY

New-Harmony, Indiana

Printed by Richard Beck and James Bennett

1832.

Explanation of Terms used in Conchology

A.

Abbreviated, shortened; shorter than some compared part.

Abdominal margin, the basal margin in bivalves; opposed to the hinge margin.

Abrupt, terminating suddenly; not drawn out to a point.

Accessory valves, the operculum of multivalves¹, consisting of several small valves.

Acephalus, destitute of a head, as the inhabitants of many shells.

Acerous, having no tentacula.

Acetabuliform, like a circular, shallow saucer, the sides of which are more or less incurved, v. calathiform.

Acicular, needle-shaped; approaching subulate, but more slender, with a more delicate and pungent point; closely allied to acerose.

Acinaciform, cimeter-shaped; sabre-shaped; one thick and straight edge, the other thin and curved.

Acuducted, scratched very finely as if with a needle-point.

Aculeate, prickly; furnished with prickles.

Aculei, prickles; small sharp points.

Acuminate, sharp-pointed; terminating acutely, the point lengthened out.

Acute, sharp-pointed or edged.

Adherent, adhering to rocks and other solid bodies, as the Ostraea, &c. and is either fixed, radicate or obtect.

Adnate, adhering or growing together; connected.

Adpressed, pressed to, or laid to.

Aereal canal, the trachea.

Aeruginous, the colour of verdigrise; light bluish green.

Alated, furnished with projecting parts somewhat like a wing or wings; winged.

Albus, white.

Alternate, so placed that between two on one side there is one on the opposite side; a series of spots on the checquer board is alternately black or alternately white. V. opposite.

Alveolate, having large cells.

Alveole, a cell like that of the honey-comb.

Ambitus, the circumference or outline of the valves. V. margin, edge.

Ambulatory, formed for walking.

Ample, large; wide.

Analogous, fossil-shells, having a great resemblance to recent species. V. identical.

Anastomosing, inosculating, or running into each other like veins.

Ancipital, two-edged; (shell) having two varices, which are lateral and continuous, as in Ranella.

.

Anfractus, a whorl.

Angustate, narrowed, becoming narrow. V. attenuate.

Animal, the molluscous artificer and inhabitant of the shell.

Annulate, marked with rings, either sculptured or differently coloured.

Annule, a ring-shaped spot.

Anterior side, or anterior slope, or anterior margin² of a bivalve, is the side on a portion of which the ligament is placed, and is anterior to the beaks; many naturalists call this the posterior side.

Anteversed, (apex) turned forward as in some Patellas and Emarginulas.

Antipenultimate, the last but two.

Antiquated, sculptured with longitudinal and transverse furrows and lines. V. cancelled.

Anus, the lunule; an identation behind the beaks of bivalves; of the animals it is the opening through which the excrements are discharged.

Apert, open.

Aperture, the entrance to the cavity of a univalve; it is divided into labium, labrum, columella, and peristome; it is deflected, reversed, symmetrical, emarginate, entire, effuse, or rostrated, angulated, rounded, orbicular, semilunar, linear, and sometimes appears double, the inner margin being surrounded by an exterior one; it is longitudinal, transverse, or oblique; it is often called mouth.

Apex, summit, the point at which the shell commences; the beak. Lamarck considers this the base in bivalves.

Apiculate, with fleshy, erect, short points. See verrucose.

Apophysis, an excrescence; a process.

Appendage, or appendice, a supplementary part.

Appendiculate, (hinge) having a recurved process, which arises from the interior of the summits, as in Pholas.

Approximate, near to; approaching near together.

Apterous, destitute of any process like a wing.

Arcuated, bent in the form of an arch; bowed; simply curved.

Arenaceous, of a sandy consistence.

Arenicolae, dwelling in the sand. See petricolae, lutricolae.

Armature, a general term to indicate spines, &c. with which some shells are beset.

Arms, the anterior part of the body of the Ligula³, &c. is furnished with two ciliated processes which are called arms.

Articulate, consisting of abbreviated lines placed longitudinally with respect to each other.

Articulation, of a redintigrate, multilocular fossil is a single cameration of a shell, the sinuous diaphragms of which have disappeared; the tentaculae of the Balani⁴ are articulated; bivalves with inserted teeth are said to have an articulated hinge.

Articulate hinge, (in bivalves) furnished with teeth, but only a small number.

Ascititious, supplemental, additional, adscitious.

Asperous, rugged; with very distinct elevated dots; more uneven than scabrous.

Assurgent, rising; declining at base and rising in a curved manner to an erect posture.

Atrous, or ater, deepest black.

Atom, a minute dot or point.

Attached, fixed to a solid body by the substance of the shell, as in Ostrea; adherent.

Attenuate, slender, drawn to a point; tapering. See augustate.

Attiguous, near, hard by.

Attrite, worn by friction; a dead shell.

Atropurpureus, dark purplish, almost black.

Atrovirens, dark green, approaching black.

Aurantiacus, orange colour, mixed yellow and red. See fulvous.

Aureus, golden-yellow.

Auricles, (in bivalves) the ear-like appendages; the lateral processes near the beaks.

Auriculate, eared, having processes like ears, as in the genus Pecten. Austral, of or belonging to the south.

Axis, the central line around which the volutions revolve; the axis of Nautilus and Planorbis is the shortest diameter, that of Fusus and Conus is the longest.

Azure, azure blue; resembling caeruleus, but more like ultramarine.

B.

Back, that portion of the body of a univalve which is opposite to the aperture; in bivalves the summit and ligament margin.

Badius, chesnut or liver brown.

Barb, a beard-like appendage; a kind of spine with teeth pointing backwards.

Basal margin, in bivalves, is the margin opposite to the beaks, corresponding with the foot of the animal. Lamarck calls it the back.

Basal, relating to the base.

Base, (in univalves) the extremity opposite to the apex; the tip of the salient part of the shell at the extremity opposite to the apex of the spire; in the rostrated kind of univalves it implies the tip of the beak; (bivalves) is at the extremity opposite to the apex; (in multivalves¹) that part of the shell on which it rests; in the lepas⁵ tribe it implies the part immediately seated upon the stem or pedicle; according to some naturalists the base is considered as situated in the external orifice of the shell or aperture of the univalve. — Linne and Lamarck considered the beaks of bivalves as the base.

Beak, the extremity of the umbo, the apex of the bivalve. The process in which the canal is situated in univalves, remarkably elongated in Fusus and rectilinear in some, turned backwards in others.

Beard, the Byssus.

Bellying, ventricose.

Belly, (of a univalve) is to be distinguished from the body as it implies only the convex or swollen part of the first whorl⁶ near the lip, it is opposed to the back. See venter.

Bicuspidate, ending in two points.

Bifarious, parting in opposite directions.

Bifid, cleft; deeply divided at tip in two parts; (umbilicus) somewhat divided in two by a kind of pillar of the callosity, in some Natices.

Bijugum, in two pairs.

Bilamellar, divided into two laminae.

Bilateral, shell, having one valve on the right and the other on the left side of the animal. See dorsal, perisomatice.

Bilobate, divided into two lobes.

Bilocular, having two cells or compartments.

Bimarginate, furnished with a double margin; (labrum) thickened within as in some species of Helix.

Binate, in pairs; consisting of a single pair.

Biradiate, consisting of two rays.

Bivalve, composed of two valves or pieces applied each upon one side of the animal, they are rarely enclosed in a calcareous tube, as in Teredo &c. See subbivalve.

Body, the ultimate and largest whorl of the univalve shell, and is inferior to the spire. Some apply this term to the whole shell.

Boreal, of or belonging to the north.

Botryoidal, clustered like a bunch of grapes.

Bourrelet, (French) See tori.

Branches, Montfort gives this name to the more or less complicated appendages in the interior of Terebratula'; sometimes called cartilages.

Branchiae, respiratory organs, which supply the place of lungs.

Breadth, (in bivalves) is the distance between the anterior and posterior extremities of the shell; the breadth of many bivalves exceeds their length; (in univalves) the

transverse diameter of the body whorl.

Bronze, the colour of old brass.

Brunneus, pure very dark brown.

Buccate, having the anterior part of the head dilated or inflated.

Bullate, of a blistered appearance.

Byssus, [in bivalves] filaments proceeding from the animal, by which it adheres to foreign bodies; it exists in Mytilus, Pinna &c.

C.

Caducous, shedding; easily and quickly falling. See deciduous.

Caesius, pale-blue; approaching gray.

Calathiform, bowl-shaped; hemispherical and concave. See crateriform.

Calcarate, having a spur.

Calcareous, of the nature of lime.

Callous, callosity, a calcareous deposition elevated above the general surface and covering the umbilicus in some univalves as in Helicina; a calcareous deposition on the labium near the superior junction of the labrum; the fulcrum in bivalves.

Calyculate, double-cupped; one cup placed within another.

Camerated, chambered; when the cavity of a univalve is divided by diaphragms into different divisions, which communicate with each other by a siphon. In some redintigrate fossils these are called articulations.

Campanulate, bell-shaped; dilated at the margin like a bell.

Canal, an elongation of the aperture of a univalve descending in a groove or gutter-like process. Some kind of rostrated shells have the canal remarkably conspicuous forming a sinus from the aperture throughout the whole length of the beak; it is elongated in Fusus, recurved and short in Cerithium, rectilinear in Pleurotoma.

Canaliculated, marked with a deeply grooved line; [umbilicus] marked within with a spiral groove, as in some Turboes and many Cerithiums.

Cancellate, latticed; with longitudinal elevated lines, decussated by transverse ones; some authors apply this term to the Scalaria and Harpa, which have only longitudinal bars. See antiquated.

Canus, hoary; with more white than gray.

Capillary, hair-like; long and slender like a hair. See filiform.

Capitate, having a head; terminating in a little head or knob; it differs from clavate by a more abrupt enlargement.

Cardinal margin, is the margin in which the teeth are situated.

Cardinal teeth, in bivalves are situated immediately under the apex or beaks. See lateral teeth.

Carinated, keeled; having a longitudinal elevation like the keel of a vessel.

Carious, as if gnawed or worm-eaten; corroded.

Carneous, fleshy; flesh colored.

Carnivorous, feeding on flesh, on the bodies of animals.

Cartilage, a flexible fibrous substance softer than horn and firmer than flesh, by which the valves are held together, and opened, situated before the beak. For the true cartilage see ligament.

Caruncle, a soft naked, fleshy excrescence.

Cast, [fossil] an extraneous substance moulded in the interior of a shell, the shell itself having disappeared. See redintigrate.

Cataphracted, invested with a hard callous skin, or with closely united scales.

Cauda, the beak of univalves; the elongation of the base; the rostrum or canal.

Caudate, having the columella elongated at base.

Cavity, the interior or hollow part of a shell.

Cephalopode, having the feet attached to the head, as in Sepia.

Cephalous, having a head.

Cernuous, bent; the apex bent downward. See nutant.

Cespitose, matted together.

Chamber, a space in the cavity of some shells, inclosed between two diaphragms.

Chambered, see camerated.

Chink, [in bivalves] a groove beneath the ligament and near the beaks.

Cicatricose, having elevated spots of a different colour from the rest of the surface, like scars.

Cicatrix, one or more impressions on the inside of the valves of a bivalve, to which the adductor muscles, serving to close the shell are affixed; the muscular impressions.

Ciliate, edged with parallel hairs, bristles or appendages; fringed.

Cinereous, ash-colour; gray a little tinged with blackish; the colour of wood ashes.

Cingula, a coloured band.

Circumvolution, a whorl.

Clathrose, having strias crossing each other at right angles.

Clavate, club-shaped; gradually thicker towards the end. See capitate.

Clavicle, the spire of a univalve; it includes all excepting the body whorl.

Clausrum, an elastic appendage which is within the aperture of the Clausiliae, a genus of land Mollusca, it is the Ossicula and Scala of O.F. Muller.

Closed, not gaping; destitute of openings; [umbilicus] covered by a callus; [aperture] protected by an operculum; [bivalve] the edges of the valves in juxtaposition all round, not gaping.

Coadunate, joined together at base; two or more joined together.

Coarctate, pupiform; somewhat cylindric, but diminishing obviously in diameter towards the extremities; contracted, compact; opposed to effuse, as in Pupa.

Coated, covered with an outer crust.

Coccineous, the colour of the blossom of saffron.

Cochleate, screw-shaped; twisted spirally.

Coeruleous, sky-colour; sky-blue.

Columella, or pillar of the univalves, that solid portion of the shell near or at the axis, around which the whorls revolve; it is often perforated by the umbilicus; it is acute when it terminates beneath in a point as in Harpa; truncated when abruptly cut off, as in Agathina, sallient when prolonged as in Terebellum; spiral when twisted at its base, as in Cerithium telescopium; folded as in Voluta. It is often naked towards the base of the aperture, having the labium above.

Columella lip, the labium.

Columnar, like the shaft of a column; it differs from cylindric by tapering to one end. Commissure, a suture.

Comose, with a tuft or brush. See plumose.

Complicated, folded together, as the tooth of a Mactra.

Compressed, flattened laterally; the transverse diameter much shorter than the vertical diameter. See depressed.

Concamerated, See camerated.

Concave, hollow; opposed to convex.

Concatenate, with a series of points placed in a regular order. See articulated.

Concealed, obtecta, hidden in a distinct tube or other foreign body. See radicate.

Concentric, having the same centre.

Conchology or Conchyliology, the science which treats of shells; synonymous with Ostracology, Testaceology.

Conchyliferous, bearing a shell; testaceous mollusca are conchyliferous.

Concretion, a deposition of a foreign body on the shell.

Conduplicate, doubled or folded together.

Confert, crowded, clustered; opposed to sparse.

Confluent, running into one another.

Congeneric, of or belonging to the same genus.

Congested, heaped together.

Conglomerate, congregated.

Conic, in the shape of a cone; the summit being at the anterior part of the aperture as in Conus. See turbinated, turriculated.

Conjugate, consisting of a single pair.

Connate, parts soddered together, that are usually separate. (This is more strictly speaking Coalite, and connate differs in having the line of union distinguished by an incisure or obsolete suture;) united at base.

Connivent, converging or approaching; closing.

Conoid, in the shape of a depressed cone.

Consolidated, [umbilicus,] an umbilicus entirely covered at base by a callous, so as to be concealed from view as in Helicina.

Contiguous, placed nearly or quite in contact; the ribs of some species of Harpa are contiguous; the whorls of most shells are contiguous. See disjoined.

Continuous, [varices] when the varices of one volution are in a right line with those of the next, as in Ranella.

Contorted, twisted; incumbent upon each other in an oblique direction.

Contour, the general form of the exterior surface.

Contractile, capable of being diminished in size; the foot of the snail is contractile. See retractile.

Convergent, approaching each other towards one end; connivent.

Convexity, [in bivalves] is indicated by the distance between the most convex part of the disk of one valve and that of the other. Blainville calls it thickness and Draparnaud names it depth.

Convoluted, rolled upon itself, like a piece of paper rolled between the finger and thumb. See revolute, involute.

Corcelet, the escutcheon.

Cordate, heart-shaped; having the form of a heart when the valves are united, in Cardium. *Cardiform*, resembling the shape of a heart.

Coriaceous, of a leather-like consistence. See pergamaceous.

Corneous, of a horn colour, resembling horn; of a horny consistence.

Corniform, horn-shaped; long, mucronate or pointed.

Coronated, crowned; girt towards the apex of the whorls with a single row of eminences, as in many Cones.

Corpus, the body.

Corrugated, wrinkled.

Cortex, the epidermis.

Corticate, covered with an epidermis.

Costated, ribbed; longitudinally marked with dilated and elevated lines, as in many Pectens.

Covering, operiens; a conic shell, without distinct spire, applied upon the animal like a lid, as in Patella.

Crassus, thick, in allusion to the thickness of each valve, but not to the general diameter.

Crateriform, somewhat like calathiform, but not so much inflated, and rather approaching to infundibuliform.

Crenulated or Crenate, scolloped at the margin, differs from serrate and dentate in having rounded teeth, not directed towards either end; (umbilicus) an umbilicus armed within with small elevated grains as in Solarium.

Cretaceous, shell, having a great proportion of calcareous matter.

Crimson, red with a tint of blue.

Crisped, (striae or varices) undulated somewhat irregularly.

Cruciate, cross-shaped; having the shape of a cross.

Crustaceous, a calcareous substance somewhat hard, elastic, resisting the pressure of the finger, like the shell of a crab.

Cucullate, hooded; cone shaped.

Cultrate, shaped like a pruning knife.

Cupreous, coppery; the colour of copper.

Curved, deviating more from rectilinear than arquated.

Cuspidate, prickly pointed; ending in a sharp point.

Cyaneus, dark blue, like prussian blue.

Cyathiform, wine-glass-shaped; more or less obconical and concave. See calathiform.

Cydariform, globose, but truncated at two opposite sides.

Cylindrical, transverse diameters somewhat equal, as in Oliva; of an elongated rounded form, preserving the same diameter throughout.

Cymbiform, boat-shaped; navicular.

D.

Dead shell, more or less discoloured, or worn by attrition.

Deciduous or deflected, (aperture) declining suddenly; not following the direction of the volutions. See resupinate.

Deciduous, falling off easily.

Decollated, (apex) cut or broken off.

Decorticated, divested of epidermis.

Decrepitant, crackling.

Decumbent, bending down; upright at base and bending down at tip. See procumbent.

Decurrent, closely attached to and running down another body.

Decurved, bowed downwards. See recurved.

Decussated, generally applied to striae which cross each other at acute angles. See antiquated and cancelled.

Deflected, bent downwards rather angularly. See reflected.

Dehiscent, (labrum) at its origin departing a little from the preceding whorl, so as to present a fissure, as in Conus; gaping.

Deltoid, triangular spear-shaped; trowel-shaped; having the general appearance of a triangle, with the terminal angle much further from the base than the lateral ones.

Dendroid, shrub-like; with the appearance of a little tree.

Dentated, toothed; [umbilicus] armed within with little teeth as in Turbo pica, (lip) armed within with elevations resembling teeth; the sides are equal, the tip being opposite the base.

Dentate-serrated, tooth serrated; the denticulations being themselves serrated on their edges.

Dentate-sinuated, toothed and indented.

Denuded or denudated, destitute of covering.

Depauperate, to degenerate; to become poor or inferior.

Dependent, hanging down.

Depressed, pressed downward; more or less flattened vertically; the vertical diameter much shorter than the transverse diameter. See compressed.

Dextral, revolving from the left of the shell to the right, from the base to the apex, the aperture being on the right of the labrum; (valve) the right valve; (apex) inclining to the right.

Diaphanous, transparent, clear, pellucid.

Diaphragm, a transverse interior division of a camerated univalve, it is either simple as in Nautilus or foliaceous as in Ammonite. There is a single incomplete diaphragm in Crepidula.

Dicerous, having two tentacula.

Dichotomous, forked; dividing by pairs.

Didymous, when a pair of spots &c. touch or are confluent.

Diffracted, bending in opposite directions.

Diffuse, spreading.

Digitated, fingered or clawed, as in the labrum of Pterocerus, &c.

Dimidiate fascia, a partial band extending only half around.

Discoidal, revolving nearly in the same plane; resembling a disk; as in Planorbis.

Discontinued, (varices) when the varices of one volution are not in a right line with those of the next, as in *Triton*. See continuous.

Disjoined, when the whorls of a univalve revolve without touching each other, as in Scalaria. See contiguous. (lips) not continuous.

Disk, that portion of the valve of a bivalve that is comprehended between the umbo and the submargin; the convex center of each valve, or exterior surface.

Dislocated, applied to designate a line or stria which is interrupted in its continuity, but of which the tips at the interrupted parts are not in a right line with each other.

Dislocated, broken in its continuity, but the tips of the interrupted part are not in a right line with each other. See interrupted.

Dissilient, bursting open elastically.

Dissivalves⁸, shells composed of many pieces separated from each other by cuticle as in Anatifa⁹. See multivalve.

Distichous, terminating in a fork.

Divaricated, spreading out widely.

Divergent, tending to different points from a centre; spreading out so as to form nearly a right angle.

Dolabriform, hatchet-shaped; compressed, with a very prominent keel and cylindrical base. See securiform.

Dorsal, shell; situated on the back as in the univalves; and in Chiton. See ventral.

Dorso-ventral, shell of two pieces of which one is dorsal and the other ventral. See bilateral.

Dorsum, the back; in bivalves, the margin in which the ligament and beaks are placed. Double, (suture) having a parallel groove.

Duplicate, double.

E.

Ears, see auricles.

Ecalcarate, destitute of a spur or horn.

Echinated, spinous, set with spines like a Hedgehog.

Edentate, or edentulous, toothless, as the hinge of Pinna and Anodon.

Edge of a bivalve, is the termination of the surface, and is bounded inwards by the margin; it forms the extreme boundary.

Effuse, the aperture not entire; having the lips separated by a sinus or gutter, so that if the shell were filled with water, it would flow out at the upper part of the aperture.

Eflected, bent outwards somewhat angularly.

Elevated, (spire) when the spiral cone advances more in height than in width.

Egg, the first state of the shell.

Elliptical, elongate oval; differs from oval by having the lines nearly parallel in the middle.

Emarginate, notched; terminating in a notch. See sinuate.

Ensiform or ensate, sword-shaped; two-edged and tapering towards the point like a sword. See ancipital.

Entire, with a simple margin, not indented on the edge.

Epidermis, the superficial or exterior covering of the shell in many species; it often scales off by desiccation; a kind of periosteum, or membranaceous coating.

Epiphragm, a membranaceous or chalky substance secreted by the animal of many univalves, and closing the aperture of the shell in winter and in very dry weather during the summer; it is the "Operculum hybernum" of Muller, and the "Hybernaculum" of Montagu.

Equal, superfices without inequalities, not canaliculated, striated, punctured, &c.; it differs from plane in not requiring the part to be level or in a rectilinear direction, but occurs in round bodies; also applied to bodies of the same length.

Equal, as applied to costae, striae, punctures, &c. indicates their similarity of magnitude, elevation, &c.; equivalved.

Equidistant, being at the same distance.

Equilateral, the anterior and posterior ends of the bivalve equal both in size and form, the beaks being in the middle of the length.

Equivalved, those shells of which the two valves are equal and similar both in diameter and convexity. See inequivalved.

Erect, upright, nearly but not absolutely perpendicular to the horizon. See vertical. *Eroded*, excavated in irregular cavities, as if gnawed.

Escutcheon, in bivalves, an elongated depression anterior to the beaks, or spatulated mark; the corcelet; Linne called it vulva, Da Costa fissura. In Limax or Slug it is a fleshy covering on the anterior part of the body, under which the head and part of the body are withdrawn in a state of contraction.

Essential Character, a peculiar trait, distinguishing the genus or species from all others. *Esurine*, corroding or eating.

Exaratus, sulcated.

Exarticulate, having no distinct joints or interruptions.

Excurved, bowed outwards. See recurved.

Exoleted, worn or faded.

Explanate, spread out; flat.

Exserted, protruded; opposed to inclosed.

External, one which appears to be exterior to the skin of the animal, as in most shells. See internal.

Extinct, fossil shell, not existing as a living species.

Exumbilicate, destitute of umbilicus.

F.

Facet, the flat elongation of the summit of the inferior valve in some bivalves. The summit of the inferior valve of Spondilus has a facet.

Falcate, sickle-shaped; convexly curved before and concave behind.

Farctus, filled full; stuffed; distended.

Fascia, a transverse band, or broad line.

Fasciated, banded; having bands. See lineated, litterate.

Fascicle, a cluster, numerous filaments or other similar objects placed closely together in a bundle.

Fascio-maculate, with spots disposed in bands.

Fascio-punctured, ornamented with coloured points disposed in bands.

Fastigiate, flat-topped; of an equal height; truncated.

Fatiscent, spontaneously mouldering and falling to pieces in the air.

Fauces, Faux, or throat, that part of the cavity of a univalve, that can be seen by looking in at the aperture.

Favose, honey-comb-like; with large deep holes like the cells of a honey-comb. See scrobiculate.

Ferruginous, colour of the oxide of iron; brown approaching yellow.

Fibrous, shell, in its fracture exhibiting fibres perpendicular to the surface, as in Pinna. *Filament*, a slender thread-like appendage.

Filiform, thread-shaped; slender and of equal diameter throughout.

Fimbriated, fringed.

Fissile, cloven; divided into parallel lamellae.

Fissure, a cleft; a little slit; sometimes applied to the aperture in the summit of Fissurella.

Fissure, (umbilicus,) an umbilicus nearly closed by calcareous deposite, leaving only a slender opening; a rima umbilicalis; Da Costa gave this name to the escutcheon in bivalves, but it is now used for the space which divides the nymphs.

Fistular, hollow; applied to hollow cylinder.

Fixed, attached to a solid body by the substance of the shell, as in Ostrea. See adherent, radicate.

Flabelliform, fan shaped.

Flaccid, limber; feeble; lax.

Flavo vireus, green verging upon yellow.

Flexuose, zig-zag without acute angles; differs from *undulated* in being alternately bet¹⁰ and nearly straight.

Fluviatile, inhabiting rivers, or other fresh waters. See marine.

Foliaceous, very thin and depressed, resembling a leaf or leaves; lamellous.

Fontinal, of springs; belonging to springs.

Foot, of the inhabitant of the shell, is that part which it applies to the earth in locomotion.

Fornicate, arched; having arched scales.

Fornix, the cavity on the inside under the hinge of a bivalve; Linne applied this term to the larger valve of an inequivalved bivalve.

Fosset, in bivalves, a cavity of the hinge to receive a tooth of the opposite valve.

Fossil shell; one that has been dead long enough to lose its animal gluten and colours, to become friable, chalky white, and adhering to the tongue.

Fossulet, a somewhat long and narrow depression.

Fragile, brittle, easily broken.

Frondose, or foliaceous, (varices,) more or less divided into leaf-like expansions, as in many species of Murex.

Front, in univalves, is that side of the shell in which the aperture is situated.

Free, liberae, unattached; as in most shells. See fixed, attached.

Fulcrum, that part of a bivalve shell to which the *cartilage* proper is attached, it is sometimes internal in the form of a cavity in the line of the teeth.

Fulgid, a bright fiery red.

Fuliginous, of the colour of soot.

Fulvous, orange yellow.

Furcated, forked; terminating in two divisions.

Fuscous, dark brown, with a slight mixture of gray; a dull brown.

Fusiform, spindle-shaped; gradually tapering towards each end, and inflated in the middle, as in Fusus.

G.

Gaping, those bivalves in which an opening remains when the valves are closed, as *Pholas, Mya*, &c., are said to be gaping shells. See *ringent*.

Gasteropode¹¹, having the foot situated under the belly.

Geminated, placed in pairs.

Geniculate, knee jointed; bending abruptly at an obtuse angle.

Genus, an assemblage of species more or less closely allied to each other by their zoological characters, and corresponding in particular traits.

Gibbous, hump-backed; bulging out; an elevation, the arc of which is not the segment of a circle.

Glabrous, of a smooth surface; opposed to hairy, downy, villous.

Glaucous, pale gray-bluish green, like the inferior page of a cabbage leaf.

Globular, those of which the diameters are nearly equal, owing to the great dilatation of the body whorl; as in Ampularia, Dolium, &c.

Glochis, a barbed point.

Glomerate, congregated.

Granulated, covered with small grain-like elevations.

Granule, a very minute elevation.

Gracile, slender.

Gregarious, living in society.

Griseous, white mottled with black or brown; light gray.

Group, an assemblage of shells having a general similarity of character.

Gutta, a roundish dot, intermediate in size between an atom or point and a macula.

H.

Habit, or Habitus, the port or aspect; used comparatively to express a resemblance in general appearance, apart from more important markings derived from organization.

Habitation, or Habitat, a situation or locality frequented by the shell.

Hastate, halbert-shaped; resembling the head of a halbert; excavated at the base and sides, but with spreading lobes or angles.

Hemispheric, convex above and flat below, like the half of a globe.

Hepatic, liver-brown.

Herbivorous, feeding on plants.

Hermaphrodite, the two sexes united in the same individual.

Heteroclite. See Heterostrophe.

Heterostrophe, revolving from right to left of the shell from the base to the apex, the aperture being on the right side of the shell¹²; synonymous with Sinistral.

Hians, gaping.

Hieroglyphic, with lines or characters, somewhat like hieroglyphics.

Hinge, the point of union between the two valves of a bivalve, formed by the connection or articulation of the teeth in both valves, or by the teeth in one valve fitting into hollows or sockets in the opposite valve; it is *inarticulate*, *articulate*, and *multiarticulate*.

Hinge margin, that margin of a bivalve on which the hinge is situated. See ligament margin.

Hirsute, rough with strong hairs; shaggy. See pilous, villous, tomentous.

Hispid, bristly; rough with short stiff bristly sparse hairs. See strigose, pilous.

Hoary, covered with a fine white silvery substance or pubescence. See pruinous.

Holosericeous, with thick set, shining, short, decumbent hairs, like silk. See sericeous.

Homotene, retaining the primitive form; not changing the form with age.

Horns, a word commonly used to designate the tentacula of the animal.

Hyaline, transparent; vitreous.

Hymen, the ligament.

Hopocrateriform, salver-shaped.

L

Identical, when a fossil shell is perfectly similar to a recent species.

Imbricate, placed one partly over another like shingles on the roof of a house.

Imbued, imbutus, coloured more or less deeply in the substance of the shell.

Immaculate, destitute of spots.

Immarginate, having no elevated or coloured margin or rim.

Imperforate, destitute of an umbilicus; exumbilicate; without perforations, or spiracles.

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Impression, a trace; imprint; the cicatrices are the muscular impressions; the attachment of the mantle forms the palleal impression.

Impression, (fossil,) the print of the exterior of a shell in stone.

Inarticulate hinge, (in bivalves) having no visible teeth, or only furnished with callosities. *Inauriculated*, destitute of ear-like processes.

Incanus, hoary.

Incisure, the suture; an impressed line marking the junction of two segments or whorls. *Incrassated*, thickened.

Incrustation, a deposition of calcareous matter upon a shell.

Incumbent, one lying over another; resting upon.

Incurved, bowed inwards. See excurved.

Indented, abruptly pressed inwards.

Inequal, unequal; with irregular elevations and depressions on the surface.

Inequilateral¹³, in bivalves, the anterior and posterior ends unequal in size and form, the beaks not being in the middle of the length.

Inequivalved, those shells of which the valves are not equal to each other as in Ostrea and Pandora. See equivalve.

Inferior margin, the basal margin.

Inferior valve, generally more convex than the superior valve and sometimes of a paler colour.

Inflected, bent inwards rather angularly. See reflected.

Infracted, bent inwards abruptly, as if broken.

Infundibuliform, funnel-shaped. See cyathiform.

Inner edge, or Interior edge, the edge or extreme boundary of the inside of the shell.

Inner margin, the margin of the inner surface.

Inside, within.

Internal, (shell,) included within the skin or other covering of the animal, generally thin, colourless, and always destitute of epidermis. See external.

Internode, the space between one knot or joint and another.

Interstitial space, or groove, or interstice, intervening between two elevated lines.

Interrupted, broken in its continuity, but the tips of the broken part are in a right line with each other. See dislocated.

Interval, the space between elevations or depressions.

Intortion, the turning or twisting in any particular direction.

Involute, rolled inwards from each side as in Cypraea, Ovula, &c.

Involution, the part which involves or inwraps another.

Involuted labrum, the labrum turned inwards at the margin, as in Cypraea.

Involuted spire, turning or revolving inside of the shell, so that the whorls are concealed within the body as the nautilus, &c.

Iridescent, reflecting the prismatic colours.

Irregular, (valve,) fixed to a solid body and modified by its form, as in Ostrea. See regular. *Irrorate*, marked with minute points; dew-like.

J.

Joint, articulation. Juncture, the meeting of the whorls of the spire; the suture.

K.

Keel. See carina.

Labium, the inner side of the aperture or columellar lip in univalves, extending from its origin at the tip of the labrum and resting on the columella. It is dentated, folded, &c.

Labrum, the exterior side of the aperture in univalves, extending from its origin on the penultimate whorl to the base; it is acute, reflected, or thickened, lobated, alated, or

digitated, involute, bimarginate.

Lacerated, ragged; torn.

Laciniated, jagged; cut into irregular segments.

Lactescent, yielding or secreting a milky fluid.

Lacteus, of a white or milky colour, slightly tinted with blue.

Lacunose, pitted; having the surface covered with small cavities.

Lageniform, dilated and ending in a narrow neck like a bottle.

Lamella or lamina, a thin plate or foliation.

Lamellated, divided into distinct plates or foliations, as in Oysters.

Lamello-fibrous, shell; when one part of the shell is composed of fibres and the other of laminae. As in Mytillus.

- Lamellous, (operculum) subconcentrically striated or imbricated, with a submarginal nucleus. See unguiculate.
- Lanate, woolly; covered with dense, fine, long, white hairs, so distinct that they may be separated. See tomentose.
- Lanceolate, lancet-shaped; oblong and tapering to the end.

Lapideous, of the nature of a stone.

Lateral, placed on one side.

Lateral teeth, in bivalves, are at a distance from the cardinal teeth, and are often elongated, lamelliform.

Lateritious, brick-colour; like miniatus, but duller, and verging towards yellow.

Latticed, cancellated.

- *Left-valve*¹⁴, when a bivalve is placed upon its base, with the ligament distant from the observer, the left valve corresponds with his left hand; many naturalists consider this the right valve.
- Length¹⁵ of a bivalve shell is measured from the cartilage or beak to the base¹⁶; that of a univalve shell is the distance between the point of the spire and the base.

Leprous, with loose irregular scales.

Lenticular, of a depressed double convex figure.

Ligament, (or cartilage) the substance, whether membranaceous or tendinous, which serves to connect the valves together and to open them; it consists of two parts or substances, of which the exterior or covering is the ligament proper, and the interior is the cartilage proper; they are sometimes widely separated.

Ligament fosset, (in bivalves) a cavity in the face of the hinge of some shells, in which the ligament is inserted as in Mactra, Lutraria &c.

Ligament margin, the margin on which the ligament is situated. See hinge margin.

Ligament perforation, (in bivalves) the opening through which a portion of the animal passes, in the genera Anomia and Terebratula, by the assistance of which, it adheres to rocks and other bodies.

Ligneous, woody; of a hard unelastic substance like wood.

Ligulate, strap-shaped; somewhat linear, much longer than broad and cut off at top.

Lilacinous, lilac colour; like violaceous, but duller, tinged with red.

Limb, the circumference of the valves within the margin.

Line, the twelfth part of an inch; a longitudinal narrow stripe.

Linear, with parallel sides, narrow and nearly of a uniform breadth.

Lineated, marked with lines.

Line of separation, the suture.

Linguiform, tongue-shaped; linear with the extremities obtusely rounded.

Lip, the outer edge of the aperture in univalves. See labrum.

Lite, (lithos, a stone) terminal syllable in the name of a petrified shell, as Nummulite¹⁷, Belemnite.

Litterate, lettered; with irregular lines, somewhat like Arabic letters. See tessellate, fasciate.

Littoral, inhabiting on or near the shore. See pelagic.

Litura, an indeterminate spot growing paler at one end, as if daubed or blotted.

Livid, pale purplish brown; the colour of a bruise.

Living shell, having all its colours and perfection as when on the animal.

Longitudinal, the direction of the longest diameter; situated longitudinally with respect to the body.

Longitudinal, [aperture] parallel to the axis; vertical.

Lubricous, with a smooth surface; as if lubricated.

Lubricous, covered with a slippery mucous¹⁸.

Lunate, crescent-shaped; shaped like a new moon.

Lunule, (in bivalves) the lunulated depression behind¹⁹ the beaks.

Lurid, dirty yellowish; yellowish with a mixture of brown.

Luteus, yellowish with a tint of red like the yolk of an egg.

Lutose, covered more or less with dirt or mud, which easily rubs off.

Lutricolae, dwelling in the mud. See petricolae.

Lyrate, cut into transverse segments, and gradually enlarging towards the extremity; lyre-shaped.

M.

Macula, a spot larger than a gutta of an indeterminate figure, and of a different colour from the general surface.

Maculated, spotted; marked with spots.

Mamillar, (apex) obtuse and rounded, as in Voluta.

- Mantle, of the animal, is the membranaceous or fleshy and muscular covering of the body which secretes the matter of which the shell is formed; it generally margins the mouth, but is in some genera, reflected so as to cover the whole shell.
- Margaritaceous, glossy-white with changeable tints of purple, green and blue; pearlaceous.

Margin, a somewhat indefinite line or space between the submargin and edge; in general it is used to indicate the circumference. The whole circumference of the outline of

the bivalve when laid down flat on one valve, within the edge.

Marginal impression, the palleal impression.

Marginal lip, the labrum.

Marginal, [apex] having the tip of the spire on the margin, as in Crepidula.

Marginated, having a prominent margin or border.

Marine, inhabiting the Sea, or other salt water and are either littoral or pelagic.

Marmorate, so variously coloured as to resemble marble;

Membranaceous, of a thin, membrane-like texture.

Meniscoidal, somewhat globular, with one side concave.

Microscopical shells, those which are so small as to render the microscope necessary to examine them.

Miniatus, red, like red-lead.

Monothalmes, See unilocular.

Moniliform, beaded like a necklace.

Mouth, the aperture; [of the animal] the opening by which nourishment is taken.

Mucous pores, small pores which supply a mucous to lubricate the surface of the body in the animal.

Mucronate, terminating in a sharp rigid point. See cuspidate.

Mullusca²⁰, the class which includes the animals artificers of shells. Their body is soft, inarticulate, destitute of vertebra or skeleton and envelloped in a muscular skin or mantle of a variable form, in or upon which is generally a calcareous body or shell, of one or two pieces. See Testacea, Conchology.

Multiarticulate hinge, [in bivalves] furnished with numerous teeth.

Multilocular, having the cavity divided into many cells or chambers. See camerated.

Multispirate, [operculum] consisting of many narrow whorls, beginning at the centre, as in trochus. See paucispiratum.

Multivalve, composed of many valves or pieces; these are either transverse and imbricated as in Chiton; or formed of five or more pieces united by the skin as in Anatifa, (Dissivalves)²¹ or they are disposed in a circular form and closely united as in balanus²¹ (subcoronal shells).

Muricated, armed with sharp elevated rigid points.

- *Muscle*, a fleshy, flexible, contractile organ, by means of which the animal is attached to its shell; they are interior and tend to keep the valves of bivalves closed; the Oyster has but one; Venus has two; the antagonist of the ligament.
- Muscular impressions, the cicatrices on the inside of a bivalve where the adductor muscles, which act as antagonists to the ligament, are affixed; the Oyster has but one, the Venus and Unio two principal ones.

N.

Nacre, iridescence.

Naked, destitute of an obvious shell, as Limax.

Natant, floating, swimming at the surface of the water; as Argonaut, &c. See fixed, attached.

Nates, in bivalves, the most prominent part of the convexity of the shell; the umbo.

Natural character, all the characters of a genus or species.

Navicular, boat-shaped; as in Argonanta²²; or transverse and truncate anteriorly, as in some species of Arca; with a concave disk and elevated margin.

Nebulous, clouded, marked with many scattered, abrupt, dilated colours or spots of various forms.

Neck, a contracted posterior termination of the head.

Niger, black, a little tinged with gray.

Nitidus, nearly synonymous with lucid, but is less brilliant, and is applied to highly polished surfaces.

Niveous, snow white.

Nodose, knotty.

Nonsymmetrical, those shells of which the apex or nucleus is lateral, and the sides dissimilar; they are more or less spirally twisted.

Nucleus, the smallest layer of the shelly cone, that first formed; the apex.

Nutant, nodding; the tip bent down towards the horizon.

Nymphae, the elongated lamina, on which the ligament is attached in bivalves.

0.

Ob, inversely; thus obovate inversely ovate, &c.

Obese, distended, enlarged.

Oblate, flattened; applied to a spheroid of which the diameter is shortened at two opposite ends.

Oblique, (aperture,) in a direction intermediate to longitudinal and transverse.

Obsolete, indistinct, inconspicuous; (whorls) when the suture is not obvious, as in ancillaria.

Obtect. See concealed.

Obtuse, blunt, the reverse of acute.

Ocelate, eye-like; resembling an eye.

Ochraceous, or Ochreous, resembling ochre; yellow with a slight tinge of brown.

Oculiferous, bearing eyes; the superior tentacula of Helix, &c., are oculiferous, having the eyes at their tips.

Olivaceous, of an olive colour.

Opaline, bluish white, iridescent; like the opal.

Operculated, having an operculum.

Operculum, (in univalves,) a corneous, or calcareous lid, with which the animals of some species close the aperture of the shell when they retire in it; (in multivalves¹,) the small valves which close the summit of the shell; in inequivalved bivalves it is the smaller valve²³.

Opposite, placed on the side opposite to another, so that the bases of the two are on the same transverse line. See alternate.

Orbicular, round and flat, the diameters of the plane equal.

Order, the subdivision of a class; consisting of a group of allied genera.

Ordinate, placed in rows or regular order.

Ostracology. See Conchology.

Oval, a rounded figure in which one diameter is a little longer than the other.

Ovate, shaped like the longitudinal section of an egg, the outlines of the ends being unequal.

Oviduct, the organs through which the eggs are excluded.

Oviposition, the act of depositing eggs; the manner in which eggs are deposited.

Oviparous, propagating by means of eggs. See viviparous²⁴.

Ovoviviparous, producing living young, the eggs being disclosed in the matrix of the parent.

P.

Paleaceous, chaffy.

Palleal line, or impression, in bivalves, a more or less impressed line on the limb of the shell, formed by the attachment of the mantle; it is sometimes sinuous anteriorly.

Pallide-flavens, pale or whitish yellow.

Pallidus, of a pale cadaverous hue.

Palmate, hand-shaped; cut down nearly half way to the base into subequal, oblong segments, leaving an entire space like the palm of the hand.

Panduriform, fiddle-shaped; oblong, at the two extremities and contracted in the middle.

Papillary, having the apex semiglobular; somewhat like a nipple; it ought to be distinguished from verucose.

Papillous, the surface covered with raised dots or pimples.

Papulous, with small dimples or cavities.

Parallelogram, a quadrilateral, right-lined figure, whose opposite sides are parallel and equal to each other.

Parasitical, inhabiting another animal.

Parietes, walls; sides of elevated bodies.

Patulous, spread open; gaping widely.

Papyraceous, thin, paper-like.

Paucispiratum, (operculum,) of but two or three whorls, which are large, with the summit subcentral; in Turbo. See unispiratum.

Pearlaceous, having the appearance of pearl.

Pectinated, cut into regular straight segments like the teeth of a comb.

Pedicle, or peduncle, the fleshy support of the anatifa.²⁵

Peduncle, the pedicle.

Pedunculated, elevated on a stalk or peduncle.

Pelagic, inhabiting the ocean, or lake at a distance from the shore. See littoral.

Pellicle, skin, or film.

Peltate, target-shaped.

Pendent, hanging down.

Penicilliform, pencil-shaped.

Pennaceous, feathered like the web of a quill. See plumous.

Perfoliated, transversely divided into thin plates, which are connected by a common stalk passing nearly through their centres.

Perforated²⁶, (in univalves,) when the umbilicus is so dilated and profound, as to permit a view of the inner summit of the shell.

Pergameneous, thin, tough, and transparent, somewhat like parchment. See coriaceous. Periostraca, the Epidermis.

Peristome, the reflected cord-like portion of the labrum in some univalves.

Petrifaction. See fossil.

Petricolae, or lithophagous; dwelling within stones. See arenicolae.

Pervious. See perforated.

Piceous, pitchy; the colour of pitch; shining reddish black.

Pillar, the columella.

Pillar cavity, the umbilicus.

Pilous, more or less covered with hair.

Plaga, a long and large spot.

Plaits, folds.

Plane, a level or rectilinear surface, destitute of elevations or depressions; a curved surface cannot be plane, because it is not rectilinear.

Plicated, folded or plaited, as on the pillar of Voluta, &c.

Plumous, feathered; with fine hairs on each side so as to resemble a feather.

Polyphagous, eating a variety of food.

Polythalmes, multilocular.

Porcate, marked with raised longitudinal, parallel ridges.

Porrect, stretched out; prominent; elongated forwards.

Posterior side, or posterior slope, (in bivalves²⁷), the portion of the shell which is on the opposite side of the beaks to that on which the ligament is situated; the side on which the lunule is placed. This is the anterior side of many naturalists. It is the side which is foremost in locomotion and opposite to that by which the food enters.

Postapical teeth, lateral teeth, situated behind the apex. See preapical.

Prasinus, grass green, without any tinge of blue.

Preapical teeth, lateral teeth, placed before the summit or apex. See postapical.

Premorse, as if bitten off; with a blunt or jagged termination.

Primary teeth, or cardinal teeth, the principal teeth of the hinge of bivalves, situated beneath the apex. See lateral teeth.

Primary valves, the principal valves of a multivalve¹. See operculum.

Prismatic or *prismoidal*, like a prism; of equal thickness and having more than four flat sides; differs from cylindrical in being angular.

Proboscis, a fleshy and contractile part containing the mouth of the animal.

Proculiform, hollow and cylindrical, with a hemispherical base, the sides at top straight and not recurved. See calathiform.

Pruinous, covered with a frosty kind of mealiness; hoary.

Pubes, the Escutcheon.

Pubescent, coated with very soft, fine wool, hair or down, which is short and not crowded.

Pulverulent, dusty.

Punctured, (colour,) when the spots are so small as to resemble points; marked with small impressed dots.

Puniceous, carmine colour.

Pyriform, pear-shaped; inflated and rounded at one end and narrowed at the other, as in *Pyrula*.

Q.

Quadrangular, having four angles. Quadrate, square; somewhat square. Quadrilateral, having four sides.

R.

Radiate, (operculum) having marginally concentric elements, cut by very fine striae radiating from one of the angles. See lamellous.

Radiated, having small lines either coloured or sculptured from the summit towards the base; or proceeding from the centre.

Radicate, adherent to a solid body by a tendinous part as in Terebratula⁷. See adherent, obtect.

Ramous, having branches, branched.

Reclivate, curved in a concave then in a convex line.

Recondite, hidden, concealed; when one part is entirely covered by another.

Rectangular, in the form of a right angle; having an angle of ninety degrees.

Rectilinear, right lined; formed in a right line.

Recurved, bowed backwards. See decurved.

Redintigrate, [fossil] a cast, an extraneous substance moulded in the interior of a shell, the shell itself having disappeared.

Reflexed, bent backwards. See deflected.

Refracted, bent backwards as if broken.

Regular, (valve) having a constant form, not modified by exterior bodies. See irregular.

Remote, further removed than distant.

Reniform, kidney-shaped.

Repand, waved; with alternate segments of circles and minute angles. See scolloped. *Replicatile*, capable of being folded back.

Resilient, having the property of springing back.

Respiratory orifice, the aperture by which air is admitted into the pulmonary cavity, it is variously situated according to the genus of the animal.

Resupinate or reversed, [aperture] suddenly recurved towards the spire, and not continuing the direction of the volutions. See desiduous.

Reticulate, resembling net-work.

Retractile, [tentacula] capable of being withdrawn, so as to be concealed. See contractile. *Retroflected*, bending in different directions.

Retrorse, (sinuate) pointing backwards; [serrate] inversely serrate.

Retroverse, [apex] turned backwards, as in septaria. See antiverse.

Retuse, ending in an obtuse sinus, or broad shallow notch; terminated by an obtuse hollow.

Reversed. See heterostrophe.

Revivescence, the awakening from torpidity; the restoration from suspended animation.

Revolute, revolving in the same plane, the volutions perfectly lateral, as in Argonauta, &c. See subrevolute.

Rhomboid, a figure approaching to a rhombus.

Rhombus, a quadrilateral figure, having its four sides equal and its opposite lines parallel, with two opposite angles acute and two obtuse.

Ribbed, See costated.

Ridge, the upper or prominent part of a slope.

*Right valve*¹³, when a bivalve is placed upon its base, with the ligament distant from the observer, the right valve corresponds with his right hand; many naturalists consider this the left valve.

Rima umbilicalis. See fissure.

Rimose, having cracks or fissures, running into each other, like the bark of a tree.

Ringent, gaping, not capable of being closed.

Rivose, having furrows which are not parallel, but sinuate.

Rolled shell, is one which has lost its asperities, or part of its surface by attrition upon the shore.

Roseus, colour of a rose, a pale blood red.

Rostrate, having a beak.

Rostrated, (in bivalves) having the anterior²⁸ extremity much narrowed.

Rostrum or cauda or beak, the elongation of the shell in which the canal is situated; as in *Fusus*; an elongation of the head of the animal.

Rotate, wheel-shaped.

Rotundate, rounded at the angles or sides.

Rudiment, the incomplete formation of a part or organ.

Rufous, reddish; a pale red.

Rugged, rough with irregular, differently shaped prominences.

Rugose, surface of the whorls marked with rugosities, or wrinkles; or with irregularly waved and elevated lines. See corrugated.

Runcinate, notched; cut into several transverse acute segments, which point backwards. Rusticated, antiquated.

S.

Saccate, gibbous or inflated towards one end.

Sagittate, arrow-shaped; triangular, and deeply emarginate at base.

Sanguineous, colour of arterial blood; duller than puniceous; red with a blackish tint. Scabrous, rough like a file, with small raised dots.

Scala. See clausium.

Scalloped, curvelinearly indented on the edges, without intervening angles.

Scriptus, lettered; marked with various characters resembling letters. See litterate. Scripta. See litterate.

Scrobiculated, pitted, having the surface more or less covered with hollows. Scrotiform, purse-shaped.

Scutate, with large, flat, scales.

Seam. the suture.

Secund, pointing one way; unilateral.

Securiform, hatchet-shaped; triangular compressed, like the iron part of a hatchet. See dolabriform.

Semicylindric, flat on one side; the form of the longitudinal half of a cylinder.

Semisagitate, half arrow-shaped; like the longitudinal half of an arrow head.

Septiform, (labrum,) resembling a septum, as in nerita.

Septum, the diaphragm.

Serioeous, having the surface shining by means of dense, minute, short, silky hair. See pubescent.

Series, a line of objects placed in succession; a series of spots, spines, points, &c.

Serrate, like the teeth of a saw; differs from crenate in having the teeth acute and directed towards one end.

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Serrulate, minutely serrated.

Sesquitertial, occupying the fourth part.

- Sessile, connected immediately with the part from which it originates, without the intervention of a peduncle.
- Setaceous, bristle-shaped; attenuated to the tip, as the spines of Murex tribulus L.

Setous, bristly; set with bristles.

- Shell, the entire calcareous covering of a mollusk; all the valves or pieces taken collectively--shells are either tubular, univalve, bivalve, or multivalve, marine, fluviatile, or terrestrial.
- Shell-fish, an improper name applied to shells and their included animals.

Shield. See escutcheon.

- Sides, those parts of a univalve seen longitudinally in profile, to the right and left, when the shell is viewed either in a front or back position; (in bivalves,) the lateral parts of a valve distinguished into anterior side and posterior side.
- Sigmoidal, in the shape of an S; lanceolate and concave on one side at base, and on the other at tip.
- Siliceous, fossil shell; changed both in its chemical and mineralogical nature, into a siliceous substance.

Simple, destitute of any remarkable process or appendage.

Sinistral. See heterostrophe; (valve,) the left valve; (apex,) inclining to the left; (shell,) having the aperture on the right¹² side of the shell.

Sinister valve, the left valve.

Sinuate, indented; cut into deep sinuses.

- Sinus, an excavation as if scooped out; a curvilinear indentation more or less profound; differs from an emargina in not being angulated. See retuse.
- Siphon or Siphunculus, a tube by which the cavities in camerated univalves, communicate with each other; it is said to be in the middle when it passes through the middle of the diaphragm, dorsal or exterior when it penetrates the diaphragm near the exterior margin; [in the animals of bivalves,] two tubes, formed by folds of the mantle and which project more or less beyond the edge of the shell, by one of which the water is received into the branchiae and the other is the conduit of the rejections.

Solid, shell; somewhat thick and firm, of a dense texture.

Sparse, scattered; spread irregularly and at a distance from each other.

Spathose, spathifacta, in fossil shells, when the substance itself is changed, not chemically, but mineralogically, so as to exhibit a calcareous crystalization, or a fibrous tissue, instead of the lamillated structure of life. See silicious.

Spatulate, battle-dore-shaped; broad and rounded at top and attenuated at base.

- *Species*, comprehends all the individuals which descend from a common parentage and those that resemble them as much as they resemble each other.
- Specific character, a character which comprehends all the individuals of a species and distinguishes them from all others of the same genus.
- Spinosoradiate, (shell,) when a range of long, spinous tubercles occupy the middle of the whorls.

Spinous, armed with acute processes or spines.

Spiracles, a series of perforations in the shell of Haliotis.

Spiral, revolving obliquely, so as to resemble a spire.

Spire, that portion of the shell which is between the body and apex; it includes all the whorls excepting that in which the aperture is situated.

Spirivalve, a spiral shell.

Spongiose, of a soft, elastic substance, like sponge.

Squamose, scaly; with small scales.

Squarrose, scurfy; consisting of scales spreading every way, or divided into pieces standing upright and not parallel with the plane.

Stellate, star-shaped; with four or five radiating lines.

Stipitate, supported on a peduncle.

Striated, marked with parallel impressed or elevated lines; scored; or covered with fine thread-like lines.

Striga, a narrow transverse line or streak. See fascia.

Strigose, clothed with rigid bristles thickest at base. See hispid.

Sub, in composition, means nearly or approaching to; as suboval, nearly oval, &c.

Subbivalve, (Blainv.,) consisting of a principal piece, as in univalves, and an accessory one closing the aperture more or less completely. Operculated.

Subconsolidated, (umbilicus,) partly covered by a callus.

Subcoronal, (shells,) those which are composed of many pieces, closely united, and disposed in a circular manner as in Balanus²⁹. See multivalve.

Subcutaneous, placed under the skin.

Subereous, of a soft elastic substance like cork.

Submargin, an indefinite line between the disk and margin of the valve of a bivalve.

Subrevolute, revolving nearly in the same plane, as in Planorbis. See revolute.

Subspirated, (operculum,) which presents the beginning only of a volution.

Subulate, awl-shaped; linear at base and attenuated at tip.

Sulcated, marked by one or more broad parallel hollow lines; grooved; furrowed.

Sulphureous, bright yellow; the colour of sulphur.

Summit, tip or apex; (in univalves,) the tip of the spire; (in bivalves,) the tip of the beaks. Superficial, colour, confined to the surface of the shell.

Suture, the line of separation between the whorls of a univalve. It is sometimes sulcated, crenulated, or somewhat projecting.

Symmetrical, those univalves of which the two sides are equal, the nucleus or apex being central, as the argonauta, patella.

T.

Tawny, pale dirty orange.

- *Teeth*, in bivalves; an arrangement of eminences and depressions on the dorsal or cardinal edge, reciprocally penetrating and interlocking and serving to fix the valves; they are cardinal and lateral.
- Tentacula, feelers of a molluscous animal of which there are two or four, situated on the head.

Tenuis, thin.

Teres, nearly cylindric.

Terebrant, [shell,] piercing and residing in solid bodies. See petricolae, xylodomae or lignivorae, arenicolae, lutricolae.

Tergum, the back.

Terrestrial, inhabiting only on land. See fluviatile.

Tesselate, checquered; figured like a chess board. See maculated; fasciate.

Testacea, the order of, including those that are covered with a testaceous shell³⁰.

Testaceology. See Conchology.

Testaceous, tile or brick coloured.

Tetragonal, having four corners or angles.

Thermal, inhabiting warm water.

Thick, crassus.

Thickness, see convexity.

Thin, papyraceous, tenuis; the valves not thick.

Throat or Fauces, that portion of the cavity of a univalve, which is visible from the aperture.

Thyrsus, a cluster.

Tomentose, covered with fine hairs so matted together that particular hairs cannot be separated. See lanate.

Toothed, dentated; armed with prominences resembling teeth.

Tori, small prominent lines, more or less dilated, in the direction of the lines of growth. See varices.

Torose, protuberating; swelling into knobs or protuberances.

Torpidity, a state of hybernation in which no exterior signs of life are exhibited. Tortilis, twisted.

Trachea, of the animal, is the passage through which air is respired. See Siphon. *Translucent*, transmitting light.

Transverse, (aperture) at right angles with the axis of the shell; horizontal.

Trapezoid, a quadrilateral figure, with none of the sides parallel.

Trichotomous, dividing by threes.

Tricuspidate, ending in three points.

Trigonate, three cornered.

Triquetrous, three-sides; with three flat sides. See trigonate.

Trochlearis, pulley-shaped; like a cylinder contracted in the middle.

Truncate, cut off square at tip. See emarginate.

Tubercle, a little solid pimple.

Tuberculous, surface of the whorls marked with tubercles.

Tubivalve, shell; composed of two principal valves, as in the bivalves, but envelloped by a piece in the form of a tube, as in Teredo, Fistulana, &c.

Tubular, (shells,) those of which the transverse diameter is much less than the longitudinal, they are not in whorls and never in regular spiral, as in Serpula³¹, Dentalium.

Tubulous, formed like a tube; fistulous.

Tunicated, composed of concentric layers enveloping one another.

Turbinate, shaped like a top, nearly conic; it differs from pear-shaped in being shorter and more attenuated at base.

Turgid, swollen.

U.

Umbilicated, having an umbilicus.

Umbilicus, a void more or less considerable, formed at the axis of the spiral revolution of univalves and often open beneath; it is consolidated or subconsolidated by a callosity, within it is crenulated, dentated, canaliculated; it sometimes exhibits all the inner space of the axis to the summit or apex.

Umbo, the prominent part which is elevated from the disk of the valve and turns sometimes over the hinge, it terminates in the apex or beak.

Umbonate, bossed; having a raised knob in the centre. See gibbous.

Umbonial slope, the oblique descent made by the umbo, towards the anterior²⁸ basal side in bivalves, (Swainson.)

Umbraculate, umbrella-shaped.

Uncinate, hooked at the end.

Undulated, waved; differs from flexuous in having all its lines curved.

Unequal, see Inequivalved.

Unequal, with very slight and indeterminate excavations or elevations.

Unguiculate, (operculum) composed of imbricate elements, placed in succession from the summit to the base. See lamellous, subspirate.

Ungulate, hoof-shaped; like a horse's hoof.

Uniform, colour; all the surface of the same colour.

Unilateral, one-sided.

Unilocular, having but a single cavity.

Unispirate, (operculum) formed of but one large whorl, with the summit almost terminal, as in *Natica*, *Nerita*. See multispirate, subspirate.

Univalve, composed of a single valve or piece – as in *Helix*, &c. sometimes concealed in the interior of the skin; or occasionally covered by the mantle.

Urceolate, swelling in the middle like a pitcher; pitcher-shaped. See infundibuliform. *Ustulate*, so marked with brown as to appear scorched.

Utriculus, a little bag, or hollow vessicle.

V.

Vaginate, enclosed in a sheath.

- Valve, a calcareous piece called a shell, of a variable form, applied upon or in the skin of a Molluscous animal; it is composed in the bivalves of disk, margin, base, summit, teeth, hinge, muscular impressions, umbo, umbonial slope, anterior side, see right valve, left valve, regular valve, irregular valve, equivalve, inequivalve &c. The two large calcareous pieces of a common muscleshell are called valves, and the single piece of a common snail shell is a valve.
- Varices, prominent lines on the surface of univalves, being so many remains of the dilated or reflected ancient labrum, and exhibiting more or less of a membranaceous lamina at their anterior edges, as in *Murex* &c. See tori.

Varicose, having many varices.

Variolous, with large, unequal, impressed points.

Variegated, ornamented with different colours. See fasciated.

Variety, a difference in colour or form not of sufficient importance to constitute a species, and not continued to succeeding generations; often dependant on climate and nourishment.

Varnished, highly polished, seeming as if covered with varnish.

Vaulted, like the roof of the mouth. See Fornicate.

Velutinous, velvet-like; covered with very thick set, upright, short hairs.

Venose, having lines which branch like veins.

Venter, that part of the body of a univalve which is opposite to the back. Blainville considers the venter corresponding with the aperture; Bruguiere calls venter that part of the last whorl which is on the right of the aperture to which the labium is attached.

Ventral, situated under the belly. Blainville supposes the shell of Umbrella to be ventral. See dorsal; dorso-ventral.

Ventricose, distended, inflated, swelling in the middle, or bellying out.

Vermicular, having the form of a worm, as in Serpula³¹

Verrucose, warted; having small lumps on the surface. See papillous.

Versatile, capable of being turned nearly round.

Vertex or apex, the top or most prominent part; the tip of the spire, or of the umbo.

Vertical, [summit] situated vertically as in Patella.

Verticillate, placed in whorls.

Vesicular, bladder-like, or having little bladder-like prominences.

Villi, soft hairs.

Villous, clothed with long soft hairs. See hirsute.

Violaceous, violet colour; a mixture of blue and red.

Viscid, covered with a resinous or greasy matter. See glutinous.

Vitellinous, yellow, with a tinge of red.

Vitta, a longitudinal coloured broad stripe.

Vulva, the escutcheon.

W.

Whorl, one complete revolution of the spiral cone in univalves.

Winged, expanded like a wing; the labrum of many species of Strombus is said to be winged; the mantle of the Cypraea is said by some to be two winged from its great expansion over the shell; the margin of some bivalves is said to be winged when it is expanded very much in a particular part; alated.

Within, [in bivalves] the concave surface.

X.

Xylodomae, those shells that penetrate and reside in wood. See terebrant.

Z.

Zoned, surrounded with one or more zones, or broad lines.

END OF THE GLOSSARY.

GENERAL RULES

RELATIVE TO DIMINUTIVE COMPOUNDS.

[From Kirby and Spence.]

RULE 1.

Terms in English ending in *cle*, *ule*, or *let*, and which in Latin add *lus*, *la*, or *lum*, to a word, *diminish* its sense. As Dentic*le*, a little tooth; Set*ule*, a little bristle; Ey*let*, a small eye; Denticu*lus*, a little dens; Guttu*la*, a little gutta; Punctu*lum*, a little punctum. Where length or breadth are concerned, the diminutive implies a diminution in the length of the predicate. As, Lineo*la*, Lineo*let*, a short line; Strio*la*, Strio*let*, a short stria; Fascio*la*, Fascio*let*, a short fascia.

RULE 2.

The preposition *sub* prefixed to any word *reduces* the sense of it. As, *Sub*punctate, not fully punctate; *Sub*hirsute, not fully hirsute, &c.

RULE 3.

The termination *culus* in Latin words added to a comparative, implies the state of the object comparatively. As, Convexius*culus*, rather convex than not; Majus*culus*, rather large than not. This is usually denoted in English by the termination *ish*, or the adverb *rather*, as, largish, rather large, &c.

RULE 4.

The participle present used instead of the adjective, implies a *tendency* to the equality expressed by it. As, *Cinerascens*, cinerascent, tending to cinereous, &c.

RULE 5.

The preposition *ob* prefixed to a term reverses it. As, *Ob*conical, *Ob*cordate, a conical or heart-shaped body, of which the narrowest part is the base.

RULE 6.

In compound terms the *last* member indicates the *preponderating* character. For instance, when it is said of a body that it is *nigro-aeneous*, it means that the aeneous tint prevails; but if it is termed *aeneo-nigrous*, the black tint is predominant.

RULES

FOR THE PRONUNCIATION OF THE LINNAEAN NAMES.

[From Withering.]

- 1. The letter *e* at the end of a name is always to be sounded: thus the word *Elatine*, is to be pronounced *E-lat-ti-ne*, with four syllables, and not *E-la-tine*.
- 2. In words ending in *ides*, the *i* is always to be pronounced long.
- 3. Ch is to be pronounced hard, like the letter k. [The Italians pronounce it soft as in Churn.]
- 4. In words beginning with *sce* and *sci*, the *c* is to be pronounced soft; some few words derived from the Greek are exceptions to this rule.
- 5. In such words as have *sch*, the *c* is to be pronounced hard. Thus *Schaenus* is to be pronounced as if it were written *Skenus*.
- 6. The c, and g, before e and i, and before ae and oe, are to be pronounced soft, but before the other vowels and dipthongs hard.

THE END.

NOTES ON SAY'S GLOSSARY.

¹ "Multivalves" here refers to barnacles.

²Now referred to as the posterior end, posterior slope, or the dorso-posterior margin or end.

⁴Balani refers to a group of barnacles.

⁵Lepus is a barnacle.

⁶The revolutions of a gastropod shell are now observed in the reverse fashion (*i.e.*, from apex to base).

⁷*Terebratula* is a brachiopod.

⁸The parts of the carapace of barnacles.

⁹Anatifa is a barnacle.

¹⁰bent.

¹¹Gasteropode is now spelled gastropod.

¹²The revolutions of a gastropod shell are now observed in the reverse fashion (*i.e.*, from apex to base), as is the position of the shell aperture (*i.e.*, with the aperture *facing* the

 $^{^{3}}$ Ligula is one of the barnacles (Crustacea), which were placed in the Mollusca during Say's time.

observer). Accordingly, sinistral shells are now described as revolving in a counterclockwise direction, and having their apertures on the left.

¹³Inequipartite (see Sterki, 1907).

¹⁴The ligament of freshwater unionacean clams is posteriorly located. Therefore, the valve called the left one by Say is now considered to be the right valve, and Say's "right valve" is actually the left one. ¹⁵Say's "length" for a bivalved shell is now referred to as the height.

¹⁶Say's "base" for a bivalved shell is now referred to as the ventral margin.

¹⁷Nummulite is a foraminiferan.

¹⁸ "Mucus" is now the spelling of the noun; "mucous" is an adjective.

¹⁹"Behind" = "in front of," in modern usage.

²⁰ "Mullusca" is now considered to be a phylum and is spelled "Mollusca."

²¹Dissivalves and Balanus are barnacles.

²²Argonauta, i.e., the egg case.

²³The smaller valve in asymmetrical bivalves is no longer referred to as the "operculum."

²⁴Say inadvertently left viviparous [which means giving birth to young snails instead of laving eggs] out of the glossary.

²⁵Anatifa here refers to a group of barnacles.

²⁶A "perforate" univalve shell is now defined as one which has a very narrow perforation in its base, as opposed to "umbilicate," in which the opening is wider. ²⁷Now referred to as the anterior end, posterior slope, or the dorso-anterior margin or

end

²⁸The end of the bivalved shell that Say called "anterior" is now the one called called "posterior."

²⁹Balanus is a barnacle.

³⁰Testacea is no longer used as a molluscan taxon name.

³¹Serpula is an annelid (polychaete).

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Walkerana, 1990 4(12): 307-316

SPOOL AND LINE TECHNIQUE FOR TRACING FIELD MOVEMENTS OF TERRESTRIAL SNAILS

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ABSTRACT — In spool and line technique for terrestrial snails, a spool of thread is glued to the shell of a snail so the thread unwinds as the snail moves, leaving a record of the movement pattern. Using spool and line to trace movement patterns of large (>13 mm diameter) land snails has distinct advantages over other methods of assessing movements in field studies including being relatively simple and inexpensive, giving a continuous record of animal positions and actual distances moved, ability to track many animals simultaneously, increasing the number of recaptures, being usable in dense cover and when the researcher is absent, and minimizing disturbance at recapture.

KEY WORDS - Spool and line, spooling, movement, dispersal, gastropod.

INTRODUCTION

Land gastropods are excellent creatures for biological studies. Many ecological, behavioral and agricultural pest studies on habitat use of land snails seek to discover the factors influencing the timing, distance and patterns of snail movement. Land snails move to find food and mates, avoid predators, and adjust their micro-environment (for example, snails may move to remain moist). Little is known about the extent of individual movement by snails (Solem, 1959: 261). Researchers may wish to determine environmental, seasonal or diurnal influences on movement patterns, to study the rate and routes of movements such as dispersal, homing and activity ranges, and to make movement comparisons among species or among different age groups within a species.

A variety of techniques have been employed in studying land snail homing and movement patterns in the past. The most common method for studying snail movements has been mark and recapture (Blinn, 1963; Newell, 1967; Shachak *et al.*, 1975; Richter, 1976; Cowie, 1980; Rollo & Wellington, 1981; Greenwood & Parkin, 1984; Asami, 1988; Auffenberg & Auffenberg, 1988; Lind, 1989; Staikou *et al.*, 1989). Time-lapse photography (Newell, 1967; Cook, 1980; Bailey, 1989a), video camera (Cook, 1979a; Bailey, 1989b), radio transmitter (Vail, 1979), metal tag and metal detector (Pearce, unpublished), visualizing mucous trails using calcium carbonate (Cook, 1977) or carbon particle (Pearce, unpublished) suspension in water, and continuous observation (Cook, 1979b; Rollo & Wellington, 1981) have also been used. Spool and line technique has been used on vertebrates, but has not been used previously with land snails.

The ideal technique for tracing movement patterns of land snails would not alter the behavior of the animal, would be inexpensive and not require much field labor, would give a continuous and accurate record of the snail's movements in time and space, and would be useful for tracing movements of numerous individuals in any habitat. Unfortunately, a single technique that satisfies all of these criteria is not currently available, and the best method for a given study will depend on the circumstances.

The thin film of mucus that snails leave behind when they move is perhaps the best record of the snail's movements, although times the snail was at a given point are not available. Mucous trails are readily visualized on smooth surfaces such as glass and plastic, but visualizing mucous trails is not practical on uneven field substrates. The thread left by a spooled snail is a visible approximation of the slime trail left by that snail, and therefore spooling is an excellent technique for accurately tracing snail movements in the field.

In this paper I discuss the advantages and disadvantages of spool and line technique, give a brief history of the uses of spooling in other animals, give details of the spool design I used for land snails, and give examples of the kind of results obtainable by spooling land snails.

SPOOL AND LINE TECHNIQUE

Spool and line technique involves attaching a spool of thread or other line to an organism whose movement patterns are to be observed, attaching the free end of the thread to a landmark, and allowing the thread to unwind from the spool as the animal moves so that a continuous record of the animal's movement is preserved as the pattern of the thread remaining where the animal was active.

Advantages of Spooling. The spool and line technique has a number of distinct advantages over other techniques of recording animal movements in the field. Major advantages are that the spooling technique is inexpensive, is accurate, gives a continuous record of an animal's position and actual distances moved, can be used on many animals simultaneously, can record movements at night and in dense brush when the researcher is absent, and can decrease disturbance at recapture.

Spooling requires less equipment and materials than radiotracking and timelapse film or video camera (Miles *et al.* 1981; Boonstra & Craine, 1986; Stott, 1987). The cost of spooling is comparable to the cost of mark and recapture techniques. Spooling is much less labor intensive and can provide information on more animals than continuous observation.

Although mark and recapture data allow one to estimate a minimum distance travelled between the mark and recapture points (Hazlett, 1984), the actual distance travelled by an animal may be much greater than this minimum. For example, researchers in a mark and recapture study concluded that the home range of the spiny rat *Proechimys guyannensis* (E. Geoffroy, 1803) was less than 100 m, but using spool and line method, Miles *et al.* (1981) found that all *P. guyannensis* travelled more than 100 m in one night. Furthermore, when an animal is found at the same location on two consecutive recaptures, mark and recapture data cannot indicate if the animal remained stationary or if it returned to the same location, but spooling data can allow the researcher to distinguish between those two possibilities.

Spooling gives a continuous record of movements (Boonstra & Craine, 1986), because it shows the actual route an animal took, including the animal's threedimensional use of the the habitat (*e.g.*, up trees, under leaves), showing vertical as well as horizontal movement (Lemen & Freeman, 1985). Such an accurate record

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is not possible with ordinary mark and recapture, metal tag and metal detector, or radiotelemetry using hand held antennae. Other techniques that can give a continuous record are film or video camera, visualizing mucous trails, continuous observations, or radiotelemetry using a grid of antennae with a continuous recorder. Some of these techniques are more difficult to use in the field and give less vertical resolution than spooling does, and spooling gives a level of finegrained resolution not possible with radiotracking (Berry *et al.*, 1987; Stott, 1987).

With spooling, many more animals can be traced simultaneously (Miles *et al.*, 1981) than is possible with radio transmitters and time-lapse film or video cameras. For spooling very large numbers of active animals in a small area, using threads of different colors would simplify tracing paths. Visualizing mucous trails could trace paths of numerous animals, but, as noted above, this technique is not applicable on rough field substrates.

Another advantage of the continuous record ability of spooling is that the researcher need not be present. The animal can be made to map its own travel route (Stickel, 1950). In this way, spooling allows mapping of nocturnal behavior and movements in dense cover (Miles *et al.*, 1981) where cameras or direct visual observation is hindered.

Spooling minimizes disturbance at recapture for animals such as snails that rest under leaves or hide in or under logs. With mark and recapture techniques, considerable effort and disturbance to the habitat can occur as researchers turn logs or stir leaf litter seeking the marked animals. The thread of a spooled individual indicates the location of the animal so habitat need not be disturbed. Furthermore, spooling increases the number of recaptured snails considerably over that of normal mark-recapture (see results).

Limitations of Spooling. Spool and line technique is limited to animals large and strong enough to carry the spool and not have their movements significantly affected by it. Spooling does not give a time record of movement; researchers must periodically put time marks on the payed out thread if a time record is desired. Spooling as described here would not work underwater.

USES OF SPOOLING

Spool and line technique has been used to trace movement patterns of turtles since the 1940's, and has been used to trace spatial relationships of other vertebrates, especially mammals, since then. This paper reports the first use of spooling on a non-vertebrate.

Here I present a summary of the types of questions spooling and other movement study techniques have addressed on vertebrates, then I discuss some additional questions that spooling can address in land snails. Spooling has been used in vertebrate animals to study activity range, navigational or foraging activity, sites of interactions, and effects of environmental factors. In addition to these topics, spooling has great potential in gastropods for studies of mucous trail interactions, and in agricultural applications.

Spooling can give a more accurate picture of the activity range of an animal than can mark-recapture technique, because animals rarely move in straight lines between recapture points. Spooling can accurately trace the positions of an animal at all times it is spooled (Miles *et al.*, 1981). Knowing activity ranges is important

for studies of territorial behavior, competitive interactions, habitat partitioning, and spacing behavior (Strang, 1983; Chitty, 1987). Spooling can indicate if animals return to a home site (Stickel, 1950; Berry, 1986; Boonstra & Craine, 1986), and when an animal is found at a given location on two consecutive recaptures, can distinguish between homing and no movement. Spooling can help locate refuges or nests (Miles *et al.*, 1981; Boonstra & Craine 1986; Berry *et al.*, 1987; Stott, 1987) and can be useful in studies of dispersal activity (Keister *et al.*, 1982; Cockburn *et al.*, 1985; Chitty, 1987), including comparing dispersal of juveniles and adults (Wygoda, 1979; McRae *et al.*, 1981).

In studies of navigational ability and foraging behavior (Berry, 1986), spooling can address whether animals move straight toward food or shelter, or if they use a systematic or random search path. The meander ratio (displacement distance divided by actual distance travelled) (Strang, 1983; B.A. Hazlett, pers. comm.) is a useful measure in comparing movement path types. Spooling with time marks added periodically by the researcher can indicate mean speeds of movement over intervals, which can be correlated to environmental factors such as presence of food, weather conditions, or habitat type.

Sites of interactions among spooled individuals can be determined. Since the animal leaving each thread is known, comparisons can be made among adults and juveniles, both intra- and interspecifically.

The effects of environmental factors (*e.g.*, rain, temperature, light) on movement patterns can be studied (Wygoda, 1979; Berry & Turner, 1986; Stott, 1987) either by correlating movements to measured variables, or by observing the effect of manipulated variables (*e.g.*, adding water) on movements. Spooling, with periodically placed time marks, can be used to study diurnal activity patterns (McRae *et al.*, 1981; Berry *et al.*, 1987) and seasonal patterns of aestivation or hibernation (Gibbons, 1986).

Two other broad topics, more relevant to land snails, can be addressed by spooling: mucous trail interactions, and agricultural applications. Recent evidence indicates that gastropod mucous trails contain information detectable by other gastropods (Ushadevi & Krishnamoorthy, 1980; Rollo & Wellington, 1981; Cook, 1985; Wareing, 1986) indicating, for example, species and direction of travel. Laboratory studies of mucous trails have been conducted on terrestrial slugs (Chelazzi *et al.*, 1988). Spooling allows field studies of land snail mucous trails to evaluate whether snails cross (= ignore), follow in direction of travel, follow in opposite direction, or are repelled when they encounter a slime trail. Comparisons can be made of responses to the snail's own trail, trails of conspecific individuals, trails of other species, and responses between juveniles and adults can be recorded. For example, Cook (1977) found that *Limax grossui* reacts to trails of *L. flavus* but not to less closely related species. Studies can indicate how long information in mucous trails persists.

Some snails are important agricultural pests, and spooling can provide information useful in controlling these pests. Understanding movements of agricultural pests is necessary to developing effective control measures. The activity range of a pest will dictate effective spacing of poison baits or distance around a crop to maintain a pest-free zone. Understanding the timing of pest activity can aid planning the timing of pest control measures to be most effective.

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SPOOLING LAND SNAILS

The spools I used for land snail movement studies are modified slightly from the spools used by Boonstra & Craine (1986). I used smaller spools, and instead of using heat shrinking plastic to enclose the thread spool, I wrapped spools in aluminum foil (Fig. 1).

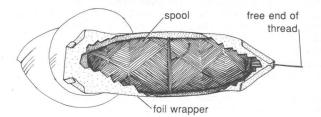


FIG. 1. Cutaway diagram showing spool and line in place on a snail shell. Free end of thread unwinds from middle of spool.



FIG. 2. Spool and line on an active Mesodon thyroidus. Arrow indicates free end of thread.

I used number 5 white nylon thread, available from Culver Textile Corp., 525 52nd St., West New York, New Jersey. The smallest spool size they had available was spindle size 60 (containing about 250 m of thread, weighing 1.63 g and measuring 31 mm long, 10 mm diameter at the middle, and tapering to 7 mm diameter at each end). The thread pulls very easily from the middle of the spool, like yarn pulls from a skein, so the spool has no moving parts except the thread.

Because size 60 spindles were too large for my needs, I rewound the thread onto a needle inserted into a variable speed electric drill, keeping the innermost end of the

thread free for later, and mimicing the morphology of the size 60 spindles so the thread traversed the length of the spool each one to three times around to prevent tangling when the thread is payed out. I wound spindles of about 80 m of thread, weighing about 0.5 g, and measuring about 25 mm long and 6-8 mm wide.

I wrapped the spools in a piece of light weight aluminum foil measuring about 4.5×5 cm, weighing about 0.1 g, folding the edges under securely to be as water tight as possible, and allowing the free end of the thread to protrude from the middle of the spool freely out one end of the foil wrapper. I flattened the other end of the foil slightly so it could be easily attached to the snail shell.

To evaluate the spooling technique, I spooled three species of large (15-25 mm diameter) land snails, Anguispira alternata (Say), Mesodon thyroidus (Say) and Neohelix albolabris (Say), in a hardwood forest in northern Michigan. I used super glue (cyanoacrylate) to attach spools to marked snails (Fig. 2). I attached the free end of the thread to a stake and noted the time and position that I released spooled snails. As the snail crawled, the thread unwound from the spool leaving a record on the ground of the snail's route. The meandering record of the snail was preserved as the thread was held by twigs and leaves when the snail turned. Periodically, I marked the snail's position with another stake to put time marks on the trails. I mapped and measured the thread trails and took them up regularly to keep the study site free from old threads.

To determine if spools affected the activity of snails, I continuously observed two spooled and two unspooled snails of each of the three species for three hours one humid night when snails were active.

RESULTS AND DISCUSSION

Spooling trials gave a continuous record of snail movement patterns. Fig. 3 shows the paths over the same 100 days of one individual of each of the three species. Movement patterns apparent from the figure are that the snails reuse refuges occasionally, but the snails do not home at the end of every night. Snails may follow their own mucous trail, not exactly, but within about 10 cm either side.

Some species differences are apparent. The Anguispira alternata seemed more arboreal, spent more time stationary or climbing trees and had a smaller activity range (ca 40 m²), the Neohelix albolabris activity pattern resembled a home range of ca 80 m², and the Mesodon thyroidus seemed more itinerant, occasionally retracing its path, and had the largest activity range (ca 800 m²). A preliminary analysis of the movement data indicates that A. alternata moved the least distance per day (76 cm, n = 19), N. albolabris moved an intermediate distance (122 cm, n=33), and M. thyroidus moved the farthest per day (225 cm, n=18).

These activity ranges are similar to or larger than activity ranges reported by other researchers on land snails. Heatwole & Heatwole (1978) found activity ranges of the pulmonate snail *Caracolus carocollus* Linnaeus 1758 between 0.08 and 59.0 m². Auffenberg & Auffenberg (1988) found activity ranges of the terrestrial prosobranch snail *Geophorus bothropoma* Moellendorff 1895 between 2.3 and 3.8 m². McCracken (1976) found a mean activity range of *Neohelix albolabris* of about 65 m².

Spooling snails was very successful for tracing movement patterns. I spooled up to 22 snails simultaneously. Spooling gave 18 times more recaptures than did mark and recapture: without spooling, recaptures ranged from 0 to 4, mean 0.8, n = 91; with spooling, recaptures (excluding no-moves) ranged from 2 to 57, mean 14.8, n = 67. As snails rested during the day and dry weather, moving more at

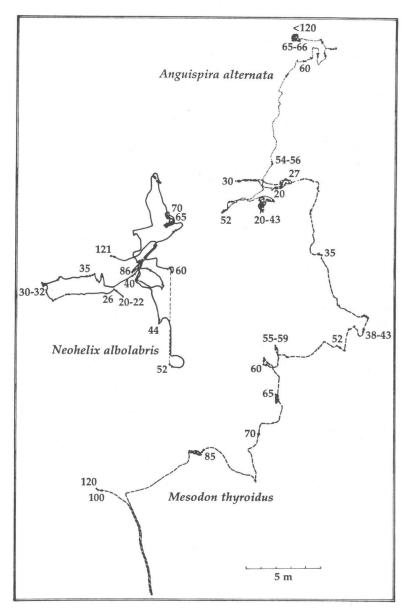


FIG. 3. Movements of Anguispira alternata, Mesodon thyroidus, and Neohelix albolabris in a hardwood forest in northern Michigan, traced by spool and line technique. Numbers on the figure indicate positions of snails that number of days after 20 June 1989.

night and during moist weather, the threads recorded the nocturnal movements of the snails whether I was present or absent. Sometimes spools fell off snail shells before the thread had completely payed out (spools that I glued to partly wet shells sometimes fell off), but more often thread payed out completely and the snails were found later with empty foil wrappers on their shells.

The only inaccuracy I noted in my trials was that sometimes when a snail reversed its direction of motion, the thread on the ground would slip back until it was caught on a projecting object, so the thread indicated less distance than the snail actually moved. Similarly, when snails climbed trees or other objects, the path of thread did not necessarily indicate the highest point the snail reached.

Spooled snails in my studies apparently behaved normally. Similarly, Stickel (1950) reported that spooled turtles behaved normally. I detected no noticeable difference in snail movement patterns when I continuously observed spooled and unspooled active snails of the three species in the field for three hours. The extra weight and drag of spools is not expected to affect snail movement because gastropods are strong (Crozier & Federighi, 1925), and snails appear to move normally in the lab even with several other snails attached to their shells. Furthermore, the weight of a spool is within the range of how much a gastropod's weight fluctuates as it gains or loses water (Blinn, 1964; Runham & Hunter, 1970). The thread pulls out of the spool very easily, so is not likely to alter snail movements. However, a few times thread became tangled within the foil wrapper, and ceased to pull out freely, especially the few times the spool got wet within the foil wrapper. Snails with tangled thread were unable to move further.

Preliminary observations indicate that mucous trail interactions can be studied in the field by spool and line technique. When snails encountered trails, individuals of all three species usually followed a conspecific trail, including their own. In addition, *Mesodon thyroidus* followed *Neohelix albolabris*, and *N. albolabris* sometimes followed *M. thyroidus; Anguispira alternata* did not follow *M. thyroidus*, and *N. albolabris* did not follow *A. alternata*.

An unexpected indication of an interspecific interaction is a spooled *Anguispira alternata* that was carried one day by a shrew a distance of more than 25 m through runways in the forest, then taken more than 1 m deep into the shrew's burrow, trailing the thread all the way. A bit of the snail's shell at the aperture was broken, but the snail was still alive when I found it the next day.

In conclusion, spool and line technique is an inexpensive method for tracing continuous movement patterns and actual distances moved by land snails in the field, useful for studying many animals simultaneously, and not requiring continuous observation. Spooling increases the number of recaptures over mark and recapture, and minimizes disturbance at recapture. Spooling did not have a detectable affect on snail movement behavior.

ACKNOWLEDGEMENTS

I am grateful to P. Myers for alerting me to the spooling technique and providing spools. My thanks go to the many people who made helpful (and skeptical!) comments about this technique, and for comments on the manuscript. J.B. Burch kindly helped with Fig. 2. A grant from the University of Michigan Biological Station and a Hinsdale-Walker Scholarship from the University of Michigan Museum of Zoology partly supported this research.

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