# WHEN SHELLS DO NOT TELL: 145 MILLION YEARS OF EVOLUTION IN NORTH AMERICA'S POLYGYRID LAND SNAILS, WITH A REVISION AND CONSERVATION PRIORITIES 

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#### Abstract

A phylogenetic hypothesis for the 274 known polygyrid species is presented, based on 115 anatomical, behavioral, and shell characters ( 39 of which are newly discovered or newly assessed), as corroborated in part by published allozyme data. The hypothesis differs little from that of Emberton (1994a), except for greatly increased resolution in the tribes Stenotremini and Polygyrini. A corresponding revision is presented that assigns species to 50 subgenera, 24 genera, seven tribes, three infrafamilies, and two subfamilies. All taxa in the revision, as well as unnamed clades, are defined phylogenetically by shared derived characters. Nine new subgeneric names are introduced: Neohelix (Asamiorbis), N. (Solemorbis), Triodopsis (Brooksorbis), T. (Pilsbryorbis), T. (Macmillanorbis), T. (Vagvolgyorbis), Stenotrema (Archerelix), S. (Pilsbrelix), and Millerelix (Prattelix).

A separate phylogenetic analysis of polygyrid subgenera was conducted based on shell morphology alone, using 71 character states in 14 characters, all new or newly assessed, including ontogenetic characters scored from shell $x$-rays. The resulting shell-based hypothesis had only one-fourth the phylogenetic resolution of, and showed major topological discrepancies from, the anatomy-behavior-shell hypothesis. Thus, at present level of knowledge, polygyrid shells are inadequate for reconstructing phylogenetic history, and identifications of preMiocene fossils should be considered dubious at best. Remaining to be evaluated, however, are shell-surface microsculptures and ultrastructural layers.

Museum and field surveys discovered the closest known polygyrid convergences in sympatry on flat, umbilicate, and tridentate shell forms: Patera laevior and Xolotrema fosteri at Hawesville, Harlan County, Kentucky; Appalachina sayana and Allogona profunda on Pine Mountain, Hancock County, Kentucky; and Inflectarius inflectus and Triodopsis fallax in Vinton County, Ohio. These provide starting points for analyses of naturally replicated experiments in evolutionary morphology, such as those already conducted on the globose shell form (Mesodon normalis and Neohelix major at numerous sites in the Southern Appalachian Mountains).

Adult Triodopsis tridentata from which apertural barriers had been removed lost water $27 \%$ faster than controls when retracted, and $9 \%$ faster when extended. Controls were 83\% more successful than barrierless snails in forming epiphragms. Epiphragms reduced the rate of water loss by 3\% in controls and by 38\% in barrierless snails. Ramsay's (1935) hypothesis is extended to suggest that barriers and epiphragms slow evaporation not directly, but indirectly by interrupting natural convection currents between the aperture and the retracted snail's body. Because T. tridentata and other triodopsins have larger barriers in more humid climates, barriers should also serve at least one other function, such as impeding invertebrate predators. A new hypothesis is proposed for the function of extremely obstructed shell apertures: to exclude water, allowing the snails to float to safety during floods. Polygyrids have many convergences on apertural obstruction by barriers, some extreme examples of which are illustrated together.

Based on the phylogenetic hypothesis/revision, the most urgent remaining targets for polygyrid conservation are (1) Colombia's Isla de Providencia, where deforestation threatens the ancient, relic, uniquely live-bearing, endemic Giffordius; and (2) the northern coves of Pine Mountain, Harlan County, Kentucky, which harbor North America's most diverse land-snail communities, including four simultaneous cases of polygyrid convergence in sympatry.

Key words: cladistics, phylogenetic taxonomy, shell ontogeny, paleontology, fossils, convergence in sympatry, functional morphology, Gastropoda, Pulmonata, Stylommatophora.


## INTRODUCTION

The Polygyridae are an endemic North American family of land snails that are remarkable for their shell convergences in sympatry (due to iterative, punctuated evolution coupled with phenotypic and genetic, adaptive parallel environmental responses); their 145-million-year biogeographic history (paralleling that of, for example, plethodontid salamanders); and their evolution of hermaphroditic, external sperm exchange via several behaviorally bizarre intermediates that remain extant (Pilsbry, 1940; Webb, 1974; Solem, 1976; Emberton, 1981, 1988a, 1991a,b 1994a,b, 1995a,b; Asami, 1988, 1993). Polygyrids currently comprise 271 nominal and three undescribed species (see below), with a maximum sympatric diversity of ten species reported from Pine Mountain, Harlan County, Kentucky, U.S.A. (Hubricht, unpublished; Emberton, 1995c), with many more species yet to be described and discovered in Mexico and Central America ( $F$. Thompson, pers. commun.), and probably with some undiscovered species remaining in the Pacific Northwest (T. Frest, pers. commun.). Phylogenetic hypotheses for the family as a whole (Webb, 1974; Pratt, 1979; Emberton, 1994a) have been to genus only, and the most recent hypothesis omitted shell characters completely and had major unresolved polytomies.

Polygyrid fossil shells of the Pleistocene and Pliocene are nearly all identical with Recent species (Hubricht, 1985, and pers. commun.; Emberton \& Bogan, unpublished). Miocene and later fossils are generally assignable to genus (Pilsbry, 1940; Auffenberg \& Portell, 1992; Roth \& Emberton, 1994). Earlier polygyrid fossils, however, which are rare but presumably valuable in reconstructing the first 125 million years of polygyrid history, could be difficult to identify because of multiconvergent, punctuated-equilibrium evolution (Emberton, 1994a). One way of testing the value of early fossils is to make an honest, concerted attempt to reconstruct polygyrid phylogeny based on Recent shells alone. This has not previously been attempted. One possible source of new and useful characters for such an analysis-and for fossil identification-is shell ontogeny as viewed in x-rays (Ramirez, 1993). For example, a recent study discovered, using x-rays, a significant difference in whorl-expansion rate between the polygyrid tribes Triodopsini and Mesodontini (Emberton, 1994a). Thus a
more general x-ray survey of polygyrid shell ontogeny could be productive.

Non-mimetic sympatric convergences are important as naturally replicated experiments in evolutionary morphology (Emberton, 1995a). Polygyrid non-mimetic convergences in sympatry fall into four distinct shell forms (Pilsbry, 1940) that have been called globose, flat, tridentate, and umbilicate shell-static clades (Fig. 1; Emberton, 1991b, 1994a). The globose clades show the closest convergences in sympatry (Solem, 1976; Emberton, 1981; Asami, 1988, 1993), of which the most extreme is between Neohelix major and Me sodon normalis. Recent analyses of these two species have yielded important new insights into the ecological, genetic, and naturalselective influences on shell morphology (Emberton, 1994b, 1995a). The most extreme cases of sympatric convergence on flat, tridentate, and umbilicate shell forms have not been analyzed or even reported, however.

Polygyrid shell evolution is further noteworthy for its convergences in extreme apertural obstruction by denticles and other shell structures (Fig. 2; Pilsbry, 1940; Zilch, 195960 ). Such apertural barriers appear in many forms among numerous land-snail clades (Zilch, 1959-60). Four hypotheses have been proposed concerning the function of these barriers: (1) to deter attacks by predatory insects (Cook, 1895; Boettger, 1921, 1935; Solem, 1972, 1974; Falkner, 1984); (2) to retard evaporative water loss (Boettger, as cited by Goodfriend, 1986; Rees, 1964; Paul, 1974; Christelow, 1992); (3) to strengthen the aperture against accidental breakage (Paul, 1974); and (4) to orient the shell during crawling (Paul, 1974). A fifth hypothesis, proposed here for the first time, is suggested by some polygyrid cases of extreme apertural obstruction existing in flood-prone environments (Hubricht, 1985; Emberton, 1986): that some barriers function (5) to trap air within the submerged shell, preventing drowning and enhancing gene flow by allowing the snail to float downstream. None of these hypotheses has been adequately tested using living snails (Goodfriend, 1986; pers. observ.).

Also untested is the likely hypothesis that some barriers perform two or more functions simultaneously. In the polygyrid tribe Triodopsini, there is a correlation in several lin-eages-including that of the common species Triodopsis tridentata-between greater apertural obstruction and increased environ-




FIG. 2. Convergent shell-apertural obstruction among various polygyrid subgenera. Species are (left to right, top row): Triodopsis (Haroldorbis) henriettae (ANSP 109734), Trilobopsis roperi (150631), Ashmunella mudgii (319743), Stenotrema (Stenotrema) unciferum (171138), Stenotrema (Stenotrema) maxillifer (170141); (bottom row): Millerelix (Millerelix) tamaulipasensis (317942), Millerelix (Prattelix) plicata (143448), Daedalochila (Upsilodon) hippocrepis (84629), Daedalochila (Daedalochila) uvulifera (10990), Inflectarius (Inflectarius) rugeli (116893).
mental moisture (Vagvolgyi, 1966; Emberton, 1988a). This implies that if apertural barriers retard evaporative water loss in T. tridentata, then they should also serve at least one additional function, such as deterring predators or trapping air.

Polygyrid conservation is relatively advanced, with at least five rare taxa currently listed as endangered or threatened: Patera clarki nantahalae, Fumonelix archeri, F. orestes, F. jonesianus, and Triodopsis playsayoides. Thanks to this recognition, these taxa are receiving the protection they need to survive. Phylogenetic analysis, however, can provide insights into conservation priorities beyond the rarity of individual taxa. Polygyrid conservation has never been considered in a phylogenetic context.

The purposes of this paper are (1) to conduct a phylogenetic analysis of the Polygyridae to the species-group/subgeneric level; to use the resulting phylogenetic hypothesis (2) to taxonomically revise the family; (3) to conduct an independent phylogenetic analysis based on shells alone, incorporating x-rays; to use the resulting cladogram (4) to assess the reliability of fossils for recon-
structing polygyrid phylogeny; (5) to find and report the closest polygyrid convergences in sympatry on the flat, tridentate, and umbilicate shell forms; (6) to test for retardation of evaporative water loss by shell apertural barriers in living Triodopsis tridentata; and (7) to assess remaining conservation priorities for the Polygyridae from a phylogenetic perspective.

## MATERIALS AND METHODS

## General Phylogenetic Analysis

Standard phylogenetic methods of character analysis were used (Hennig, 1966; Wiley, 1981; Wiley et al., 1991; Brooks \& McLennan, 1991). The outgroups used were the type genera of the bradybaenids, helminthoglyptids, thysanophorids, camaenids, and sagdids, plus Cepolis to represent the xanthonycids (Emberton, 1991c). Data sources were from anatomical and behavioral characters compiled by Emberton (1994a: appendix A), with added anatomical character analyses using illustrations of Pilsbry (1940), Archer
(1948), Metcalf \& Riskind (1979), Pratt (1981a), and Emberton (1988a, 1991a), and shell character analyses using the collection of the Department of Malacology, Academy of Natural Sciences of Philadelphia (ANSP). Shell characters were limited as much possible to those involving complex apertural barriers. No anatomy of Pilsbry's (1940) "Polygyra plicata group" had ever been adequately published (W. G. Binney's [1878: plate 15 , fig. I] sketch of the genitalia of "Polygyra troostiana Lea" is uninformative and untrustworthy, appearing as it does beside a totally inaccurate depiction of the genitalia of "P. tridentata [Say]"). Therefore, all the (limited) ANSP alcohol material of " $P$. plicata Say" was examined, and one adult was chosen for dissection and illustration of the shell and the reproductive system, which were included in the general character analysis.

Based on experience with anatomical-shell comparisons in the context of an anatomicalallozymic phylogenetic hypothesis among all species of both the Triodopsini and the Mesodontini (Emberton, 1988a, 1991a), anatomically unknown polygyrid species were tentatively assigned to subgenus by shell characters alone. Thus, subgenus was used as the operational taxonomic unit for this phylogenetic analysis, even though any given subgenus may have been represented by up to eleven species that were each scored for each character. For this reason, all "autapomorphies" defining subgenera were retained in the data matrix.

Polygyrid allozyme data (Emberton, 1988a, 1991a, 1994a) were not used in this analysis because data were lacking for many subgenera and because existing data were from two separate analyses involving only partially overlapping sets of loci. Instead, relevant portions of this phylogentic hypothesis were visually compared for topological congruency with previously published, allozymebased hypotheses (Emberton, 1988a, 1991a, 1994a).

Phylogenetic analysis was conducted by hand and was interactive with construction of the data matrix. The analysis progressed along successively more restricted ingroups, each of which was compared with its closest possible outgroup. Thus, the resulting cladogram and its coordinate subgenus-by-character-state matrix were superficially free of certain homoplasies that would have resulted from a non-hierarchical, single-outgroup analysis.

## Taxonomic Revision

The revision was based on the general phylogenetic hypothesis and followed basic principles of phylogenetic taxonomy (Queiroz \& Gauthier, 1990), which are becoming well established among vertebrate systematists and have recently been introduced to malacology by Roth (1995). The method, as employed here, designates as taxa clades that are defined by shared derived characters (synapomorphies), regardless of subsequent evolutionary modifications of those characters. For a discussion of the naturalness of this method and its great advantages over traditional taxonomy, see Queiroz \& Gauthier (1990).

## Shell-Based Phylogenetic Analysis

Previous studies had shown the extents and limits of intraspecific variation in polygyrid shell morphology (Emberton, 1988a, 1988b, 1994a, 1994b), which were considered during character analysis. In general, one intact adult shell of the type species was chosen to represent each subgenus, but for subgenera with extreme shell variation, two or more representative species were selected. Outgroups were represented by one shell each of the type species of the type genus of each of the six closest polygyrid outgroup families (Emberton, 1991c), except when the type genus happened to have a highly derived shell morphology.

Shells were mounted in the planes simultaneously of both the rotational axis and the aperture (Emberton, 1988a: fig. 29b, d) on clear acetate sheets using thick rubber cement, then x-rayed over single-coat SR-5 Industrex R film. Contact prints were made from the x-ray negatives. Shell "apertures" at half-whorl intervals were drawn, with accompanying $3-\mathrm{mm}$ scale lines, from the contact prints using a camera lucida mounted on a Wild M-5 dissecting microscope. The drawings were inked, reduce-xeroxed until all of about the same size, and mounted in regular array, arranged by a former classification (Webb, 1974; Richardson, 1986) that has since been revised (Emberton, 1994a, this paper).

The demounted shells themselves, as well as the x-ray drawings of their ontogenies, were compared in a standard phylogenetic character analysis (Wiley, 1981; Wiley et al., 1991; Brooks \& McLennan, 1991: chapter 2).

Conchological differences known to occur among closely related species within subgenera of the Triodopsini and the Mesodontini (Emberton, 1988a, 1991a) were discounted as characters.

The resulting shell-character by subgenus matrix was analyzed phylogenetically using Hennig86 (Farris, 1988), assigning equal weights to all characters. A Nelson semistrict consensus tree (Farris, 1988) was computed from the set of resulting, equally and maximally parsimonious cladograms.

## Reliability of Fossils

To qualitatively assess the reliability of fossils for reconstructing polygrid phylogeny, the shell-based and anatomy-behavior-shellbased phylogenetic hypotheses were compared for their degrees of phylogenetic resolution among subgenera. Resolution in both cases was quantified as the number of nodes relative to the maximum number of possible nodes for the given number of taxa.

## Closest Convergences in Sympatry

Closest potential polygyrid shell convergences in sympatry on the flat, tridentate, and umbilicate shell forms were searched for using Pilsbry (1940), Hubricht (1985), and the collections of the Field Museum of Natural History, Chicago. Actual sympatry was tested by field work conducted during the spring months of 1979, 1981, 1982, and 1983.

## Shell Barriers and Water Loss

Twenty-five adult Triodopsis tridentata were collected during five field trips in the spring and fall of 1970. Twenty-three were from Athens County, Ohio, and two from Monongahela County, West Virginia. Initial weights ranged from 0.39 to 1.06 gm . From ten of these snails, all three apertural denticles were completely removed using a tablemounted dentist's drill. These barrier-less nails were given 20 hours to recuperate from the operation, and seven appeared at that time to be uninjured and normally active.

All snails were weighed and placed into individual rubber-stoppered Erlenmeyer flasks in which were suspended 10.0 gm of the desiccant calcium sulfate in a cheesecloth bag. Temperature was maintained at $14-15^{\circ} \mathrm{C}$ in a walk-in refrigerator. Each snail was weighed on a tortion balance every hour for 18 hours.

Weighing took about two minutes per snail. At each weighing, the snail's activity state was recorded as (a) fully extended, (b) partially extended, (c) retracted without epiphragm, (d) retracted with partial epiphragm, or (e) retracted with complete epiphragm. Periods of individual fully extended activity were also recorded when they occurred between weighings.

Each recorded weight was expressed as a percentage of the snail's initial weight, then the percent decrease from the previous hour's weight was calculated for each "snailhour'" that proved usable. Mean percent decreases were calculated for each of eight aperture/activity categories. Differences among categories were expressed as percent changes in rates of evaporative water loss. The study was conducted some 25 years ago, and since that time the raw data were lost, so no statistical analysis could be performed.

## Remaining Conservation Priorities

Phylogeny-based conservation priorities were assessed for the categories of (1) radiating, endemic clades; (2) extremely autapomorphic, endemic taxa; (3) relic sister groups to major clades; and (4) sites rich in convergences in sympatry (Emberton, 1992). Priorities in these categories were judged from the general polygyrid phylogenetic hypothesis/ revision (this paper; Emberton, 1988a, 1991a) and from known species distributions (Hubricht, 1985) and sites of known high diversity (Solem, 1976; Emberton, 1995c, unpublished; Hubricht, unpublished). The current conservation status of each high-priority taxon or site was evaluated based on the U.S. Federal Endangered Species List and the locations of national and regional parks and forest preserves.

## RESULTS

## General Phylogenetic Analysis

Table 1 defines the 115 characters used for phylogenetic analysis, with references to illustrations of the characters. I had not previously used or detected some of these characters (39, or 34\%) (Emberton, 1988a, 1991a, 1994a), primarily those dealing with (a) penial morphology within the tribe Stenotremini (Fig. 3), (b) reproductive-system morphology

TABLE 1. Anatomical, behavioral, and shell characters used for a phylogenetic hypothesis (Fig. 8) and a revision (text) of the Polygyridae. Citations refer to papers of Emberton, unless otherwise indicated.

1. Nodulose fertilization pouch-seminal receptacle complex (1994a: fig. 2: character-state 2.2).
2. Anteriorly united retractor muscles (1994a: fig. 2: character-state 3.2).
3. Deeply excavated ureteric interramus (1994a: fig. 2: character-state 4.2).
4. Single, dorsal, penial pilaster (1994a: fig. 2: character-state 5.2).
5. Proximally swollen, internally lamellate vas deferens (1994a: fig. 2: character-state 8.2).
6. Terminally papillate penial verge (1988a: figs. 2f, 3b, 4b, 5e, 7b, 7d, 8c).
7. Two, flat terminal papillae on a terminal penial verge (1988a: fig. 6a).
8. Distinct but pustulate lappets (= transversely, partially fused pustules) on the penial pilaster (1988a: figs. 2b, 5c, 5f).
9. Doubled density of pustulate lappets on the penial pilaster (1988a: figs. 5a, 5d).
10. Smooth lappets (= transversely, completely fused pustules) on the penial pilaster (1988a: fig. 2e).
11. Halved density of smooth lappets on the penial pilaster (1988a: figs. 2d, 4a).
12. Smooth penial-pilastral lappets, plus in adulthood a short vas deferens (only about twice as long as the penis) and a penial-retractor-muscle attachment near the penis (on the vas deferens within one-third penis-length of the apex of the penis) (1988a: table 4).
13. Greatly enlarged pustules on the penial pilaster (1988a: fig. 7).
14. Penial-wall columns that merge mid-ventrally into 6-10 U-shapes that are tapered and slightly separated and that bear unequally sized pustules (1988a: fig. 8).
15. Penial-pilastral pustules forming a single column of abutting cubes (1988a: fig. 8a).
16. A ventrally subterminal penial verge (1988a: fig. 7).
17. Penial-pilastral pustules that are knob-like, unfused, and abruptly larger than the penial-wall pustules (1988a: figs. 9a, 9c), or derivatives thereof.
18. 15-20 penial-wall columns unmerging and radiating directly from the ejaculatory pore (1988a: figs. 9a, 9c), or derivatives thereof.
19. Club-shaped penis with a ventrally subterminal ejaculatory pore about $1 / 5$-way from the apex and indented into the penial wall (Webb, 1959: figs. 22, 27, 34, 38; 1988a: fig. 9), or derivatives thereof (characters 28-30).
20. Penial-pilastral pustules fused into two interdigitating columns of rectangular boxes (1988a: fig. 12).
21. Penial-pilastral polygons 4-10 times the size of penial-wall pustules and armed with pustulesized knobs, or derivatives thereof (characters 22-24).
22. Penial-pilastral polygons fused into a single mass or into large, irregular masses (1988a: fig. 11).
23. Ventral penial-wall columns with pustules indistinct (1988a: fig. 11).
24. Penial pilaster $3 / 4$ the length of the penis and bearing polygons armed with blunt spurs (1988a: figs. 13a, 14a, 14b, 16a).
25. Indistinct pustules on the ventral-most radiating penial-wall columns (1988a: fig. 18b).
26. Penial-wall columns merging mid-ventrally into 5-7 acute, equilateral, widely separated V-shapes bearing equally sized pustules (1988a: figs. 14a, 15b, 16a).
27. Extremely long, narrow penis (at least 25 times as long as wide) (1988a: fig. 13).
28. Mace-shaped penis with a ventrally subterminal ejaculatory pore and with a sub-pore region erectile as a fleshy peduncle, and derivations thereof (characters 29, 30).
29. Ejaculatory-pore position approximately $1 / 4$-way from the penial apex, peduncle small (Webb, 1948: fig. 4; Webb, 1959: figs. 14, 25a, 40, 43; 1988a: figs. 14a-b, 15-17).
30. Ejaculatory-pore position approximately $2 / 5$-way from the penial apex, peduncle large (Webb, 1959: figs. 12, 13, 15, 41; 1988a: figs. 14c-d, 18a, 18c).
31. A discernible clasping disc during mating (1994a: fig. 2: character-state 1.4), or derivatives thereof.
32. An unfanned origin of the penial retentor muscle (1994a: fig. 2: character-state 7.3).
33. An epiphallus and flagellum (1994a: fig. 2: character-state 9.2), or derived loss thereof.
34. A constriction in the epiphallus from the penial apex part-way toward the flagellum (1994a: fig. 2: character-state 9.3).
35. A fleshy protuberance near the apex of the penis (Roth \& Miller, 1992: fig. 6).

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36. Conical, non-papillate verge at the apex of the penis (Pilsbry, 1940: fig. 512Bb; Webb, 1970: plate 35, fig. 5; Roth \& Miller, 1993: figs. 19, 24).
37. Clasping disc during mating that is as voluminous as the inserted portion of the penis (1994a: fig. 2: character-state 1.5), or derivatives thereof.
38. Minutely pustulate sculpture on the dorsal penial wall (1994a: fig. 2: character-state 5.4).
39. Paired dorsal penial pilasters (Pilsbry, 1940: fig. 496Aa, Bb', D), or derivative thereof (character 42).
40. Rugose clasping disk (Webb, 1990: plate 6, figs. 1-4).
41. Nearly effaced paired dorsal pilasters (1994a: appendix B, character state 5.4).
42. Single dorsal pilaster, plus a clasping disc that is twice as voluminous as the inserted portion of the penis (1994a: fig. 2: character-state 1.5).
43. One or more small, pointed, fleshy processes on the clasping disc, and derivatives thereof (characters 44, 45).
44. A single large, pointed, fleshy process on the clasping disc (Pilsbry, 1940: fig. 506, 1d-e; Webb, 1948: figs. 3, 3a).
45. Two large, pointed, fleshy processes on the clasping disc (Pilsbry, 1940: fig. 510: 2a, 5a).
46. Clasping disc divided peripherally into two or three broad, unpointed lobes (Webb, 1965: plate 27, figs. 1-4).
47. Epiphallus longer than the prostate-uterus (Pilsbry, 1940: figs. 524, 525).
48. Chitinous, ornate spermatophore (Webb, 1954).
49. No penial insertion during mating (1994a: fig. 2: character-state 1.8).
50. Lateral pilaster(s) on the clasping disc (= basal penis) (1994a: fig. 2: character-state 5.5).
51. A (secondarily) slender spermathecal duct (1994a: fig. 2: character-state 10.4).
52. (Basal) penial lateral pilasters apically modified into two fleshy-walled cups half as long as the penis (Fig. 3E).
53. Shell aperture with a complete basal lamella having a central trough half or more as broad as the lamella, and derivatives thereof.
54. Shell bearing a straight, even-height parietal apertural denticle isolated from both the umbilicus and the aperture (Fig. 6: character-state 5a), and derivatives thereof.
55. During mating, bearing an everted female organ that receives ejaculate from a pocket at tip of the penis (1994a: fig. 2: character-state 1.8).
56. Apertural-basal-lamellar central trough about one-third or less as broad as the lamella (Fig. 6: character-state 4b), and derivatives thereof.
57. Parietal apertural denticle extending from the umbilicus into the aperture (Fig. 6: character-state 5b), and derivatives thereof.
58. A single penial lateral pilaster apically modified into a symmetrical, fleshy-walled cup one-third as long as the penis, with a medial branch leading to a medial fleshy protuberance (Fig. 3C).
59. Lower apertural shell lip joined to the basal body whorl as a thin callus (Fig. 5, character-state 3 b ), and derivatives thereof.
60. Two large, fleshy penial lateral pilasters, both bearing apical V- or U-shaped structures, one up and one down (Fig. 3A).
61. Two large, fleshy penial lateral pilasters, neither bearing apical V - or U -shaped structures, and one or none bearing an apical, cup-like depression (Fig. 3T, S, P), and derivatives thereof.
62. One of the two large, fleshy penial lateral pilasters bearing an apical, cup-like depression about one-tenth as long as the penis (Fig. 3T).
63. The two large, fleshy penial lateral pilasters free of apical, cup-like structures (Fig. 3S).
64. One of the two large, fleshy penial lateral pilasters bearing an apical, cup-like depression one-fifth to one-half as long as the penis (Fig. 3P).
65. Penial-retractor-muscle insertion on or near penial apex (1994a: fig. 2, character-state 7.5-7.8).
66. Penial sheath (secondarily) completely absent (1994a: fig. 2, character-state 7.8).
67. Only a vestigial flagellum near the penial apex (1994a: fig. 2, character-state 9.5), and derivatives thereof.
68. Shell bearing a triangular parietal denticle (Fig. 6: character-state 6a), and derivatives thereof.
69. Ovoviviparity (Pilsbry, 1930a).

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70. Shell apertural expansion rate abruptly increasing then decreasing such that successive whorls are nearly equal in volume (Fig. 6: character-state 2b), and derivatives thereof.
71. At least one full whorl of growth beyond the expansion-rate increase (Fig. 6: character-state 2 c -right).
72. Shell bearing a V- to U-shaped parietal denticle (Fig. 6: character-state 6b).
73. Shell with a narrow baso-palatal interdenticular notch (Pratt, 1981a: fig. 3i).
74. Complete loss of pustulation in the penial apex (1994a: fig. 2, character-state 5.6).
75. A small, sac-like, glandular diverticulum of the lower penis (Fig. 5Ln), and derivatives thereof.
76. Patches of glandular cells on the penial wall above the diverticulum (Fig. 5Ln).
77. Penial diverticulum large, one-third to equal the volume of the penis (Fig. 5Lb).
78. Shell apertural expansion rate (secondarily) regular throughout ontogeny.
79. A secondary lobe on the penial diverticulum (Fig. 5Lb).
80. A (secondarily) globose shell with the aperture entirely free of denticles (Pilsbry, 1940: figs. 425-429).
81. Adnate penial diverticulum (Fig. 5PrF).
82. Penial diverticulum long and at least twice the volume of the penis (Fig. 5PrP, PrX).
83. Shell depressed, broadly umbilicate (Zilch, 1959-1960: fig. 2036).
84. Spiral, threadlike sculpture on the embryonic shell (Pilsbry, 1940: 689).
85. A bifurcate or trifurcate penial retractor muscle (Fig. 5PrP).
86. A vestigial epiphallus without a flagellum (Fig. 5MiM, MiP).
87. A slender penis (width $\leq 0.12$ length) with an apical, pendant, conical projection (Fig. 5 MiM , $\mathrm{MiP})$, and derivatives thereof.
88. An extremely long and slender penis (width $\leq 0.06$ length) (Fig. 5 MiM ).
89. A greatly enlarged, muscular, proximal vas deferens (Figs. 7MiP, 13).
90. Even-diameter vas deferens with no trace of epiphallus (Fig. 5DD, DU).
91. A stout penis (length/diameter <3.5) with a straight apex (Fig. 5DU).
92. A moderately long penis ( 4 < length/diameter < 10) with a bent or convoluted apex (Fig. 5DD).
93. A downward curve on the lower limb of the parietal apertural denticle (Pilsbry, 1940: figs. 384-387).
94. A raised parietal callus (Pilsbry, 1940: figs. 384-387).
95. A penial apical chalice formed by the junction of lateral pilasters (1991a: fig. 27).
96. An even-diameter distal vas deferens with no trace of flagellum or epiphallus (1994a: fig. 2: character-state 9.6).
97. An arched parietal apertural denticle (Fig. 13: character-state 9b), and derivatives thereof.
98. A depressed, hairless shell (height/diameter 0.4-0.6) (1991a: figs. 49,50), and derivatives thereof.
99. A regularly oval-shaped aperture with the reflected lip uniform in width throughout its palatal and basal regions, with no basal dentition (1991a: fig. 48a).
100. A basal apertural lamella (1991a: figs. 46, 47).
101. A pronounced, blade-like parietal apertural denticle (1991a: figs. 46, 47).
102. A straight basal region of the aperture with only a vestigial lamella (1991a: fig. 10b).
103. A barrel-shaped, solid pedestal underlying the penial chalice (1991a: fig. $45 \mathrm{c}-\mathrm{d}$ ).
104. A small, globose or subglobose shell (diameter $8-15 \mathrm{~mm}$, height/diameter 0.6-0.7) (1991a: figs. 35a,b, 40a,b), and derivatives thereof.
105. A globose, hairless shell (1991a: figs. 35a,b).
106. A subglobose shell (height/diameter 0.5-0.6) bearing periostracal scales, with the umbilicus broadly covered by an extension of the basal apertural lip, and with palatal and basal apertural denticles (1991a: figs. 40a,b), and derivatives thereof.
107. A thick-walled, hooded, cup-shaped penial chalice (1991a: figs. 7, 8, 9b).
108. Penial chalice with a higher left than right wall (1991a: fig. 27, transformation 21).
109. Shell very broadly umbilicate (1991a: figs. 39a,c).
110. Dorsal penial sculpture (1991a: fig. 28, transformations 31-33).
111. Dorsal penial sculpture consisting of 4-10 cord-like, subparallel, anastomosing ridges, running Iongitudinally to 30 -degrees obliquely (1991a: figs. 4, 6, 16a).

TABLE 1. Anatomical, behavioral, and shell characters used for a phylogenetic hypothesis (Fig. 8) and a revision (text) of the Polygyridae. Citations refer to papers of Emberton, unless otherwise indicated. (Continued)
112. Dorsal penial sculpture consisting of 8-12 cord-like, subparallel, anastomosing ridges, running Iongitudinally to 30 -degrees obliquely, many of which are contiguous with one or both lateral pilasters, and many of which enlarge basally to form a network of large basal bulges (1991a: figs. 2b, 11b,c, 15c).
113. Penial chalice a deep, thin-walled scoop, with the left wall much higher than the right (1991a: figs. 2b, 11b,c, 15c).
114. Dorsal penial sculpture consisting of about 8-12 thin parallel ridges, equal in diameter, which is constant or gradually increases basally (1991a: figs. 15a,b, 16b,c).
115. Penial chalice a thick-walled, rounded or pointed ear-like flap, flared to the left (1991a: figs. 15a,b, 16b,c).
within the tribe Polygyrini (Figs. 4, 5), and (c) shell ontogenetic and apertural morphology within-primarily-the tribes Stenotremini and Polygyrini (Fig. 6).

Figure 7 shows the distributions of all 115 characters among polygyrid subgenera (as revised below).

Figure 8 gives the maximum-parsimony cladogram of polygyrid subgenera (as revised below), based on the data presented in Figure 7. Each node in the cladogram is supported by one to three characters, numbered as in Table 1.

## Taxonomic Revision

The following revision exactly follows the phylogenetic hypothesis of Figure 8. For brevity's sake, definitions employ character numbers as defined in Table 1. Species with only tentative assignment to subgenus are preceded by a question mark.

Family POLYGYRIDAE Pilsbry, 1894
Definition: The first stylommatophoran pulmonate gastropod to possess characters \#1, 2 , and 3 , and all of its descendants.

Subfamily TRIODOPSINAE Pilsbry, 1940
Definition: The first Polygyridae to possess characters \#4 and 5, and all of its descendants.

## Tribe TRIODOPSINI

Definition: as for the subfamily.

Unnamed Clade Comprising Webbhelix, Neohelix, and Xolotrema
Synonym: "Xolotrema Rafinesque" (Webb, 1952)

Definition: The first Triodopsinae to possess character \#6, and all of its descendants.

Genus Webbhelix Emberton, 1988
Type species: Helix multilineata Say, 1821, by original designation.

Definition: The first Triodopsinae to possess character \#7, and all of its descendents.

Species: W. multilineata (Say, 1821).
Genus Neohelix Ihering, 1892
Type species: Helix albolabris Say, "1816" 1817, by subsequent designation (Pilsbry, 1930a).

Definition: The first Triodopsinae to possess character \#8, and all of its descendents.

Subgenus Neohelix (Asamiorbis) subgen. n .
Type species: Helix dentifera Binney, 1837.
Definition: The first Neohelix to possess character \#9, and all of its descendents.
Etymology: Dr. Takahiro Asami, land-snail ecologist and geneticist, who has worked extensively with $N$. (A.) dentifera and other polygyrids in Virginia (Asami, 1988, 1993); orbis (Latin) "disc" or "coil."

Species: N. (A.) dentifera (Binney, 1837); N. (A.) divesta (Gould, 1851); N. (A.) lioderma (Pilsbry, 1902).

Unnamed clade comprising subgenera N. (Neohelix) s.s. and
$N$. (Solemorbis) subgen. n .
Definition: The first Neohelix to possess character \#10, and all of its descendents.


FIG. 3. Character-state analysis of penial-functional-surface anatomy of the Stenotremini; see Table 1, characters \#52, 58, 60-64. Characters are delineated by solid lines; arrows are hypothesized transformations among characters. Anatomical figures (at different size scales) are from Archer (1948). A, Stenotrema (Archerelix) subgen. n.; C Stenotrema (Cohutta); E, Euchemotrema; P, Stenotrema (Pilsbrelix) subg. n.; S, Stenotrema (Stenotrema); T, Stenotrema (Toxotrema); aa, S. altispira altispira; ad, S. altispira depilatum; bb, S. barbatum; bd, S. blandianum; bg, S. barbigerum; bv, S. brevipila; cd, S. caddoense; ch, S. cohuttense; dc, S. deceptum; eg, S. edgarianum; ev, S. edvardsi; ex, S. exodon; ext, S. exodon turbinella (= S. turbinella); fl , S. florida; ft, E. fraternum; h S. hirsutum; I, S. labrosum, ma, E. monodon aliciae; mg, S. magnifumosum; mn, E. monodon, mx, S. maxillatum; pb, S. pilsbryi; pl, S. pilula; sp, S. spinosum; st, S. stenotrema; u, S. unciferum.


FIG. 4. Reproductive system (minus ovotestis) and shell (umbilical view) of Millerelix (Prattelix) plicata (ANSP A2423-A) from Knox County, Tennessee. $\mathrm{a}=$ atrium, $\mathrm{ag}=$ albumen gland, $\mathrm{ap}=$ apical, pendant, conical projection of the penis, $\mathrm{fpsc}=$ fertilization pouch-seminal receptacle complex ( $=$ talon $=$ carrefour $), \mathrm{gp}=$ gonopore, $\mathrm{hd}=$ hermaphroditic duct, $\mathrm{mf}=$ mantle-cavity floor, $\mathrm{o}=$ oviduvt, $\mathrm{p}=$ penis, $\mathrm{pr}=$ penial retractor muscle, pt = prostate, $\mathrm{sd}=$ spermathecal duct (= bursa copulatrix duct = gametolytic duct), u = uterus, v $=$ vagina, vd = vas deferens.

Subgenus Neohelix (Neohelix) s.s.
Synonym: Neohelix albolabris group (Emberton, 1988).

Definition: The first Neohelix to possess character \#11, and all of its descendents.

Species: N. (N.) albolabris (Say, 1817); N. (N.) major (Binney, 1837).

Subgenus Neohelix (Solemorbis) subgen. n .
Type species: Neohelix solemi Emberton, 1988.

Synonym: Neohelix alleni group (Emberton, 1988).

Definition: The first Neohelix to possess character \#12, and all of its descendents.

Etymology: The late Dr. Alan Solem, long


FIG. 5. Character-state analysis of the lower-reproductive-tract anatomy of the Polygyrini; see Table 1, characters \#75-92. Characters are delineated by solid lines; arrows are hypothesized transformations among characters. Anatomical figures (at different size scales) are from Pilsbry (1940), Metcalf \& Riskind (1979), Pratt (1981a), and this paper (Fig. 4). DD, Daedalochila s.s.; DU, Daedalochila (Upsilodon); G, Giffordius; Lb, Lobosculum; Ln, Linisa; MiM, Millerelix s.s.; MiP, Millerelix (Prattelix); Po, Polygyra; PrF, Praticolella (Farragutia); PrP, Practicolella (Praticolella); PrX, Praticolella (Filapex); be, Pr. berlandieriana; bu, D. burlesoni; ch, D. chisosensis; cr, Po. cereolus; df, Mi. doerfeuilliana; hp, D. hippocrepis; Ip, D. leporina; Iw, Pr. lawae; mb, Pr. mobiliana; mp, D. multiplicata; mr, Mi. mooreana; pi, G. pinchoti; pl, Mi. plicata; pu, Lb. pustula; sp, Po. septemvolva volvoxis; tm, Ln. tamaulipasensis; tx, Ln. texasiana; uv, D. uvulifera.


FIG. 6. Character analysis of shell morphologies of the Stenotremini and the Polygyrini; Table 1, characters \#53, 54, 56, 57, 59, 70-72.













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FIG. 8. Phylogenetic hypothesis for polygyrid subgenera based on the data in Fig. 7. Synapomorphies supporting each node and defining each subgenus are numbered as in Table 1. " $23 \mathrm{MeK}^{\prime}$ " $=112,113 \mathrm{MeK}$. " 1145 MeM " $=114,115 \mathrm{MeM}$.
one of the world's leading and most prolific specialists on land snails, who did some important work on polygyrids (Solem, 1976); orbis (Latin) "disc" or "coil."

Species: N. (S.) alleni (Sampson, 1883); N. (S.) solemi Emberton, 1988.

Genus Xolotrema Rafinesque, 1819
Type species: Helix denotata Férussac, 1821 (= Helix notata Deshayes, 1830) by subsequent designation (Pilsbry, 1940).

Definition: The first Triodopsini to possess characters \#13 and 14, and all of its descendents.

## Subgenus Xolotrema (Wilcoxorbis) <br> Webb, 1952

Type species: Polygyra appressa fosteri F. C. Baker, 1932, by original designation.

Definition: The first Xolotrema to possess character \#15, and all of its descendents.

Species: X. (W.) fosteri (F. C. Baker, 1932); X. (W.) occidentalis (Pilsbry \& Ferriss, 1907).

## Subgenus Xolotrema (Xolotrema) s.s.

Definition: The first Xolotrema to possess character \#16, and all of its descendents.

Species: X. (X.) caroliniensis (Lea, 1834); X. (X.) denotata (Férussac, 1821); X. (X.) obstricta (Say, 1821).

Genus Triodopsis Rafinesque, 1819
Type species: Helix tridentata Say, "1816" 1817, by original designation.

Definition: The first Triodopsinae to possess characters \#17 and 18, and all of its descendants.

## Subgenus Triodopsis (Shelfordorbis) Webb, 1959

Type species: Triodopsis fraudulenta vulgata Pilsbry, 1940, by original designation.

Synonym: species group Triodopsis vulgata (Emberton, 1988).

Definition: The first Triodopsis to possess character \#19, and all of its descendents.

Species: T. (S.) claibornensis Lutz, 1950; T. (S.) fraudulenta (Pilsbry, 1894); T. (S.) picea Hubricht, 1958; T. (S.) vulgata Pilsbry, 1940.

Subgenus Triodopsis
(Brooksorbis) subgen. n.
Type species: Polygyra platysayoides Brooks, 1933.
Synonym: species group Triodopsis platysayoides (Emberton, 1988).

Definition: The first Triodopsis to possess character \#20, and all of its descendents.

Etymology: The late Dr. Stanley T. Brooks, who described the type species; orbis (Latin) "disc" or "coil."

Species: T. (B.) platysayoides (Brooks, 1933).

Unnamed Clade Comprising Triodopsis
Subgenera T. (Pilsbryorbis) subgen. n., T. (Macmillanorbis) subgen. n., T.
(Haroldorbis), T. (Triodopsis), and $T$. (Vagvolgyorbis) subgen. n.
Definition: The first Triodopsis to possess character \#21, and all of its descendents.

## Subgenus Triodopsis (Pilsbryorbis) subgen. n.

Type species: Polygyra tridentata tennesseensis Walker \& Pilsbry, 1902.

Synonym: species groups Triodopsis tennesseensis and $T$. burchi (Emberton, 1988a).

Definition: The first Triodopsis to possess characters \#22 and 23, and all of its descendents.
Etymology: The late Dr. Henry A. Pilsbry, for some 70 years the world's best known and most productive land-snail specialist, who wrote the definitive monograph on polygyrids (Pilsbry, 1940); orbis (Latin) "disc" or "coil."

Species: T. (P.) burchi Hubricht, 1950; T. (P.) complanata (Pilsbry, 1898); T. (P.) tennesseensis (Walker \& Pilsbry, 1902).

Unnamed Clade Comprising Triodopsis
Subgenera T. (Macmillanorbis) subgen. n.,
T. (Haroldorbis), T. (Triodopsis), and $T$.
(Vagvolgyorbis) subgen. n.
Definition: The first Triodopsis to possess character \#24, and all of its descendents.

## Subgenus Triodopsis (Macmillanorbis) subgen. n .

Type species: Triodopsis tridentata rugosa Brooks \& MacMillan, 1940.

Synonym: species group Triodopsis rugosa (Emberton, 1988).

Definition: The first Triodopsis already having character \#24, to possess character \#25, and all of its descendents.

Etymology: The late Gordan K. MacMillan of the Carnegie Museum, Pittsburg, who collected and coauthored the type species; orbis (Latin) "disc" or "coil."

Species: $T$. (M.) fulciden Hubricht, 1952; $T$. (M.) rugosa Brooks \& MacMillan, 1940.

Unnamed Clade Comprising Triodopsis Subgenera T. (Haroldorbis), T. (Triodopsis), and $T$. (Vagvolgyorbis) subgen. n .

Definition: The first Triodopsis already having character \#24, to possess character \#26, and all of its descendents.

## Subgenus Triodopsis (Haroldorbis) Webb, 1959

Type species: Triodopsis cragini Call, 1886, by original designation.

Synonyms: "Triodopsis copei (Wetherby)" (Vagvolgyi, 1968; species group Triodopsis cragini Call (Emberton, 1988a).

Definition: The first Triodopsis already having characters \#24 and 26, to possess character \#27, and all of its descendents.

Species: T. (H.) cragini Call, 1886; T. (H.) henriettae (Mazÿck, 1877); T. (H.) vultuosa (Gould, 1848).

## Unnamed Clade Comprising Triodopsis Subgenera $T$. (Triodopsis) and $T$. (Vagvolgyorbis) subgen. n.

Definition: The first Triodopsis already having characters \#24 and 26, to possess character \#28, and all of its descendents.

Subgenus Triodopsis (Triodopsis) s.s.
Synonym: species groups Triodopsis tridentata (Say) and T. fallax (Say) (Emberton, 1988a).

Definition: The first Triodopsis already having characters \#24, 26, and 28, to possess character \#29, and all of its descendents.

Species group $T$. (T.) tridentata s.s.: T. (T.) anteridon (Pilsbry, 1940); T. (T.) tridentata (Say, 1817).

Species group $T$. (T.) fallax: T. (T.) alabamensis (Pilsbry, 1902); T. (T.) fallax (Say, 1825); T. (T.) hopetonensis (Shuttleworth, 1852); T. (T.) obsoleta (Pilsbry, 1894); T. (T.) palustris

Hubricht, 1958; T. (T.) soelneri (Henderson, 1907); T. (T.) vannostrandi (Bland, 1875).

## Subgenus Triodopsis (Vagvolgyorbis) subgen. n .

Type species: Polygyra tridentata juxtidens Pilsbry, 1894b.

Synonym: species group Triodopsis juxtidens (Pilsbry) (Emberton, 1988).

Definition: The first Triodopsis already having characters \#24, 26, and 28, to possess character \#30, and all of its descendents.

Etymology: Dr. Joseph Vagvolgyi, author of a conchological monograph on the Triodopsinae and Cryptomastix (Vagvolgyi, 1968); orbis (Latin) "disc" or "coil."

Species: T. (V.) discoidea (Pilsbry, 1904); T. (V.) juxtidens (Pilsbry, 1894b); T. (V.) neglecta (Pilsbry, 1899); T. (V.) pendula Hubricht, 1952.

Subfamily POLYGYRINAE s.s.
Definition: The first Polygyridae to possess characters \#31, 32, and 33, and all of its descendents.

Tribe VESPERICOLINI Emberton, 1994
Type genus: Vespericola Pilsbry, 1939, by original designation.

Definition: The first Polygyrinae to possess character \#34, and all of its descendents.

Genus Hochbergellus Roth \& Miller, 1992
Type species: Hochbergellus hirsutus Roth \& Miller, 1992, by original designation.

Definition: The first Vespericolini to possess character \#35, and all of its descendents.

Species: H. hirsutus Roth \& Miller, 1992.
Genus Vespericola Pilsbry, 1939
Type species: Polygyra columbiana pilosa Henderson, 1928, by original designation.

Definition: The first Vespericolini to possess character \#36, and all of its descendents.

Species: V. armigera (Binney, 1885); V. columbianus (Lea, 1838); V. euthales (Berry, 1939); V. hapla (Berry, 1933); V. karokorum Talmadge, 1962; V. marinensis Roth \& Miller, 1993; V. megasoma (Dall, 1905); "V. sp. n. 1" (Roth \& Miller, 1993); "V. sp. n. 2" (Roth \& Miller, 1993); V. orius (Berry, 1933); V. pilosus
(Henderson, 1928); V. pinicola (Berry, 1916); V. pressleyi Roth, 1985; V. shasta (Berry, 1921); V. sierrana (Berry, 1921).

> Unnamed Clade Comprising Tribes Allogonini and Ashmunellini and Infrafamily Polygyrinai

Definition: The first Polygyrinae to possess character \#37, and all of its descendents.

Tribe ALLOGONINI Emberton, 1994
Type genus: Allogona Pilsbry, 1939, by original designation.

Definition: The first Polygyrinae already having character \#37, to possess character \#38, and all of its descendents.

## Genus Cryptomastix Pilsbry, 1939

Type species: Polygyra mullani olneyae Pilsbry, 1928, by original designation.

Synonym: Triodopsis Rafinesque (in part) (Pilsbry, 1940; Vagvolgyi, 1968).

Definition: The first Allogonini to possess character \#39, and all of its descendents.

Subgenus C. (Bupiogona) Webb, 1970
Type species: Polygyra mullani hendersoni Pilsbry, 1928, by original designation.

Definition: The first Cryptomastix to possess character \#40, and all of its descendents.

Species: C. (B.) hendersoni (Pilsbry, 1928).

## Subgenus C. (Cryptomastix) s.s.

Definition: (as for the genus).
Species: C. (C.) devia (Gould, 1846); C. (C.) mullani (Bland \& Cooper, 1862); C. (C.) sanburni (Binney, 1886).

Subgenus C. (Micranepsia) Pilsbry, 1940
Type species: Helix germana Gould, 1851, by original designation.

Definition: The first Cryptomastix to possess character \#41, and all of its descendents.
Species: C. (M.) germana (Gould, 1851).

## Unnamed Clade Comprising Allogona and Trilobopsis

Definition: The first Allogonini to possess character \#42, and all of its descendents.

Genus Allogona Pilsbry, 1939
Type species: Helix profunda Say, 1821, by original designation.

Definition: The first Allogonini already having character \#42, to possess character \#43, and all of its descendents.

Subgenus A. (Allogona) s.s.
Definition: The first Allogonini to possess character \#44, and all of its descendents.

Species: A. (A.) profunda (Say, 1821)
Subgenus A. (Dysmedoma) Pilsbry, 1939
Type species: Helix townsendiana Lea, 1838, by original designation.

Definition: The first Allogonini to possess character \#45, and all of its descendents.

Species: A. (D.) lombardii Smith, 1943; A. (D.) ptychophora (Brown, 1870); A. (D.) townsendiana (Lea, 1838).

Genus Trilobopsis Pilsbry, 1939
Type species: Helix Ioricata Gould, 1846, by original designation.

Definition: The first Allogonini already having character \#42, to possess character \#46, and all of its descendents.

Species: T. Ioricata (Gould, 1846); T. penitens (Hanna \& Rixford, 1923); T. roperi (Pilsbry, 1889); T. tehamana (Pilsbry, 1928); T. trachypepla (Berry, 1933).

## Tribe ASHMUNELLINI Webb, 1954

Type genus: Ashmunella Pilsbry \& Cockerell, 1899, by original designation.

Definition: The first Polygyrinae already having character \#37, to possess characters \#47 and 48, and all of its descendents.

## Genus Ashmunella Pilsbry \& Cockerell, 1899

Type species: Polygyra miorhyssa Dall, 1898 [= Ashmunella rhyssa miorhyssa (Dall, 1898)], by subsequent designation (Pilsbry, 1905).

Definition: (as for the tribe).
Species ( $\mathrm{n}=49$ ): A. altissima (Cockerell, 1898); A. angulata Pilsbry, 1905; A. animasensis Vagvolgyi, 1974; A. ashmuni (Dall, 1896); A. auriculata (Say, 1818); A. bequaerti Clench \& Miller, 1966; A. binneyi Pilsbry \& Ferriss, 1917; A. carlbadensis Pilsbry, 1932;
A. chiricahuana (Dall, 1896); A. cockerelli Pilsbry \& Ferriss, 1917; A. danielsi Pilsbry \& Ferriss, 1915; A. edithae Pilsbry \& Cheatum, 1951; A. esuritor Pilsbry, 1905; A. ferrissi Pilsbry, 1905; A. harrisi Metcalf \& Smartt, 1977; A. hawleyi Metcalf, 1973; A. hebardi Pilsbry \& Vanatta, 1923; A. intricata Pilsbry, 1948; A. jamesensis Metcalf, 1973 (fossil); A. juarezensis Pilsbry, 1948; A. kochi Clapp, 1908; A. lenticula Gregg, 1953; A. lepidoderma Pilsbry \& Ferriss, 1910; A. levettei (Bland, 1881); A. macromphala Vagvolgyi, 1974; A. mearnsi (Dall, 1896); A. mendax Pilsbry \& Ferriss, 1917; A. meridionalis Pilsbry, 1948; A. mogollonensis Pilsbry, 1900; A. montivaga Pilsbry, 1948; A. mudgei Cheatum, 1971; A. organensis Pilsbry, 1936; A. pasonis (Drake, 1951); A. pilsbryana Ferriss, 1914; A. proxima Pilsbry, 1905; A. pseudodonta (Dall, 1897); A. rhyssa (Dall, 1897); A. rileyensis Metcalf \& Hurley, 1971; A. ruidosana Metcalf, 1973 (fossil); A. salinasensis Vagvolgyi, 1974; A. sprouli Fullington \& Fullington, 1978; A. tegillum Metcalf, 1973; A. tetrodon Pilsbry \& Ferriss, 1915; A. thomsoniana (Ancey, 1887); A. todseni Metcalf \& Smartt, 1977; A. tularosana Metcalf, 1973; A. varicifera Ancey, 1901; A. walkeri Ferriss, 1904; A. watleyi Metcalf \& Fullington, 1978.

## Infrafamily POLYGYRINAI s.s.

Definition: The first Polygyrinae already having character \#37, to possess characters \#49, 50, and 51, and all of its descendents.

Tribe STENOTREMINI Emberton, 1994
Type genus: Stenotrema Rafinesque, 1819.

Definition: The first Polygyrinai to possess characters \#52, 53, and 54, and all of its descendents.

## Genus Euchemotrema Archer, 1939

Type species: Helix monodon Rackett, 1821, by subsequent designation (Pilsbry, 1940).

Definition: The first Stenotremini to possess character \#55, and all of its descendents.

Species: E. fasciatum (Pilsbry, 1940); E. fraternum (Say, 1824); E. hubrichti (Baker, 1937); E. leai (Binney, 1840); E. monodon (Rackett, 1821); E. occidaneum Roth \& Em-
berton, 1994 (early Miocene fossil); E. wichitorum Branson, 1972.

## Genus Stenotrema Rafinesque, 1819

Type species: Stenotrema convexa Rafinesque, 1819 [nomen nudum = Helix stenotrema Pfeiffer, 1842].

Definition: The first Stenotremini to possess characters \#56 and 57, and all of its descendents.

## Subgenus Stenotrema (Cohutta) <br> Archer, 1948

Type species: Polygyra cohuttensis Clapp, 1914, by original designation.

Definition: The first Stenotrema to possess character \#58, and all of its descendents.

Species: S. (Cohutta) cohuttensis Archer, 1948

Unnamed Clade Comprising Stenotrema
(Archerelix), S. (Pilsbrelix), S. (Stenotrema) s.s., and S. (Toxotrema)

Definition: The first Stenotrema to possess character \#59, and all of its descendents.

## Subgenus Stenotrema (Archerelix) subgen. $n$.

Type species: Helix barbigera Redfield, 1856.

Description: The first Stenotrema to possess character \#60, and all of its descendents.

Etymology: The late Dr. Allan F. Archer, who contributed "information, notes, and manuscript" (Archer, 1948: 8) to Pilsbry's (1940) monograph on Stenotrema and wrote a revision and ecological manual on the genus (Archer, 1948); helix (Latin) "coil" or "snail."
Species: S. (A.) barbigerum (Redfield, 1856); S. (A.) edgarianum (Lea, 1841); S. (A.) edvardsi (Bland, 1858); S. (A.) pilsbryi (Ferriss, 1900).

Unnamed Clade Comprising S. (Pilsbrelix), S. (Stenotrema) s.s., and S. (Toxotrema)

Definition: The first Stenotrema to possess character \#61, and all of its descendents.

Subgenus S. (Toxotrema) Rafinesque, 1819
Type species: Helix hirsuta Say, 1817, by subsequent designation (Pilsbry, 1930).

Definition: The first Stenotrema to possess character \#62, and all of its descendents.

Species: S. (T.) barbatum (Clapp, 1904); S. (T.) hirsutum (Say, 1817); S. (T.) labrosum (Bland, 1862); ?S. (T.) simile Grimm, 1971.

Subgenus Stenotrema (Stenotrema) s.s.
Synonyms: Stenotrema (Stenostoma) Rafinesque, 1831 (Archer, 1948); Stenotrema (Maxillifer) Pilsbry, 1940 (Archer, 1948); Stenotrema (Coracollatus) Archer, 1948.

Definition: The first Stenotrema to possess character \#63, and all of its descendents.

Species and subspecies: S. (S.) altispira (Pilsbry, 1894); S. (S.) altispira depilatum (Pilsbry, 1895); ?S. (S.) angellum Hubricht, 1958; S. (S.) brevipila (Clapp, 1907); S. (S.) caddoense (Archer, 1935); ?S. (S.) calvescens Hubricht, 1961; S. (S.) florida Pilsbry, 1940; S. (S.) magnifumosum (Pilsbry, 1900); S. (S.) maxillatum (Gould, 1848); ?S. (S.) morosum Hubricht, 1978 (PleistoceneRecent fossil); S. (S.) pilula (Pilsbry, 1900); S. (S.) spinosum (Lea, 1831); S. (S.) stenotrema (Pfeiffer, 1842); S. (S.) unciferum (Pilsbry, 1900); ?S. (S.) waldense Archer, 1938.

## Subgenus Stenotrema (Pilsbrelix) subgen. $n$.

Type species: Polygyra stenotrema exodon Pilsbry, 1900.

Description: The first Stenotrema to possess character \#64, and all of its descendents.

Etymology: The late Dr. Henry A. Pilsbry, who wrote the definitive monograph on polygyrids (Pilsbry, 1940), and who described the type species; helix (Latin) "coil" or "snail."

Species: S. (P) blandianum (Pilsbry, 1903); S. (P) deceptum (Clapp, 1905); S. (P.) exodon (Pilsbry, 1900); S. (P) turbinella (Clench \& Archer, 1933).

## Unnamed Clade Comprising Polygyrini and Mesodontini

Definition: The first Polygyrinai to possess characters \#65, 66, and 67, and all of its descendents.

## Tribe POLYGYRINI s.s.

Definition: The first Polygyrinai already having characters \#65, 66, and 67, to possess character \#68, and all of its descendents.

Genus Giffordius Pilsbry, 1930
Type species: Giffordius pinchoti Pilsbry, 1930, by original designation.

Definition: The first Polygyrini to possess character \#69, and all of its descendents.

Species: G. corneliae Pilsbry, 1930; G. pinchoti Pilsbry, 1930.

Unnamed Clade Comprising Polygyra, Linisa, Lobosculum, Praticolella, Millerelix, and Daedalochila

Definition: The first Polygyrini to possess character \#70, and all of its descendents.

Genus Polygyra Say, 1818
Type species: Polygyra septemvolva Say, 1818, by subsequent designation (Herrmannsen, 1847).

Definition: The first Polygyrini already having character \#70, to possess character \#71, and all of its descendents.

Species: P. caloosaensis Johnson, 1899 (Pliocene fossil); P. cereolus (Mühlfeld, 1818); P. paludosa (Wiegmann, 1839); P. plana (Dunker, 1843); P. septemvolva Say, 1818.

> Unnamed Clade Comprising Linisa, Lobosculum, Praticolella, Millerelix, and Daedalochila

Definition: The first Polygyrini already having character \#70, to possess characters \#72, 73, and 74, and all of its descendents.

## Unnamed Clade Comprising Linisa, Lobosculum, and Praticolella

Definition: The first Polygyrini already having characters \#70, 72, 73, and 74, to possess character \#75, and all of its descendents.

Genus Linisa Pilsbry, 1930
Type species: Helix (Polygyra) anilis Gabb, 1865, by original designation.
Synonyms (fide Pratt, 1981a): Polygyra (Daedalochila) texasiana group (in part) (Pils-
bry, 1940); Polygyra (Erymodon) Pilsbry, 1956; Polygyra (Monophysis) Pilsbry, 1956; Polygyra (Solidens) Pilsbry, 1956; Polygyra (Linisia) (Pratt, 1981a,b); Daedalochila (in part) (Richardson, 1986).

Definition: The first Polygyrini already having characters \#70, 72, 73, 74, and 75, to possess character \#76, and all of its descendents.

Species: ?L. adamnis (Dall, 1890) (Upper Oligocene fossil); L. albicostulata (Pilsbry, 1896); L. anilis (Gabb, 1865); ?L. aulacomphala (Pilsbry \& Hinkley, 1907); L. behri (Gabb, 1865); ?L. bicruris (Pfeiffer, 1857); ?L. cantralli (Solem, 1957); ?L. couloni (Shuttleworth, 1852); ?L. dissecta (Martens, 1892); ?L. dysoni (Shuttleworth, 1852); ?L. euglypta (Pilsbry, 1896); ?L. hertleini Haas, 1961; ?L. hindsii (Pfeiffer, 1845); ?L. idiogenes (Pilsbry, 1956); ?L. matermontana (Pilsbry, 1896); ?L. nelsoni (Dall, 1897); L. pergrandis (Solem, 1959); ?L. plagioglossa (Pfeiffer, 1859); L. polita (Pilsbry \& Hinkley, 1907); ?L. ponsonbyi (Pilsbry, 1896); L. richardsoni (Martens, 1892); ?L. suprazonata (Pilsbry, 1900); L. tamaulipasensis (Lea, 1867); L. texasiana (Moricand, 1833); L. ventrosula (Pfeiffer, 1845); ?L. yucatanea (Morelet, 1853).

## Unnamed Clade Comprising Lobosculum and Praticolella

Definition: The first Polygyrini already having characters \#70, 72, 73, 74, 75, and 76, to possess characters \#77 and 78, and all of its descendents.

## Genus Lobosculum Pilsbry, 1930

Type species: Helix pustula Férussac, 1822, by subsequent designation (Pilsbry, 1930b: 320).

Definition: The first Polygyrini already having characters \#72, 73, 74, 75, 76, 77, and 78 , to possess character \#79, and all of its descendents.

Species: L. pustula (Férussac, 1822); L. pustuloides (Bland, 1858).

Genus Praticolella Martens, 1892
Type species: Praticola ocampi Strebel \& Pfeffer, 1880 (= Helix ampla Pfeiffer, 1866), by original designation.

Definition: The first Polygyrini already having characters \#72, 73, 74, 75, 76, 77, 78, to
possess character \#80, and all of its descendents.

## Subgenus Praticolella (Farragutia) Vanatta, 1915

Type species: Helix mobiliana Lea, 1841, by original designation.

Definition: The first Praticolella to possess character \#81, and all of its descendents.

Species: P. (F.) mobiliana (Lea, 1841).
Unnamed Clade Comprising Praticolella (Eduardus), P. (Filapex), and P. (Praticolella) s.s.

Definition: The first Praticolella to possess character \#82, and all of its descendents.

Comment: The membership of $P$. (Eduardus) in this clade needs to be tested by dissection, because Pilsbry (1936) was inexplicit about the size of the appendix.

## Subgenus Praticolella (Eduardus) <br> Pilsbry, 1930

Type species: Polygyra martensiana Pilsbry, 1907, by original designation.

Definition: The first Praticolella already having character \#82, to possess character \#83, and all of its descendents.

Species: P. (E.) martensiana (Pilsbry, 1907).

Subgenus Praticolella (Filapex) Pilsbry, 1940
Type species: Helix jejuna Say, 1821, by original designation.

Definition: The first Praticolella already having character \#82, to possess character \#84, and all of its descendents.

Species: P. (F.) bakeri (Vanatta, 1915); P. (F.) jejuna (Say, 1821); P. (F.) lawae (Lewis, 1874).

Subgenus Praticolella (Praticolella) s.s.
Definition: The first Praticolella already having character \#82, to possess character \#85, and all of its descendents.

Species: P. (P.) ampla (Pfeiffer, 1866); P. (P.) berlandieriana (Moricand, 1833); P. (P.) candida Hubricht, 1983; P. (P.) flavescens (Pfeiffer, 1848); P. (P.) griseola (Pfeiffer, 1841); P. (P.) pachyloma (Pfeiffer, 1847); P. (P.) strebeliana Pilsbry, 1899; P. (P.) taeniata Pilsbry, 1940; P. (P.) trimatris Hubricht, 1983.

## Unnamed Clade Comprising Millerelix and Daedalochila

Definition: The first Polygyrini already having characters \#70, 72, 73, and 74, to possess character \#86, and all of its descendents.

Genus Millerelix Pratt, 1981 (see below)
Type species: Helix mooreana W. G. Binney, 1857, by original designation.

Definition: The first Polygyrini already having characters \#70, 72, 73, 74, and 86, to possess character \#87, and all of its descendents.

## Subgenus Millerelix (Millerelix) s.s. <br> Pratt, 1981

Definition: The first Millerelix to possess character \#88, and all of its descendents (Pratt, 1981b).

Species: M. doerfeulliana (Lea, 1838); M. gracilis (Hubricht, 1961); ?M. implicata (Martens, 1865); M. lithica (Hubricht, 1961); M. mooreana (Binney, 1857); ?M. rhoadsi (Pilsbry, 1900); M. tholus (Binney, 1857).

Subgenus Millerelix (Prattelix) subgen. n .
Type species: Polygyra plicata Say, 1821.
Synonyms: Polygyra plicata group (Pilsbry, 1940); Daedalochila plicata group = unnamed subgenus (Pratt, 1981a).

Definition: The first Millerelix to possess character \#89, and all of its descendents.

Comments: The shell of the type species is sparsely and evenly covered with long, conspicuous periostracal hairs, seemingly round in cross-section and slightly curved at the tip, that fade out toward the umbilicus (Fig. 13). They are easily broken, hence Pilsbry's (1940: 626) mildly erroneous, "a few short hairs, usually preserved only in the umbilicus and behind the lip." The long hairs were found in all four of the Academy of Natural Sciences's alcohol-preserved lots of D. plicata: Alabama, Madison County (ANSP A 2423-B); Tennessee, Marion County (A 2423C); Tennessee, Knox County (A 2423-A, Fig. 13); and Kentucky, Barren County (A 2387-B, most hairs broken).

Etymology: The subgenus is named in honor of Will Pratt.

Species: deltoidea (Simpson, 1889); fatigiata (Say, 1829); jacksoni (Bland, 1866); peregrina (Rehder, 1932); plicata (Say, 1821); simp-
soni (Pilsbry \& Ferriss, 1907); troostiana (Lea, 1838).

## Genus Daedalochila Beck, 1837

Type species: Helix auriculata Say, 1818, by subsequent designation (Herrmannsen, 1847).

Definition: The first Polygyrini already having characters \#70, 72, 73, 74, and 86, to possess character \#90, and all of its descendents.

## Subgenus Daedalochila (Upsilodon) Pilsbry, 1930c

Type species: Helix hippocrepis Pfeiffer, 1848, by original designation.
Synonym: Daedalochila (Acutidens) Pilsbry, 1956.

Definition: The first Daedalochila to possess character \#91, and all of its descendents.
Comment: The recurved palatal apertural denticle of $D$. acutidentata also occurs in the otherwise very different shell of $D$. poeyi, so does not seem to be a reliable character for defining a clade.
Species: ?D. (U.) acutedentata (Binney, 1858); D. (U.) burlesoni (Metcalf \& Riskind, 1979); D. (U.) chisosensis (Pilsbry, 1936); D. (U.) dalli (Metcalf \& Riskind, 1979); D. (U.) hippocrepis (Pfeiffer, 1848); D. (U.) leporina (Gould, 1848); D. (U.) multiplicata (Metcalf \& Riskind, 1979); ?D. (U.) poeyi (Aguayo \& Jaume, 1947); D. (U.) sp. n. A (Pratt, 1981a); D. (U.) sterni (Metcalf \& Riskind, 1979).

Subgenus Daedalochila (Daedalochila) s.s.
Synonym: Polygyra auriculata group (Pilsbry, 1940).

Definition: The first Daedalochila to possess characters \#92, 93, and 94, and all of its descendents.

Comments: The downward curve on the lower limb of the parietal apertural denticle is a newly discovered synapomorphy. Pratt (1981a) stated (without giving evidence) that ?D. ariadne and ?Mi. implicata are members of a new genus; this needs to be investigated.

Species: ?D. (D.) ariadne (Pfeiffer, 1848); D. (D.) auriculata (Say, 1818); D. (D.) auriformis (Bland, 1862); D. (D.) avara (Say, 1818); D. (D.) delecta (Hubricht, 1976); D. (D.) hausmani (Jackson, 1948); ?D. (D.) oppilata (Morelet,
1849); D. (D.) peninsulae (Pilsbry, 1940); D. (D.) postelliana (Bland, 1862); D. (D.) subclausa (Pilsbry, 1899); D. (D.) uvulifera (Shuttleworth, 1852).

Tribe MESODONTINI Emberton, 1991
Type genus: Mesodon Férussac, 1821.
Definition: The first Polygyrinai already having characters \#65, 66, and 67, to possess characters \#95, 96, and 97, and all of its descendents.

Genus Patera Albers, 1850
Type species: Helix appressa Say, 1821, by subsequent designation Pilsbry, 1930c: 326).

Definition: The first Mesodontini to possess character \#98, and all of its descendents.

## Subgenus Patera (Vesperpatera) Emberton, 1991

Type species: Polygyra binneyana Pilsbry, 1899, by original designation.

Definition: The first Patera to possess character \#99, and all of its descendents.

Species: P. (V.) binneyana (Pilsbry, 1899); P. (V.) clenchi (Rehder, 1932); P. (V.) indianorum (Pilsbry, 1899); P. (V.) kiowaensis (Simpson, 1888); P. (V.) leatherwoodi (Pratt, 1971); P. (V.) roemeri (Pfeiffer, 1848).

Unnamed Clade Comprising P. (Patera) and P. (Ragsdaleorbis)

Definition: The first Patera to possess character \#100, and all of its descendents.

## Subgenus Patera (Patera) s.s.

Definition: The first Patera already having character \#100, to possess character \#101, and all of its descendents.

Species: P. (P.) appressa (Say, 1821); P. (P.) clarki (Lea, 1858); P. (P.) laevior (Pilsbry, 1940); P. (P.) panselena (Hubricht, 1976); P. (P.) perigrapta (Pilsbry, 1894b); P. (P.) sargentiana (Johnson \& Pilsbry, 1892).

Subgenus Patera (Ragsdaleorbis)
Webb, 1954
Type species: Helix pennsylvanicus Green, 1827, by original designation.

Definition: The first Patera already having
character \#100, to possess characters \#102 and 103, and all of its descendents.

Species: P. (R.) pennsylvanica (Green, 1827).

Genus Inflectarius Pilsbry, 1940
Type species: Helix inflecta Say, 1821, by original designation.
Definition: The first Mesodontini to possess character \#104, and all of its descendents.

## Subgenus Inflectarius (Hubrichtius) <br> Emberton, 1991

Type species: Mesodon kalmianus Hubricht, 1965, by original designation.

Definition: The first Inflectarius to possess character \#105, and all of its descendents.

Species: I. (H.) downieanus (Bland, 1861); I. (H.) kalmianus (Hubricht, 1965)

Subgenus Inflectarius (Inflectarius) s.s.
Definition: The first Inflectarius to possess character \#106, and all of its descendents.
Species group I. (I.) edentatus: I. (I.) edentatus (Sampson, 1889); I. (I.) magazinensis (Pilsbry \& Ferriss, 1907).
Species group I. (I.) smithi: I. (I.) smithi (Clapp, 1905).
Species group I. (I.) inflectus: I. (I.) approximans (Clapp, 1905); I. (I.) inflectus (Say, 1821); I. (I.) rugeli (Shuttleworth, 1852); I. (I.) verus (Hubricht, 1954).
Species group: I. (I.) ferrissi: I. (I.) ferrissi (Pilsbry, 1897); I. (I.) subpalliatus (Pilsbry, 1893).

## Genus Fumonelix Emberton, 1991

Type species: Helix wheatleyi Bland, 1860, by original designation.

Definition: The first Mesodontini to possess character \#107, and all of its descendents.
Species: F. archeri (Pilsbry, 1940); F. christyi (Bland, 1860); F. jonesiana (Archer, 1938); F. orestes (Hubricht, 1975); F. wetherbyi (Bland, 1874); F. wheatleyi (Bland, 1860).

## Unnamed Clade Comprising Appalachina and Mesodon

Definition: The first Mesodontini to possess character \#108, and all of its descendents.

Genus Appalachina Pilsbry, 1940
Type species: Polygyra sayana Pilsbry, 1906, by original designation.

Definition: The first Mesodontini already having character \#108, to possess character \#109, and all of its descendents.
Species: A. chilhoweensis (Lewis, 1870); A. sayanus (Pilsbry, in Pilsbry \& Ferriss, 1906).

Genus Mesodon Férussac, 1821
Type species: Helix thyroidus Say, 1817, by monotypy.

Definition: The first Mesodontini already having character \#108, to possess character \#110, and all of its descendents.

## Subgenus Mesodon (Aphalogona) Webb, 1954

Type species: Helix elevata Say, 1821, by original designation.

Definition: The first Mesodon to possess character \#111, and all of its descendents.
Species: M. (Aph.) elevatus (Say, 1821); M. (Aph.) mitchellianus (Lea, 1838); M. (Aph.) zaletus (Binney, 1837).

## Subgenus Mesodon (Akromesodon) Emberton, 1991

Type species: Polygyra andrewsae normalis Pilsbry, 1900, by original designation.

Definition: The first Mesodon to possess characters \#112 and 113, and all of its descendents.

Species: M. (Akr.) altivagus (Pilsbry, 1990); M. (Akr.) andrewsae Binney, 1879; M. (Akr.) normalis (Pilsbry, 1900).

Subgenus Mesodon (Mesodon) s.s.
Definition: The first Mesodon to possess characters \#114 and 115, and all of its descendents.

Species: M. (M.) clausus (Say, 1821); M. (M.) sanus (Clench \& Archer, 1933); M. (M.) thyroidus (Say, 1817); M. (M.) trossulus Hubricht, 1966.

Shell-Based Phylogenetic Analysis
Figures 9-11 present x-ray outlines of 57 shells representing polygyrid subgenera and outgroups. These outlines were used for phylogenetic character analysis. Also included in the character analysis were the $x$-rayed
shells themselves, plus four shells from the ANSP collection representing four additional species: Ashmunella angulata, Stenotrema (Archerelix) barbigerum, S. (Pilsbrelix) exodon, and S. (Toxotrema) hirsutum. No shell was available of Hochbergellus hirsutus, but its published description (Roth \& Miller, 1992) was used to score as many characters as possible. Thus, a total of 62 species were included, of which only five lacked x-ray data.

Table 2 defines the 14 characters and 71 character states scored for phylogenetic analysis, which are illustrated in Figures 12, 13 , and 6 . All of these characters and characters states are new or newly evaluated.

Figure 14 shows the distributions of shell characters among subgenera and species. Figure 15 diagrams shell characters that were excluded from phylogenetic analysis because of known high levels of homoplasy within subgenera of the Triodopsini and Mesodontini.

Figure 16 shows the results of cladistic analysis of the data in Figure 14. In total, Hennig86 generated 1,529+ equally and maximally parsimonious cladograms with a consistency index of 0.34 and a retention index of 0.68 , of which Figure 16 is the Nelson consensus tree.

Reliability of Fossils
Comparison of shell-based and anatomy-behavior-shell-based phylogenetic hypotheses revealed conspicuous differences in resolution and topology. Among 54 ingroup (polygyrid) taxa, with a maximum possible resolution of 53 nodes, the shell hypothesis (Fig. 16) had 10 nodes ( $19 \%$ of maximum) and the anatomy-behavior-shell hypothesis (Fig. 8) had 40 nodes ( $75 \%$ of maximum). Thus, the anatomy-behavior-shell hypothesis had four times the resolution of the shellbased hypothesis.

Topologically, the only congruence between the two hypotheses was in the Stenotremini, which both showed as a monophyletic clade with Euchemotrema and Stenotrema (Cohutta) at its base. Other clades showed major discrepancies between the two phylogenetic hypotheses. Thus, relative to the anatomy-behavior-shell hypothesis/revision, the shell-based hypothesis (a) grouped Vespericola and Appalachina, Daedalocheila (Upsilodon) hippocrepis and Lobosculum, and Polygyra and Millerelix (Prat-










FIG. 9.

FIGS. 9-11. Shell ontogenies, from x-rays of adult shells, of representatives of polygyrid subgenera and of polygyrid closest outgroup families. The representatives are type species unless otherwise indicated. All scale bars $=3 \mathrm{~mm}$. The shells are arranged by a previous classification (Webb, 1974; Richardson, 1986), since revised (Emberton, 1994a, this paper). Dotted lines indicate portions of the x-rays that were difficult to interpret. By chance the x-rayed shell representing Ashmunella (As) was broken internally; all characters could be scored from this drawing, however, so the specimen was not replaced. Specimen abbreviations, defined in alphabetical order with their catalog numbers at the Academy of Natural Sciences of Philadelphia, are: AIA, Allogona (Allogona) profunda, 77867; AID, Allogona (Dysemdoma) townsendiana, 100390; App, Appalachina sayana, 139140; As, Ashmunella rhyssa, 166077; CB, Cryptomastix (Bupiogona) hendersoni, 171267; CC, Cryptomastix (Cryptomastix) mullani, 171245; CM, Cryptomastix (Micranepsia) germana, 11154; DD, Daedalochila (Daedalocheila) auriculata, 57070; DU, Daedalochila (Upsilodon) hippocrepis, 84629; DUa, D. (U.) acutidentata, 166418; E, Euchemotrema leai, 172539; F, Fumonelix wheatleyi, 169691; G, Giffordius pinchoti, 150735; IH, Inflectarius (Hubrichtius) downieanus (non-type), 91035; II, Inflectarius (Inflectarius) inflectus, 91616; Ilf, I. (I.) ferrissi, 98085; Lb, Lobosculum pustula, 86968; Ln, Linisa anilis, 166371; Lnb, Linisa behri, 166487; MeA, Mesodon (Aphalogona) elevatus, 81161; MeK, Mesodon (Akromesodon) normalis, 169640; MeM, Mesodon (Mesodon) thyroidus, 71950; MiM, Millerelix (Millerelix) mooreana, 158375; MiP, Millerelix (Prattelix) plicata, 143448; NA, Neohelix (Asamiorbis) dentifera, 78876;


FIG. 10.

[^0]

FIG. 11
telix), each pair of which has been classified into two widely separated clades; and (b) split Ashmunella rhyssa and A. angulata, Daedalocheila (Upsilodon) hippocrepis and D. (U.) acutidentata, Praticolella and Lobosculum, Linisa anilis and Linisa behri, Millerelix (Millerelix) and M. (Prattelix), and Polygyra and Giffordius, each pair of which has been classified into a single, closely related clade. Among outgroups, the shell-based hypothesis conflicted with a previous, anatomybased hypothesis (Emberton, 1991c; Fig. 8)
by joining Cepolis in a clade with Pleurodonte and Sagda.

## Closest Convergences in Sympatry

Figure 1 shows the closest known, fieldvalidated, polygyrid convergences in sympatry on the globose, umbilicate, flat, and tridentate shell forms. As mentioned in the Introduction, the globose case is the closest convergence and has received detailed

TABLE 2. Shell characters used for a separate phylogenetic analysis of the Polygyridae (Fig. 16).

1. Shape of the aperture's generating curve throughout late-juvenile ontogeny (Fig. 12: 1). 1a, "egg," "pinto bean," or "lima bean." 1b, "kidney bean." 1c, "bulging kidney bean."
2. Approximate number of complete adult whorls (Fig. 12: 2, which shows the shell apex down). 2 a , four. 2 b , five. 2 c , six. 2d, eight. 2 e , nine.
3. Approximate ratio of apertural areas three whorls apart, beginning near the apex and ending at least 3/4-whorl before the aperture (Fig. 12: 3). 3a, 40:1. 3b, 32:1. 3c, 15:1. 3d, 9:1. 3e, 7:1.
4. Columellar surface of the body whorl approximately $1 / 4$-whorl before the adult aperture (Fig. 12: 4). 4a, flat or slightly concave, but convex at the suture. 4b, flat or slightly concave, flat at the suture. 4 c , convex throughout.
5. Umbilical shape (Fig. 12: 5, which outlines the x-rayed umbilici). 5a-5h, extremely narrow to broad (some intergradation among categories).
6. Umbilical sutures (Fig. 13: 6). 6a, strongly to weakly shouldered. 6b, rounded, unshouldered.
7. Umbilical-wall whorls (Fig. 13: 7). 7a, flat. 7b, slightly flat. 7c, round.
8. Basal denticle(s) (Fig. 13: 8). 8a, absent. 8b, baso-columellar shoulder or knob parallel to apertural plane. 8c, partial lamella parallel to apertural plane. 8d, basal denticle parallel to apertural plane. 8e, denticle or lamella(e) transverse to apertural plane. 8f (= Fig. 6: character 4), complete lamella parallel to apertural plane.
9. Parietal denticle shape (size variable) (Fig. 13: 9). 9a, absent. 9b, linear, curved toward the umbilicus, higher toward the aperture. 9c (= Fig. 6: character 5), linear, straight, even in height. 9d (= Fig. 6: character 6), Triangular to spatulate. 9e, linear, curved away from the umbilicus, higher away from the aperture.
10. Size (Fig. 13: 10). 10a-10i, gigantic to minute (some intergradation among categories).
11. Gradually increasing outward tilt of the long axis of the aperture (= Fig. 6: character 1). 11a, throughout ontogeny or until tilting upward slightly. 11b, until tilting upward conspicuously.
12. Whorl expansion rate (= Fig. 6: character 2). 12a, constant. 12b, increasing then decreasing, with successive whorls always larger. 12c, increasing then decreasing, such that successive whorls are equal.
13. Lower apertural lip (= Fig. 6: character 3). 13a, separate from basal shell. 13b, joined to basal shell as a thin callus.
14. Palatal denticle (= Fig. 6: character 7). 14a, absent. 14b, discrete, parallel to apertural plane. 14 c , non-discrete, forming a thin shelf grading into the basal denticle, parallel to apertural plane. 14d, semidiscrete, with bottom tapering and thinning, basally slanted inward into the apertural plane.
study, including discoveries of several sites of sympatry (Emberton, 1994b, 1995b).

The second closest shell-form convergence in sympatry is on the flat form, exhibited by the mesodontin Patera (Patera) laevior and the triodopsin Xolotrema (Wilcoxorbis) fosteri. Fieldwork in April 1981 along the lower Ohio River Valley, visiting all stone bluffs reasonably accessible by road, accumulated collections at 22 stations (numbered as "H-1" through "H-22"), all material from which is catalogued at the Field Museum of Natural History. Both species had been reported from Grand Chain, Indiana (Pilsbry, 1940), but extensive search failed to find both in 1981, perhaps due to recent floods. Sympatry between $P$. laevior and $X$. fosteri was discovered at only one station: on a sand-
stone wall above the Ohio River at the Fern Cliff estate, Hawesville, Hancock County, Kentucky, 21 April 1981.

Figure 17 illustrates the external anatomies, shells, and dissected reproductive anatomies of representative specimens of Patera laevior and Xolotrema fosteri from the Hawesville, Kentucky, site, and summarizes their mating-behavioral differences according to Webb (cited in Emberton, 1994a). The shells and external bodies were virtually identical in size and shape (Figs. 1, 17), but internally $X$. fosteri differed from $P$. laevior by its penial sheath, penial retentor muscle, retrac-tor-muscle attachment on the vas deferens, and thick gametolytic-gland (= spermathecal) duct, all correlating with its internal (vs. external) sperm exchange (Fig. 17). Ecologi-
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: SBSB

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6



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FIG. 13.
cal and conchological data on the two sympatric populations (Emberton, unpublished) are archived at the Academy of Natural Sciences of Philadelphia.

The third closest shell-form convergence in sympatry is on the umbilicate form, exhibited by the mesodontin Appalachina sayana and the allogonin Allogona (Allogona) profunda. In the northern Midwest, these species' ranges overlap extensively (Hubricht, 1985), but examination of Field Museum collections indi-
cated only a few cases of documented sympatry, of which the most conchologically similar case was at Burnside, Pulaski County, Kentucky (Fig. 1). Extensive search of that region in spring of 1982 failed to yield both species, perhaps due to degradation of remnant forest. Sympatry was discovered, however, at a site on the northern slope of Pine Mountain, Harlan County, Kentucky (station "GS-116"). At that site, the shell convergence was not as extreme as in Figure 1, because


FIG. 14. Distributions of shell characters among polygyrid subgenera. Characters are numbered as in Table 2 , but character-states are converted to letters ( $a=1, b=2$, etc.).



FIG. 15. Shell variation discounted as characters: a, low-to-high spires are documented within Patera s.s.; b, rounded-to-angulate-to-keeled peripheries occur within Xolotrema s.s., X. (Wilcoxorbis), and Patera s.s.; c, covered-to-open umbilici are known within both Patera (Vesperpatera) and Mesodon s.s.; d, smooth-to-ribbed sculpture appears within Xolotrema s.s., Triodopsis s.s., T. (Pilsbryorbis), and T. (Haroldorbis); e, bald-to-hirsute sculpture occurs within Xolotrema s.s., Inflectarius (Summinflectarius), and Fumonelix; f, unicolor-to-color-banded shells are known within both Mesodon s.s. and M. (Aphalogona).

App. sayana tended to have a smaller shell than AI. profunda. The northern Midwest was not extensively surveyed during 1982 and 1983 fieldwork, however, so closer convergences in sympatry on the umbilicate shell form may exist in that region.

Least close-but still remarkable, espe-
cially in apertural-barrier construction-of the four polygyrid shell-form convergences in sympatry (Fig. 1) is on the tridentate form. The closest field-documented case of tridentate convergence in sympatry comprises the mesodontin Inflectarius (Inflectarius) inflectus and the triodopsin Triodopsis (Triodopsis) fal-


FIG. 16. Shell-based consensus tree of polygyrid subgenera resulting from cladistic analysis of data in Fig. 14.


Lengthy courtship and mating Intertwining of penes

External deposition of sperm mass on mate's everted penis


- 4


Brief courtship and mating Insertion of penes

Internal deposition of sperm mass in spermathecal duct


FIG. 17. Closest known convergence in sympatry on the flat shell form: Patera laevior (left) and Xolotrema fosteri (right) from Hawesville, Hancock County, Kentucky. Center: external anatomies and shells in two views. Bottom: dissected reproductive anatomies. Sides: mating-behavioral differences according to Webb (cited in Emberton, 1994a).
lax, which I collected together under the same log in dense woods, Vinton County, Ohio, in 1979 (vouchers at Field Museum of Natural History, Chicago). The ranges of these two species overlap moderately in the central Midwest, and other cases of sympatry are documented-sometimes as inadvertently mixed lots-in the collection of the Academy of Natural Sciences of Philadelphia (Emberton, unpublished).

Shell Barriers and Water Loss
Table 3 gives the results of the experiment on Triodopsis tridentata. A total of 280 "snailhours" were recorded. Snails from which apertural barriers had been removed lost water by evaporation faster than those with barriers left intact: $27 \%$ faster when inactive (retracted into the shell) and 9\% faster when active (extended from shell).

Snails with intact barriers were 83\% more successful than those from which barriers had been removed in forming complete or partial epiphragms. Epiphragms slightly reduced the rate of evaporative water loss in snails with barriers intact (by 3\% for both partial and complete epiphragms). In snails from which barriers had been removed, however, epiphragms greatly reduced the rate of water loss: by $22 \%$ for partial epiphragms and by $38 \%$ for complete epiphragms.

## Remaining Conservation Priorities

Table 4 gives highest priorities for polygyrid conservation for each of four, phylogenybased categories. In the category of radiating, endemic clades, Fumonelix must rank very high; the genus is restricted to the southern Appalachians, and three of its six species are narrow-range endemics that have been officially designated as endangered or threatened: F. archeri, F. jonesianus, and $F$. orestes. In the same category, although Mesodon (Akromesodon) contains the widespread and relatively common species $M$. normalis, its other two species both have narrow, high-altitude ranges: M. altivagus on summits of the Great Smoky Mountains, and $M$. andrewsae on the summit of Mount Rogers, Virginia.

Four species have been listed as high priorities for conservation in the category of extremely autapomorphic endemics. The twospecies genus Giffordius, endemic to Colombia's tiny Isla de Providencia (off the eastern coast of Nicaragua), is unique within the family for its ovoviviparity; Giffordius pinchoti by far is the rarer and most endangered of the two species (Emberton, unpublished). Inflectarius ferrissi, endemic to high elevations of the Smoky Mountains, represents
extreme phylogenetic shifts in both shell morphology (Emberton, 1991a, 1991b) and in penial morphology (Emberton, 1991a). Triodopsis platysayoides, endemic to a few bluffs along the New River Gorge of northeastern West Virginia, U.S.A., also embodies extreme phylogenetic divergences in both shell and penis (Emberton, 1988a). Mesodon chilhoweensis is remarkable for its gigantic, broadly umbilicate shell, exhibiting nearly regular, log-spiral growth (Emberton, 1994a: fig. 1) and for its extremely long penis, much longer than the diameter of the shell (Emberton, 1991a).
Giffordius also deserves high priority for conservation in another category, as relic sis-ter-group to a major clade. According to the general phylgenetic hypothesis (Fig. 8), Giffordius is basal to the Polygyrini, hence is sister-group to the remaining Polygyrini, a highly diverse and speciose clade.
The conservation category of localities with diverse sympatric convergences is led by the northern slope of Pine Mountain, Harlan County, Kentucky. This is the only known site where convergences on all four polygyrid shell forms (Fig. 1) coexist. There the globose form is represented by Mesodon zaletus and Neohelix albolabris; the umbilicate form by Appalachina sayana and Allogona profunda (mentioned above); the flat form by Patera appressa and Xolotrema denotata; and the tridentate form by Inflectarius inflectus, Triodopsis vulgata, and T. tridentata (Emberton, 1995c). This site is also important as North America's most diverse known locality for land snails (Emberton, 1995c).
Thus, Table 4 lists seven high priorities (including a double listing of Giffordius) for polygyrid conservation, based on phylogenetic criteria. Five of these priorities are currently under protection. The Smoky Mountains are a

TABLE 3. Effect of apertural dentition and epiphragm on the rate of evaporative water loss in Triodopsis tridentata.

| Category | Number of <br> "Snail-Hours", | Mean Rate of <br> Water Loss |
| :--- | :---: | :---: |
| Toothed, no epiphragm | 70 | $3.86 \%$ |
| Toothed, partial epiphragm | 59 | $3.74 \%$ |
| Toothed, complete epiphragm | 26 | $3.73 \%$ |
| Toothless, no epiphragm | 63 | $4.90 \%$ |
| Toothless, partial epiphragm | 7 | $3.97 \%$ |
| Toothless, complete epiphragm | 20 | $3.06 \%$ |
| Toothed, after activity | 25 | $15.80 \%$ |
| Toothless, after activity | 10 | $17.18 \%$ |
| Total "Snail-Hours" | 280 |  |

TABLE 4. Conservation high priorities for polygyrids, based on four phylogenetic criteria.

| Criterion | High Priority | \#Spp | Locality | Protected? |
| :---: | :---: | :---: | :---: | :---: |
| Radiating, endemic clade | Fumonelix | 6 | Southern Blue Ridge, U.S.A. | Yes |
| Radiating, endemic clade | Mesodon (Akromesodon) | 3 | Southern Blue Ridge, U.S.A. | Yes |
| Extremely autapomorphic endemic | Giffordius pinchoti | 1 | Isla de Providencia, Colombia | No |
| Extremely autapomorphic endemic | Inflectarius ferrissi | 1 | High Smoky Mountains, U.S.A. | Yes |
| Extremely autapomorphic endemic | Triodopsis platysayoides | 1 | New River Gorge, U.S.A. | Yes |
| Extremely autapomorphic endemic | Mesodon chilhoweensis | 1 | Smoky Mountains, U.S.A. | Yes |
| Relic sister-group to major clade | Giffordius | 2 | Isla de Providencia, Colombia | No |
| Diverse sympatric convergences | four shell-form convergences | 11 | Pine Mountain, Kentucky, U.S.A. | No |

U.S. National Park and International Biosphere Reserve, protecting four species of Fumonelix, two species of Mesodon (Akromesodon), Inflectarius ferrissi, and Mesodon chilhoweensis. The remaining Fumonelix are protected in U.S. National Forests, and the remaining M. (Akromesodon) is protected by Mount Rogers State Park. Triodopsis platysayoides is somewhat protected in Coopers Rock State Forest, West Virginia, U.S.A.

Two high-priority sites remain unprotected. There is a "Pine Mountain State Park," Bell County, Kentucky, but it is about 64 km away from and has a much lower diversity than the Harlan-County Pine Mountain site listed in Table 4 (Emberton \& Petranka, unpublished). Thus, the Pine Mountain site, U.S.A., is unprotected.

Also unprotected is the conservationally important, small Isla de Providencia, Colombia. In 1987, both species of Giffordius were still surviving on the island in remnant patches of forest, primarily at higher elevations, but deforestation had already destroyed the type locality of G. pinchoti and seemed to be rapidly advancing up the central peak (Emberton, 1992, unpublished).

## DISCUSSION

General Phylogenetic Hypothesis/Revision
This hypothesis/revision culminates the author's 15 years of work on polygyrid systematics, and hopefully provides a replicable data set and a fully testable hypothesis upon which future workers may build. For allozyme
data and for more detailed phylogenetic hypotheses on the Triodopsini and the Mesodontini, see Emberton (1988a, 1991a, 1994). For a polygyrid biogeographic/historical hypothesis, see Emberton (1994a). Clearly, this is not the final word; much remains to be learned.

Shell-Based Phylogenetic
Analysis/Reliability of Fossils
Despite the discovery of many new characters, shell-based phylogenetic analysis resulted in very low resolution. Two possible sources of additional shell characters were neglected, however: shell-surface microsculpture (Emberton, 1995b) and shell ultrastructural layers (Bøggild, 1930; Wilbur \& Saleuddin, 1983; Roth, 1987; Watabe, 1988). Both of these should be investigated. Qualitative character analysis of $x$-ray data failed to detect a difference in whorl expansion rate between the Triodopsini and the Mesodontini suggested by quantitative analysis (Emberton, 1994a). Thus, more subtle analysis of x-rays could yield more characters for phylogenetic resolution. Based on current data, however, "shells do not tell" the estimated 145 million years of phylogenetic history of the Polygyridae in North America (Emberton, 1994a). This implies that identification of preMiocene polygyrid fossils may be very difficult at best.

Thus, based on the general phylogenetic hypothesis/revision, convergences in shell morphology were rampant within the Polygyridae. "Kidney-bean" generating curves cropped up in one subgenus each of Poly-
gyra and Daedalochila. Whorl-counts of over six hypothetically evolved one or more times each in the Triodopsini, Vespericolini, Stenotremini, Polygyrini, and Mesodontini. Extremely low whorl-expansion rates (<2.7 per 360-degree rotation) seemingly evolved independently in the Triodopsini, Stenotremini, and Polygyrini. Convergences on a columellarly flattened body whorl seem to have occurred in all polygyrid tribes except the Ashmunellini. Expanded umbilici (Fig. 12: char $5 \mathrm{e}-\mathrm{g}$ ) appeared in all tribes but the Vespericolini. Rounded, unshouldered umbilical sutures seems to be a good synapomorphy of the genus Triodopsis, but nevertheless this character-state was apparently reversed in the nominal subgenus and seems to have been converged upon in the outgroup family Camaenidae. Slightly flattened umbilical-wall whorls seemingly arose convergently within one or more subgenera each of the Triodopsini, Allogonini, and Mesodontini. Although transverse-to-spiral basal lamellae in Ashmunella, Daedalochila, and Appalachina were hypothetically plesiomorphic and hence not necessarily convergent, all other forms of basal denticles and lamellae seem to have been converged upon repeatedly in the Polygyridae, with the single exception of the complete basal lamella, which is a hypothetical synapomorphy of the Stenotremini. Two types of parietal denticles-straight and tri-angular-to-spatulate-seem to be good synapomorphies, with additional phylogenetic information, for the Stenotremini and the Polygyrini, although the latter was apparently lost secondarily in Practicolella; a downcurved parietal denticle, however, seems to have evolved independently in all other tribes of the Polygyridae (non-type species of Vespericola also have it: Pilsbry, 1940). Both extremes of shell size occur among the outgroups, and various intermediate and small sizes recur repeatedly among polygyrid subgenera, with only very slight tendencies toward trends within and among tribes. Rapid shifts in apertural tilt and expansion rate are apparent synapomorphies for a subset of the Polygyrini, yet both were hypothetically reversed in type species of some genera. An adnate, callus-like apertural basal lip may seem a perfect synapomorphy for four of Stenotrema's five subgenera, but was apparently reversed in S. (Archerelix) barbigerum (Pilsbry, 1940). Regarding apertural palatal denticles, discrete denticles (apertural barriers) seem to appear sporadically in nearly all
polygyrid tribes; and semidiscrete, basally recessed denticles seem to be only an inconsistent synapomorphy of the Polygyrini; but a non-discrete "shelf" seems to be a good synapomorphy of the Stenotremini.

## Closest Convergences in Sympatry

Identifications and field verifications of the closest convergences in sympatry on the flat, umbilicate, and tridentate polygyrid iterated shell forms (Fig. 1) provide starting points for analyses of these naturally replicated experiments in evolutionary morphology, such as those already conducted on the globose shell form (Emberton, 1994b, 1995a). Although these four cases of polygyrid shell convergence in sympatry (Fig. 1; Emberton, 1994a) are the most precise known in North America, they are representative of numerous less precise cases involving the same four basic shell forms. Among and within these four shell forms, there are other examples of convergence (Emberton, 1988a, 1991a, 1994a), the most striking (and informative for polygyrid evolution) of which is between Inflectarius ferrissi and Neohelix dentifera (Emberton, 1991b).

## Shell Barriers and Water Loss

The experimental results from Triodopsis tridentata suggest that apertural barriers reduce the rate of evaporative water loss both directly and indirectly, by aiding in the formation of an epiphragm. The manner in which barriers and epiphragms retard water loss may be counter-intuitive, judging from Ramsay's (1935) experiments on evaporation rates from vertical tubes. Ramsay observed faster water loss when the evaporating surface was at the bottom of the tube than at the top, but found that the presence of a permeable occluder tended to diminish the difference. He hypothesized therefore that "when [the evaporating surface] is at the bottom . there is an upward current of moist air which sets up a circulation in the system." Ramsay's hypothesis has not been tested, to my knowledge. Extending his hypothesis to land snails, when a snail withdraws deeply (to escape predation, for example) into the coiled tube of its shell, its apertural barriers (and the epiphragm they aid in forming) may function not so much to physically block diffusing water vapor as to interrupt the convection cur-
rents that normally result from tubular evaporation.

The trend for apertural barriers in T. tridentata and other triodopsins to be larger in moister habitats (Emberton, 1988a) suggests that their demonstrated retardation of evaporative water loss is not their only-or even primary-function. Other hypothesized functions are given in the Introduction.

Polygyrids provide some fascinating examples of apertural obstruction that could be used to test these and other hypotheses. Figure 2 presents some extreme examples from several clades, most of which have arisen by evolutionary convergence. The most extreme cases are in the genus Stenotrema; it is a memorable experience to watch one of these snails extend, its body "pouring" like molasses through the slit-like, convoluted aperture. This slit seems to be at its most narrow in $S$. (Pilsbrelix) uncifera, but is augmented in S. (Stenotrema) maxillatum (both in Fig. 2) by recession of the basal lamella, which lacks a notch and which is overlapped by the parietal lamella to form a three-dimensional baffle.

Species of Daedalochila have some complex apertural conformations, the most bizarre of which are the deeply recessed parietal scoop in D. (Upsilodon) hippocrepis and the convoluted apertural lip incorporating the parietal scoop and augmented by recessed denticles in D. (Daedalochila) uvulifera (both in Fig. 2). Other notable examples occur in Triodopsis, Lobosculum, Ashmunella, Linisa, Lobosculum, and Inflectarius (some are illustrated in Figs. 1 and 2).

Remaining Conservation Priorities
The evaluation of conservation priorities presented in this paper is doubtless biased by the author's limited experience with the western and subtropical species. Table 4 is intended only as a preliminary guideline and as a possible format for future, more enlightened assessments.
Given these caveats, Table 4 suggests that most phylogenetically important polygyrids are reasonably well protected against extinction due to habitat loss. How well they and other polygyrid species will withstand environmental degradation due to acid rain (Graveland et al., 1994), local extinctions of forest-canopy tree species (Getz \& Uetz, 1994), and global warming, remain to be discovered, however. Unfortunately, there is no long-term monitoring study being conducted
on any polygyrid population or community, to my knowledge.

Two remaining conservation priorities do demand rapid attention, however: Isla de Providencia, Colombia, and Pine Mountain, Harlan County, Kentucky, U.S.A. (Table 4). The high conservation importance of these sites almost assuredly applies to many other, lesser-known, leaf-litter/soil invertebrates that polygyrids represent.

## ACKNOWLEDGEMENTS

Supported in part by National Science Foundation grants BSR-8700198 and DEB9201060 and by Academy of Natural Sciences of Philadelphia (ANSP) discretionary funds. I am also grateful to S. Schaefer and G. Bohlke for access to the x-ray facility, Ichthyology Department, ANSP; to E. Gittenberger for steering me to the Christelow and Falkner papers; and especially to T. Pearce, B. Roth, and an anonymous reviewer for very useful comments on a previous draft of the manuscript. I would like to take this opportunity to thank fellow polygyrid workers who have generously helped me with this and other projects during the past 15 years: T. Asami, K. Auffenburg, N. Babrakzai, A. Bogan, J. Burch, R. Caldwell, H. L. Fairbanks, H. Feinberg, H. B. Foster, R. Fullington, G. Goodfriend, F. W. Grimm, L. Hubricht, E. Keferl, G. Long, C. Mather, R. Maze, G. McCracken, W. Miller, J. Murray, R. Neck, T. Pearce, J. Petranka, W. Pratt, R. Reeder, B. Roth, R. Selander, the late A. Solem, A. Stiven, R. Taylor, F. Thompson, J. Vagvolgyi, A. Van Devender, W. Van Devender, and G. Webb.

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Revised MS. accepted 10 January 1995


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[^0]:    NN, Neohelix (Neohelix) albolabris, 75843; NS, Neohelix (Solemorbis) solemi, 182281; OB, outgroup Bradybaenidae: Bradybaena similaris, 174469; OC, outgroup Camaenidae Pleurodonte lynchnuchus, 32588; OH outgroup Helminthoglyptidae: Helminthoglypta tudiculata, 112911; OS, outgroup Sagdidae: Sagda cookiana, 139388; OT, outgroup Thysanophoridae: Thysanophora impura, 177310; OX, outgroup Xanthonychidae: Cepolis cepa, 33301; PaP, Patera (Patera) appressa, 335137; PaR, Patera (Ragsdaleorbis) pennsylvanica, 251512; PaV, Patera (Vesperpatera) binneyana, 176765; Po, Polygyra septemvolva, 69117; PrE, Praticolella (Eduardus) martensiana, 98578; PrF, Praticolella (Farragutia) mobiliana, 105999; PrP, Praticolella (Praticolella) ampla, 131749; PrX, Praticolella (Filapex) jejuna, 77035; SC, Stenotrema (Cohutta) cohuttensis, 170118; SS, Stenotrema (Stenotrema) stenotrema, 169148; SSm, S. (S.) maxillatum, 170141; SSp, S. (S.) spinosum, 11383; ST, Stenotrema (Toxotrema) hirsutum, 11396; Tb, Trilobopsis loricata, 11149; TdB, Triodopsis (Brooksorbis) platysayoides, 183201; TdH, Triodopsis (Haroldorbis) cragini, 186723; TdM, Triodopsis (Macmillanorbis) rugosa, 174909; TdP, Triodopsis (Pilsbryorbis) tennesseensis, 139143; TdS, Triodopsis (Shelfordorbis) vulgata, 68807; TdT, Triodopsis (Triodopsis) tridentata, 211921; TdV, Triodopsis (Vagvolgyorbis) juxtidens, 64720; V, Vespericola columbiana, 158355; W, Webbhelix multilineata, 190168; XW, Xolotrema (Wilcoxorbis) fosteri, 157255; XX, Xolotrema (Xolotrema) denotata, 128444.

