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Zoogeography of North American hydrobiid cavesnails

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Summary

North American hydrobiid cavesnails are moderately diverse taxonomically, including 36 species representing 15 genera and four subfamilies. This exclusively freshwater fauna is deployed in eastern United States and small areas of south-central Texas and northeast Mexico. Most of the snails are stygobionts (obligate aquatic subterranean forms without eye and body pigment), while five species of *Fontigens* are stygophiles (occurring in both epigean and hypogean habitats). Three of the above subfamilies are old freshwater groups (probably predating break-up of Laurasia) with no close relationships to brackish water, coastal taxa. Both *Amnicola* (Amnicolinae) and *Fontigens* (Emmericiinae) include epigean or stygophile species as well as stygobionts, and are closely similar to European snails, while affinities of an undescribed stygobiont amnicolid genus from Alabama are uncertain. Lithoglyphine stygobionts comprise two groups of old relicts presumably derived from epigean, lotic ancestors: one from Texas (*Phreatodrobia*), and the other from widely disjunct locales in Mexico (*Pterides*), Alabama (n. gen.), and Virginia (*Holsingeria*). Littoridinine stygobionts (comprising two groups from Texas/northern Mexico and one from Upper Mississippi drainage) have close relatives in coastal/brackish waters and some may be relicts that invaded freshwater following regression of late Cretaceous marine embayments.

Résumé

La diversité taxonomique des gastropodes aquatiques souterrains d'Amérique du Nord est modérée: 36 espèces appartenant à 15 genres et 4 sous-familles. Cette faune exclusivement d'eau douce cst représentée à l'est des Etats Unis et dans de petits territoires du centre-sud du Texas et du Mexique du nord-est. La plupart de ces gastropodes sont des stygobiontes (formes aquatiques strictement souterraines dépourvues d'yeux et de pigment du corps), tandis que 5 espèces de *Fontigens* sont stygophiles, présentes dans des habitats aussi bien épigés que souterrains. Trois des sous-familles sont des groupes dulcicoles anciens (probablement plus anciens que la séparation de la Laurasie) et ne présentent pas d'étroites affinités avec les taxa côtiers d'eau saumâtre. Les genres *Amnicola* (Amnicolinae) et *Fontigens* (Emmericiinae) comprennent des espèces épigées, stygophiles, ainsi que stygobiontes, présentant une forte similarité avec des gastropodes d'Europe, tandis quc lcs affinités d'un genre d'amnicolides encore non décrit, d'Alabama, restent incertaines. Les stygobiontes de la sous-famille des Lithoglyphinae sont représentés par deux groupes de relictes anciens descendant peut-être d'ancêtres épigés lotiques; un groupe est représenté par le genre *Phreatodrobia* du Texas, le second habite des zones largemcnt disjointes: Mexique (*Pterides*), Alabama (n. gen.), Virginie (*Holsingeria*). Les stygobiontes de la sous-famille des Littoridininae (comprenant deux groupes au Texas et au nord du Mexique, et un autre dans le bassin supérieur du Mississippi) ont de proches parents dans des eaux côtières (saumâtres); certaines de ces espèces pourraient être des relictes ayant envahi les eaux douces à la suite d'une regression marine au niveau de baics du Crétacé Supérieur.

Introduction

Prosobranch snails of the family Hydrobiidae are the only molluscan group extensively deployed in underground aquatic habitats. Apart from the huge subterranean hydrobiid (hereafter referred to as cavesnails) assemblage of Europe, which totals over 250 species in 60 genera (Willman & Pieper, 1978; Bole & Velkovrh, 1986), there are smaller but significant faunas in North America, Japan, and New Zealand; as well as cavesnail records from many other areas where this cosmopolitan family occurs. Bole & Velkovrh (1986) estimated that 97% of all

Table 1. Subterranean hydrobiid snails of North America (including northern Mexico). Totals include undescribed forms.

Taxon	Total species	Stygobiont species	Distribution
Amnicolinae			
Amnicola	12	2	Eastern, northern United States
N. gen. 1	1	1	Enconfina Basin (northwest Florida)
Emmericiinae			
Fontigens	9–10	4*	Eastern, central United States
Lithoglyphinae			
Holsingeria	1	1	Powell, Shenandoah Basins (Virginia)
Phreatodrobia	8	8	South-central Texas
Pterides	3	3	Rio Panuco Basin (northeast Mexico)
N. gen. 2	1	1	Coosa Basin (northeast Alabama)
Littoridininae			
Antrobia	1	1	White Basin (southwest Missouri)
Antroselates	1	1	Ohio Basin (Kentucky, Illinois)
Balconorbis	1	1	Nueces Basin (south-central Texas)
Coahuilix	2	2	Rio Salado Basin (northeast Mexico)
Emmericiella	2	2	Rio Panuco Basin (northeast Mexico)
Paludiscala	1	1	Rio Salado Basin (northeast Mexico)
Phreatoceras	1	1	Southwest Texas, northeast Mexico
Stygopyrgus	1	1	Colorado Basin (south-central Texas)
N. gen. 3	1	1	Devils, Rio Grande Basins (south-central Texas)

*Remaining congeners occur in both epigean and subterranean aquatic habitats.

mollusks associated with continental subterranean waters are hydrobiids.

Hydrobiid cavesnails of North America (including northern Mexico) are a modest-sized group (ranking second to that of Europe among continental faunas) comprising 36 species representing 15 genera and four subfamilies (Table 1). Cavesnails occur in many of the major limestone areas of North America, although their absence from karst areas of western United States and poor representation in the Interior Low Plateaus are noteworthy (Fig. 1). All of these snails are exclusively freshwater: they may be collected from subsurface habitats that include outflows of springs of various sizes, cave streams, and phreatic waters delivered by wells. Local diversity usually is low, with a maximum of two sympatric species found at most localities (note, however, that five *Phreatodrobia* spp. have been collected from orifices of the large San Marcos Springs, Hays County, Texas). Of the 36 species, thirty-one (86%) are stygobionts, or obligate subterranean species, characterized by loss of body and eye pigment. Another five species (all members of the genus *Fontigens*) may be termed stygophiles, as they occur in both epigean and hypogean habitats.

While the first North American cavesnail was described in 1838 (*Paludina nickliniana* Lea), most of the fauna (including virtually all of the stygobionts) was only recently discovered by or through the efforts of Leslie Hubricht and Joseph Morrison, who commenced their long field careers during the 1930s. Modern taxonomic study of the fauna was initiated during the past decade, and descriptions of shell and anatomy of most of the known taxa now are published or in press. The senior author participated in much of this taxonomic work (see Hershler, 1985, 1989; Hershler & Hubricht, 1988; Hershler & Longley, 1986a, 1986b, 1987; Hershler & Thompson, in press; Hershler *et al.*, in preparation; Thompson & Hershler, in preparation) and has studied virtually all members of this fauna.

The purpose of this paper is to describe zoogeographic patterns of the North American cavesnails. Basic data including distributions and phylogenetic relationships of the snails (at the generic level) are summarized and briefly analyzed in relation to

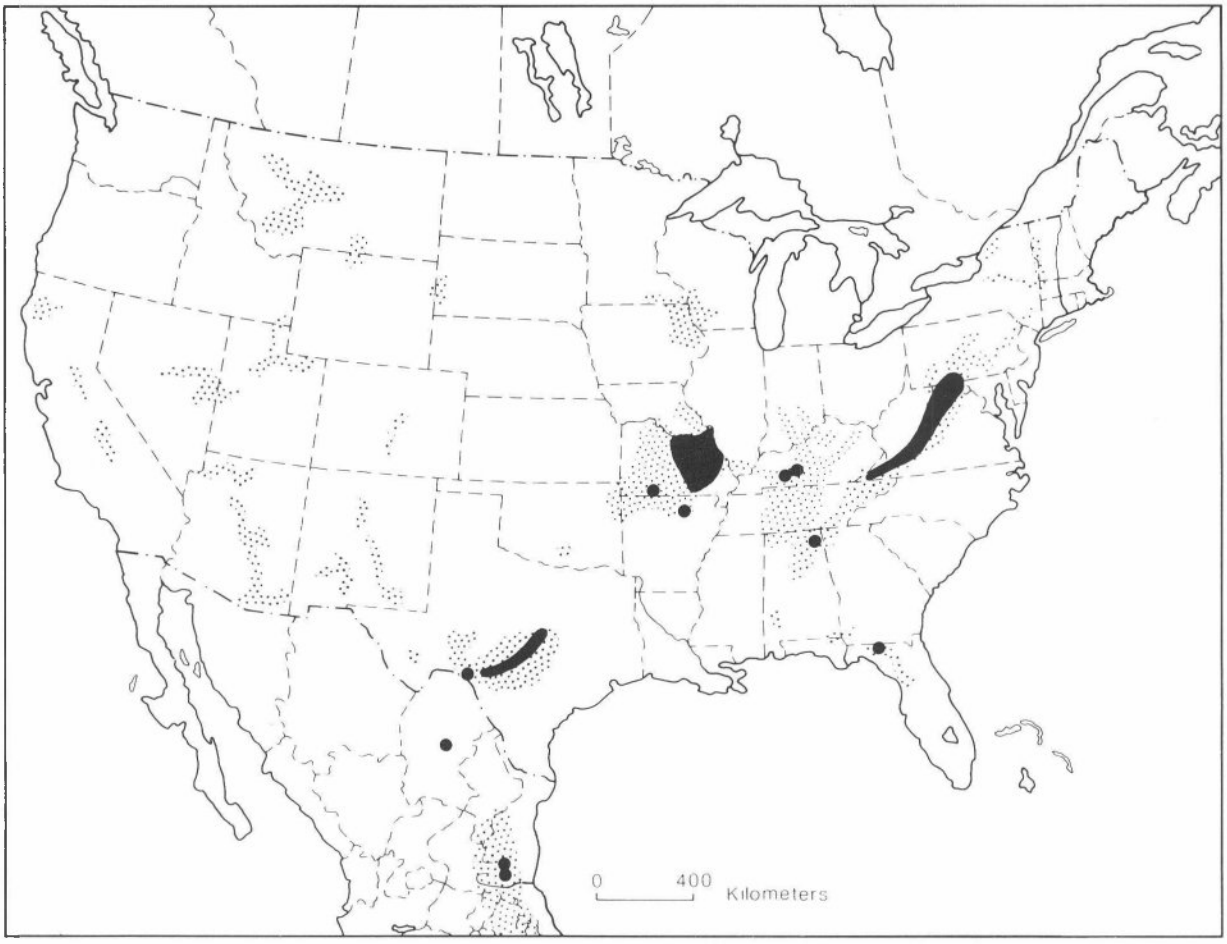

Fig. 1. Map of the conterminous United States and northern Mexico showing distribution of major limestone cave areas (stipple) and occurrences of stygobiont hydrobiid cavesnails (filled circles and black areas) (modified from Tamayo 1964; Barr & Holsinger 1985).

hypothesized vicariant and/or dispersal events of presumed importance to the evolutionary history of these snails. This paper updates an earlier review by Morrison (1949), whose conclusions in part are supported by additional evidence provided herein.

Our conclusions are preliminary, as both the distribution and phylogenetic relationships of North American cavesnails require much additional study. Sampling by no means is routine: while collection of live examples of suspected cavesnails usually can be accomplished given sufficient time, effort and ingenuity, detailed documentation of subterranean range of these organisms presents enormous difficulties that rarely have been overcome in anything other than relatively small regions. Further, robust assessments of phylogenetic relationships using morphological criteria are particularly difficult to obtain for cavesnails because of anatomical simplification and convergence associated with their characteristic reduced size (compared to epigean counterparts, an anecdotal trend lacking statistical confirmation). Features apparently associated with snail miniaturization (which itself may be an ecological correlate of a stygobiont habit) include complex coiling of the intestine, loss or reduction of ctenidium, simplification of gonadal morphology, and loss of sperm sacs. Given this situation, together with the currently inadequate supra-generic classification of hydrobiids (in which various family-level groups probably represent grades rather than clades), the cladistic analyses presented below must be considered "working

hypotheses'' to be modified pending acquisition of additional morphological and (hopefully) genetic data.

Methods

Distributional data for North American hydrobiids were obtained from recent literature (notably Taylor, 1966a; Andrews, 1977; Burch & Tottenham, 1980; Davis *et al.*, 1982; Heard, 1982; Thompson, 1984; various papers of the senior author cited above) and unpublished data of the senior author. *Probythinella* is considered a senior synonym of *Vioscalba*, following Heard (1979), and *Emmericiella* is elevated to full generic status, as advocated by Bole & Velkovrh (1986).

Separate phylogenetic analyses were performed for Lithoglyphinae, Amnicolinae and Emmericiinae (comprising hydrobiids having males with tubular penial glands), and Littoridininae. Subterranean and relevant epigean genera were considered, and non-North American taxa were included where possible. Morphological data are from the literature or from the senior author's unpublished observations. *Hydrobia* was used as an outgroup to root all trees because it appears to be the most primitive extant hydrobiid group (partly based on aspects of development of its female reproductive system; see Ponder 1988 and references cited therein) and because relationships among hydrobiid subfamilies are not sufficiently clear at this time to justify selection of other taxa. Data used to generate cladograms are in Tables 2–5. Multistate characters were treated as unordered. For small data sets, cladograms were prepared by hand. For the Littoridininae (22 taxa; 20 characters), trees were generated using HENNIG86 on an IBM PS/2 microcomputer. The non-exhaustive ''M*bb'' tree-searching command was used because more exhaustive algorithms were too time-consumptive and because an approximate solution was considered acceptable given the preliminary nature of the data set.

Zoogeographic patterns

Lithoglyphinae. The North American fauna includes four genera (one undescribed) of stygobionts sharing a simple penis and capsule gland with ventral channel (Figs. 2, 3), a groundplan common to snails of various faunas throughout the world. The difficulty of assigning such snails to existing subfamilies has been discussed previously (Hershler, 1989: 99–100), but placement of the North American stygobionts in the Lithoglyphinae rather than the Hydrobiinae appears warranted, as indicated in Fig. 4. The cladogram suggests that these stygobionts were derived from the epigean lithoglyphines, a group of genera highly adapted for life in lotic waters (Thompson, 1984), whose collective distribution in North America encompasses much of the United States east of the Mississippi and portions of the western states (Fig. 3). Epigean lithoglyphines also occur in Europe, whose *Lithoglyphus* was considered synonymous with western American *Fluminicola* by Taylor (1966b: 131; but see Thompson 1984), and South America.* Given the morphological similarity among North American epigean lithoglyphines, it presently cannot be determined whether the stygobiontic forms were derived from western or eastern fauna (although highly derived *Lepyrium*, from Coosa-Cahaba River basins, certainly is the least likely candidate progenitor). The stygobionts comprise two groups. *Phreatodrobia*, from caves and deep phreatic waters in south-central Texas, is a distinct group characterized in part by wrinkled protoconch sculpture, and is not closely similar to other lithoglyphines. The other three genera, local endemics from widely separated areas of eastern United States and northeastern Mexico, are united by possession of spirally arranged tubercles on the protoconch and appear to comprise a clade. Relationships among these three taxa (which comprise a trichotomy in the cladogram) are unclear.

Amnicolinae. Amnicolids are represented by an undescribed genus from a single cave in northern

* South American *Potamolithus* is sufficiently differentiated morphologically (see Davis & Pons da Silva 1984) from northern genera to merit a re-examination of its taxonomic affinities.

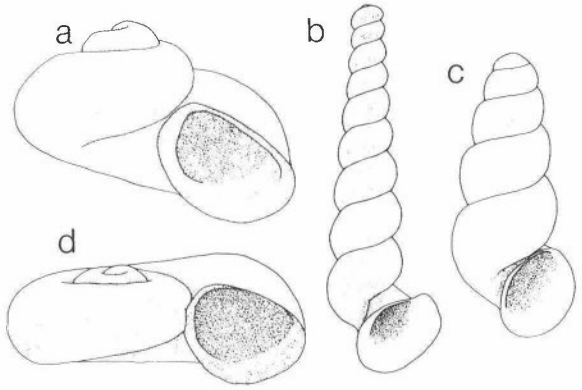

Fig. 2. Representative stygobiont Lithoglyphinae (not drawn to same scale) of North America: **a**, *Phreatodrobia nugax*; **b**, *Pterides* cf. *pterostoma*; **c**, *Holsingeria unthanksensis*; **d**, n. gen., n. sp. (Alabama).

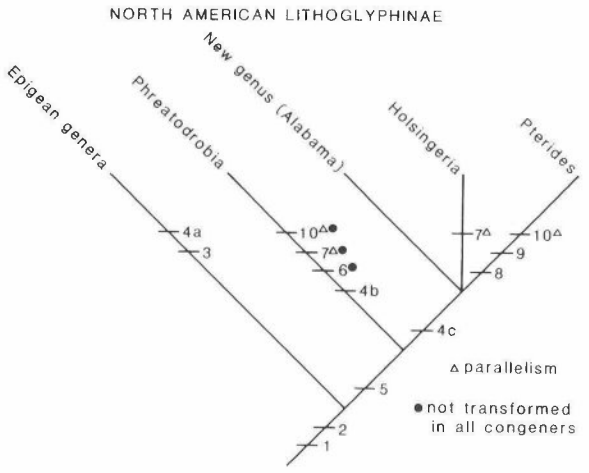

Fig. 4. Cladogram showing relationships among Lithoglyphinae genera of North America.

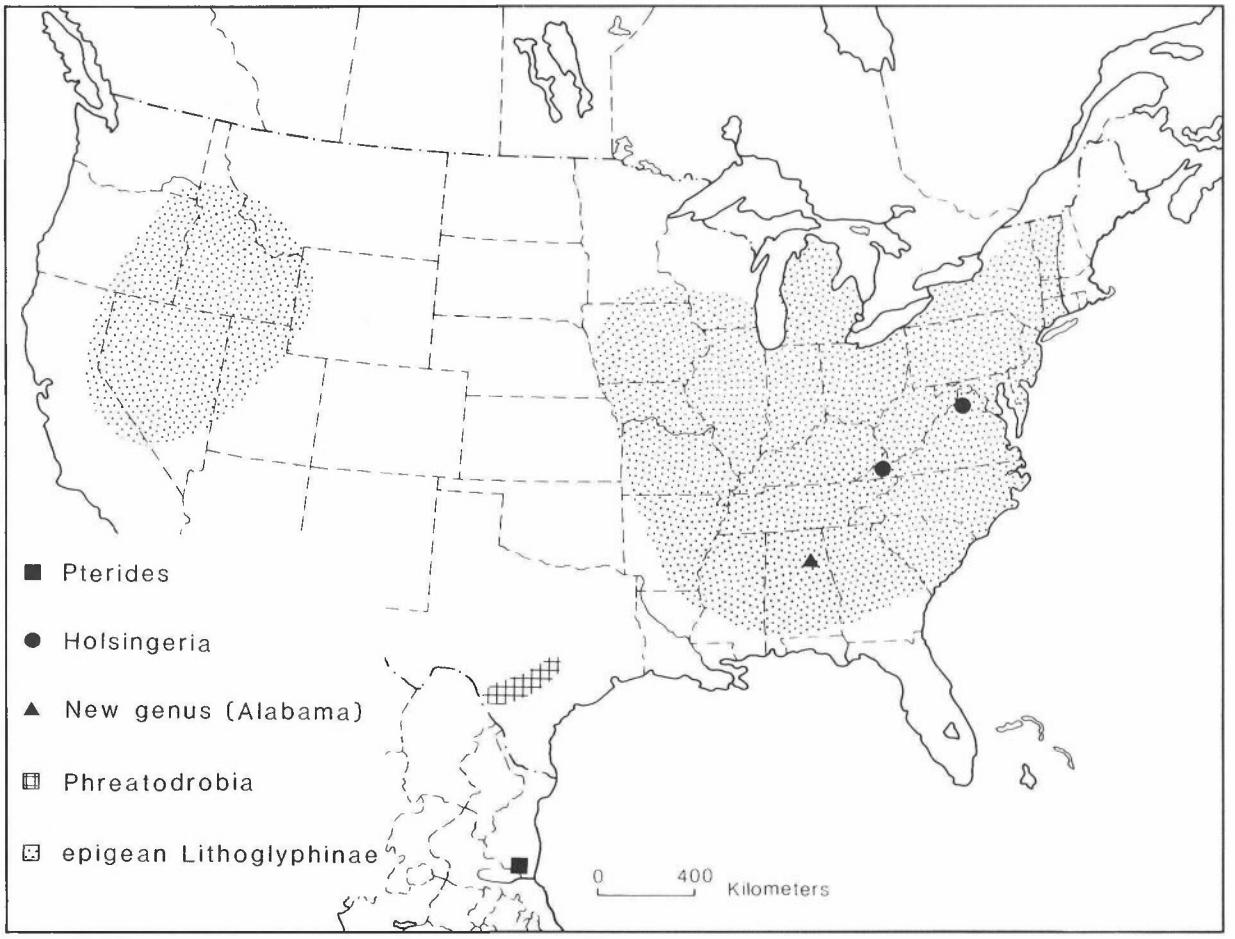

Fig. 3. Distribution of Lithoglyphinae genera of North America. Epigean genera are *Clappia* (Alabama), *Fluminicola* (northwest United States), *Lepyrium* (Alabama), and *Gillia* (eastern United States).

Table 2. Characters used to analyze phylogenetic relationships among North American lithoglyphinae genera (see cladogram in Fig. 4).

Character	Plesiomorphic state	Apomorphic state(s)
1. Penial lobe	Present	Absent
2. Renal oviduct	Complex coils, pigmented	Simple, unpigmented
3. Shell appearance	Simply ovate-conic, aperture small	Squat, aperture enlarged
4. Protoconch	Smooth	With spiral lines (a); wrinkled (b); spirally arranged tubercles (c)
5. Gonad appearance	Lobate	Sac-like
6. Basal cusps of central radular teeth	Present	Absent
7. Ventral operculum	Simple	With corneous peg
8. Seminal receptacle	Present	Absent
9. Bursa copulatrix	Much small than pallial oviduct	Sub-equal to pallial oviduct
10. Ctenidium	Present	Absent

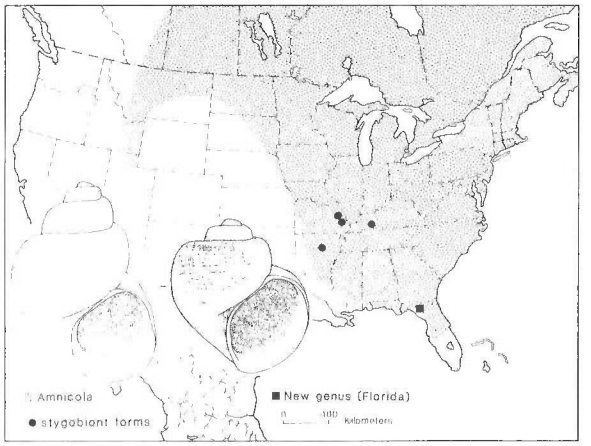

Fig. 5. Distribution of Amnicolinae genera of North America. *Amnicola* includes stygobionts from northeast Arkansas (*A. cora*) and eastern Missouri (*A. stygia*) as well as a population of uncertain status from a cave in southwest Kentucky.

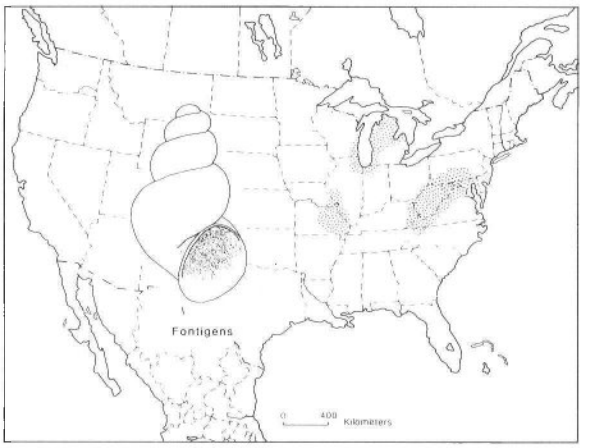

Fig. 7. Distribution of *Fontigens* (Emmericiinae). Cave populations (of stygobiont and stygophile species) occur only in the Ozark and Appalachian regions.

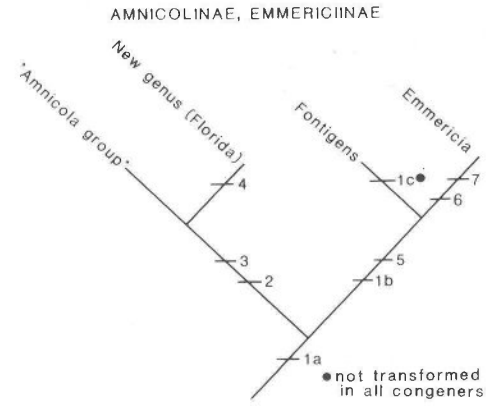

Fig. 6. Cladogram showing relationships among Amnicolinae and Emmericiinae genera.

Florida; and *Amnicola*, which includes epigean species in (usually lentic) waters of eastern and northern North America, as well as two stygobiont species from Mississippi drainage and a recently discovered form (of uncertain status) from a cave in Ohio-Tennessee drainage of southwestern Kentucky (Fig. 5). The only other amnicolids are three European genera, *Bythinella, Marstoniopsis*, and

Table 3. Characters used to analyze phylogenetic relationships among emmericiine and amnicoline genera (see cladogram in Fig. 6).

Character	Plesiomorphic state	Apomorphic state(s)
1. Penis	Without large glands	With single tubular gland (a); two tubular glands (b); third, slightly different gland (sometimes replacing one of above)(c)
2. Egg capsule	Simple	With dorsal keel
3. Spermathecal duct	Absent	Present
4. Teleoconch	Smooth	With raised spirally arranged ridges
5. Seminal receptacle	Present	Absent
6. Cusps of central and lateral radular teeth	Present	Absent
7. Bursa copulatrix	Partly posterior to albumen gland	Entirely overlapped by albumen gland

Parabythinella, the former two of which are widespread and partly deployed in subterranean habitats. *Amnicola* scarcely is differentiated from *Marstoniopsis*, with which it has been synonimized by at least one author (Morrison 1947: 86–87). The undescribed genus from Florida, distinguished by unusual shell features, is a stygobiont derivative of this basal group (Fig. 6) and possibly a sister genus to poorly known European *Parabythinella* (rather than to local *Amnicola*), with which it shares a loss of the bursa copulatrix (see Radoman 1983: 181).

Emmericiinae. *Fontigens* occurs in three largely disjunct areas of eastern and central United States: Great Lakes region, Appalachian Mountains and environs, and Mississippi drainage of eastern Missouri and western Illinois (Fig. 7). Five of the species are stygophiles, including *F. nickliniana*, which is notable for its broad distribution in the former two areas. In addition there are four stygobionts, which are restricted to either the Ozarks or Appalachian Mountains (pairs of species from these disjunct areas are closely similar). *Fontigens* is well differentiated from the only other emmericiine, *Emmericia* (from Adriatic coast of Italy and Yugoslavia), in aspects of shell, radular and female reproductive morphology; further, it may be the more primitive of the two genera based on the derived aspect of central and lateral tooth structure of *Emmericia*.

Littoridininae. The littoridinids include nine genera (one undescribed from south-central Texas) of North American cavesnails (Fig. 8). They were included in a phylogenetic analysis (Fig. 9) together with all other genera known from North America and northern Mexico (insufficient data were available for extra-limital fauna). For purposes of discussion, the fauna is divided into three informal groups characterized, in part, by penial morphology: a) *Heleobops* group, in which penes are lobate and bear apocrine glands (also found in Europe and South America); b) *Littoridinops* group, in which males have lobate penes, usually bearing glandular papillae (North and Central America); and c) *Onobops* group (uncertain distribution outside North America), in which penes are simple, lacking both lobes and glands. These groupings were present in all four trees generated, although their placement varied somewhat, and in some topologies the branching order of genera within the groups was reversed. This division of genera agrees closely with the tribal arrangement of Thompson (1968: 19), although he placed *Hydrobia* in the group of taxa having glandular penial papillae.

We suspect that at least the first two groups are clades, although only the *Heleobops* group appears monophyletic in the cladogram. Polyphyly of the *Littoridinops* group is unlikely because complex glandular penial papillae probably have not have arisen more than once in the family. The two genera (*Spurwinkia, Durangonella*) having penial lobes,

but lacking papillae may represent either a precursor stage (to the papillate condition) or one derived by loss of glands. The *Onobops* group is the most likely candidate for polyphyly, as conceivably it may include snails having simple penes as a primitive condition and those in which the condition was derived secondarily by loss of lobes and glands.

Stygobionts of the *Heleobops* group occur in south-central Texas and northeastern Mexico. Among these, a close relationship exists between *Coahuilix* and *Paludiscala*, local (and syntopic) endemics in the Cuatro Cienegas Basin of northern Coahuila, which comprise a clade defined by having a uniquely positioned sperm storage site. Epigean members of the group occur in tidal marshes and bays along the Gulf of Mexico and

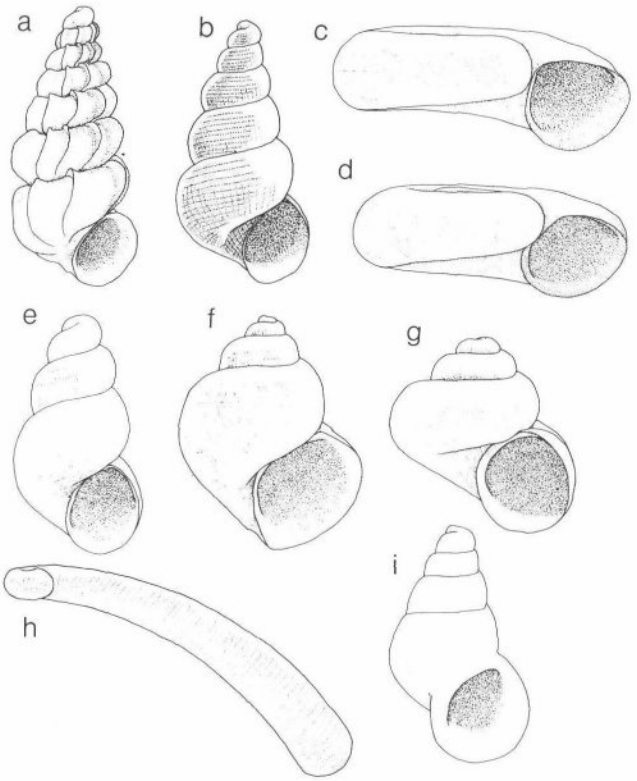

Fig. 8. Representative stygobiont Littoridininae of North America: **a**, *Paludiscala carambae*; **b**, n. gen., n. sp. (Del Rio, Texas); **c**, *Balconorbis uvaldensis*; **d**, *Coahuilix hubbsi*; **e**, *Stygopyrgus bartonensis*; **f**, *Antroselates spiralis*; **g**, *Antrobia culveri*; **h**, *Phreatoceras taylori*; **i**, *Emmericiella novimundi*.

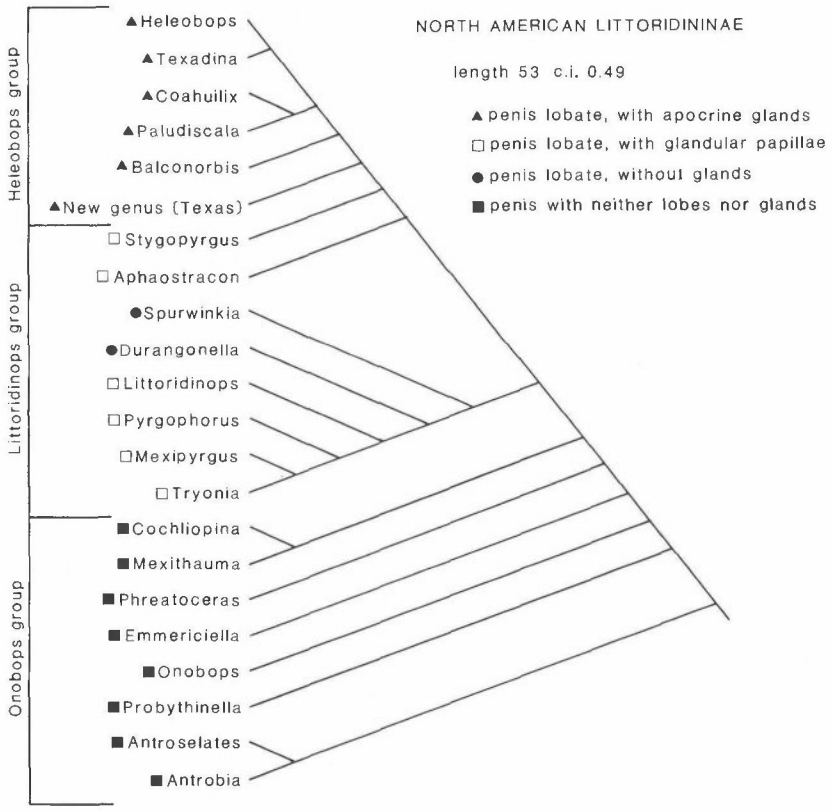

Fig. 9. Cladogram showing relationships among North American Littoridininae.

Table 4. Characters used to analyze phylogenetic relationships among North American Littoridininae genera.

1. Protoconch:
   1) smooth (0)
   2) spiral striae or grooves (1)
   3) wrinkled (2)
2. Teleoconch:
   1) coiled (0)
   2) horn-like (1)
3. Operculum:
   1) paucispiral (0)
   2) concentric (1)
4. Ventral operculum:
   1) smooth (0)
   2) with peg (1)
5. Transverse ciliary tracts of left cephalic tentacle:
   1) absent (0)
   2) present (1)
6. Pallial tentacle or papilla:
   1) present (0)
   2) absent (1)
7. Mantle edge:
   1) simple (0)
   2) frilled (1)
8. Penial lobes:
   1) present (0)
   2) absent (1)
9. Subterminal constriction of penis:
   1) absent (0)
   2) present (1)
10. Distal penis:
    1) smooth (0)
    2) striated (1)
11. Penial gland:
    1) absent (0)
    2) papilla (1)
    3) apocrine (2)
12. Ovary:
    1) overlapping stomach (0)
    2) filling significant portion of digestive gland posterior to stomach (1)
    3) filling a very small portion of digestive gland posterior to stomach (2)
13. Oviduct coil:
    1) pigmented (0)
    2) unpigmented (1)
14. Spermathecal duct:
    1) absent (0)
    2) short (1)
    3) long (2)
15. Posterior albumen gland:
    1) simple (0)
    2) with posterior fold (1)
16. Albumen gland:
    1) sub-equal to caplule gland in size (0)
    2) highly reduced in size (1)
17. Number of sperm pouches:
    1) two (0)
    2) absent or one (1)
18. Seminal receptacle:
    1) on left lateral side of pallial oviduct (0)
    2) on right lateral side (1)
19. Duct to albumen gland:
    1) issuing from oviduct (0)
    2) separate from oviduct (1)
20. Seminal receptacle and oviduct:
    1) connected by duct of seminal receptacle (0)
    2) connected by sperm duct (1)
21. Capsule gland or common genital aperture:
    1) simple (0)
    2) with muscularized sphincter (1)
    2) with muscularized bend (2)

portions of the Atlantic Coast (Fig. 10). Although the cladogram illustrated indicates that North American epigean taxa were derived from stygobionts, other equally parsimonious solutions showed the reverse relationship which we favor.

Stygopyrgus, from the Austin area of south-central Texas, is the sole stygobiont member of the *Littoridinops* group, whose epigean representatives range along Gulf of Mexico and Atlantic coasts as well as in interior western United States (*Tryonia*) and Mexico (*Durangonella, Mexipyrgus*) (Fig. 11). Based on the cladogram *Stygopyrgus* appears closest to *Aphaostracon* (a freshwater Florida endemic), and these are distinct from remaining genera which comprise a clade defined by possession of a sperm duct connecting the seminal receptacle and oviduct.

Of the stygobiont members of the *Onobops* group, *Antrobia* and *Antroselates*, both from Mississippi Basin in east-central United States, are very close in numerous morphological features and probably are sister taxa, although no unique synapomorphy defines them as such. Their closest relative is *Probythinella*, which ranges widely in central

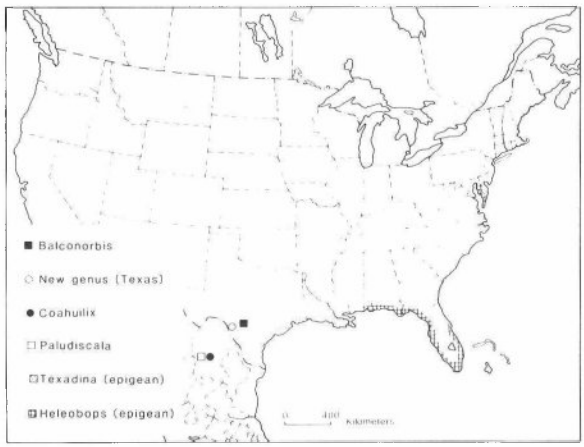

Fig. 10. Distribution of North American Littoridininae genera of the *Heleobops* group.

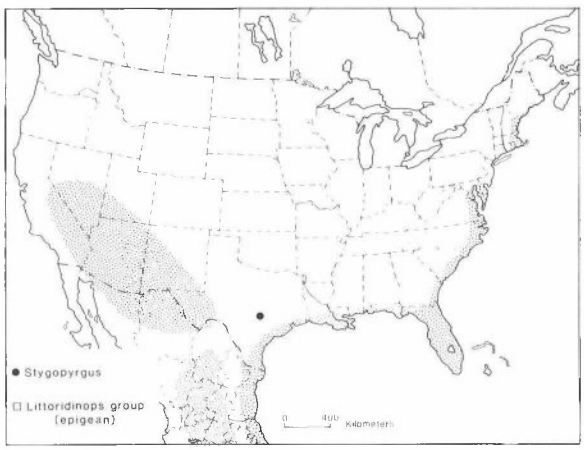

Fig. 11. Distribution of North American Littoridininae genera of the *Littoridinops* group. Epigean genera are *Aphaostracon* (Florida), *Durangonella* (northern Mexico), *Littoridinops* (East and Gulf Coasts, United States; Bahamas [not shown]), *Mexipyrgus* (northeast Mexico), *Pyrgophorus* (circum-Caribbean; Mississippi), *Spurwinkia* (Northeast Coast, United States), and *Tryonia* (Southwest United States, Northern Mexico).

United States from brackish, coastal waters of Louisiana to the Great Lakes region (Fig. 12). The remaining two stygobionts, *Emmericiella* from northeastern Mexico and *Phreatoceras* from south-central Texas and northern Mexico, are close in the cladogram, but probably are not sister groups. *Phreatoceras*, from south-central Texas and northern Mexico, is particularly well differentiated, having various autopomorphies relating to shell and operculum. *Emmericiella* and *Phreatoceras* ap-

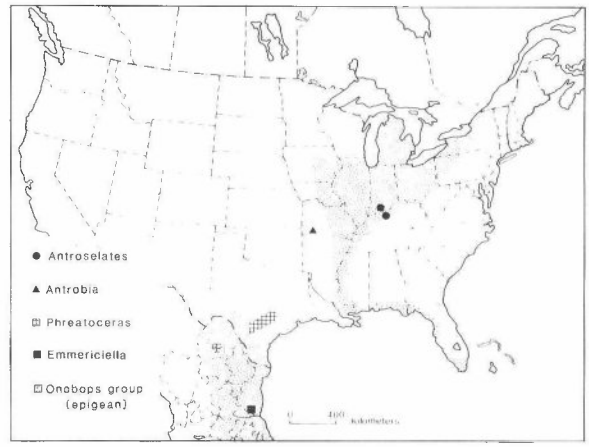

Fig. 12. Distribution of North American Littoridininae genera of the *Onobops* group. Epigean genera are *Cochliopina* (Texas, Mexico), *Mexithauma* (northeast Mexico), *Onobops* (East and Gulf Coasts, United States), and *Probythinella* (East-central United States, northern Gulf Coast).

parently are offshoots of epigean taxa: *Onobops*, a brackish-water genus from Atlantic and Gulf Coasts and Caribbean, is the most likely progenitor.

Discussion

The North American cavesnails exhibit two basic zoogeographic patterns. One set of taxa belongs to old freshwater groups (Amnicolinae, Emmericiinae, Lithoglyphinae) that apparently were established before Laurasia separated into North America and Eurasia during the Late Mesozoic. This is suggested by the close taxonomic relationship between their genera of North America and Europe, and the exclusively freshwater habitat of these snails. All three groups generally occur in cold waters (groundwaters of caves and springs, lotic streams and rivers, lakes), although some western American *Fluminicola* are found in thermal spring brooks. Stygobiont lithoglyphines located near the coastal plain in Alabama, Texas, and northeast Mexico apparently were derived from inland progenitors. While the North American amnicoline and emmericiine cavesnails are closely similar to epigean genera (of Europe), the lithoglyphine stygobionts are not, and appear to be old (presuma-

Table 5. Data matrix used to generate cladogram shown in Fig. 9.

Genus	Character (and states)																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Outgroup (*Hydrobia*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antrobia	1	0	0	0	0	1	0	1	0	0	0	0	1	2	0	0	0	0	1	0	0
Antroselates	1	0	0	0	0	1	0	1	0	1	0	0	1	2	0	0	0	0	1	0	0
Aphaostracon	0	0	0	0	1	1	0	0	0	0	1	1	1	2	1	0	0	0	0	0	1
Balconorbis	1	0	0	0	0	1	0	0	0	0	2	0	1	2	1	0	1	–	0	–	0
Coahuilix	0	0	0	0	0	1	0	0	0	0	2	1	1	2	0	0	1	1	–	–	0
Cochliopina	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	1	0	0	0	0	2
Durangonella	0	0	0	0	0	1	0	0	0	0	0	2	1	2	1	1	0	0	0	1	1
Emmericiella	0	0	0	0	1	1	0	1	0	0	0	2	1	2	0	0	1	–	0	–	0
Heleobops	0	0	0	0	1	1	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0
Littoridinops	0	0	0	0	1	1	0	0	0	0	1	1	1	2	1	1	0	0	0	1	1
Mexipyrgus	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	1	1
Mexithauma	0	0	0	0	1	1	1	1	1	0	0	2	1	2	1	1	0	0	0	0	2
Onobops	0	0	0	0	1	1	0	1	0	0	0	0	1	1	0	0	1	–	1	–	0
Paludiscala	0	0	0	0	0	1	0	0	0	0	2	1	1	2	0	0	0	1	0	–	0
Phreatoceras	0	1	1	1	0	1	0	1	0	0	0	1	1	2	1	0	1	–	0	–	0
Probythinella	0	0	0	1	1	0	1	0	0	0	0	1	2	0	0	0	0	0	1	0	0
Pyrgophorus	0	0	0	0	1	1	0	0	0	0	1	1	1	2	1	1	0	0	0	1	1
Spurwinkia	0	0	0	0	1	1	0	0	0	0	0	1	1	2	1	0	0	0	0	1	1
Stygopyrgus	0	0	0	0	0	1	0	0	0	0	1	1	1	2	0	0	1	0	0	0	1
Texadina	0	0	0	0	1	1	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0
Tryonia	0	0	0	0	0	1	0	0	0	0	1	2	1	1	1	1	0	1	0	1	1
New genus (Texas)	0	0	0	0	0	1	0	0	0	0	2	1	1	2	1	0	1	0	0	0	1

Missing or non-applicable data are indicated by a dash.

bly pre-Pliocene) relicts. The close-knit group comprising *Holsingeria, Pterides*, and a new genus from Alabama presumably are remnants of a group once-continuously distributed from Virginia to Mexico. Relict status is particularly evident for *Pterides* (from northern Mexico) and *Phreatodrobia* (Texas) as these snails are totally disjunct from epigean (as well as subterranean) relatives.*

Contrasting with the above is the Littoridininae which, while also an old group (Holarctic and Nearctic), has a closer marine affinity than the above. Coastal members of this group often dwell in brackish bays or marshes, and some have planktonic veliger larvae. Inland forms occupy a broad range of habitats including those mentioned for the above subfamilies as well as brackish and/or thermal spring-fed waters. Stygobiont genera of northeast Mexico and south-central Texas occur in areas inundated by late Cretaceous oceanic embayments, and appear to be stranded relicts that colonized freshwater habitat as marine waters regressed during the early Cenozoic. A particularly strong case for the above can be made for stygobionts of the *Heleobops* group, as all North American epigean members occur in brackish water coastal habitats. A similar origin has been proposed for diverse stygobiont Crustacea from south-central Texas and northern Mexico (Holsinger & Longley 1980; Holsinger 1986).

* Suggestions that stygobionts from Texas and Mexico are closely related to cavesnails from the Mediterranean region (Pilsbry 1909; Taylor 1966a, 1988: table vi) are based on similarities of shell; that involving *Phreatodrobia* and *Horatia* has been refuted (Hershler & Longley 1986a) while others cannot be addressed at this time for lack of anatomical data. The relationship between similar-shelled stygobiont snails of these two regions remains one of the more intriguing problems of hydrobiid systematics.

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