JOSEPH C. BRITTON, JR.

Two New Species and a New Subgenus of Lucinidae (Mollusca: Bivalvia), with Notes on Certain Aspects of Lucinid Phylogeny

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY NUMBER 129

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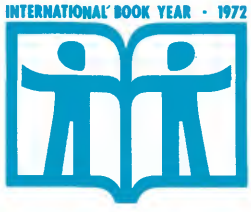

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ABSTRACT

Britton, Joseph C. Two New Species and a New Subgenus of Lucinidae (Mollusca: Bivalvia), with Notes on Certain Aspects of Lucinid Phylogeny. *Smithsonian Contributions to Zoology,* number 129, 19 pages, 6 figures, 1972.—Two new western Atlantic species of Lucinidae, *Lucina (Pleurolucina) hendersoni,* new species, and *Parvilucina (Bellucina) rehderi,* new species, are described and figured. A new subgenus, *Radiolucina* (type-species, *Phacoides amiantus* Dall, 1901), of the genus *Parvilucina* is proposed. Certain aspects of the shell morphology of several groups of Lucinidae with similar hinge structure are compared. The nature of radial ornamentation in the subgenus *Pleurolucina* appears to differ significantly from that of *Parvilucina* or *Radiolucina,* suggesting the former should be considered distinct from the latter groups. Certain aspects of the shell morphology of *Bellucina* is demonstrated to be sufficiently distinct from that of species such as *Parvilucina amiantus* (Dall, 1901) to justify the establishment of a new subgenus, *Radiolucina,* for the latter. Several additional aspects of lucinid phylogeny are considered.

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Joseph C. Britton, Jr.

Two New Species and a New Subgenus of Lucinidae (Mollusca: Bivalvia), with Notes on Certain Aspects of Lucinid Phylogeny

Introduction

Within the family Lucinidae (Mollusca: Bivalvia) there is a large, complex assemblage of species sharing several similar morphological characteristics, the most noticeable being the similarity of hinge structure. Because previous authors have assigned these species to several different supraspecific categories, each of the supraspecific taxa discussed herein must be defined. Table 1 contains a list of the taxa and their type-species.

Except for minor modifications, all of the groups listed in Table 1 possess a full complement of lucinid dental elements. The following Bernard dental formula (see Cox, et al., 1969:N56, for an explanation of the Bernard formula) characterizes the hinge of this assemblage:

AIII		3a	3b		PIII
AII	AIV	2	4b	PII	PIV

In some species of each of the groups except *Lucina,* sensu stricto, and *Bellucina,* the right anterior cardinal tooth (3a) fails to develop or is obscured by encroachment of the lunule; whereas in some groups (particularly *Bellucina*) the left dorsal lateral teeth (*AIV* and *PIV*) may be reduced. Considering the total variation of dentition within the entire family, these variations are slight and suggest that these groups are more closely related to each other than to any other group (s) of Lucinidae (e.g., *Codakia* has weak or obsolete posterior laterals, *Miltha* lacks lateral dentition entirely, and *Anodontia* is edentulate).

Previous authors (particularly Dall, 1901; Chavan, 1937, 1938, 1969; and Bretsky, 1969) have recognized the basic similarity of dentition among the groups listed in Table 1, but their phylogenetic and systematic interpretations vary according to the degree of emphasis each author places upon (1) subtile variations of hinge dentition, (2) other aspects of shell morphology, or (3) a combination of these two.

Although there were several earlier works which purported to be revisionary, Dall (1901) should be considered the "first reviser" of the Lucinidae. He recognized the tremendous diversity of the lucinids and attempted to demonstrate this knowledge nomenclatorially. Unfortunately, many of his nomenclatorial opinions were to confuse rather than to clarify lucinid phylogeny. Dall recognized only six genera of Lucinidae: *Lucina* Bruguière, 1797 [type-species considered by Dall to be *Lucina edentula* (Linnaeus, 1758), by subsequent monotypy, Lamarck, 1799]; *Loripes* Cuvier, 1799; *Codakia* Scopoli, 1777; *Myrtea* Turton, 1822; *Phacoides* Blainville, 1825; and *Divaricella* von Martens, 1880. He subdivided each of these genera into several subgenera and sections. He considered all of

Joseph C. Britton, Department of Biology, Texas Christian University, Fort Worth, Texas 76129.

TABLE 1.—*Supraspecific taxa of Lucinidae receiving primary consideration in this publication*

Taxon	Synonym	Type-species
Pleurolucina Dall, 1901		*Lucina leucocyma* Dall, 1886, o.d.[1]
	Dallucina Olsson and Harbison, 1953	*Lucina (Here) amabilis* Dall, 1898, o.d.
	Paslucina Olsson, 1964	*Lucina (Paslucina)* follis Olsson, 1964, o.d.
Lucina Bruguière, 1797		*Venus pensylvanica* Linnaeus, 1758, s.d.[2], Schumacher, 1817
	Linga deGregorio, 1885	*Lucina columbella* Lamarck, 1819 s.d., Sacco, 1889 [fide Chavan, 1969]
	Quasilucina Stewart, 1930	*Lucina carnifera* Conrad, 1933, o.d.
Here Gabb, 1866		*Lucina (Here) richtofeni* Gabb, 1866 (=*Lucina excavata* Carpenter, 1857), s.d. Stoliczka, 1871
Parvilucina Dall, 1901		*Lucina tenuisculpta* Carpenter, 1864, o.d.
Bellucina Dall, 1901		*Parvilucina eucosmia* Dall, 1901 (= *Lucina semperiana* Issel, 1869), o.d.
Radiolucina, new subgenus		*Phacoides (Bellucina) amiantus* Dall, 1901, designated herein
Cavilinga Chavan, 1937		*Lucina trisulcata* Conrad, 1841, o.d.

[1] o.d.=original designation.
[2] s.d.=subsequent designation.

the species mentioned in Table 1 to be within his largest and most inclusive genus, *Phacoides* (see Table 2).

The most important aspect of this first revision of the Lucinidae is the phylogenetic relationships which can be inferred from it. Assuming Dall's "subgenera" to roughly correspond to Bretsky's (1971) higher "phenon groups," Dall recognized two basic lineages: the *Here* lineage (corresponding to the *Lucina* lineage of this paper) including the species *Phacoides richtofeni, P. pensylvanica, P. leucocyma,* and *P. trisulcata;* and the *Parvilucina* lineage (the *Parvilucina,* sensu lato, lineage or the *Parvilucina-Radiolucina-Bellucina* complex of this paper) including the species *Phacoides tenuisculpta, P. semperiana,* and *P. amiantus.* As will be shown, there is considerable merit to an arrangement of this type.

Chavan (1937, 1938) obviously drew heavily from Dall's classification of the Lucinidae, but his interpretation of the family was influenced by two new opinions: that *Phacoides* was a term introduced in the vernacular and was not a name available for zoological nomenclature, and that *Lucina jamaicensis* (Spengler, 1784) [1] (=*Tellina pectinata* Gmelin, 1791) was the type-species of *Lucina* according to subsequent designation. The problem of the type-species of *Lucina* is a complex nomenclatorial matter. Except as indicated here it is beyond the scope of the present paper. (For additional information, see Chavan, 1937, 1938, 1952;

[1] Chavan (1937) and several other authors have cited Spengler, 1784, as the author of *L. jamaicensis.* Chemnitz (1784) described *Venus jamaicensis* from the cabinet of Spengler. The specimens Chemnitz described were apparently labeled *"jamaicensis"* in Spengler's hand for purposes of identification *within the collection* ("Diese muschel wird im Spenglerischen Cabinette Venus Jamaicensis genannt, welche Benennung ich sehr gerne behbehalte," Chemnitz, 1784). Spengler did not publish the name *jamaicensis* prior to publication of *Tellina pectinata* Gmelin, 1791. Thus, Chemnitz (1784), not Spengler, should be credited with the first use of *jamaicensis* in a published work. Note that Chemnitz (1784) is on the list of officially rejected works of the International Commission on Zoological Nomenclature.

TABLE 2.—*Comparison of supraspecific assignments by previous authors of certain species of Lucinidae*

(Type-species are indicated by an asterisk (*) in each column according to the interpretation of the author whose name appears at the top of each classification. Only those species which were explicitly specified by a particular author as belonging to a particular taxon are included in that author's classification.)

Dall, 1901	Chavan, 1937, 1938	Bretsky, 1969, 1971	Chavan, 1969
Genus *Phacoides*	Genus *Linga*	Genus *Lucina*	Genus *Linga*
Subgenus *Here*	Subgenus *Linga* s.s.	Subgenus *Lucina* s.s.	Subgenus *Linga* s.s.
	*columbella	*pensylvanica	*columbella
Section *Here* s.s.[1]	*pensylvanica*		
*richtofeni		Subgenus *Here*	Subgenus *Pleurolucina*
pensylvanica	Subgenus *Here*	*richtofeni	*leucocyma
	*richtofeni		
Section *Pleurolucina*		Subgenus *Pleurolucina*	Subgenus *Bellucina*
*leucocyma	Subgenus *Pleurolucina*	*leucocyma	*semperiana
	*leucocyma		
Section *Cavilucina* Fischer, 1887	*amiantus*	Subgenus *Cavilinga*	Genus *Here*
trisulcata		*trisulcata	
	Subgenus *Cavilinga*		Subgenus *Here* s.s.
Subgenus *Parvilucina*	*trisulcata	Subgenus *Parvilucina*	*richtofeni
		*tenuisculpta	
Section *Parvilucina* s.s.	Subgenus *Parvilucina*		Genus *Parvilucina*
*tenuisculpta	*tenuisculpta	Subgenus *Bellucina*	
		*semperiana	Subgenus *Parvilucina* s.s.
Section *Bellucina*	Subgenus *Bellucina*	*amiantus*	*tenuisculpta
*semperiana	*semperiana		
amiantus			Subgenus *Cavilinga*
			*trisulcata

[1] s.s.=sensu stricto.

Bretsky, 1969; Britton, 1970.) Thus, instead of the groups of Table 1 being considered of the genus *Phacoides,* Chavan placed them in the genus *Linga.* He affirmed that phylogenetic relationships between and among these taxa were very difficult to understand, and proposed a taxonomic solution whereby each of the major lineages within his genus *Linga* were subgenera with more-or-less equal status. Like Dall, Chavan recognized all of the groups of Table 1 to be more closely related to each other than to other Lucinidae, a fact which becomes less obvious in his more recent classification (Chavan, 1969). The details of both Chavan classifications are given in Table 2. Note that Chavan (1937, 1938) considered *Phacoides amiantus* Dall, 1901, to be a member of the subgenus *Pleurolucina* rather than *Bellucina* to which it was originally referred by Dall. Much more will be said of this matter shortly.

In the more recent Chavan classification (1969), several groups previously considered subgenera are elevated to genera, including *Here* and *Parvilucina* (Table 2). *Pleurolucina* and *Bellucina* are considered subgenera of the genus *Linga;* whereas *Cavilinga* is a subgenus of the genus *Parvilucina.* Hence, Chavan (1969) does not consider *Bellucina* to be as closely related to *Parvilucina* as it was originally considered by Dall (1901).

A few months before publication of Chavan's more recent classification, Bretsky (1969) completed a doctoral dissertation on phenetic and phylogenetic classifications of the Lucinidae. Bretsky's systematic treatment of the *Lucina,* sensu lato, complex is quite similar to that of Chavan (1937, 1939), as she considers each of the groups subgenera of a single taxon (Table 2). Yet her classification differs in several details from both of Chavan's classifications. For example, Bretsky gives a very convincing argument (accepted in this paper) favoring Schumacher's (1817) subsequent designation of *Venus pensylvanica* Linnaeus, 1758, as the first valid type-species designation of *Lucina.* She also rejects Chavan's contention that *Phacoides amiantus* Dall, 1901, is a *Pleurolucina,* placing it in the subgenus *Bellucina.* Bretsky indicates, however, that specimens of the type-species of *Bellucina* (i.e., speci-

mens of *Lucina semperiana* Issel, 1869) were not available for her examination. Hence, Bretsky's concept of *Bellucina* is based on *P. amiantus* and its close relatives rather than upon the type-species. Some of these data have subsequently been published (Bretsky, 1971).

While preparing a monograph of the Western Atlantic Lucinidae, I discovered two new species which help to clarify relationships among the taxa of Table 1. One of the new species also has been influential in the decision to designate a new subgenus, although it is not of the new subgenus itself. The new species and new subgenus are described below, followed by a discussion of their significance and relationship to the taxa of Table 1.

Acknowledgments

This paper is based on data obtained in part during preparation of a doctoral dissertation for The George Washington University, under the direction of Dr. Harald A. Rehder, National Museum of Natural History, Smithsonian Institution. I would like to express my gratitude to Dr. Rehder for many valuable hours of consultation which helped make this work possible, and for numerous helpful suggestions during preparation of the manuscript. I am also indebted to Dr. Joseph Rosewater, also of the National Museum of Natural History, for additional guidance and criticism.

Lucina (Pleurolucina) hendersoni, new species

FIGURES 1, 2, and 6*c*

TYPE.—Holotype, USNM 503399; type-locality, off English Harbor, Antigua in 120 fms.

DESCRIPTION.—*General Form:* Shell attaining 12.5 mm in length and 12.3 mm in height, more or less trigonal, equivalve, inequilateral with beaks posterior to midlength, valves moderately inflated; posterodorsal margin gently curving from beak to beyond posterior termination of hinge plate; posterior margin gently curving to marginal termination of posterior sulcus, there becoming indented; posteroventral, ventral, and anteroventral margins smoothly curving (see p. 6); anterior margin slightly projecting, indented at marginal termination of dorsalmost anterior sulcus; anterodorsal margin slightly arching above hinge plate.

Beaks, Umbos: Beaks coiled under umbos, posterior to midlength of shell. Umbos coiled, prosogyrate, distinctly projecting above body of shell.

Sulci, Folds, Ridges: Posterior sulcus strong, extending from beak to ventral margin; posterior

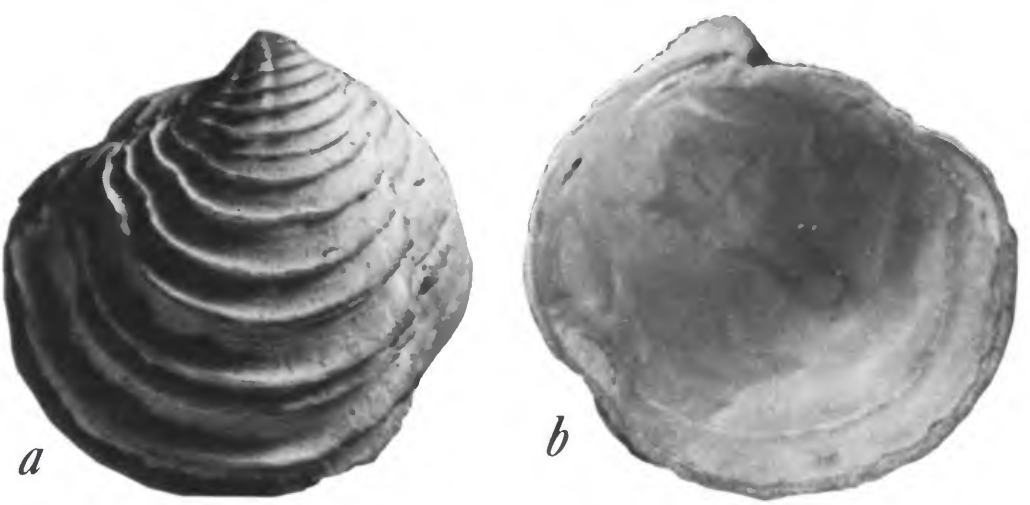

FIGURE 1.—*Lucina (Pleurolucina) hendersoni*, new species, holotype, USNM 503399: *a*, external aspect of left valve; *b*, internal aspect of left valve. Length, 12.3 mm.

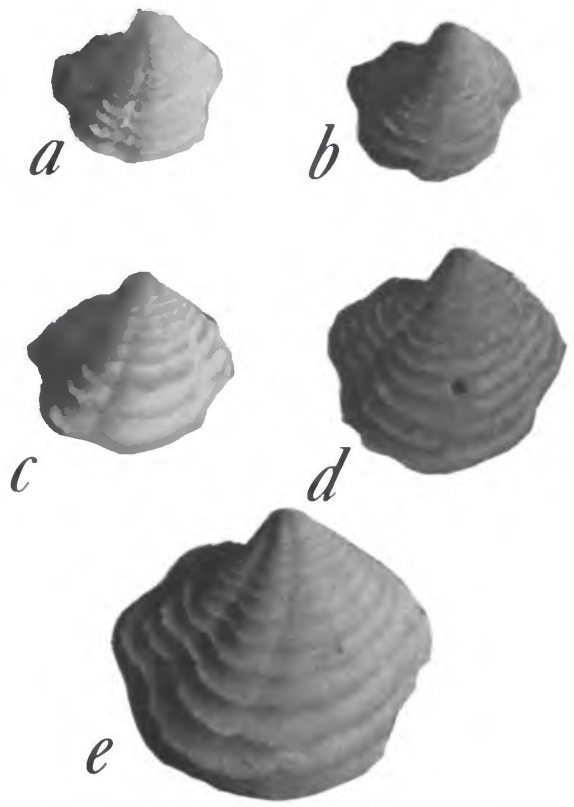

FIGURE 2.—Paratype specimens of *Lucina (Pleurolucina) hendersoni*, new species, USNM 712452. Note how ventral marginal outline becomes less irregular with increase in size. Length of (*e*), 10.2 mm; others to scale.

dorsal area bearing sculpture as on body of shell. Three or four anterior sulci variably expressed; dorsalmost anterior sulcus strongly impressed, extending from beak to anterior margin, forming distinct anterior dorsal area or pseudolunule; second or next posteriormost sulcus relatively strong on dorsal half of valve, but becoming weak or obscure toward margin; third sulcus restricted to umbo, centrally located, crossing few strongly elevated concentric lamellae; fourth sulcus extremely obscure, occuring only on dorsal portion of umbo between third sulcus and posterior sulcus.

Lunule, Escutcheon, External Ligament Area: Lunule very small, slightly depressed, located immediately ventral of and extending slightly posterior to beaks, essentially symmetrical, not projecting. Escutcheon absent. Insufficient material to describe ligament suture or nature of external ligament area.

Ornamentation: Except for sulci noted above, radial ornamentation absent; concentric sculpture consisting of several widely spaced, distinctly erect, concentric lamellae, fewer than one lamella per millimeter at a point between 4 and 5 millimeters ventral to umbo, dorsal edge of each lamella sharply formed; secondary concentrics present on interspaces between primary lamellae, low, feeble, numerous in each interspace; primary lamellae interrupted by posterior and first anterior sulcus, interrupted on dorsal half of shell by second anterior sulcus, and interrupted on umbo by third anterior sulcus.

Internal Shell Morphology: Hinge plate moderately thickened; ligament opisthodetic, moderately inset, relatively short; dorsal lamellar layer very thin, extending from beak to half-way to anterior termination of posterior laterals, in contact with ventral fibrous layer along entire length of latter; fibrous layer separated from posterior laterals by undifferentiated portion of hinge plate almost equal to length of posterior laterals, moderately thickened centrally, separated from ventral margin of hinge plate by undifferentiated region narrower than width of ligament area.

Dentition of right valve including anterior lateral tooth (A III), opisthocline, narrow, sharply pointed, distinctly protruding, separated from anterodorsal margin by shallow groove, ventral portion of tooth on distinct ridge of hinge plate and with cusp to receive left ventral anterior lateral; hinge plate narrowing toward cardinal area; anterior lateral separated from anterior termination of lunule; lunule not jutting, majority of lunule under and posterior to beaks; anterior cardinal tooth (3a) small, feeble, slightly elevated, essentially orthocline, positioned on ventral portion of hinge plate and slightly posterior to anterior termination of lunule, separated from posterior cardinal by small narrow socket to receive left anterior cardinal; posterior cardinal tooth (3b) moderately enlarged, prosocline, bifid, situated on ventral margin of hinge plate, anterior portion projecting slightly ventrad, separated from ligament area by broad shallow socket to receive left posterior cardinal; posterior lateral tooth (P III) prosocline, moderately elongate, distinctly elevated but less so

than right anterior lateral, separated from posterodorsal margin by narrow groove, ventral surface with distinct cusp to receive left ventral posterior lateral.

Dentition of left valve including two orthocline anterior lateral teeth with ventral member somewhat anterior to dorsal member; dorsal anterior lateral tooth (A IV) not strongly elevated, separated from dorsal margin by broad shallow groove, separated from ventral anterior lateral by broad, deep socket to receive right anterior lateral; left ventral anterior lateral tooth (A II) bluntly pointed, distinctly projecting, located on ventral portion of hinge plate posterior and immediately dorsal to dorsal termination of anterior adductor muscle impression; anterior laterals separated from cardinal area by undifferentiated portion of hinge plate extending approximately three times length of left dorsal anterior lateral; lunule as in right valve; anterior cardinal tooth (2) essentially orthocline, distinctly projecting, located on ventral projection of hinge plate, not elongate in dorsoventral axis, dorsal termination of tooth separated from ventral rim of lunule by narrow depression, apex of tooth lying almost ventral and slightly anterior to anterior termination of posterior cardinal, separated from latter by relatively deep, broad socket to receive right posterior cardinal, less remote from beak than corresponding tooth in *P. leucocyma;* posterior cardinal tooth (4b) prosocline, lamelliform, distinctly elevated, separated from ligament area by narrow undifferentiated portion of hinge plate; posterior lateral teeth prosocline; dorsal posterior lateral tooth (P IV) very weak, slightly elevated, separated from ventral posterior lateral by elongate socket to receive right posterior lateral; left ventral posterior lateral tooth (P II) strongly elevated, elongate, apex bluntly rounded and almost appearing flattened, posterior termination of tooth immediately dorsal to dorsal termination of posterior adductor muscle impression.

Anterior adductor muscle impression elongate, more or less typically lucinoid, somewhat L-shaped, pallial line junction slightly dorsal to midlength of adductor impression, dorsal and ventral portions of impression undifferentiated, anterior pedal retractor impression small, separated from anterior adductor impression, located immediately above dorsal termination of latter and immediately below anterior termination of anterior laterals; pallial line typical, relatively narrow; posterior adductor muscle impression relatively small, ovate, bluntly pointed dorsally, rounded ventrally, pallial line junction slightly above distalmost portion of impression. Line of gill attachment and pallial blood vessel impression faintly indicated. Internal ventral margin finely crenulate.

Soft Parts: Neither living specimens nor specimens with preserved soft parts were available for study.

Color of Shell: All fresh specimens examined possessed uniformly chalky white shells.

Measurements: There are no paired valves of this species available for study. Measurements below are in millimeters.

length	*height*	*inflation*	
12.3	12.3	4.4	holotype
9.4	9.1	3.0	paratype
6.5	6.5	2.0	paratype
4.4	4.0	1.6	paratype
12.5	12.0	4.0	Off Payne's Bay Church, Barbados
9.9	10.9	3.6	Off Payne's Bay Church, Barbados
9.8	9.9	3.1	Off Telegraph Station, Barbados
9.2	9.5	2.9	Off La Habana, Cuba
9.1	8.9	2.7	Off Payne's Bay Church, Barbados
8.5	8.5	2.7	Off Payne's Bay Church, Barbados
6.5	6.1	1.9	Off Telegraph Station, Barbados
5.2	4.9	1.7	Off Pelican Id., Barbados

VARIATION.—With very few specimens available for examination, only a few remarks on variation are possible here. Marginal outline changes noticeably with the growth of the shell (Figure 2). In younger shells (6 mm or less in length) there are two distinct marginal indentations: one on the posteroventral margin at the termination of the posterior sulcus, and the other on the anteroventral margin at the termination of the second anterior sulcus. As the shell increases in size, the second anterior sulcus becomes progressively weaker until it is no longer impressed in the ventral portion of the shell. Concurrently the anteroventral indention of the shell margin becomes less noticeable. In the adult (8 mm or more) this area is smoothly curving without a trace of indentation.

The spacing of primary concentric lamellae on the shell exterior of the holotype is representative of the condition observed in most specimens available for study. In one valve (a single specimen from off La Habana, Cuba) these lamellae are more numerous than on the holotype and considerably more closely spaced (about two per millimeter).

The lamellae of this specimen does not approach even closely the high density condition of the lamellae of *L. leucocyma,* but it certainly demonstrates that a potential for more numerous, more closely spaced primary concentrics exists within the lineage.

REMARKS.—This species is named in honor of J. B. Henderson, Jr., a collector *extraordinaire* during the early years of this century.

L. hendersoni is a species linking *Lucina,* sensu stricto, with *Pleurolucina.* The nature of the external sculpture is very similar to that of *Lucina pensylvanica,* and *L. hendersoni* also possesses a distinct pseudolunule or anterior dorsal area quite similar to that of the *Lucina,* sensu stricto, assemblage. The secondary sulcations, however, are decidedly as in *Pleurolucina,* even if they are incompletely indicated in the adult. These sulcations are discussed in considerable detail below. The nature of the shell interior further establishes the affinities of *L. hendersoni* with *Pleurolucina.* This species and *L. leucocyma* are almost identical in all characters of internal shell morphology except in the left valve the anterior cardinal of *L. hendersoni* is less ventrally jutting on the hinge plate, less remote from the beak, and the socket between this tooth and the posterior lateral is shallower and narrower than in *L. leucocyma. L. hendersoni* shares many common characteristics with the fossil *Lucina (Paslucina) follis* Olsson, 1964, from the early Miocene of Ecuador.

RANGE.—Based on the present records for this species, *L. hendersoni* is assumed to occur in moderate depths from Cuba to the Lesser Antilles. It appears to be quite uncommonly collected.

MATERIAL EXAMINED.—CUBA: off La Habana in 127 fms (USNM). LESSER ANTILLES: off English Harbor in 120 fms, off Paynes Bay Church in 50 fms, off Telegraph Station in 50 to 60 fms, and off Pelican Is. in 100 fms, Barbados (all USNM).

Parvilucina (Bellucina) rehderi, new species

FIGURE 3

TYPE.—Holotype, USNM 208255; type-locality, Brazil.

DESCRIPTION.—*General Form:* Shell attaining 4.2 mm in length and 4.2 mm in height, subtrigonal, equivalve, slightly inequilateral with beaks posterior to midlength, valves moderately inflated. Posterodorsal margin slightly curving from beak to point near posterior termination of hinge plate, thereafter passing rather abruptly ventrad; posterior margin straight; posteroventral margin rather sharply angular; posterior margin gently curving to about midlength of shell, thereafter arc of curve becomes sharper; anteroventral margin somewhat produced but smoothly curving; anterior margin dorsoventrally straight for short distance; anterodorsal margin arching above anterior laterals.

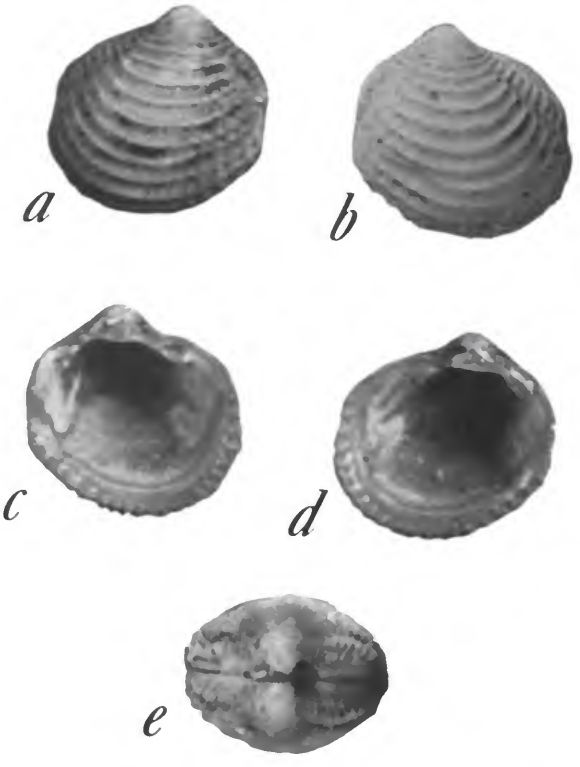

FIGURE 3.—*Parvilucina (Bellucina) rehderi,* new species, holotype, USNM 208255: *a,* external aspect of the left valve; *b,* external aspect of right valve; *c,* internal aspect of left valve; *d,* internal aspect of right valve; *e,* dorsal aspect of paired valves. Length, 4.2 mm.

Beaks, Umbos: Beaks small, depressed, adjacent but not touching. Umbos moderately projecting above body of shell.

Sulci, Folds, Ridges: Posterior sulcus broad and widening ventrally, sufficiently depressed to indi-

cate posterior dorsal area; posterior dorsal area distinct, tending to be elevated marginally. Anterior sulcus poorly impressed; anterior dorsal area poorly differentiated.

Lunule, Escutcheon, External Ligament Area: Lunule distinct, approximately as long as wide, inserted slightly beneath beak, extending from there to point immediately posterior to posterior termination of anterior laterals, depressed, slightly unsymmetrical with portion on right valve projecting and portion on left valve recessed. Escutcheon absent. External ligament area quite short, about one-half width of lunule.

Ornamentation: Dominant sculpture concentric, lamellae elevated, thickened, moderately spaced, interspaces between lamellae at least width of lamellae and usually broader, lamellae on ventral portion of valve usually more elevated than those on upper third of valve, lamellae often appear scalloped by forming nodules in positions adjacent to elevated regions of radial sculpture; radial ribs present but poorly distinguished, best developed in interspaces between concentric lamellae particularly on dorsal third of valve, appearing as poorly elevated columnar elements between concentrics, rarely sufficiently distinct so as to appear to cross concentrics although ventral nodes on some concentric lamellae may be fused with some ribs; ribs broad, separated by very shallow, narrow interspaces; ribs tend to become progressively less distinct toward ventral margin or to lie primarily upon dorsal surface of the broadest concentric lamellae instead of being located only in interspaces between lamellae. Very low scales formed by local elevations of concentric lamellae tend to occur on posterior dorsal area.

Internal Shell Morphology: Hinge plate noticeably thickened; ligament opisthodetic, slightly inset, quite short, extending from beak to approximately midlength between beak and apex of posterior laterals, extending only slightly beyond posterior termination of cardinal plateau; material insufficient to determine nature of ligament layers.

Dentition of right valve including anterior lateral tooth (A III), large, bulbous, prominently elevated, located immediately in front of and ventral to anterior termination of lunule, resting on ventrally projecting ridge of hinge plate, separated from anterodorsal margin by broad groove, possessing cusp on ventral surface to receive left ventral anterior lateral; right anterior cardinal tooth (3a) present, opisthocline, small, slightly crowded by encroachment of lunule, more or less lamelliform, extending from point ventral and anterior to posterior termination of lunule and passing anteroventrally, not in contact with ventral margin of hinge plate, separated from ventral surface of lunule by shallow groove, contacting dorsal termination of right posterior cardinal but separated from remainder of latter by triangular socket receiving left anterior cardinal; right posterior cardinal tooth (3b) prosocline, large, well elevated, separated from ligament area by elongate socket receiving left posterior cardinal; right posterior lateral tooth (P III) elongate, anteriorly broad, posterior portion centrally excavated to receive left posterior lateral, separated from posterodorsal margin by broad groove, separated from cardinal area by undifferentiated portion of hinge plate less than length of posterior lateral.

Dentition of left valve including two anterior lateral teeth; dorsal anterior lateral tooth (A IV) extremely feeble, essentially obsolete; ventral anterior lateral tooth (A II) bluntly pointed, moderately elevated, occupying ventrally projecting ridge of hinge plate, located noticeably in front of and ventral to dorsal anterior lateral, separated from latter by deep socket receiving right anterior lateral; left cardinal teeth lamelliform; anterior cardinal tooth (2) orthocline, noticeably elevated, extending from posterior termination of lunule toward but not reaching ventral termination of hinge plate, separated from greater portion of lunule by narrow socket receiving right anterior cardinal, separated from left posterior cardinal by broad triangular socket receiving right posterior cardinal; left posterior cardinal tooth (4b) prosocline, extending from near posterior termination of lunule toward ventral margin of hinge plate, essentially adjacent and in contact with ligament area; two posterior lateral teeth; dorsal posterior lateral tooth (P IV) extremely feeble, essentially obsolete; ventral posterior lateral tooth (P II) bulbous, elevated, positioned on ventrally projecting ridge of hinge plate, located behind and below dorsal posterior lateral, separated from latter by broad, elongate socket receiving right posterior lateral.

Anterior adductor muscle impression longer than wide but very short, pallial line joining anterior adductor impression near ventral termina-

tion of latter; anterior pedal retractor muscle impression small, separate from anterior adductor muscle impression, ovate, located on lower surface of anterior lateral tooth of each valve; posterior pedal retractor impression obscure. Line of gill attachment and pallial blood vessel impression not indicated on specimens available for study. Ventral margin dentate, almost appearing fluted.

Soft Parts: Neither living specimens nor specimens with preserved soft parts were available for study.

Color of Shell: All specimens examined possessed uniformly chalky white shells.

MEASUREMENTS.—Including the holotype, there were 26 left valves and 30 right valves of the new species *P. rehderi* available for study. Measurements (in mm) given below are of a representative series selected from this material.

length	*height*	*width* (paired values)	*inflation* (unpaired values)	
4.2	4.2	4.1	–	holotype
3.7	3.7	–	1.9	paratype
3.5	3.6	–	1.8	paratype
3.2	3.2	–	1.4	paratype
3.1	3.0	–	1.4	paratype
3.0	3.0	–	1.4	paratype
2.8	2.9	–	1.3	paratype
2.7	2.7	–	1.3	paratype
2.4	2.4	–	1.1	paratype
2.3	2.4	–	1.2	paratype

VARIATION.—The most noticeable variation observed among the specimens available for study concerns the thickness and spacing of concentric lamellae and the degree to which radial elements of sculpture are developed and expressed on the shell exterior. Radial sculpture never approaches the degree of expression demonstrated by that of *Parvilucina (Bellucina) semperiana.*

In *Parvilucina rehderi,* the posterior sulcus tends to be more deeply impressed in some specimens than in others. In those specimens with a more deeply impressed posterior sulcus the angles formed along the posterior margins of the shell tend to be more acute.

The degree to which the shell is produced anteroventrally is variable. Some specimens possess an anteroventral margin only slightly produced, whereas others demonstrate a markedly extended anteroventral margin.

Among those characters which demonstrate very little variation are the nature of the hinge and dentition, the nature of the lunule, and the nature of the anterior adductor impression and its junction with the pallial line.

REMARKS.—The species name honors Harold A. Rehder of the National Museum of Natural History, Smithsonian Institution.

Although the hinge plate of *P. rehderi* is not quite as broad as that of *P. semperiana* (Figures 3 and 4*a*), these two species demonstrate virtually identical hinge structure and dentition. Most other species of shell morphology correspond closely between the two species. *P. semperiana* differs from *P. rehderi,* however, in being larger, with a slightly shorter and more noticeably unsymmetrical lunule. The anterior dorsal area of *P. semperiana* tends to be slightly more distinct than that of *P. rehderi.* Similarly, the radial sculpture of the former species is more apparent but by no means dominant. Most aspects of the internal shell morphology of the two species are identical, including the nature of the anterior adductor impression and its junction with the pallial line.

Some criticism may be leveled at the description of a new species based on one lot from such a generalized locality as Brazil. Were it not for the fact that significant sculptural and other differences tend to separate *P. rehderi* and *P. semperiana,* I would be hesitant to describe the new form. However, there is definite morphological differentiation between the two. It is with some reluctance, therefore, that the new species is proposed; perhaps workers in the western South Atlantic region will be advised to search for additional records of this small species.

Parvilucina rehderi is certainly closely related to *Parvilucina (Bellucina) semperiana* (Issel, 1869). The latter is of the type of the subgenus *Bellucina,* hence *P. rehderi* is a member of the subgenus *Bellucina.* Thus, *P. rehderi* is the first species of *Bellucina* described from the Western Atlantic.

RANGE AND MATERIAL EXAMINED.—The species is known only by a single lot of material. The only locality record given is "Brasil."

Genus *Parvilucina*
Subgenus *Radiolucina,* new subgenus

TYPE-SPECIES.—*Phacoides amiantus* Dall, 1901

DIAGNOSIS.—Shell suborbicular to slightly elongate, equivalve, moderately to well inflated, usually

less than 20 mm. Anterior and posterior dorsal areas moderately to weakly indicated; lunule moderately elongate, narrow, unsymmetrical with portion in right valve slightly wider, not inserted beneath beaks, slightly to moderately depressed; escutcheon absent or very narrow. Dominant sculpture radial, consisting of less than 20 broad, prominently elevated ribs; concentric sculpture consisting of numerous fine lamellae, moderately spaced, elevated on and between ribs, definitely secondary in prominence to radials. Periostracum thin, obscure; ligament external, poorly depressed, extremely short. Hinge plate usually dorsoventrally broad; anterior and posterior lateral teeth well developed, single in right, paired in left valve; two cardinal teeth in left valve, right anterior cardinal tooth (3a) usually present but weak, right posterior cardinal tooth (3b) strong. Anterior adductor muscle impression relatively short, junction with pallial line usually ventral to midlength of muscle impression; anterior pedal retractor muscle impression separate from anterior adductor impression. Ventral margin crenulate.

REMARKS.—Since the original description of *Phacoides amiantus* Dall, 1901, the systematic position of this species has been subjected to several interpretations (Table 2). Most recently, Bretsky (1969) suggested the possibility that *P. amiantus* might represent a lineage distinct from any previously designated group. She rejected Chavan's (1937, 1938) assignment of *P. amiantus* to *Pleurolucina* on grounds never adequately explained but presumably according to some of the points developed in the discussion below. Because she lacked specimens of the type-species of *Bellucina* (*Lucina semperiana* Issel, 1869) with which she could compare *P. amiantus,* Bretsky accepted Dall's assignment of the latter to *Bellucina,* noting that *P. amiantus* and *L. semperiana* could be of distinct lineages.

I have had an opportunity to compare *Phacoides amiantus* with specimens of *Lucina semperiana* and several other species (Figure 4, Table 3). I believe *P. amiantus* represents a distinct lineage within the Lucinidae, for reasons given in the discussion. Thus, I propose the new subgenus, *Radiolucina,* for those species similar to *Phacoides amiantus* Dall, 1901. This includes the Recent Eastern Pacific species *Lucina cancellaris* Philippi, 1846, and several Tertiary fossils, including *Phacoides wacamawensis* Dall, 1903, *Phacoides tuomeyi* Dall, 1903, *Lucina katherinepalmerae* Weisbord, 1964, *Phacoides nereidedita* Maury, 1910, and *Phacoides euphaea* Gardner, 1926.

DISCUSSION.—The discussion is primarily concerned with two considerations previously noted by Bretsky (1969): (1) the possibility that *Parvilucina, Bellucina* (fide Bretsky; that is, those species of *Radiolucina* herein), and *Pleurolucina* form "a phyletic progression with sequential decrease in number and increase in size of radial ribs" (Bretsky, 1969:72); and (2) the possibility that "the type of *Bellucina* is actually a *Parvilucina* [or otherwise not related to *Lucina amiantus,* JCB] in which case a new subgeneric name would have to be proposed for the distinctive group of species to which *L. amiantus* belongs" (Bretsky, 1969:278).

RADIAL ORNAMENTATION AND THE CONDITION IN PLEUROLUCINA.—Both of the above considerations involve, to a greater or lesser degree, the nature of radial ornamentation on *Pleurolucina.* It is generally agreed among the major revisers of the Lucinidae that *Pleurolucina* possesses radial "ribs." An undefined assumption seems to hold that these ribs are primary elevations upon the shell exterior and arise in a manner analogous with the ribs of certain species of *Parvilucina* and *Radiolucina.* By comparing the radial ornamentation of several species of each of these groups, certain trends or central tendencies within and between the groups become apparent. Phylogenetic interpretations may vary according to the direction one assigns to these tendencies. For example, Bretsky (1969) presents evidence which favors recognition of a *Parvilucina-Radiolucina* lineage (Figure 5). I concur with Bretsky's hypothesis, considering the lineage as possessing "true" radial ribs (i.e., ribs formed as primary localized elevations above an external shell base) which demonstrate the tendency to become more prominently elevated and fewer in number. Bretsky also suggests that *Pleurolucina,* with a few broad radial "ribs," could form a terminal element of the *Parvilucina-Radiolucina* lineage. I disagree.

The radial ribs of *Pleurolucina* do not seem to be analogous to those of the *Parvilucina-Radiolucina* complex. The ribs of the former apparently are not primary elevations above the shell base; rather they are secondary "elevations" formed subsequent to and mostly as a result of the formation

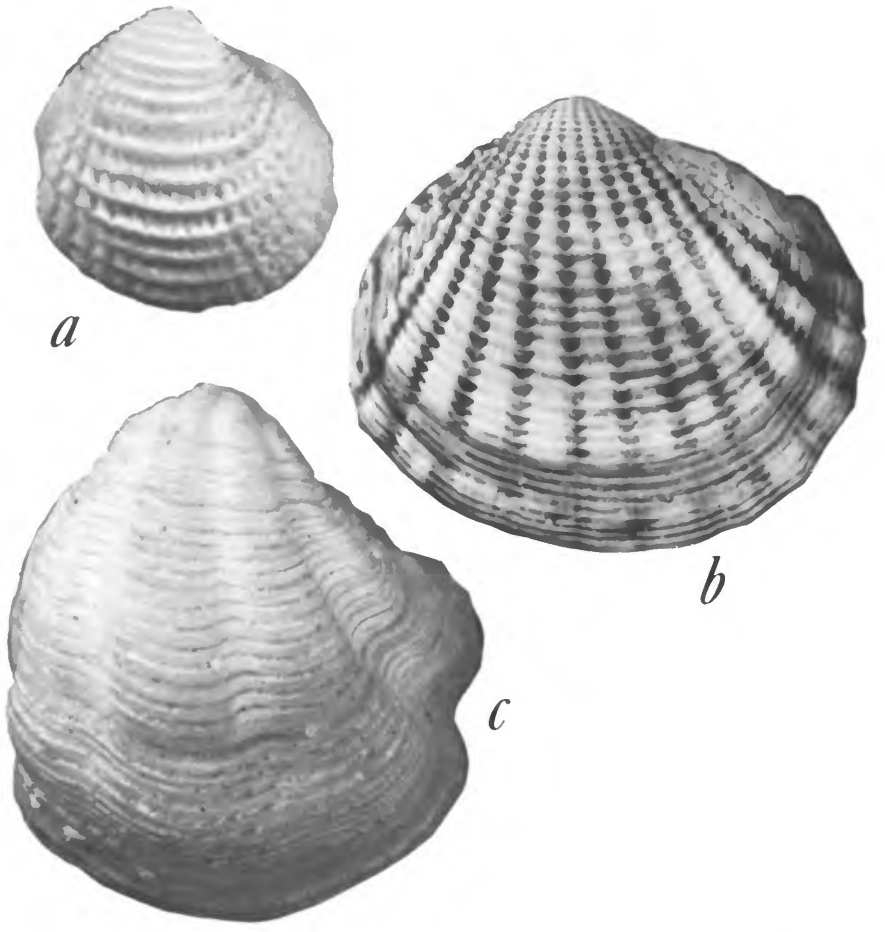

FIGURE 4.—Comparison of the type-species of the subgenera *Bellucina, Radiolucina,* and *Pleurolucina: a, Parvilucina (Bellucina) semperiana* (Issel, 1869), USNM 598440, right valve exterior, length 3.2 mm; *b, Parvilucina (Radiolucina) amiantus* (Dall, 1901), USNM 64276, right valve exterior, length 8.6 mm; *c, Lucina (Pleurolucina) leucocyma* Dall, 1886, USNM 83140, right valve exterior, length 6.8 mm.

of radial sulci (i.e., localized depressions below the shell base).

Consider the condition of *L. (Pleurolucina) hendersoni,* new species. The crest or high point of each of the "ribs" of *L. hendersoni* is equivalent to the base level of elevation on the shell exterior. Concentric lamellae are elevated above this base level, while several shell sulci or grooves are incised below it. [According to a figure (Keen, 1958: 97), *L. leucocymoides* (Lowe, 1935) of the eastern Pacific has radial elements of sculpture almost identical to that of *L. hendersoni.* I have not seen specimens of *L. leucocymoides.*] When sulci fail to be impressed on the ventral third of the valve, the base level is essentially at the same relative elevation as the "rib" crests on the more dorsal portion of the valve. The condition of *L. hendersoni* is in contrast to that of certain *Radiolucina*

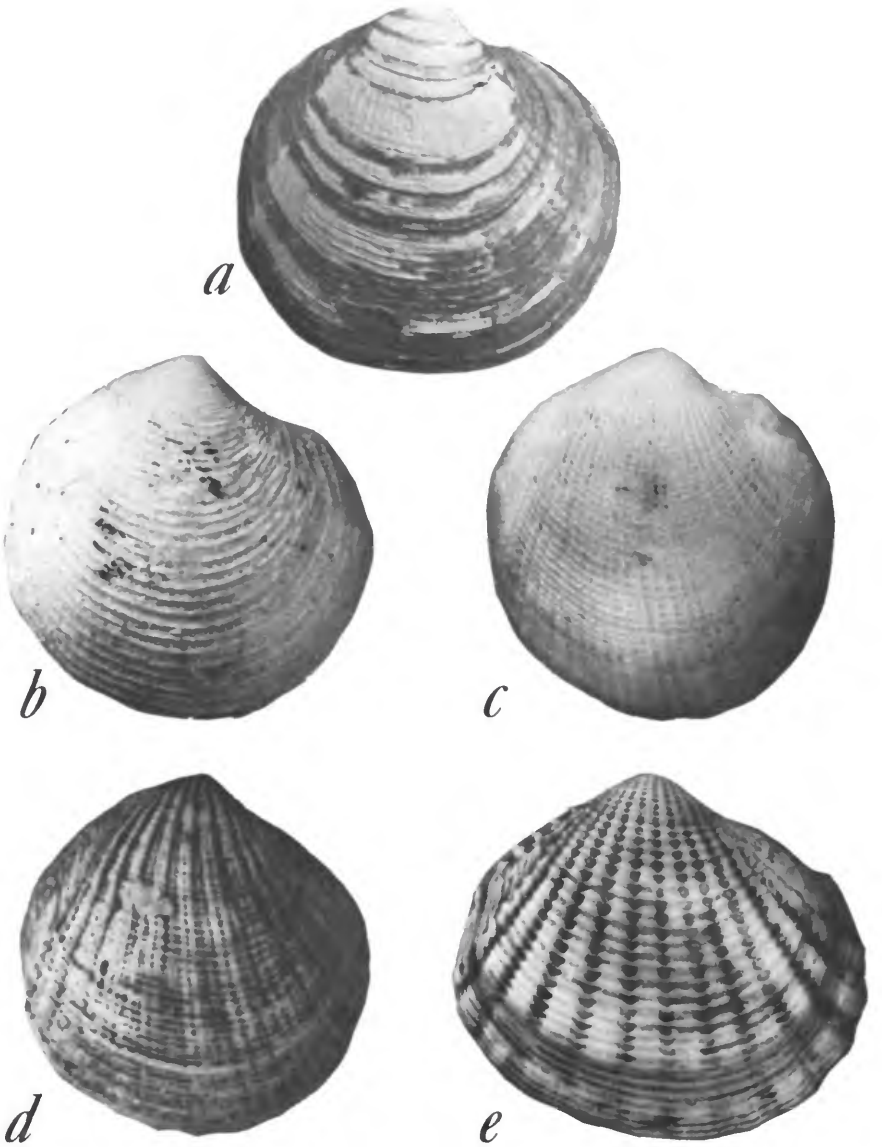

FIGURE 5.—Possible sequence of a *Parvilucina–Radiolucina* lineage with Recent species as examples. All specimens right valves with external view: *a*, *Parvilucina (Parvilucina) tenuisculpta* (Carpenter, 1864), USNM 108826, length 13.6 mm; *b*, *P. (P.) multilineata* (Tuomey and Holmes, 1856), USNM 60981, length 5.1 mm; *c*, *P. (P.) pectinella* (C. B. Adams, 1852), MCZ 155597, length 6.8 mm; *d*, *P. (P.) costata* (d'Orbigny, 1842), USNM 683297, length 9.4 mm; *e*, *P. (Radiolucina) amiantus* (Dall, 1901), USNM 64276, length 8.6 mm.

which also demonstrate a slight tendency toward ventral obsolescence of radial sculpture [e.g., *Parvilucina (Radiolucina) waccamawensis* (Dall, 1903) of the South Carolina Pliocene, or *P. (R.) tuomeyi* (Dall, 1903), a Miocene species from the same geographic region]. In these species the base level on the central valve exterior corresponds not with the crests of the ribs, but with the floor of the grooves between the ribs as they exist on the more dorsal portions of the valve exterior.

An alternative to Bretsky's (1969) *Parvilucina,* sensu lato, *Pleurolucina* progression hypothesis takes into consideration the nature of radial ornamentation in *L. hendersoni.* According to the new hypothesis *Pleurolucina* is visualized acquiring radial "ribs" secondarily after sulci formation rather than as primary formations elevated above a shell base. The radial ornamentation of *L. leucocyma* could have arisen just as easily by this secondary, sulci-related process.

The first stage of the progression might be similar to the condition in *L. sombrerensis* (Dall, 1901), a Recent western Atlantic species. The shell of this species almost lacks radial ornamentation. On the anterior slope of each valve, however, are two radial sulci. The anteriormost sulcus is slightly weaker than the other but extends entirely to the anterior margin. The second or more posteriorly located sulcus fails to extend entirely to the anteroventral margin. Figure 6*a* illustrates the external ornamentation on the shell of *L. sombrerensis.*

The next stage of the series is represented by a form like *L. hendersoni,* or the fossil *L. follis* Olsson, 1964, and has been described (Figure 6*c*). The dominance of sulci over "ribs" is obvious in this stage.

L. leucocyma (Figure 6*d*) is an example of the final stage where the radial "ribs" take the form of definite elevations. This seems to have been achieved by two simultaneous developments: (1) the sulci deepen and widen, while (2) the shell undergoes a moderate anteroposterior compression (i.e., a dorsoventral elongation). These two processes acting together cause slight folding of the radial ornamentation, additional deepening of the sulci, and elevation of the "ribs."

If *Pleurolucina* originated in a manner such as has just been postulated, perhaps additional evidence could be presented suggesting a closer relationship between it and some other lucinid group lacking primary radial elevations of the shell exterior (i.e., lacking ribs). Such is the case between *Pleurolucina* and *Lucina,* sensu stricto.

THE RELATIONSHIP BETWEEN LUCINA, SENSU STRICTO, AND PLEUROLUCINA.—A cursory examination of the type-species of *Lucina,* sensu stricto, and *Pleurolucina* gives one cause to doubt that these species are closely related. Not only is *L. leucocyma* considerably smaller than *L. pensylvanica* and, unlike the latter, possesses "radial" ornamentation, but the concentric ornamentation of the valve exterior appears to be different. *L. leucocyma* possesses relatively broad concentric lamellae separated by narrow interspaces, whereas *L. pensylvanica* has fewer narrow primary concentrics separated by wider interspaces. Closer examination of the shell morphology of the two groups reveals, however, several important similarities between them.

The similarity of hinge structures has already been mentioned. This similarity is an inconclusive correspondence shared by a number of lucinid groups. Other common features of *Lucina,* sensu stricto, *Pleurolucina,* and *Here* (a group very closely related to *Lucina,* sensu stricto, but differing from it primarily by the nature of the lunule) can be listed and compared with corresponding features of the *Parvilucina-Radiolucina* complex.

1. The lunule of *Pleurolucina* is either very small and inserted below and posterior to the beaks as in *Lucina,* sensu stricto, or deeply incised in a manner similar to the condition in *Here;* whereas the lunule of *Parvilucina,* sensu lato, tends to be more elongate.

2. Most species of *Pleurolucina* possess a relatively broad anterior dorsal area or pseudolunule as in *Lucina,* sensu stricto, and *Here;* whereas the anterior dorsal area in *Parvilucina,* sensu lato, usually is considerably narrower and less noticeable.

3. The junction of the pallial line with the anterior adductor muscle impression in *Pleurolucina* is located dorsal to midlength of the muscle scar as in the genus *Lucina;* whereas this condition is observed rarely among species of *Parvilucina,* sensu lato.

4. The posterior sulcus of *Pleurolucina* is usually well impressed and the posteroventral margin

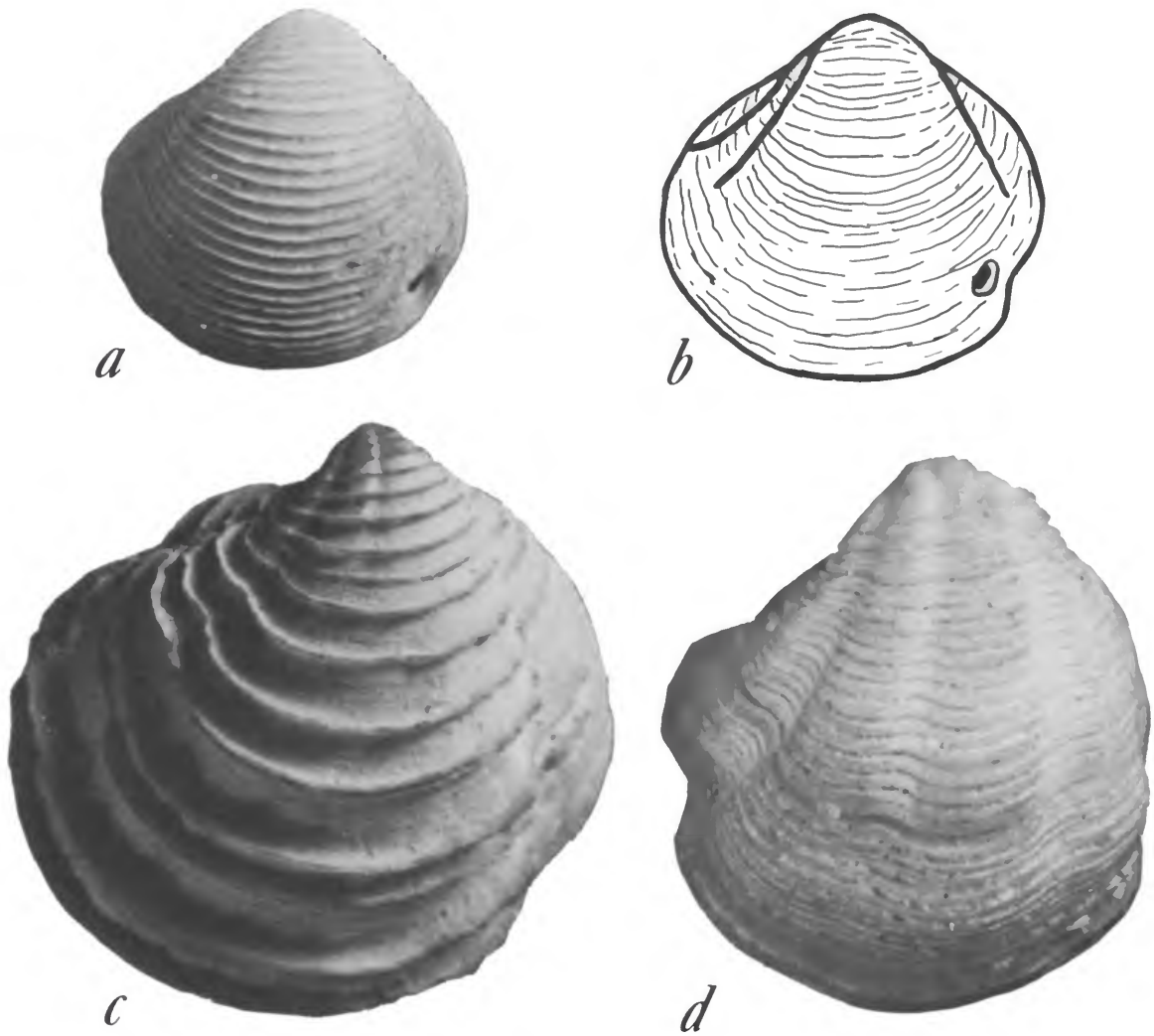

FIGURE 6.—Possible derivation of radial ornamentation in *Pleurolucina: a, Lucina (Pleurolucina) sombrerensis* (Dall, 1901), USNM 329253, length 5.9 mm, left valve exterior; *b,* line drawing of preceding, indicating position of radial ornamentation; *c, L. (P.) hendersoni,* new species, USNM 503399, length 12.3 mm, left valve exterior; *d, L. (P.) leucocyma* Dall, 1886, USNM 83140, length 6.8 mm, right valve exterior photographically reversed to facilitate comparison with other specimens.

is noticeably incised at the termination of this sulcus; this condition occurs in *Lucina,* sensu stricto, and *Here,* but is expressed weakly or not at all in *Parvilucina,* sensu lato.

The major weakness in the case for a close phylogenetic relationship between *Pleurolucina* and *Lucina,* sensu stricto, has been the nature of external ornamentation of the two groups. Simi-

larly, this has seemed to be one of the major arguments for a relationship between *Pleurolucina* and *Parvilucina*, sensu lato. If differences of shell ornamentation between the former pair could be satisfactorily accounted for, the case for a closer relationship between these groups would be considerably strengthened. By resolving the matter of radial ornamentation in *Pleurolucina* in the preceding section, there remains only to demonstrate some degree of relationship between the two groups with regard to concentric lamellae. *L. hendersoni*, new species, can be employed again to represent an intermediate stage between the two types.

There should be little doubt that *L. hendersoni* is a *Pleurolucina*, considering the typical five sulci of the shell exterior and the close correspondence of its internal shell morphology with that of *L. leucocyma*. Its concentric lamellae are quite unlike those of *L. leucocyma*, being very narrow, well elevated, and broadly spaced in a manner similar to that expressed by *L. pensylvanica*. Thus, species such as *L. hendersoni* seem to suggest a transitional stage betwene *Lucina*, sensu stricto, and *Pleurolucina* with respect to concentric ornamentation and the other morphological shell characters mentioned above.

A good case can be made, then, for a close phylogenetic relationship between *Pleurolucina* and *Lucina*, sensu stricto. Now consider the relationships of *Pleurolucina* and *Parvilucina*, sensu lato.

RELATIONSHIPS OF RADIOLUCINA, BELLUCINA, AND PLEUROLUCINA.—*Radiolucina*, *Bellucina*, and *Pleurolucina* are compared primarily to demonstrate the need for the new subgeneric designation, and also to establish a basis for additional phylogenetic considerations (Figure 4). Table 3 summarizes certain morphological shell characteristics of each of the type-species. Most species of *Parvilucina*, sensu stricto, produce weak or relatively feeble elements of radial ornamentation; hence, this subgenus is omitted from the present discussion. Bretsky (1969) has pointed out the tendency of some *Parvilucina*, sensu stricto, species to produce relatively stronger radial elements which approach the condition of *Radiolucina*.

Radiolucina and *Bellucina* share a number of very similar morphological shell characters including several not included in Table 3. Hence, both are considered of the *Parvilucina*, sensu lato, lineage (see Bretsky, 1969). The justification for designating the former group as a new subgenus, however, is based primarily on differences with respect to (1) the nature of the ventral margin, (2) certain aspects of cardinal and lateral dentition, and especially (3) the nature of external ornamentation. The latter difference is particularly pronounced. Radial ribs of *Radiolucina* are unquestionably dominant over concentric lamellae, usually tending to obscure the latter. In *Bellucina* the condition is reversed with the concentric lamellae being dominant. Radial sculpture in *Bellucina* is restricted to interspaces between concentrics giving the appearance of numerous separate, short columnar elements.

The basic difference between *Pleurolucina* and *Radiolucina* with respect to radial ornamentation has already been discussed. In addition, there are a number of other dissimilarities between analgous characters of the two groups. These include (1) the nature of the lunule, (2) the position of the junction of the pallial line with the anterior adductor impression, (3) the nature of the anterior dorsal area, and to a lesser degree (4) the nature of the ventral margin and (5) certain aspects of hinge dentition (Table 3). Similar differences exist between *Pleurolucina* and *Bellucina*. Thus, *Pleurolucina* appears to be more remotely related to *Radiolucina* and *Bellucina* than the latter two are related to one another. This is an additional justification, then, for considering *Pleurolucina* outside the *Parvilucina*, sensu lato, lineage.

CONCLUSIONS.—A systematic revision of those groups listed in Table 1 is proposed. A summary of the revision follows, including names of only those species given primary consideration herein.

Genus *Lucina*
- Subgenus *Lucina*, sensu stricto, including *L. pensylvanica*.
- Subgenus *Here*, including *L. richtofeni*.
- Subgenus *Pleurolucina*, including *L. leucocyma*, *L. hendersoni*, and *L. sombrerensis*.

Genus *Parvilucina*
- Subgenus *Parvilucina*, sensu stricto, including *P. tenuisculpta*.
- Subgenus *Radiolucina*, including *P. amiantus*.
- Subgenus *Bellucina*, including *P. semperiana* and *P. rehderi*.

TABLE 3.—*Comparison of certain morphological shell characters for three lucinid subgenera*

Characters	*Radiolucina*	*Bellucina*	*Pleurolucina*
ORNAMENTATION			
Radial elements	Strongly elevated ribs, crossing or superimposed over concentrics	Poorly elevated ribs, not crossing or superimposed over concentrics	Sulci and sometimes secondarily-formed ribs
Concentric elements	Lamellae	Lamellae	Lamellae
DORSAL AREAS			
Anterior dorsal area	Poorly differentiated	Poorly differentiated	Moderately distinct
Posterior dorsal area	Distinct with portion of area consisting exclusively of concentric sculpture	Moderately expressed with portion of area consisting exclusively of concentric sculpture	Distinct
LUNULE	Usually as long as wide, never deeply excavated, slightly unsymmetrical	Usually as long as wide, never deeply excavated, slightly unsymmetrical	Either obscure and deeply inserted beneath beaks or noticeably excavated, symmetrical
LOCATION OF JUNCTION OF ANTERIOR ADDUCTOR IMPRESSION AND PALLIAL LINE	Pallial line joining anterior adductor impression near ventral termination of latter; pallial line appears fused to outer surface of anterior adductor impression along most of length of latter	As in *Radiolucina*	Pallial line joining anterior adductor impression dorsal to midlength of latter; pallial line appears to be free of anterior adductor impression for about 2/3 length of latter
HINGE STRUCTURE			
Appearance of hinge plate	Strongly thickened	Moderately thickened	Moderately thickened
Length of ligament area	Very short	Very short	Short
Left dorsal lateral teeth (AIV and PIV)	Present but weaker than typical	Essentially obsolete	Well developed
Right anterior cardinal (3a)	Faintly indicated or obsolete	Present	Obsolete
VENTRAL MARGIN	Coarsely crenulate	Very coarsely crenulate, almost fluted	Finely crenulate

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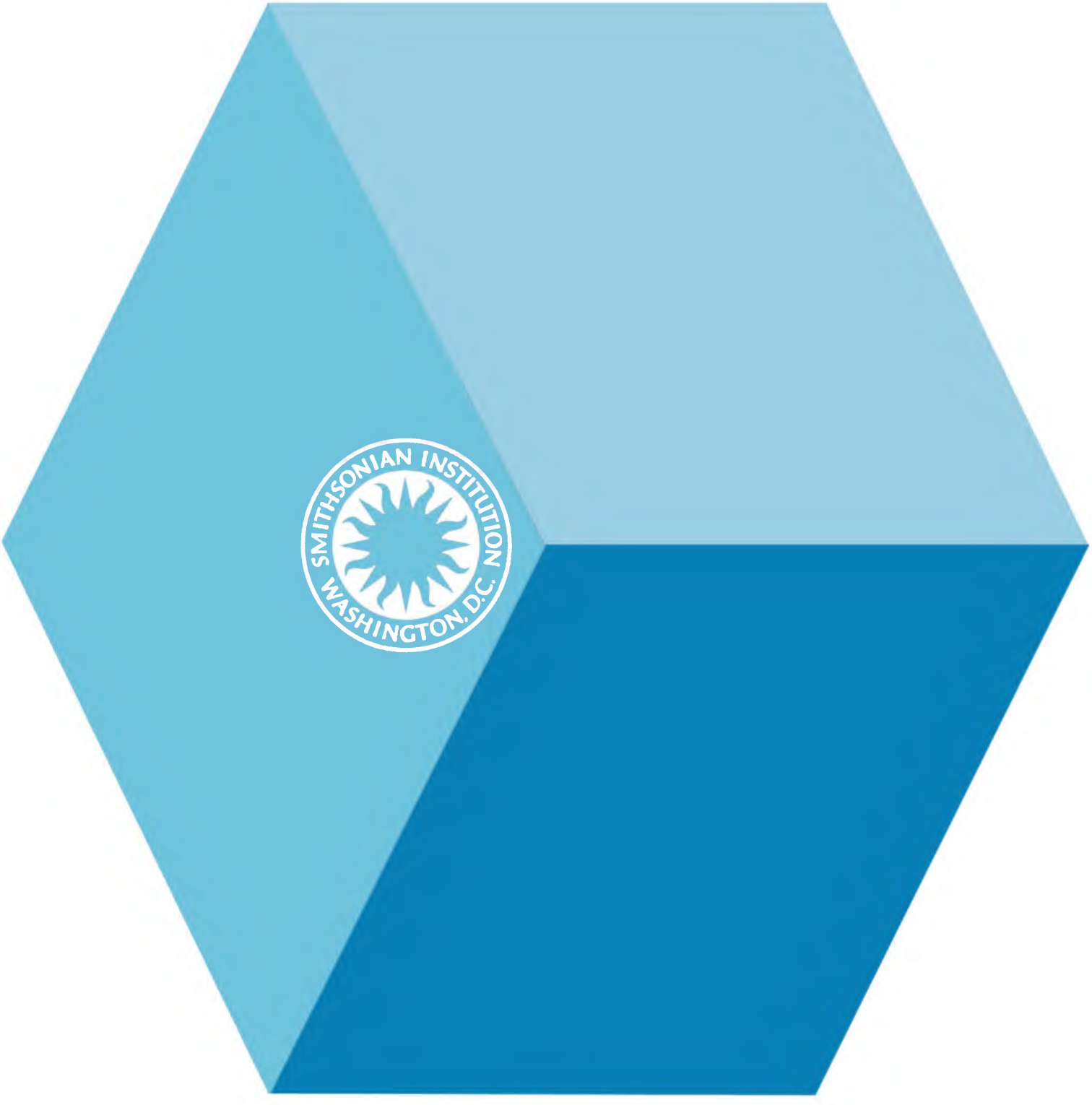
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