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UTTERBACKIA PENINSULARIS, A NEWLY RECOGNIZED FRESHWATER MUSSEL (BIVALVIA: UNIONIDAE: ANODONTINAE) FROM PENINSULAR FLORIDA, U.S.A.

Arthur E. Bogan[1,2] and Walter R. Hoeh[3]

ABSTRACT – An eastern Gulf Slope freshwater mussel species, *Utterbackia peggyae* (Johnson 1965), was found to contain a cryptic species, ***Utterbackia peninsularis, nova species,*** rendering a total of three currently recognized species in this anodontine genus. Diagnosis of the new species was effected by comparisons of allozymes and stomach anatomy. The *U. penisularis-U. peggyae* species pair spans the hypothesized Suwannee Straits area of northern Peninsular Florida, therefore providing further evidence consistent with the submergence of this area during the Late Cenozoic. Repeated cycles of marine incursions and regressions in the Suwannee Straits area have likely had a profound effect on faunal diversification in the region.

Keywords: biodiversity, cryptic species, allozymes, stomach anatomy, southeastern United States, biogeography, Unionidae, *Utterbackia*.

INTRODUCTION

It has been hypothesized that portions of Peninsular Florida have been isolated from the southeastern United States mainland as a result of multiple marine incursions during the Late Cenozoic. These marine incursions may have played a major role in the diversification of the freshwater and terrestrial biota of the region (*e.g.*, see Dall, 1903; Hubbell, 1932; Carr, 1940; Cooke, 1945; Olson *et al.*, 1954; Clench & Turner, 1956; Neill, 1957; Johnson, 1970, 1972; Burgess & Franz, 1978; Riggs, 1984; Bert, 1986; Bermingham & Avise, 1986; Swift *et al.*, 1986; Gilbert, 1987; Dillon & Popenoe, 1988; Moler & Kezer, 1993). Freshwater mollusk distributional patterns have been used to both support and discount the hypothesis that an isolated Peninsular Florida was a significant factor in the genesis of the current freshwater molluscan fauna of the area (*e.g.*, see Dall, 1903; Clench & Turner, 1956; Thompson, 1968; Johnson, 1972, 1973).

Utterbackia peggyae (Johnson 1965) (Bivalvia: Unionidae: Anodontinae) is a freshwater mussel species that occurs in many of the Eastern Gulf Slope drainages flowing through the Florida Panhan-

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dle and northern Peninsular Florida region (*e.g.*, see Johnson, 1965; Heard, 1979; Butler, 1989). The type locality, located in the Florida Panhandle region (*sequens* Butler, 1989), is the southeastern shore of Lake Talquin (an impoundment of the Ochlockonee River), Leon County, Florida (Johnson, 1965). However, phylogenetic analyses of allozyme variation (Hoeh, 1991; Hoeh *et al.*, 1995) suggest that the populations of *U. peggyae* from the Peninsular Florida drainages (herein inclusive of the drainages from the Suwannee River to the Hillsborough River) form a monophyletic group distinct from populations in the panhandle drainages. This inference is corroborated by a preliminary analysis of mitochondrial DNA restriction fragments (estimated sequence divergence of 12% between panhandle and peninsula populations; Hoeh, unpublished data). The estimated average level of allozyme divergence (Nei's D, 1978; based on 25 presumptive genetic loci) between panhandle and peninsular populations was 0.354 (Hoeh *et al.*, 1995). Furthermore, the analyses suggest that the peninsular populations of *U. peggyae* are more closely related to *U. imbecillis* (Say 1829) than to the panhandle populations of *U. peggyae*. A subsequent examination of soft-tissue anatomy supported the distinction of the peninsular drainage populations from those of the panhandle drainages. In summary, the allozymic, anatomical, and geographic cohesion evinced by the populations of *U. peggyae* from the peninsular drainages is evidence consistent with species-level recognition for these populations.

MATERIALS AND METHODS

Type materials of *Utterbackia peninsularis* are deposited in the following institutions: University of Michigan Museum of Zoology (UMMZ), Florida Museum of Natural History (UF), Academy of Natural Sciences, Philadelphia (ANSP), Carnegie Museum of Natural History (CMNH).

The specimens used herein for anatomical comparisons were chosen from among those that had been previously analyzed for allozyme variation (Hoeh, 1991; Hoeh *et al.*, 1995) (see Table 1). Stomachs of two or more specimens from each locality were examined whenever possible. In this way, evaluations of the degree of congruence between the anatomical observations and those of the allozyme analyses were facilitated.

Soon after specimen collection, gill and mantle tissues were excised (from only one side of the animal, if possible, in order to maximize the utility of the specimen for subsequent anatomical comparisons) and cleaned of macroscopic parasites and debris, frozen in liquid nitrogen, and subsequently stored at -70°C. The remainder of each animal (*i.e.*, shell, visceral mass, and remaining gill/mantle) was fixed in 10% sodium phosphate buffered (pH 7.0) formalin, rinsed with multiple washes of tap water, and preserved in 70% ethanol. Gill tissues were homogenized with a glass pestle in conical-bottomed 1.5 ml microcentrifuge tubes. The gill tissues contained sufficient water to eliminate the

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METHODS

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need for homogenization buffer. The resultant homogenate was centrifuged at 13,605 x g for 10 minutes at 4°C.

Horizontal starch gel electrophoresis (12% starch gels; 51 g Connaught starch in 425 ml of gel buffer) was used to detect electromorphs at 25 putative genetic loci using five buffer systems (see Hoeh, 1990, 1991).

Stomach floor observations were enabled by an anterior-dorsal incision that opened, initially, the mouth/esophagus region and, subsequently, the stomach proper. This dorsal entry into the stomach minimized mechanical disruption of the stomach floor. The nomenclature used for areas and landmarks on the stomach floor closely followed Kat (1983). However, we have chosen not to follow Kat's numbering scheme for the sorting areas (Kat, 1983; Graham, 1949). At this time, there is insufficient evidence to rigorously assess the potential homology of these sorting areas among different orders of bivalves. The voucher specimen of *Utterbackia peggyae* used for the stomach anatomy illustration (Fig. 3b) has been deposited at the University of Michigan, Museum of Zoology, Malacology Collections (UMMZ 253585).

TABLE 1. Locality information and abbreviations for electrophoretic specimens used and number of specimens (Hoeh, 1991, p. 41).

1. ACH – Attapulgus Creek, at Florida County Route 159, Gadsden County, Florida. (N = 16) [*Utterbackia peggyae*]
2. CSL – Chumuckla Springs Lake, Santa Rosa County, Florida (N = 15) [*U. peggyae*]
3. ERF – Escambia River, at FL County Route 4, Escambia County, Florida (N = 1) [*U. peninsularis*]
4. GCP – Gator Creek, at Florida County Route 471, Polk County, Florida (N = 14) [*U. peggyae*]
5. HCC – Holmes Creek, at US Route 90, Holmes County, Florida (N = 8) [*U. peggyae*]
6. HRH – Hillsborough River, at Florida County Route 579, Hillsborough County, Florida (N = 13) [*U. peninsularis*]
7. HRP – Hillsborough River, at Florida Route 39, Pasco County, Florida (N = 5) [*U. peninsularis*]
8. LRG – Little River, at Florida Route 12, Gadsden County, Florida (N = 16) [*U. peggyae*]
9. LTC – Ochlockonee River, Lake Talquin, Coe's Landing, Leon County, Florida (N = 15) Topotypes [*U. peggyae*]
10. NRB – New River, at Florida County Route 231, Bradford County, Florida (N = 5) [*U. peninsularis*]
11. ORT – Ochlockonee River, at US Route 84, Thomas County, Georgia (N = 1) [*U. peggyae*]
12. RCA – Rocky Creek, at FL County Route 235, Alachua County, Florida (N = 20) [*U. peninsularis*]
13. SHF – sink hole, at Florida Caverns State Park, Jackson County, Florida (N = 19) [*U. peggyae*]
14. SR – canal off of the Suwannee River, at Dilger's Campground, Dixie County, Florida (N = 20) Type locality [*U. peninsularis*]
15. YRC – Yellow River, at US Route 90, Okaloosa County, Florida (N = 10) [*U. peggyae*]

SPECIES ACCOUNT

Utterbackia peninsularis Bogan & Hoeh, new species

Common name: peninsular floater

(Figs. 1; 3a)

Synonymy: *Anodonta imbecillis* Say 1829
Clench & Turner, 1956:187-189 (*partim*)

Anodonta peggyae Johnson 1965
Johnson, 1965, pp. 1-7 (*partim*)
Johnson, 1970, pp. 272, 362, 364, 366 (*partim*)
Johnson, 1972, pp. 228-230, fig. 3B (*partim*)
Burch, 1973, pp. 17 (*partim*)
Burch, 1975, pp. 15 (*partim*)
Heard, 1979, pp. 28 (*partim*)
Kat, 1983, (*partim*)
Butler, 1989, pp. 244 (*partim*)

Diagnosis: This species is included in *Utterbackia* based on a phylogenetic analysis of allozyme data (Hoeh, 1991; Hoeh *et al.*, 1995). Species in the genus *Utterbackia* can be differentiated from those in *Pyganodon* (a closely related genus in the subfamily Anodontinae) by the position of the umbo in relation to the hinge line; in *Utterbackia* the umbos are not raised above the hinge line as they are in *Pyganodon*. *Anodonta couperiana* Lea 1840 and *Anodonta suborbiculata* Say 1831 can be distinguished from *Utterbackia* based on the raying patterns on the shell and degree of ventral shell margin curvature. The raying pattern in *Utterbackia* typically covers the majority of the shell disc while rays are typically restricted to the posterior half of the disc in *A. couperiana* and *A. suborbiculata*. Within *Utterbackia*, *U. imbecillis* can be distinguished from *U. peggyae* and *U. peninsularis* based on the shape of the ventral margin of the shell: typically, *U. imbecillis* has a relatively straight ventral margin which is parallel with the hinge line while those of *U. peggyae* and *U. peninsularis* are somewhat rounded.

Utterbackia peninsularis can be distinguished from *U. peggyae* by the presence of five diagnostic electromorphs at four genetic loci: Aconitase Hydratase (ACOH1-b), Aspartate Aminotransferase (AAT-b), Fumarate Hydratase (FUMH-d), Glucose-6-phosphate Isomerase (GPI-b, GPI-e). Electromorph designations are those presented in Hoeh (1991) and Hoeh *et al.* (1995). *U. peninsularis* can also be diagnosed from *U. peggyae* based on the shape of the right lateral sorting area of the stomach: *U. peninsularis* has a narrow

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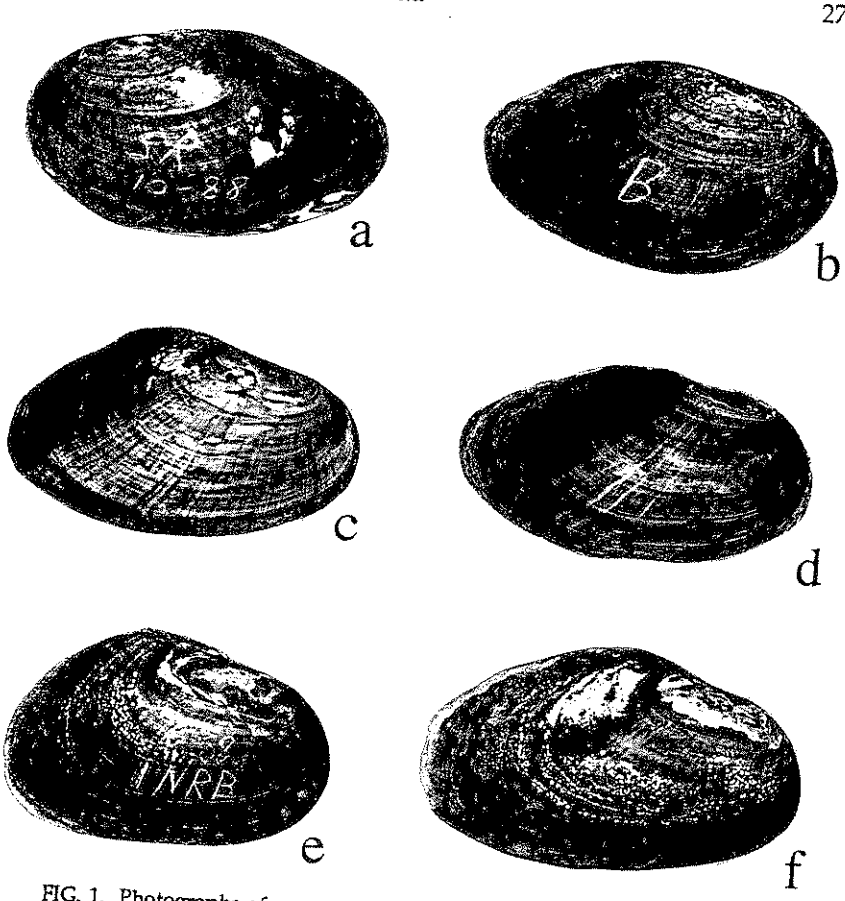

FIG. 1. Photographs of representative shells of *Utterbackia peninsularis* Bogan and Hoeh, new species. (For locality information see Table 1). **a**, Holotype, left valve, SR (B) 10-88, length: 55.8 mm; height, 32.2 mm; width: 22.0 mm. **b**, Holotype, right valve. **c**, HRH (3) 6-88, length: 54.5 mm. **d**, RCA (6) 6-88, length: 75.1 mm. **e**, NRB (1) 6-88, length: 50.8 mm. **f**, GCP (2) 6-88, length: 58.3 mm.

row sorting area which is extended laterally contrasting with the same area in *U. peggyae* which is markedly expanded anteriorly (Fig. 3a,b; Table 2).

Holotype: UMMZ 253583; Collectors: W.R. Hoeh and R.S. Butler; 17 October 1988.

Paratypes: UMMZ 253584 (two specimens); ANSP A18104 (two specimens); CMNH 47384 (two specimens); UF 211099 (two speci-

TABLE 2. Diagnostic anatomical characters for *Utterbackia penisularis* and *U. peggyae.*

Characters	*Utterbackia peggyae*	*Utterbackia peninsularis*
1. General body color:	usually orangish-brown	usually yellowish-cream color
Characters of the stomach		
2. Shape of major typhlosole:	usually more elongate to oval	more or less evenly rounded
3. Shape of conical mound depression:	depression is elongate	depression evenly rounded
4. Mound on left lateral wall of stomach (shape):	mound is obvious and somewhat elongate like the depression	mound is usually less obvious and rounded
5. Shape of right lateral sorting area:	elongate anterio-posteriorly, narrow medio-laterally	narrower anterio-posteriorly, wider medio-laterally

mens); authors collections; all specimens are from the type locality. Collectors: W.R. Hoeh and R.S. Butler; 17 October 1988.

Type Locality: Unnamed canal adjacent to the Suwannee River at Dilger's Campground, near intersection of U.S. Highway 19 and Suwannee River, southeast of Old Town, Dixie County, Florida.

Description

Shell (Fig. 1): The shell is elongate oval in outline and the maximum observed shell length is 76 mm, shell valves are moderately inflated but thin, the anterior end of the shell is evenly rounded, the posterior end of the shell is squared off to a rounded point, ventral margin in some animals is straight like *Utterbackia imbecillis* but varying to a broadly curved ventral margin, the shell dorsal margin is straight like in *U. peggyae* (Fig. 2) and *U. imbecillis*, the posterior ridge is round and not very distinct, the umbos are low, not extending above the hingeline, the beak sculpture is broad undulations varying to double looped, the periostracum is smooth and shining, becoming roughened on the posterior slope. The periostracum is covered with fine green rays over the entire shell, with broad green

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rays on the posterior slope; some individuals have a greenish background with yellowish rays. Periostracum color varies from light yellowish to green or brown. There is no hinge plate and the shell lacks any indication of teeth or vestigial swellings. Nacre color is bluish-white to iridescent.

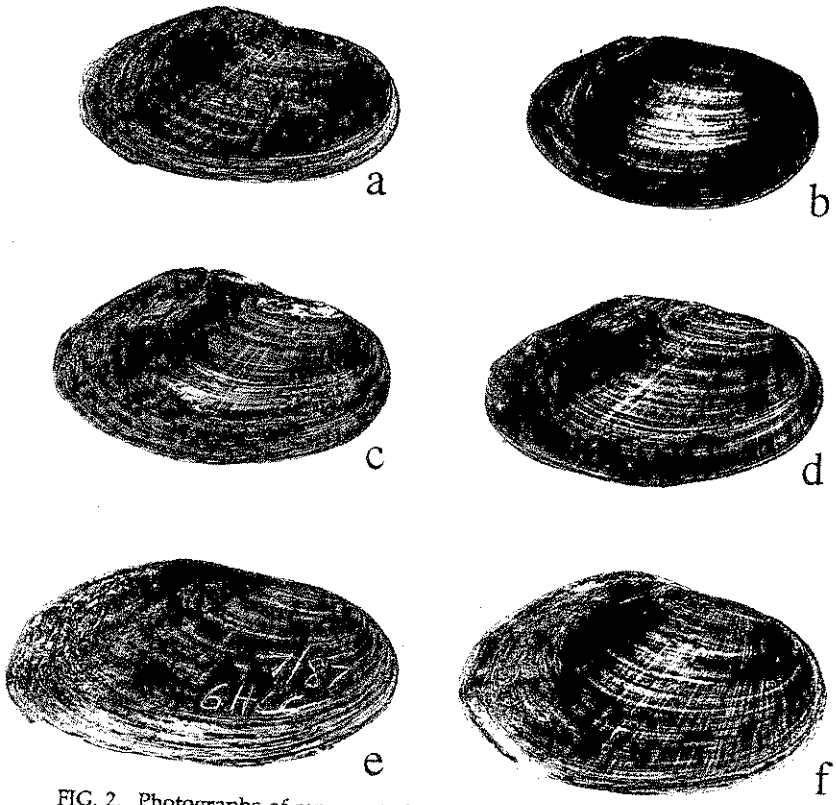

FIG. 2. Photographs of representative shells of *Utterbackia peggyae* (Johnson 1965). (For locality information see Table 1). a, YRC (8) 7-87, length: 70.8 mm. b, LTC (1) 2-88, length: 66.2 mm. c, CSL (1) 7-87, length: 54.6 mm. d, SHF (6) 10-88., length: 75.7 mm. e, HCC (6) 7-87, length: 86.6 mm. f, ORT (13) 10-88, length: 60.9 mm.

Stomach Anatomy: The stomach floor of the holotype is illustrated in Fig. 3a. The most striking feature of the stomach floor of *Utterbackia peninsularis* is the shape of the right lateral sorting area (Fig. 3a). This rather narrow sorting area is extended laterally

and is in marked contrast to the anterior extension of the same area in *U. peggyae* (Fig. 3b; Table 2).

Allozyme Analysis: Allozymically distinct from *Utterbackia peggyae* (see above and Hoeh, 1991, table 4, pp. 44-46).

Habitat: Sand and/or muddy substrates in canals, creeks, and rivers with slight to moderate current.

Distribution: Fig. 4. Northwestern portion of Peninsular Florida from the lower Suwannee and Sante Fe rivers south to the Hillsborough River, including the Withlacoochee River.

Etymology: The name is based on the Peninsular Florida distribution of the new species.

Comments: Kat's (1983, p. 368, fig. 5) illustration of the stomach anatomy of *Anodonta peggyae* is, in fact, an illustration of *Utterbackia peninsularis*.

Discussion: The description of *Utterbackia peninsularis* brings to three the total number of currently recognized species within the genus *Utterbackia* (*i.e., U. imbecillis, U. peggyae* and *U. peninsularis*). However, this small number of recognized species is not likely representative of the actual biodiversity extant within the genus. An allozymically distinct entity, conchologically similar to *U. imbecillis*, exists in multiple drainages of the Southern Atlantic Slope (Hoeh, 1991; Hoeh *et al.*, 1995). Furthermore, specimens of *Utterbackia* that are conchologically similar to *U. peggyae* have been recently noted by us from 1) near Alamo, Veracruz, Mexico (UMMZ 248931) and 2) Drake's Creek at Lookout Road, Vernon Parish, Louisiana (Vidrine, 1993). It is probable, given their geographically disjunct locations, that the latter two populations represent genetically distinct taxa. This hypothesis should be evaluated.

The occurrence of closely related and parapatrically distributed freshwater taxa (often abutting near the hypothesized Suwannee Straits area of northen Peninsular Florida [Swift *et al.*, 1986]) in eastern Gulf of Mexico drainages has been documented in fish (Burgess & Franz, 1978; Bermingham & Avise, 1986; Gilbert, 1987; Gilbert *et al.*, 1992) salamanders (Moler & Kezer, 1993), pleurocerid gastropods (Genus *Elimia;* our reinterpretation of data presented in Chambers, 1980, 1982) and viviparid gastropods (Katoh & Foltz, 1994. The relative importance of historical marine incursions on the evolution and present distribution of freshwater mollusks of this region has been discussed by Dall (1903), Clench & Turner (1956, pp.

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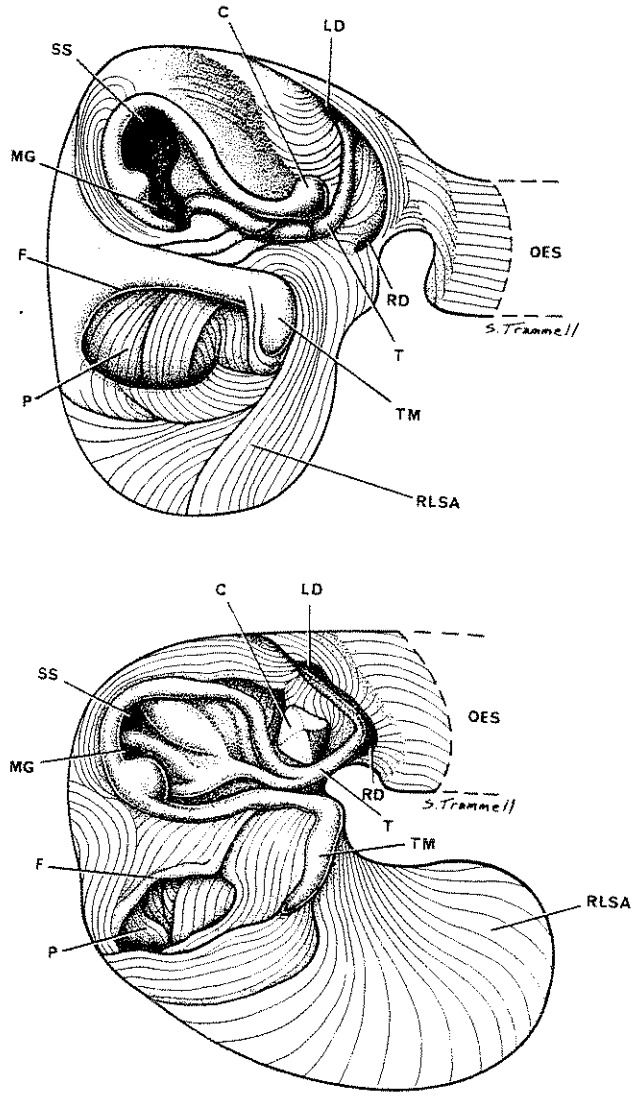


FIG. 3. Stomach Anatomy. a, Stomach anatomy of *Utterbackia peninsularis* Bogan and Hoeh, New Species. SR (B) 10-88, Holotype UMMZ, canal off of Suwannee River, Dixie County, Florida. b, Stomach anatomy of *Utterbackia peggyae* (Johnson 1965). ORT (13) 10-88, Ochlockonee River, Thomas County, Florida. Abbreviations: C-conical mound, F-fold, LD-left digestive diverticula, MG-midgut, OES-oesophagus, P-pouch, RD-right digestive diverticula, RLSA-right lateral sorting area, SS-style sack, T-major typhlosole, TM-minor typhlosole.

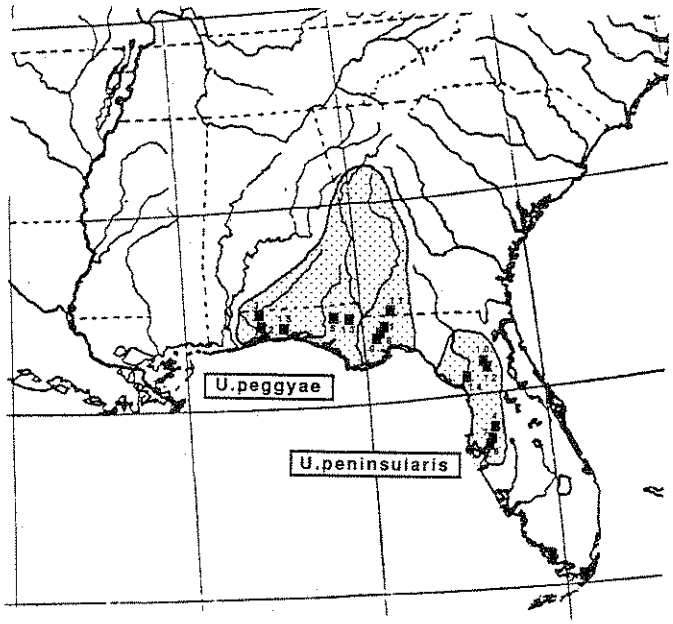
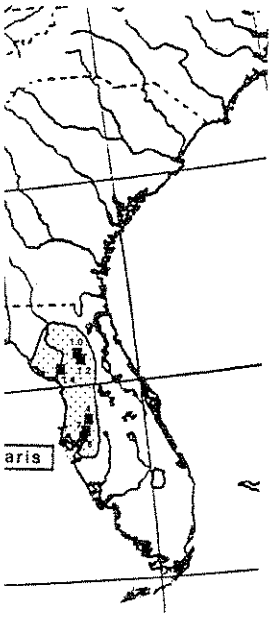


FIG. 4. Distribution of the populations of *Utterbackia peninsularis* Bogan and Hoeh, new species and *Utterbackia peggyae* (Johnson 1965) used in these analyses. The northern extension of the range of *U. peggyae* is based upon recent records from J. Brim-Box and J.D. Williams, National Biological Survey, Gainesville, Florida.

104-108), Thompson (1968, pp. 14-16) and Johnson (1972, pp. 183, 185-186). Impediments to a consensus on this issue can be attributed to 1) the likely existence of multiple cryptic species of freshwater mollusks in the region (as evinced by *Utterbackia* and *Elimia*), 2) the lack of well corroborated phylogenetic hypotheses for the groups in question, and 3) the problems of dating the coastal plain terraces (see Johnson, 1970). Hoeh *et al.* (1995) argued that the Suwannee Straits area of northern Florida was submerged multiple times during the Late Cenozoic and that these vicariant events were likely responsible for early differentiation within the *Utterbackia* clade. The geographic placement of the distributional discontinuity between *U. peggyae* (Florida Panhandle distribution; Escambia River to the Ochlockonee River) and *U. peninsularis* (Peninsular Florida distribution; Suwannee River to Hillsborough River) is consistent with the hypothesis of an insularized peninsula of Florida during the Late Cenozoic.



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Other nominal unionid species with distributions that span the Suwannee Straits area of northern Florida need to be carefully examined for potential anatomical and/or molecular discontinuities that, if present, may be causally related to the hypothesized insularization. The elucidation of the actual freshwater mollusk biodiversity of the region is a necessary prelude to phylogenetic analyses of the pertinent higher taxa. Furthermore, the availability of well corroborated phylogenetic hypotheses for the freshwater biota of the southeastern United States is fundamental to any explication of the sequence of Late Cenozoic marine insularization events in the Peninsular Florida region.

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