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A new species of freshwater mussel (Bivalvia: Unionidae), *Pleurobema athearni*, from the Coosa River Drainage of Alabama, USA

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Abstract

The Mobile Basin historically supported one of the most diverse freshwater mussel (Bivalvia: Unionidae) assemblages in North America. More than 65 species of mussels are known from the Basin, but it is difficult to determine how many species were present historically. The drainage's unique physical habitat was largely destroyed between the late 1800s and mid-1900s by impoundment and channel modifications of most of the larger rivers. Many species that were once common are now restricted to small headwater rivers and mid-sized tributaries. Recent Coosa River tributary surveys revealed a new, undescribed species of *Pleurobema*. This new species, *Pleurobema athearni*, is distinctive in outward appearance, shell morphometry and reproductive morphology, and can be distinguished from other Coosa River drainage unionids. Our analysis indicates that *P. athearni* is morphologically different from other similar taxa. It differs both in shell width/length and width/height ratios and thus provides a simple, quantitative means to differentiate this species from *P. georgianum* (Lea, 1841) *Fusconaia barnesiana* (Lea, 1838), and *F. cerina* (Conrad, 1838), which it superficially resembles and that also occur in the area. Our morphological diagnosis of this species is supported by recent molecular analyses that suggest this species is a *Pleurobema* and one closely related to other endemic Coosa River drainage unionids. The discovery of a new species of large, long-lived macroinvertebrate from a relatively well-sampled drainage in a populated region of the southeast United States underscores the need for more detailed surveys in isolated stretches of tributary streams. It should also serve as a reminder that almost 40 species of aquatic mollusks have been extirpated from the Mobile Basin before anything could be learned about their habitat or life history requirements.

Key words: Big Canoe Creek, freshwater mussel, Mobile Basin, mollusk biodiversity, Unionoida, endemic species

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Introduction

The Mobile River Basin historically supported one of North America's most species-rich mussel assemblages, with more than 70 species, including 30 endemic taxa (Hurd 1974; Lydeard and Mayden 1995; Neves et al. 1997; Lydeard et al. 1999). *Pleurobema* is the most diverse genus with 45 nominal species described between 1831 and 1931 from the Mobile Basin. Many species of this phenotypically variable genus were described from morphologically extreme shells and are currently considered synonyms (Turgeon et al. 1998; Kandl et al. 2001). Unfortunately, most of the Mobile Basins large-river habitat that supported this assemblage was destroyed by channel modifications and impoundments beginning in the late 1800s and continuing through the mid 1900s. It is difficult to ascertain how many species were lost because no comprehensive baseline mussel inventories were conducted prior to channel modifications and construction of impoundments.

Freshwater mussels have received many superfluous species descriptions and the literature is rife with synonyms of morphologically variable taxa (e.g., Simpson 1914; Ortmann 1923; Burch 1973). Few morphological characters are evident, making quantitative morphologically based unionid taxonomy difficult (Roe and Hoeh 2003) Understanding of relationships within Unionidae has greatly increased over the last 20 y largely as a result of molecular data. However, use of molecular tools presents obvious temporal and financial obstacles to monitoring or ecological studies. Morphologic diagnoses offer an intuitive means for identification of problematic specimens in the field or post-hoc assessments of characters using measurements of shell morphometric ratios. It bears noting that some morphometric analyses have successfully diagnosed cryptic taxa that were supported by subsequent molecular studies (Clarke 1981; 1985; King et al. 1999).

Recent accounts recognize as many as 20 species of *Pleurobema* in the Mobile Basin (Neves et al. 1997; Turgeon et al. 1998). After thorough examination of the types and evaluation of recent molecular data, the number of valid species appears to be 12, of which five appear to be extinct (Williams et al. unpubl. data). Seven species of Mobile Basin *Pleurobema* are protected under the U.S. Endangered Species Act and the surviving members of the genus are largely confined to isolated, forested watersheds with high water quality (USFWS 1989; 2000; Evans 2001). A recent molecular phylogeny of the unionid subfamily Ambleminae revealed that *Pleurobema* as currently recognized is paraphyletic (Campbell et al. 2005). The analyses presented in Campbell et al. (2005) also suggest strong phylogeographic patterns in *Pleurobema;* many Coosa drainage taxa form a distinct clade, but one distinct from *Pleurobema* species restricted to Coastal Plain drainages of the Mobile Basin [e.g., *P. perovatum* (Conrad, 1834) and *P. taitianum* (Lea, 1834) are restricted to Mobile Basin but not found in Coosa above Wetumpka, Campbell et al. 2005].

Between 1999 and 2002, we conducted surveys in the Coosa and Tallapoosa river drainages to assess the distribution and status of unionid mussels (Gangloff 2003). During our surveys we encountered a *Pleurobema*-like mussel in Big Canoe Creek in east central Alabama that did not fit into currently accepted species descriptions. We initially identified these specimens as *P. georgianum* (Lea, 1841), a small, ovate and compressed mussel that is now restricted to Coosa River headwater tributaries in Alabama and the Upper Conasauga River system in northeast Georgia. Historically, *P. georgianum* was found throughout the Coosa River Drainage in Alabama, Georgia and Tennessee. Most other Mobile Basin *Pleurobema* species are more elongate and/or inflated (e.g., *P. decisum* (Lea, 1831), *P. hanleyianum* (Lea, 1852), and *P. taitianum*; Parmalee and Bogan 1998; USFWS 2000).

Materials and methods

We examined the type material of all species of *Pleurobema* described from the Mobile Basin. We also examined shell and soft tissue morphology of *Pleurobema* and *Fusconaia* specimens from the Mobile Basin and adjacent drainages housed in the Academy of Natural Sciences Philadelphia, (ANSP), Auburn University Natural History Learning Center and Museum Invertebrate Collection (AUM), Florida Museum of Natural History (FLMNH), Museum of Fluviatile Mollusks (MFM; Cleveland, Tennessee), North Carolina State Museum of Natural Sciences (NCSMN), Ohio State University Museum of Zoology (OSUM), University of Michigan Museum of Zoology (UMMZ), and U.S. National Museum (USNM) to ensure that no other names existed for this species.

We measured maximum length, height, and width of *P. athearni* shells from Big and Little Canoe creeks, *P. georgianum* from Hatchet, Little Canoe and Shoal creeks and the Conasauga River, *P. hanleyianum* from Hatchet Creek, Little Canoe Creek and the Conasauga River, *F. barnesiana* (Lea, 1838) from the Paint Rock River (Tennessee River Drainage), and *F. cerina* from the Alabama, Cahaba, and Tallapoosa river drainages (Table 1). Digital calipers were used to measure specimens to the nearest 0.01 mm. These species were chosen for quantitative comparisons because their shell morphology very closely resembles *P. athearni*.

We computed height/length, width/length, and width/height ratios for all specimens and then used an arcsine transformation to normalize ratio data (Sokal and Rohlf 2001). Normality was confirmed using a Kolmogov-Smirnov test. We calculated principal component analysis (PCA) scores to describe differences in shell ratios among specimens. We then used Discriminant Function Analysis (DFA) to determine how frequently PC scores correctly distinguished *P. athearni* from other similar-appearing *Pleurobema* species, *F. barnesiana*, and *F. cerina*. All statistical analyses were conducted using SPSS software (version 11.5.0, SPSS Inc., 2002).

TABLE 1. Specimens used in morphometric analyses. Specimens with no lot numbers were measured alive and returned to the stream.

Lot Number	Locality	Identity	N
USNM 1078388	Big Canoe Creek	*Pleurobema athearni (holotype)*	1
ANSP 412952	Little Canoe Creek	*Pleurobema athearni (paratype)*	1
AUM 290	Big Canoe Creek	*Pleurobema athearni (paratopotype)*	1
AUM 1758	Little Canoe Creek	*Pleurobema athearni (paratype)*	4
AUM 2296	Big Canoe Creek	*Pleurobema athearni (paratype)*	1
	Big Canoe Creek	*Pleurobema athearni*	2
MFM 14828	Little Canoe Creek	*Pleurobema athearni (paratype)*	2
MFM 20689	Big Canoe Creek	*Pleurobema athearni (paratype)*	4
MFM 20706	Big Canoe Creek	*Pleurobema athearni (paratype)*	2
AUM 1578, 1610, 1624, 1642	Conasauga River	*Pleurobema georgianum*	24
AUM 1362, 1531	Hatchet Creek	*Pleurobema georgianum*	60
AUM 102, 108, 221, 450, 850, 4603, 6596, 6738, 8101	Shoal Creek	*Pleurobema georgianum*	31
AUM 1759	Little Canoe Creek	*Pleurobema georgianum*	9
AUM 1364, 1532	Hatchet Creek	*Pleurobema hanleyianum*	19
AUM 1759, 1760	Little Canoe Creek	*Pleurobema hanleyianum*	3
AUM 1580, 1610, 1611,	Conasauga River	*Pleurobema hanleyianum*	6
AUM 22454, 2996, 4004, 6631, 6671	Paint Rock River	*Fusconaia barnesiana*	21
AUM 2344, 2382, 2422	Big Swamp Creek	*Fusconaia cerina*	6
AUM 4487, 8222, 8507	Cahaba River	*Fusconaia cerina*	17
AUM 1552, 1708	Kelly Creek	*Fusconaia cerina*	2
AUM 7246	Pintlala Creek	*Fusconaia cerina*	3
AUM 518, 548	Chewacla Creek	*Fusconaia cerina*	2
AUM 805, 1408	Choctafaula Creek	*Fusconaia cerina*	18

***Pleurobema athearni*, new species**
Canoe Creek Clubshell, Figure 1

Synonymy

Pleurobema perovatum (in part): Hurd (1974), Collection number 758 Little Canoe Creek (Station 95).

TABLE 2. Locality, number and mean shell morphometry ratios for specimens examined.

Taxa (Location)	N	Height/ Length	Width/ Length	Width/ Height
Pleurobema athearni (Canoe Creeks)	18	0.71	0.31	0.44
Pleurobema georgianum (Conasauga)	24	0.70	0.43	0.61
Pleurobema georgianum (Hatchet)	60	0.70	0.41	0.59
Pleurobema georgianum (Shoal)	31	0.69	0.39	0.56
Pleurobema georgianum (Little Canoe)	10	0.68	0.39	0.57
Pleurobema hanleyianum (Coosa tribs.)	28	0.66	0.42	0.63
Fusconaia barnesiana (Paint Rock)	21	0.74	0.37	0.50
Fusconaia cerina (Alabama R. tribs.)	28	0.82	0.51	0.63
Fusconaia cerina (Uphapee sub-basin)	20	0.71	0.38	0.58

Material Examined

Holotype. USNM 1078388, Alabama, St. Clair County, Big Canoe Creek, ~1 km downstream of St. Clair County Road 36 near mouth of Mukleroy Creek (33°50'13"N, 86°16'55.5"W), 23 September 2001, collected by M. M. Gangloff, L. Siefferman, W. Weidenbach, and E. Wiggins.

Paratopotypes. AUM 2296 (1) taken with the holotype.

Paratypes. ANSP 412952 (1), Alabama, Etowah/St. Clair counties, Little Canoe Creek, 2.1 miles E of Steele (33° 55' 54.9" N, 86° 10' 0.8"W), 3 October 1973, collected by J. C. Hurd; AUM 1758 (4), Alabama, Etowah/St. Clair counties, Little Canoe Creek, 2.1 miles E of Steele (33° 55' 54.9" N, 86° 10' 0.8"W), 3 October 1973, collected by J. C. Hurd; MFM 14821 (2), Alabama, Etowah/St. Clair counties, Little Canoe Creek, 3.7 km E of Steele, collected by H. D. Athearn; AUM 290 (1), Alabama, St. Clair County, Big Canoe Creek, ~0.1 km downstream of St. Clair County Road 31 (33° 48' 16.2" N, 86° 25' 10.2"W), collected by M. Gangloff and M. Buntin; MFM 20689 (4), Alabama, St. Clair County, Big Canoe Creek, 6 km ENE of Springville, collected by H. D. Athearn; MFM 20706 (2), Alabama, St. Clair County, Big Canoe Creek near U.S. Hwy 231, 1 km NE of Ashville (33° 50' 24.2" N, 86° 15' 46.9" W collected by H. D. Athearn).

Diagnosis. A species of *Pleurobema* as diagnosed by Walker (1918), Ortmann (1923), and Hurd (1974) by having only the outer gills marsupial and appearing smaller but not obviously marsupia-like. Specimens of *P. athearni* are distinguished from other closely related or similar appearing taxa primarily by shell morphology. *Pleurobema athearni* is typically more compressed and round in outline than *P. georgianum* (Fig. 2). It is less elongate and more compressed than *P. decisum* and *P. hanleyianum*. Larger specimens of *P. athearni* may exhibit slight corrugations approximately parallel to the posterior ridge along the posterior-dorsal shell slope that are not found in *P. georgianum* and *F. cerina*. Additionally, the umbo cavity in *P. athearni* is typically intermediate in depth between that of *P. georgianum* (shallower) and *F. cerina* (deeper). *Pleurobema athearni* conglutinates (Fig. 3B) are elongate and red to dark pink and similar in appearance to those of *F. cerina*. *Pleurobema georgianum* conglutinates are lighter and appear less elongate (Fig. 3A). Further, *P. georgianum* conglutinates appear to consist of a clear central core with glochidia encrusted on the outer surface, whereas those of *P. athearni* appear to be darker at their core with a lighter outer covering suggesting glochidia retained within the conglutinate (Fig. 3).

Description. Shell ovate to sub-ovate in outline, with slight corrugations or sculpturing on posterior-dorsal third of valves (Fig. 1). Posterior ridge rounded, evident on some specimens; valves compressed laterally. Maximum shell length to 93 mm, height to 65 mm, width to 31 mm. Periostracum brown to dark yellow with faint green growth rests present on small individuals (<40 mm). Shell disk moderately thick, maximum thickness anteriorly and thinnest posteriorly near apertures. Nacre white, usually iridescent posteriorly.

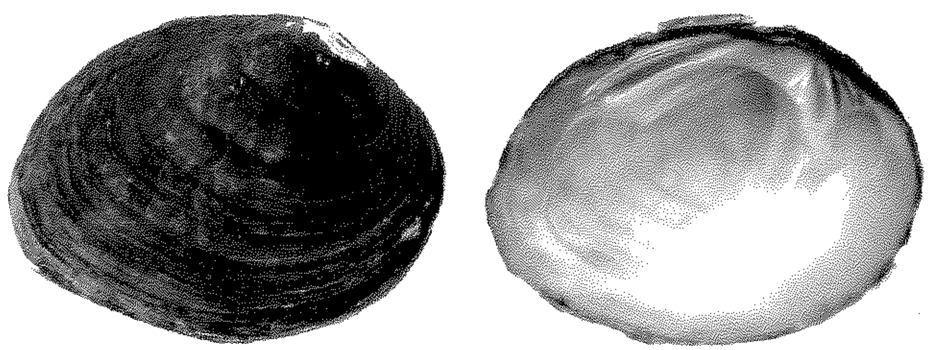

FIGURE 1. Shell morphology, external and internal, of *Pleurobema athearni*. Holotype AUM 999, 8.44 cm. Big Canoe Creek, St. Clair County, Alabama. Photo © Richard T. Bryant.

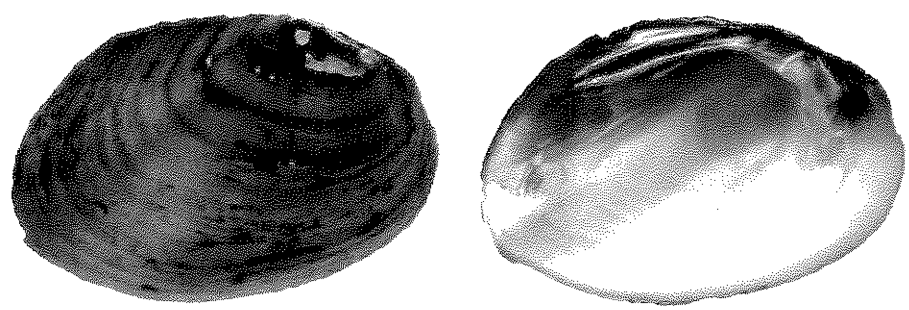

FIGURE 2. Shell morphology, external and internal, of *Pleurobema georgianum*. Specimen length 58 mm. Shoal Creek, St. Clair County, Alabama, October 1914. UF 66700. Photo © Richard T. Bryant.

FIGURE 3. *Pleurobema georgianum* conglutinate recovered from a specimen taken in Shoal Creek, Cleburne County, Alabama, 2 May 2005 (A) and *Pleurobema athearni* conglutinates recovered from specimen taken from Big Canoe Creek near the U.S. Highway 231 bridge crossing, St. Clair County, Alabama, 26 May 2004 (B). Coin diameter approximately 18 mm.

Umbos low and do not protrude above hinge line. No beak sculpture evident on any specimens examined, however, umbos usually eroded. Left valve with two thick, elongate, slightly curved lateral teeth projecting slightly past hinge ligament; two low, triangular, ventrally directed pseudocardinal teeth. Right valve with single, elongate lateral tooth, two pseudocardinal teeth, one large, one small. Interdentum moderately long and wide on both valves. Umbo cavity usually moderately deep, extending dorsally beneath interdentum.

Anterior adductor scar deeply incised into nacre, just anterior to pseudocardinal teeth in both valves. Posterior adductor scar incised, positioned behind and below lateral hinge tooth. Pallial line complete, roughly parallel to shell margin. Pallial distance greatest anteriorly, decreasing posteriorly.

Soft tissues salmon orange in living animals. Aperture margins from brown to black, typically reddish-brown or brown. Papillae either single or bifid, usually larger along margin of incurrent aperture. Large, bifid papillae interspersed with smaller, single bifid papillae along apertures.

Inner gills approximately 1.5 times larger in surface area than outer gills. No mature or developing glochidia observable in individuals collected in September and October, conglutinates present in late May, suggesting species tachytictic (i.e., short-term brooder). Conglutinates elongate, length 10–15 mm, width ~1–2 mm, red or dark pink (Fig. 3B).

Discussion

We found that 2 PC scores with eigenvalues ≥ 1 explained >99% of the variability in shell ratios across measured taxa. PC_1 explained 66.6 % of the variability and both width-to-length ratio and width-to-height ratio loaded most heavily on PC_1. PC_2 explained another 33.3% of the variability and shell height-to-width ratio loaded most heavily on PC_2. PC scores were plotted to assess their ability to separate putative species and then we used DFA to describe how well PC scores are able to separate *P. athearni* from all specimens examined and from other similar-appearing Coosa River Drainage *Pleurobema* species. DFA revealed that PC scores correctly distinguished *P. athearni* from other species examined 90% of the time, and that it was distinguishable from other Coosa River Drainage *Pleurobema* species 94% of the time. *Pleurobema athearni* was the most readily categorized unionid species examined and was more accurately classified by PC scores than other species examined.

The shell morphology of *P. athearni* is thus distinctive from other *Pleurobema* species in the Mobile Basin for at least two reasons: 1) it is more compressed than its congeners, and 2) it has a deeper umbo cavity than many other Coosa or Tennessee drainage *Pleurobema* species, a trait characteristic of many *Fusconaia* species. PC scores of *P. athearni* overlapped more extensively with those of *F. barnesiana* and *F. cerina* than with those of other Coosa Drainage *Pleurobema* species which may be why this species was initially diagnosed as *Fusconaia* by Athearn and other malacologists familiar with the regional unionid fauna. Compared with its congeners, differences in morphometry and overall appearance of *P. athearni* indicate that this mussel should be recognized as a distinct species.

Ortmann (1920) was among the first to apply quantitative measurements of freshwater mussel (*Pleurobema*, *Fusconaia*, and *Obovaria*) shell morphology to examine ecophenotypic variability along longitudinal riverine sections. That study established Ortmanns Rule which stated that mussels in headwater streams tend to have much more laterally compressed (expressed as maximum width to length ratio) shells than conspecifics in larger streams and rivers. Interestingly, *P. athearni* is much more compressed than even headwater *P. georgianum* occurring in Shoal Creek (Cleburne County, Alabama), suggesting that observed morphometric differences were not attributable to physico-chemical differences among streams.

Unfortunately, recent molecular analyses (Campbell et al. 2005) do not provide sufficient evidence to resolve whether *P. athearni* is distinct from *P. georgianum*. The 50% majority-rule consensus tree, depicted in Campbell et al. (2005) appears to support the hypothesis that *P. athearni* (*P. georgianum* 3) is a distinct taxon and one most closely related to *P. georgianum*. However, the strict consensus tree produced by Campbell et al. (2005) indicates a polytomy between *P. athearni* and *P. georgianum*. However, other molecular data suggest that more substantial differences exist between the nuclear, ITS-1 genes of *P. athearni* and *P. georgianum* (D. Campbell, pers. comm.). Recent studies using the ITS-1 marker in unionids suggest that it can provide useful information about divergence rates that may be more conservative than more commonly-used mtDNA markers (King et al. 1999; Kallersjo et al. 2005). Additionally, some strictly mtDNA-based studies have failed to diagnose cryptic unionid species that appear to be supported by ITS-1 data (Buhay et al. 2002; Jones 2004).

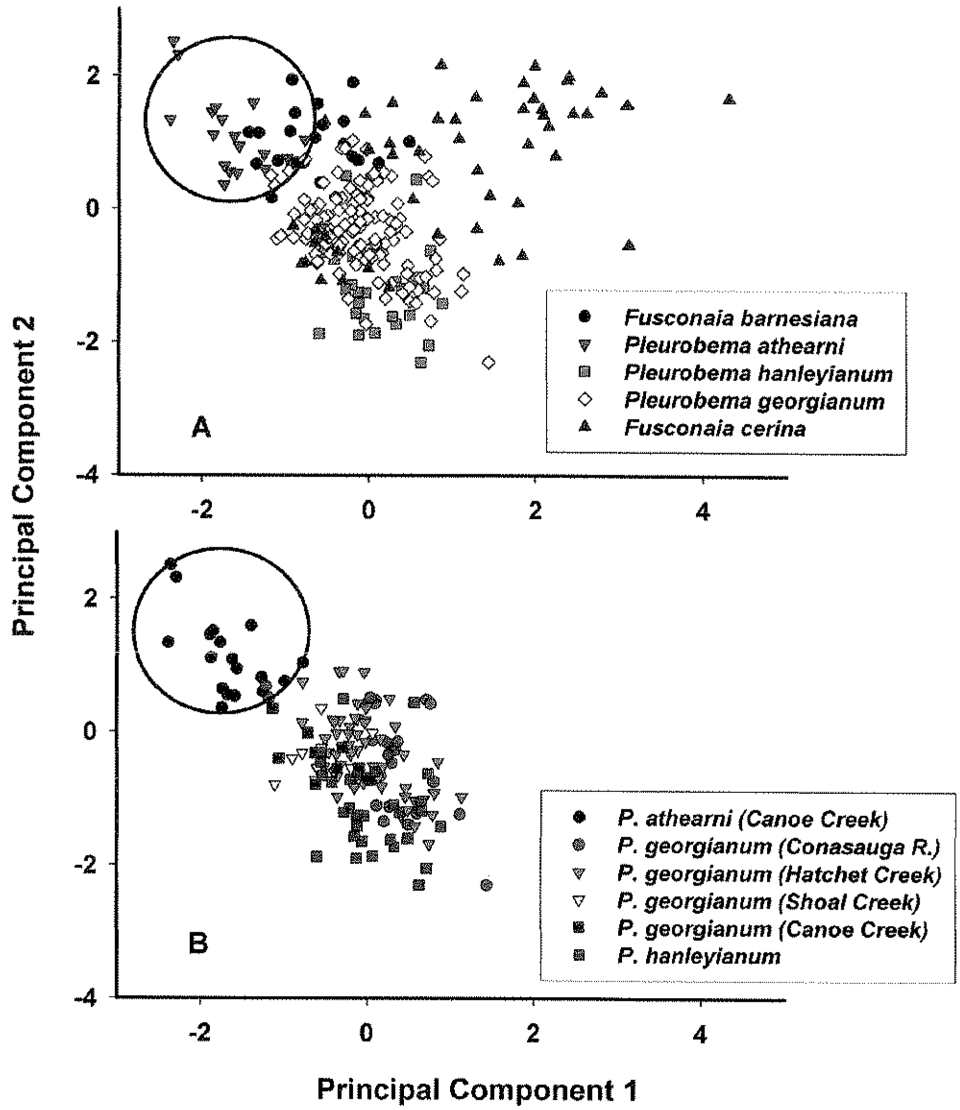

FIGURE 4. Plot of scores for principal components 1 (width-to-length and width to height ratios) and 2 (height-to-length ratio) for all (A) and for only Coosa Drainage *Pleurobema* (B) specimens measured. Circles show boundaries of *P. athearni* PC score plots. Tables 1 and 2 provide detailed information about specimen morphometric ratios and collecting localities.

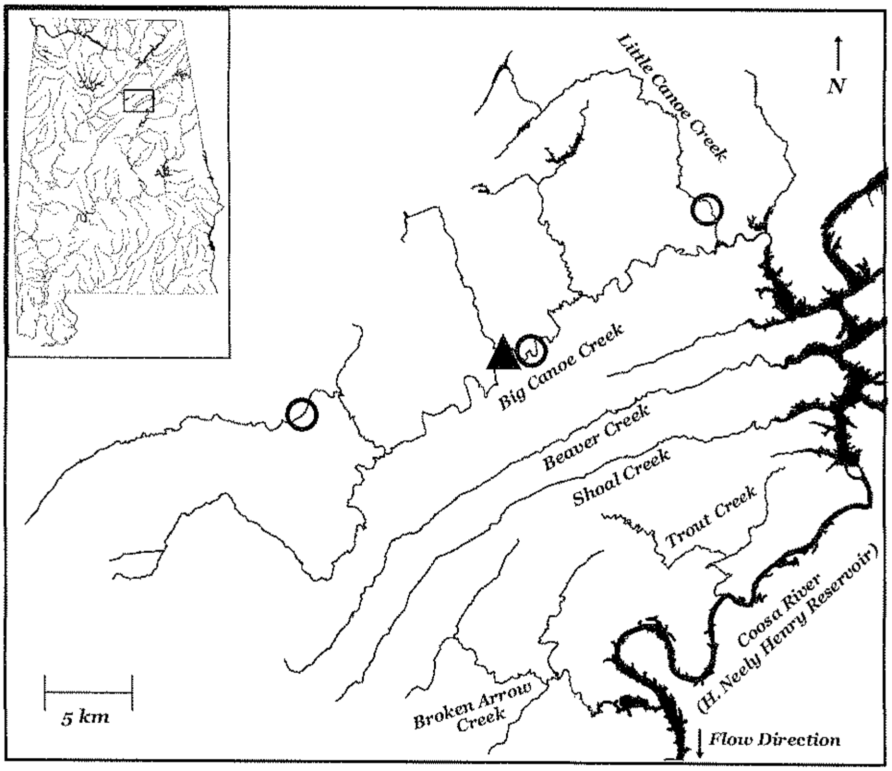

FIGURE 5. Distribution of *Pleurobema athearni* in Big Canoe Creek sub-basin, St. Clair and Etowah counties, Alabama. The triangle (▲) indicates the location where the holotype and paratopotype were collected, open circles (○) represent paratype collection localities.

Relatively small mtDNA differences between *P. athearni* and *P. georgianum* suggest that *P. athearni* may represent a recent evolutionary divergence from *P. georgianum*. Other mtDNA-based studies of Mobile Basin unionids have indicated similarly small genetic differences between species (Mulvey et al. 1997; Roe et al. 2002). However, Berg and Berg (2000) urged caution in synonymyzing species based on sequences from only one or a few individuals as this may not take into account the often considerable range of mitochondrial haplotypes within a species. Given the limited data available (i.e., 2 mtDNA sequences from 1 *P. athearni* and 5 mtDNA sequences from 2 *P. georgianum*) it is difficult to be certain if *P. athearni* represents a distinct phylogenetic entity or is simply an artifact of phylogeographic structure within *P. georgianum*. Clearly more molecular sequence data from Coosa River Drainage *Pleurobema* species are needed to adequately resolve this question.

More importantly the data presented by Campbell et al. (2005) support our hypothesis that *P. athearni* is a valid member of the genus *Pleurobema* and not a *Fusconaia* as suggested by shell morphometric ratios and internal morphology. This finding is significant because a number of recent molecular studies have demonstrated the apparent misplacement of a number of unionid species within the wrong genera (Lydeard et al. 2000; Serb et al. 2003; Campbell et al. 2005). Additionally, the phylogenetic structure within *Pleurobema* suggests that *P. athearni* forms a clade with other Coosa drainage endemic *Pleurobema* species and is therefore not a recent introduction from the nearby Tennessee River Drainage. Given the high rate of extinction within Mobile Basin *Pleurobema* species, we feel it is prudent to recognize *P. athearni* as a distinct species, as species-level recognition will greatly facilitate conservation of *P. athearni* and protection of its habitat (Hurd 1974; Neves et al. 1997; Evans 2001; Gangloff 2003; Mirarchi 2004).

Distribution. *Pleurobema athearni* is known only from the Big Canoe Creek watershed, a western tributary of the Coosa River, northeast Alabama. This stream originates in the Ridge and Valley Physiographic Province near the town of Springville (Shelby County) and flows northeast to its juncture with Little Canoe Creek and H. Neely Henry Reservoir (Fig. 5). For much of its length below Ashville, Big Canoe Creek forms the boundary between St. Clair and Etowah counties. Historically, Big Canoe Creek flowed for another ~15 km, prior to impoundment of this reach of the Coosa River by H. Neely Henry Dam. Despite loss of 15 km of habitat, the mussel assemblage in Big Canoe Creek still supports at least 21 unionid species (Gangloff 2003). Mussels have continued to survive in Big Canoe Creek because land use in the watershed is predominantly agricultural and/or forested land with largely intact riparian forest has remained intact, and it receives good ground water flow.

Conservation Status. *Pleurobema athearni* appears to be restricted to one small (<500 km^2) watershed in northeast Alabama, and, because of its rarity, may qualify for endangered status under the Endangered Species Act. Only 19 specimens are known but only one-third of these were recent collections. We found four specimens alive between 2000–2004. One gravid individual was found on 26 May 2004, indicating that *P. athearni* remains reproductively viable.

Pleurobema is one of the most imperiled genera of North American freshwater mussels (Lydeard et al. 1999; Kandl et al. 2001). Unfortunately, the number of valid species of *Pleurobema* may never be known because many species are apparently extinct (Neves et al. 1997; Parmalee and Bogan 1998; Evans 2001; Gangloff 2003). The discovery of a new, undescribed species of freshwater mussel in northeast Alabama is unusual for several reasons. First, this area was extensively sampled by H. H. Smith during the early 1900s. Second, this area is heavily developed with the study area falling between two large cities, Birmingham and Gadsden, Alabama. Big Canoe Creek is one of a very few Coosa tributaries that has not lost the majority of its mussel species, as recent surveys found 21 of 32 (66%) historical species there (Gangloff 2003).

This new, previously unknown species demonstrates the need for careful, intensive surveys if rare species of aquatic organisms are to be detected and conserved. Most mussel surveys have been confined to stream reaches adjacent to bridge crossings and have not made use of small boats to survey more stable intact habitats and their associated mussel populations. Discovery of *P. athearni* demonstrates that even highly surveyed aquatic systems in the Mobile Basin may support new taxa that have been overlooked.

The Coosa River ecosystem has been reduced to a number of highly fragmented tributary refugia. Only five tributary sub-basins were found to have mollusk species-richness levels that approach historic reports (Gangloff 2003). These watersheds, along with tributaries of the Black Warrior, Tombigbee, Cahaba and Conasauga drainages, represent most of what remains of a unique and species-rich aquatic ecosystem (Williams et al. 1992; Lydeard and Mayden 1995; McGregor et al. 2000). Protection of these few remaining fragments is critical to preserving populations of mussels and other aquatic species in the Mobile Basin (USFWS 1989; 2000).

Etymology. We take great pleasure in naming this species for Mr. Herbert D. Athearn, of Cleveland, Tennessee, who first collected this species. Herb Athearn has sampled mussels in the southeastern U.S. from the mid 1950s until 2002. He maintains his personal collection in his home.

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