

Historical and Ecological Factors in the Evolution, Adaptive Radiation, and Biogeography of Freshwater Mollusks¹

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SYNOPSIS. There are some 36 families that are wholly freshwater or with representative species in freshwater. There are virtually no phylogenetic analyses for these families. Zoogeographic analyses of freshwater molluscan faunas are hindered by a lack of significant systematic studies of these faunas. Such studies are essential if one hopes to develop hypotheses about phylogeny or biogeography.

It is clear from a phylogenetic analysis of the Pomatiopsidae that phylogenetic, vicariance, dispersal, and ecological factors all have significant effects on the patterns of distribution of this family. At one stage in history vicariance may be a dominant factor while during another stage of history, dispersal may be a dominant factor. At every stage, ecological considerations are necessary to understand the phenotypes seen and the spatial relationships among taxa. In examining the distribution patterns of dominant freshwater families with regard to their biological, ecological, and overall phylogenetic relationships it is evident that ecology plays a major role along with dispersal and vicariance. Clearly a synthesis is needed in biogeographical studies that incorporates vicariance dispersal, ecology, and geology-paleontology.

INTRODUCTION

For some years I have been attempting to understand something about the origins, pathways of evolution, modes and tempos of evolution, adaptive radiations, and distributions of freshwater molluscan faunas. In my pursuits it has become increasingly clear that in beginning a biogeographical analysis involving organisms about which little is known, one does not start with a single hypothesis (only vicariance) or with a single analytic tool for the systematic study (only multivariate phenetics by UPGMA). So diverse are the ways in which organisms can respond to environmental change and so diverse are the geological-ecological changes through time as they impinge on diverging grades and clades, that there is no a priori way of knowing the initial boundaries within which to assess relationships or origins. If one is interested in a group of taxa, for whatever reason, in the absence of a data base suitable for phylogenetic analysis one must

begin by collecting data on all their close relatives in faunas throughout the world.

In this paper I use as my major example the analysis of the origin and evolution of the Pomatiopsidae with its two subfamilies: Triculinae and Pomatiopsinae (Davis, 1979a). In brief, this family is considered to have a Gondwanaland origin with vicariance accounting for the relict elements in South America, South Africa, and Australia, the delivery via the Indian Plate to continental Asia.² Additionally there was long range dispersal through China to Japan, the Philippines, to the United States (Fig.

² The origin of continental S.E. Asia is complex. There is evidence that the Thai-Malay peninsular section separated from northern Gondwanaland mid-Palaeozoic and that collision with mainland Asia was in the late Triassic (Ridd, 1980). This early accretion of a "microcontinent" to mainland Asia does not alter the scenario for the introduction of the Pomatiopsidae to Asia from the Indian Plate. The Indian Plate had a profound impact on Tibet, Burma and western China in the Tertiary at a time coincident with the availability of freshwater snails of hydrobioid grade organization. The mid-Palaeozoic considerably predates freshwater hydrobioids. The Ridd (1980) report provides a strong reminder that with each new geological find involving land mass movements and formulations, biogeographic hypotheses must be re-evaluated.

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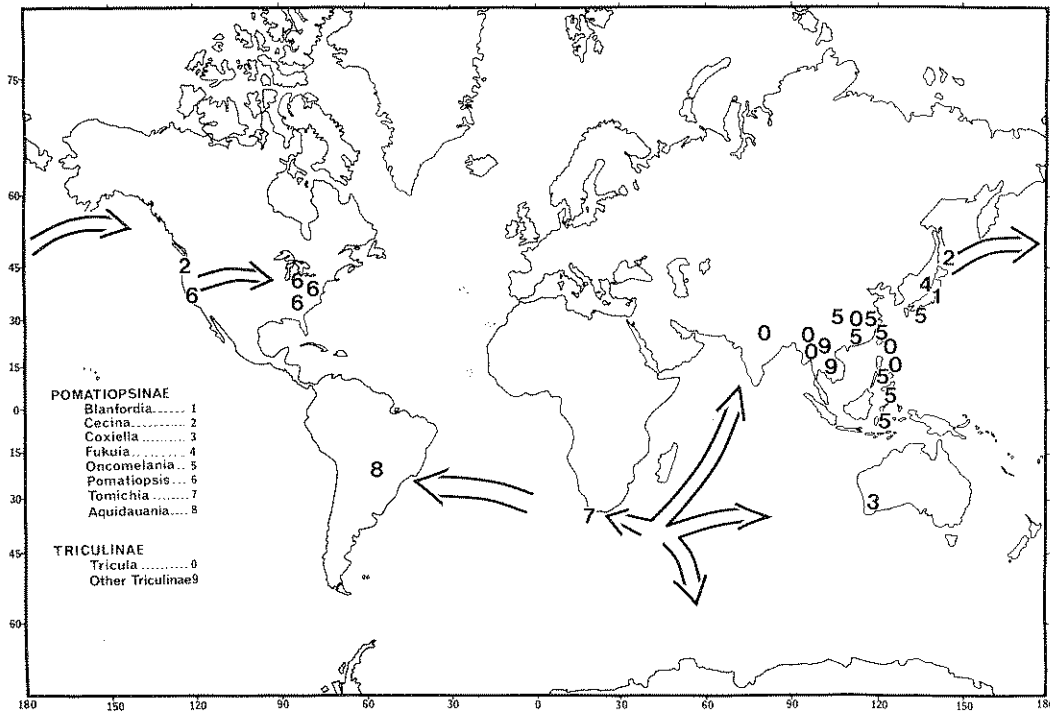


FIG. 1. The current distribution of pomatiopsid species, the hypothesized area where the Pomatiopsidae flourished over 100 million years ago, and the pathway of distribution following the breakup of Gondwanaland. (From Davis, 1979a)

1). One subfamily, the Triculinae, underwent an explosive adaptive radiation in the Mekong River, yielding three tribes, 11 genera and at least 92 species within the past 10 to 12 million years.

In the first half of this paper I ask general questions pertaining to biogeographical studies including my own approach, operational methods of systematic analysis, the relationship of systematic studies to biogeographic hypotheses, and constraints in structuring a phylogeny. I then provide examples relevant to these general issues from my studies of the Pomatiopsidae. The second half of the paper involves dispersal, vicariance and ecological considerations.

My general approach to these issues and my understanding of constraints follow: 1) Certainly evolutionary and biogeographical hypotheses should be falsifiable if they are to be valid (Popper, 1960, 1968a, b; Wilson, 1965; Platnick and Gaffney, 1977).

2) Sound biogeographic analyses are dependent on sound systematic analyses. Today systematic analyses should be done within the framework of population ecology, population genetics and modern ecological theory (Davis, 1979b, p. 161). 3) Only after a thorough systematic study is it possible to attempt to assess phylogeny and in many, if not most cases there will be insufficient data to make an *objective* hypothesis about phylogeny (Cain and Harrison, 1960). 4) Recent literature concerned with methods in systematics and biogeography is full of polemics and some read like religious dogma. To quote Eldredge (1979): "The dialogue has been marred at times by shouting (as a substitute for careful thought), confusion of exposition (with consequent misunderstanding on the part of opponents), and a tendency to characterize the opposition in monolithic terms. There has been as much tilting at windmills as reasoned discourse."

Avoid dogma and consider carefully the value of each position. In establishing positions recent authors have frequently set up straw men to bring greater attention to their points and often ignored early papers in which the same issues are discussed (often with greater clarity). With time and new discoveries, older and mistaken concepts are rapidly replaced with the new and more sound ideas. In so doing the best of the old should be incorporated with the new. 5) Vicariance, dispersal, and ecology are all important in understanding the distribution of organisms throughout the biosphere. 6) It is most desirable to test the congruence between hypotheses about phylogeny and hypotheses of biogeographical patterns. Phenetic and cladistic analyses should be used to complement each other. Cladistic analyses can be done with different operational methods. No single method is the best or only method. 7) One should be wary of extreme models. There is more to biogeographic analysis than looking for congruence of Hennig's (1966) complete-rule cladistic analysis and a vicariant model of area cladograms. One should indeed examine the congruence of a cladistic analysis and the temporal aspects of geologic change if the data permit it. However, one should use all possible operations to test the soundness of results based on the initial method, and one should consider the impacts of ecology and dispersal on present and past distributions.

SYSTEMATIC STUDIES AND BIOGEOGRAPHIC HYPOTHESES

Which comes first: systematic analyses with development of hypotheses about phylogenies, or biogeographic models? While the pros and cons of one or the other of these positions have been argued (Rosen, 1975; Ball, 1975; McDowall, 1978), the answer clearly depends on the kinds of data available. One could argue that biogeographic models for groups of fish, mammals, etc. could serve to predict aspects of phylogeny of a group of freshwater snails (concept of Rosen, 1975). This might be the case; it equally could be wrong. Each group must be considered in

terms of its own history only after sound systematic analyses have been done.

There are virtually no objective phylogenetic analyses for groups of freshwater Mollusca (Table 1). Accordingly, one should not score geographic regions for presence, absence, and/or diversity of a family of freshwater mollusks with a goal of preparing a sophisticated biogeographic model, until one can be sure 1) that each group concerned is monophyletic, and 2) that the systematic relationships to supposedly related groups in other localities are worked out.

The value of having at least a three-taxa data set for initiating or testing hypotheses concerning biogeography has been discussed (Platnick and Nelson, 1978; Rosen, 1978). Data available from three or more taxa of different geographic localities may make possible an initial hypothesis that leads to targeting new localities and faunas for future studies. Subsequent data collection and reformulated hypotheses may go through several cycles to produce a satisfactory and congruent set of hypotheses for phylogeny and biogeography. Any hypotheses about biogeography or phylogeny for most freshwater molluscan groups prior to the above steps would have the highest probability of being wrong.

CLADES, CLADISTICS, AND PHYLOGENY

As pointed out elegantly by Cain and Harrison (1960) and Sokal and Camin (1965) there are three components to a phylogeny: phenetic, cladistic, chronistic. A clade is a monophyletic assemblage (Huxley, 1959) and a cladogram is a hypothesis about phylogeny by ordering the branching sequences (*i.e.*, sequence of clades). By ordering the branches, one implies direction of change through time.

The need for techniques in phylogenetic systematics for formal analysis that would enable one to test hypotheses, and establishment of criteria and techniques were subjects addressed by Hennig (1950, 1957, 1965, 1966), Cain and Harrison (1958, 1960), Wilson (1965), Sokal and Camin (1965) and others. With the English edition of Hennig's (1966) operational criteria

for phylogenetic reasoning, cladism became enthusiastically endorsed by many and the polemics began. Cladistic analysis is essential to formulate an hypothesis about phylogeny. A cladistic analysis is not necessarily equated with Hennig's (1966) cladism. Further, we see that many excellent systematic works, pre-cladism, used set theory as a mental process and unique and unreversed characters to group taxa often without formally stating their techniques or without making a formal analysis that would make their hypotheses falsifiable. With appropriate operational criteria, cladistic analysis had come into its own, but it is not necessary to denigrate excellent contributions of the past. The practitioners of cladistic analysis face all the constraints and problems faced by pre-cladistic systematists (Cain and Harrison, 1960).

The gap between collecting a thorough morphological data base for systematic analyses, and producing a phylogeny is enormous. Cain and Harrison (1960) have fully discussed the problem involved. To establish a clade, one must establish monophyly. To consider a group monophyletic, one must eliminate cases of convergence. Convergence is probably the most underestimated problem in systematics (see also Davis, 1979a), is widespread in mollusks, and may not be detectable in poorly known groups.

Having identified convergent taxa, the task of establishing clades arises. Many who engage in cladistic analysis insist on selecting primitive character states and derived character states for those suites of characters that permit discrimination among sets of taxa. The problems with selecting primitive character states are considerable (Cain and Harrison, 1960; Cain, 1964; Davis, 1980a; Davis and Greer, 1980) and summarized with regard to assessing molluscan phylogeny by Davis (1981a).

There is little fossil record preserving the most important suite of characters for assessing phylogeny within subclass or superfamily level taxa of the Mollusca. These characters are from internal organs, the soft parts. The shell is of little value because of convergence (Davis, 1979a). Many of the most useful characters have several

unordered states (Davis, 1979a). Given numerous unordered multistate characters, each choice of the most primitive state and the most derived state increases considerably the probability of error.

There is, of course, uncontested approval among malacologists of the primitive status of many gastropod character states. The three-chambered heart is primitive, two-chambered derived; the rhipidoglossate radula is primitive, taenioglossate derived; the zygobranch gill primitive, pectinobranched gill derived; ctenidium primitive, lung derived, etc. These do serve at present to separate subclasses and some orders. The problem is selecting primitive characters at the superfamily or lesser taxonomic levels. Consider the freshwater Rissoacea (Table 1) with its several families where the Hydrobiidae are, after removal of the Pomatiopsidae, still probably polyphyletic, and where each family may have derived from a different marine rissoacean group or where one or another freshwater family evolved from a species of an existing freshwater family. There are at least 19 families with a rissoacean grade of organization (Taylor and Sohl, 1962; Davis, 1979a) about which we have very little morphological detail. We are a long way from designating primitive and derived character states for the Rissoacea.

AN EXAMPLE: THE POMATIOPSIDAE

An aquatic snail in the Mekong River and an amphibious snail of China have an important characteristic in common: both transmit a species of *Schistosoma* infecting man. The former is a species of *Tricula* (Triculinae), the latter is a species of *Oncomelania* (Pomatiopsinae). The *Tricula* species is part of a large endemic radiation in the Mekong River. Both genera had once been classified as Hydrobiidae. *Tricula* has been classified as Hydrobiidae Lithoglyphinae (Brandt, 1974). These opinions raised a series of questions (Davis *et al.*, 1976). How were these taxa related? Were they indeed Hydrobiidae? What can we learn of the origin of these taxa? Was the Mekong River assemblage that Brandt (1974) classified as Lithoglyphinae monophyletic?

Anatomical studies of all organ systems of the Mekong River taxa yielded data that when compared with similar data for Hydrobiidae s.s. of Europe, made the following clear: The Mekong River taxa in question are monophyletic: the Triculinae. The Triculinae and Pomatiopsinae are monophyletic: the Pomatiopsidae. The family Hydrobiidae of Brandt (1974) and previous authors is polyphyletic, a worldwide assemblage of taxa grouped on characters of shell, radula, penis, and operculum (Davis, 1979a). So similar were shells and radula of *Lithoglyphus* s.s. of Europe and pomatiopsids called *Lithoglyphus* or *Lithoglyphopsis* of China, as well as *Lacunopsis* of the Mekong River, that they were all considered Hydrobiidae Lithoglyphinae (Brandt, 1974). Ensuing studies (Davis, 1979a) made clear that Hydrobiidae s.s. are primarily northern continental, especially European and North American, while taxa of similar grade of organization of the Yangtze River drainage and drainages to the south and west of it including all rivers of Southeast Asia and India, are Pomatiopsidae. Convergence in a few character states had masked the considerable differences between these two families. Any biogeographical analysis involving the Hydrobiidae *sensu lato* would have been in error.

With the Hydrobiidae excluded from consideration of the origin of the Asian Pomatiopsidae, attention was focused on taxa of similar grade of organization from the southern continents. On the basis of anatomy, *Tomichia* of South Africa has a close phenetic relationship to *Oncomelania* of Asia. With the discovery that *Coxiella* of Australia is more phenetically similar to *Tomichia* than either is to *Oncomelania*, a tentative hypothesis involving historical biogeography was formulated. The Pomatiopsidae are of Gondwanaland origin and the direction of evolution was from Gondwanaland to western Asia to Japan. Research was intensified on potential pomatiopsid taxa of South America, South Africa, Southeast Asia, and Asia from India to Japan. It was found that pomatiopsid genera of South America, South Africa, and Australia differed little phenetically, that derived character states doubled in

TABLE 1. Families of freshwater molluscs exclusive of brackish-water taxa and Opisthobranchia, and references for those few families in which phylogenetic analysis has been extensive enough to permit biogeographical analyses involving origins, vicariance and dispersal.

Class	Gastropoda	
Subclass	Prosobranchia	
Superfamily	Neritacea	
Family	Neritidae	
	Hydrocenidae	
	Viviparacea	
	Ampullariidae	
	Viviparidae	
	Valvatacea	
	Valvatidae	
	Cerithiacea	
	Pleuroceridae	
	Melanopsidae	
	Syrnolopsidae	
	Thiaridae	
	Rissoacea	
	Assimincidae	
	Baicaliidae	
	Bithyniidae	
	Hydrobiidae	
	Lepyrriidae	
	Pomatiopsidae (Davis, 1979, 1980; Davis and Greer, 1980)	
	Pyrgulidae	
	Stenothyridae	
	Buccinacea	
	Buccinidae	
	Volutacea	
	Marginellidae	
Subclass	Pulmonata	
Order	Basommatophora	
Family	Acroloxidae	
	Ancylidae	
	Chiliniidae	
	Latiidae	
	Lymnaeidae	
	Physidae	
	Planorbidae (Hubendick, 1956; Meier-Brook, 1982)	
Class	Bivalvia	
Superfamily	Unionacea	
Family	Etheriidae	
	Hyriidae	
	Mutelidae	
	Unionidae (Heard and Guckert, 1971; Davis and Fuller, 1981)	
	Corbiculacea	
	Corbiculidae	
	Pisidiidae	
	Arcacea	
	Arcidae	
	Mytilacea	
	Mytilidae	
	Solenacea	
	Solenidae	
	Dreissenacea	
	Dreissenidae	

number with *Oncomelania* (Pliocene of Burma, living in western China to Japan) and they doubled in number yet again in the pomatiopsine radiation that began in the late Tertiary of Japan. Upper Cretaceous fossils of South Africa and northern India are strikingly similar and of pomatiopsid phenotype. *Tricula* lives today across northern India. These facts coupled with the late Miocene-Pliocene beds containing clearly pomatiopsid taxa in northern Burma justify an hypothesis of introduction of the fauna to Asia via the Indian Plate (Davis, 1979a).

The Cain and Harrison (1960) criteria for discussing phylogeny were met as regards the Pomatiopsidae (Davis, 1979a, 1980a, b, 1981b; Davis and Greer, 1980). Two of the three tricoline tribes, with the most derived taxa, are endemic in the Mekong and possibly, to a lesser extent, in the Yangtze River drainages. Taxa of one tribe with the most generalized taxa are widely distributed from India throughout Southeast Asia. There are a sufficient number of unique and unreversed characters to establish discrete sets of taxa. As a result, a phenetic analysis without weighting characters coupled with a timetable of events made clear by geological and paleontological data made possible a phyletic topology (Fig. 2), the main branches of which are consistent with a cladistic analysis (Davis, 1979a, 1980a). A Prim Network superimposed after multidimensional scaling (multivariate analysis, NT-SYS: phenetic method), rooted as a tree by establishing *Tricula* as the most generalized taxon, yields a branching pattern consistent with a cladistic analysis using Wilson's (1965) operational method (Davis, 1979a, 1980a). With the discovery of the tricoline genus *Robertsella* in the Malaysian peninsula, sufficient qualitative data were available to attempt a cladistic analysis based on the selection of primitive character states. The cladistic analysis was to assess the relationships among genera most closely related to *Tricula* (i.e., genera of the tribes Triculini and Lacunopsini). Critical to the analysis was the primitive position of the seminal receptacle (refer to Davis and Greer, 1980, for details). As

there is a directional sequence of moves of the seminal receptacle from the bursa copulatrix out along the common sperm duct to the sperm duct to the oviduct, the question is: Which end of the sequence is the original position? Two cladograms were developed (using Hennig's 1966 operational criteria) based on the two possible choices (Fig. 3). The "s" on the branches indicated the potential of taxa in that clade to transmit *Schistosoma* infecting man or mammals (snails resistance to or potential for infection with this parasite are under snail oligogenic control [Davis, 1980a]). Then a cladogram was developed using Wilson's (1965) operational method in which one does not select primitive character states (Fig. 4). The congruence between cladograms A of Figure 3, and Figure 4 coupled with the fact that lineages with genes associated with the transmission of *Schistosoma* are unbroken in A indicates that A is probably correct while cladogram B has been falsified. In summary, a cladogram based on Wilson's operational method of weighting unique character states has falsified one of two cladograms based on choosing primitive and derived character states.

In summary, and with consideration of the general remarks made earlier: 1) Any biogeographic model involving *Tricula* or *Oncomelania* classified as Hydrobiidae would have been in serious error. The family Hydrobiidae *sensu lato* is polyphyletic and many relationships implied by such a classification are incorrect. 2) A biogeographical model of the Pomatiopsidae could only come after a thorough systematic analysis. 3) By identifying cases of convergence and establishing monophyly (clades) it became possible to initiate hypotheses about the histories of these groups. 4) Combinations of systematic methodologies involving phenetics and cladistics were useful in establishing clades and relationships among clades. 5) It was clear that the weakest approach to developing clades would have been the method involving selection of primitive character states. 6) The distribution of pomatiopsid taxa and the direction of evolution in terms of derived character states is con-

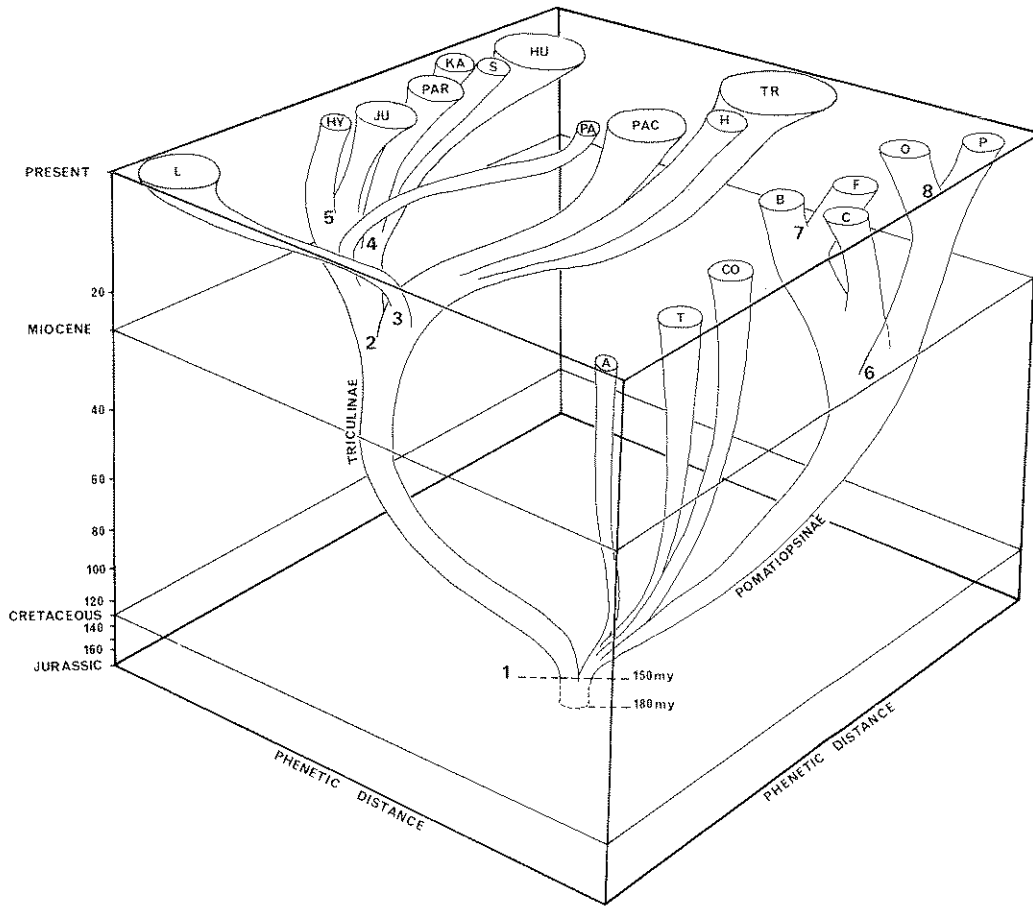


FIG. 2. Phylogenetic diagram in three dimensions, with time given in millions of years (on a log scale) from the Jurassic to the present. Branching Points: 1. Triculine and pomatiopsine lineages established in Gondwanaland prior to the breakup of the southern continents. 2. Divergence to form the Jullieniini (left grouping) in the Miocene. 3. Radiation of specialized *Lacunopsis* (*Lacunopsini*), which diverges from the Triculini. *Lacunopsis*, on shell characters, resembles marine and freshwater Neritidae. Some species converge on *Anculosa* (*Pleuroceridae*), *Littorina* (*Littorinidae*), or *Calyptrea* (*Calyptraeidae*). 4. Seven genera evolved in the Miocene, probably much at the same time, *Pachydrobiella* (PA) converges on *Pachydrobia* (PAC) of the Triculini in shell shape and structure. 5. Anatomical and shell data clearly indicate that *Hydrorissoia* (HY) and *Jullienia* (JU) diverged from a common ancestor. 6. A late Miocene radiation took place in Japan, giving rise to endemic genera *Blanfordia* (B) and *Fukuia* (F), and *Cecina* (C). *Cecina* spread to western North America, while *Pomatiopsis* (P) occurs only in the USA. 7. *Blanfordia* and *Fukuia* have either diverged from a common ancestor or are the same genus. Data thus far available support the former interpretation (see Davis, 1979a).

A. *Aquidauania*, South America. B. *Blanfordia*, Japan. C. *Cecina*, Japan, Manchuria, USA. CO. *Coxiella*, Australia. F. *Fukuia*, Japan. H. *Halewsia*, Mekong River. HU. *Hubendickia*, Mekong River. HY. *Hydrorissoia*, Mekong River. JU. *Jullienia*, Mekong River. KA. *Karelaimia*, Mekong River. L. *Lacunopsis*, Mekong River, Yangtze River. O. *Oncomelania*, China, Japan, Philippines, Sulawesi. P. *Pomatiopsis*, USA. PA. *Pachydrobiella*, Mekong River. PAC. *Pachydrobia*, Mekong River. PAR. *Paraprososthenia*, China, Mekong River (Thailand, Laos). S. *Saduniella*, Mekong River. T. *Tomichia*, South Africa. TR. *Tricula*, India, Burma, China, Philippines, Mekong River. (From Davis, 1979a)

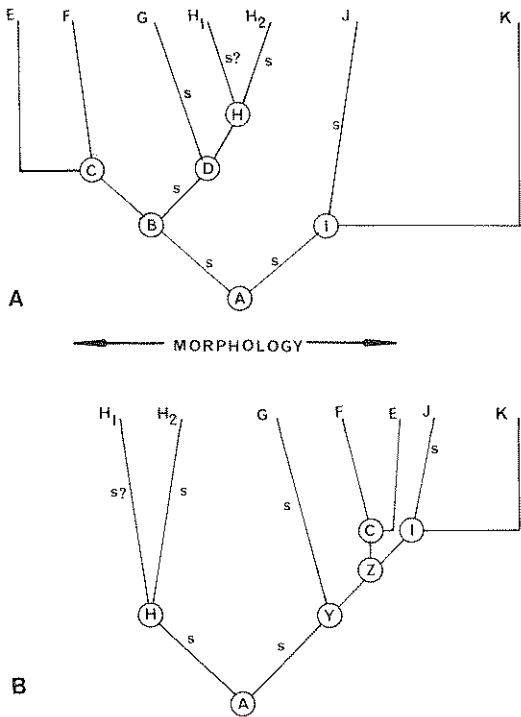


FIG. 3. Cladograms showing possible relationships among taxa of Triculini and *Lacunopsis*. The cladograms are based on characters of the female reproductive system. A is based on the concept that the primitive position of the seminal receptacle is on the oviduct; B is based on a primitive position of the seminal receptacle attached to the bursa copulatrix. See Davis and Greer (1980:268-270) for details. E, *Halewsia*; F, *Pachydrobia*; G, *Robertsia*; H, *Tricula*; H₁, *T. burchi*; H₂, *T. aperta*; J, *T. bollingi*; K, *Lacunopsis*. A, B, C, D, H, I, Y, Z are ancestral taxa; s indicates the potential of taxa in that clade to transmit *Schistosoma*. (From Davis and Greer, 1980)

gruent with the timing and location of geological-paleontological events.

Vicariance and dispersal biogeography

Is it true that "in biogeography, the contrast is between the concepts of chance dispersal and vicariance" (Croizat, 1978)? Are "the differences between traditional and vicariance biogeography . . . analogous to the differences between phenetic and cladistic taxonomy" (Nelson and Platnick, 1978)? Is there really the polarity that on one hand the traditionalists cling to "determining centers of origin and direction of dispersal" while on the other hand the

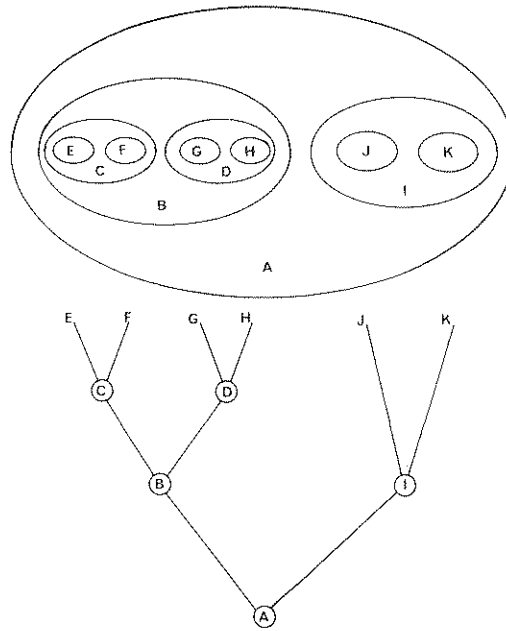


FIG. 4. Set-theory solution for demonstrating relationships among taxa E-H, J-K based on unique and unreversed characters *sensu* Wilson (1965). Character-states upon which each set is based are given in Davis and Greer, 1980. E, *Halewsia*; F, *Pachydrobia*; G, *Robertsia*; H, *Tricula*; J, "*Tricula*" *bollingi*; K, *Lacunopsis*. (From Davis and Greer, 1980)

"vicariance approach" attempts to unite "phylogenetic theory, concepts of distributional congruence, and theories of earth history" (Rosen, 1978)? Must a discussion of dispersal be tied to centers of origin? Is it true that taxa are distributed where they are today "because their ancestors originally occurred in the areas where they occur today, and the taxa now there evolved in place" (Platnick and Nelson, 1978)?

The answer to all these questions is no. Given historical developments and massive evidence for plate tectonics, the traditionalist approach to historical "centers of creation," and routes for dispersal from these centers had to undergo radical reappraisal. It is to make a straw man out of "traditionalist" to pit the 19th century against the syntheses possible given from late 20th century facts about plate tectonics. The concepts of vicariance in terms of the importance of barriers, plate movements,

and theories of earth history were being conscientiously applied (Scientific American, 1952–1972) before the so-called vicariance paradigm started its exponential phase of development in the decade of 1970. The straw man problem is compounded with vicariance enthusiasts redefining dispersal to suit their own ends.

I use the term dispersal as it has long been considered, *i.e.*, in terms of 1) a taxon increasing its range without crossing barriers and without fragmenting; 2) a taxon increasing its range without crossing barriers but with subsequent fragmentation; 3) a taxon increasing its range by crossing barriers. It is self serving to state that type-2 dispersal is "vicariance in disguise" (Platnick and Nelson, 1978).

As discussed above, phenetics is not incompatible with cladistics; likewise I maintain that both vicariance and dispersal are important to both understanding the origin of new taxa and the distribution of world biotas. It is irrelevant to ask which is the more important aspect. It is relevant to question the relative contribution of each to the origin and distribution of the taxa in question. It is important to realize that at one stage in the history of a stock, vicariance may be a dominant factor while at another stage in history, dispersal may be the dominant factor. Further explanations about biogeographic patterns may change as one varies the time frame and geographic scale (Simberloff *et al.*, 1981).

The origin and evolution of the Pomatiopsidae (Davis, 1979a) provide an example for discussing these issues as they relate to freshwater mollusks. From the Upper Cretaceous to the present, vicariance and dispersal have played different roles at different times with regard to the subfamilies Pomatiopsinae and Triculinae. From the Upper Cretaceous to the Miocene, vicariance was a dominant factor with faunal elements rafted to their current South American, South African, and Australian localities and an additional segment carried to mainland Asia via the Indian Plate. With the initiation of the Himalayan orogeny began the formation of those major river systems that provided highways of dispersal. The amphibious pomatiopsine

Oncomelania dispersed along the Yangtze, throughout southern China to reach Japan and eventually North America. The aquatic Triculinae dispersed along three arcs; northern India through China to the Philippines; northern India through northern Burma to western Yunnan, China; down along the Mekong River; and from northern India through northern Burma down through western Thailand into Malaysia (Davis, 1980a; Davis and Greer, 1980).

Concentrating on the Triculinae, it is reasonable to consider three centers of evolution (not to be confused with historical centers of creation or centers of origin), *i.e.*, localized areas in which evolved species-rich faunas. Centers of evolution are recognized by zones of high species diversity comprising one or more monophyletic groups. I do not consider a center of evolution simply to be a locality where the first fossil species, possibly attributed to the group of interest, is found. Species may disperse to new drainages from such centers. Lineages diverging through time may swell into species-rich centers at different places and in different times. Those centers increasing in numbers of species and diversity of species are centers of evolution as within them and from them come the various morphological or physiological variations that lead to new lineages and perhaps new species-rich centers later on. The first triculine center is recorded in the fossil record on the Indian Plate in the Upper Cretaceous; the second center is recorded in the late Miocene-Pliocene fossil beds and existing lake faunas of northern Burma and western Yunnan, China; the third is seen in the living fauna concentrated within 300 river miles of the Mekong River from Khemarat, Thailand to Kratie, Cambodia.

Considering the first discernible center, these ancestral populations were not divided by the appearance of a barrier. The underriding of the Asian mainland and initiation of the Himalayan orogeny allowed for dispersal from the Indian Plate into newly forming aquatic systems. In rapid order micro-vicariations and dispersal were associated with stream captures, lake formations, lake basin disruptions,

etc. From this first recorded center, the fauna spread into virgin freshwater environments, so that diversity increased in northern Burma and western Yunnan.

With the Himalayan orogeny and the initiation of the Yangtze and Mekong rivers in the late Miocene, there opened vast new ecological space for the radiating pomatiopsids. As the rivers evolved, habitats and tributaries suitable for triculines opened up further and further downstream. The tributaries became highways for colonization. Further downriver the river became wider and ecological space more complex.

Today, the greatest diversity in the world of a monophyletic assemblage of freshwater snails is found in the third center of evolution. This assemblage of some 92 species now occurs on either side of the great falls of the Mekong River near the Cambodian border. Considering the biology of these snails, speciation could readily occur without macrobarriers (of the vicariance paradigm) dividing the ancestral biota. The snails are small, mostly <12 mm maximum shell dimension, and r-selected (Davis, 1979a) in that they live one year or less, putting relatively immense amounts of energy into a one-time reproductive effort. They are opportunistic species living in a river that goes through an annual cycle of flooding and low water associated with the monsoon cycle. The annual catastrophic floods cause immense density-independent mortality. There are continuous shifts of habitats as the river destroys them and creates them. During various stages of low water various species grow to maturity and quickly reproduce at slightly different times. Thus several different species may occupy the same space but at different times (Davis, 1979a). Newly created habitats are rapidly colonized due to rapid dispersal mechanisms. These are ideal conditions for parapatric speciation (Endler, 1977).

The distributions of species and populations in this modern center of diversity appear continuous viewed in terms of macro-zoogeography but break up into nodes of diversity and patchiness of populations as one increases magnification of space.

Close examination reveals numbers of contiguous or barely disjunct demes. There is probably little or no gene flow among many demes over a number of years where habitats are infrequently destroyed by flooding. I have sampled such pockets along the Mekong River over five years. In other localities habitats are regularly created and destroyed with low probability of stability over periods of time such as five years. Recruitment into these low-stability areas presumably involves individuals from numbers of demes. Considering the habitat complexity and width of the 300 mile stretch of river that also includes major tributaries, and the patchiness and small area of species and deme patches throughout this area, it is highly probable that speciation has taken place in this center as habitats evolved and diversity increased. Speciation could still be occurring since in this evolving river system there is no ecological steady-state. Considering arguments of Ehrlich and Raven (1969) and Endler (1973, 1977), micro-allopatric or parapatric speciation can take place in a very small geographic area where geographic ranges of closely related species are nested.

Some triculine genera endemic in the Mekong River have more than eight to ten species and there are races of species. The impression gained is that demes diverged into races, races to species until within the ecological space, stabilizing selection restricted speciation.

What dispersal mechanisms are there? Dispersal across barriers leading to the introduction of freshwater molluscan fauna to new aquatic systems can occur in several ways. All of these mechanisms were undoubtedly involved in the formation of species-rich pomatiopsid centers of evolution. Consider the invasion of brackish-water Stenothyridae up the Mekong River system to reach headwaters that occupy an enormous area while the Triculinae were dispersing down evolving river systems. The stenothyrids, like the triculines, are mostly negative rheotropic and thus push upstream. Over time, waterfalls and rapids do not seem to dampen chance dispersal into tributaries and headwaters. Local

endemism of the stenothyrids and certain Triculinae in tributaries and certain headwaters attest to highly local speciation and lack of gene flow, or survival.

1. The foremost mechanism is stream capture. There is extensive geological evidence of stream capture in the upper Mekong-Yangtze River drainages. A common sequence would be a lake being tilted, and the contents subsequently flowing into an existing but previously separate stream; two faunal elements are thus joined.

2. Faunal elements are swept downstream throughout the year. I have collected algal masses floating downstream filled with 200+ individuals of four different species. I have collected sticks floating downstream, covered with typical triculine sand encrusted egg capsules. I collected one such branch just after it was swept over the falls of the Mekong. Maintained in an aquarium, the eggs hatched yielding over 100 healthy young snails. It is easy to see how new habitats are colonized and how a species can increase its range far downstream.

While such downstream movement could restrict parapatric differentiation and speciation along certain naturally channeled sections of the Mekong River, other vast sections of river are so complex due to thousands of islands creating natural backwaters and barriers to dispersal that conditions for parapatric speciation are found.

3. The distribution of freshwater molluscs, particularly pulmonate gastropods and bivalves, has, in great part, been accomplished by passive dispersal (Russell-Hunter *et al.*, 1964; Lassen, 1975; Russell-Hunter, 1979). In England, it has been calculated that isolated ponds receive an average of one species every 9 years (Boycott, 1930, 1936), and that species diversity in these ponds relates to the age of the ponds. Lassen (1975) documented the introduction of pulmonate species into one small pond where he estimated that the pond equilibrated at 4 species with immigration and extinction rates at equilibrium of 0.8 species per year.

The transport of molluscs by various animals, particularly by birds and insects has

been well documented (Kew, 1893; Rees, 1965; Fryer, 1974; Russell-Hunter, 1979), and some distribution patterns of freshwater molluscs reflecting bird migration routes (Russell-Hunter and Warwick, 1957; Russell-Hunter, 1979). Fryer (1974) noted that 20% of the corixid bugs of an English pond had one or more specimens of the tiny bivalve *Pisidium* clamped to an appendage, a situation previously reported (Fernando, 1954). Given that these insects do fly long distances, it is clear that *Pisidium* transport by bugs is much more probable than generally thought. Smaller species of operculate snails are particularly well-suited for transport by birds, and authentic cases of passive aerial transport have been documented (Russell-Hunter *et al.*, 1964). Limpets are transported on the elytra of aquatic beetles and *Hemiptera*, and lymnaeids, unionids, physids, and land snails have been commonly found on the feet and plumage of birds, including birds in long distance migration (Rees, 1965). Egg masses of physids can pass through the digestive system of ducks and a few eggs can survive to hatching (Malone, 1965).

Unionid clams, for the most part, disperse with fish since the glochidial larvae of the clams are parasitic on fish. However, clams do clamp onto the feet of migratory water-fowl. Kew (1893) documented a case where a duck was shot on the wing with a clam clamped onto a foot. The leg was cut off and after a day placed into a pan of water upon which the clam opened its valves and released the foot. Transport of amphibious or aquatic snails and/or eggs on mud stuck to hooves or birds' feet is too highly probable to reject (Lassen, 1975). In short, stepping-stone dispersal (from aquatic system to aquatic system) leads to long range dispersal given sufficient time.

I have seen birds along the Mekong River fly off with small sticks from the river and fly upstream a considerable distance with them. Presumably some of these sticks will fall back into the water. Examining the area from which these sticks were gathered, other similar sticks were frequently covered with eggs. It should be remarked that during low water in this river, snails

cover all solid objects with eggs to the point that space for eggs appears to be a limiting factor.

In the pomatiopsid dispersal to North America via Japan (Davis, 1979a), of special note is the amphibious habit of Asian *Oncomelania* and American *Pomatiopsis*, the high density populations in which they occur, and their proven ability to withstand long periods of desiccation—all important attributes for passive dispersal. The *Pomatiopsis* radiation in North America is an extension of *Oncomelania hupensis* of Japan (Davis, 1979a). The Pliocene pomatiopsid radiation of Japan produced the marine genus *Cecina* that probably dispersed along Beringia to the northwestern United States where it is also found today (Davis, 1979a). Precisely how pomatiopsids reached the Philippines is unknown but the arcs of distribution are consistent with a hypothesis of dispersal mixed with some vicariance events.

In summary, modern pomatiopsid diversity today is not where the pomatiopsid ancestors occurred 10 million years ago. Tracing backward in time, we can identify a series of centers of evolution. Pomatiopsid history is best interpreted in terms of both vicariance and dispersal. The roles of vicariance and dispersal varied significantly over time. Passive dispersal by birds, insects, and fish plays an important role in the distribution and local species diversity of freshwater molluscs. The explanations do change as one varies the time frame and geographic scale. Rapid and episodic speciation occurring in a relatively small area (by continent size standards) coupled with geographic expansion can be perceived as a blur of vicariance and dispersal.

ECOLOGICAL DETERMINISM

Are ecology and biogeography (based on sound systematics) mutually exclusive as stated by Rosen (1978)? I maintain that they are not, and that what is needed is a synthesis that links ecology, systematics, geological history and biogeography. Ecological considerations are essential for sound systematic studies, assessing distributions of living biotas, and analyzing changes in distribution through time. En-

vironmental equilibria and steady states are short term at best even over periods of geological time relevant to speciation events, *i.e.*, 500, 1,000, 10,000 years. Continuous environmental changes drive evolution. Diversity of organisms arises from continuous adaptation to shifting selective pressures.

Ecological principles are important to systematic analyses that are the foundations for biogeographical models, and to understanding the distribution of taxa throughout the world. First consider the ecology-systematic link. Ignorance of, or neglect of ecological principles still contributes to serious errors in systematics of freshwater mollusks. Consider the results of ignoring the impact of both environmental variables and species interactions on convergence, polymorphisms, color patterns, character displacement, sibling species, adaptive radiation. The foremost problem is convergence (Davis, 1979a) as discussed earlier. Genera around the world have been placed into higher taxa on the basis of greatly convergent character states. Systematists have failed to realize that species of different phylogenies occurring in different areas often converge phenotypically in adapting to similar ecological conditions. In Figure 5 are shown species belonging to three different superfamilies, yet on the basis of shell phenotype, phylogenetic relationships are masked by phenotypes adapted to similar ecological conditions, *i.e.*, living on solid objects such as rocks in high energy environments (Davis, 1979a). Considering the prominent degree to which shell phenotype has been used in molluscan systematics, no further comment should be necessary.

The systematics of the pomatiopsid genus *Tomichia* simply cannot be done on the traditional basis of comparative anatomy. While species of this genus have remained morphologically similar, they have radiated ecologically with different physiological requirements. An understanding of the climatic changes in South Africa from the Miocene onward is essential to understanding the physiological-ecological radiation. With the onset of aridity in west-

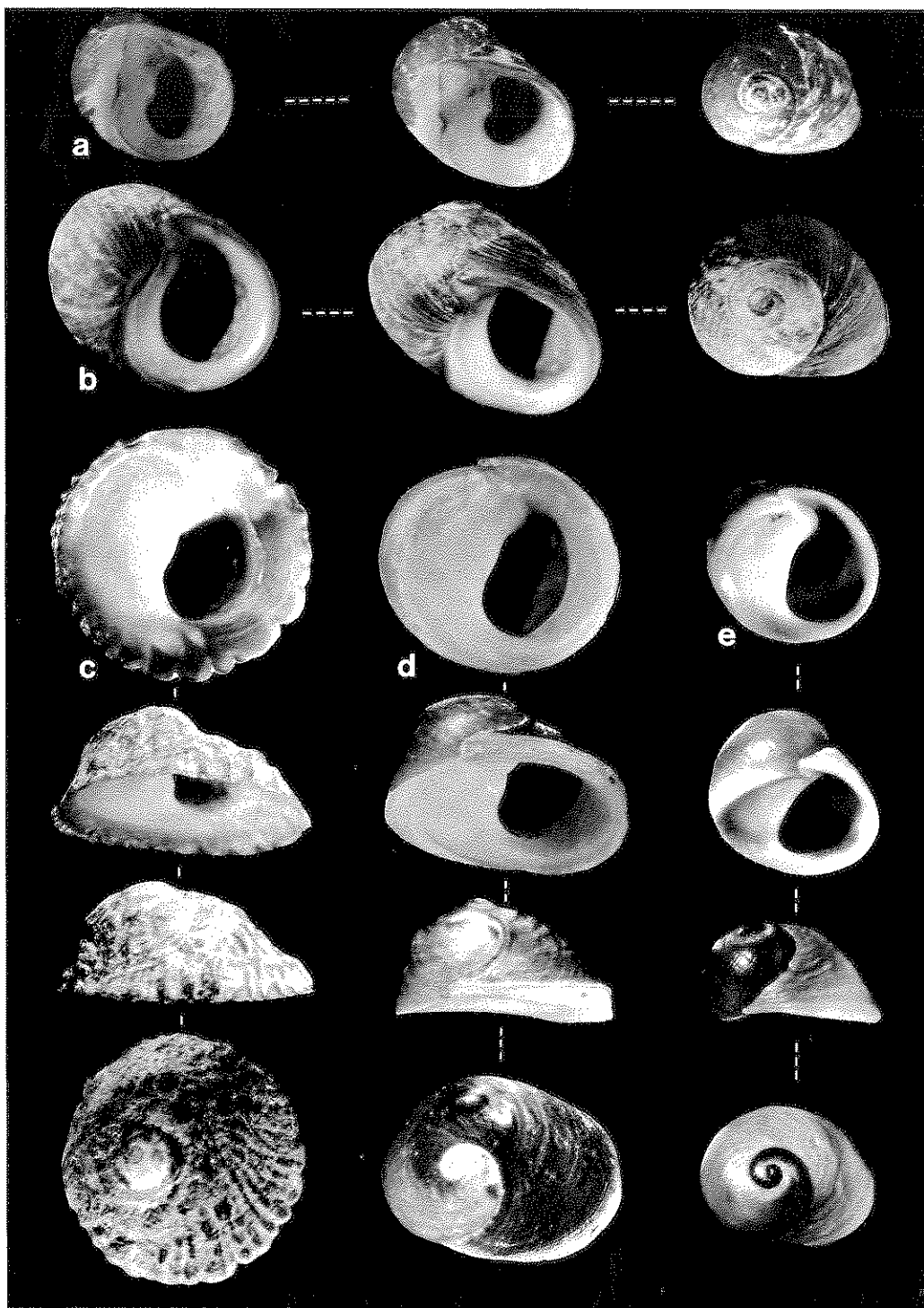


FIG. 5. Shells from three superfamilies demonstrating convergence. Rissoacea, Pomatiopsidae: Triculinae: Lacunopsini of the Mekong River; a) *Lacunopsis globosa* (length = 11.0 mm), c) *L. fischerpietti* (diameter = 16.3 mm), d) *L. harmandi* (d = 8.1 mm). b) Littorinacea, Littorinidae: *Littorina obtusata* (l = 13.7 mm) marine, northeast USA. e) Cerithiacea: *Spekia zonata* (d = 11.0 mm) Africa, Lake Tanganyika. (From Davis, 1979a)

ern South Africa, there has been a continuing climatic change towards desert formation (Tankard and Rogers, 1978; Axelrod and Raven, 1978). With the drying up of perennial freshwater, snails adapted or became extinct. We see today species adapted to cycles of freshwater evaporating to hypersaline water, and to amphibious, terrestrial, as well as completely freshwater aquatic conditions (Davis, 1980*b*, 1981*b*). An understanding of changing ecological conditions from the Miocene to the present is essential to understanding modern and past distributions of South African Pomatiopsidae.

Now consider ecology and the distribution worldwide of freshwater molluscan taxa. By comparison with terrestrial and oceanic biomes, freshwater habitats are transient short-lived systems. The total area of freshwater systems is not large (1/70th ocean's area; Russell-Hunter, 1979) and is broken up into small discontinuous units (excepting the few large river systems). Additionally, most lakes and ponds accounting for about 80% of the world's freshwater area are <100 km² (Russell-Hunter, 1979). The life expectancy for such lakes is only about 10³-10⁴ years with many existing only 10² (Russell-Hunter, 1979).

In such systems (<100 km², <10³ years duration) one finds a considerable amount of between-systems population diversity but low speciation. It appears that there is a premium on adaptive plasticity, dispersibility, and dampened speciation (Russell-Hunter, 1979). High diversity and considerable speciation are found only in those few systems (lakes and rivers) exceeding 10⁶ years in age and/or in new ecological space opened by tectonic activity (Davis, 1979*a*; Boss, 1979). Considering the constraints of the above, and with regard to freshwater dispersal, overall deployment, diversity and adaptive radiation, it appears that the following factors are important: 1) reproductive strategy, 2) respiration, 3) biological-habitat constraints, 4) size, 5) physical-ecological parameters.

It is clear from Table 2 that wherever a large endemic radiation is described, it is

dominated by cerithiaceans or hydrobioids, not by bithyniids, viviparids, pulmonates, etc. (Davis, 1979*a*). The cerithiaceans or hydrobioids occur in lakes or rivers and there is no geographic exclusion of one type or another, *i.e.*, all cerithiacean radiations are not restricted to Africa, etc. Where one group radiates, the other is absent or minimally present. Clearly these facts result from ecology, not history.

It further seems evident that ecology, not history is involved in the ampullariid and Viviparidae Bellamyiinae radiations, and the fact that cerithiaceans dominate in Africa, not hydrobioids. The ampullariids and Bellamyiinae are clearly of Gondwanaland origin. The ampullariids have modern radiations confined to tropical areas in South America, South Africa, India-Ceylon, and Southeast Asia (Pain, 1972). The viviparids are fossil in South America (Parodiz, 1969) with proven Bellamyiinae radiating in Africa, India, and Southeast Asia. Thus the individual track of the Pomatiopsinae involving Africa, India, and Southeast Asia is part of a generalized track involving the Ampullariidae and Bellamyiinae (also certain Thiaridae and Planorbidae Bulininae). Given that these distributions were most probably derived by vicariant historical events involving plate tectonics, the Ampullariidae and Thiaridae radiated extensively in Africa, but not in the hotbed of endemism in Southeast Asia where the hydrobioid Triculinae and Viviparidae now dominate (Table 3). The relatively great amounts of slow moving, muddy-bottom and muddy-water rivers or streams and expanses of swamp land of tropical Africa may account for the larger bithyniid and ampullariid radiations of Africa. One innovation in the Ampullariidae, the sinistral genus *Lanistes* accounts for 18 (69%) of the African ampullariid species. This genus is not found in Southeast Asia. On the other hand, viviparids radiated more extensively in Southeast Asia. Hydrobioids do not do well in Africa in spite of the fact that the first freshwater fossil record of hydrobioids is from the Permian of Africa (Knight *et al.*, 1960). This lack of hydrobioid radiation and di-

TABLE 2. World-wide distribution of large endemic freshwater gastropod radiations with taxa that are dominant in them in numbers of species.

Cerithiacean	
Lakes	Rivers
Tanganyika, Africa	Tennessee system, U.S.A.
Sulawesi (Celebes)	Coosa*, U.S.A.
Biwa, Japan	
Hydrobioid	
Lakes and Springs	Rivers
Baikal, U.S.S.R.	Mekong, Southeast Asia
Cuatro Ciénegas, Mexico	La Plata, South America
Ohrid, Yugoslavia	
Titicaca, South America	
Peninsular Florida, U.S.A.	

* Some 12 species of the hydrobioid genera *Somatogyrus* and *Clappia* were presumably endemic in the Coosa River (Walker, 1918) but these were overshadowed by the numerous pleurocerid species of this river. Most of this endemic fauna is now extinct due to damming of the river.

iversity is apparently due to a paucity of limestone-rich outcroppings and suitable substrates in perennial rivers of tropical Africa. Hydrobioids do not thrive in muddy-bottom rivers, rivers with a pH <7.0, or in aquatic systems that dry out regularly.

Bithyniids, viviparids, and ampullariids have not radiated to the extent of cerithiaceans or hydrobioid prosobranchs primarily for reasons related to feeding and/or habitat restrictions. Bithyniids and viviparids are adapted for filter feeding (Cook, 1949; Lilly, 1953; Taylor, 1966a; Owen, 1966; Monakov, 1972; Meier-Brook and Kim, 1977) and hence considerable ecological space is apparently closed to them. The ampullariids are macrophagous herbivores with some carnivorous tendencies (van Benthem Jutting, 1956; Demain and Lutfy, 1965; Demain and Ibrahim, 1969) but are amphibious with both pulmonary and ctenidial respiration. Ampullariids, the largest of all freshwater snails, can spend long periods of time on land and withstand long periods of desiccation when their source of water evaporates away.

Taxa of these three families inhabit quiet, muddy ponds, lakes, canals, and for the ampullariids, paddy fields and swamps.

TABLE 3. Numbers of species of prominent entirely freshwater prosobranchs of Africa and continental Southeast Asia.

	Central to South Africa	Southeast Asia (continental)
Bithyniidae	29	12
Viviparidae	19	42
Ampullariidae	26	5
Thiaridae	95 to 100	29
Hydrobioids	~20*	100
Stenothyridae	0	20
Buccinidae	0	8 to 10

References:

Brandt, 1974; Boss, 1979; Davis, 1979a; Hoagland and Davis, 1979; Brown, 1980; Davis, 1980a, b.

* Exact number of purely freshwater hydrobioid taxa not precisely known; 8 of the 20 are South African *Tomichia* (Pomatiopsidae).

In my observations, the bithyniids tolerate the muddiest environments followed by the ampullariids with viviparids requiring the least muddy conditions.

Viviparids worldwide have not rivaled cerithiaceans in numbers or nominal subgeneric taxa and in no large geographical area do they come close to rivaling hydrobioids. In continental Southeast Asia, however, they do slightly exceed freshwater cerithiaceans (Table 3). Viviparids have probably had greater success than bithyniids and ampullariids in Southeast Asia because they tolerate less muddy conditions, can live in many rivers and lakes not suitable for habitation by bithyniids or ampullariids (too strong a current, and/or too little mud), and because at least some viviparids have been shown to supplement their diets by scavenging (Allison, 1942; van der Schalie, 1965). The viviparid *Mekongia* is particularly successful in continental Southeast Asia with seven nominal species and an additional five nominal subspecies of which five taxa live in the Mekong River (contrasted with one species of cerithiacean).

A number of families with representatives in freshwater are marine-brackish water groups with a limited modern invasion into freshwater, e.g., families of the Neritacea, Buccinacea, Volutacea, Arcaea, Mytilacea, Solenacea, and Dreissena-

cea. Some rissoacean families likewise are included here: Assimineidae, Stenothyridae. There are ecological reasons for the successful, relatively species-rich stenothyrid and buccinid radiations in freshwater as well as the limited marginellid, mytelid, arcid, dreissenid, and solenid incursions into freshwater. The freshwater stenothyrid, buccinid, mytilid and arcid radiations as well as the single marginellid occurrence are uniquely Southeast Asian and explained by the reported dynamic sea level changes over the shallow Sunda shelf. The repeated transitions from marine to brackish to freshwater to brackish to marine as continental Southeast Asia gained and lost connection with Indonesia and Borneo is sufficient to explain the adjustments of some taxa of these families to freshwater where river beds extend far out into the vast Sunda platform. I know of no other place, including Brazil, where sea level fluctuations have affected such a large area with major river systems to produce the kind of result seen in Southeast Asia.

Endemism and adaptive radiations are associated with tectonic events (Taylor, 1966*b*; Davis, 1979*a*). Tectonic events open new ecological space and variously affect molluscan populations. Spectacular freshwater molluscan endemism in Southeast Asia is associated with the Himalayan orogeny,² Pleistocene sea level changes over the Sunda platform, and climatically favorable conditions. Areas of little or no tectonic activity from the early Tertiary onward have slight faunal changes and little endemism. An example is the Blancan and recent faunas of the southern Great Plains of the United States (Taylor, 1966*b*).

The biology of certain of the groups discussed restrict them to different habitat types. These constraints are important in accounting for some of the biogeographical patterns involving cerithiaceans, hydrobioids, ampullariids, bithyniids, and viviparids. Let us now examine aspects of reproductive strategy, respiration, size, and the combination of these factors on species diversity, patterns of distribution, and passive dispersal.

Pulmonates have not radiated to the

same extent as prosobranchs. It has been calculated that prosobranchs are 1.5 to 10 times more endemic than aquatic pulmonates (Boss, 1979). As the vast majority of pulmonates must obtain atmospheric oxygen to fill their lungs, they must live in the shallows of lakes, ponds, standing water, or pools of quietly flowing streams. They cannot survive the turbulence of large rivers. For example, while pulmonates abound in Thailand and Laos, they are totally absent from the Mekong River. Because of ctenidial respiration prosobranchs can remain submerged and exist at considerable depths. Depth zonation is an important niche variable exploited by prosobranchs (Boss, 1979; Davis, 1979*a*). Only some minute planorbids and lymnaeids have succeeded in adapting to continuous immersion at some depth (Boss, 1979; Russell-Hunter, 1979).

Another factor is reproductive strategy. A single hermaphrodite or brooding female of a monoecious species can establish a new colony (Lassen, 1975). Of importance, also, are size and weight of an individual in addition to habitat position and population density relative to passive dispersal already discussed. Pulmonates are hermaphrodites and live at relatively high densities in the shallows of freshwater lakes and ponds that are among the most transient and ephemeral of biomes. Pulmonate species exhibit remarkable tolerances to varying environmental factors, well suited for the necessities of dispersal and colonization (Russell-Hunter, 1979). Besides ecological tolerances, the short-duration transience of most freshwater habitats clearly limits the number of generations per population, per system, and dispersal capabilities apparently restrict speciation (Russell-Hunter, 1979). Given all factors, it is not surprising that pulmonate species are the most widespread and least speciose of freshwater gastropods. Such taxa are seemingly less prone to extinction than species with limited ranges. Local environmental changes causing extinction of an endemic species within a zone of environmental change may eliminate only some populations of a wide-ranging species. On the other hand, as mentioned above, dis-

persal capabilities associated with widespread taxa apparently dampen speciation with resultant low species diversity among such taxa.

Generally, sexually reproducing pulmonates that can self fertilize have distributions \geq parthenogenetic prosobranchs and brooding bivalve Corbiculidae and Pisidiidae, \geq brooding Viviparidae and cerithiaceans, and $>$ egg-laying dioecious prosobranchs. The same hierarchy holds for spatial extent of species distributions. Consider the wide-ranging distribution of the sexually reproducing pulmonates *Radix auricularia* and *Indoplanorbis exustus*. The former ranges over Europe, Asia, India, Southeast Asia, and northeast Africa. The latter is widespread throughout India and Southeast Asia.

The cerithiaceans *Thiara scabra* (Müller) and *Melanooides tuberculata* (Müller) are parthenogenetic (or at least have numerous parthenogenetic races) and brood their young as do all *Thiara*, *Melanooides*, and *Brotia*. They are Gondwanaian with a present-day distribution in Africa, India, and Southeast Asia; they have been further distributed by man. Many Corbiculidae and Pisidiidae have widespread distributions because they are small, brood young, and are well-known to clump onto animal agents of dispersal as discussed above. The rapid spread into, and colonization of rivers throughout the United States in recent years (following introduction into the west coast) of *Corbicula manilensis* can be attributed to effective dispersal and wide ecological tolerances of this small brooding clam (Britton, 1979). However, in the hotbed of endemism in Thailand, Laos, Burma, Cambodia, Malaysia, Indonesia, and Vietnam, there are 36 nominal species of the bivalve family Corbiculidae and Pisidiidae of which 31 (86%) are endemic to the region (Brandt, 1974). The few non-endemic species are all tiny *Pisidium* (<5.0 mm length, 8 species in this region); one species, *P. annandalei* Prasad, ranges from Sicily, Greece, Israel to Southeast Asia. This regional diversity rivals that seen in North America, *i.e.*, 34 nominal species of Corbiculidae (Herrington, 1962). Colonization ability of the larger *Corbicula*

(mostly >12 mm length; ranging to 46 mm length) has not dampened speciation in this region any more than is seen in the Viviparidae and cerithiaceans.

Large outbreeding and brooding snails (>20 mm shell length) are next in order of extensive species distributions. Examples are the cerithiacean *Brotia costula* (Rafinesque) and *Semisulcospira libertina* (Gould). The former extends from the Himalayas of India through Southeast Asia to Indonesia. The latter occurs in Japan, the Ryukyu Islands, Taiwan, and southern China.

Hydrobioids are small (<15 mm shell length; mostly <10 mm) primarily aquatic, predominately outbreeding snails (except the parthenogenetic *Potamopyrgus*). No Asian or African hydrobioid has the extended range of *Brotia costula* or *Semisulcospira libertina*.

In summary it is evident that the general ecological requirements required of the morphological-physiological ground-plans of the various families of freshwater snails have a great deal to do with their diversity and distributions after the major vicariant event of Gondwanaland disruption. Pulmonates are excellent colonizers of transient habitats and have broad niches with regard to physiological tolerances. Conversely, small outbreeding hydrobioids apparently can specialize in relatively small areas (Davis, 1979a), have narrow niches and narrow ecological tolerances. Ecological constraints associated with mode of respiration, habitat, and reproduction impact on speciation, dispersal and adaptive radiation. Small brooding bivalves are good colonizers and readily dispersed by various animal agents; they are more cosmopolitan than non-brooding outbreeding prosobranchs.

The relative roles of history and ecology are clear in some cases and not in others. Given the disruption of Gondwanaland, the role of vicariance is reasonably clear in understanding the South American-African-India/Asian distribution of Pomatiopsidae (as discussed) and Ampullariidae, and the African-Indian-Southeast Asian distribution of the Viviparidae Bellamyinae, Planorbidae Buliniinae, and certain

Thiaridae. On a more local level, in Japan the cerithiacean pleurocerid *Semisulcospira* radiated in the absence of hydrobioids. The fossil record indicates an absence of hydrobioids and the availability of *Semisulcospira* for colonization. In this case the historical argument is apparently correct (Davis, 1979a).

The picture is more complicated in Southeast Asia. The cerithiacean *Brotia* is widespread throughout Southeast Asia as are the hydrobioid Triculinae. The Triculinae dominate the molluscan fauna of the Mekong River; *Brotia costula* is found as the sole cerithiacean in the river; it is not, compared with triculine species, abundant in the river. There is a radiation of *Brotia* in streams and rivers of Southeast Asia. There are at least nine species in Thailand (Brandt, 1974). At least 11 species of *Brotia* have radiated in lakes of Sulawesi (Celebes); considering lakes and rivers of Sulawesi there may be 15 or more species (Sarasin and Sarasin, 1898). No Triculinae have thus far been reported from Sulawesi; no Triculinae are known from lakes or ponds of Thailand, Laos, or Malaysia, but are known from lakes of Yunnan, China and the Philippines (Davis, 1979a, 1980a). When *Brotia* is found in rivers there is usually one species, two at the most. The exception to this is the small radiation in the Koek Noi River (north central Thailand) of the Nan-Chao Phraya drainage ultimately flowing through Bangkok (Brandt, 1974). The river is small, flowing from the mountains over numerous small waterfalls. There are five species, subspecies, or phenotypically different populations along this river (Brandt, 1974). Of all species of *Brotia*, *Brotia costula* is the most widespread with a distribution extending from the Indian Himalayas through Thailand, Laos, Malaysia, and Indonesia.

I have recently surveyed the Pahang River system of Pahang State, Malaysia. Two species of gastropod dominate this river system, *Brotia costula* in great abundance in the quiet, marginal areas, and a spiny species of *Brotia* among rocks in the rapids. In three or four tributaries of tertiary rank, one genus and two species of

Triculinae: Triculini are found (Davis and Greer, 1980). These triculines have restricted habitat types while *Brotia costula* is found in every stream type from primary to quaternary. *Brotia* is found in every habitat type where other mollusks are found, and in many streams where no other mollusks are found. *Brotia* lives on rocks, mud, sand, in root systems, under and among piles of leaf litter in the water.

Is it history or ecology that limits *Brotia* in the Mekong River? Is it history or ecology that limits the Triculinae in the Pahang River? Did the Triculinae invade and radiate in the Mekong River before *Brotia* arrived and is a *Brotia* radiation prevented by competition? Is the niche of *Brotia costula* so large that an adaptive radiation of *Brotia* within the river is dampened? Why are Triculinae not found in the Celebes? These are ecological questions that must be answered before one can determine the relative role of history in explaining the distribution of freshwater cerithiaceans and hydrobioids.

SUMMARY

1. Mapping and accounting for contemporaneous distributions of freshwater mollusks is hindered by the virtual lack of synthetic systematic and phylogenetic analyses for most families.

2. Understanding the origin of a modern distribution of any group is dependent on a phylogenetic analysis involving phenetics, cladistics, and chronistics. An objective phylogenetic analysis can only be done with an adequate data base allowing one to identify convergences, establish monophyly, establish clades and, by use of the fossil record and/or geological events, establish the direction and rate of evolution. In many cases data may not be sufficient to permit a phylogenetic analysis and all that may be possible is a phenetic analysis.

3. There is more than one way to establish clades. Extreme caution is necessary in selecting primitive character states for molluscan taxa within or below superfamily level. Given an adequate data base one should test the congruence among different methodologies to establish the best possible hypothesis of phylogeny.

4. A synthesis is needed in biogeographical study that incorporates vicariance, dispersal, ecology, geology-paleontology. At one stage in history vicariance may be a dominant factor while during another stage of history, dispersal may be a dominant factor. At every stage ecological considerations are necessary to understand the phenotypes seen and the spatial relationships among taxa. Interpretations of the vicariance and dispersal components very much depend on the scale of observing involving time and space.

5. It is relevant to discuss centers of evolution and route of dispersal. Through geological time one may be able to identify several centers of evolution, as a diverging lineage undergoes an explosive adaptive radiation, with new morphological innovations giving rise to yet newer clades. In many cases where one now sees a center of diversity, it is not the place where the ancestors of the taxa in question evolved.

6. Freshwater systems are relatively temporary over geologic time, and freshwater steady states are of particularly short term duration. It is clear from the example of the Pomatiopsidae that vicariance and dispersal both have been involved throughout the history of this family. New ecological space with resulting adaptive phenotypes are associated with the formation of new rivers, lakes and the changes in these aquatic systems. It is also clear that many freshwater mollusks are adapted to a stepping-stone model of passive dispersal as well as continuous active dispersal (migration) along and among aquatic systems.

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
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