2013 SOUTHEASTERN NATURALIST 12(3):534–551

Crayfishes of the Apalachicola Ravines, Northern Florida: A Search for the Fireback Crayfish, *Cambarus pyronotus*

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Abstract - The series of steep, wooded ravines along the eastern side of the Apalachicola River in Gadsden and Liberty counties, FL, is recognized for its rich biodiversity. Little recent information is available on crayfishes of this unique ecosystem. During surveys conducted from 1939–1941, 5 taxa, including one undescribed species (now *Cambarus pyronotus* [Fireback Crayfish]), were recorded. No crayfish studies were conducted in the Apalachicola Ravines in the ensuing 60 years, and the conservation status of *C. pyronotus* remained unknown. From June 1999–February 2002, we surveyed the Apalachicola Ravines to determine distributional limits and stream-by-stream occurrence of *C. pyronotus* and evaluate its conservation status in relation to the regional system of protected lands. We recorded 8 species of crayfishes, including 4 primary burrowers and 4 aquatic species. Members of each of these 2 groups exhibited distinct microgeographic and microhabitat selection patterns, with several species showing non-overlapping microdistributions. We documented *C. pyronotus* from only 12 of 29 stream drainages surveyed, all within the middle region of the survey area, for a total range estimate of about 80 km^2. Most of the inhabited streams within this small range occur on protected lands and include multiple habitable branches.

Introduction

The lower Apalachicola River basin is recognized as a global center of biodiversity and a priority for conservation (Knight et al. 2011, Stein et al. 2000, Whitney et al. 2004). The uniqueness and diversity of the region's biota extend to both plants and animals in terrestrial and aquatic systems. The Apalachicola River system is the only river with its headwaters in the Appalachian foothills and its mouth in the Florida coastal plain, and many species have close affinities with more northern biotas. Among vertebrates, the area supports one of the highest numbers of species of reptiles and amphibians in North America north of Mexico (Means 1977). The Apalachicolan Region is equally well known for supporting high levels of endemism among fishes and aquatic macroinvertebrates (Williams and Fradkin 1999), with nearly 30 species of endemic mussels (Butler 1989, US Fish and Wildlife Service 1994), more than 20 species of aquatic snails, and 16 crayfish species (Hobbs 1942; P. Moler, FL Fish and Wildlife Conservation Commission [FWC], Gainesville, FL, unpubl. data).

Within Florida, a physiographically and biologically unique set of ravines dissects the upland escarpment along the eastern side of the Apalachicola River from just below Lake Seminole (an impoundment of the river along the Georgia state line) to the vicinity of Bristol, Liberty County, 30 km to the south. The "Apalachicola Ravines" (formerly "Torreya Ravines") provide an especially

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important refugium for plants (Harper 1914, Kurz 1933, Platt and Schwartz 1990), amphibians (Carr 1940, Means 1975), and invertebrates (Berner and Pescador 1988, Harris et al. 1998, Hubbell 1936); many species apparently extended their ranges southward during the Pleistocene. A particularly interesting component of this biota is the suite of species, including crayfishes and salamanders, that occur at the interface of terrestrial and aquatic systems.

Crayfishes of the Apalachicola Ravines: existing knowledge

Most of Florida's 50 taxa of crayfishes, allocated to 6 genera (Franz and Franz 1990), are endemic to the state. The fauna is concentrated in western and northern Florida, with only 3 species occurring in the southern half of the peninsula (south of Tampa Bay). Little recent information is available on crayfishes of the Apalachicola Ravines in Gadsden and Liberty counties, in the northwestern Florida Panhandle (Table 1). Surveys from 1934 to 1941 identified 4 species of crayfish—*Cambarus diogenes* (Devil Crayfish), *Cambarus latimanus* (Variable Crayfish), *Procambarus spiculifer* (White Tubercled Crayfish), and *Procambarus versutus* (Sly Crayfish)—and referred to the presence of a fifth unknown taxon in the ravines (Hobbs 1942). Because of small sample size and uncertainty regarding its uniqueness, Hobbs (1942) deferred formal description of a new species. Nearly 4 decades later and based solely on Hobbs' original material, Bouchard (1978) named this fifth species *Cambarus* (*Depressicambarus*) *pyronotus* (Fireback Crayfish; Taylor et al. 2007) for its unique orange-red coloration. Little crayfish collecting was conducted in the ravines for 60 years following Hobbs' work.

Cambarus pyronotus remains one of the most poorly known animals in Florida. Based on its rarity in collections, presumed dependence on fragile and restricted habitats known as steepheads (Means 1981, Whitney et al. 2004), and its small geographic range, Franz (1994) listed *C. pyronotus* as rare in an unofficial list of sensitive species, and Taylor et al. (2007) subsequently categorized it as endangered. Whether the species was widespread within the Apalachicola Ravines system or instead restricted to a limited subset of streams remained unknown, as did all aspects of its life history. Because this knowledge is critical to establishing effective conservation measures, our study sought to determine the precise distribution of *C. pyronotus* and describe the distributions, microhabitats, and species associations of other crayfishes that inhabit this small but biologically rich ravine ecosystem. We recorded observations on the reproductive habits of the crayfish subgenus *Depressicambarus* (especially of *C. pyronotus*), to increase the limited information currently available.

Field-Site Description

From June 1999–February 2002, we surveyed the Apalachicola Ravines principally for primary burrowing crayfishes, and to a lesser extent co-occurring aquatic crayfishes. Lands within the potential range of *C. pyronotus* span a north–south ecological and physiographic gradient that may regulate the species' distribution. The area encompasses an important privately owned preserve near the southern end (The Nature Conservancy's Apalachicola Bluffs and Ravines

Table 1. Previous knowledge about crayfishes of the Apalachicola Ravines and nearby stream systems, Liberty and Gadsden counties, FL. Habitat: A = aquatic, P = primary burrower, S = secondary burrower, T = tertiary burrower. Common names follow Taylor et al. (2007).

Species	Habitat	Known sites	References
Cambarus (*Lacunicambarus*) *diogenes* Girard (Devil Crawfish)	P	Apalachicola Ravines	Hobbs, 1942
Cambarus (*Depressicambarus*) *latimanus* (LeConte) (Variable Crayfish) —Locally abundant; variable, indistinguishable from north GA (type locality) specimens.	A/S	Two ravines in original Torreya State Park	Carr 1940, Hobbs 1942
Cambarus (*Depressicambarus*) *pyronotus* Bouchard (Fireback Crayfish)	P	Vicinity of Torreya State Park, including Rock Creek addition	Bouchard 1978, Hobbs 1942, Means and Studenroth 1995
Cambarus (*Depressicambarus*) *striatus* Hay (Ambiguous Crayfish) —As *C. floridanus*	P	Undocumented from Apalachicola Ravines though confirmed from streams and seepages along Chipola River (Apalachicola River tributary)	Hobbs 1942
Procambarus (*Ortmannicus) leonensis* Hobbs (Blacknose Crayfish)	A[A]	Liberty County but not Apalachicola Ravines	Hobbs 1942
Procambarus (*Hagenides*) *rogersi* Hobbs (Seepage Crayfish)	P	Nearly all counties bordering Apalachicola River but not from Apalachicola Ravines	Hobbs and Hart 1959
Procambarus (*Pennides*) *spiculifer* (LeConte) (White Tubercled Crayfish) —Often abundant in streams, does not invade shallow headwaters	A/T	FL Panhandle rivers, including lower reaches of Apalachicola Ravines	Hobbs, 1942, Hobbs and Hart 1959
Procambarus (*Pennides*) *versutus* (Hagen) (Sly Crayfish) —*C. latimanus* present in many Apalachicola Ravines streams that lack *P. versutus*	A/T	Mobile Bay drainage east to Apalachicola-Chattahoochee drainage; Little Sweetwater Creek within Apalachicola Ravines, though absent from many other streams	Hobbs 1942, 1981; Hobbs and Hart 1959

[A]Lentic but occasional in streams.

Preserve), a recently enlarged state park (Torreya State Park) near the northern end, and a high-priority state land-acquisition project (Apalachicola River Florida Forever project; Florida Department of Environmental Protection 2011) that, if completed, would consolidate and expand protected lands within the Apalachicola Ravines system (Fig. 1).

All stream systems surveyed empty into the eastern side of the Apalachicola River, which is bordered by an escarpment as high as 60 m and an alluvial swamp

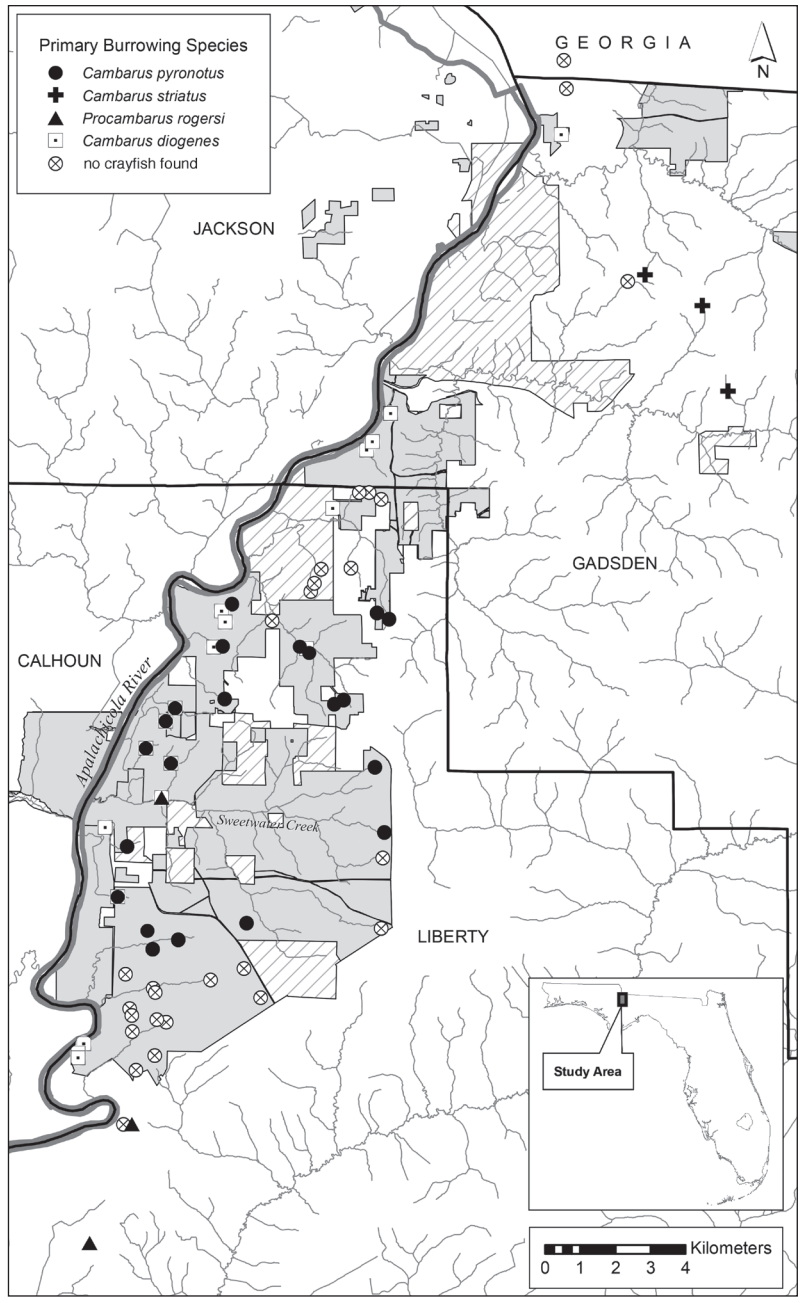

Figure 1. Map of Apalachicola Ravines study area indicating survey sites, Florida counties, state of Georgia (upper right corner of map), and principal stream branches. See Appendix 1 for all species recorded at each site. Shading = conservation lands, hatching = private lands proposed for protection.

of variable width (though typically much narrower than the broad floodplain west of the river). The study area spanned 34 km in latitudinal extent, from 1 km north of the Georgia state line (Decatur County) to 2.5 km south of Florida Highway 20 in northern Liberty County (Fig. 1). For this study, each stream system was considered to be independent if its mouth emptied separately onto the river floodplain (as seen on USGS 7.5' topographic maps). The total sample included 68 sites (accessed from different points and extending 25 to >600 m each) representing 29 stream systems.

The headwater tributaries of Apalachicola Ravines stream systems are of two types: typical gully-eroded streams that erode from the land surface, and steepheads (Means 1975, 1981; Means and Karlin 1989; Whitney et al. 2004). Means (1975) described the latter as perennially wet stream sources (first order) that originate at the foot of valley headwalls. Their side-walls are very steep (40°–90°), up to 30 m deep, and generally support mesic hardwood forests (Kwit et al. 1998, Platt and Schwartz 1990). More xerophilic, pine-dominated vegetation ocurrs on the upper slopes of gully-ravines. In both types of ravines, more hydrophilic species occupy the lower slopes and valley floors. Steepheads generally occur south of the mainstem of Sweetwater Creek (Fig. 1), with gully ravines mostly to the north (Means 1975, Means and Karlin 1989).

Though low in volume, the flows of both gully and steephead streams are relatively swift compared to many streams on the lower Coastal Plain, including most in the Florida peninsula. The smaller headwater streams in the region normally have compacted clay bottoms, which are often covered by fine sand, with increasing amounts of silt and detritus downstream. A few regional streams cut through calcareous sediments with exposed limestone.

Methods

Sampling

Based on characteristics of sites from which *C. pyronotus* had been collected in the past, specific sampling sites were identified from 7.5' USGS topographic maps, aerial photographs, and field reconnaissance. Preliminary reconnaissance of selected sites consisted of walking along first- and second-order steephead streams to find chimneys of crayfish burrows. We classified a burrow as potentially inhabited if it included one or more open entrances surrounded by relatively fresh balls of mud. Fresh burrows were excavated by hand, small shovel, and garden trowel. *Cambarus pyronotus*' habit of building deep, complex burrows among tree roots along streams rendered this task difficult and slow, yet it was still an effective method of obtaining specimens. When possible, we excavated burrows to the level of the local water table, where most specimens were situated.

To supplement manual excavation, we constructed 50 PVC pipe-traps similar to those described by Norrocky (1984). These traps provided a non-invasive sampling method with the advantage of rapid installation, minimal disruption to habitat and no need for frequent checking. PVC traps extend burrows upward artificially to lure movement of crayfishes past a one-way door into the trap. Each trap consisted of a 30–40-cm length of 5-cm-(OD) PVC pipe with a flat piece of

aluminum wired loosely just inside one end to serve as a one-way door. We used a rubber band to secure a piece of cheesecloth or vinyl screen-wire to the top of the trap to prevent crayfish escape. Traps were inserted vertically to diagonally into entrances of active burrows; this placement usually required slight enlargement of burrow openings by hand. Trapping efforts included 6 to 14 traps at selected sites for 1–24 nights. Though the method was marginally successful (6 crayfish/418 trap-nights), it was later abandoned as too time-consuming because it required return visits to a site.

We also developed a second trapping method, but we discontinued its use. For this trap, we fashioned small single-entrance funnel-traps from standard window screen. We inserted a small piece of cheesecloth-wrapped canned cat food as bait, and placed the trap in a burrow that had been excavated by hand to reach the water table. One of these traps captured a small *C. diogenes*, but most of the traps were disturbed by vertebrate animals. Additionally, although lifting potential natural cover objects (logs) may potentially yield specimens, it was ineffective in our study. We also used a dipnet to sample for aquatic crayfish at all stream sites visited as we surveyed for burrowing species.

Species identification

Crayfish identities were confirmed by R. Franz, mainly by comparison with Hobbs (1942, 1981, 1989). Diagnostic features included structure of the first pleopod of Form I males (gonopods), configuration of the annulus ventralis of females, and distinctive color patterns. We use currently accepted scientific names, though we acknowledge that 2 of the taxa (*C. diogenes* and *C. striatus* [Ambiguous Crayfish]) are not monophyletic and likely represent multiple species (Breinholt et al. 2012). A small series of voucher specimens of *C. pyronotus* from No Name Creek was preserved in 70% ethanol and deposited in the invertebrate collection of the Florida Museum of Natural History.

Results

This survey identified 8 species of crayfish: 4 taken principally from burrows, and 4 predominantly from streams. Here we present notes on taxonomy, morphology, microhabitat, natural history, local distribution of species by stream drainage (Table 2), locations of primary burrowing species (Fig. 1), and species recorded at each survey site (Appendix 1).

Survey results

Cambarus diogenes. This large species was documented in 17 of 29 streams spanning much of the study area, although not from the 2 northernmost or 3 southernmost drainages examined. Populations were abundant in the river floodplain and extended upstream in many stream systems to at least third order, and occasionally, second order tributaries. Typically, *C. diogenes* occurred downstream of other primary (and generally smaller) burrowers (Table 2, Fig. 1), with minimal overlap. However, at least 2 cases of overlap (25 m or more) with *C. pyronotus* (No Name Creek, Camp Torreya Creek) were noted; one of these involved adults of both species.

Table 2. Summary of crayfish species by stream drainage within the Apalachicola Ravines system. Stream drainages are listed from north to south by relative position of the mouth on the river floodplain. Unnamed streams were assigned names based on nearby physical or cultural features. For specific collection localities, see Appendix 1. Question marks indicate tentative identifications based on small juveniles. *P.* = *Procambarus*, *C.* = *Cambarus*.

	Primary burrowers				Stream inhabitants			
	C. diogenes	*C. striatus*	*C. pyronotus*	*P. rogersi*	*C. latimanus*	*P. spiculifer*	*P. versutus*	*P. latimanus*
Campground Creek (CC)	-	-	-	-	-	-	-	-
Northwest Chattahoochee Creek (NC)	-	-	-	-	+	-	-	-
Chattahoochee Nature Park Creek (CN)	+	-	-	-	?	-	-	-
Mosquito Creek (MC)	-	+	-	-	+	-	-	-
Flat Creek (FC)	-	+	-	-	+	+	-	-
Boat Ramp Creek (BR)	+	-	-	-	-	+	-	-
North of Aspalaga Landing Creek (AN)	+	-	-	-	+	-	-	-
Aspalaga Landing Creek (AL)	+	-	-	-	+	+	-	-
Short Creek (SC)	+	-	+	-	+	+	-	-
Graham Cemetery (GC)	-	-	-	-	+	+	-	-
Rock Creek (RC)	+	-	+	-	+	+	-	-
Mile 95 Creek (MF)	-	-	+	-	+	-	-	-
Indian Relic Creek North (IN)	+	-	-	-	-	-	-	-
Indian Relic Creek South (IS)	+	-	-	-	-	-	-	-
Weeping Ridge Creek (WR)	+	-	+	-	+	-	-	-
Rock Bluff Landing Creek (RB)	-	-	+	-	+	-	-	-
Long Branch (LB)	+	-	+	-	+	-	-	-
Camp Torreya Creek (CT)	+	-	+	-	-	-	-	-
Mile 90 Creek (MN)	+	-	+	-	-	-	-	-
Sweetwater Creek (SW)	+	-	+	+[1]	-	+	+	-
St. Stephens Creek (SS)	+	-	+	-	-	+	-	-
No Name Creek (NN)	+	-	+	-	+	+	-	-
Beaverdam Creek (BD)	-	-	+	-	-	+	+	-
Little Sweetwater Creek (LS)	-	-	-	-	-	-	+	-
Alum Bluff Creek (AB)	+	-	-	-	-	-	-	-
Alum Bluff Seep (AS)	+	-	-	-	-	-	-	-
Kelley Branch (KB)	-	-	-	-	?	-	+	-
St. Luke Creek (SL)	-	-	-	+	-	-	-	+
First Street Creek (FS)	-	-	-	+	-	-	-	+

[1]Presence based on a June 2009 collection by P. Moler.

All but the smallest juveniles of *C. diogenes* from the Apalachicola Ravines were olive to tan in color, with red to purplish-red cheliped tips, rostrum, and cephalic portions of the cephalothorax and abdomen; a reddish band crosses each abdominal segment. This coloration is similar to the concolorous pattern noted in Georgia specimens by Hobbs (1981), but is distinctly different from the pattern observed in other northwestern Florida populations (R. Franz, pers. observ.), which supports suggestions (Breinholt et al. 2012, Hobbs 1942) that the *C. diogenes* group is in need of review.

Cambarus latimanus. Dipnet sampling yielded many, mostly juvenile *C. latimanus* from first-order and small second-order streams within at least 13 stream systems, but we did not detect the species in the 7 southernmost ravines. We observed a few adult individuals in-stream, and others were taken from burrows, including a Form I male on 22 March 2001 and an adult female on 3 April 2003.

Cambarus pyronotus. This species was found at 21 sites within 12 drainages, including streams both north and south of the original boundaries of Torreya State Park. No *C. pyronotus* were collected from the 8 northernmost and 6 southernmost streams in the study area. We supplemented our observations with earlier unpublished sightings (all from within our determined range); P. Moler collected the species during the early 1990s from St. Stephens Creek (P. Moler, FWC, Gainesville, FL, unpubl. data; Appendix 1), K. Studenroth captured several specimens in pitfall traps associated with drift fences during a 1994–1995 herpetological survey of the Rock Creek addition to Torreya State Park (K. Studenroth, Northwest FL Environmental Conservancy [NWFLEC], Marianna, FL, unpubl. data), and S. Humphrey provided behavioral notes to accompany a photograph taken in 1978 (S. Humphrey, FL Museum of Natural History [FLMNH], Gainesville, FL, unpubl. data). Though often abundant where found, *C. pyronotus* may inhabit a range that extends no more than 13 km from north to south and 8 km from east to west.

Observations confirm that *C. pyronotus* is a primary burrower restricted to first- and second-order tributaries flowing through closed-canopy hardwood forests. Crayfishes of all demographic classes were removed from burrows constructed within a few centimeters to several meters from stream edges. Burrow size and complexity generally increased with crayfish size. Burrows of small juveniles were relatively simple, often with a single entrance. Those of adults had one to 5 entrances, with tunnels extending laterally to vertically for as much as a meter or more in each direction. Burrow depth varied with the upslope distance of the burrow entrance from the stream; thus, depths ranged from a few centimeters (typical of small juveniles that burrowed just above the stream) to an estimated 1.5 m (too deep and with too many plant roots to be excavated). All burrows had at least one tunnel leading to a chamber that reached groundwater. Most crayfishes were encountered only after digging to this chamber.

Cambarus striatus. The current study collected *C. striatus* (name subject to future revision: Breinholt et al. 2012) only from burrows in stream systems north of those inhabited by *C. pyronotus*. Specifically, *C. striatus* occurs along tributaries of Mosquito and Flat creeks, both in Gadsden County, just north of Liberty

County. These are the only relatively large and complex drainages among the 8 streams surveyed north of Short Creek, the northernmost creek confirmed in this study to support *C. pyronotus*. On 10 November 2000 along Flat Creek, tiny but free young were observed cohabiting in burrows with 2 adult females.

Procambarus leonensis. Within the current study area, this species was captured with dipnets only in the 2 southernmost streams (St. Luke and First Street creeks). Because these 2 ravines have lower topographic profiles as a result of sand overburden reduction from Pleistocene erosion, they qualify only marginally as true Apalachicola Ravines.

Procambarus rogersi. This primary burrower was excavated along the two southernmost streams in the present survey, the same ones that produced the only *P. leonensis* collected. These sites are separated from the southernmost occurrence of *C. pyronotus* by 7 km. Subsequent to the current survey, P. Moler collected *P. rogersi* at a site along lower Sweetwater Creek (SW-2) during June 2009 (P. Moler, FWC, Gainesville, FL, unpubl. data).

Procambarus spiculifer. Dipnetting yielded mostly small specimens from second-order and, very rarely, first-order tributaries in 10 drainages that spanned much of the study area, though none south of the range of *C. pyronotus*. Our surveys were concentrated in shallower first- and second-order streams, and we did not sample the lower portions of other systems where *P. spiculifer* may also be present

Procambarus versutus. We found this species in only 4 drainages, all in the southern half of the study area. We located none north of the large Sweetwater Creek system that physiographically separates steephead-dominated from gully-dominated drainages. Form I males were taken on 16 June 2000, 18–19 September 1999, and 6 November 1999.

Life-history data for *Cambarus pyronotus*

The current survey revealed that *C. pyronotus* maintained at least some activity year-round, though burrows were frequently plugged during cold weather and during droughts. Individuals collected during colder months (December–February) were often lethargic until handled. Although numbers of burrows were not recorded, the species was clearly abundant at some sites and rare at others. We obtained crayfish only from burrows and never observed surface activity, though there is evidence that the latter occurs at least occasionally. Studenroth intercepted both immature and mature specimens, including an ovigerous female (2 April 1995), at drift fences placed adjacent to streams during a herpetological survey of Torreya State Park in May–June 1994 and April 1995 (K. Studenroth, NWFLEC, unpubl. data). Humphrey photodocumented abundant and active *C. pyrontus* on the surface, during mid-morning observations in 1978 (S. Humphrey, FLMNH, Gainesville, FL, unpubl. data).

Although not recorded for all specimens, data revealed the following demographic classes by dates—Form I males (including one freshly molted): 16–17 June and 19 October 1999; Form II males: 9 Janauary, 9 March, 21 May, and 4–6 and 17 June 2000; ovigerous females: 2 April 1995 (K. Studenroth, NWFLEC,

unpubl. data), 5 June 1999; female with free young in burrow: 16 June 2000; non-ovigerous females: 16 April 2000, 23 May 2001, 4–6 June 1999, 11 August 2001, 24 and 30 September 1999, and 17 and 23 November 1999; and juveniles (< 4 cm total length): 9 January, 9 March, and 16 April 2000, 23 May 2001, 4–6 and 17 June 2000, and 18 September 1999. An increase in intensity of red pigmentation with age (size) was conspicuous; small juveniles typically ranged from brownish to pale salmon, which changed to bold orange-red to red in adults.

The ovigerous female collected 5 June 1999 at No Name Creek carried 38 orange-colored eggs; diameters of 5 eggs averaged 2.3 mm. The burrow was located in the bank 2.1 m from a small, sand-bottomed tributary with a maximum water depth of 3 cm and width of 1.3 m; the burrow opened 30 cm above water level. Water and burrow-mud temperatures were 23 °C. The 2 to 3 dozen tiny young discovered sharing a female's burrow on 16 June 2000 at Camp Torreya Creek were ≈6 mm in total length.

Discussion

The range of *C. pyronotus*, as delimited by this study, consists of a series of small stream systems with a latitudinal extent of 13 km, longitudinal extent of 8 km, and an area of 80 km^2. These parameters indicate that this species is one of the most geographically restricted surface (non-stygobitic) crayfishes in North America (NatureServe 2012, Taylor et al. 2007). Interestingly, this range is bisected by a geological break described by Means (1998) as the most important in the Panhandle of Florida. Streams north of the break (at Sweetwater Creek) are gully-eroded ravines formed in Miocene clays, sands, and gravels, whereas streams to the south are steephead valleys developed in deep, porous Plio-Pleistocene sand deposits (Means 1998).

Our life-history observations supplement those provided by Bouchard (1978), who recorded ages and sexes of the type series (Hobbs collection) as follows. The sole Form I male (holotype) was collected 28 November 1941, along with 8 females, one of which was listed as a juvenile. The sample also included a Form II male collected 8 April 1941; 7 juvenile males collected on 3 dates (17 March 1939, 13 December 1939, and 8 April 1941); an adult female collected 8 April 1941; and 4 juvenile females collected on 2 dates (17 March 1939 and 8 April 1941). Table 3 depicts minimal seasonal occurrence of demographic classes

Table 3. Monthly distributions of observed demographic classes of *Cambarus pyronotus* (+), including data from Hobbs'1939–1941 collection (H) as presented by Bouchard (1978).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
♂ I						+				+	H	
♂ II	+		+	H	+	+						
♀, ovigerous				+		+						
♀ with young						+						
♀, non-ovigerous				+/H	+	+		+	+		+/H	
Juvenile <4 cm	+		+/H	+/H	+	+			+		H	H

based on our combined data sets, although neither study attempted to spread survey efforts evenly across the year. The small number of ova and neonates found with reproductive females in our study, if representative of entire clutches, contrasts with parameters normally seen in crayfishes, but larger samples are needed to corroborate this potential difference.

Type locality of *Cambarus pyronotus*

Some confusion exists about the type locality of *C. pyronotus* as well as Hobbs' other collecting sites as listed by Bouchard (1978). The first site, a ravine in the northern part of Torreya State Park (TSP), was mentioned by Hobbs (1942) and must be either our Mile 95 Creek or the lowermost tributary of Rock Creek (both of which support the species). The second site, Rock Bluff, is described as a deep ravine in TSP. However, Rock Bluff, as shown on topographic maps, is 3 km southeast of the original park, at the headwaters of the Rock Creek drainage; our Rock Bluff Landing Creek is a deep ravine emerging on the river at Rock Bluff Landing, but this drainage lies immediately south of the original park. Whether Hobbs meant this creek or a large tributary of Rock Creek that occupies much of the eastern portion of the original park is uncertain, although the latter is suspected. The third and fourth sites listed by Bouchard (1978) are ravines south of Indian Lodge and south of Indian Ridge, both in TSP. In all likelihood, Bouchard mistakenly used the word "lodge" for "ridge" and these represent the same site. Because it produced the only Form I male available to Hobbs, Bouchard selected this as the type locality. However, he then declared this creek to be Beaver Dam Creek, but the only creek known locally by that name (though more often spelled Beaverdam) lies 8 km south of TSP. Clearly, the description of the type locality as lying south of Indian Ridge in TSP and possessing a waterfall can only be the unnamed creek that we herein call Weeping Ridge Creek, after the park's Weeping Ridge Campground situated above its northern slope. *Cambarus pyronotus* was readily found here in this study, and hence we redesignate the type locality as Weeping Ridge Creek in Torreya State Park, Liberty County, FL.

Microdistributional patterns

The Apalachicola Ravines study area supports a crayfish fauna that includes 4 primary burrowing species and 4 principally aquatic species; the ranges of some appear to be parapatric to the restricted range of *C. pyronotus*. Although our principal goal was to determine the extent of occurrence of *C. pyronotus*, our data suggest a number of distributional relationships among the 8 species. Foremost among them are the essentially non-overlapping distributions of the three smaller primary burrowing species (*C. pyronotus, C. striatus,* and *P. rogersi*) that occupy headwater tributaries within the Apalachicola Ravines. Along first- and smaller second-order streams, we found *C. striatus* only in drainages north of the range of *C. pyronotus*. This observation supports the suggestion of Hobbs (1942), who collected *C. striatus*, (which he referred to as *C. floridanus*) only from seepages and creeks along the Chipola River (an Apalachicola River tributary) and Ochlockonee River (just east of the Apalachicola), but who speculated that it might

eventually be found in some small tributaries of the Apalachicola River, though perhaps not sympatrically with *C. pyronotus*.

Similarly, we collected *P. rogersi* only from drainages south of the range of *C. pyronotus*, although Moler found it in Sweetwater Creek, but downstream of tributaries inhabited by *C. pyronotus*. The much larger *C. diogenes* inhabits the entire study area (and beyond) but mostly occurs in floodplain habitat and the lower portions of stream drainages, exhibiting only minimal within-stream overlap with the 3 smaller species.

Our data for principally aquatic crayfishes are less comprehensive but suggest potential microgeographic differences similar to those noted for primary burrowers. Within the study area, *C. latimanus*, *P. versutus*, and *P. leonensis* appear to have complementary distributions. *Procambarus leonensis* was collected from only the 2 southernmost streams, as was the primary burrower *P. rogersi*. Only 4 streams, all in the southern half of the area (Sweetwater Creek and 3 smaller drainages to the south), were found to support *P. versutus*. In contrast, *C. latimanus* occupies at least 12 of 19 streams north of Sweetwater Creek, but was found in only one to the south (No Name Creek, which may lack *P. versutus*). Thus, we observed no instances of co-occurrence of these 3 species. *Procambarus spiculifer*, on the other hand, shared multiple streams with both *C. latimanus* and *P. versutus*, although all *P. spiculifer* captured in first- (infrequent) and second-order (more frequent) streams were juveniles. Hobbs (1942) also found the local distributions of *P. versutus* and *C. latimanus* in the Apalachicola Ravines to be complementary, and noted that *P. versutus* penetrated further upstream than *P. spiculifer* in shared drainages.

Conservation status of the Apalachicola Ravines crayfish fauna

Because of land acquisition efforts by the State of Florida and The Nature Conservancy, a substantial portion of the Apalachicola Ravines ecosystem is now protected. Torreya State Park was established in 1944 with the protection of 430 ha that included a few smaller ravines, but a series of land acquisitions begun in 1990 (including much of the Rock Creek and Sweetwater Creek drainages) vastly expanded its size to 5558 ha. The Nature Conservancy began acquiring lands south of the original park for its Apalachicola Bluffs and Ravines Preserve (ABRP) in 1982 and now manages 2548 ha (Florida Natural Areas Inventory 2012). Most of the range of *C. pyronotus* is encompassed by these combined protected lands. North of the range of *C. pyronotus*, much of the remaining private land bordering the river and extending to within 2.5 km of the Georgia border is under consideration for acquisition by the state (Apalachicola River Florida Forever project), although funding to secure this land remains problematic. The city of Chattahoochee owns a 51-ha nature park with two small ravines located 2 km south of the Georgia border. Despite these efforts, the two large drainages at the northern end of our study area, Mosquito and Flat creeks, remain unprotected, although portions are under consideration for state protection. Thus, among primary burrowers, most of the range of *C. pyronotus* is now protected;

many of these same lands also support *C. diogenes*. *Cambarus striatus* is virtually unprotected in this region, as may be *P. rogersi*, although the latter might occur on protected lands elsewhere in Florida. Among stream forms, *P. versutus*, *P. spiculifer*, and *C. latimanus* all occur in several protected Apalachicola Ravines stream systems; *P. leonensis* does not, but is more widely distributed in lentic habitats elsewhere in the Florida Panhandle.

It is noteworthy that within one sampled stream system (Graham Cemetery Creek), crayfish burrows as well as aquatic crayfishes appeared to be absent from first-order streams exhibiting extensive disturbance from rooting and wallowing by *Sus scrofa* L. (Feral Hogs). Aquatic crayfish did occur in undisturbed higher order reaches of Graham Cemetery Creek. Headwaters of stream systems immediately north and south of this stream support *C. pyronotus* as well as aquatic species, which underscores the value of bringing the remaining private holdings within the Apalachicola Ravines system into public or conservation ownership, where threats such as disturbance by Feral Hogs can be addressed. Private lands important for acquisition include stream systems occurring both north and south of the range of *C. pyronotus*. However, even on protected lands, Feral Hogs constitute a continuing threat that requires regular control, as evidenced by increased hog populations on the ABRP in 2003–2004. Even if eliminated within protected areas, hogs readily reinvade from adjacent private lands. For example, although SW-1 (on ABRP) still supported a robust *C. pyronotus* population in March 2004, evidence of hog rooting in the streamside microhabitat used by this crayfish raises concerns.

On remaining private lands, commercial silviculture threatens the ecological integrity of inhabited streams. Recent clearcutting of timber along Short Creek at the time of our study produced erosion and siltation of that stream system, which supports the northernmost known population of *C. pyronotus*. Similarly, Means and Studenroth (1995) noted heavy sedimentation in the middle reaches of Rock Creek, the second largest drainage supporting the species, as a result of mechanical disturbance associated with silviculture, excavation of borrow pits, and construction of roads in the uplands. Thus, even though land protection efforts have secured a substantial portion of the Apalachicola Ravines ecosystem that supports *C. pyronotus* and a variety of other rare species, long-term conservation efforts will require continued vigilance and action by land managers charged with preservation of this globally significant biota.

Acknowledgments

We thank The Nature Conservancy, especially Rick Studenmund and Jon Blanchard, for funding our field work. The St. Joe Company, The Nature Conservancy, and the Florida Department of Environmental Protection Division of Recreation and Parks granted permission to conduct research on their lands. Grayal Farr, Karl Studenroth, and Mike Wilson provided invaluable field assistance. Dick Bartlett, Steve Humphrey, Barry Mansell, Bruce Means, Paul Moler, and Karl Studenroth shared data and photographs. Bruce Means and Paul Moler reviewed the manuscript, and Mike O'Brien and David Almquist

assisted with figure preparation. The Florida Fish and Wildlife Conservation Commission, courtesy of Stasey Whichel, supported publication through administration of a State Wildlife Grant funded by the US Fish and Wildlife Service.

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Appendix 1. Collection sites for crayfish within the Apalachicola Ravines system; all sites except Campground Creek are in Florida stream drainages and are listed from north to south by relative position of stream mouth on the river floodplain. Approximate midpoints of latitude and longitude are provided for stream stretches covering several hundred meters, and for groups of subsites (lower case letters following site number; typically these comprise nearby first-order and adjacent second-order streams) sufficiently close to be considered a single site. Species collected follow site coordinates and are indicated by 2-letter acronyms (absence of acronyms indicates no crayfish collected at site). Primary burrowers: *CD = Cambarus diogenes*, *CS = Cambarus striatus*, *CP = Cambarus pyronotus*, *PR = Procambarus rogersi*. Aquatic inhabitants: *CL = Cambarus latimanus*, *PS = Procambarus spiculifer*, *PV = Procambarus versutus*, *PL = Procambarus leonensis*.

Campground Creek, Decatur County, GA.
CC-1: 30°42'57"N, 84°50'59"W
Northwest Chattahoochee Creek, Gadsden County
NC-1: 30°42'31"N, 84°50'56”W; *CL*
Chattahoochee Nature Park Creek, Gadsden County
CN-1: 30°41'48"N, 84°51'01"W; *CD*, *CL*?[A]
Mosquito Creek, Gadsden County
MC-1: 30°39'39"N, 84°49'31"W; *CS*, *CL*
Flat Creek, Gadsden County
FC-1: 30°39'11"N, 84°48'29"W; CS, PS
FC-2: 30°39'33"N, 84°49'49"W; *CS*?, *CL*, *PS*
FC-3: 30°37'52"N, 84°48'01"W; *CS*
Boat Ramp Creek, Gadsden County
BR-1: 30°37'29"N, 84°54'02"W; *CD*, *PS*
North of Aspalaga Landing Creek, Gadsden County
AN-1: 30°37'03"N, 84°54'21"W; *CD*, *CL*
Aspalaga Landing Creek, Gadsden County
AL-1: 30°36'55"N, 84°54'27"W; *CD*, *CL*, *PS*
Short Creek, Liberty County
SC-1: 30°34'25"N, 84°54'15"W; *CP, CL*, *PS*
SC-2: 30°36'16"N, 84°54'24"W; *CL*
SC-3: 30°36'16"N, 84°54'35"W; *CL*
SC-4: 30°36'01"N, 84°55'03"W; *CD*
SC-5: 30°36'10"N, 84°54'11"W; *CL*
SC-6: 30°35'06"N, 84°54'43"W; *CL*, *PS*
SC-7: 30°34'19"N, 84°54'02"W; *CP*, *CL*, *PS*
Graham Cemetery Creek, Liberty County
GC-1:30°34'44"N, 84°55'26"W; *CL*
GC-2:30°34'52"N, 84°55'22"W
GC-3:30°35'05"N, 84°55'15"W; *CL*, *PS*
Rock Creek, Liberty County
RC-1: 30°33'53"N, 84°55'37"W; *CP*
RC-2: 30°33'47"N, 84°55'27"W; *CP*
RC-3: 30°34'17"N, 84°56'07"W; *CD?*
RC-4: 30°33'04"N, 84°54'50"W; *CP*, *CL*
RC-5: 30°33'00"N, 84°55'00"W; *CP*, *CL*
RC-6: 30°33'52"N, 84°55'30"W; *PS*
RC-7: 30°33'51"N, 84°55'30"W; *CD*, *CL*

Mile 95 Creek, Liberty County
MF-1: 30°34'32"N, 84°56'50"W; *CP*, *CL*
Indian Relic Creek North, Liberty County
IN-1: 30°34'25"N, 84°57'01"W; *CD*
Indian Relic Creek South, Liberty County
IS-1: 30°34'15"N, 84°56'57"W; *CD*
Weeping Ridge Creek, Liberty County
WR-1: 30°33'53"N, 84°57'00"W; *CP*
WR-2: 30°33'52"N, 84°57'09"W; *CD, CL*
Rock Bluff Landing Creek, Liberty County
RB-1: 30°33'04"N, 84°56'57"W; *CP*, *CL*
Long Branch, Liberty County
LB-1 ab: 30°32'55"N, 84°57'50"W; *CD*, *CP*, *CL*
Camp Torreya Creek, Liberty County
CT-1: 30°32'43"N, 84°58'00"W; *CD*, *CP*
Mile 90 Creek, Liberty County
MN-1: 30°32'18"N, 84°58'21"W; *CD*, *CP*
Sweetwater Creek, Liberty County
SW-1 abc: 30°32'04"N, 84°57'54"W; *CD*, *CP*, *PS*
SW-2: 30°31'32"N, 84°58'04"W; CD^{B}, PR^{B}, *PS*
SW-3: 30°32'02"N, 84°54'16"W; *CP*, *PV*
SW-4: 30°31'02"N, 84°54'05"W; *CP*, *PV*
SW-5: 30°30'38"N, 84°54'07"W; *PV*
SW-6: 30°29'33"N, 84°54'08"W; *PV*
SW-7: 30°29'37"N, 84°56'32"W; *CP*, *PV*
St. Stephens Creek, Liberty County
SS-1 abcdef: 30°30'47"N, 84°58'40"W; *CP*, *PS*
SS-F: 30°31'04"N, 84°59'04"W; *CD*
No Name Creek, Liberty County
NN-1: 30°30'00"N, 84°58'50"W; *CD*, *CP*, *CL*, *PS*
Beaverdam Creek, Liberty County
BD-1: 30°29'21"N, 84°57'45"W; *CP*, *PS*, *PV*
BD-2: 30°29'12"N, 84°58'12"W; *CP*, *PV*
BD-3: 30°29'29"N, 84°58'18"W; *CP*
Little Sweetwater Creek, Liberty County
LS-1 abcdef: 30°28'44"N, 84°57'10"W; *PV*
LS-2: 30°28'28"N, 84°56'16"W; *PV*
LS-3: 30°28'49"N, 84°58'41"W
LS-4: 30°28'55"N, 84°56'34"W; *PV*
LS-5: 30°28'32"N, 84°58'9"W
LS-6: 30°28'36"N, 84°58'11"W; *PV*
LS-7: 30°28'17"N, 84°58'36"W
LS-8: 30°28'11"N, 84°58'34"W; *PV*
Alum Bluff Creek, Liberty County
AB-1: 30°27'44"N, 84°59'25"W; *CD*
Alum Bluff Seep, Liberty County
AS-1: 30°27'35"N, 84°59'31"W; *CD*
AS-F: 30°27'31"N, 84°59'31"W; *CD*

Kelley Branch, Liberty County
KB-1: 30°27'34"N, 84°58'9"W; *CL?*, *PV*
KB-2: 30°28'5"N, 84°57'57"W; *PV*
KB-3: 30°28'7"N, 84°58'7"W; *PV*
KB-4: 30°27'56"N, 84°58'33"W; *PV*
KB-5: 30°27'20"N, 84°58'29"W; *PV*
St. Luke Creek, Liberty County
SL-1: 30°26'30"N, 84°58'42"W
SL-2: 30°26'30"N, 84°58'33"W; *PR*, *PL*
First Street Creek, Liberty County
FS-1: 30°24'40"N, 84°59'17"W; *PR*, *PL*

[A]Question marks indicate tentative identification based on small juveniles.
[B]Based on June 2009 collection by P.E. Moler.