Crayfishes of Mississippi: A Provisional Checklist with Distributions and Discussion of Unresolved Taxonomic Issues

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Abstract - Recent state crayfish records, species descriptions, taxonomic revisions, and extensive additional collecting have rendered the previous Mississippi crayfish list, published in 2002, outdated. We compiled 9597 crayfish collection records from multiple sources, georeferencing localities that lacked coordinates. The new state list includes 65 species and possibly 5 subspecies. Thirteen species and 1 subspecies are endemic to the state, and another 21 species occur in only 1 other state. We created species lists by county and 4- and 8-digit hydrologic unit codes (HUCs) and discussed taxa whose presence in the state was recorded but questionable or not recorded but plausible. We coarsely estimated that 175–200 records were necessary to consider a county well-sampled; 18% of counties met that threshold. Finally, we summarized numerous, unresolved taxonomic issues.

Introduction

Mississippi has among the highest freshwater crayfish diversity in the world but lacks a taxonomically current, comprehensive list of the state's crayfishes. Lyle (1937, 1938) produced the first statewide list of crayfishes, which documented 22 species, including several species new to science. Joseph F. Fitzpatrick Jr. produced 2 lists of Mississippi crayfishes. The first (Fitzpatrick 1996), a technical report, included 60 described species plus 2 subspecies but focused on the distributions of 24 species of conservation concern. The second (Fitzpatrick 2002) was comprehensive of all 78 "population groups", including undescribed species and "lumped species complexes", that Fitzpatrick thought were in the state. The second, and presumably the first, included numerous unverifiable records. While those publications have proven useful, extensive taxonomic changes since 2002, recently described species, new state records of existing species, and uncertainty surrounding Fitzpatrick's personal records have rendered the lists outdated.

Numerous crayfish systematic changes have been made recently at family to species taxonomic levels (e.g., Crandall and De Grave 2017, Glon et al. 2018). The family Cambaridae still includes all crayfishes native to North America east of the Continental Divide. Crandall and De Grave (2017) recommended the following changes relevant to Mississippi: removing recognition of the subfamily Cambarinae so the family Cambaridae has no recognized subfamilies; removing recognition of all subgenera within Cambaridae except for 2 in the genus *Cambarellus*;

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elevating some subgenera to genus level; and moving numerous species to new genera (Table 1). The most significant of these changes for Mississippi taxa included moving all the state's *Orconectes* and *Fallicambarus* species to the newly elevated genera *Faxonius* and *Creaserinus*, respectively. Also, *Cambarellus* retained 2 subgenera, but the subgenus *Dirigicambarus* was eliminated and its species moved to the subgenus *Pandicambarus,* which now includes all *Cambarellus* species in Mississippi (Crandall and De Grave 2017). Subsequently, Glon et al. (2018) elevated the subgenus *Lacunicambarus* (formerly in the genus *Cambarus*) to genus level, leaving the state with 3 *Cambarus* species, 2 of which are restricted to the Tennessee River drainage in extreme northeast Mississippi. We followed Crandall and De Grave's recommendations, except for reference to 1 subgenus each in *Procambarus* and *Faxonius* where they improved clarity. The remaining taxonomic changes have been at the species level and included synonymizing several species and describing new ones (Table 1).

Currently in Mississippi, as in several other southeastern states, the ability of biologists, students, and the public to document, manage, and study crayfishes is severely hampered by the lack of a guide to identification and distribution of the state's crayfish fauna. The only neighboring state with a published guidebook to crayfishes is Louisiana (Walls 2009), although a book on Alabama crayfishes is forthcoming (Schuster et al., in press). A major hindrance to publishing a book on Mississippi's crayfish fauna continues to be the large number of taxonomic uncertainties, including groups or species complexes requiring taxonomic revision, and a lack of clarity guiding identification of some presumably valid species. In recent years, several systematic questions have been resolved (e.g., Glon et al. 2018, 2019; Schuster et al. 2015), or at least addressed (Taylor et al. 2014), and work on others is in progress. However, the plethora of taxonomic changes creates its own set of challenges for those identifying crayfishes, making a revised checklist of species a necessity.

Interest in crayfish conservation has increased over the past 10 years in Mississippi, due in part to the Center for Biological Diversity (CBD) petition to list 404 southeastern aquatic species, including 17 crayfish taxa in Mississippi, as threatened or endangered under the US Endangered Species Act (CBD 2010). Therefore, waiting to publish a revised checklist until after the major systematic issues are resolved is no longer an appropriate option. Consequently, we based this checklist on current systematic understanding but acknowledge that it is far from the final word, and we highlighted the major remaining systematic concerns and sampling needs.

Methods

We compiled a spreadsheet of crayfish records from Mississippi derived from multiple databases. The largest data source was the Mississippi Department of Wildlife, Fisheries, and Parks, Museum of Natural Science (MMNS) database (4184 records exported on 12 December 2018). The MMNS acquired the Tulane University Museum of Natural History (TUMNH) crayfish collection in 2011, so the MMNS database included 756 records of Mississippi crayfishes from the TUMNH

Table 1. Taxonomic changes and species additions to Mississippi since 2002.

Current name	Recent previous name(s)	Citation(s) for change
Genus changes		
Creaserinus	*Fallicambarus (Creaserinus)*	Crandall and De Grave 2017
Faxonius	*Orconectes* [multiple subgenera]	Crandall and De Grave 2017
Lacunicambarus	*Cambarus (Lacunicambarus)*	Glon et al. 2018
Subgenus changes		
Cambarellus (Pandicambarus) shufeldtii	*Cambarellus (Dirigicambarus) shufeldtii*	Crandall and De Grave 2017
Cambarus	All subgenera eliminated	Crandall and De Grave 2017
Faxonius	All former *Orconectes* subgenera eliminated	Crandall and De Grave 2017
Procambarus	All subgenera eliminated	Crandall and De Grave 2017
Species synonymized		
Procambarus hagenianus vesticeps	*Procambarus (Girardiella) cometes*	Schuster at al. 2015
Procambarus hagenianus vesticeps	*Procambarus (Girardiella) connus*	Schuster at al. 2015
Procambarus hagenianus vesticeps	*Procambarus (Girardiella) pogum*	Schuster at al. 2015
Faxonius etnieri spp. complex	*Orconectes (Trisellescens) etnieri; O. (T.) chickasawae; O. (T.)* sp.	Taylor et al. 2014
Recently described species		
Lacunicambarus erythrodactylus	*Cambarus (Lacunicambarus) diogenes; C.* aff. *diogenes; L.* aff. *diogenes*	Simon and Morris 2015; Glon et al. 2018
Lacunicambarus dalyae	*Cambarus (Tubericambarus)* sp. A*; C.* aff. *polychromatus; L.* aff. *polychromatus*	Glon et al. 2019
Lacunicambarus freudensteini	*L.* aff. *miltus*	Glon et al. 2020
Lacunicambarus mobilensis	*L.* aff. *miltus*	Glon et al. 2020
Faxonius yanahlindus	*Orconectes (Procericambarus)* sp., ref.*: spinosus; O. spinosus; O. putnami*	Taylor et al. 2016; Adams and Jones 2018
Range extensions into MS		
Cambarus girardianus	*Cambarus (Hiaticambarus) girardianus*	Adams et al. 2010
Cambarus rusticiformis	*Cambarus (Erebicambarus) rusticiformis*	Adams et al. 2010
Faxonius erichsonianus	*Orconectes* (*Crockerinus*) *erichsonianus*	Adams and Jones 2018
Faxonius placidus	*Orconectes (Procericambarus) placidus*	Adams and Jones 2018
Faxonius wrighti	*Orconectes* (*Faxonius*) *wrighti*	Adams et al. 2010
Faxonius yanahlindus	*Orconectes (Procericambarus)* sp., ref.: *spinosus; O. spinosus; O. putnami*	Adams et al. 2010; Adams and Jones 2018

collection. The next largest source included 2 US Forest Service (USFS) databases (3142 records): the Center for Bottomland Hardwoods Research (USFS_CBHR) database, including the first author's collections and material that others sent to her, and the Fish Index of Biotic Integrity (USFS_FIBI) database that resulted from a USFS effort to sample fishes and crayfishes from wadeable streams across National Forests in Mississippi from 1999 to 2003 (Warren et al. 2003). Early records in the USFS_FIBI collection were identified by Dr. Chris Taylor at the Illinois Natural History Survey (INHS) and subsequent records by the first author. Many lots from the 2 USFS collections were transferred to the MMNS collection; however, we attempted to avoid double-counting records. The third data source was the Smithsonian National Museum of Natural History (USNM; 2146 records exported 11 December 2018), and the final source was the INHS collection (125 records exported 1 September 2007). Each record represented 1 species from 1 collection (i.e., 1 locality sampled on 1 day); however, some species-by-collection combinations were represented by more than 1 record. In the USNM and MMNS data, this sometimes occurred when individuals were designated as different types (e.g., allotype, morphotype) or when tracking individual specimens was desired (e.g., for genetic analyses). In the USFS_CBHR data, it occurred when some crayfish of a taxon from 1 collection were retained while others were released.

With some hesitation, we included subspecies in our taxa lists. Neither of us has made much effort to identify specimens to subspecies, in part because identifying to species presents challenge enough. But also, many—if not most—described subspecies were not clearly identifiable based on the subspecific descriptions. The subspecific descriptions were often based entirely on form I males (the reproductive form), leaving us without a reliable method for identifying form II males and females to subspecies. Nonetheless, we opted to retain subspecies in the lists to illustrate additional diversity and to retain information about subspecies that may eventually be elevated to species.

We manually georeferenced many USNM, MMNS, and TUMNH records that lacked a latitude and longitude by employing TopoUSA digital maps (DeLorme, Yarmouth, ME), Google Maps, and when necessary, historic county maps to locate features that had been moved or renamed. If site descriptions were vague or contained ambiguities, we did not assign coordinates.

We then used ArcGIS Pro 2.4 (ESRI, Redlands, CA) to assign each record with coordinates to United States Geological Survey (USGS) hydrologic unit codes (HUCs) from the USGS Watershed Boundary Dataset (USGS 2013). The HUC scheme is hierarchical, with each 2-digits that are appended to codes representing finer spatial subdivisions. In Mississippi, the 2-digit HUCs are roughly equivalent to Jones et al.'s (2005, 2019) "drainage basins" and the 4-digit HUCs to their "drainages"; however, HUCs are not synonymous with watersheds (Omernik et al. 2017). In Mississippi, one important example of this is that the HUC scheme combined independent Gulf Coastal streams in the same 4-digit HUC as the Pascagoula River, rather than grouping them independently (Table 2); the grouping did not appear to have any biological justification. The HUC scheme was chosen because it

offered GIS data useful in compiling crayfish records in a practical and biologically relevant fashion. Using the same GIS software, we obtained areas of counties and HUCs that we used to calculate the density of crayfish records (number of records per ha) by county and 8-digit HUC.

Records were culled for a variety of reasons. Some records included county designations but could not be confidently georeferenced; therefore, more records contributed to species lists by counties than by HUCs. Some records did not include identifications to species; in lists by county and drainage, we included records identified to genus level only if no records identified to species level existed within the same genus and geographic area. In some records, the person identifying the specimens indicated uncertainty about their identification; in such cases, we either excluded the records from lists or included them with a question mark. Finally, we excluded a small number of records that we strongly suspected of being incorrect (see Results).

Species distributions from select recent publications (Glon et al. 2019, 2020) were also included in our lists. On the other hand, Fitzpatrick (1996, 2002) listed many species as present in geographic areas within Mississippi without providing any supporting evidence. Presumably, evidence was in his "personal records" that he referred to in Fitzpatrick (2002); however, he died in 2002, and despite efforts by several biologists, none have found and obtained access to those records. We do not even know if collections exist for all of his records. Therefore, we did not include distributions from the Fitzpatrick publications that were not supported by records in our database.

Cautionary notes

At least one of us has personally examined nearly all material from the USFS collections and the MMNS collections acquired since 2002, including the

Table 2. Four-digit hydrologic unit codes (HUC4), acronyms (as used in Appendix 1) and names, and major water bodies in each HUC4. MS = Mississippi; TN = Tennessee.

HUC4	Acronym: name	Major waterbodies included in HUC4
0316	TO: Mobile–Tombigbee	Tombigbee, Buttahatchee, Noxubee, and Sucarnoochee rivers; Tibbee and Luxapallila creeks.
0317	PA: Pascagoula	Chickasawhay, Chunky, Leaf, Pascagoula, Escatawpa, Biloxi, Wolf (southern MS), Jourdan, and Tchoutacabouffa rivers.
0318	PE: Pearl	Pearl, Strong, and Bogue Chitto rivers.
0603	EL: Middle TN–Elk	Pickwick Lake, Bear Creek.
0604	LT: Lower TN	Beech Creek.
0801	HA: Lower MS–Hatchie	Wolf (northern MS) and Hatchie rivers; Horn Lake.
0802	SF: Lower MS–St. Francis	Mississippi River.
0803	YA: Lower MS–Yazoo	Tallahatchie, Yocona, Coldwater, Yalobusha, Yazoo, and Big Sunflower rivers.
0806	BB: Lower MS–Big Black	Mississippi, Big Black, Homochitto, and Buffalo rivers; Bayou Pierre; Coles Creek.
0807	MA: Lower MS–Lake Maurepas	Amite and Tangipahoa rivers; Bayou Sara; Thompson Creek.

TUMNH collections. However, we have examined only small percentages of the MMNS collection acquired prior to 2002 and the USNM collection and none of the INHS collection. Based on the samples we have examined, we assumed that portions of the MMNS and USNM collections were misidentified. Some older lots in the MMNS collection even contain multiple species. The pre-2002 MMNS collections were identified primarily by Fitzpatrick, often with identifications based on juveniles or females, which can be challenging to identify. Furthermore, as new species have been described, many relevant collections were not revisited to determine whether species assignments should be changed. For these reasons, as well as the taxonomic uncertainties described below, this must be considered a provisional species checklist, intended to assist others in advancing knowledge of Mississippi crayfishes.

Results

Of the 9597 records we compiled, 38 lacked a county and 409 were not confidently georeferenced and, therefore, lacked coordinates. Many more lacked identifications to species level or reflected uncertainty in identifications.

Sampling adequacy

Records were far from evenly distributed throughout the state (Fig. 1). Mississippi has 82 counties, so 9559 records with county designations equated to 117 records per county, on average. Actual coverage by records was quite uneven, with a low of 6 records in Coahoma County and high of 714 in Lafayette County. The counties with highest densities of records ([# of records/ha] x 10,000) were Lafayette, where investigators with the University of Mississippi and the USFS sampled extensively, and Oktibbeha, where investigators with Mississippi State University sampled extensively. Whether considering total records or densities of records, the 5 counties with the fewest records were all in the Lower Mississippi Alluvial Valley (LMAV; Fig. 1). Visual examination of a graph showing the number of species / number of records versus the number of records by county suggested that once a county reached ~175–200 records, the return on sampling investment in terms of new county species records was quite low (Fig. 2). Fifteen counties (18%) had at least 175 records.

Fifty-three 8-digit HUCs (HUC8) include more than 100 ha within Mississippi. The least-sampled HUC8 was the Tickfaw in Amite County, with no records; the most-sampled HUC8 by number of records was the Yalobusha (1077 records) and by record density was the Lower Hatchie (44.6 records/10,000 ha) (Fig. 3).

Crayfish taxa and distributions

Records indicated 8 genera in Mississippi, up from 6 in 2002 (Fitzpatrick 2002). In the state list, we included 65 species, including several species complexes (Appendix 1, which includes the authorities and common names for all species in our State checklist). Additionally, we included 5 subspecies, including 1 subspecies (*Faxonius palmeri creolanus*) whose presence we found questionable in the state. We also found that 4 additional species, including 1 non-native, were of

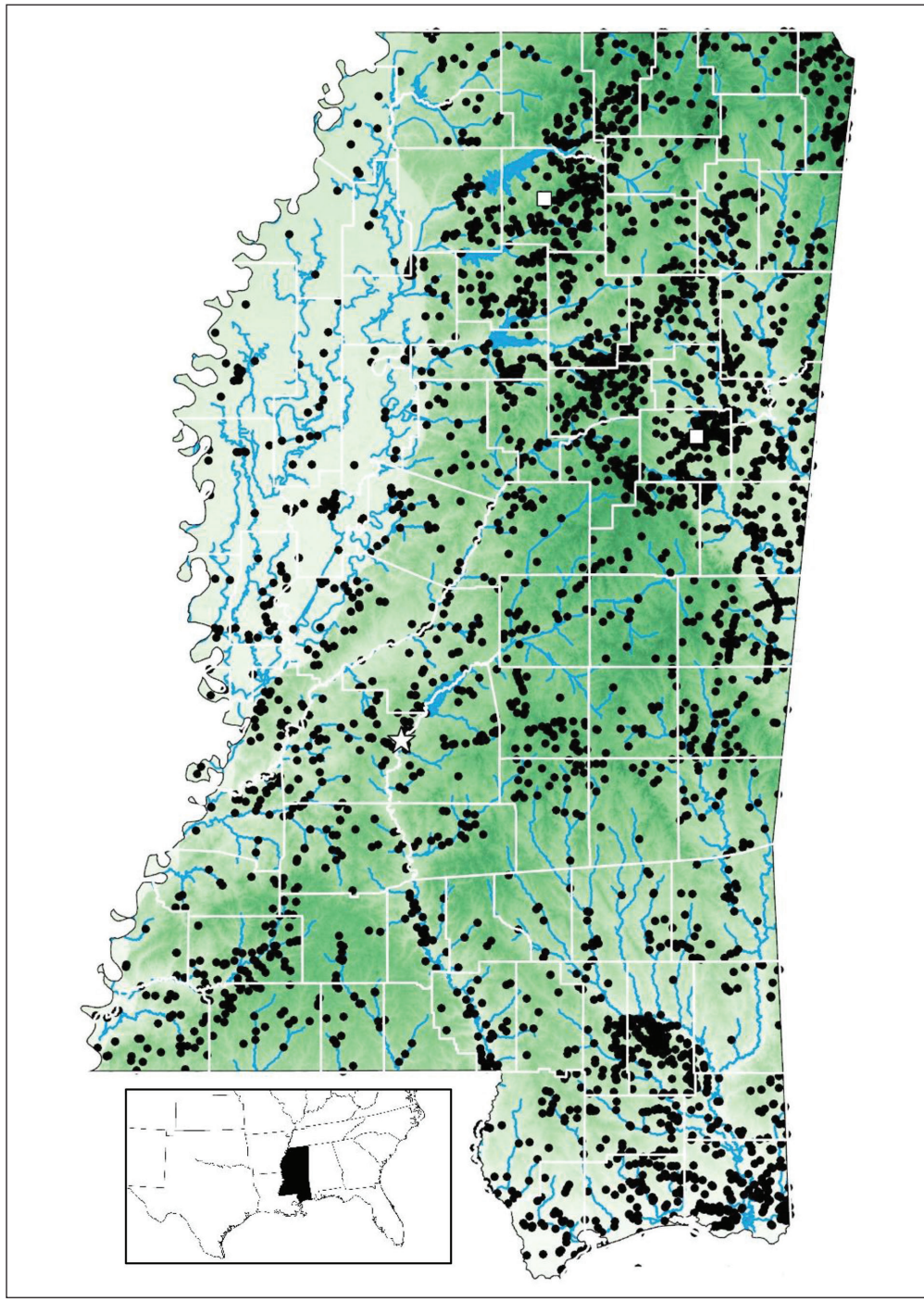

Figure 1. Distribution of crayfish records with coordinates in Mississippi. Black dots indicate records (many dots are superimposed on others). Shading indicates elevational relief, with darker shades indicating higher elevations. Major rivers and reservoirs are shown. White star locates Jackson, and white squares locate Oxford (north) and Starkville (south). Inset shows state's location in southeastern US.

questionable occurrence in the state. Thirteen species and 1 subspecies were endemic to the state, and another 22 species and 1 subspecies occurred in just 1 other state (Appendix 1)—so over half of the species were restricted to 1 or 2 states.

At the 4-digit HUC level, we documented variation of taxa numbers from 1 in the Lower Mississippi–St. Francis (code 0802; Fig. 3) to 41 in the Pascagoula (0317, which included independent coastal rivers; Appendix 2). To meet the needs of various readers, we also listed taxa by county (see Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s20-1-S2658-Adams-s1, and for BioOne subscribers, at https:dx.doi.org/10.1656/S2658.s1) and by 8-digit HUC (see Supplemental File 2, available online available online at http://www.eaglehill.us/SENAonline/suppl-files/s20-1-S2658-Adams-s2, and for BioOne subscribers, at https:dx.doi.org/10.1656/S2658.s2).

Taxa excluded

Faxonius alabamensis (Faxon) (Alabama Crayfish). Fitzpatrick (2002) reported *F. alabamensis* from Alcorn and Tishomingo counties. Taylor et al. (2007) also listed it as occurring in Mississippi; however, that was likely based on an identification that was later changed to *F. etnieri* spp. complex (C. Taylor, INHS, Champaign, IL, pers. comm.). Specimens that Fitzpatrick identified as *F. alabamensis* in 1 Tishomingo County collection were re-identified by Jones as *F. compressus*. We found no other records of *F. alabamensis* in the state. However, given that *F. alabamensis*

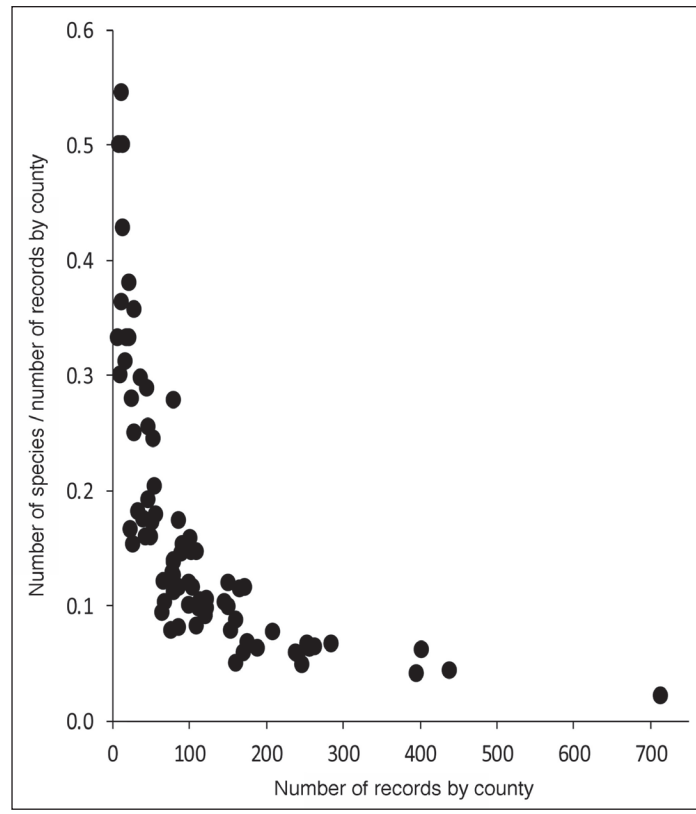

Figure 2. Number of records by Mississippi county versus the number of species / number of records for the county.

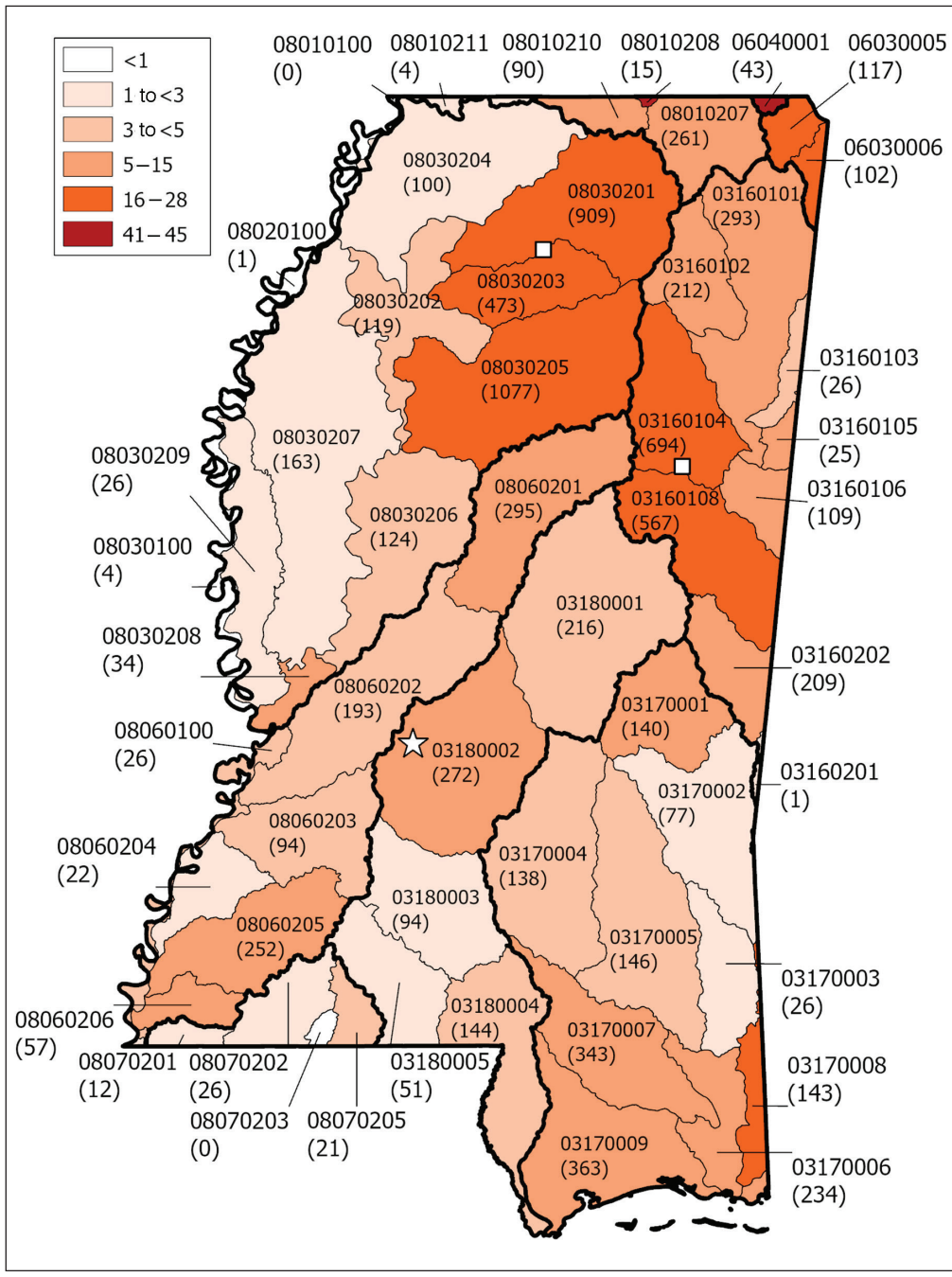

Figure 3. Sampling intensity. Heat map indicating density of crayfish records ([# of records/ha] x 10,000) by USGS 8-digit hydrologic unit code (HUC8) in Mississippi. Darker shades indicate higher density of records. Those HUCs with <100 ha in the state were excluded from calculations. Labels indicate HUC8 codes, with number of records in parentheses. Thicker lines indicate boundaries of 4-digit HUCs (HUC4 codes are the first 4 digits of HUC8 codes), roughly equivalent to "drainages" in Jones et al. (2019).

occurs just across the Tennessee River in northwest Alabama (Schuster et al., in press), future sampling may more clearly document it in a Tennessee River tributary in Mississippi.

Faxonius validus. Although we included *F. validus* in the state species list, we removed one 1985 record of the species from the Yazoo River drainage in Lafayette County (MMNS catalog # 534, 2 form II males, 1 female; identified by J.F. Fitzpatrick Jr.). Despite extensive subsequent sampling in the county, the species has not been encountered again, and we found no records of it from elsewhere in Mississippi outside of the Tennessee or Tombigbee drainages. We assume the Yazoo River drainage record represents a misidentification of a specimen belonging to the *F. etnieri* spp. complex.

Faxonius virilis (Hagen) (Virile Crayfish). A 1967 record of *F. virilis* from Clay County in the USNM database (catalog # 145455) has caused confusion for years about whether the species exists in Mississippi. *Faxonius virilis* is highly invasive where introduced, including in Alabama (Schuster et al., in press), but the species has not been documented in Mississippi beyond that 1 record. We concluded that it was either an erroneous record or a failed introduction and so did not include the species in the state taxa list. That said, given that the species is widely established in Alabama, it may yet appear in Mississippi.

Procambarus v. vioscai Penn (Percy's Creek Crayfish). Four records of *P. v. vioscai*, identified by J.F. Fitzpatrick Jr., from Amite (3) and Hinds (1) counties in the Homochitto and Lower Big Black HUC8s, respectively, were in the MMNS database. In his description of *P. v. paynei*, Fitzpatrick (1990) listed additional Mississippi counties with the nominate species and mentioned that intergrades between *P. v. paynei* and *P. v. vioscai* were possible; however, no subsequent MMNS collections from Mississippi were identified as *P. v. vioscai* by Fitzpatrick or any others. Fitzpatrick (2002) included *P. v. paynei* and *P. v. vioscai* x *paynei* but not *P. v. vioscai*, implying to us that the nominate subspecies does not occur in Mississippi; therefore, we excluded *P. v. vioscai* from distribution lists.

Procambarus cuevachicae (Hobbs). Two records of *P. cuevachicae*, 1 each from Grenada (MMNS catalog # 1352, 1 form I male, 1 female; identified by J.F. Fitzpatrick Jr.) and Yalobusha (USFS_FIBI Collection ID 265, 1 female; identified by S.B. Adams) counties, existed but were not included because of taxonomic uncertainties (see Discussion).

Procambarus elegans Hobbs (Elegant Creek Crayfish). *Procambarus elegans* occurs in northeastern Louisiana and southeastern Arkansas, so Fitzpatrick's (2002) report of the species from the northern Pearl River drainage (Montgomery and Simpson counties) seemed "odd" to Walls (2009). Because our database contained no records of the species from Mississippi, we did not include it in our lists.

Discussion

In his accounting of Mississippi crayfishes, Fitzpatrick (2002) listed 78 taxa, including subspecies, undescribed taxa, and species complexes. Several of those species have since been synonymized with other species (Schuster et al. 2015).

Other taxa have been described as new species (e.g., Glon et al. 2019). Some of Fitzpatrick's undescribed taxa were either unclear to us or were included with species complexes in our lists. Unquestionably, though, the state still contains undescribed crayfish diversity.

Several taxa seem likely to occur in Mississippi based on their distributions in neighboring states. Some *Faxonius* species present in the Tennessee River drainage in extreme northwest Alabama may also occur in Mississippi, including *F. durelli* (Bouchard and Bouchard) (Saddle Crayfish), *F. forceps* (Faxon) (Surgeon Crayfish), *F. mirus* (Ortmann) (Wonderful Crayfish), and *F. alabamensis* (Adams et al. 2010). *Creaserinus hortoni* (Hobbs and Fitzpatrick) (Hatchie Burrowing Crayfish) is a primary burrowing crayfish most closely related to the *C. fodiens* species complex and is known from Chester and McNairy counties, TN (Ainscough et al. 2013, Hobbs and Fitzpatrick 1970). Therefore, it, too, may be present in extreme northern Mississippi. *Procambarus versutus* (Hagen) (Sly Crayfish) is widespread below the Fall Line in Alabama, including in 3 southwest Alabama counties (Choctaw, Washington, and Mobile) that border Mississippi (Schuster et al., in press); the Okatuppa and Escatawpa drainages would be likely places for the species to occur in Mississippi. Similarly, *Procambarus spiculifer* (Le Conte) (White Tubercled Crayfish) also occurs in Washington and Mobile counties, AL, including 1 known locality in the Escatawpa drainage (Schuster et al., in press), and so might occur in Mississippi. *Procambarus hinei* (Ortmann) (Marsh Crayfish) is a small species primarily restricted to west of the Mississippi River in Louisiana; however, because it has been found several km east of the river in East Baton Rouge Parish, LA (Walls 2009), it may also occur near the Mississippi River in southwest Mississippi.

The distribution of crayfish records across Mississippi reflects past and present locations of astacologists, as well as the goals of particular studies or sampling efforts. For example, National Forests were over-represented in the records because of a 5-year effort to sample fishes and crayfishes of wadeable streams within those forests. Many crayfish records were byproducts of efforts to sample fishes. That has introduced biases into the locations and habitat types sampled and the seasons when sampling occurred. Ichthyologists may have focused more on habitat types likely to contain certain fish families, such as darters (Percidae), meaning that crayfishes of more swiftly flowing, perennial streams may be overrepresented. Additionally, fish sampling was often conducted during summer when reproductive-form male crayfishes of many genera were less likely to be collected. Due to this uneven application of sampling effort, some parts of the state and some habitat types have remained woefully undersampled for crayfishes.

The 82% of Mississippi counties that had fewer than 175 records (min–max: 6–172 records) probably need additional sampling to fully capture their crayfish diversity. Although we found that the crayfish fauna was likely well-characterized in counties with 175–200 records, that amount of records should be taken as an extremely rough estimate of what is needed to accurately sample a county's diversity; several problems and confounding factors marked our analysis. Ideally the analysis would have been based on sampling effort rather than the number of records, but

given the nature of our dataset, we were unable to analyze the data that way. Three problems arose from the data themselves. First, by definition, higher diversity led to more records per collection. Second, records with uncertain crayfish identifications were excluded from the taxa counts, for the most part (e.g., except in instances where the species likely to be confused were combined into a single taxon, as for *F. chickasawae* (M.R. Cooper and Hobbs) (Chickasaw Crayfish) and *F. etnieri* being combined into *F. etnieri* spp. complex). Third, as previously mentioned, some species-by-collection combinations were represented by more than 1 record. The most obvious confounding factors were that counties certainly varied in the actual number of species they contained and the areas they encompassed. Another was that more sampling effort focused on counties known for high diversity (e.g., Jackson County) than on those expected to have low diversity, including counties falling completely within the LMAV.

By highlighting undersampled areas, the density of records by watershed may be useful in informing future sampling needs. For example, watersheds in the Chickasawhay River drainage and in southwest Mississippi, and those falling entirely within the LMAV, had relatively few records per ha in the database (Fig. 3). Although actual numbers of records from the Tennessee River Basin watersheds were not high, the record densities were high because only a small area of each watershed fell within Mississippi (Fig. 3); nonetheless, those watersheds remain likely candidates for containing new state species records.

Three additional categories of sampling needs were harder to quantify given the available information in most collection records. The first was large water bodies (i.e., those too large for wading). Plotted collection points revealed a paucity of samples from large water bodies; however, when such waters were sampled, coordinates may have been recorded at access points, making it difficult to determine where sampling actually occurred. Small numbers of crayfishes caught incidentally while sampling for fishes or other taxa may mean that plotted points over-represented actual sampling of large water bodies for crayfishes. A collateral benefit of sampling large water bodies is that it may increase the chances of detecting invasive crayfishes, which often first appear in recreational lakes or reservoirs (e.g., Adams et al. 2015).

At the other extreme, the second undersampled category was very small ephemeral and intermittent water bodies (e.g., vernal and floodplain pools, roadside ditches, headwater streams). These have received little sampling, in part because people seldom sampled such habitat types for fishes, but also because they can only be sampled efficiently when adequate water is present, so summer sampling presumably overlooked crayfishes in such habitats (Adams et al. 2018). Evidence of this omission due to undersampling of such habitats was recent (2018) USFS sampling of 30 ephemeral and intermittent water bodies (e.g., roadside ditches) in the Upper Big Black River watershed and finding *Hobbseus* sp. in 20 of the sites, despite the genus never having been reported from the drainage before.

The third category of sampling needs related to crayfish behavior. Crayfishes are often broadly categorized as primary, secondary, or tertiary burrowers (Hobbs

1942, 1981), with each level spending progressively less time in burrows and more in surface waters. Although we were unable to quantify the sampling effort applied to each burrowing category, we determined from examining records, and from personal experience, that by far the most effort has been expended sampling secondary and tertiary burrowers in surface waters. Primary burrowing species appeared to be poorly sampled throughout the state, as was the case until recently in Alabama, where only 4.9% of all records were of primary burrowing species (Schuster et al. 2008). Consequently, Mississippi probably harbors undiscovered diversity of primary burrowers. As an example, intensive, targeted sampling of primary burrowers over 10 days during winter in southern Mississippi and Alabama recently revealed 2 new *Lacunicambarus* species (Glon et al. 2020) and produced many reproductive-form males and ovigerous females.

Taxonomic issues

Numerous taxonomic issues need clarification to facilitate species identifications, conservation assessments, and effective management. Below is a synopsis of major issues by taxon.

Cambarus rusticiformis. *Cambarus rusticiformis* occurs in the Tennessee River drainage in northeast Mississippi; however, the records appear to represent a species complex, with distinct color morphs in different parts of the range. Taxonomic work on the complex is ongoing (Jeff Simmons, Tennessee Valley Authority, Chattanooga, TN, 13 May 2020 pers. comm.) and will likely result in a new species in Mississippi.

Creaserinus byersi. Three records of *C. byersi* from Mississippi were in the USNM database. All were collected and identified prior to 1976, and *C. burrisi* was not described until 1987. Given that no *C. byersi* have been identified from Mississippi since the description of *C. burrisi*, specimens from the 3 collections need to be re-examined to determine if they should be reassigned to *C. burrisi*. That said, in Alabama, *C. byersi* were found in the Escatawpa River drainage that flows into Mississippi; therefore, we retained the species in the state species list for now.

Creaserinus danielae. Both *C. danielae* and *C. oryktes* are reported from Mississippi (Taylor et al. 2007); however, in a phylogenetic analysis, Ainscough et al. (2013:315) noted that the 2 are "very difficult to distinguish from each other, and further work should be done to determine whether they truly are separate species". The *C. oryktes* specimens in that study were identified based on form II males, which introduced uncertainty about their identifications. Several records in the USNM collection have had identifications changed back and forth between these 2 species several times by various experts. Walls (2009) reports only *C. oryktes* from Louisiana, and Schuster et al. (in press) report only *C. danielae* from Alabama. Morphologic and genetic comparisons of the 2 species are ongoing (R. Garrick, University of Mississippi, Oxford, MS, and S.B. Adams, unpubl. data).

Creaserinus fodiens. *Creaserinus fodiens* is a paraphyletic species complex with high diversity that, upon revision, will likely result in multiple species, with at least 1 new species in Mississippi (Ainscough et al. 2013).

Faxonius species formerly assigned to the Trisellescens subgenus of Orconectes. Perhaps the largest crayfish systematic conundrum in the state involves members of the former subgenus *Trisellescens*. This confusion also extends to crayfishes in streams below the Fall Line in Alabama and in western Tennessee (Taylor et al. 2014). *Faxonius etnieri* and *F. chickasawae* were both described species in the subgenus *Trisellescens*; however, the morphologic and geographic criteria separating them did not hold up under closer genetic and morphometric scrutiny, and identification was fraught; therefore, until the taxonomy is further clarified, we referred to both as "*F. etnieri* species complex", as recommended by Taylor et al. (2014). In addition, populations in the Pascagoula River drainage and parts of the Yazoo River drainage probably represent additional diversity, but we included those populations in the species complex. The closely related and morphologically similar species *F. jonesi* and *F. mississippiensis* were not placed in the species complex but remain of questionable validity with uncertain ranges. For the time being, Taylor et al. (2014) recommended restricting the name *F. jonesi* to individuals with short pleopods and wide areolas from the Sucarnoochee River drainage. The findings of Taylor et al. (2014:11) were inconclusive with respect to the validity of *F. mississippiensis*, but pending further study, they recommended applying the name to populations with long pleopod elements and closed areolas "in eastern flowing tributaries of the Tombigbee River drainage upstream of the Sucarnoochee River and in adjacent headwaters of the Yalobusha River drainage". Regardless of taxonomic status, an important management consideration is that considerable diversity exists within the group, and genetic diversity exists among watersheds (Taylor et al. 2014).

Faxonius hartfieldi. Although *F. hartfieldi* appears to be a valid species, specimens from several localities had characteristics attributable to both *F. hartfieldi* and the closely related *F. perfectus*. In 2 localities in Abiaca Creek (Carroll County) both up- and downstream of Sanders Lake, we found specimens that looked like *F. hartfieldi* except for having strong carinas, open areolas with room for 1–2 punctations, and weak suborbital angles. No form I males were caught, but gonopods of form II males resembled those of *F. hartfieldi*. At 1 of the localities, juveniles had bearded chelae, but setae were less prominent on adults. At another Carroll County locality (Big Sand Creek), specimens were identified as *F.* sp. cf *perfectus* based on females (no adult males were captured). The annulus ventralis resembled that of *F. hartfieldi*, but specimens had open areolas, weak to strong carinas, mesial margins of the palm with cristate spines, and less setae on chelae/fingers than seen on other *F. hartfieldi* specimens; however, the rostrum shape and annulus ventralis differed from *F. perfectus*. Similarly, in Buck and Little Topashaw creeks (Webster County), specimens were identified as *F*. sp. cf *hartfieldi* (USFS-CBHR catalog # 4657 and 4662).

The *F. hartfieldi* species description notes in 2 places that the species lacks a carina. Also, as described, *F. hartfieldi* lacks a suborbital angle and has an areola that is obliterated through most of its length (Fitzpatrick and Suttkus 1992). In contrast, *F. perfectus* has an areola that is closed to narrowly open with 1 row of punctations

and an obtuse suborbital angle (Walls 1972). Areola width is not necessarily a reliable character in other *Faxonius*, including in the subgenus *Trisellescens* (Taylor et al. 2014) and in *F. palmeri* (Penn 1957). The presence or absence of a carina seemed to be a reliable species-level character in the subgenus *Trisellescens* (Taylor et al. 2014), but the presence/absence and prominence of a carina varied in *F. palmeri* (Penn 1957).

Whether the specimens in question represent previously undocumented variation within *F. hartfieldi*, *F. perfectus* x *F. hartfieldi* hybrids, or a new species is important to resolve because *F. hartfieldi* is an at-risk species, considered threatened by the American Fisheries Society (Taylor et al. 2007), vulnerable by the IUCN (Adams and Jones 2010), and petitioned for listing under the Endangered Species Act (CBD 2010). Other Mississippi records of *F. perfectus* outside of the Tombigbee River basin might also belong with this group because *F. perfectus* is likely restricted within the state to the Tombigbee River Basin.

Faxonius hobbsi. Although the species description restricted *F. hobbsi* to tributaries of Lake Ponchartrain, LA, as did Penn (1957) and Walls (2009), records for the species occur much more broadly in Mississippi. We suspect this widespread reported occurence has resulted from the difficulty of distinguishing between *F. hobbsi* and *F. palmeri* after preservation. The 2 species are most easily separated based on life colors (Walls 2009), making identification of preserved specimens more difficult. According to its species description, *F. palmeri* has a closed areola (Faxon 1884), but across the species' range, the percentage of specimens with slightly open areolas generally increased from west to east and north to south, with only 17.5% of specimens examined in the Homochitto River drainage having a closed areola (Penn 1957). We suspect that many *F. palmeri* specimens in Mississippi were identified as *F. hobbsi* because of their slightly open areolas and that most, if not all, of the specimens from outside of the Lake Ponchartrain basin are *F. palmeri*.

Hobbseus. Of the 7 *Hobbseus* species, only *H. orconectoides* is easily identifiable to species. The other 6 are each difficult to separate from at least 1 other species, and the species descriptions apparently failed to document the extent of morphologic variation within species. Some of the key characters used in describing species were shapes and lengths of terminal processes of form I male gonopods, but these characters do not appear to be diagnostic, at least as described. Although some specimens we have examined closely resembled described species, many appeared to be intermediate between species. In several instances, the left and right gonopod of a single specimen resembled different species. The shape and orientation of the mesial process, in particular, appeared highly variable, possibly changing after preservation.

Lacunicambarus erythrodactylus. Until recently, the only described *Lacunicambarus* species in Mississippi were *L. diogenes* and *L. ludovicianus*. In 2015, *L. erythrodactylus* was described from the *L. diogenes* species complex (Simon and Morris 2015). Subsequently, *L. diogenes* was redescribed and restricted to Atlantic Coast drainages (Glon et al. 2018). Glon et al. (2018:609) noted that "specimens

of *Lacunicambarus* from the Gulf of Mexico are distinct from *L. diogenes* and will need to be elevated to the species level. Such change will require a review of the taxonomic validity of … *L. erythrodactylus* …, whose description has proven puzzling." That review is ongoing but will likely point to all *L. diogenes* and *L.* aff. *diogenes* in Mississippi being reassigned to *L. erythrodactylus* (M. Glon, Ohio State University, Columbus, OH, 14 May 2020 pers. comm.). Therefore, for the purposes of this checklist, we listed all such records as *L. erythrodactylus* without examining the specimens.

Procambarus acutus species complex. The *P. acutus* species complex, including *P. acutus*, *P. zonangulus*, and *P. cuevachicae* has troubled astacologists for decades. *Procambarus zonangulus* was described as a species distinct from *P. acutus* in 1990, but its range was not delineated because the authors were in the midst of a never-completed revision of the entire species complex (Hobbs and Hobbs 1990). The native ranges of these 3 taxa may never be fully known, given their extensive introductions via aquaculture and the live crawfish food trade. Walls (2009) suggested that occurrences of *P. zonangulus* more than a few km east of the Mississippi River may represent introductions but did not explain his reasoning for the statement. The species' northern distribution limit is unclear (Walls 2009). Misidentifications of *P. acutus* and *P. zonangulus,* including by the authors, are assumed to be rampant, so the distributions of both species in Mississippi remain unclear. Individual records, especially those lacking form I males, should be viewed with caution. *Procambarus cuevachicae* was initially thought to be restricted to Mexico (Hobbs et al. 1989), but 2 records of it exist in Mississippi (see Taxa excluded). These may be misidentifications of *P. acutus* or *P. zonangulus*; however, some discussion among astacologists has suggested that *P. cuevachicae* may, in fact, occur in Mississippi and as far north as southern Illinois. The following excerpt summarizes Fitzpatrick's understanding of the situation shortly before his passing (Fitzpatrick 2002:26–27):

> "Discussions between us about the status of the several populations (Hobbs, Jr., pers. comm.) led Hobbs, Jr., Hobbs III, and me to the conclusion that *P. cuevachicae* rather than occupying a somewhat restricted distribution in Mexico, existed throughout west Texas and west of the Mississippi River to the northern limit of the complex; east of the river, it extends into western Mississippi and into the Mississippi River basin of the Midwest. Christopher Taylor and Larry Page confirmed that the populations of Illinois should be assigned to *P.* (*O.*) *cuevachicae* (Taylor, pers. comm.). The range of *P. acutus* interdigitates in Mississippi, but *acutus* then extends from the Tombigbee River basin to the Atlantic Coastal Plain. Except for the instance cited above, these opinions are not yet validated with detailed information in the published literature."

This understanding was confirmed in a recent personal communication with C. Taylor (Illinois Natural History Survey, Champaign, IL, 9 April 2020). Walls (2009) retained use of *P. acutus* subspecies and suspected that *P. a. cuevachicae* (or *P. cuevachicae*) may have been restricted to west of the Mississippi River; however, he recommended against use of the subspecies until the taxonomy was clarified.

Given the great uncertainty surrounding *P. cuevachicae*, we chose to not include it in the state list at this time, while acknowledging that it may occur in the state. The *P. acutus* species complex is in dire need of revision, which needs to be undertaken across the entire range of the species complex.

Procambarus clemmeri vs P. penni. These 2 species have created confusion for many years because they are difficult to distinguish from one another. Based on morphology alone, we suspected that for the most part, *P. clemmeri* occurred in the Pascagoula River drainage and *P. penni* occurred in the Pearl River drainage; however, ongoing genetic work indicates greater complexity in systematics and distributions, especially when intervening Gulf Coastal drainages are included (S. Feist, US Army Corps of Engineers, Vicksburg, MS, and R.L. Jones, unpubl. data). Several possible taxonomic resolutions remain open.

Procambarus aff. viaeviridis. Ongoing genetic and morphologic work (J. Fetzner, Carnegie Museum of Natural History, Pittsburgh, PA, and S.B. Adams, unpubl. data) suggests 1 or possibly 2 new species in Mississippi that are closely related to *P. viaeviridis*. The most certain to be a new species is known from the southern and western portions of the LMAV, and the other is from central Mississippi. We distinguished only the former, *P. viaeviridis* sp. A, from *P. viaeviridis* in this checklist.

Procambarus vioscai subspp. Walls (2009) questioned Fitzpatrick's (1990) designation of *P. vioscai* populations in the Florida Parishes of Louisiana as intergrades between *P. v. vioscai* and *P. v. paynei*. Although Walls indicated that designation of the populations as intergrades was the most conservative approach to take in 2009, he found it problematic given the difficulty in distinguishing between the 2 subspecies, much less in distinguishing *P. v. paynei* from intergrades between the two. We accept Walls' (2009) interpretation and assume that *P. vioscai* populations in Mississippi drainages adjacent to the Florida Parishes may also be intergrades. However, as Walls (2009) stated, great uncertainty surrounds this designation, and a re-examination of the taxonomic status and distributions of *P. vioscai* subspecies is warranted.

Conclusions

Although progress has occurred in documenting species distributions and clarifying the taxonomy of Mississippi's rich crayfish fauna, much work remains. The taxonomic issues raised present excellent opportunities for graduate research studies. Additional sampling is especially needed to target undersampled watersheds, primary burrowing crayfishes, and crayfishes in large water bodies. We hope that the current species list will facilitate the next decade of crayfish research and management in the state.

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Literature Cited

Adams, S.B., and R.L. Jones. 2010. *Orconectes hartfieldi.* The IUCN Red List of Threatened Species 2010:e.T15441A4585752. https://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T15441A4585752.en.

Adams, S.B., and R.L. Jones. 2018. Range extensions of three crayfishes (*Faxonius yanahlindus*, *F. placidus*, and *F. erichsonianus*) into Mississippi. Southeastern Naturalist 17:N6–N9.

Adams, S.B., C.A. Taylor, and C. Lukhaup. 2010. Crayfish fauna of the Tennessee River drainage in Mississippi, including new state species records. Southeastern Naturalist 9:521–528.

Adams, S.B., C. Roghair, C. Krause, M.L. Warren, Jr, J.A. Cochran, A. Dolloff, J. Moran, S.W. McGregor, G.A. Schuster, M. Gangloff, D.R. DeVries, M.R. Kendrick, G.L. Grove, and R.A. Wright. 2015. New crayfish species records from the Sipsey Fork drainage, including Lewis Smith Reservoir (Alabama, USA): Native or introduced species? Freshwater Crayfish 21:17–32.

Adams, S.B., B.A. Davis, and D.A. Miller. 2018. *Hobbseus yalobushensis*, a crayfish of intermittent streams: Biotic and habitat associations, life-history characteristics, and new localities. American Midland Naturalist 179:126–149.

Ainscough, B.J., J.W. Breinholt, H.W. Robison, and K.A. Crandall. 2013. Molecular phylogenetics of the burrowing crayfish genus *Fallicambarus* (Decapoda: Cambaridae). Zoologica Scripta 42:306–316.

Center for Biological Diversity (CBD). 2010. Petition to list 404 aquatic, riparian, and wetland species from the southeastern United States as threatened or endangered under the Endangered Species Act. Tuscon, AZ. 1145 pp.

Crandall, K.A., and S. De Grave. 2017. An updated classification of the freshwater crayfishes (Decapoda: Astacidea) of the world, with a complete species list. Journal of Crustacean Biology 37:615–653.

Faxon, W. 1884. Descriptions of new species of *Cambarus*, to which is added a synonymical list of the known species of *Cambarus* and *Astacus*. Proceedings of the American Academy of Arts and Sciences 20:107–158.

Fitzpatrick, J.F., Jr. 1990. *Procambarus* (*Pennides*) *vioscai paynei*, a new subspecies of crawfish from east of the Mississippi River (Decapoda, Cambaridae). American Midland Naturalist 123:259–267.

Fitzpatrick, J.F., Jr. 1996. Rare and endangered crawfishes of Mississippi. Museum Technical Report No. 93, Mississippi Department of Wildlife, Fisheries, and Parks, Jackson, MS. 67 pp.

Fitzpatrick, J.F., Jr. 2002. The conservation status of Mississippi crawfishes (Crustacea: Decapoda: Cambaridae). Louisiana Academy of Sciences 63:25–36.

Fitzpatrick, J.F., Jr., and R.D. Suttkus. 1992. A new crawfish of the genus *Orconectes* from the Yazoo River system of Mississippi (Decapoda: Cambaridae). Proceedings of the Biological Society of Washington 105:70-–76.

Glon, M.G., R.F. Thoma, C.A. Taylor, M. Daly, and J.V. Freudenstein. 2018. Molecular phylogenetic analysis of the devil crayfish group, with elevation of *Lacunicambarus* Hobbs, 1969 to generic rank and a redescription of the devil crayfish, *Lacunicambarus diogenes* (Girard, 1852) comb. nov. (Decapoda: Astacoidea: Cambaridae). Journal of Crustacean Biology 38:600–613.

Glon, M.G., B.W. Williams, and Z.J. Loughman. 2019. *Lacunicambarus dalyae*: A new species of burrowing crayfish (Decapoda: Cambaridae) from the southeastern United States. Zootaxa 4683:361–380.

Glon, M.G., S.B. Adams, Z.J. Loughman, G.A. Myers, C.A. Taylor, and G.A. Schuster. 2020. Two new species of burrowing crayfish in the genus *Lacunicambarus* (Decapoda: Cambaridae) from Alabama and Mississippi. Zootaxa 4802:401–439.

Hobbs, H.H., Jr. 1942. The crayfishes of Florida. Biological Science Series, University of Florida Publications 3:1–79.

Hobbs, H.H., Jr. 1981. The crayfishes of Georgia. Smithsonian Contributions to Zoology 318:1–549.

Hobbs, H.H., Jr., and J.F. Fitzpatrick, Jr. 1970. A new crayfish of the genus *Fallicambarus* from Tennessee (Decapoda, Astacidae). Proceedings of the Biological Society of Washington 82:829–836.

Hobbs, H.H., Jr. and H.H. Hobbs, III. 1990. A new crayfish (Decapoda: Cambaridae) from southeastern Texas. Proceedings of the Biological Society of Washington 103:608–613.

Hobbs, H.H., III, J.P. Jass, and J.V. Huner. 1989. A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). Crustaceana 56:299–316.

Jones, R.L., W.T. Slack, and P.D. Hartfield. 2005. The freshwater mussels (Mollusca: Bivalvia: Unionidae) of Mississippi. Southeastern Naturalist 4:77–92.

Jones, R.L., M.D. Wagner, W.T. Slack, S. Peyton, and P. Hartfield. 2019. Guide to the Identification and Distribution of Freshwater Mussels (Bivalvia: Unionidae) in Mississippi. Mississippi Department of Wildlife, Fisheries, and Parks, Jackson, MS. 339 pp.

Lyle, C. 1937. The crawfishes of Mississippi, with special reference to the biology and control of destructive species. M.Sc. Thesis. Iowa State College, Ames, IA. 140 pp.

Lyle, C. 1938. The crawfishes of Mississippi, with special reference to the biology and control of destructive species. Iowa State College Journal of Science 13:75–77.

Omernik, J.M., G.E. Griffith, R.M. Hughes, J.B. Glover, and M.H. Weber. 2017. How misapplication of the hydrologic unit framework diminishes the meaning of watersheds. Environmental Management 60:1–11.

Penn, G.H. 1957. Variation and subspecies of the crawfish *Orconectes palmeri* (Faxon) (Decapoda, Astacidae). Tulane Studies in Zoology 5:231–262.

Schuster, G.A., C.A. Taylor, and J. Johansen. 2008. An annotated checklist and preliminary designation of drainage distributions of the crayfishes of Alabama. Southeastern Naturalist 7:493–504.

Schuster, G.A., C.A. Taylor, and S.B. Adams. 2015. *Procambarus* (*Girardiella*) *holifieldi*, a new species of crayfish (Decapoda: Cambaridae) from Alabama, with a revision of the Hagenianus Group in the subgenus *Girardiella*. Zootaxa 4021:1–32.

Schuster, G.A., C.A. Taylor, and S.W. McGregor. In press. Crayfishes of Alabama. University of Alabama Press, Tuscaloosa, AL.

Simon, T.P., and C.C. Morris. 2015. *Cambarus* (*Lacunicambarus*) *erythrodactylus*, a new species of crayfish (Decapoda: Cambaridae) of the *Cambarus diogenes* complex from Alabama and Mississippi, USA. Proceedings of the Biological Society of Washington 127:572–584.

Taylor, C.A., G.A. Schuster, J.E. Cooper, R.J. DiStefano, A.G. Eversole, P. Hamr, H.H. Hobbs III, H.W. Robison, C.E. Skelton, and R.F. Thoma. 2007. A reassessment of the conservation status of crayfishes of the United States and Canada after 10+ years of increased awareness. Fisheries 32:372–389.

Taylor, C.A., S.B. Adams, and G.A. Schuster. 2014. Systematics and biogeography of *Orconectes*, subgenus *Trisellescens*, in the southeastern United States: A test of morphology-based classification. Journal of Crustacean Biology 34:1–14.

Taylor, C.A., C.M. Rhoden, and G.A. Schuster. 2016. A new species of crayfish in the genus *Orconectes* (Decapoda: Cambaridae) from the Tennessee River Drainage with comments on and key to members of the *O. juvenilis* species complex. Zootaxa 4208:161–175.

US Geological Survey (USGS). 2013. Hydrologic unit maps. http://water.usgs.gov/GIS/huc.html. Accessed 9 July 2020. Available online at http://water.usgs.gov/GIS/huc.html. Accessed 9 July 2020.

Walls, J.G. 1972. Three new crayfishes related to *Orconectes difficilis* (Faxon) (Decapoda: Astacidae). Proceedings of the Biological Society of Washington 84:449–458.

Walls, J.G. 2009. Crawfishes of Louisiana. Louisiana State University Press, Baton Rouge, LA. 240 pp.

Warren, M.L., S. Adams, W. Haag, J.G. McWhirter, and L.G. Henderson. 2003. Fish and fish habitat survey in Mississippi National Forests: Fish community sampling 1999–2002. Technical Report. Mississippi National Forests, Jackson, MS. CD-ROM.

Appendix 1. Mississippi crayfish species checklist. Numbers in parentheses indicate number of full species per genus. Sixty-five species total, excluding subspecies. Does not include any species mentioned in literature but not included in the database used. Species preceded by an asterisk are endemic to the state. "Taxa excluded" are those with at least 1 record in the database but with uncertainty surrounding whether they actually occur in the state. Four-digit hydrologic unit code (HUC4) names abbreviated as in Table 2. A "?" after a HUC4 abbreviation indicates that either (1) all identifications of the species in the HUC4 were indicated as uncertain by the determiner, or (2) we questioned the species' presence in the HUC based on other information.

Taxon	Common name	HUC4
Genus *Cambarellus* (*Pandicambarus*) (4)		
C. diminutus[1] Hobbs 1945	Least Crayfish	PA
C. lesliei[1] Fitzpatrick & Laning 1976	Angular Dwarf Crawfish	PA
C. puer Hobbs 1945	Swamp Dwarf Crayfish	BB, YA
C. shufeldtii (Faxon) 1884	Cajun Dwarf Crayfish	BB, PA, PE, TO, YA
Genus *Cambarus* (3)		
C. girardianus Faxon 1884	Tanback Crayfish	EL
C. rusticiformis Rhoades 1944	Depression Crayfish	EL
C. striatus Hay 1902	Ambiguous Crayfish	BB, EL, HA, LT, PA, PE, TO, YA
Genus *Creaserinus* (6)		
C. burrisi[1] (Fitzpatrick) 1987	Burrowing Bog Crayfish	PA
C. byersi (Hobbs) 1941	Lavender Burrowing Crayfish	PA?
C. danielae[1] (Hobbs) 1975	Speckled Burrowing Crayfish	PA
C. fodiens[2] (Cottle) 1863	Digger Crayfish	BB, HA, MA, PA, PE, TO, YA
**C. gordoni* (Fitzpatrick) 1987	Camp Shelby Burrowing Crayfish	PA
C. oryktes[1] (Penn & Marlow) 1959	Flatwoods Digger	PA, PE
Genus *Faxonella* (1)		
F. clypeata (Hay) 1899	Ditch Fencing Crayfish	BB, PA, PE
Genus *Faxonius* (14)		
F. compressus (Faxon) 1884	Slender Crayfish	EL, TO
F. erichsonianus (Faxon) 1884	Reticulate Crayfish	EL
F. etnieri (R.W. Bouchard & J.W. Bouchard) 1976 spp. complex	Ets Crayfish	BB, EL, HA, LT, PA, TO, YA
**F. hartfieldi* (Fitzpatrick & Suttkus) 1992	Yazoo Crayfish	BB, YA
F. hobbsi[1] (Penn) 1950	Pontchartrain Painted Crawfish	BB?, MA, PA?, PE?, YA?
F. jonesi[1] (Fitzpatrick) 1992	Sucarnoochee River Crayfish	PA?, TO
F. lancifer (Hagen) 1870	Shrimp Crayfish	BB, PA, PE, TO, YA
**F. mississippiensis* (Faxon) 1884	Mississippi Crayfish	BB?, PE?, TO
F. palmeri (Faxon) 1884		BB, HA, MA, PA, PE, TO?, YA
F. p. creolanus[1] (Creaser) 1933	Creole Painted Crayfish	BB?, PA?, PE?
F. p. palmeri (Faxon) 1884	Gray-speckled Crayfish	BB, HA, MA, PA, PE, TO?, YA
F. perfectus[1] (Walls) 1972	Complete Crayfish	TO
F. placidus (Hagen) 1870	Placid Crayfish	EL
F. validus (Faxon) 1914	Powerful Crayfish	EL, LT, TO
F. wrighti[1] (Hobbs) 1948	Hardin Crayfish	LT
F. yanahlindus (Taylor et al.) 2016	Spinywrist Crayfish	EL

Taxon	Common name	HUC4
Genus *Hobbseus*[1] (7)		
**H. attenuatus* Black 1969	Pearl Rivulet Crayfish	PA, PE, TO
**H. cristatus* (Hobbs) 1955	Crested Rivulet Crayfish	PA, TO
**H. orconectoides* Fitzpatrick & Payne 1968	Oktibbeha Rivulet Crayfish	TO
**H. petilus* Fitzpatrick 1977	Tombigbee Rivulet Crayfish	TO
H. prominens[1] (Hobbs) 1966	Prominence Rivulet Crayfish	TO
**H. valleculus* (Fitzpatrick) 1967	Choctaw Rivulet Crayfish	PE, TO
**H. yalobushensis* Fitzpatrick & Busack 1989	Yalobusha Rivulet Crayfish	BB?, TO?, YA
Genus *Lacunicambarus* (5)		
L. dalyae Glon et al. 2019	Jewel Mudbug	EL, HA, TO, YA
L. erythrodactylus (Simon & Morris) 2015	Warpaint Mudbug	BB, EL, HA, LT, PA, PE, TO, YA
L. freudensteini[1] Glon 2020	Banded Mudbug	PA
L. ludovicianus (Faxon) 1884	Painted Devil Crayfish	BB, HA, MA, PA, PE, SF, TO, YA
L. mobilensis[1] Glon 2020	Lonesome Gravedigger	PA
Genus *Procambarus* (25)		
P. ablusus[1,3] Penn 1963	Hatchie River Crayfish	EL, HA, LT
P. acutissimus (Girard) 1852	Sharpnose Crayfish	BB?, PA, PE, TO, YA
P. acutus (Girard) 1852	White River Crawfish	BB, EL, HA, LT, MA, PA, PE, TO, YA
**P. barbiger* Fitzpatrick 1978	Jackson Prairie Crayfish	PA, PE
P. bivittatus Hobbs 1942	Ribbon Crayfish	PA, PE
P. clarkii (Girard) 1852	Red Swamp Crawfish	BB, HA, PA, PE, TO, YA
P. clemmeri[1,3] Hobbs 1975	Cockscomb Crayfish	BB?, PA, PE
P. evermanni (Faxon) 1890	Panhandle Crayfish	PA
**P. fitzpatricki* Hobbs 1971	Spinytail Crayfish	PA
P. hagenianus[1] (Faxon) 1884		PE, TO, YA
P. h. hagenianus[1] (Faxon) 1884	Southeastern Prairie Crayfish	PE, TO
**P. h. vesticeps* Fitzpatrick 1978	Egyptian Crayfish	TO, YA
P. hayi (Faxon) 1884	Straightedge Crayfish	BB?, HA, TO, YA
P. hybus[1] Hobbs & Walton 1957	Smoothnose Crayfish	BB, PA, PE, TO, YA
P. jaculus[1] Hobbs & Walton 1957	Javelin Crayfish	BB, PA, PE, YA
P. lagniappe[1,3] Black 1968	Lagniappe Crayfish	TO
P. lecontei[1] (Hagen) 1870	Mobile Crayfish	PA
**P. lylei*[3] Fitzpatrick & Hobbs 1971	Shutispear Crayfish	YA
**P. mancus*[4] Hobbs & Walton 1957	Lame Crayfish	PA, PE?, TO
P. ouachitae[1,3] Penn 1956	Ouachita River Crayfish	BB, HA, YA
P. penni[1,3] Hobbs 1951	Pearl Blackwater Crayfish	BB?, MA?, PA?, PE
P. planirostris Penn 1953	Flatnose Crayfish	MA, PA, PE
P. shermani Hobbs 1942	Gulf Crayfish	PA, PE
P. aff. *viaeviridis* sp. A		YA
P. viaeviridis (Faxon) 1914	Vernal Crayfish	BB, EL, HA, LT, PA?, PE, TO, YA
P. vioscai[3] Penn 1946		BB, HA, MA, PA, PE, TO, YA

Taxon	Common name	HUC4
P. v. paynei[3] Fitzpatrick 1990	Payne's Creek Crayfish	BB, HA, PA, PE, TO, YA
P. zonangulus Hobbs & Hobbs 1990	Southern White River Crawfish	BB, PA, PE, TO
Taxa excluded		
Faxonius alabamensis (Faxon) 1884	Alabama Crayfish	
Faxonius virilis (Hagen) 1870	Virile Crayfish	
Procambarus cuevachicae (Hobbs) 1941		
Procambarus v. vioscai Penn 1946	Percy's Creek Crayfish	

[1]Known distribution extends into only 1 other state.
[2]A species complex (Ainscough et al. 2013).
[3]In subgenus *Pennides*, which seems to remain a particularly useful subgenus of *Procambarus*.
[4]May also occur in Alabama.

Appendix 2. Crayfish species by USGS 4-digit Hydrologic Unit (HUC4). HUC4 code and name given (number of useable records in database in parentheses). A "?" indicates uncertainty about identification indicated by either the person who identified the specimens or by the authors.

0316 Mobile-Tombigbee (*n* = 2136)
Cambarellus shufeldtii
Cambarus striatus
Creaserinus fodiens
Faxonius compressus
Faxonius etnieri spp. complex
Faxonius jonesi
Faxonius lancifer
Faxonius mississippiensis
Faxonius p. palmeri?
Faxonius perfectus
Faxonius validus
Hobbseus attenuatus
Hobbseus cristatus
Hobbseus orconectoides
Hobbseus petilus
Hobbseus prominens
Hobbseus valleculus
Hobbseus yalobushensis?
Lacunicambarus erythrodactylus
Lacunicambarus dalyae
Lacunicambarus ludovicianus
Procambarus acutissimus
Procambarus acutus
Procambarus clarkii
Procambarus h. hagenianus
Procambarus. h. vesticeps
Procambarus hayi
Procambarus hybus
Procambarus lagniappe
Procambarus mancus
Procambarus viaeviridis
Procambarus vioscai paynei
Procambarus zonangulus

0317 Pascagoula (*n* = 1612)
Cambarellus diminutus
Cambarellus lesliei
Cambarellus shufeldtii
Cambarus striatus
Creaserinus burrisi
Creaserinus byersi?
Creaserinus danielae
Creaserinus fodiens
Creaserinus gordoni
Creaserinus oryktes
Faxonella clypeata
Faxonius etnieri spp. complex
Faxonius hobbsi?
Faxonius jonesi?
Faxonius lancifer
Faxonius palmeri creolanus?
Faxonius p. palmeri
Hobbseus attenuatus
Hobbseus cristatus
Lacunicambarus erythrodactylus
Lacunicambarus freudensteini
Lacunicambarus ludovicianus
Lacunicambarus mobilensis
Procambarus acutissimus
Procambarus acutus
Procambarus barbiger
Procambarus bivittatus
Procambarus clarkii
Procambarus clemmeri
Procambarus evermanni
Procambarus fitzpatricki
Procambarus hybus
Procambarus jaculus
Procambarus lecontei
Procambarus mancus
Procambarus penni?
Procambarus planirostris
Procambarus shermani
Procambarus viaeviridis?
Procambarus vioscai paynei
Procambarus zonangulus

0318 Pearl (*n* = 777)
Cambarellus shufeldtii
Cambarus striatus
Creaserinus fodiens
Creaserinus oryktes
Faxonella clypeata
Faxonius hobbsi?
Faxonius lancifer
Faxonius mississippiensis?
Faxonius palmeri creolanus?

Faxonius p. palmeri
Hobbseus attenuatus
Hobbseus valleculus
Lacunicambarus erythrodactylus
Lacunicambarus ludovicianus
Procambarus acutissimus
Procambarus acutus
Procambarus barbiger
Procambarus bivittatus
Procambarus clarkii
Procambarus clemmeri
Procambarus hagenianus
Procambarus hybus
Procambarus jaculus
Procambarus mancus?
Procambarus penni
Procambarus planirostris
Procambarus shermani
Procambarus viaeviridis
Procambarus vioscai paynei
Procambarus zonangulus

0603 Middle Tennessee–Elk (*n* = 219)
Cambarus girardianus
Cambarus rusticiformis
Cambarus striatus
Faxonius compressus
Faxonius erichsonianus
Faxonius etnieri spp. complex
Faxonius placidus
Faxonius validus
Faxonius yanahlindus
Lacunicambarus erythrodactylus
Lacunicambarus dalyae
Procambarus ablusus
Procambarus acutus
Procambarus viaeviridis

0604 Lower Tennessee (*n* = 43)
Cambarus striatus
Faxonius etnieri spp. complex
Faxonius validus
Faxonius wrighti
Lacunicambarus erythrodactylus
Procambarus ablusus
Procambarus acutus
Procambarus viaeviridis

0801 Lower Mississippi–Hatchie (*n* = 370)
Cambarus striatus
Creaserinus fodiens
Faxonius chickasawae
Faxonius etnieri spp. complex
Faxonius p. palmeri
Lacunicambarus erythrodactylus
Lacunicambarus dalyae
Lacunicambarus ludovicianus
Procambarus ablusus
Procambarus acutus
Procambarus clarkii
Procambarus hayi
Procambarus ouachitae
Procambarus viaeviridis
Procambarus vioscai paynei

0802 Lower Mississippi–St. Francis (*n* = 1)
Lacunicambarus ludovicianus

0803 Lower Mississippi–Yazoo (*n* = 3035)
Cambarellus puer
Cambarellus shufeldtii
Cambarus striatus
Creaserinus fodiens
Faxonius chickasawae
Faxonius etnieri spp. complex
Faxonius hartfieldi
Faxonius hobbsi?
Faxonius lancifer
Faxonius p. palmeri
Faxonius sp. cf *perfectus*
Hobbseus yalobushensis
Lacunicambarus erythrodactylus
Lacunicambarus dalyae
Lacunicambarus ludovicianus
Procambarus acutissimus
Procambarus acutus
Procambarus clarkii
Procambarus hagenianus vesticeps
Procambarus hayi
Procambarus hybus
Procambarus jaculus
Procambarus lylei
Procambarus ouachitae
Procambarus sp. cf *viaeviridis* sp. A
Procambarus viaeviridis
Procambarus vioscai paynei

0806 Lower Mississippi–Big Black (*n* = 939)

Cambarellus puer
Cambarellus shufeldtii
Cambarus striatus
Creaserinus fodiens
Faxonella clypeata
Faxonius etnieri spp. complex
Faxonius hartfieldi
Faxonius hobbsi?
Faxonius lancifer
Faxonius mississippiensis?
Faxonius palmeri creolanus?
Faxonius p. palmeri
Hobbseus yalobushensis?
Lacunicambarus erythrodactylus
Lacunicambarus ludovicianus
Procambarus acutissimus?
Procambarus acutus
Procambarus clarkii
Procambarus clemmeri?
Procambarus hayi?
Procambarus hybus
Procambarus jaculus
Procambarus ouachitae
Procambarus penni?
Procambarus viaeviridis
Procambarus vioscai paynei
Procambarus zonangulus

0807 Lower Mississippi–Lake Maurepas (*n* = 59)

Creaserinus fodiens
Faxonius hobbsi
Faxonius p. palmeri
Lacunicambarus ludovicianus
Procambarus acutus
Procambarus penni?
Procambarus planirostris
Procambarus vioscai