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PHENETIC AND PHYLOGENETIC CLASSIFICATIONS OF THE LUCINIDAE (MOLLUSCA, BIVALVIA)

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Abstract. In order to test the hypothesis that phenetic and phylogenetic classifications should closely correspond, a numerical taxonomic study was carried out using 42 species of the bivalve Family Lucinidae. Study of the phylogeny of the lucinids permitted the assignment of these species to seven genera and 28 subgenera. The phenetic study was carried out using both correlation and distance coefficients. Some 45 characters were recorded for each species. The correlation and distance phenograms, constructed by the weighted pair-group method, were quite similar at the high and intermediate similarity levels, but the contents of the major groups formed at low similarity levels were rather different. Likewise, clusters formed at high similarity levels generally contained species of either the same subgenus or of closely related subgenera, but generic-level relationships reflecting inferred phylogeny were very poorly represented in both the phenetic classifications.

INTRODUCTION

For the past few years there has been increasing interest in the possibility of arriving at sounder and more stable biological classifications by the use of large numbers of taxonomic characters. The methods of numerical taxonomy, as outlined by Sokal and Sneath (1963), are techniques for classifying organisms into taxa on the basis of numerous characters, each of which is to be given equal importance or weight. Proponents of the numerical or phenetic (Cain & Harrison, 1960) approaches to taxonomy believe that the most stable, repeatable, and objective taxonomies will be those based on empirical determination of the degree of similarity among organisms, and that speculations on phylogenetic pathways should be excluded from the classificatory process. They have generally indicated, however, that by using as many characters as possible, the proportionate contribution to overall similarity made by characters affected by convergence will not be significant; phenetic and phylogenetic classifications should therefore be closely similar. Most pheneticists, however, have been interested in groups of organisms which have a meager fossil record or none. The pheneticists have thus insisted strongly on the highly speculative nature of many of the phylogenetic hypotheses on which classifications have been based. Most phylogeneticists who have dealt with the relationship between phenetic and phylogenetic taxonomy have been concerned principally with refuting the conceptual basis of the phenetic argument and have not tested its methodology. Few studies incorporating paleontological evidence into a phenetic study have been made. Even when data from paleontology have been available, critiques of the phenetic method have usually revolved about whether numerical taxonomy gave results agreeing with a conventionally accepted classification, not whether the results were consistent with the phylogeny of the organisms.

The present study is an attempt to determine, for a taxon whose evolutionary history can be documented with considerable accuracy, the degree of coincidence or discrepancy between phenetic and phylogenetic classifications. The group chosen is the Cenozoic members of the Family Lucinidae (Mollusca, Bivalvia). The lucinids have an extensive fossil record beginning in Silurian time; the taxon is particularly well represented in Cenozoic strata and has numerous living representatives. Allen (1958) conducted an extensive study of the functional morphology of the Lucinidae, emphasizing the unique method of feeding. The evolutionary significance of the taxon as one of the

earliest bivalve groups with the heterodont pattern of dentition and as a possible direct descendant of a monoplacophoran ancestor has been explored by McAlester (1964, 1965, 1966). It is hoped that, by providing an example of a phenetic study whose results can be evaluated by reference to a phylogenetic classification based on considerable fossil evidence, light can be thrown on both the practical utility and the theoretical validity of the phenetic approach to taxonomy.

MATERIALS AND SCOPE OF THE PHENETIC STUDY

The Family Lucinidae was chosen as the subject for the phenetic study because of its good fossil record, the considerable degree of knowledge of the ecology and anatomy of its recent representatives, and the fact that its taxonomy is well worked out at the specific level. For all these reasons, it posed an intriguing problem in classification and an excellent test case for the simultaneous application of the phenetic and phylogenetic methodologies.

The Lucinidae are one of an ensemble of families included in the Superfamily Lucinacea. As many as nine families may belong to the Lucinacea, but the study by Allen (1958) dealt only with the three largest and best-represented in the Recent fauna, the Lucinidae, Thyasiridae, and Ungulinidae. In all major classifications of the Bivalvia, these three families have been considered closely related. On the basis of their gill structure and dentition, the Lucinacea have been placed in the higher categories Eulamellibranchia and Heterodonta. Allen showed, however, that the Lucinacea have a feeding mechanism which is virtually unique among eulamellibranch heterodonts. Most eulamellibranch bivalves have a posterior inhalant feeding current entering through an aperture created by the fusion of the mantle edges; the posterior inhalant and exhalant apertures are often produced into siphons, permitting the animal to burrow into the substratum. In the Lucinacea, in contrast, the inhalant feeding current enters anteriorly (Fig. 1) through a tube constructed of sediment particles cemented together by mucus produced by glands in the foot. The tube serves the same function as the siphon in other bivalves. The anterior adductor muscle in the Lucinacea is considerably longer than the posterior one, in contrast to the situation in most infaunal bivalves,

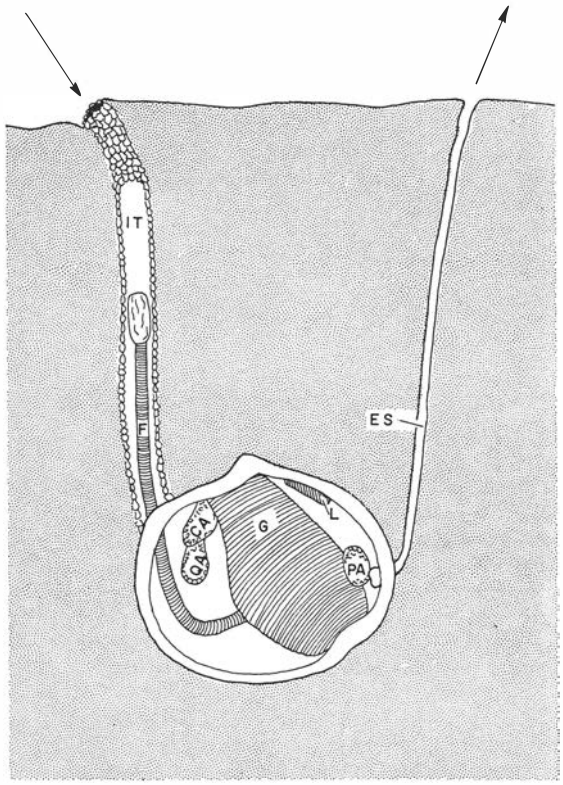

Fig. 1. Living position of the lucinoid *Loripes lacteus* (Lucinidae), modified from Allen (1958) and Kauffman (1967). Anterior inhalant tube broken away to show shape of foot. Grains of tube enlarged to show structure, and no size selection implied. Arrows show direction of inhalant and exhalant currents. *IT*, inhalant tube; *F*, foot; *CA*, catch portion of anterior adductor; *QA*, quick portion of anterior adductor; *G*, gill; *PA*, posterior adductor; *L*, ligament; *ES*, exhalant siphon.

whose adductors are about equal in size. The elongation of the anterior adductor serves two functions: keeping detritus particles which enter through the feeding tube from going into the mouth before being sorted to separate out particles not usable for food; and carrying out, by means of cilia on the epithelium of the muscle, some or most of the sorting process. (In non-lucinoid eulamellibranch bivalves, the sorting process is done entirely by cilia on the gills and labial palps.)

McAlester (1965, 1966) noted that the anterior inhalant current of the lucinoids is also a characteristic of the Recent protobranch bivalves considered by Yonge (1939) to be most closely similar to the primitive bivalve condition. Because the Lucinacea are first represented in rocks of Silurian

age, whereas nearly all other eulamellibranch families are first known from Mesozoic rocks, McAlester hypothesized that the lucinoids are rather primitive, and that their resemblances to the eulamellibranch heterodonts with which they are traditionally associated are the result of convergent evolution. He considered it possible in fact, that the Lucinacea were derived, through the Middle Ordovician Czechoslovakian bivalve *Babinka,* from a monoplacophoran ancestor. This speculation, based on the similarity between the pattern of muscle scars marking the attachment of the pedal retractors and the probable line of gill attachment in *Babinka* to the muscle patterns in the Recent monoplacophoran *Neopilina,* would make the Lucinacea evolutionarily independent not only of the other Eulamellibranchia but also of all other bivalves. The hypothesis of a monoplacophoran ancestry for the Lucinacea, implying a polyphyletic origin of the Bivalvia, has not been generally accepted. The conclusion that *Babinka* is the earliest member of the Lucinacea (or the sole representative of a Superfamily Babinkacea ancestral to the Lucinacea, depending on one's taxonomic philosophy) and that the lucinoids are the oldest known heterodont eulamellibranchs has, however, found more favor (Vokes, 1967; Pojeta, in press). Allen (1968) has shown that a recent astartoid bivalve, *Crassinella,* resembles the lucinoids in having an elongate anterior adductor. The Astartacea are the only heterodont, eulamellibranch superfamily other than the Lucinacea definitely known from Paleozoic rocks, being probably of Silurian origin (Stanley, 1968). Saleuddin (1965) and Stanley (1968) consider the Astartacea morphologically well suited to represent the primitive eulamellibranch heterodont. It is thus possible that *Babinka* gave rise to two major bivalve lineages, one leading to the Lucinacea and the other to the Astartacea and thence to such bivalves as the Veneracea, Cardiacea, Myacea, and Mactracea.

The Lucinidae, the family with which the phenetic study deals, are the oldest of the lucinoid families. They are well represented in Silurian and Devonian rocks, but are virtually unknown from the span of time from the Mississippian through the Triassic Period. They are present in Jurassic, particularly Upper Jurassic, strata and have a practically continuous record from Late Cretaceous time to the present. Vokes (1967) lists 109 genus-group names (names proposed for either genera, subgenera, or sections) which have been validly applied to lucinids. Over a thousand species of the Lucinidae have been named. There are several major monographs of the taxonomy of the Lucinidae (Dall, 1901, 1903; Lamy, 1920; Chavan, 1937–38). The last of these works, in particular, incorporated data on both fossil and recent lucinids into an evolutionary scheme used as the basis for classification. In several subsequent papers, Chavan has proposed some new genera and subgenera, modified the scope of some of those discussed in the 1937–38 work, and revised some of his thoughts on phylogeny. He has not, however, proposed any unified, integrated revision of phylogenetic classification. It appeared, therefore, that a taxonomic revision of the Lucinidae at the generic and subgeneric levels would be a useful contribution (species-level taxonomy in the Lucinidae is reasonably well worked out; there has been little suggestion that the lucinids are either oversplit or overlumped at the specific level) and would provide a forum for testing phenetic against phylogenetic classifications.

For practical reasons, I decided initially to limit the study to the Cenozoic Lucinidae of North America, since specimens of these species were readily available for study in the collections accessible to me. (Later, two recent European species of which a number of specimens were available and which had a prominent position in Chavan's evolutionary system were added.) Because both fossil and recent species were to be represented, the phenetic study was restricted to characters of the shell. Since numerical taxonomists have emphasized the necessity of basing phenetic studies on a large number of characters—not less than 40, preferably 60 or more (Sokal & Sneath, 1963) —specimens of Paleozoic and Mesozoic lucinids were excluded because in general they are much more poorly preserved, and thus show fewer useful characters, than their Tertiary counterparts. (There are, of course, exceptions to this general rule, because the preservation of fossil species is a function of the nature of the environmental conditions under which they were deposited, the nature of the enclosing sediment, the degree of diagenetic change which they have undergone, and the amount of deformation to which the rocks have undergone. None of these factors has any necessary correlation with the antiquity of the fossil.) With these geographic and stratigraphic

restrictions, 29 genus-group taxa were selected for inclusion in the phenetic study. It was decided to represent most by a single species, following the exemplar method of Sokal and Sneath (1963), who state that in a study of taxa of supraspecific rank any one member of the taxon can be chosen to give an estimate of the resemblances among the taxa, since presumably intrataxon variability should be less than intertaxon variability. To test the exemplar method, therefore, in some cases I included two species of a given genus to determine whether on the average they were more similar to each other than to species of other

Table I. *Species of the Lucinidae included in the phenetic study*

Code No.	Species
1	**Anodontia alba* Link
2	**Armimiltha disciformis* (Heilprin)
3	*Bellucina amiantus* (Dall)
4	*Callucina lampra* (Dall)
5	*Callucina lingualis* (Carpenter)
6	*Callucina papyracea* (Lea)
7	**Callucina radians* (Conrad)
8	*Cavilinga pomilia* (Conrad)
9	**Cavilinga trisulcata* (Conrad)
10	**Claibornites symmetricus* (Conrad)
11	*Codakia distinguenda* (Tryon)
12	**Codakia orbicularis* (Linné)
13	*Ctena costata* (d'Orbigny)
14	**Ctena mexicana* (Dall)
15	*Ctena orbiculata* (Montagu)
16	**Dallucina amabilis* (Dall)
17	*Divalinga eburnea* (Reeve)
18	**Divalinga quadrisulcata* (d'Orbigny)
19	*Egracina dentata* (Wood)
20	*Eomiltha pandata* (Conrad)
21	* *Eophysema subvexa* (Conrad)
22	* *Epilucina californica* (Conrad)
23	* *Eulopia sagrinata* (Dall)
24	* *Here excavata* (Carpenter)
25	**Loripes lacteus* (Poli)
26	**Lucina pensylvanica* (Linné)
27	**Lucinisca nassula* (Conrad)
28	*Lucinisca nuttalli* (Conrad)
29	**Lucinoma filosa* (Stimpson)
30	*Miltha xantusi* (Dall)
31	*Myrtea lens* (Verrill and Smith)
32	* *Myrtea spinifera* (Montagu)
33	*Parvilucina multilineata* (Tuomey and Holmes)
34	* *Parvilucina tenuisculpta* (Carpenter)
35	* *Pegophysema philippiana* (Reeve)
36	* *Phacoides pectinatus* (Gmelin)
37	* *Plastomiltha claibornensis* (Conrad)
38	* *Pleurolucina leucocyma* (Dall)
39	*Pleurolucina undatoides* (Hertlein and Strong)
40	* *Recurvella dolabra* (Conrad)
41	* *Stewartia anodonta* (Say)
42	*Stewartia floridana* (Conrad)

* Type species of the genus.

Table II. *Lucinid characters and states*

Shell exterior

1. Type of surface sculpture
   - Concentric only 1
   - Concentric and radial 2
   - Concentric and divaricate 3
2. Quality of surface sculpture
   - Fine 1
   - Distinct 2
   - Coarse 3
   - Rugose 4
3. Type of concentric ribbing
   - Growth rings absent 1
   - Growth rings irregularly spaced, not deep 2
   - Growth rings fairly regular, deep 3
   - Fine and coarse ribs both present, and regularly spaced; growth rings absent 4
4. Prominence of radial ribs
   - All equally prominent 1
   - Less prominent toward center of disk 2
   - Most prominent anteriorly and at umbo 3
5. Bifurcation of radial ribs
   - Absent 1
   - Variable 2
   - Present 3
6. Dominant type of sculpture
   - Radial faint, concentric dominant 1
   - Radial distinct, concentric dominant 2
   - Radial dominant, concentric distinct 3
7. Number of primary radial ribs
   - 3 to 7 1
   - 8 to 12 2
   - More than 12 3
8. Undulatory surface
   - Absent 1
   - Present 2
9. Posterior dorsal spinosity
   - Absent 1
   - Present 2
10. Anterior dorsal area
    - Not set off 1
    - Faint 2
    - Distinct 3
    - Conspicuous 4
11. Posterior dorsal area
    - Not set off 1
    - Faint 2
    - Distinct 3
    - Conspicuous 4
12. Periostracum
    - Absent 1
    - Present, thin 2
    - Conspicuous 3
13. External color
    - Absent 1
    - Variable 2
    - Present 3

43. Kind of anterior dorsal area
    - Pseudo-lunule 1
    - Change in sculpture 2

Table II. (*continued*)

44. Continuity of radial sculpture
    Continuous 1
    Discontinuous 2

45. Elevation of beaks
    Slight 1
    Moderate 2
    Great 3

Lunule

14. Lunule width
    Narrow 1
    Wide 2

15. Lunule shape
    Triangular 1
    Rectangular to oval 2
    "Figure 8" 3

16. Lunule symmetry
    Symmetrical 1
    Slightly asymmetrical 2
    Distinctly asymmetrical 3

17. Lunule depth
    Shallow 1
    Deep 2
    Excavated 3

18. Distinctness of lunule
    Not perceptible 1
    Poorly defined 2
    Well defined 3

19. Lunule length
    Short 1
    Long 2

Ligament

20. Position of ligament
    External, slightly inset 1
    Deeply inset 2
    Completely internal 3

Muscle scars

21. Anterior muscle scar length
    Short 1
    Normally long 2
    Very long 3

22. Anterior muscle scar width
    Narrow 1
    Normal 2
    Wide 3

23. Anterior muscle scar shape
    Straight 1
    Curved or bent 2

24. Anterior muscle scar position
    Parallelling pallial line 1
    Diverging from pallial line 2

25. Posterior muscle scar shape
    Round 1
    Elliptical 2

Table II. (*continued*)

26. Position of pedal retractor scars
    Neither evident 1
    Anterior separate, posterior not evident 2
    Anterior separate, posterior above and partly separate from adductor 3
    Anterior not evident, posterior inside and partly separate from adductor 4

Hinge line

27. Anterior lateral—right valve
    Absent 1
    Obsolescent 2
    Present 3

28. Posterior lateral—right valve
    Absent 1
    Obsolescent 2
    Present 3

29. Cardinal teeth
    Absent 1
    Obsolescent 2
    Present 3

30. Bifidity of right posterior cardinal
    Absent 1
    Slight 2
    Distinct 3

31. Number of cardinals—right valve
    One 1
    Two, anterior much smaller than posterior 2
    Two, anterior about same size as posterior 3

32. Lateral(s)—left valve
    Single 1
    Double 2

33. Hinge plate
    Narrow 1
    Wide 2

34. Relationship of cardinals—left valve
    Subparallel 1
    Diverging widely 2

Shell interior—miscellaneous characters

35. Internal color
    Absent 1
    Variable 2
    Present 3

36. Pallial blood vessel scar
    Absent 1
    Present 2

37. Denticulation of inner margin
    Absent 1
    Present 2

Size and shape

38. Shell thickness
    Thin 1
    Average 2
    Thick 3

39. Adult size
    5–9 mm (very small) 1
    1.0–2.0 cm (small) 2
    2.0–4.0 cm (medium) 3
    4.0–8.0 cm (large) 4
    > 8.0 cm (very large) 5

Table II. (*continued*)

40. Height/length ratio	
0.80–0.89	1
0.90–0.99	2
1.00–1.09	3
>1.09	4
41. Inflation (depth of one valve/length ratio)	
<0.20	1
0.20–0.29	2
0.30–0.39	3
>0.39	4
42. Anterior expansion (anterior length/total length)	
0.40–0.44	1
0.45–0.49	2
>0.49	3

genera. I also included a few common North American species whose generic position had been questioned in earlier works. In all, the phenetic study included 42 species. Whenever possible, I included the type species of each genus-group taxon as its representative in the phenetic study. This practice should not be construed as an emphasis on typological thinking. It represents, rather, an attempt to approach as nearly as possible the concept of the describer of the genus; this appeared particularly important because many of the lucinid genera were described in only a few words, and consideration of the species believed by their authors to be representative of them is

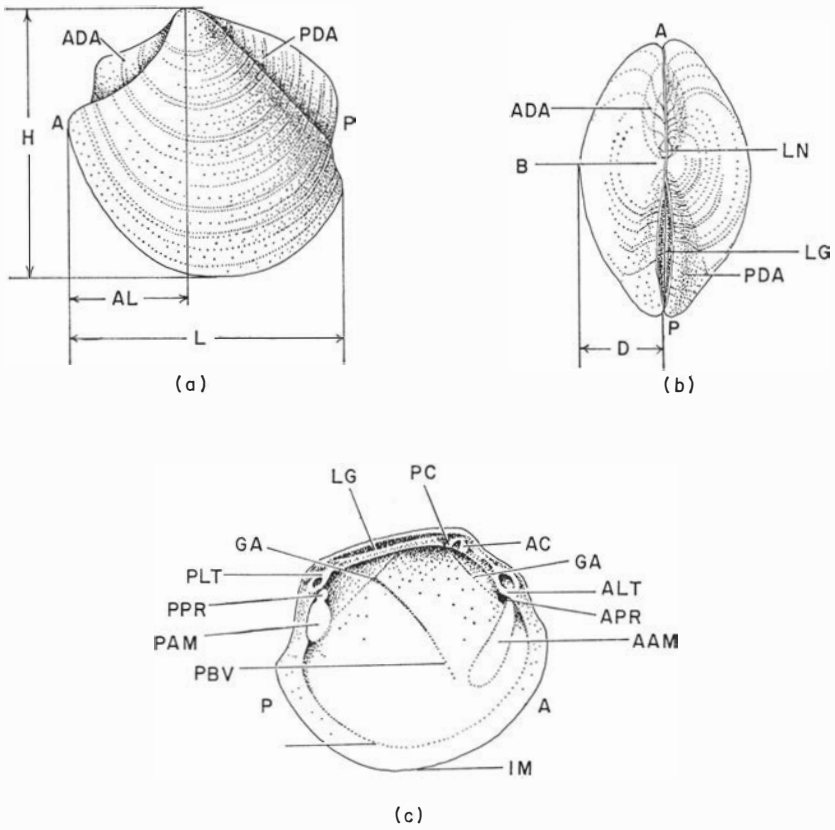

Fig. 2. Morphology of the shell of a generalized lucinid. *a.* Exterior of left valve. *b.* Interior of left valve. *c.* Top view of articulated shell, showing relationships between dorsal areas, lunule, and ligament. A, anterior; AAM, anterior adductor muscle scar; AC, anterior cardinal tooth; ADA, anterior dorsal area; AL, anterior length; ALT, anterior lateral teeth; APR, anterior pedal retractor scar; B, beak; D, depth of one valve; GA, trace of gill attachment on interior of shell; H, height of shell; IM, inner margin of shell; L, length of shell; LG, ligament; LN, lunule; P, posterior; PAM, posterior adductor muscle scar; PBV, pallial blood vessel scar; PC, posterior cardinal tooth; PDA, posterior dorsal area; PL, pallial line; PLT, posterior lateral teeth; PPR, posterior pedal retractor scar.

necessary to provide an estimate of their morphological scope.

The species included in the phenetic study are listed in Table I, with the code numbers by which each was identified in the computer. The generic assignments for species other than type species are those indicated in the study by Chavan (1937–38).

Fig. 2 illustrates the morphology of the shell of a generalized lucinid. The characters of the shell used in the phenetic classification are listed in Table II (since both fossil and recent species were included in the study, it was possible to use for the phenetic study only shell characters, the soft-part anatomy of the fossils being unknown). I use the term "character" in the way that it is generally understood in numerical taxonomy, that is, as a "feature which varies from one kind of organism to another" (Sokal & Sneath, 1963) and thus occurs in two or more alternative conditions or states. For example, the character "type of surface sculpture" in the Lucinidae has three states, "concentric only", "concentric and radial", and "concentric and divaricate". Table II also gives the code numbers assigned to the characters and to the states of each.

NUMERICAL METHODS

A numerical taxonomic classification is constructed as follows: After the taxonomic entities to be studied [operational taxonomic units, or OTU's (Sokal & Sneath, 1963)] have been chosen and the characters listed and divided into states, the state of each character for each OTU is recorded in an $n \times t$ matrix (n being the number of characters and t the number of taxa). This matrix is used for calculation of the similarities between all possible pairs of OTU's, summed over all the characters in the study. This technique, which aims at finding groups of similar organisms, is the Q-technique of Cattell (1952). The similarity coefficients are then arranged in a $t \times t$ matrix and used as the basis for forming groups whose members have a high degree of mutual similarity. Finally, the results are represented in diagrammatic form, showing the contents of the groups constructed on the basis of similarity and the relationship of each group to the other.

When the taxonomic data are such that some or all of the characters have more than two states, the similarity coefficients most commonly used are the Pearson product-moment correlation coefficient and the average taxonomic distance (Sokal, 1961). When the number of states varies from character to character, the calculation of similarity is preceded by standardization of the states; that is, each character state is transformed by subtracting from it the mean of the row of character states to which it belongs, and dividing this value by the standard deviation of the row. This procedure ensures that all the standardized character states have the same mean, 0, and the same variance, 1.

Arrangement of OTU's into groups is carried out by cluster analysis (Tryon, 1939). The cluster analysis generally used in numerical taxonomy are the group methods, which yield a hierarchical arrangement of taxa [see Sokal & Sneath (1963) for a more detailed discussion]. All begin by finding pairs of OTU's which have their highest similarity with each other, and successively adding to these original clusters the unclustered OTU's, or other clusters, which have the highest average similarity with the members of the cluster. Only one new member at a time may be added to a cluster in the pair-group method; in the variable-group method, new members may be added to a cluster as long as the average similarity among clusters is not reduced by more than a certain amount (empirically determined for a given study). The average similarity between the members of a cluster and a prospective new member may be carried out either by weighting all members of the cluster equally (unweighted group method); or by giving greater weight to the later members of the cluster than to those which joined earlier, by treating each subcluster within the cluster (rather than each of its component OTU's) as an individual in computing the average similarity (weighted group methods). The average similarity between two clusters or between a cluster and an unclustered individual may be calculated by using simple arithmetic averages of the coefficients of similarity between the members of cluster A and of cluster B, or between OTU C and the members of cluster A. When correlation coefficients are used, however, arithmetic averaging may give spurious results because the variance of correlation coefficients depends on their magnitude. Averages can be used, however, if the correlations are first transformed to Fisher's z; or the recalculation of similarity coefficients may be carried out by Spearman's (1913) sums of variables method (Sokal & Sneath, 1963).

In this study, standardized character values were used for the calculation of similarity both by correlations and by average taxonomic distances. Both coefficients were clustered by the weighted pair-group method, Spearman's sums of variables being used for calculating average similarities among correlation coefficients.

It was predicated that, of the two phenetic classifications, the one based on correlations would be less satisfactory than that based on distances. This prediction results from two considerations. First, correlation coefficients are much more sensitive to arbitrariness in coding than are distances (Eades, 1965; Minkoff, 1965). Two OTU's could be perfectly correlated, for example, even though they differed in every character, if the state code for each character of OTU 1 happened to be twice that of the corresponding character for OTU 2. Correlation coefficients appear to give the most satisfying results when most of the characters used in a study are measurements of various parts of an organism (Rohlf & Sokal, 1965). In the lucinid study, however, nearly all the characters were qualitative, and many were difficult to arrange in a non-arbitrary sequence. Second, the use of Spearman's method in a taxonomic context creates difficulties, in that reversals of correlation are possible—the correlation be-

tween OTU 3 and a cluster containing OTU's 1 and *s* may be slightly higher than the correlation between OTU's 1 and 2. Taxonomically, this would imply that, e.g., two different subgenera were more closely similar to each other than the constituent species of one were to each other. This problem does not exist with arithmetic averages. Reversals are particularly likely when very small or negative values of the average correlation are involved, and since standardization of characters reduces the average correlation within a matrix to approximately zero (Rohlf & Sokal, 1965), Spearman's method is likely to give poorer results with standardized characters (as in the present study) than with unstandardized ones.

PHYLOGENY OF THE LUCINIDAE

Much of the dissatisfaction of pheneticists with phylogenetic taxonomy doubtless stems from the fact that it is much more difficult to explain how one sets up a phylogenetic scheme than to present formulae for calculating similarity among organisms and for clustering the organisms on the basis of these similarities. Sokal and Camin (1965) have criticized the phylogenetic approach to taxonomy as being "nonoperational"; that is, there are no clearly defined, objective sets of instructions which can be followed to determine the degree of phylogenetic relationship between two species or other taxa. To draw inferences about the course of evolution within a family, one must be familiar with a great deal of information about the morphology and the geographic and stratigraphic occurrence of a large number of its constituent species and genera. Even if one conscientiously avoids any *a priori* inference that some characters or character-complexes define one taxon or are diagnostic at a particular categorical rank, it is difficult to eliminate such simplifying assumptions just because of the sheer mass of data which has to be mentally processed. It is not surprising that the procedures of phylogenetic taxonomy may seem at best mystical and at worst circular.

Although the phylogenetic method of taxonomy may never be fully operational in the sense of Sokal and Camin, I believe that some general rules or guidelines for evolutionary taxonomy can be formulated. These guidelines, summarized below, owe much to the detailed and lucid discussions by Simpson (1961) and Mayr (1965). I have purposely used the vague terms "organism", "taxon", and "form" to indicate that these guidelines should be valid at any taxonomic level, though some may be of greater practical utility at the lower taxonomic levels and others at the higher.

1. Organisms which resemble each other in the great majority of their characters are probably closely related. The magnitude of the resemblance is likely to be inversely proportional to the amount of time which has elapsed since their divergence from a common ancestor, but frequently it can be shown that many of the similarities are responses to similar modes of life (or many of the dissimilarities are due to exploitation of rather different environments). The relationship between degree of dissimilarity and remoteness of common ancestry is thus not a strict rule.

2. Organisms which resemble each other in few characters, but which are connected by a chain of morphologically intermediate forms (for contemporaneous taxa) or stratigraphically and morphologically intermediate forms (for diachronous taxa), such that each pair of organisms along the chain meets criterion 1, are presumably related to each other through a phylogenetic continuum whose course approximates that of the morphological and/or stratigraphic one. Evidence from fossils, since it includes a time sequence, is likely to be more convincing phylogenetically than that based only on recent organisms; however, the gaps in the fossil record should be small enough to permit inferring with considerable confidence that taxa from different horizons were indeed connected by intermediate forms. (One would be cautious, for example, about inferring genetic relationship between a Devonian and a Cretaceous species, though they were morphologically quite alike, if no intervening similar forms were known. With closely similar Middle Eocene and Late Eocene species, for example, the hypothesis of genetic relationship would seem much more reasonable.)

3. Organisms which are dissimilar as adults but which have similar larvae, embryos, or juvenile stages are likely to be closely related; related organisms may, however, have quite dissimilar juveniles if the juveniles are subject to different ecological conditions. If two organisms are dissimilar as adults, but the adult stage of one is much like the juvenile stage of the other, genetic relationship is also likely.

4. A fossil organism which is morphologically intermediate between stratigraphically younger,

more or less dissimilar organisms can reasonably be inferred (subject to the temporal limitations mentioned in 2) to be, if not their actual common ancestor, closely similar to it. The term "intermediate" does not imply a condition exactly halfway between the characters in which the younger organisms differ; it means possession of characters which, by transformations known or inferred to be reasonably likely in the group under study, could be changed to yield the relevant character states of each of the younger organisms. A living organism or one occurring too late in the fossil record to be an actual common ancestor of two or more taxa, but morphologically intermediate between them, may be a little-modified descendant of the common ancestor of the group. The inference is more likely to be warranted if the organism in question inhabits an ecological niche or geographic locality which is likely to have been that of the ancestral form, or to have been relatively isolated (e.g. oceanic trenches, island continents) from invasion by the descendant forms.

5. Phylogenetic trees worked out by the application of the preceding criteria to the analysis of morphological similarity should be reflected in classification by application of Simpson's (1961) criterion of monophyly: "the derivation of a taxon through one or more lineages from one immediately ancestral taxon of the same or lower rank." [Birch and Ehrlich (1967) have pointed out that a definition of monophyly as "species combined in a taxon must be descendants of a common ancestor" (Mayr, 1965) applies to any group of organisms whatsoever. This sort of objection, however, was anticipated by Simpson and is nullified by the framing of the definition of monophyly in relative rather than absolute terms and by including the phrase *immediately ancestral*.] It is not necessary, however, that *all* descendants of the ancestral taxon be included in *the same* taxon; in a lineage some of whose members have diverged strongly from the ancestral condition, it is perfectly proper to include the ancestral group and its slowly evolving descendants in the same taxon and to recognize a distinct taxon for the rapidly evolving members.

Application of these principles to a study of the fossil and recent Lucinidae has permitted the recognition of five major evolutionary lineages; two additional distinctive morphological groups are also recognized, but sufficient evidence is not yet available to determine whether the latter groups are monophyletic. The phylogenetic classification is based on study of actual specimens of about 250 species, supplemented by information gained from figures and descriptions of many others. The species most intensively studied were those from Cenozoic (i.e. Tertiary, Pleistocene, and Recent) time in North America, since these are deposited in the museums accessible to me at the time of the study, are almost always well preserved, and are sufficiently well distributed throughout the fossil record to provide a close approximation to a continuous evolutionary sequence. (I consider the latter criterion to be satisfied when the maximum length of the gaps in the record is less than the probable average length of existence of the individual lowest-level taxonomic units—species in this case—in the study.)

The phylogenetic study was carried out by taking each species in the phenetic study as a starting point and listing first the contemporaneous species which appear most closely similar to it, and then, in stratigraphic sequence, the older (and, if a fossil species was used as the starting point, younger) species which most closely resemble it. In this way it was possible to recognize chains of closely similar species which intergraded through time. Eventually many distinctive morphological groups disappeared from the record. A number of early forms similar to members of two or more of the later groups were found. The duration of phyletic lines and their probable ancestry could thus be established. Comparisons were, of course, facilitated because most of the species chosen for the phenetic study are type species of various genus-group taxa, and the authors of these taxa had in most cases enumerated the species which they considered the new taxon to include. In most cases the evolutionary sequences worked out on the basis of the North American material were quite comparable to those suggested by Chavan (1937–1938), who worked primarily with European lucinids.

As previously noted, it was possible to recognize seven principal divisions of the Lucinidae; these divisions are here given the rank of genera. The five which appear to be monophyletic are here referred to as *lineages*. The two based only on similarity in morphology (because members of them were not sufficiently well represented in the phylogenetic study to permit decision on their

Table III. *Phylogenetic classification of the Lucinidae*

Genera	Subgenera
	Phacoides (36)
	—
	Lucina (26)
	—
	Here (24)
Phacoides	—
Lucina	*Stewartia a.* (41)
Here	*Stewartia f.* (42)
Stewartia a.	—
Stewartia f.	
	Pleurolucina *a.* (16)
Pleurolucina a.	*Pleurolucina l.* (38)
Pleurolucina l.	*Pleurolucina u.* (39)
Pleurolucina u.	—
Bellucina	*Bellucina* (3)
Lucinisca na.	
Lucinisca nu.	—
Parvilucina m.	*Lucinisca na.* (27)
Parvilucina t.	*Lucinisca nu.* (28)
Parvilucina? c.	—
Callucina r.	*Parvilucina m.* (33)
Callucina? r.	*Parvilucina t.* (34)
Cavilinga p.	—
Cavilinga t.	Parvilucina? *c.* (13)
Cavilinga la.	—
Cavilinga ll.	*Callucina r.* (7)
Recurvella	—
	Callucina? p. (6)
	—
	Cavilinga p. (8)
	Cavilinga t. (9)
	Cavilinga la. (4)
	Cavilinga ll. (5)
	—
	Recurvella (40)
—	—
	Codakia d. (11)
Codakia d.	*Codakia o.* (12)
Codakia o.	—
Ctena m.	*Ctena m.* (14)
Ctena o.	*Ctena o.* (15)
Claibornites	—
	Claibornites (10)
—	—
	Miltha (30)
Miltha	—
Eomiltha	*Eomiltha* (20)
Plastomiltha	—
Lucinoma	*Plastomiltha* (37)
Armimiltha	—
	Lucinoma (29)
	—
	Armimiltha (2)
—	—
	Myrtea (32)
Myrtea	—
Eulopia	*Eulopia* (23)
Myrteopsis?	—
Epilucina	Myrteopsis? (31)
	—
—	*Epilucina* (22)
	—
	Eophysema (21)
Eophysema	—
Anodontia a.	*Anodontia a.* (1)

Table III. (*continued*)

Anodontia p.	Anodontia p. (35)
	—
Loripes	*Loripes* (25)
	—
Divalinga e.	*Divalinga e.* (17)
Divalinga q.	*Divalinga q.* (18)
Egracina	—
	Egracina (19)

Table IV. *Clusters formed at selected phenon levels in correlation phenogram* (*Fig. 3*)

0.0 Phenons	0.25 Phenons	0.50 Phenons
		Recurvella (40)
	Recurvella	*Lucina* (26)
	Lucina	—
	Pleurolucina a.	Pleurolucina a. (16)
Recurvella	*Pleurolucina l.*	*Pleurolucina l.* (38)
Lucina	*Pleurolucina u.*	*Pleurolucina u.* (39)
Pleurolucina a.	—	—
Pleurolucina l.		*Callucina? p.* (6)
Pleurolucina u.		*Callucina r.* (7)
Callucina? p.		—
Callucina r.	*Callucina? p.*	*Parvilucina m.* (33)
Parvilucina m.	*Callucina r.*	—
Parvilucina t.	*Parvilucina m.*	*Parvilucina t.* (34)
Cavilinga la.	*Parvilucina t.*	—
Cavilinga ll.	Cavilinga la.	Cavilinga la. (4)
Cavilinga p.	Cavilinga ll.	Cavilinga ll. (5)
Cavilinga t.	*Cavilinga p.*	—
Parvilucina? c.	*Cavilinga t.*	*Cavilinga p.* (8)
—	Parvilucina? c.	*Cavilinga t.* (9)
	—	Parvilucina? c. (13)
		—
Divalinga e.	*Divalinga e.*	*Divalinga e.* (17)
Divalinga q.	*Divalinga q.*	*Divalinga q.* (18)
Ctena m.	—	—
Ctena o.	*Ctena m.*	*Ctena m.* (14)
Egracina	*Ctena o.*	*Ctena o.* (15)
Eophysema	—	—
Codakia d.	*Egracina*	*Egracina* (19)
Codakia o.	*Eophysema*	—
	—	*Eophysema* (21)
		—
	Codakia d.	*Codakia d.* (10)
	Codakia o.	*Codakia o.* (11)
—		—
	—	*Eulopia* (23)
Eulopia	*Eulopia*	*Myrtea* (32)
Myrtea	*Myrtea*	—
Epilucina	*Epilucina*	*Epilucina* (22)
Bellucina	*Bellucina*	—
Lucinisca na.	*Lucinisca na.*	*Bellucina* (3)
Lucinisca nu.	*Lucinisca nu.*	*Lucinisca na.* (27)
Here	*Here*	—
		Lucinisca nu. (28)
		—
		Here (24)
—	—	—
		Miltha (30)
	Miltha	*Plastomiltha* (37)
Miltha	*Plastomiltha*	*Stewartia a.* (41)

Table IV. (*continued*)

Plastomiltha	*Stewartia a.*	*Stewartia f.* (42)
Stewartia a.	*Stewartia f.*	—
Stewartia f.	*Anodontia a.*	*Anodontia a.* (1)
Anodontia a.	Anodontia p.	—
Anodontia p.	Myrteopsis?	Anodontia p. (35)
Myrteopsis?		—
Armimiltha		Myrteopsis? (31)
Lucinoma	—	—
Eomiltha	*Armimiltha*	*Armimiltha* (2)
Loripes	*Lucinoma*	*Lucinoma* (29)
Claibornites	*Eomiltha*	—
Phacoides	*Loripes*	*Eomiltha* (20)
		—
	—	*Loripes* (25)
		—
	Claibornites	*Claibornites* (10)
	Phacoides	—
		Phacoides (36)

Table V. (*continued*)

Anodontia a.	—
Anodontia p.	Myrteopsis? (31)
Ctena m.	*Anodontia a.* (1)
Ctena o.	Anodontia p. (35)
Cavilinga p.	—
Cavilinga t.	*Ctena m.* (14)
Parvilucina t.	*Ctena o.* (15)
Parvilucina? *c.*	*Cavilinga p.* (8)
Cavilinga la.	*Cavilinga t.* (9)
Cavilinga ll.	*Parvilucina t.* (34)
Callucina? p.	Parvilucina? c. (13)
Callucina r.	Cavilinga la. (4)
Parvilucina m.	Cavilinga ll. (5)
Loripes	*Callucina? p.* (6)
	Callucina r. (7)
	Parvilucina m. (33)
	—
	Loripes (25)

Table V. *Clusters formed at selected phenon levels in distance phenogram* (*Fig. 4*)

1.50 Phenons	1.15 Phenons
	Recurvella (40)
	—
Recurvella	Pleurolucina a. (16)
Pleurolucina a.	*Pleurolucina l.* (38)
Pleurolucina l.	*Pleurolucina u.* (39)
Pleurolucina u.	—
Here	*Here* (24)
Lucina	*Lucina* (26)
—	—
Divalinga e.	*Divalinga e.* (17)
Divalinga q.	*Divalinga q.* (18)
—	—
	Stewartia a. (41)
	Stewartia f. (42)
Stewartia a.	*Plastomiltha* (37)
Stewartia f.	*Eomiltha* (20)
Eomiltha	—
Miltha	*Miltha* (*30*)
Codakia d.	—
Codakia o.	*Codakia d.* (11)
Egracina	*Codakia o.* (12)
Armimiltha	—
Lucinoma	*Egracina* (19)
	Armimiltha (2)
	Lucinoma (29)
—	—
	Claibornites (10)
	—
	Phacoides (36)
Claibornites	—
Phacoides	*Bellucina* (3)
Bellucina	*Lucinisca na.* (27)
Lucinisca na.	*Lucinisca nu.* (28)
Lucinisca nu.	—
Epilucina	*Epilucina* (22)
Myrtea	*Myrtea s.* (32)
Eulopia	*Eulopia* (23)
Eophysema	—
Myrteopsis?	*Eophysema* (21)

phyletic status) are referred to as *groups*. In two cases, it is possible to tentatively divide a lineage into two segments which seem to be monophyletic at the subgenetic level; however, the evidence is not sufficiently firm nor the limits of the subdivisions sufficiently clear to warrant there being given independent status at this time. It is difficult to suggest relationships among the lineages which would serve as the basis for proposing subfamilies; nearly all the lineages are represented as early as Jurassic time, and some may have existed as distinct entities even in Silurian or Devonian time. The first very well-preserved lucinids appear to be those of the French Upper Jurassic described by Chavan (1952); more detailed study of them may shed light on the subfamily-level relationships of the Lucinidae.

The lucinid genera recognized here, and their inferred durations, are the following:

Lucina lineage—Devonian? Jurassic–Recent
Codakia lineage—Jurassic–Recent
Miltha lineage—Silurian? Jurassic–Recent
Myrtea lineage—Jurassic? Cretaceous–Recent
Anodontia lineage—Eocene–Recent
Loripes group—Paleocene–Recent
Divaricella group—Cretaceous–Recent

Table III gives the phylogenetic classification of the lucinid species included in the phenetic study. The right-hand column gives the classification of the species into subgenera; the left-hand column shows the assignment of the species to the genera (lineages and groups) listed above. The sequence

of the major divisions of the chart corresponds to the sequence of genera in the list above. This mode of representation was adopted to facilitate comparison between the phylogenetic and the phenetic (Tables IV, V) classifications. Since in most cases only one species of each subgenus was included in the phenetic study, only the subgeneric name (and, where necessary to distinguish between two or more species of the same subgenus, the initial one or two letters of the specific name) of each taxon is given in Table III. The code numbers used in Table I and in the phenograms are given in the Subgenera-column for each taxon. Question marks indicate generic or subgeneric assignments which are doubtful; OTU names not italicized are those of taxa whose subgeneric assignment is changed on the basis of phylogenetic evidence from that given in Table I. Plates I and II illustrate representative species of the lucinid genera.

Detailed documentation of the phylogenetic classification proposed here is given in Bretsky (1969). I no longer hold the opinion noted in the abstracts for the Prague Symposium that the *Lucina* and *Anodontia* lineages are closely related. Rather, the *Anodontia* lineage is probably closest either to the *Myrtea* lineage or to members of the *Loripes* group. The *Myrtea* and *Codakia* lineages may have a common Jurassic ancestry; it is possible, however, that the *Codakia* lineage is derived from an early member of the *Miltha* lineage. The last three members of the *Miltha* lineage in Table III may actually be derived from an early Tertiary member of the *Lucina* lineage, but it is more likely that they are descendants of the Jurassic species also ancestral to *Miltha* and *Eomiltha*.

COMPARISON OF THE PHENETIC AND PHYLOGENETIC CLASSIFICATIONS

Correlation phenograms

Fig. 3 presents the results of clustering of correlation coefficients by the weighted pair-group method, Spearman's sums of variable technique being used to calculate the average correlations among clusters. Subdivisions of the phenogram are defined by drawing lines across the phenogram at correlation levels of 0.75, 0.50, 0.25, and 0.0. These lines of equal phenetic similarity are called phenon lines; the groups which they delimit are phenons (Sokal & Sneath, 1963). The stems of the four clusters present at the 0.0 correlation level are numbered. The contents of the three latter phenons are summarized in Table IV (nomenclature and symbolism as in Table III). Only three clusters are present at the 0.75 correlation level; each consists of a pair of Recent species of the same subgenus, one member of the pair being found on the Atlantic and one on the Pacific coast of southern North America. Presumably, such Atlantic–Pacific species pairs belonged to an interconnected gene pool until the Pliocene emergence of the Isthmus of Panama.

Nearly all the clusters which form above the 0.50 correlation closely reflect inferred phylogenetic relationships, as shown by the fact that most of these clusters contain two or three members of the same subgenus or of closely related subgenera (cf. Table III). There are a few discrepancies, such as the clustering of the two *Stewartia* species with *Miltha s.s.* and *Plastomiltha*. This cluster, incidentally, illustrates reversal of correlation level, since the *Miltha–Plastomiltha* and *Stewartia anodonta–S. floridana* clusters were formed at a slightly lower level than that at which the two clusters joined, as given by Spearman's method. The cluster is plotted as a quadruple furcation at the highest of the similarity levels involved. The clustering of *Recurvella* and *Lucina s. s.* may be phylogenetically justified, since the former rather aberrant Eocene subgenus may be derived from an early species of *Lucina s. s.*

The 0.25 phenons should correspond in general, if the hypothesis of congruence between phenetic and phylogenetic classifications is to be accepted, to the major lineages and groups. This hypothesis is not well borne out in the correlation phenogram. Reasonable results are, however, obtained in the first two 0.25 phenons. The first indicates a close relationship between *Lucina s. s.* and *Pleurolucina*; the latter subgenus is probably closest to *Bellucina* but may have been derived from Obligocene or Miocene species of *Lucina s. s.* The second phenon includes most of the species of the *Lucina* lineage below the dotted line in Table III. The next four 0.25 phenons are identical to the corresponding 0.50 phenons, except for the junction of *Egracina* (probably most closely related to *Divalinga*) and *Eophysema* (an Eocene member of the *Anodontia* lineage). The seventh 0.25 phenon combines most of the species of the *Myrtea* lineage with a few of the *Lucina* lineage. The next includes some species of the *Miltha* lineage plus the edentulous members

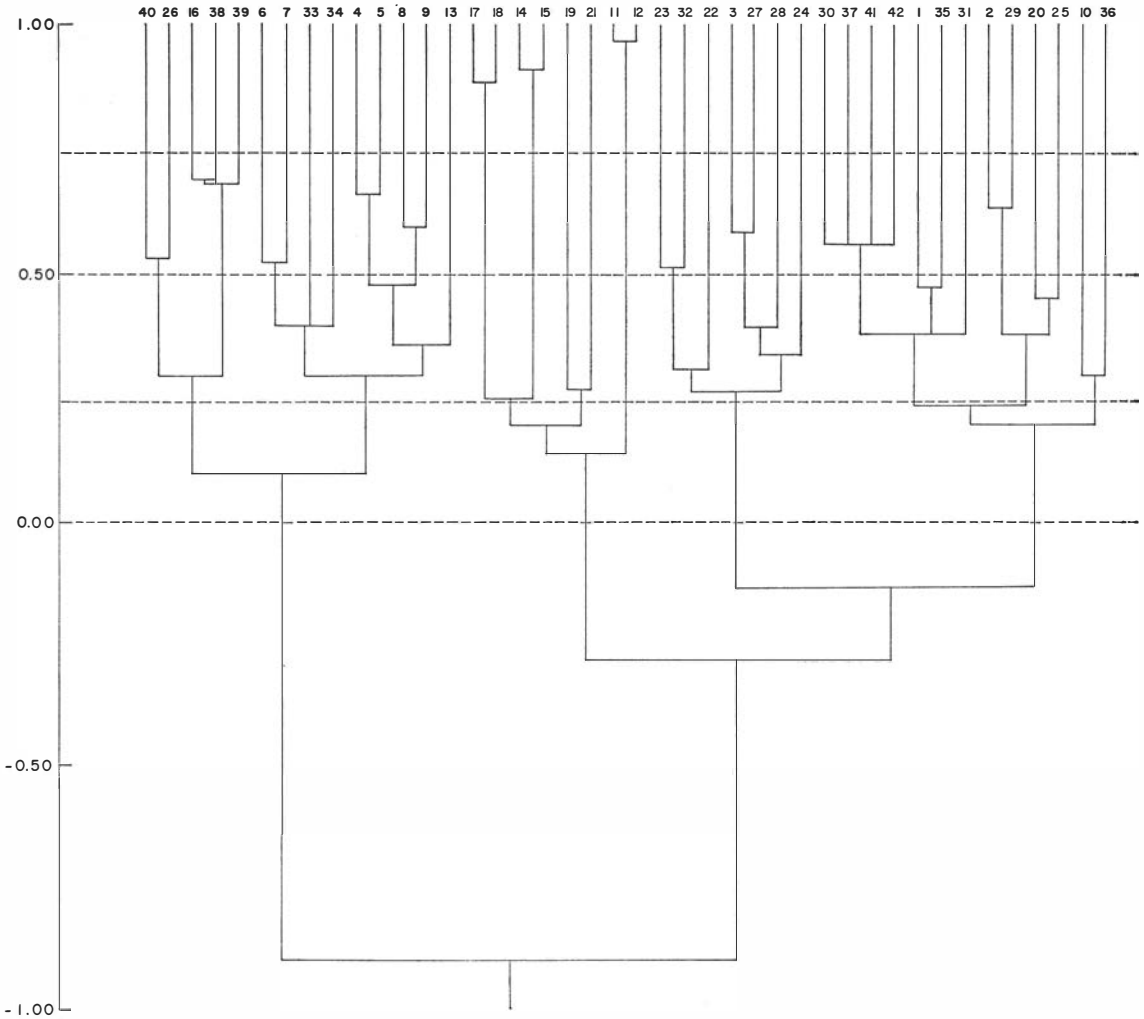

Fig. 3. Correlation phenogram.

of the *Lucina, Anodontia,* and *Myrtea* lineages. The last two are composed of, respectively, the remaining members of the *Miltha* lineage, with *Loripes*, (of uncertain affinity, probably related to the *Anodontia* lineage); and *Claibornites,* an Eocene taxon of uncertain affinity probably belonging to the *Codakia* lineage and possibly linking the *Codakia* and *Miltha* lineage, and *Phacoides,* probably most closely related to *Lucina s. s.* (and perhaps ancestral to *Plastomiltha, Lucinoma,* and *Armimiltha*).

The 0.0 phenons of Table IV are the major clusters numbered in Fig. 3. The first contains most of the members of the *Lucina* lineage; the second, the *Divalinga* group and *Codakia* lineage, plus *Eophysema,* with the order of clustering of the species of these genera being quite different from their inferred phylogenetic relationships. The third is the same as the 0.25 phenon containing most of the *Myrtea* and part of the *Lucina* lineage. The fourth is the *Miltha* lineage plus edentulous members of the *Anodontia, Lucina,* and *Myrtea* lineage, with the addition of *Loripes, Claibornites,* and *Phacoides;* again, the subclusters within this major cluster correspond poorly to groupings based on inferred phylogeny.

The considerable degree of isolation between the major clusters in the correlation phenogram,

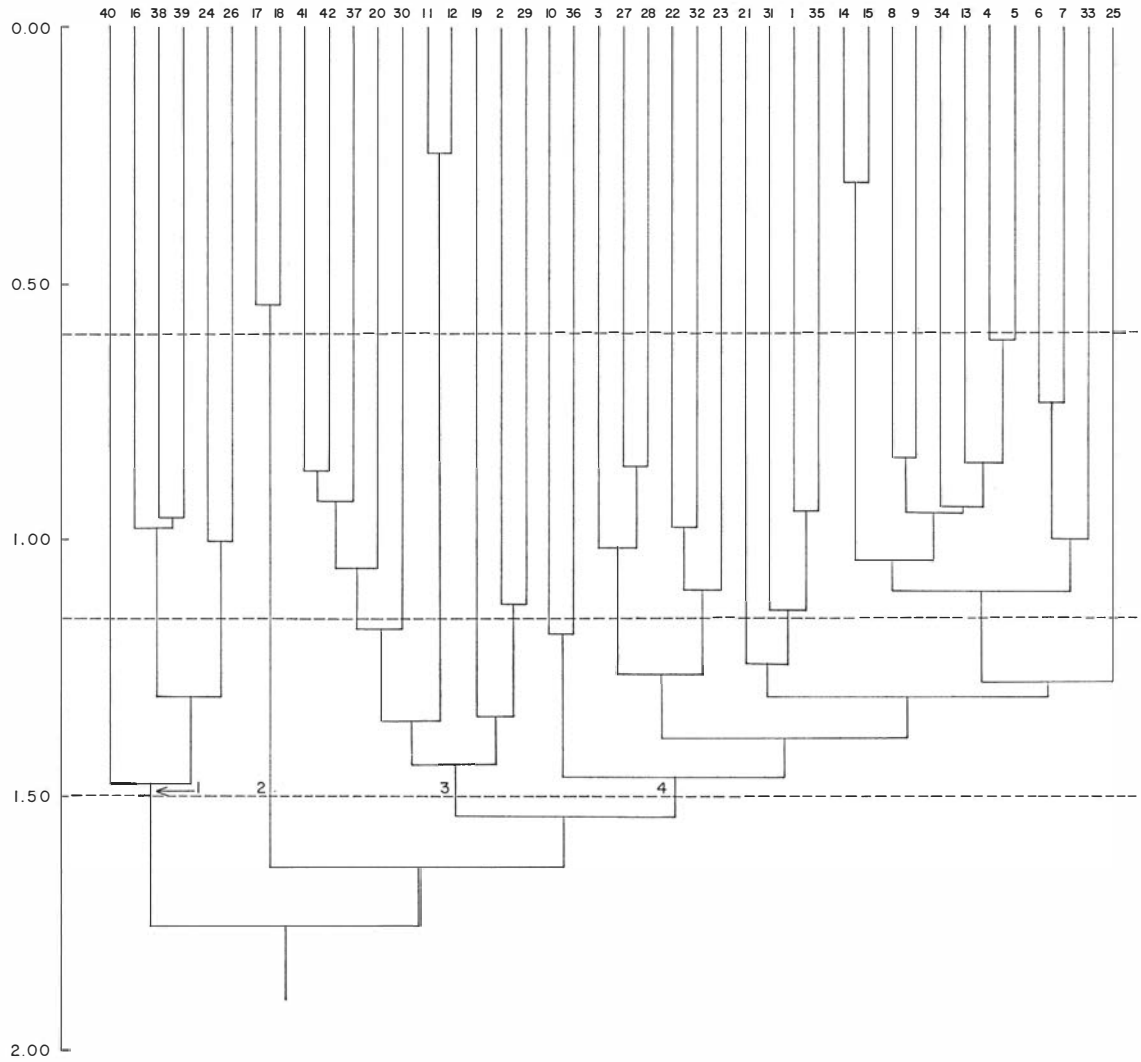

Fig. 4. Distance phenogram.

particularly of Major Clusters 1 and 2, is evidently a result of reversal of correlation occurring in a negative direction when the average correlation among members of a cluster becomes very small or negative. Similar results occurred in the studies by Moss (1967), Rowell (1967), and Thornton and Wong (1967) when Spearman's method was used.

Distance phenogram

Fig. 4 presents the result of clustering of distance coefficients by the weighted pair-group method, using arithmetic averages. (Smaller distance values imply closer similarity.) The structure within this phenogram is much less clear-cut than that of the correlation phenogram, and the choice of levels for phenon lines seems more arbitrary. Phenon lines have been drawn at the 0.60, 1.15, and 1.50 distance levels. The last of these phenon lines delimits four major clusters, whose stems are numbered. Table V records the composition of the 1.15 and 1.50 phenons, the 0.60 phenons being identical to the 0.75 phenons of the correlation phenogram.

In most cases, species having mutually highest correlations are also found to pair when distances are used. Because of the differences between the

correlation and distance formulas, however, when three OTU's are closely similar, OTU 1 may cluster first with 2 when correlation coefficients are used and with 3 with distances. The different modes of calculating average similarity may further alter the order of clustering. Thus the phenons formed at the 1.15 distance level are closely similar to but not identical with the 0.50 or 0.25 correlation phenons. Where differences between the phenograms exist at these intermediate levels, in some cases the changes are improvements from the phyletic standpoint and in others they are not. As an example of improvement, in the distance phenogram *Here* is placed with *Lucina s. s.,* with which it probably had a common early Tertiary ancestry. The original correlation matrix also indicates similarity between these OTU's, but similarity was not reflected in the clustering of correlation coefficients. As an example of worsening of phyletic relationships in the distance phenogram, *Ctena mexicana* and *C. orbiculata,* members of the *Codakia* lineage, are placed with some species of the *Lucina* lineage. This clustering probably reflects their resemblance (particularly in sculpture) to *Lucina* (*Parvilucina*?) *costata,* originally considered a species of *Ctena* (Table I).

The four major clusters defined by the 1.50 phenon line very poorly reflect any inferred generic-level or subfamilial-level relationships within the Lucinidae. Major Cluster 1 contains a few members of the *Lucina* lineage; except for the addition of *Here,* it is the same as the first 0.25 phenon of the correlation phenogram. Major Cluster 2 is composed of only two species, the *Divalinga* Atlantic-Pacific species pair. Major Cluster 3 includes the *Miltha* lineage, plus *Stewartia, Codakia s. s.,* and *Egracina* (with considerable discrepancy between the probable phylogenetic affinities of these species and their calculated similarities). The 24 remaining species are in Major Cluster 4, containing the entire *Myrtea* and *Anodontia* lineages and members of the *Codakia* and *Lucina* lineages and *Loripes.*

COMPARISON OF THE CORRELATION AND DISTANCE PHENOGRAMS

Although in the distance phenogram the affinities of several individual species and subgenera are better reflected than they were in the correlation phenogram, the major clusters of the distance phenogram are less similar to the principal phyletic divisions than are those of the correlation phenogram. Sokal and Rohlf (1962) developed the method of cophenetic correlations (calculating the correlation between the similarity level at which two taxa join in a phenogram and the actual calculated similarity between them) to measure the degree of distortion introduced by representing in two-dimensional space the multidimensional similarity between taxa. The cophenetic correlation for the correlation phenogram is 0.51; that for the distance phenogram is 0.66. The distortion in the correlation phenogram seems attributable to the considerable depression of similarity levels in the last few cluster cycles, by negative reversals. This distortion is a common feature of phenograms constructed by Spearman's method. In the distance phenogram, the rather low cophenetic correlation seems to be related to the extreme degree of isolation in the phenograms of some OTU's, particularly the *Divalinga* species, which have their second-order and lower-order similarities with species which are closer to still other species. The averaging feature of the pair-group clustering method means that OTU's which are somewhat isolated will remain unclustered until the average similarity level within one of the clusters decreases to the average level of similarity of the isolated OTU's with the other OTU's in the study. Their degree of isolation is thus exaggerated and their cophenetic values are unrealistically low (Sokal & Sneath, 1963).

Considerations such as those outlined above raise some doubt as to the common practice in phenetic studies of constructing phenograms by a variety of methods and selecting for comparison with the inferred phylogeny or traditional classification only the one or two phenograms with the highest cophenetic coefficient (e.g., Rowell, 1967). Perhaps more cogently, they support the contention of Ehrlich and Ehrlich (1967)—who are definitely not phylogeneticists (see, for example, P. R. Ehrlich, 1961)—that there is no one unequivocal measure of overall similarity. These authors consider difficulties to be introduced both by problems in deciding how to recognize and code different degrees of similarity, and by ambiguity in determining which of several methods of calculating similarity and of clustering is to be used.

CONCLUSIONS

Both the phenetic classification of the Lucinidae based on correlations and that based on distances gave results which from a phylogenetic viewpoint appeared reasonable at the subgeneric level. In other words, species considered on the basis of phylogenetic evidence to belong to the same subgenus were almost always placed close together by phenetic methods. These results generally validated Sokal and Sneath's (1963) exemplar method, at least for the specific and intraspecific levels. Clustering of the pairs or groups of closely related lucinid species with each other and with species which were the sole representative in the phenetic study of their subgenus, however, did not give groupings closely approximating the phylogenetically-based genera. In many cases several closely related subgenera clustered first with each other, but then with a group of interrelated subgenera from another lineage, rather than with the more distant members of their own lineage. It almost appeared that the phylogenetic lineages had been chopped into segments and these segments arbitrarily rearranged—once by the correlation method and then by the distance method. The poverty of the results at the generic level precludes any attempt to base subfamilies on the results of the phenetic classifications.

The results of the study are not particularly encouraging to the contention that phenetic and phylogenetic classifications should be closely similar. At least in the Bivalvia, convergence appears to become a troublesome problem at the generic level. Several cases of independent origin of characters which could not be distinguished phenetically can be documented by knowledge of the evolutionary history of the Lucinidae. A few examples are the loss of both cardinal and lateral teeth in the *Lucina, Myrtea,* and *Anodontia* lineages; the development of prominent radial ribbing in the *Codakia* and *Lucina* lineages; the loss of lateral dentition in most members of the *Lucina* lineages; and the attainment of very large size in the *Miltha* and *Codakia* lineages.

It is rarely possible, because as yet we know little about the ecology of bivalves by comparison to, for example, our knowledge of the ecology of terrestrial vertebrates, to adduce precise explanations for a particular case of convergence in the Lucinidae. The general evolutionary pattern seen in the Lucinidae—rapid divergence into a number of different lineages in late Jurassic time, with smaller radiations taking place early in Tertiary time and again near the Oligocene-Miocene boundary—can, however, be understood by considering their ecology. Recent Lucinacea are unusual among bivalves in that several lucinid species (both of the same and of different lineages) are frequently found living together and that members of other higher taxa, except for the deposit-feeding Protobranchia, are less common in or excluded from areas with a high concentration of lucinoids. The Lucinacea are especially characteristic of areas with a low oxygen content (which the presence of the anterior inhalant tube presumably makes more tolerable for the lucinoids) and of meager food supply (their relatively undiscriminatory sorting apparatus and specialization of the stomach for dealing with large food particles facilitate their utilizing all available food) (Allen, 1958; Moore *et al.,* 1968). The Jurassic lucinid radiation (with, as well, the mid-Cretaceous emergence of the other two principal lucinoid families, the Thyasiridae and Ungulinidae) may be related to the evolution in Mesozoic time of a number of infaunal eulamellibranch bivalve taxa, whose exploitation of the infaunal niche was related to the development of siphons (Stanley, 1968). Pushed into the less desirable marginal environments [Speden (1969) has documented the dominance of the Lucinidae in marginal environments in Upper Cretaceous time in the Western Interior of the United States], the lucinids were able to survive by dividing up their restricted environment into a number of microniches. These niches may well have been primarily defined by different depths of burrowing; Kauffman (1967) has postulated such depth zonation for Upper Cretaceous thyasirids, again in the Western Interior. Differences in size (shell size being strongly correlated with length of the inhalant tube and thus with depth of burrowing), shape (especially degree of inflation, compressed forms being able to burrow more rapidly), coarseness of sculpture, degree of development of the dorsal areas, strength of the musculature, and degree of development of the dentition (the first two factors probably being related to anchoring in the substratum, the others to interlocking and alignment of the valves, and all to degree of exposure to disturbance, as by wave activity or predation, which is partly a function of depth of burial) are the principal features on which major

lucinid taxa have been defined. The most viable combinations may have become established rather rapidly so that intrafamily competition might be minimized. Thus the species which were competitively most successful in mid-Mesozoic time became the ancestors of major lineages.

The radiations in latest Cretaceous, early Tertiary and mid-Tertiary time, except for the Eocene origin of the *Anodontia* lineage, generally can be considered as elaborations on the major adaptive themes inherited from the Jurassic radiation. None of the major lineages was replaced, but subgenera became extinct, new ones originated, and the relative dominance and diversity of the various lineages changed. Such changes in the fauna are documented for many other molluscan groups (Stewart, 1930; Stanley, 1968), and, indeed, for many other phyla. The Mesozoic–Cenozoic and Paleogene–Neogene boundaries coincide approximately with times of major tectonic events in, respectively, the North American Cordillera and the Eurasian Tethys. Though many factors other than tectonism must be considered, it is reasonable to suppose that the breakup of major seaways was responsible for extinction of some groups and stimulated evolutionary innovation in others—both within the Bivalvia and in their competitors and predators.

In a few cases, instances of convergence in the Lucinidae seem likely to be related directly to evolutionary replacement (e.g., the large size of the Paleogene species of *Miltha* and the Neogene species of *Codakia*, which have the same compressed shape and may have occupied a similar niche; the *Miltha* lineage was quite diverse in Paleogene time but is much less important in the modern fauna). The adaptive significance of others, such as the partial or complete loss of the dentition, remains speculative. Yet it is clear that in the Lucinidae it is possible to propose a well-documented phylogenetic scheme and a classification consistent with it, and to suggest many promising areas of future research into the causes of notable similarities and differences.

It is easy to understand the pessimism of the pheneticists apropos of phylogenetic classification, considering the nature of the material with which most of them have worked. But where fossil evidence is available, it would appear fruitless to ignore it. It is interesting to note that organisms which are too poorly preserved to yield enough characters to permit their inclusion in a phenetic study may, if they are strategically located in the fossil record, provide information of lines of descent. It seems clear that more information can be gained from attempting to determine how and why particular combinations of characters recur than from simply listing the characters as separate items in a similarity calculation.

Pheneticists have countered the arguments expressed above by stating that they consider evolutionary studies to be an indispensable part of the broad field of systematics, but too speculative and subjective to be included in the formal act of classifying. I consider, however, that much of the phenetic argument against phylogenetic classification is semantic in nature and results from misunderstanding of the requisites of evolutionary taxonomy. Simpson (1961), in fact, preferred to use the term "evolutionary" rather than "phylogenetic" to emphasize that classification is "inevitably an inadequate expression of phylogeny", with always some compromise between horizontal and vertical classification, some disagreement on question of homology, and some arbitrariness in subdividing continuously evolving lineages. He pointed out that it is preferable to consider evolutionary classification not as *expressing* phylogeny but as being *consistent* with it. Mayr (1965) further clarified the phylogenetic viewpoint by remarking that phylogenetic relationship has two aspects, genetic (number of characters or, ultimately, genes in common) and genealogical or cladistic (temporal location of branching points in phylogeny), and that phylogenetic classification takes into account both, not merely the cladistic dimension.

I believe that this study bears out with the statement by Michener (in Michener & Sokal, 1957) that the best approach to classification is one "utilizing information gained by the statistical method but modifying it with knowledge of probable actual phylogenies gained in a variety of ways". The phenetic methodology can be an excellent means of summarizing what is and is not known about a taxon and for assuring that all available information is used without *a priori* weighting in constructing a classification. Construction of phenograms followed by their critical examination to determine which clusters seem phylogenetically valid and which do not, and attempts to determine the causes of anomalous results, can suggest weaknesses in previous classifications and areas of future inquiry.

A principal reason for the rapid acceptance of the theory of evolution by natural selection was the way in which the theory provided a rational explanation for the existence of a natural system of classification. One of Darwin's predictions on the effect of the general acceptance of his views was that "our classification will come to be, as far as they can be so made, genealogies" (Darwin, 1859). As yet, the phenetic method does not seem to provide an improvement on this approach to classification.

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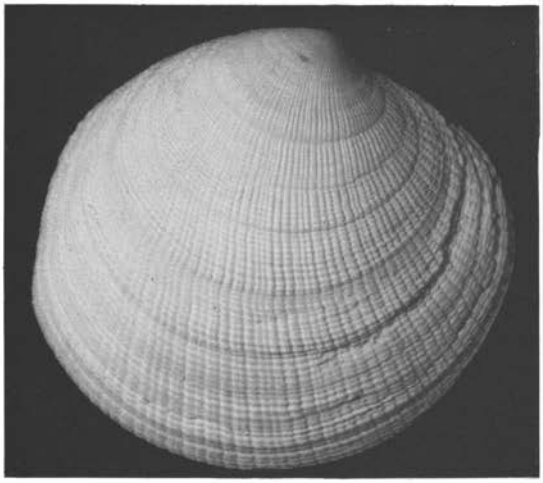
Sommaire. L'évolution de la famille bivalve Lucinidae est tracée en l'Amérique du Nord du Crétacé jusqu'à présent et la classification revisée pour mettre en lumière la marche probable de l'évolution de cette famille. Une seconde classification a été basée sur l'application de méthodes de la taxonomie numérique à une ou plusieurs espèces représentatives de chaque genre de Lucinides. Environ 45 caractéristiques de la morphologie du test sont prises en considération pour chacune des 42 espèces; des coefficients de correlation et de distance sont obtenus et groupés. Les deux classifications devraient être semblables si les suppositions de la taxonomie numérique sont valables. Des dissemblances entre les classifications phénétique et phylogénétique peuvent indiquer l'inexactitude de quelquesunes de ces suppositions, mais elles peuvent aussi rappeler qu'une combinaison des deux procédés a l'avantage de donner plus d'information que chacun d'eux tout seul.

1

2



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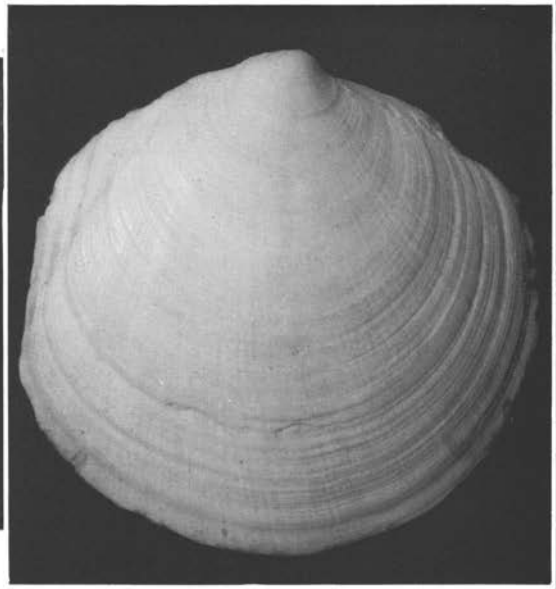

4

Representative species of the lucinid genera.
Lucina lineage: Fig. 1. *Lucina (Lucina) pensylvanica* (Linné). Fig. 2. *Lucina (Parvilucina) tenuisculpta* Carpenter.
Codakia lineage: Fig. 3. *Codakia (Codakia) orbicularis* (Linné).
Miltha lineage: Fig. 4. *Miltha (Miltha) xantusi* (Dall).

Plate II

1

2

3

4

Representative species of the lucinid genera.
Anodontia lineage: Fig. 1. *Anodontia (Anodontia) alba* Link.
Myrtea lineage: Fig. 2. *Myrtea (Myrtea) spinifera* (Montagu).
Loripes group: Fig. 3. *Loripes (Loripes) lacteus* Poli.
Divaricella group: Fig. 4. *Divaricella (Divalinga) quadrisulcata* (d'Orbigny).