Article

Two new species of freshwater crayfish of the genus *Faxonius* (Decapoda: Cambaridae) from the Ozark Highlands of Arkansas and Missouri

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Abstract

Two new species of freshwater crayfish are described from the Ozarks Plateau of northern Arkansas and southern Missouri. Both species are restricted to the mainstem of rocky streams that are at least fourth-order or greater in size. Recent genetic and morphological investigations of the coldwater crayfish, *Faxonius eupunctus* Williams, 1952, indicated that it was actually composed of several undescribed species. *Faxonius eupunctus* is herein restricted to just the Eleven Point River system. *Faxonius roberti*, new species is found in the mainstem of the Spring and Strawberry river systems in northern Arkansas. It differs from *F. eupunctus* by lacking a male Form-I gonopod with a distal spatulate mesial process, and presence of two spines on the dorsal side of the merus, where *F. eupunctus* typically has 1 spine. *Faxonius wagneri*, new species is known from a 54 mile (86 km) stretch of the Eleven Point River mainstem, ranging from just southeast of Greer, Missouri to just north of Birdell, Arkansas. *Faxonius wagneri* can be differentiated from both *F. eupunctus* and *Faxonius roberti* **sp. nov**. by using the male Form-I and Form-II gonopods, the shape of the chelae, and the female annulus ventralis. In *F. wagneri*, the terminal elements of the first pleopod are almost twice as long as those in *F. eupunctus* and *F. roberti*, with the tips of the appendage reaching the posterior base of the first pereiopod when the abdomen is flexed forward, whereas, in the other two species, these elements only reach the base of the second pereiopod. The species also possesses two spines on the dorsal side of the merus of the first pereiopod, which helps distinguish it from *F. eupunctus*.

Key words: crayfish, *Faxonius*, life history, morphology, new species, *Orconectes*, phylogeny

Introduction

The Ozark Highlands of Arkansas and Missouri contain a diverse array of unique aquatic taxa that are known only from this physiographic region. Among these taxa are a variety of freshwater crayfish that can be found nowhere else. As a result, many of these species are of conservation concern for reasons such as overall rarity, restricted geographic distributions, impacts of invasive aquatic species (including other crayfish), or anthropogenic modifications to their freshwater environments.

Faxonius eupunctus Williams, 1952, formerly of the genus *Orconectes* (see Crandall & De Grave 2017), is a species of greatest conservation need in both Arkansas and Missouri due to its limited geographic distribution and overall rarity, even though at some sites it may be locally abundant (e.g., near Greer Spring in Missouri). The species is known only from the mainstems of the Eleven Point, Spring and Strawberry river systems in Arkansas and Missouri. Until recently, there was very little known about this species aside from a general notion of its geographic distribution (e.g., Pflieger 1996), thus, the Missouri Department of Conservation (MDC), Arkansas Game and Fish Commission (AGFC), and the US Fish & Wildlife Service all had vested interests in discerning more about this species to inform their species status assessments and long-term conservation strategies, especially since the species was being considered as a possible candidate for listing under the *Endangered Species Act* (ESA).

Prior to this study, it was also noted by an ADFC researcher that some specimens from the Eleven Point River

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in northern Arkansas appeared to have slightly different coloration and that the terminal elements of the male Form-I first pleopod was longer in these individuals. Initially, it was thought that these specimens might represent *F. eupunctus* × *F. ozarkae* hybrids, but that has since been ruled out based on genetic analyses (Fetzner *et al*. 2013). Several projects examining the ecology, distribution, genetics and morphological variaion were ultimately funded by these agencies. These projects resulted in the discovery that *F. eupunctus* was actually comprised of several cryptic species, and these new forms are herein described.

Materials and methods

Materials Examined. For the morphological analyses, preserved specimens contained in the crustacean collections at the Carnegie Museum of Natural History (CMNH), Pittsburgh, Pennsylvania and the Illinois Natural History Survey (INHS), Champaign, Illinois were examined and measured. Genetic samples for phylogenetic analyses consisted of recently collected specimens by the first author, as well as some data that was generated as part of a previous project (Fetzner *et al*. 2013).

Morphological Analyses. A variety of morphological measurements and meristic characters were captured for each of the 196 specimens, including some from the carapace (n=15), rostrum (n=11), chela (n=20), male gonopod (n=7) or female annulus ventralis (n=4), as well as other characters (n=18), such as spine counts. Measurements were captured using a digital Vernier caliper (Mitutiyo Absolute Digimatic Caliper, model CD-8"CX), with a direct computer connection, to the nearest 0.01 mm. Measurements were entered directly into a web form and saved to an online CMNH database (Crayfish Morphology Database). Photos of each specimen were captured from different angles to highlight structures or features and were uploaded to the database.

After individual measurements were captured, a set of 18 morphometric ratios were calculated based on features that are commonly used to distinguish crayfish species. These ratios were: 1. carapace length/maximum carapace width (CPL.CPW), 2. carapace length/maximum carapace depth (CPL.CPD), 3. postorbital carapace length/maximum carapace width (POCL.CPW), 4. postorbital carapace length/maximum carapace depth (POCL.CPD), 5. rostrum length/carapace length (RL.CPL), 6. areola length/carapace length (AL.CPL), 7. areola length/areola width at its narrowest point (AL.AW), 8. chela length/carapace length (CL.CPL), 9. chela length/ maximum chela width (CL.CW), 10. chela length/chela depth (CL.CD), 11. palm length/chela length (PL.CL), 12. dactyl length/chela length (DL.CL), 13. propodus length/chela length (PPL.CL), 14. central projection length/total gonopod length (CePL.TGL), 15. mesial process length/total gonopod length (MPL.TGL), 16. annulus ventralis width/annulus ventralis length (AVW.AVL), 17. antennal scale length/maximum antennal scale width (ASL.ASW), and 18. Acumen Length/Rostrum Length (AcL.RL). A single meristic character, the number of spines on the dorsal surface of the merus of the cheliped (DMS), was also used in the analysis since there appeared to be a geographic pattern associated with this character. Other meristic characters and spine counts contained too much variation and overlap between groups to be considered useful.

Statistical Analyses. All statistical analyses were carried out in version 3.4.1 of the R statistical software program (R Core Team 2017). Prior to the analyses, any individual with missing data for one or more of the variables was excluded from the dataset. Specimens possessing only regenerated chelae, which were measured due to a lack of normal chelae, were also removed before analysis. The average differences of 18 morphometric ratios and 1 meristic character were analyzed using one-way ANOVAs to characterize the amount of variation present in each variable. Each morphometric ratio was considered the response variable while species was used as the predictor variable. Post-hoc analyses were conducted using a TukeyHSD test from the R package *psych* (Revelle 2016).

Multivariate analyses utilized non-metric multidimensional scaling (NMDS) to reduce the morphometric ratio matrix to two dimensions using the *metaMDS* function in the *vegan* package (Oksanen *et al.* 2012). Since several important characters in the set of ratios were sex-related, several independent NMDS analyses were conducted. The first excluded the gonopod (CePL.TGL and MPL.TGL) and annulus ventralis (AVW.AVL) characters so all individuals could be run in the same analysis. The second analysis created separate datasets for females and males, with males also being subset into Form-I and Form-II datasets. The ordination in each analysis was based on the Bray-Curtis distance measure. An ordination plot was then generated based on the Pearson Correlation Coefficient for each ratio against the NMDS axis. A stress value ≤ 0.20 was considered to be an adequate solution (McCune & Grace 2002), while those ≤ 0.1 are considered fair and those ≤ 0.05 indicate a good fit.

Genetic Analyses. DNA was extracted using a high salt precipitation method described in detail by Fetzner and Crandall (2003). PCR amplifications of the mitochondrial DNA (mtDNA) cytochrome c oxidase subunit I gene (COI; EC 1.9.3.1) were conducted in a total volume of 25 μL. Each PCR reaction utilized a PCR master mix which contained the following components: 4 mM magnesium chloride, 400 μM each dNTP, and GoTaq® G2 Hot start DNA polymerase (Promega). To this mix was added 1 μM of each primer and 300 ng of sample DNA. PCR cycling conditions included an initial denaturizing step of 2:00 min at 95°C followed by 50 cycles performed at 95°C for 0:30 sec, 50°C for 0:30 sec, and 72°C for 1:30 min. A final extension at 72°C for 10 min was conducted, followed by a final soak at 4°C (usually overnight) until samples could be processed further. Primers used in the reaction were the standard set of Folmer *et al.* (1994) primers, except that a universal primer sequence was added to the 5' end of the Forward and Reverse COI primers (T7 and T3, respectively). These non-degenerate, non-homologous 5' tails (in bold) were then used to sequence all resulting PCR products. Primer sequences used were: HybLCO 5'– **TAATACGACTCACTATAGG**GGGTCAACAAATCATAAAGATATTGG–3' and Hyb2HCO 5'– **ATTAACCCTCACTAAAG**TAAACTTCAGGGTGACCAAAAATCA–3'. The PCR reactions were checked for amplification products in the correct size range (~700 bp) by electrophoresis through a 1% agarose gel (run at 140 volts for 20 min in TAE buffer). Viable PCR products were then cleaned and purified using MultiScreen PCR$_{\mu 96}$ plates (Millipore, Cat#: LSKMPCR50) in preparation for DNA sequencing by a commercial sequencing service (Eurofins Genomics). Sequences obtained from the sequencing facility were initially corrected and aligned using the program Sequencher v5.01 (GeneCodes Corp, Inc.), and then adjusted, as necessary, by eye.

After alignment in Sequencher, the COI barcode sequence data were checked for indels and also translated into the corresponding amino acids using Mesquite v3.04 (Maddison & Maddison 2015) to verify the presence of an open reading frame (i.e., no stop codons or indels), and to avoid incorporating mtDNA nuclear pseudogenes (=numts) in the analysis. The data were then imported and analyzed using PAUP* v4.0a158 (Swofford 2002) in order to output a matrix of uncorrected p-distances, which were used to calculate average within and among species divergences.

Phylogenetic analyses were conducted to examine relationships among the taxa of interest as well as among other crayfish species from both east and west of the Mississippi River (Appendix 1). Different models of DNA sequence evolution were tested for their fit to the COI dataset. Twenty-four different models (three substitution schemes) of DNA sequence evolution were tested using jMODELTEST v2.1.15 (Darriba *et al.* 2012) with the best model selected by BIC for the Bayesian analyses. The estimated phylogeny was generated using MrBayes v.3.2.6 (Ronquist & Huelsenbeck 2003). Two simultaneous independent runs were conducted with one cold chain and three hot chains. The program was run for 2.5×10^6 generations, with sampling every 1000 generations. Split frequencies below 0.01 were used to check for convergence, and the first 25% of trees were discarded as burn-in. The two independent runs were then combined after the deletion of burn-in and a majority rule consensus tree was created with nodal confidence for the trees assessed using node posterior probabilities. Trees were then examined in FigTree v1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/).

Results

A variety of morphological measurements were gathered from a total of 196 specimens of *F. eupunctus*, *F. roberti* **sp. nov.**, and *F. wagneri* **sp. nov.**, which represented 41 different specimen lots and 20 distinct localities. Specifically, 87 specimens (22 lots) came from the CMNH collection, 106 specimens (17 lots) from the INHS and 3 specimens (3 lots. #129200, #1437738, #1437739, *F. eupunctus* types) from the National Museum of Natural History (NMNH). When considered by species, 83 specimens (20 MI, 21 MII, 42 F; 15 lots) were examined for *F. eupunctus* (see Appendix 2 for specimen localities), 76 specimens (27 MI, 20 MII, 29 F; 13 lots) for *F. roberti*, and 37 specimens (19 MI, 6 MII, 12 F; 12 lots) for *F. wagneri*. Only adult specimens or larger juveniles (>15 mm carapace length) were measured because smaller juvenile crayfish can often display higher levels of variation in morphological features, such as spination (Fetzner, personal observation). The Eleven Point River was represented by the greatest number of specimens (61.2%, 28 lots, 120 specimens), followed by the Spring River (21.5%, 9 lots, 43 specimens) and then the Strawberry River (16.8%, 4 lots, 33 specimens). Measurements from the holotype, allotype and morphotype of all three species were also included in the analyses. Additional specimen lots were examined, but were not measured, and are included in the respective specimens examained sections as "Additional Collections".
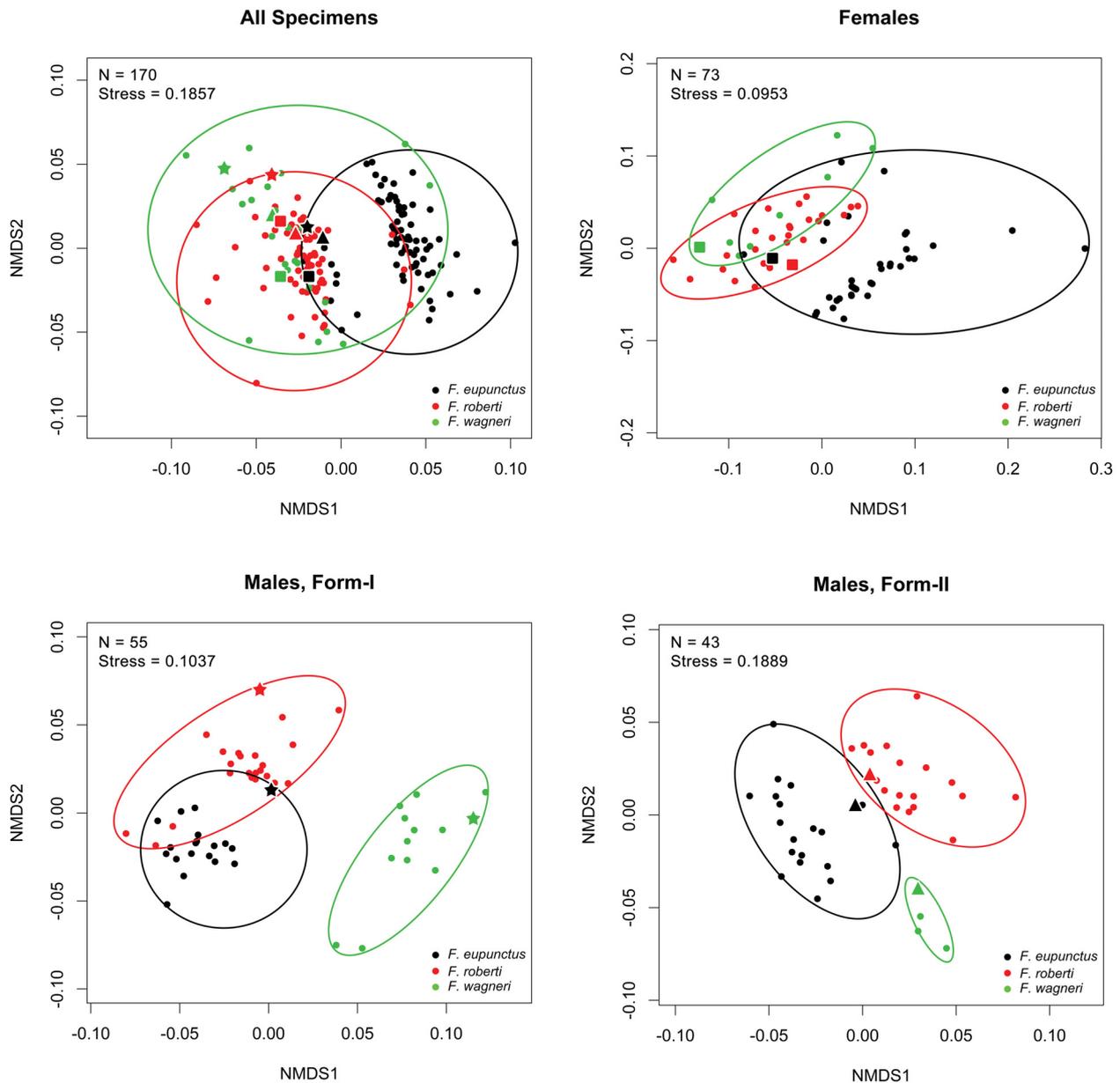
FIGURE 1. Nonmetric Multidimensional Scaling (NMDS) graphs showing similarity among specimens. **A).** All specimens in the dataset, generated by dropping any ratios that were non-significant or sex-related. **B).** Females only, generated by dropping non-significant and male only ratios. **C).** Form-I males only and **D).** Form-II males only. Colored lines were drawn by hand and circumscribe the region that contains all of the data points for the indicated species.

Morphometric ratio comparisons. The results from the one-way ANOVAs (Table 1) suggested that there were significant differences detected among the species for all morphological measurements examined, except two (POCL.CPD and AcL.RL). As a result, these two non-significant ratios were dropped from further analyses. The Tukey HSD posthoc tests indicated that *Faxonius wagneri* differed significantly from the other species for six of the measured ratios, including shape of the carapace (POCL.CPW), chela (DL.CL and PPL.CL), male gonopod (CePL.TGL and MPL.TGL), and female annulus ventralis (AVW.AVL) (Table 2). In comparisons with *F. eupunctus*, it differed significantly for 17 of 19 examined characters. *Faxonius wagneri* differed significantly from *F. roberti* for 11 of 19 characters. These were dimensions of the carapace (POCL.CPW) antennal scale (ASL.ASW), chela (CL.CPL, CL.CW, CL.CD, PL.CL, DL.CL, and PPL.CL), gonopod (CePL.TGL and MPL.TGL) and annulus ventralis (AVW.AVL) (see Table 2). *Faxonius roberti* differed from *F. eupunctus* for 11 of 19 characters, mainly in the carapace (CPL.CPW, CPL.CPD, RL.CPL, AL.CPL, AL.AW and ASL.ASW), chelae (CL.CPL, CL.CW, CL.DC, PL.CL) and number of dorsal merus spines (DMS).

TABLE 1. Averages and standard errors for each of the morphometric ratios as well as the mode and standard error for the single meristic character (DMS) analyzed among species. *F*-value and *p*-value are those from the one-way ANOVA analysis for the listed ratio. Significant trait differences are listed in bold italic font. The significance level for the posthoc TukeyHSD multiple comparisons of means test was *p* < 0.05.

Morphometric	Average Values									F value	p value	Tukey HSD (*p*-value)		
	F. eupunctus		*F. roberti*		*F. wagneri*							eup–rob	eup–wag	rob–wag
Ratio	n	mean (± SE)	n	mean (± SE)	n	mean (± SE)								
Carapace Measures														
CPL.CPW	83	2.00 (0.01)	76	2.06 (0.01)	35	2.10 (0.01)				14.15	<0.001	*0.002*	*<0.001*	0.066
CPL.CPD	83	2.25 (0.01)	76	2.30 (0.01)	37	2.32 (0.02)				9.68	<0.001	*0.004*	*<0.001*	0.362
POCL.CPW	83	1.57 (0.00)	76	1.59 (0.01)	35	1.62 (0.01)				10.57	<0.001	0.145	*<0.001*	*0.007*
POCL.CPD	83	1.77 (0.01)	76	1.78 (0.01)	37	1.79 (0.01)				2.25	0.108	0.632	0.088	0.361
RL.CPL	83	0.30 (0.00)	76	0.32 (0.00)	37	0.31 (0.00)				18.45	<0.001	*<0.001*	*0.001*	0.707
AL.CPL	83	0.35 (0.00)	76	0.34 (0.00)	37	0.34 (0.00)				15.84	<0.001	*<0.001*	*<0.001*	0.577
AL.AW	83	5.54 (0.11)	76	6.29 (0.11)	37	6.64 (0.25)				16.71	<0.001	*<0.001*	*<0.001*	0.246
ASL.ASW	83	2.60 (0.03)	76	2.69 (0.03)	37	2.98 (0.03)				35.79	<0.001	*0.038*	*<0.001*	*<0.001*
AcL.RL	83	0.29 (0.00)	76	0.28 (0.00)	37	0.28 (0.01)				2.59	0.078	0.065	0.478	0.798
Chela Measures														
CL.CPL	81	0.76 (0.01)	76	0.82 (0.01)	36	0.90 (0.02)				23.38	<0.001	*0.001*	*<0.001*	*0.001*
CL.CW	81	2.16 (0.01)	76	2.28 (0.01)	36	2.45 (0.03)				71.19	<0.001	*<0.001*	*<0.001*	*<0.001*
CL.CD	81	3.50 (0.02)	76	3.75 (0.03)	35	3.95 (0.04)				52.49	<0.001	*<0.001*	*<0.001*	*0.001*
PL.CL	81	0.32 (0.00)	76	0.32 (0.00)	36	0.30 (0.00)				28.44	<0.001	*0.035*	*<0.001*	*<0.001*
DL.CL	81	0.58 (0.00)	74	0.57 (0.00)	36	0.60 (0.00)				14.57	<0.001	0.680	*<0.001*	*<0.001*
PPL.CL	81	0.45 (0.00)	74	0.45 (0.00)	36	0.48 (0.00)				19.58	<0.001	0.978	*<0.001*	*<0.001*
DMS	83	1 (0.04)	76	2 (0.04)	37	2 (0.07)				129.2	<0.001	*<0.001*	*<0.001*	0.213
Gonopod Measures (males only)														
CePL.TGL	41	0.19 (0.01)	46	0.20 (0.01)	25	0.37 (0.02)				89.88	<0.001	0.683	*<0.001*	*<0.001*
MPL.TGL	41	0.20 (0.01)	47	0.19 (0.01)	25	0.32 (0.02)				43.68	<0.001	0.597	*<0.001*	*<0.001*
Annulus Ventralis Measures (females only)														
AVW.AVL	42	1.65 (0.03)	29	1.72 (0.03)	12	1.50 (0.05)				6.89	0.002	0.259	*0.021*	*0.001*

TABLE 2. Pairwise genetic distances (below diagonal: uncorrected p-distances and above diagonal: absolute number of mutational differences) among species of *Faxonius* from the Ozarks. Red boxes indicate divergence values among the three focal species.

ID	Species	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	*F. roberti*	7	1.1%															
2	*F. wagneri*	5	1.9%	0.1%														
3	*F. eupunctus*	3	6.0%	5.6%	0.1%													
4	*F. durelli*	2	4.9%	4.7%	5.1%	0.3%												
5	*F. putnami*	4	5.4%	5.1%	4.9%	4.8%	0.7%											
6	*F. cristavarius*	1	5.2%	4.5%	5.1%	3.7%	2.3%	—										
7	*F. peruncus*	2	10.2%	9.7%	9.4%	9.2%	8.0%	8.5%	0.2%									
8	*F. hylas*	1	10.7%	10.3%	10.4%	10.2%	9.3%	9.4%	4.2%	—								
9	*F. quadruncus*	2	9.5%	9.1%	9.1%	8.8%	7.9%	7.9%	2.9%	4.1%	0.2%							
10	*F. ozarkae*	4	9.2%	8.7%	9.9%	8.6%	8.6%	8.0%	6.7%	6.9%	6.6%	3.7%						
11	*F. marchandi*	2	8.5%	8.0%	9.2%	8.4%	8.0%	7.8%	8.4%	8.2%	7.6%	6.3%	2.4%					
12	*F. neglectus*	2	9.3%	8.7%	9.2%	8.6%	8.3%	8.7%	8.7%	9.0%	8.2%	7.6%	8.1%	6.1%				
13	*F. medius*	1	8.5%	7.8%	8.3%	8.1%	6.9%	7.3%	7.5%	9.0%	7.2%	7.5%	6.7%	6.0%	—			
14	*F. luteus*	1	9.9%	9.3%	10.4%	9.8%	9.4%	9.4%	8.5%	9.7%	8.2%	7.9%	9.0%	6.8%	5.5%	—		
15	*F. longidigitus*	1	9.0%	8.4%	8.3%	8.8%	7.5%	7.8%	7.7%	8.8%	7.4%	7.7%	7.9%	6.9%	6.2%	6.8%	6.2%	
16	*F. punctimanus*	1	9.8%	9.4%	8.9%	8.7%	8.1%	8.1%	7.1%	8.2%	6.6%	6.4%	7.1%	6.8%	5.8%	6.5%	6.2%	—
17	*F. acares*	1	11.0%	10.8%	11.5%	10.3%	11.4%	10.9%	10.4%	11.6%	10.7%	10.1%	10.6%	11.6%	10.6%	11.7%	10.3%	11.4%
18	*F. leptogonopodus*	1	10.7%	10.3%	11.8%	10.6%	11.5%	11.6%	11.0%	12.5%	11.7%	11.4%	11.3%	11.3%	11.9%	12.1%	11.2%	11.1%
19	*F. menae*	1	10.6%	10.0%	10.4%	10.0%	10.5%	10.6%	10.1%	11.2%	10.0%	9.5%	10.4%	10.0%	9.7%	9.9%	9.9%	9.6%
20	*F. saxatilis*	1	11.3%	10.9%	11.8%	10.7%	11.0%	10.3%	10.6%	12.2%	10.9%	10.7%	11.1%	12.1%	12.5%	12.2%	11.4%	11.2%
21	*F. macrus*	1	9.5%	8.8%	9.7%	8.5%	9.3%	9.1%	9.8%	10.8%	10.0%	10.3%	11.3%	9.8%	9.3%	10.4%	10.8%	9.9%
22	*F. palmeri*	1	9.7%	9.3%	9.8%	8.7%	9.4%	9.4%	10.0%	10.9%	10.1%	9.2%	8.7%	9.2%	8.5%	10.3%	9.7%	9.4%
23	*F. williamsi*	1	11.0%	10.4%	9.8%	9.3%	9.4%	9.9%	10.1%	11.1%	9.7%	8.6%	9.0%	9.2%	8.4%	10.1%	9.6%	8.7%
24	*F. forceps*	1	9.0%	8.4%	8.4%	7.6%	6.9%	7.4%	8.0%	8.8%	8.2%	8.4%	8.8%	8.9%	8.2%	9.3%	8.4%	7.8%
25	*F. pardalotus*	1	8.7%	8.1%	8.7%	7.2%	7.1%	7.1%	8.5%	9.6%	8.3%	8.1%	8.8%	9.0%	8.2%	9.9%	9.1%	8.1%
26	*F. placidus*	1	9.0%	8.7%	8.7%	9.1%	7.9%	7.4%	8.5%	9.6%	7.7%	9.0%	8.5%	8.8%	8.8%	9.4%	8.4%	8.7%
27	*F. placidus*	1	9.0%	8.7%	8.7%	9.1%	7.9%	7.4%	8.5%	9.6%	7.7%	9.0%	8.5%	8.8%	8.8%	9.4%	8.4%	8.7%
28	*F. yanahlindus*	2	9.0%	8.4%	9.9%	8.3%	8.2%	7.8%	8.8%	9.7%	8.6%	8.4%	8.1%	8.8%	8.4%	9.3%	9.6%	8.2%
29	*F. barrenensis*	1	10.1%	9.9%	11.0%	10.0%	10.3%	9.9%	10.4%	10.8%	9.9%	10.8%	10.0%	10.2%	9.4%	11.1%	10.3%	10.6%
30	*C. hubbsi*	4	14.8%	14.2%	14.0%	13.7%	13.5%	13.7%	14.2%	15.6%	13.6%	13.1%	14.2%	14.2%	14.2%	13.7%	14.7%	14.1%

TABLE 2. Extended.

ID	Species	N	17	18	19	20	21	22	23	24	25	26	27	28	29	30
17	*F. acares*		—													
18	*F. leptogonopodus*		5.6%	—												
19	*F. menae*	1	8.1%	8.3%	—											
20	*F. saxatilis*	1	9.7%	8.8%	8.2%	—										
21	*F. macrus*	1	11.9%	12.1%	11.9%	11.6%	—									
22	*F. palmeri*	1	10.8%	12.4%	11.7%	12.6%	10.4%	—								
23	*F. williamsi*	1	12.1%	12.1%	12.1%	13.0%	11.2%	3.6%	—							
24	*F. forceps*	1	12.0%	12.4%	11.4%	11.4%	10.4%	7.9%	8.4%	—						
25	*F. pardalotus*	1	12.3%	12.6%	11.6%	11.2%	10.2%	7.9%	8.3%	2.0%	—					
26	*F. placidus*	1	11.1%	11.9%	10.2%	9.9%	11.4%	10.8%	10.9%	8.7%	8.8%	—				
27	*F. placidus*	1	11.1%	11.9%	10.2%	9.9%	11.4%	10.8%	10.9%	8.7%	8.8%	0.0%	—			
28	*F. yanahlindus*	2	11.9%	12.5%	10.5%	11.1%	11.7%	10.2%	9.6%	8.2%	8.1%	7.8%	7.8%	0.0%		
29	*F. barrenensis*	1	12.3%	12.9%	10.9%	12.5%	12.0%	11.1%	12.1%	9.7%	10.0%	9.7%	9.7%	8.8%	—	
30	*C. hubbsi*	4	13.9%	14.4%	14.3%	13.3%	15.3%	14.1%	15.1%	12.1%	12.4%	12.9%	12.9%	13.7%	14.5%	0.5%
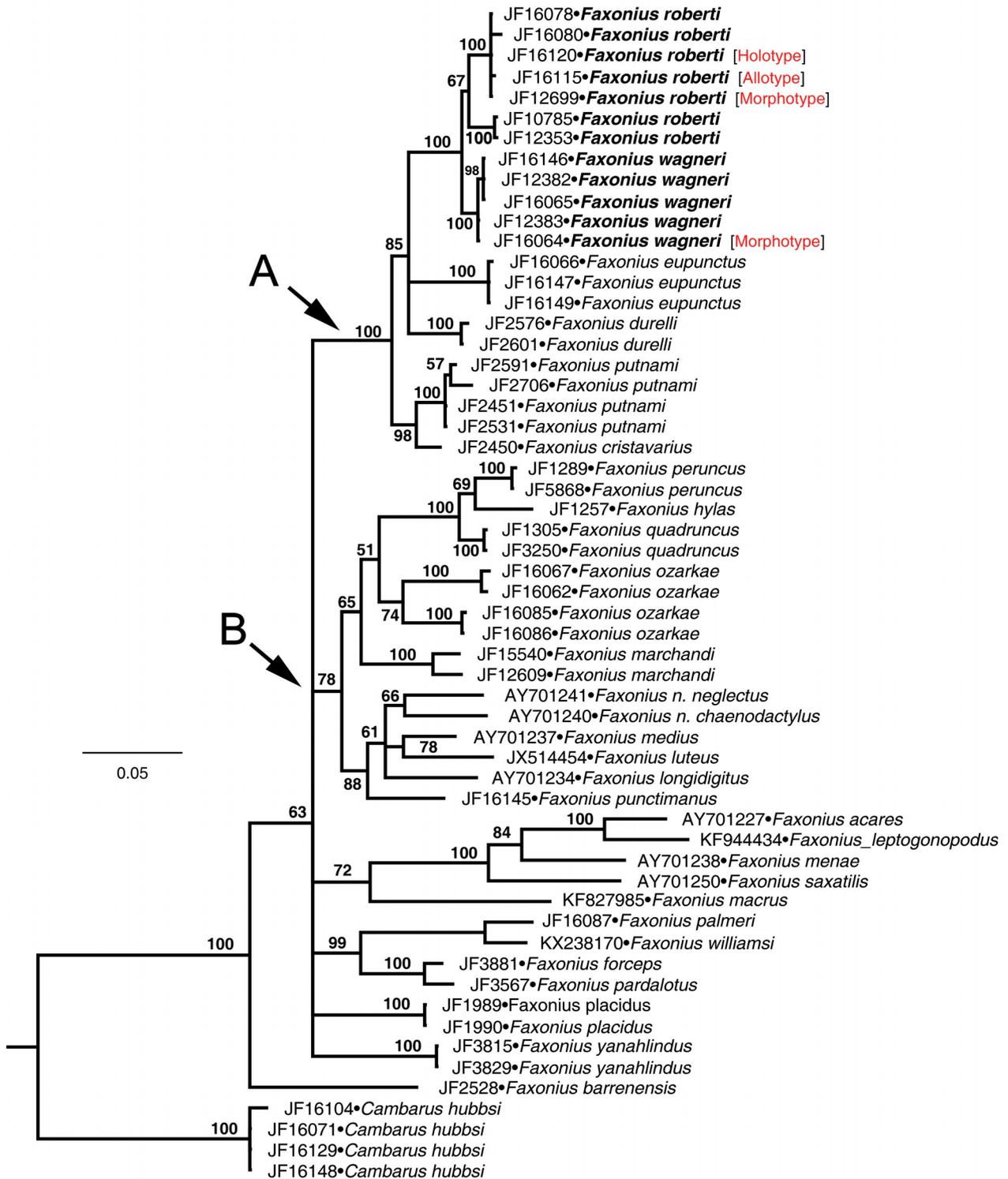
FIGURE 2. Bayesian phylogeny depicting relationships among the new species and several other members of the genus from the Ozark Highlands. Numbers at the nodes indicate bayesian posterior probabilities. Clades A and B as discussed in text.

The number of dorsal merus spines (DMS) on the first pereiopod appeared to separate *F. eupunctus* from the other two species, however, this was not 100% diagnostic. In fact, while the most common condition for *F. eupunctus* was to have a single dorsal merus spine (86% of individuals)(Fig. 9J), the specimens designated as the holotype, allotype and morphotype each exhibited two spines. In contrast, specimens of *F. wagneri* and *F. roberti*

tended to have two spines (81% and 88%, respectively), while the remainder ranged from one to three spines. It was noted that additional spines tended to appear more frequently on regenerated chelae. While we attempted to include only normal, non-regenerated chelae in the analysis, it is possible that a regenerated chela could have been mistaken for a normal chela if it happened to have a similar shape. In animals with one normal and one regenerated chela, the regenerated one typically had an additional spine or spines, and in some cases one to several raised tubercles. One specimen had four distinct spines on a regenerated chela. Spine count variation did not seem to be sex-based, as observed variants were scattered in roughly equal proportions among females, and both Form-I and Form-II males.

The terminal elements of *F. wagneri* male Form-I and Form-II gonopods are roughly twice as long as those of *F. eupunctus*. This is the most prominent character that can be used to easily distinguish between the two species. When the abdomen is flexed, the tip of the gonopod elements of *F. wagneri* reach to the posterior edge of the base of pereiopod I, whereas those of *F. eupunctus* only extend to the posterior base of pereiopod II. The gonopods of *F. roberti* are most similar to those seen in *F. eupunctus*, however, in the Form-I male, the tip of the mesial process in *F. eupunctus* is spatulate, whereas in *F. roberti*, it tapers to an acute tip. The terminal elements of the Form-II gonopod in *F. eupunctus* tended to be thickened, blunt and straight, whereas, in *F. roberti*, they are thinner and the mesial process is bent halfway along its length in a mesialcephalic direction.

The ratio of the length to width of the female annulus ventralis differed significantly between *F. wagneri* and both *F. roberti* and *F. eupunctus*. The structural features of the annulus also differed in *F. wagneri*. Females of *F. wagneri* contained a deep fossa, while specimens of *F. roberti* and *F. eupunctus* were more similar to one another in that this deep fossa was lacking or greatly reduced (e.g., compare Figures 4I, 7I, and 9I). Some slight differences in the height, positioning and angles of the anterior bumps of the annulus could also be seen among species. Among specimens of all three species, there did appear to be a handedness to the sinus (i.e., right hand or left hand facing), as the features were sometimes flipped right or left in some specimens, and this handedness has been commonly noted in the literature for other species (e.g., Johnson 2010).

The chela of *F. wagneri* tended to be longer ($\bar{x}$ = 23.7 mm, range = 12.9–35.5, SD = 6.0, n = 34), wider ($\bar{x}$ = 9.7 mm, range=5.4–13.9, SD = 2.5, n = 34), and thicker ($\bar{x}$ = 6.0 mm, range = 3.4–8.7, SD = 1.6, n = 33) while in *F. eupunctus* it was typically shorter ($\bar{x}$ = 18.7 mm, range = 9.0–30.0, SD = 5.0, n = 75), narrower ($\bar{x}$ = 8.7 mm, range = 3.8–13.7, SD = 2.3, n = 75) and thinner ($\bar{x}$ = 5.4 mm, range = 2.4–8.4, SD = 1.4, n = 75). The chela palm, dactyl and propodus lengths also differed among the two species. The chela of *F. roberti* tended more toward *F. eupunctus* in terms of the length of the palm, dactyl and propodus, whereas in other measurements it tended to fall in between the other two species.

The results from the NMDS analyses showed that there was a fair bit of overlap between the three species in general (Fig. 1A), but when analyzed by individual sex and form, the differences between them were more readily apparent (Fig. 1B–D). This analysis showed the importance of the dorsal merus spine counts and the gonopod characters in separating the species. For the females, there was some separation between *F. eupunctus* and the other two species, but *F. wagneri* and *F. roberti* overlapped to a large extent (Figure 1B). The three species were most distinct when the male specimens were considered separately by gonopod Form (Figure 1C, D), and the distinctness of *F. wagneri* was quite apparent. The number of dorsal median spines provided good separation between *F. eupunctus* and the other two species, although some specimens with abberant spine counts did not cluster as one might expect given their species affiliation.

Phylogenetics. A total of fifty seven specimens were included in a Bayesian phylogenetic analysis using DNA sequences from the standard barcode region of the COI gene. These included specimens of *Faxonius eupunctus* (n=3), *F. roberti* **sp. nov** (n=5) and *F. wagneri* **sp. nov** (n=5), along with all but one of the species with geographic distributions west of the Mississippi River that were from the former *Orconectes* subgenera *Crockerinus* and *Procericambars* (Appendix 1). In addition, several sequences from seven other species of *Faxonius* from east of the Mississippi River were also included. Several of these sequences were obtained from Genbank and are indicated by their Genbank IDs. Four specimens of *Cambarus hubbsi,* an Ozark native, were included in the analysis as an outgroup. Sequences for *F. roberti* included samples from the holotype, allotype and morphotype, while for *F. wagneri*, a sample of the morphotype was included. All of the new COI sequences generated as part of this study have been deposited in GENBANK under accession numbers (MG872915–MG872960).

Genetic divergences, as pair-wise uncorrected p-distances, were generated between all sampled individuals (Table 2, lower diagonal) using PAUP* v4.0a (build 158)(Swofford 2002). The average within and among species

divergences were calculated from the initial matrix by grouping samples according to the clades recovered by the phylogenetic tree (Fig. 2). Within species, these divergence values ranged from a low of 0.12% to a high of 6.1% (see Table 2, values along diagonal). The highest value was seen in *F. neglectus*, which was represented in the dataset by sequences from the two known subspecies. The higher value (1.14%) seen within *F. roberti* was due to the presence of distinct and somewhat divergent haplotypes occurring in the Spring versus the Strawberry rivers. Morphologically, however, specimens from these two rivers are essentially indistinguishable. Based on estimates of catch-per-unit-effort when sampling recently in the Strawberry River basin, the density of individuals (and thus the overall size of the population) seems to be quite low. Under these conditions, random genetic drift can play an important role in changing haplotype frequencies each generation, which could explain the levels of genetic divergence detected in this species between the Spring and Strawberry River drainages.

The best model selected by jMODELTEST for the Bayesian analysis, using the BIC criterion, was the HKY+I+G model with the following settings: base=(0.2867 0.1176 0.1856) nst=2 tratio=6.0169 rates=gamma shape=1.1660 ncat=4 pinvar=0.6130.

The resulting Bayesian phylogenetic tree grouped *Faxonius roberti* and *F. wagneri* as sister taxa, with *F. eupunctus* being more basal (Fig. 2, Clade A). Both of the newly described species formed monophyletic groups, however, *F. roberti* contained two slightly divergent clades that were geographically delimited based on the river drainages where they were sampled (e.g., Spring vs. Strawberry rivers). All three of the focal species discussed herein fell into a highly supported clade (PP = 100) that also contained *F. durelli*, *F. putnami* and *F. cristavarius*. This is an interesting relationship, as this clade brings together species that are geographically distributed both east and west of the Mississippi River, rather than grouping species that are geographically proximal. This same relationship was also found by Taylor & Knouft (2006), but their tree also adds *F. juvenilis*, *F. jeffersoni*, and *F. sloanii* to the group, all of which are geographically distributed east of the Mississippi River. Most of the other Ozark Highland species included in the analysis formed a separate moderately supported (PP = 78) group (Fig. 2, Clade B), while the remaining *Faxonius* taxa clustered as part of a multiclade polytomy with *F. barrenensis* as the most basal taxon of the genus.

Systematics

Faxonius roberti, new species
Figures 3–4, Table 3

Orconectes eupunctus Williams, 1952:334, pl. 1: figs. 1–8 [in part]; 1954:840, figs. 41–49 [in part].—Hobbs, 1974:19, fig. 116 [in part].
Orconectes (Crockerinus) eupunctus.—Fitzpatrick, 1987:51 [in part], Hobbs, 1989:36, fig. 154 [in part].
Faxonius eupunctus.—Crandall and De Grave, 2017:629 [in part].

Diagnosis. Body and eyes pigmented (Fig. 3). Rostrum deeply excavated, terminating in long acumen; median carina absent. Rostral margins thickened; straight, subparallel or slightly concave; terminating in spines (Fig. 4H). Areola 31.9–39.2% ($\bar{x}$ = 34.7%, n = 76, SD = 0.01) of total length of carapace, narrowest part at midpoint, 4.7–9.2 ($\bar{x}$ = 6.3, n = 76, SD = 0.9) times as long as wide, with one to three (mode = 2, n = 76, SD = 0.4) punctations across narrowest part (Fig. 4H). One (rarely zero (1.3%) or two (3.9%)) corneous cervical spine on each side of carapace (Fig. 4A). Postorbital ridges well developed, terminating in corneous spines (Fig. 4H). Suborbital angle obsolete (Fig. 4A). Antennal scale broadest distal to midlength, thickened lateral margin terminating in large corneous spine (Fig. 4G). Ischia of third pereiopods of males with hooks; hooks overreaching basioischial articulation in Form-I males only. Chela with two or three rows of tubercles (see Variation) along mesial margin of palm, usually five to 11 tubercles in mesialmost row and four to ten in dorsomesial row, third row, if present, with few scattered tubercles; dorsal surfaces of fingers lacking well defined longitudinal ridges (Fig. 4K). Mandible with serrate-edged incisor region. Cephalomedian lobe of epistome subpentagonal to subtriangular without cephalomedian projection; epistomal zygoma forming weak arch. First pleopods of Form-I male symmetrical, extending to posterior edge of base of second pereiopods when abdomen flexed. First pleopod of Form-I male without shoulder on cephalic surface at base of central projection; central projection corneous, constituting 20.2–27.6% ($\bar{x}$ = 23.9, n = 27, SD = 0.02) of total length of first pleopod, continuous with main shaft of pleopod, tapering to a pointed tip,

FIGURE 3. Dorsal view of *Faxonius roberti* new species, holotype**,** male form-I (CMNH 38749) from the type locality.

tip slightly arched caudolaterally; mesial process equal to or slightly subequal in length to central projection, non-corneous, tapering to an acute tip, tip arched cephalomesially (Figs. 4B, C, F). First pleopod of Form-II male non-corneous, extending to posterior edge of bases of second pereiopods when abdomen flexed forward; central projection straight, mesial process arched slightly cephalomesially and subequal in length; both elements tapering to rounded tips (Figs. 4D, E). Annulus ventralis immovable, subrhomboidal; cephalic half with wide median trough and two caudally directed weak protuberances overhanging centrally located fossa; sinuate sinus running from center of fossa to slightly raised caudal edge (Fig. 4I).

   Description of holotypic male, form I. Body slightly depressed dorsoventrally, carapace wider than abdomen (17.4 and 15.2 mm, respectively). Greatest width of carapace larger than height at caudodorsal margin of cervical groove (17.4 and 15.8 mm, respectively). Postorbital carapace length 78.1% of total length of carapace. Areola 5.3 times longer (11.4 mm) than wide (2.1 mm) with three punctations across narrowest part; length of areola 34.9% of total length of carapace. Rostrum deeply excavated dorsally, floor smooth, lacking carina; margins thickened, straight and slightly converging, terminating in corneous spiniform marginal tubercles. Acumen long and terminating in corneous spine, reaching posterior margin of third antennal peduncle. Postorbital ridges well developed, terminating in corneous spines. Suborbital angles obsolete. Two corneous cervical spines on righthand side, dorsal most spine less than half the length of more ventrally located spine, single spine on lefthand side broken off. Antennal scale as in Diagnosis. Right antennal scale 7.0 mm long, 2.5 mm wide. Epistome as in **Diagnosis.** Abdomen longer than carapace (34.7 and 32.5 mm, respectively). Cephalic section of telson bearing two spines in each caudolateral corner, more mesial pair movable. Proximal podomere of uropod with spine extending over mesial ramus and spine in caudolateral corner extending over lateral ramus. Caudal margin of cephalic section of lateral ramus with 18 (left) and 15 (right) fixed spines and one movable spine in caudolateral corner, lateral ramus with median ridge terminating in spine. Lateral margin of mesial ramus terminating in spine; mesial ramus with prominent median ridge terminating in premarginal spine. Dorsal surfaces of telson and uropods setiferous.

   Mesial surface of palm of left chela with two rows of tubercles, nine tubercles in each row, with an additional three interspersed tubercles between. Mesial and lateral surfaces of chela, and opposable margins of fingers, covered with punctations; dorsal surface with scattered punctations, ventral side with scattered puncations mostly

along lateral edge. Dorsal surface of finger of propodus with slight submedian longitudinal ridge, more pronounced near tip of finger; basal half of opposable margin with six tubercles, first two roughly the same size, third tubercle from base of finger largest, remaining three tubercles slightly decreasing in size toward tip of finger. Dorsal surface of dactyl with weak submedian longitudinal ridge flanked by setiferous punctations; basal half of opposable margin with five tubercles, first three of roughly the same size, fourth tubercle largest, fifth slightly smaller than first three. Propodus and dactyl with subterminal corneous tip.

Right carpus with deep oblique furrow dorsally; dorsal surface with one large corneous spine at distolateral corner; mesial margin with one large corneous procurved spine at midpoint; ventral surface with one large corneous spine just lateral to midpoint of distal margin, one large spine just mesial to midpoint of distal margin. Dorsodistal surface of merus with two large corneous spines; ventral surface with one large corneous spine at distolateral corner and mesial row of six spines, row terminating in large corneous spine. Ischium lacking corneous spine just proximal to midlength of mesial margin, one large tubercle on distal end of mesial margin.

Hook on ischium of third pereiopod only; hook simple, overreaching basioischial articulation, not opposed by tubercle on basis. First pleopod of Form-I male without shoulder on cephalic surface at base of central projection; central projection corneous, constituting 20.2% of total length of first pleopod, parallel to main shaft of pleopod, tapering to pointed tip, tip directed caudomesially; mesial process slightly subequal in length to central projection, non-corneous, tapering to acute tip, tip arched cephalolaterally (Figs. 4B, C, F).

Description of allotypic female. Except for secondary sexual characteristics, differing from holotypic male in the following respects. Areola constituting 34.6% of length of carapace and seven times longer than wide. Postorbital carapace length 79.7% of length of carapace. Abdomen wider than carapace (20.3 and 19.4 mm, respectively). Left cheliped regenerated. Mesial surface of palm of right chela with two rows of tubercles, nine tubercles in mesialmost row and eight tubercles in dorsomesial row. One small tubercle adjacent to distal-most tubercle in second row. Finger of propodus with basal half of opposable margin with eight tubercles, first two roughly the same size, third and sixth tubercles largest, remaining tubercles smaller and slightly decreasing in size toward tip of finger. Eighth tubercle offset mesially from others. Basal half of opposable margin of dactyl with seven tubercles, first four of roughly the same size, remaining four slightly decreasing in size toward tip of dactyl. Seventh tubercle offset slightly laterally. Caudal margin of cephalic section of lateral ramus of uropod with 17 fixed spines.

Sternum between third and fourth pereiopods narrowly V-shaped. Postannular sclerite 64% as wide as annulus ventralis (described in Diagnosis). First pleopod uniramous, barely reaching caudal margin of annulus when abdomen flexed.

Description of morphotypic male, form II. Differing from holotype as follows: Areola constituting 33.5% of length of carapace, 5.6 times longer than wide. Postorbital carapace length 76.8% of length of carapace. Ventral surface of right merus with mesial row of five spines. Hook on ischium of third pereiopod not overreaching basioischial articulation. First pleopod as described in Diagnosis.

Type locality. Spring River just upstream of the AGFC Bayou Access boat ramp off County Road 2027, 7.0 km S Mammoth Spring, Fulton County, Arkansas (36.43396, -91.52714, WGS84, 134 m) (Fig. 5). The type series was collected from a riffle with cobble, approximately 135 m upstream of the boat ramp. The Spring River is a large cool river that is directly fed by Mammoth Spring, which is the largest spring in Arkansas and the third largest in the Ozarks Plateau region. At the time of collection (15 April 2017), the river was 35–40 m wide near the type locality with a swift flow. Water temperature was 64.4°F (the temperature of water emerging upstream from Mammoth Spring is 58°F) and water depth at the riffle was roughly 0.5 m. The river was rocky, containing what appeared to be a gravel to cobble substrate and occasional larger rocks. Stream banks were well vegetated and the surrounding land was densely forested. The river at this access point receives a considerable amount of traffic from public users, including activities such a boating, camping, canoeing and fishing.

Disposition of primary types. The holotypic male (form I), allotypic female, and morphotypic male (form II), are housed in the crustacean collection of the Carnegie Museum of Natural History (CMNH; accession numbers 38749, 38750, and 38751, respectively). Paratypes have also been deposited at CMNH (38758, 38759) and the Illinois Natural History Survey (INHS; catalog numbers: 6920, 10704, 10785, 12343, 12822). The localities and dates of collection are provided in the following range and specimens examined section.

Range and specimens examined. Endemic to the Spring and Strawberry river drainages in the Ozark Highlands physiographic province of northern Arkansas and southern Missouri. This species can be found in
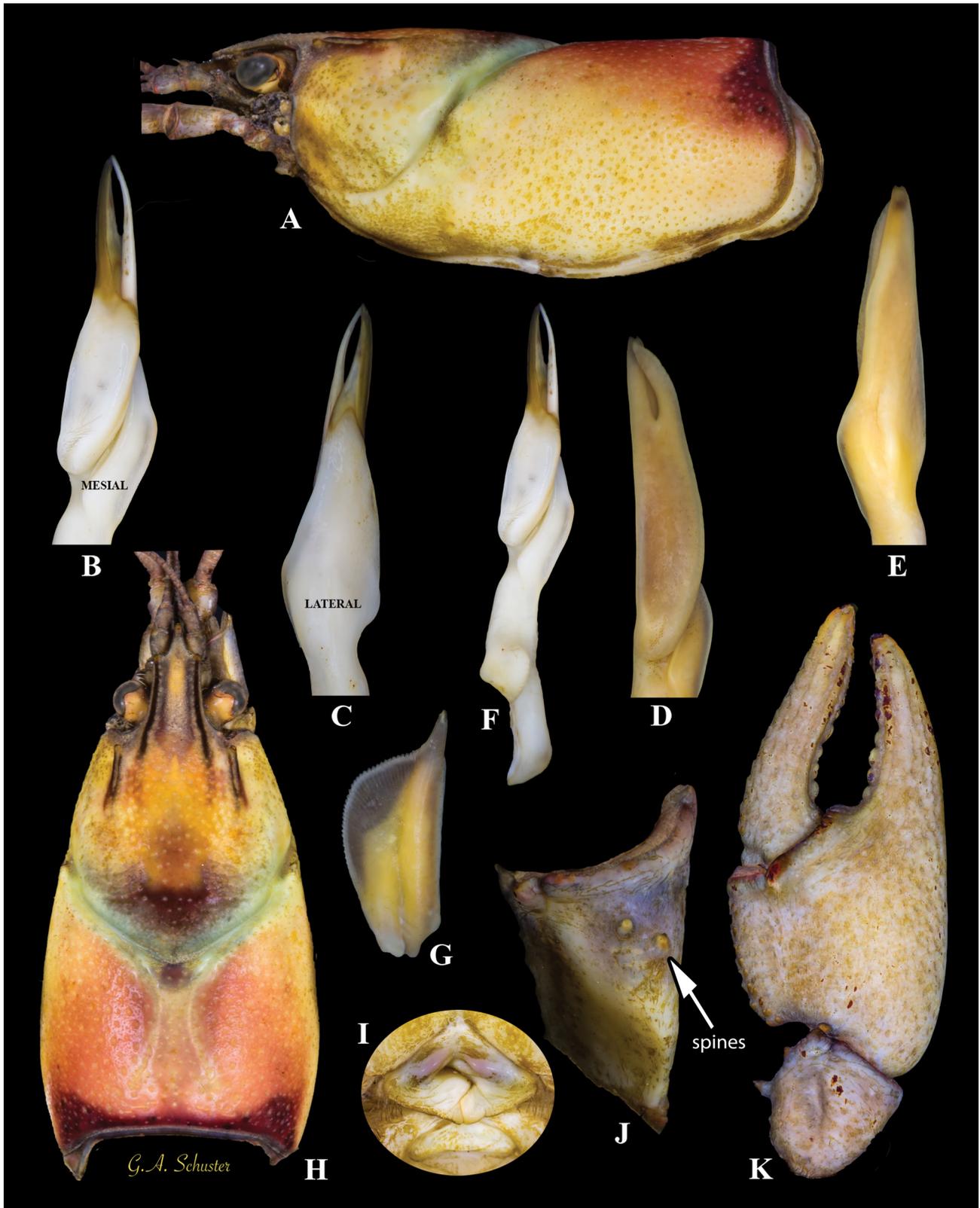
FIGURE 4. *Faxonius roberti*, new species; all from holotype male Form-I (CMNH 38749), except D and E from morphotype male Form-II (CMNH 38751), and I from allotype female (CMNH 38750). A) lateral aspect of carapace; B–C) mesial and lateral aspect of Form-I male gonopod, respectively; D–E) mesial and lateral views of Form-II male gonopod, respectively; F) mesial view of entire gonopod of male Form-I gonopod; G) dorsal aspect of antennal scale; H) dorsal veiw of carapace; I) ventral aspect of the female annulus ventralis; J) dorsal aspect of merus of first pereiopod (=cheliped) showing location of spines; K) dorsal aspect of distal podomeres of the right cheliped. Plate by Guenter A. Schuster.

Fulton, Lawrence, and Sharp counties Arkansas and Howell County, Missouri (Fig. 10). In both river drainages, the species is known only from the mainstems, except in the Spring River drainage where it is also found in the mainstems of the more southern major tributaries (e.g., South Fork Spring River and West Fork Spring Creek). The collection lots from CMNH and INHS below are referenced using their museum accession numbers. MI=male Form-I, MII=male Form-II, F=female, MDC = Missouri Department of Conservation.

A total of 76 specimens have been examined from the following nine localities: ARKANSAS: *Fulton County:* **(1).** Spring River at Many Islands, 0.4 km SSW Many Islands, 36.386, -91.5307 (WGS84), 25-May-2006, coll: BK Wagner, M Kottmyer, J Koppleman and Fry, INHS-10704, 1 MII, 1 F. **(2).** Spring River at Bayou Access, 7 km S Mammoth Spring, 36.433389, -91.528396 (WGS84), 20-May-2014, coll: C Ames, M Mabery, C Knerr and L Bachmann, CMNH-38782, 1 MI, 6 MII, 5 F; CMNH-38751, 1 MII (Morphotype). **(3).** TYPE LOCALITY: Spring River upstream of Bayou Access boat ramp, 7 km S Mammoth Spring, 36.433396, -91.52714 (WGS84), 15-Apr-2017, coll: JW Fetzner Jr., CMNH-38759, 2 MI, 3 MII; CMNH-38749, 1 MI (Holotype); CMNH-38750, 1F (Allotype). **(4).** Spring River just upstream of Big Creek confluence, 7.6 km SSE Mammoth Spring, 36.42934, -91.520324 (WGS84), 24-Oct-1998, coll: C Flinders, INHS-6920, 3 MI. *Sharp County:* **(5).** Strawberry River at Barnes Road crossing, 5.3 km W Poughkeepsie, 36.07815, -91.53805 (WGS84), 02-Oct-2014, coll: BK Wagner and A Daniel, CMNH-38765, 7 MI, 3 F. **(6).** Strawberry River at Barnes Road crossing, 7.3 km E Evening Shade, 36.07808, -91.5381 (WGS84), 21-Sep-2006, coll: BK Wagner, M Kottmyer and S Henry, INHS-10785, 8 MII, 9 F. **(7).** Strawberry River downstream of Barnes Road, 5.3 km W Poughkeepsie, 36.07624, -91.53778 (WGS84), 03-Sep-2010, coll: BK Wagner, CMNH-38766, 3 MII, 1 Fjuv. **(8).** Strawberry River upstream of Piney Fork, 6.9 km WNW Poughkeepsie, 36.09137, -91.55379 (WGS84), 09-Aug-2011, coll: BK Wagner, CMNH-38767, 1 MII, 1 F. MISSOURI: *Howell County*: **(9).** West Fork Spring Creek at Hwy-142 bridge, 4.9 km W Lanton, 36.5114, -91.85616 (WGS84), 18-Sep-1984, coll: WL Pflieger, INHS-12343, 13 MI, 8 F; 1984-03-22, coll: WL Pflieger and HV Wheeler, INHS-12822, 2 MI. ***Additional Collections*** *(examined but not measured)*: ARKANSAS: *Fulton County*: **(10).** South Fork Spring River at Sunrise Road crossing, 1.0 km ESE Sturkie, 36.455383, -91.86197 (WGS84), ??-???-2010, MDC Crayfish Crew, CMNH-38769, 1 MII, 1 F. **(11).** Spring River upstream of Bayou Access, 7 km S Mammoth Spring, 36.433396, -91.52714 (WGS84), 15-Apr-2017, coll: JW Fetzner Jr., CMNH-38759, 2 MI, 3 MII. *Lawrence County:* **(12).** Spring River at the AGFC Imboden boat ramp, 0.6 km ENE Imboden, 36.203904, -91.167702 (WGS84), ??-???-2010, coll: MDC Crayfish Crew, CMNH-38768, 1 MII, 1 Fjuv. *Sharp County:* **(13).** Spring River at Hardy Beach, 1.0 km ESE Hardy, 36.31236, -91.4724 (WGS84), 24-Aug-2011, coll: MDC Crayfish Crew, CMNH-38770, 5 MII, 5 F. **(14).** South Fork Spring River at Griffith Park, 2.5 km WSW Hardy, 36.30947, -91.5097 (WGS84), 14-Apr-2017, coll: JW Fetzner Jr., BK Wagner and D Filipek, CMNH-38758, 4 MII, 1 F; 36.30948, -91.50984 (WGS84), 24-Aug-2011, coll: MDC Crayfish Crew, CMNH-38771, 5 MII, 5 F. For a few additional published localities for this species (as *Orconectes eupunctus*) see Flinders & Magoulick (2005) and examine Figure 11 (gray dots) herein. Additional historical records from the Strawberry River depicted on the map (Fig. 10) are from the AGFC crayfish distribution database (B.K. Wagner, personal communication).

Size. The largest specimen examined was a 38.1 mm CL Form-II male. Females (n = 29) ranged in size from 16.5 to 36.3 mm CL ($\bar{x}$ = 25.6 mm). Form-I males (n = 27) ranged from 16.1 to 32.5 mm CL ($\bar{x}$ = 23.2 mm). Form-II males (n = 20) ranged from 15.6 to 38.1 mm CL ($\bar{x}$ = 25.1 mm).

Color. Base color of dorsal and lateral surfaces of cephalothorax dark brown to dark orange, fading to cream near ventral edges. Portion anterior to cephalic groove light brown to olivaceious green. Black saddle just anterior to cephalic groove, with black dot appearing just posterior to cephalic groove in center of triangle produced by the cephailc groove and the branchiocardial grooves (= areola). An additional black saddle crossing the juncture of posterior edge of carapace and anterior edge of abdomen, roughly equally divided onto both surfaces. Lateral sides of first abdominal pleuron with orangish, cream or yellowish patch that interrupts the saddle, making these patches stand out. Dorsal surface of abdomen with posteriorly tapering black stripe, fading out just before reaching tailfan. Lateral surfaces of abdomen light orange/brown to light yellowish orange. Tailfan olivaceous green with light orange highlights. Walking legs olivaceous green with hints of light orange at articulation joints, fading to light orange near junction with body. Chelae and carpus overall olivaceous green, with some individuals more infused with light orange closer to lateral margin of palm, thus making the dactyl and propodus appear a darker green than palm region. Tips of both fingers light orange to light red, then quickly transitioning into olivaceous green. Spines and tubercles on chela carpus same color as base color. First quarter of anterior part of merus olivaceous green, the remainder cream colored. Ventral surfaces of cephalothorax and abdomen cream to white with hints of light orange
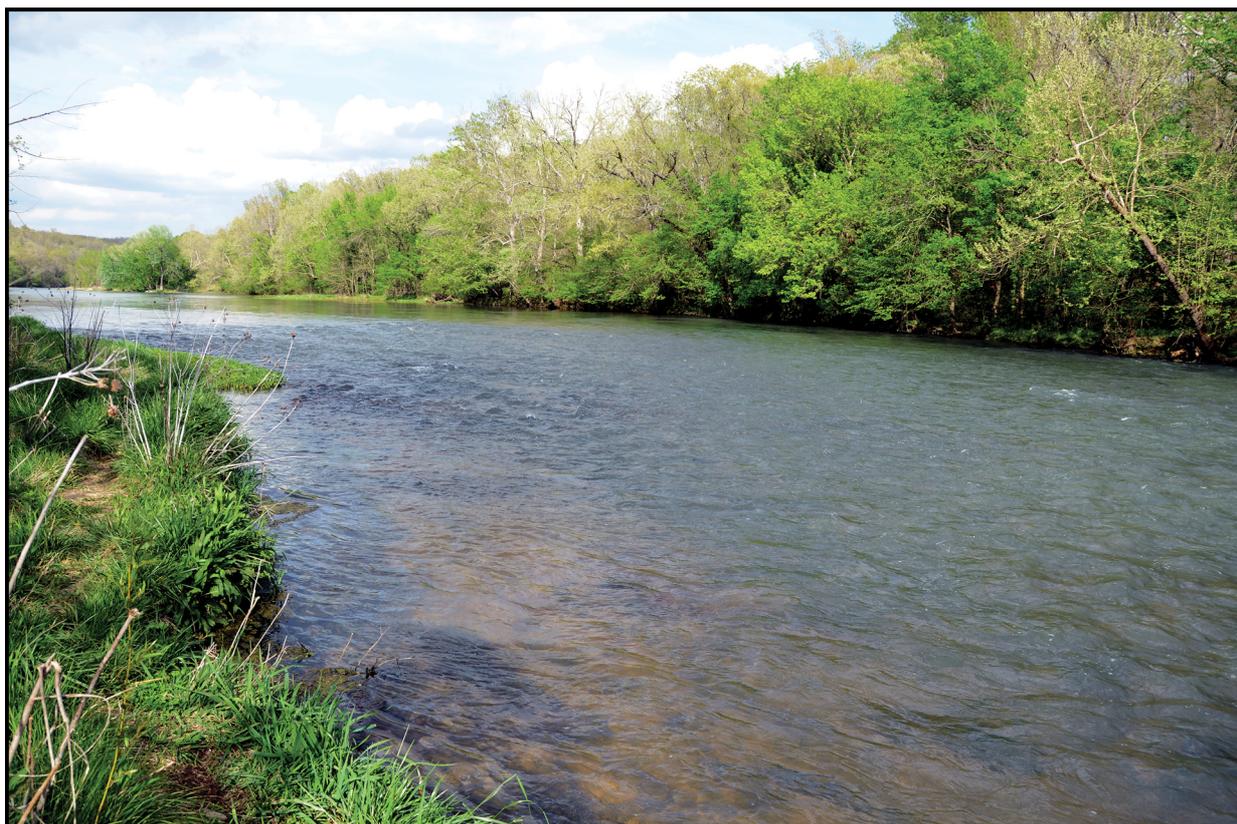
FIGURE 5. Photo of the type locality of *Faxonius roberti*, new species, taken on the mainstem of the Spring River, 135 meters upstream of the Bayou Access boat ramp (36.433959, -91.527190 ,WGS84).

on basal segment of walking legs. Ventral surface of chelae are mostly cream colored, especially on lateral half, but mesial one third can be light olivaceous green. In Form-II males, the first and second pleopods have hints of light orange (similar to base of walking legs), with the tips of the first pleopod darker orange.

On very rare occasion, variant individuals that are bright orange in color over the entire body surface have been reported in the Strawberry River basin (B.K. Wagner, personal communication).

Habitat and life history notes. *Faxonius roberti* occurs in mainstem streams of fourth order or larger, with substrates of cobble and gravel. Within these streams, the species was most commonly encountered in cobble in areas with moderate to fast flow. The cobble under which the species occurred was variable in size, ranging from 5 cm^2 to 20 cm^2. It seemed to be most commonly encountered in riffle areas.

While occurrence data are only limited to currently available museum collections, they indicate that Form-I males are present in the population during the months of March, April, May, September and October. Form-II males were recorded during April, May, August and September. No ovigerous females were available in collections, however, the Allotype female, which was collected in mid-April, did carry 212 young attached to the underside of her abdomen.

Etymology. It is our great pleasure to name this species in honor of Robert (Bob) J. DiStefano of the Missouri Department of Conservation (MDC). Bob has worked tirelessly over his career to help understand and conserve the crayfish fauna of the Ozarks in general, and Missouri in particular, so it is fitting that this Ozarkian species be named in his honor. This new species should not be confused with "*Orconectes bobi*", the ficticious species name assigned to Bob when he was wearing his full crayfish costume while conducting public outreach programs for the MDC.

Crayfish associates. The following species were collected from habitats containing *Faxonius roberti,* new species: *Faxonius ozarkae* (Williams, 1952); *Faxonius marchandi* (Hobbs, 1948) and *Cambarus hubbsi* Creaser, 1931.

Variation. In addition to the range of ratios and counts given in the Diagnosis section, several ontogenetic variations were observed in *F. roberti* new species, none of which show a geographic pattern of variation. The number of palmar tubercle rows is variable, usually with two but sometimes a partial third row being present. The marginal spines of the rostrum varied between pronounced spines, weak spines and tubercles. The cervical spines ranged from zero to two, with one being most common (95%). In one individual, the spine was replaced with a tubercle.

TABLE 3. Measurements (mm) made from the primary types of *Faxonius roberti*, new species.

Measurement	Holotype	Allotype	Morphotype
Carapace:			
Total length	32.49	36.34	33.96
Postorbital length	25.38	28.96	26.07
Width	17.42	19.44	16.87
Depth	15.80	16.86	14.16
Areola:			
Length	11.35	12.59	11.39
Width	2.13	1.79	2.04
Rostrum:			
Length	9.81	10.74	10.90
Width (at base)	3.90	4.24	3.68
Chela (right):			
Total length	35.52	30.86	31.30
Total width	16.30	15.13	14.25
Palm depth	9.69	8.81	8.61
Length, palm mesial margin	11.58	10.00	9.97
Dactyl length	19.91	16.31	17.71
Propodus length	15.46	12.07	13.86
Abdomen:			
Length	34.7	41.18	34.57
Width	15.2	20.27	15.12
First Pleopod:			
Total length	14.06	-	12.00
Width	1.79	-	1.67
Length, central projection	2.84	-	1.61
Annulus ventralis:			
Length	-	5.51	-
Width	-	3.54	-

Comparisons. *Faxonius roberti*, new species, differs from all other members of the genus by possessing a unique combination of Form-I first pleopod characters. The Form-I male pleopod of *F. roberti*, new species, is most similar in length and general shape to other members of the former subgenus *Crockerinus* Fitzpatrick, 1987, which occur throughout the central and eastern United States. This subgenus, and all other subgenera formerly in the genus *Orconectes*, were not recognized by Crandall and De Grave (2017) in their world classification of freshwater crayfish based on recent phylogenetic evidence. All members of the former subgenus *Crockerinus* generally possessed short, straight first pleopod elements which may or may not curve at their distal tips and a central projection accounting for between 20 and 33% of the total first gonopod length. *Faxonius roberti* differs from all other *Crockerinus* members occurring west of the Mississippi River in possessing a Form-I first pleopod mesial process that is equal in width at its base to the central projection, which tapers to an acute tip, and is not curved caudodistally.

FIGURE 6. Dorsal view of *Faxonius wagneri*, new species, morphotype, male form-II (CMNH 38752) from near Dalton, Arkansas.

Relationships. See the Phylogenetics text in the Results section for a discussion of the relationships of this species to other taxa. See also Fig. 2.

Common name. The suggested common or vernacular name for this species is the Spring River Crayfish, which is in reference to its affinity for the mainstem channels of the two spring-fed rivers where the species occurrs.

Conservation status. Given *F. roberti*'s limited distribution in only two major Black River drainages and the known introduction of the non-native Ringed Crayfish (*F. neglectus*) in portions of the Spring River drainage (Larson & Magoulick 2008), we recommend a status of Vulnerable following the criteria of the American Fisheries Society as outlined by Taylor *et al*. (2007). These same factors warrant a classification as Vulnerable following the criteria of the International Union for the Conservation of Nature (IUCN).

Faxonius wagneri, **new species**
Figures 6–7, Table 4

Orconectes eupunctus.—Williams, 1952 [in part].
Orconectes (Crockerinus) eupunctus.—Fitzpatrick, 1987 [in part], Hobbs, 1989 [in part].
Faxonius eupunctus.—Crandall and De Grave, 2017:629 [in part].

Diagnosis. Body and eyes pigmented (Fig. 6). Rostrum deeply excavated, terminating in long acumen; no median carina. Rostral margins thickened; margins straight, subparallel and slightly converging; terminating in spines (Fig. 7H). Areola 32.3–38.7% ($\bar{x}$ = 34.0%, n = 32, SD = 0.01) of total length of carapace, narrowest part at midpoint, 3.8–10.9 ($\bar{x}$ = 6.6, n = 32, SD = 1.6) times as long as wide, with two to three (mode = 2, n = 32, SD = 0.5) punctations across narrowest part (Fig. 7H). One (rarely two (6.3%)) corneous cervical spines on each side of carapace (Fig. 7A). Postorbital ridges well developed, terminating in corneous spines (Fig. 7H). Suborbital angle obsolete (Fig. 7A). Antennal scale broadest distal to midlength, thickened lateral margin terminating in large corneous

spine (Fig. 7G). Ischia of third pereiopods of males with hooks; hooks overreaching basioischial articulation in Form-I males only. Chela with two or three rows of tubercles (see Variation) along mesial margin of palm, usually six to ten tubercles in mesialmost row and four to ten in dorsomesial row, third row, if present, with few scattered tubercles; dorsal surfaces of fingers lacking well defined longitudinal ridges (Fig. 7K). Mandible with serrate-edged incisor region. Cephalomedian lobe of epistome subpentagonal to subtriangular without cephalomedian projection; epistomal zygoma forming weak arch. First pleopods of Form-I male symmetrical, extending to posterior edge of base of first pereiopods when abdomen flexed forward. First pleopod of Form-I male with shoulder on cephalic surface at base of central projection (Fig. 7B, C, F); central projection corneous, constituting 37.4–45.5% ($\bar{x}$ = 41.3%, n = 16, SD = 0.02) of total length of first pleopod, continuous with main shaft of pleopod, tapering to a pointed tip, slightly arched and twisted caudolaterally; mesial process equal to or slightly subequal in length to central projection, non-corneous, tapering to an acute tip, tip arched cephalomesially (Figs. 7B, C, F). Central projection of Form-II male non-corneous, constituting 20.6–25.1% ($\bar{x}$ = 23.3%, n = 6, SD = 0.02) of total length of first pleopod, extending to posterior edge of bases of first pereiopods when abdomen flexed forward; central projection straight, mesial process arched slightly cephalolaterally and subequal in length; both elements tapering to rounded tips (Figs. 7D, E). Annulus ventralis immovable, subrhomboidal; cephalic half with deep and wide median trough and two caudally directed protuberances overhanging centrally located cavernous fossa; sinuate sinus running from near center of fossa to caudal edge on a raised centrally located rounded hump (Fig. 7I).

Description of holotypic male, form I. Specimen slightly soft, a recently molted individual. Body slightly depressed dorsoventrally, carapace wider than abdomen (15.9 and 13.0 mm, respectively). Greatest width of carapace larger than height at caudodorsal margin of cervical groove (15.9 and 13.8 mm, respectively). Postorbital carapace length 82.4% of total length of carapace. Areola 7.4 times longer (11.2 mm) than wide (1.5 mm) with two punctations across narrowest part; length of areola 37.0% of total length of carapace. Rostrum deeply excavated dorsally, floor smooth, lacking carina; margins thickened, straight and slightly converging, terminating in corneous marginal spines. Acumen long and terminating in corneous spine, reaching posterior margin of third antennal peduncle. Postorbital ridges well developed, terminating in corneous spines. Suborbital angles obsolete. One corneous cervical spine on both sides. Antennal scale as in Diagnosis (Fig. 7G). Right antennal scale 5.9 mm long, 2.4 mm wide. Epistome as in Diagnosis.

Abdomen longer than carapace (31.6 and 30.3 mm, respectively). Cephalic section of telson bearing two spines in each caudolateral corner, more mesial pair movable. Proximal podomere of uropod with spine extending over mesial ramus and spine in caudolateral corner extending over lateral ramus. Caudal margin of cephalic section of lateral ramus with 20 (left) and 23 (right) fixed spines and one larger movable spine in caudolateral corner, lateral ramus with median ridge lacking terminal spine. Lateral margin of left mesial ramus terminating in spine, spine missing on right; mesial ramus with prominent median ridge terminating in premarginal spine. Dorsal surfaces of telson and uropods setiferous.

Mesial surface of palm of right chela with two rows of tubercles, those more distal less well defined, ten tubercles in mesialmost row, six tubercles in second dorsomesial row, with several additional tubercles interspersed in between these two rows. Mesial and lateral surfaces of chela, and opposable margins of fingers, covered with numerous punctations; dorsal surface with scattered punctations, ventral side with scattered puncations mostly on lateral half. Dorsal surface of finger of propodus with weak submedian longitudinal ridge, more pronounced near tip of finger; basal half of opposable margin with seven tubercles, first two roughly the same size, third tubercle from base of finger largest, remaining tubercles slightly smaller with sixth the smallest. One additional large tubercle offset mesially onto inner margin of finger half-way between seventh tubercle and tip. Dorsal surface of dactyl with weak submedian longitudinal ridge flanked by setiferous punctations; basal half of opposable margin with eight tubercles, first three of roughly the same size, fourth tubercle from base of finger largest, fifth through seventh roughly the same size, eighth smallest of all and slightly offset. Dactyl with subterminal corneous tip, corneous tip on propodus broken off.

Right carpus with moderately deep oblique furrow dorsally; dorsal surface with one spiniform tubercle at distomesial corner; mesial margin with one large corneous procurved spine at midlength, and small bump posteriorly; ventral surface with one large corneous spine just lateral to midlength of distal margin, one spiniform tubercle just mesial to midlength of distal margin (Fig. 7K). Dorsal surface of merus with two centrally located large corneous spines (Fig. 7J); ventral surface with one large corneous spine at distolateral corner and mesial row of five spines, row terminating in large corneous spine. Ischium lacking corneous spine just proximal to midlength of mesial margin, one large tubercle on distal end of mesial margin.
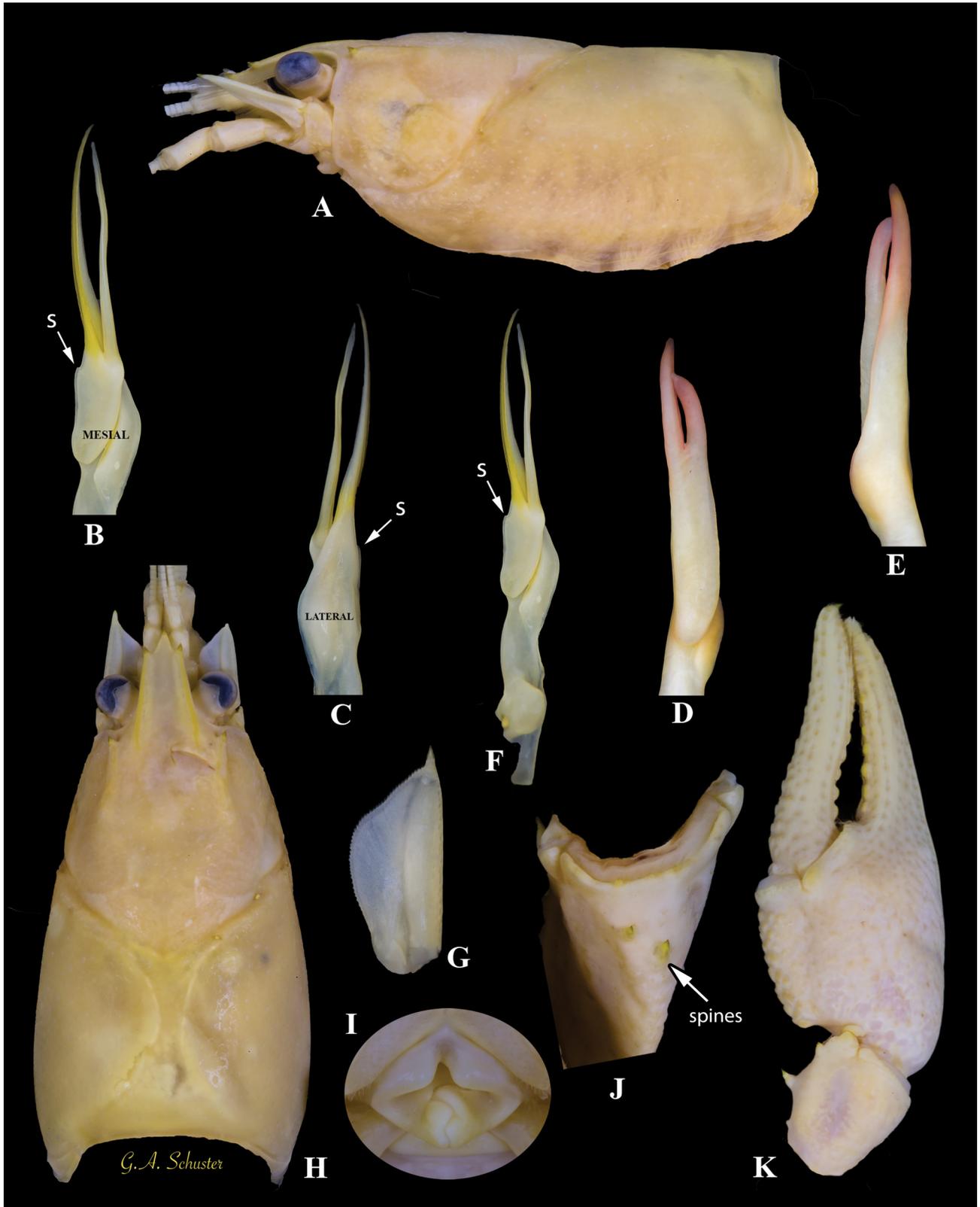
FIGURE 7. *Faxonius wagneri*, new species; all from holotype male Form-I (CMNH 38752), except D and E from morphotype male Form-II (CMNH 38754), and I from allotype female (CMNH 38753). A) lateral aspect of carapace; B–C) mesial and lateral aspect of Form-I male first pleopod, respectively; D–E) mesial and lateral views of Form-II male first pleopod, respectively; F) mesial view of entire first pleopod of male Form-I gonopod; G) dorsal aspect of antennal scale; H) dorsal veiw of carapace; I) ventral aspect of the female annulus ventralis; J) dorsal aspect of merus of first pereiopod (=cheliped) showing location of spines; K) dorsal aspect of distal podomeres of the right cheliped. Plate by Guenter A. Schuster.

Hook on ischium of third pereiopod only; hook simple, overreaching basioischial articulation, opposed by low tubercle on basis. First pleopod of Form-I male with shoulder on cephalic surface at base of central projection; central projection corneous, constituting 42.9% of total length of first pleopod, parallel to main shaft of pleopod, tapering to pointed tip, tip directed caudolaterally; mesial process subequal in length to central projection, non-corneous, tapering to acute tip, tip arched cephalomesially (Figs. 7B, C, F).

Description of allotypic female. Except for secondary sexual characteristics, differing from holotypic male in the following respects. Areola constituting 32.6% of length of carapace and eight times longer than wide, with three punctations across narrowest part. Postorbital carapace length 77.0% of length of carapace. Abdomen wider than carapace (12.7 and 10.3 mm, respectively). Mesial surface of palm of right chela with two full rows of tubercles, nine tubercles in dorsomesial row. Two tubercles in third row adjacent to distal-most tubercles in second row. A few other scatterd tubercles, one between the two main rows and a few on inner surface of palm margin. Finger of propodus with basal half of opposable margin with ten tubercles, first three roughly the same size, fourth tubercle from base of finger largest, remaining tubercles decreasing in size toward tip of finger. Tenth tubercle larger and offset distally and mesially from others. Basal half of opposable margin of dactyl with ten tubercles, first four of roughly the same size, with fourth slightly larger, remaining six slightly decreasing in size toward tip of dactyl with last two small and hard to distinguish. Caudal margin of cephalic section of lateral ramus of uropod with 19 fixed spines.

Sternum between third and fourth pereiopods narrowly V-shaped. Postannular sclerite 78% as wide as annulus ventralis (described in Diagnosis)(Fig. 7I). First pleopod uniramous, barely reaching caudal margin of annulus when abdomen flexed.

Description of morphotypic male, form II. Differing from holotype as follows. Areola constituting 33.8% of length of carapace, 6.8 times longer than wide, and with 3 punctations across its narrowest part. Postorbital carapace length 78.1% of length of carapace. Left chela regenerated. Mesial surface of palm of right chela with two irregular rows of tubercles, nine tubercles in dorsomesial row. Numerous interspersed scattered tubercles. Extra two tubercles in partial third row located near distal end. Ventral surface of right merus with two large corneous spines at distolateral corner, with mesial row of six spines. Hook on ischium of third pereiopod not overreaching basioischial articulation. First pleopod as described in Diagnosis.

Size. The largest specimen examined was a 33.1 mm CL Form-I male. Females (n = 10) ranged in size from 18.6 to 30.9 mm CL ($\bar{x}$ = 23.6 mm). Form-I males (n = 16) ranged from 19.2 to 33.1 mm CL ($\bar{x}$ = 28.1 mm). Form-II males (n = 6) ranged from 18.9 to 31.2 mm CL ($\bar{x}$ = 24.2 mm).

Color. Base color of dorsal and lateral surfaces of cephalothorax brown to dark brown (Fig. 6), rarely appearing more reddish to purplish. Black saddle crossing the juncture of posterior edge of carapace and anterior edge of abdomen, roughly equally divided onto both surfaces. Lateral sides of first abdominal pleuron with orangish, cream or yellowish patch that interupts saddle, making patches stand out. Dorsal surface of abdomen with broken or irregular triangular-shaped posteriorly tapering blackish stripe, fading out just before reaching tail fan. Posterior margin of each abdominal segment sometimes highlighted in red, especially in recently molted individuals. Lateral surfaces of abdomen and tailfan olivaceous green, with distal margins of latter sometimes appearing light yellow to cream. Walking legs olivaceous green, fading to cream near junction with body, with hints of light yellow or light red at articulation joints. Chelae and carpus overall olivaceous green, with dactyl and propodus appearing a darker green than palm region. Tips of both fingers light orange to light red, then quickly transitioning to olivaceous green. Spines and tubercles on chela carpus same color as base color. Distal half of merus olivaceous green, the remainder cream colored. Ventral surfaces of cephalothorax and abdomen cream to white with hints of light yellow on basal segement of walking legs. Ventral surface of chelae are mostly cream colored, especially on lateral half, but mesial one third can be light olivaceous green. Fingers olivaceous green or combination of cream and olivaceous green. In Form-II males, the first and second pleopods have hints of light pink or light red, with the tips of the first pleopod typically having a much darker shade than rest of the appendage.

Type locality. Eleven Point River at confluence with Diles Creek, 5.1 km NW Dalton, Randolph County, Arkansas (36.453906, -91.180904, WGS84, 104 m).

Disposition of types. The holotypic male (Form-I), allotypic female, and morphotypic male (Form-II), are housed in the crustacean collection of the Carnegie Museum of Natural History (accession numbers 38752, 38753, 38754, respectively). Paratypes consisting of seven lots are housed at CMNH (38760, 38761, 38762, 38763, 38764 and 38775) and INHS (10504).

FIGURE 8. Photo of Eleven Point River just downstream of the Dalton boat ramp (36.421044, -91.139249 ,WGS84). This is the location where the morphotype of *Faxonius wagneri* was collected, just five kilometers south (downstream) of the type locality.

Range and specimens examined. Currently known to be endemic to the mainstem of the Eleven Point River from Oregon County, Missouri to Randolph County, Arkansas. The collection lots from CMNH and INHS below are referenced using their museum accession numbers.

ARKANSAS: *Randolph County:* **(1).** Eleven Point River downstream of Dalton boat ramp, 0.2 km E Dalton, 36.421044, -91.139249 (WGS84), 15-Apr-2017, coll: JW Fetzner Jr., BK Wagner and D Filipek, CMNH-38754, 1 MII (Morphotype). **(2).** Eleven Point River above Dalton, 2.1 km N Dalton, 36.43988, -91.14478 (WGS84), 04-Aug-2011, coll: BK Wagner, CMNH-38761, 1 MI, 1 F. **(3).** Eleven Point River at Vern's Hole (Jones Creek confluence), 3.9 km SE Dalton, 36.3935, -91.1147 (WGS84), 30-Aug-2005, coll: BK Wagner, K Irwin and B Posey, INHS-10540, 3 MI. **(4).** Eleven Point River downstream of Diles Creek confluence, 4.4 km NW Dalton, 36.45033, -91.17533 (WGS84), 01-Aug-2005, coll: BK Wagner and K Irwin, INHS-10591, 2 F. **(5).** Eleven Point River upstream of Diles Creek confluence, 4.7 km NNW Dalton, 36.4599, -91.1629 (WGS84), 16-Aug-2005, coll: BK Wagner and K Irwin, INHS-10509, 5 MI. **(6).** Eleven Point River at Woody's Run, 5.1 km NW Dalton, 36.45509, -91.18096 (WGS84), 03-Aug-2011, coll: BK Wagner, CMNH-38760, 2 MI, 2 MII, 3 F; CMNH-38752, 1 MI (Holotype); CMNH-38753, 1 F (Allotype). **(7).** Eleven Point River just above confluence with Diles Creek, 5.1 km NW Dalton, 36.453906, -91.180904 (WGS84), 24-Jul-2012, coll: M Nolen, CMNH-38762, 2 MI, 1 MII, 2 F. **(8).** Eleven Point River at Woody's Run, 5.2 km NW Dalton, 36.456, -91.1802 (WGS84), 17-Aug-2005, coll: BK Wagner and K Irwin, INHS-10504, 3 MI, 1 F. **(9).** Eleven Point River below Dalton, 2.3 km SSE Dalton, 36.40308, -91.12985 (WGS84), 04-Aug-2011, coll: BK Wagner, CMNH-38775, 4 MI, 2 MII, 3 F. MISSOURI: *Oregon County:* **(10).** Eleven Point River at the U.S. Forest Service Riverton East River Access, 0.2 km NE Riverton, 36.649041, -91.2000 (WGS84), 16-Apr-2017, coll: JW Fetzner Jr., CMNH-38764, 1 MII. ***Additional Collections (examined but not measured):*** ARKANSAS: *Randolph County:* **(11).** Eleven Point River downstream of Dalton boat ramp, 0.2 km E Dalton, 36.421044, -91.139249 (WGS84), 15-Apr-2017, coll: JW Fetzner Jr., BK Wagner and D Filipek, CMNH-38763, 2 MI. MISSOURI: *Oregon County:* **(12).** Eleven Point River at the U.S. Forest Service

TABLE 4. Measurements (mm) made from the primary types of *Faxonius wagneri*, new species.

Measurement	Holotype	Allotype	Morphotype
Carapace:			
Total length	30.27	25.28	27.27
Postorbital length	24.93	19.47	21.31
Width	15.91	11.85	13.14
Depth	13.76	10.31	12.01
Areola:			
Lenght	11.19	8.23	9.21
Width	1.51	1.03	1.35
Rostrum:			
Length	8.36	8.14	8.31
Width (at base)	3.62	2.92	3.38
Chela (right):			
Total length	33.10	19.33	26.32
Total width	12.83	8.38	10.59
Palm depth	8.03	4.96	6.96
Length, plam mesial margin	9.71	5.84	7.54
Dactyl length	18.40	11.34	15.43
Propodus length	15.33	9.11	12.28
Abdomen:			
Length	31.56	28.14	27.91
Width	12.98	12.73	12.14
First Pleopod:			
Total length	13.18	-	11.88
Width	1.71	-	1.44
Length, central projection	5.65	-	2.51
Annulus ventralis:			
Length	-	2.66	-
Width	-	3.31	-

Riverton East River Access, 0.2 km NW Riverton, 36.64937, -91.20001 (WGS84), 17-Sep-1984, coll: WL Pfleiger, INHS-13206, 1 F, 1 F$_{juv}$. **(13).** Eleven Point River, 9.8 km NE Myrtle, 36.56004, -91.179781 (WGS84), 02-Aug-2017, coll: CJ Rice, INHS-15712, 1 MII, 3F. **(14).** Eleven Point River, 18.3 km NNE Myrtle, 36.6620, -91.1936 (WGS84), 25-Jul-2017, coll: CJ Rice, INHS-15714, 1 MI. **(15).** Eleven Point River, 14.2 km ENE Alton, 36.7536, -91.2595 (WGS84), 17-Jul-2017, coll: CJ Rice, INHS-15716, 2F. Additional historical records depicted on the map (Fig. 10) are from the AGFC crayfish distribution database (B.K. Wagner, personal communication).

Habitat and life history notes. *Faxonius wagneri* has only been found in the mainstem of the Eleven Point River, typically associated with gravel or coble substrates. The species was most commonly encountered in areas of the river with lower water flow (side channels, along banks, etc.). The species seems to be more common in the Arkansas portion of its range, being known from only ten specimens from four sites in Missouri.

Occurrence data are currently limited to the available museum collections. These collections were only made during three months out of the year, April, July and August, so the presence of various forms for other months is unknown. These data indicate that Form-I and Form-II males are both present in the population during all three months. No ovigerous females or females carying young were available in the collections. No other life history data are available for this species.
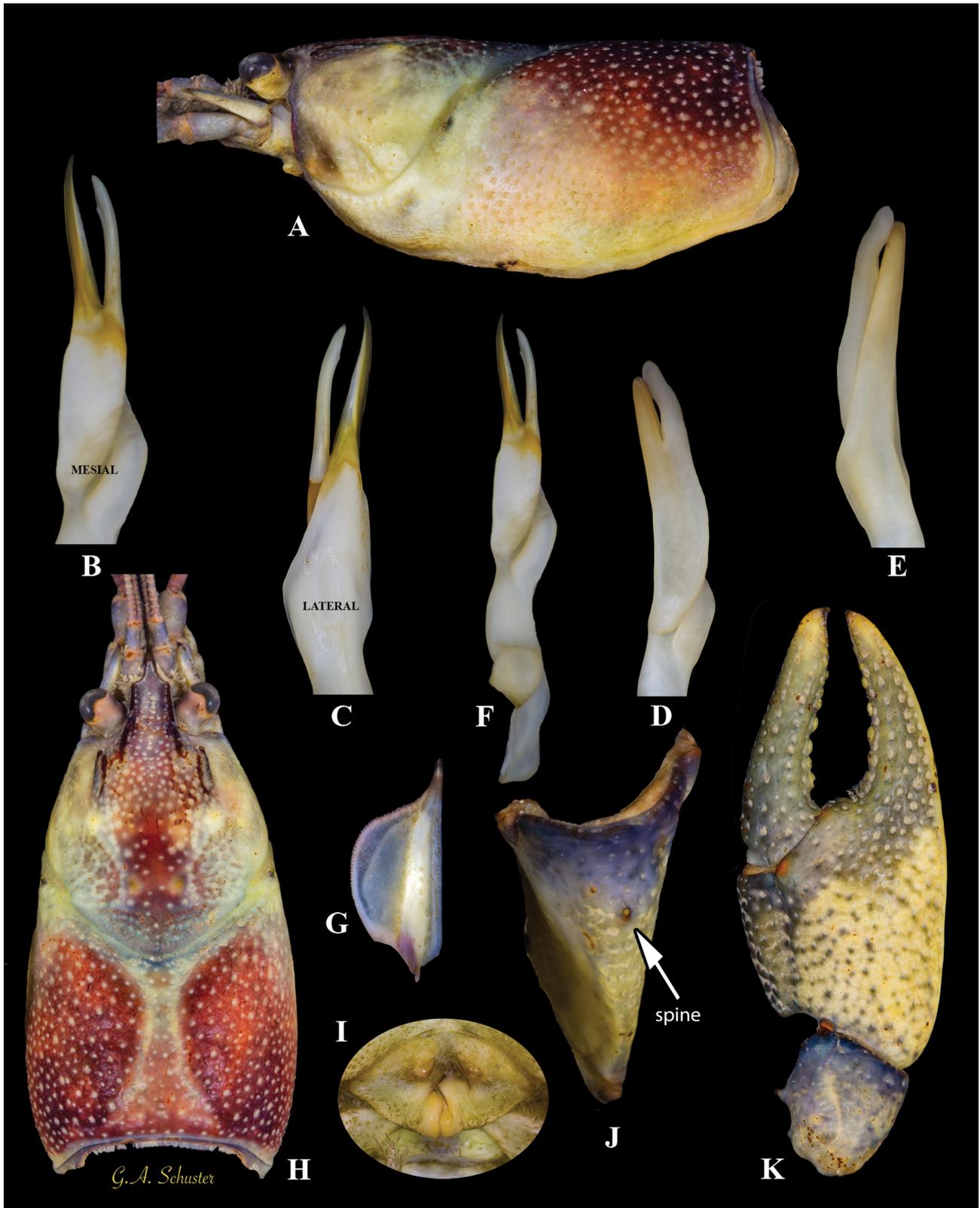
FIGURE 9. *Faxonius eupunctus* Williams, 1952; all from a recently collected male Form-I (CMNH 38755), except D and E from a male Form-II (CMNH 38757), and I from a female (CMNH 38756). A) lateral aspect of carapace; B–C) mesial and lateral aspect of Form-I male first pleopod, respectively; D–E) mesial and lateral views of Form-II male first pleopod, respectively; F) mesial view of entire first pleopod of male Form-I gonopod; G) dorsal aspect of antennal scale; H) dorsal veiw of carapace; I) ventral aspect of the female annulus ventralis; J) dorsal aspect of merus of first pereiopod (=cheliped) showing location of spines; K) dorsal aspect of distal podomeres of the right cheliped. Plate by Guenter A. Schuster.
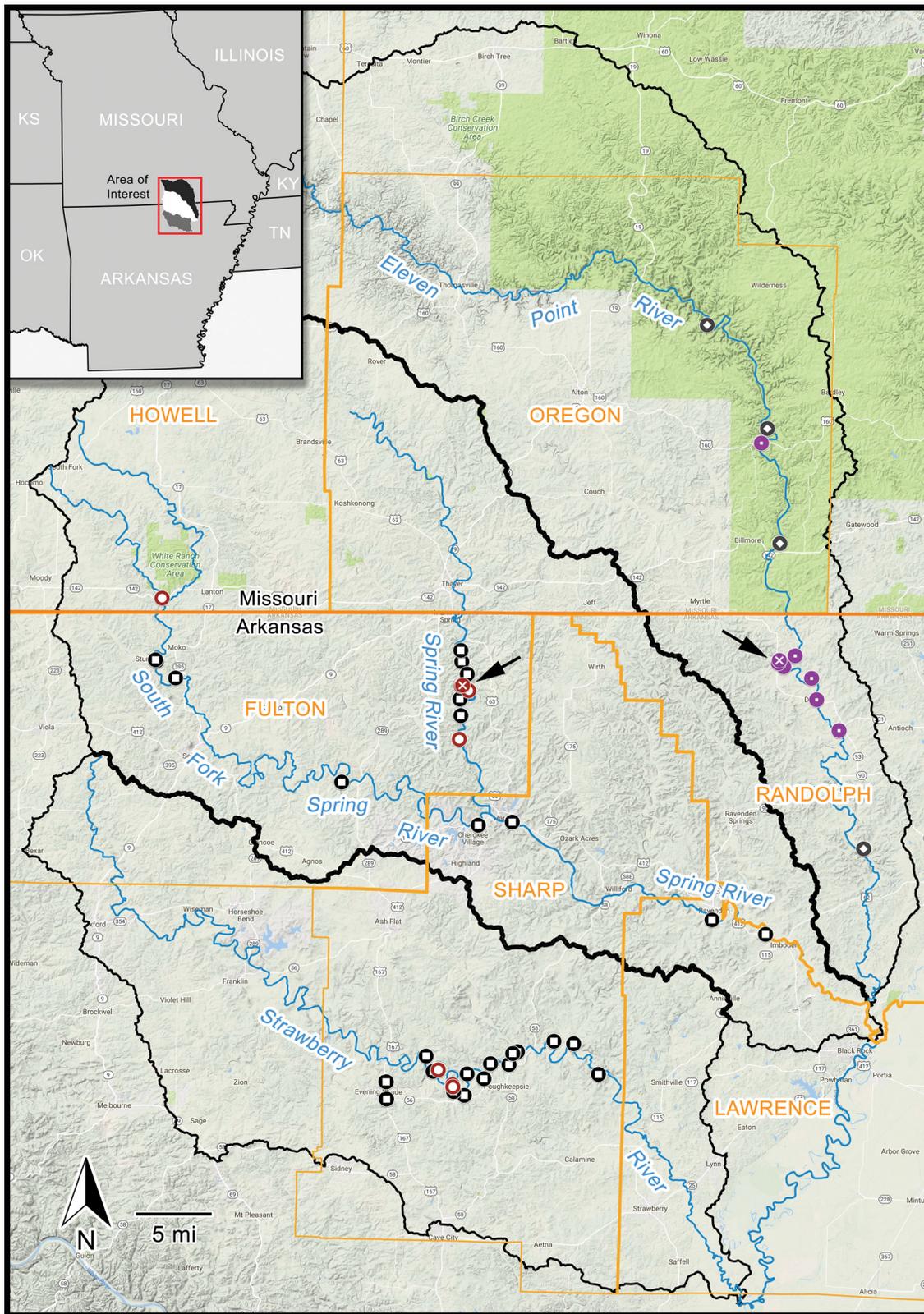
FIGURE 10. Map showing the location of museum specimens lots that were examined and measured morphologically as part of this study. *Faxonius roberti* lots examined are shown as red open circles and the type locality is depicted as an open red circle with a cross. Recent historical locality records (specimens not measured) for *F. roberti* are indicated with black circles with squares. *Faxonius wagneri* lots are shown as purple closed circles and the type locality is indicated with a purple closed circle with a cross. Black circles with diamonds indicate other known localities for *F. wagneri* that were not measured as a part of this study. Black arrows indicate the location of the type localities for both species. Orange lines indicate county boundaries. Black lines indicated HUC8 watershed boundaries. Blue lines indicate major rivers. Map was generated using Google MyMaps.

Etymology. This species is named in honor of Brian K. Wagner of the Arkansas Game and Fish Commission. Brian initially collected specimens of this species and noted that they looked different from the typical *F. eupunctus,* which are found in the same streatch of the Eleven Point River. Brian has worked extensively with the crayfish fauna of Arkansas, and it is our pleasure to name this species after him.

Crayfish associates. Other crayfish found in association with *Faxonius wagneri* include *F. eupunctus* (Williams, 1952), *F. ozarkae* (Williams, 1952), *F. punctimanus* Creaser, 1933 and *Cambarus hubbsi* Creaser, 1931.

Variation. In addition to the range of ratios and counts given in the Diagnosis section, other morphological variations seen in *F. wagneri* include the following. On the chela palm margin, there were either two or three rows of tuberlces (third only a partial row), and occasional scatered tubercles that may be interspersed between the rows or as a small cluster of tubercles distolateral to the lateral-most tubercle row. The number of spines on the ventral side of the carpus was variable, ranging from one to five (mode = 4). Some aspects of the dorsal color pattern of the carapace in this species can be variable, as described in the Color section.

Comparisons. *Faxonius wagneri* new species, differs from all other members of the genus by possessing a unique combination of male Form-I first pleopod, carapace, and rostrum characters. The Form-I male pleopod of *F. wagneri*, new species, is most similar in length and general shape to other members of the former subgenus *Procericambarus* (Fitzpatrick 1987), which occur across the central and eastern United States. This subgenus, and all others in the former genus *Orconectes*, were not recognized in the latest world classification of freshwater crayfish (Crandall & De Grave, 2017). All members of the former *Procericambarus* subgenus generally possess long, straight first pleopod elements which may or may not curve at their distal tips and a central projection accounting for at least 33% of the total first pleopod length. *Faxonius wagneri* differs from all sixteen of the former *Procericambarus* members that occur west of the Mississippi River in possessing a Form-I first pleopod mesial process that is equal in width at its base to the central projection, a central projection which is 37–45% of total pleopod length, cervical spines, and relatively wide rostrum which lacks a median carina.

Relationships. See the Phylogenetics text in the Results section for a discussion of the relationships of this species to other taxa. See also Fig. 2.

Common name. The suggested common or vernacular name for this species is the Eleven Point River Crayfish, in reference to the river where the species is found.

Conservation status. Given *F. wagneri*'s currently known limited distribution in an approximate 85 km stretch of a single river (Eleven Point R.) and the known introduction of the non-native Ringed Crayfish (*F. neglectus*) in one tributary of the Eleven Point River upstream of *F. wagneri*'s range (Imhoff *et al.* 2012), we recommend a status of Endangered following the criteria of the American Fisheries Society (Taylor *et al.* 2007). These same factors warrant a classification of Endangered following the criteria of the International Union for the Conservation of Nature (IUCN).

Discussion

Faxonius eupunctus was first described by Williams (1952) and since that time the species has received little attention, aside from being noted in various state checklists and added to state conservation lists. Only recently has the species been considered a possible candidate for listing under the federal *Endangered Species Act* (ESA), which prompted additional research into its distribution, habitat use, life history and levels of genetic and morphological variation.

The genetic and morphological datasets examined as part of this study both indicated that *Faxonius roberti* and *F. wagneri* were distinct from *F. eupunctus*. While there was some overlap in the NMDS graphs when considering all specimens together (Fig. 1A), and females only (Fig. 1B), the graphs for males (Figs. 1C, D) showed complete or almost complete separation of the species. These results show the importance of both the first pleopod measurements and dorsal merus spine counts as characters for separating these three species. The overlap between species seen in some of these graphs was interesting, given that statistical differences were detected among the species for most of the measured ratios that were examined (Table 1). Given this, we would have predicted greater separation among the species in the graphs than was actually apparent.

Geneticaly, the new species described here differed from *F. eupunctus* by roughly a six percent sequence digergence. This is significant, especially given that *F. wagneri* and *F. eupunctus* can be found sympatically and

can be caught together from the same habitat in the same seine haul. It seems clear that these are two distinct species, which apparently do not interbreed. *Faxonius wagneri* was also clearly distinct morphologically, having much longer terminal elements on the male Form-I pleopod, a very distinct female annulus ventralis, differences in the shape of the chela, live coloration, and for the most part, 2 dorsal merus spines, instead of the single spine most commonly encountered in *F. eupunctus*. *Faxonius roberti* differed morphologically from *F. eupunctus* as well, although many of the features of these two species were quite similar (i.e., shape of the chelae). *Faxonius roberti* differed from *F. eupunctus* in features of the Form-I male gonopod (pointed versus spatulate tip of the mesial process), the female annulus ventralis, antennal scale shape, dorsal merus spine count and live coloration. For the two new species, the uncorrected percent sequence divergence detected between *F. roberti* and *F. wagneri* was found to be just under two percent. This suggests these species are closely related, but the differences seen in their morphology clearly separate them from one another.

All three of the species discussed herein appear to be very closely related to one another. To illustrate this, we conducted a Bayesian phylogenetic analysis that included almost all of the species from the former subgenera *Crockerinus* and *Procericambarus* that can be found west of the Mississippi River (plus several taxa that are found to the east). Based on this analysis, *F. roberti* and *F. wagneri* appear to be sister taxa, while *F. eupuctus* was more basal. It was interesting that these three species appeared to be more closely related to species that are geographically distributed east of the Mississippi River, rather than related to other species from the Ozarks. Currently, our understanding of the phylogeographic history of this group of crayfish is limited, and further research will be needed to sort out these complex genetic relationships and their associated geographic distributions. These results also illustrate why a recent revision to the world-wide classification of crayfish was made (Crandall & De Grave 2017), and why the subgeneric rankings for many North American genera were eliminated.

Ozark crayfish, and crayfish in general, face many threats, the most important of which are probably the continued introduction and subsequent spread of other invasive crayfish species and changes to stream environments caused by the intensifying effects of global climate change. Thus, it is critically important that we closely monitor our freshwater aquatic resources, not only for changes in stream quality, but also the taxa they contain. We are at a point in histroy where such monitoring efforts will be crucial to preserving native aquaitic taxa for future generations to enjoy, and along the way, we will likely discover additional new species.

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SampleID	Species	State	County	River @ Location	Latitude	Longitude	Genbank	Type
JF16078	*Faxonius roberti*	AR	Sharp	South Fork Spring River @ Griffith Park	36.30947	-91.50970	MG872915	
JF16080	*Faxonius roberti*	AR	Sharp	South Fork Spring River @ Griffith Park	36.30947	-91.50970	MG872916	
JF16120	*Faxonius roberti*	AR	Fulton	Spring River @ Bayou Access	36.43396	-91.52714	MG872917	Holotype
JF16115	*Faxonius roberti*	AR	Fulton	Spring River @ Bayou Access	36.43396	-91.52714	MG872918	Allotype
JF12699	*Faxonius roberti*	AR	Fulton	Spring River @ Bayou Access	36.43324	-91.52836	MG872919	Morphotype
JF10785	*Faxonius roberti*	AR	Sharp	Strawberry River	36.07262	-91.52230	MG872920	
JF12353	*Faxonius roberti*	AR	Sharp	Strawberry River @ Barnes Road	36.07817	-91.53796	MG872921	
JF16146	*Faxonius wagneri*	MO	Oregon	Eleven Point River @ Riverton	36.64904	-91.20001	MG872922	
JF12382	*Faxonius wagneri*	AR	Randolph	Eleven Point River @ Woody's Run	36.45509	-91.18069	MG872923	
JF12383	*Faxonius wagneri*	AR	Randolph	Eleven Point River @ Woody's Run	36.45509	-91.18069	MG872924	
JF16064	*Faxonius wagneri*	AR	Randolph	Eleven Point River @ Dalton	36.42104	-91.13925	MG872925	Morphotype
JF16065	*Faxonius wagneri*	AR	Randolph	Eleven Point River @ Dalton	36.42104	-91.13925	MG872926	
JF16066	*Faxonius eupunctus*	AR	Randolph	Eleven Point River @ Dalton	36.42104	-91.13925	MG872927	
JF16147	*Faxonius eupunctus*	MO	Oregon	Eleven Point River @ Riverton	36.64957	-91.19985	MG872928	
JF16149	*Faxonius eupunctus*	MO	Oregon	Eleven Point River @ Greer	36.79403	-91.33368	MG872929	
JF2576	*Faxonius durelli*	TN	Humphreys	Blue Creek @ SR-13	36.05517	-87.77892	MG872930	
JF2601	*Faxonius durelli*	TN	Williamson	Trib. Watson Creek	35.92140	-86.84493	MG872931	
JF2706	*Faxonius putnami*	KY	Allen	Casey Branch @ K. Brown Road	36.70194	-86.22028	MG872935	
JF2591	*Faxonius putnami*	KY	Barren	Peter Creek @ SR-249	36.80506	-85.91764	MG872934	
JF2451	*Faxonius putnami*	KY	Monroe	Town Creek @ SR-163	36.70063	-85.68910	MG872932	
JF2531	*Faxonius putnami*	KY	Monroe	Salt Lick Creek @ Bugtussle Road	36.65650	-85.92117	MG872933	
JF2450	*Faxonius cristavarius*	TN	Johnson	Doe Creek @ fishing area	36.41905	-81.95133	MG872936	
JF1289	*Faxonius peruncus*	MO	Madison	Dry Creek @ CR-414	37.38277	-90.38339	MG872937	
JF5868	*Faxonius peruncus*	MO	Madison	Twelvemile Creek @ CR-416	37.37404	-90.39560	MG872938	
JF1257	*Faxonius hylas*	MO	Reynolds	Logan Creek @ CR-422	37.25301	-90.92771	MG872939	
JF1305	*Faxonius quadruncus*	MO	Madison	Upper Rock Creek @ CR-535	37.58537	-90.50898	MG872940	
JF3250	*Faxonius quadruncus*	MO	Iron	Trib. Marble Creek @ SR-E	37.45200	-90.58594	MG872941	
JF16067	*Faxonius ozarkae*	AR	Randolph	Eleven Point River @ Dalton	36.42104	-91.13925	MG872942	
JF16062	*Faxonius ozarkae*	AR	Lawrence	Spring River @ Ravenden	36.22481	-91.25059	MG872943	

APPENDIX 1. (Continued)

SampleID	Species	State	County	River @ Location	Latitude	Longitude	Genbank	Type
JF16085	*Faxonius ozarkae*	AR	Sharp	Strawberry River @ Barnes Road	36.07836	-91.53840	MG872944	
JF16086	*Faxonius ozarkae*	AR	Sharp	Strawberry River @ Hulett Road	36.09648	-91.47673	MG872945	
JF15540	*Faxonius marchandi*	AR	Sharp	Rock Creek @ Rock Creek Road	36.22642	-91.43903	MG872946	
JF12609	*Faxonius marchandi*	AR	Sharp	Spring River @ Hardy Beach	36.31241	-91.47267	MG872947	
INHS8789	*Faxonius n. neglectus*	MO	Stone	Indian Creek @ Hwy-86	36.50570	-93.52683	AY701241	
INHS8887	*Faxonius n. chaenodactylus*	MO	Ozark	Lick Creek @ Hwy-J	36.55010	-92.34370	AY701240	
INHS8891	*Faxonius medius*	MO	Washington	Mill Creek @ Hwy-47	37.97898	-90.66557	AY701237	
KC278	*Faxonius luteus*	AR	Benton	Deer Creek @ Fowlers Ranch *	36.49329	-94.42604	JX514454	
INHS5850	*Faxonius longidigitus*	AR	Carroll	Osage Creek @ CR-705	36.29998	-93.49713	AY701234	
JF16145	*Faxonius punctimanus*	MO	Oregon	Eleven Point River @ Riverton Access	36.64957	-91.19985	MG872948	
INHS8898	*Faxonius acares*	AR	Polk	Robinson Creek @ Hwy-88	34.58533	-93.99693	AY701227	
G148	*Faxonius leptogonopodus*	—	—	From German aquarium trade	—	—	KF944434	
INHS8896	*Faxonius menae*	AR	Polk	Robinson Creek @ Hwy-88	34.58533	-93.99693	AY701238	
INHS6296	*Faxonius saxatilis*	OK	La Flore	Pigeon Creek @ Hwy-63	34.64511	-94.53762	AY701250	
KC218	*Faxonius macrus*	MO	McDonald	Big Sugar Creek @ SR-E	36.62162	-94.18013	KF827985	
JF16087	*Faxonius palmeri*	AR	Stone	Meadow Creek @ Meadow Creek Road	35.76964	-92.34784	MG872949	
KC230	*Faxonius williamsi*	AR	Madison	White River @ SR-16 *	35.81863	-93.77986	KX238170	
JF3881	*Faxonius forceps*	AL	Madison	West Fork Flint River @ SR-231/431/1	34.96074	-86.57013	MG872950	
JF3567	*Faxonius pardalotus*	IL	Pulaski	Ohio River @ Lock & Dam 53	37.20273	-89.04215	MG872951	
JF1989	*Faxonius placidus*	IL	Hardin	Big Creek @ CR-400E *	37.54499	-88.33975	MG872952	
JF1990	*Faxonius placidus*	IL	Hardin	Big Creek @ CR-400E *	37.54499	-88.33975	MG872953	
JF3815	*Faxonius yanahlindus*	TN	Wayne	Middle Butler Creek @ Fantail Branch Road	35.09935	-87.68141	MG872954	
JF3829	*Faxonius yanahlindus*	TN	Wayne	Middle Butler Creek @ Fantail Branch Road	35.09935	-87.68141	MG872955	
JF2528	*Faxonius barrenensis*	KY	Monroe	Salt Lick Creek @ Bugtussle Road	36.65650	-85.92117	MG872956	
JF16104	*Cambarus hubbsi*	AR	Fulton	Spring River @ Bayou Access	36.43396	-91.52714	MG872957	
JF16071	*Cambarus hubbsi*	AR	Randolph	Eleven Point River @ Dalton	36.42104	-91.13925	MG872958	
JF16129	*Cambarus hubbsi*	MO	Oregon	Eleven Point River @ SR-19	36.79393	-91.33407	MG872959	
JF16148	*Cambarus hubbsi*	MO	Oregon	Eleven Point River @ Riverton Access	36.64957	-91.19985	MG872960	

APPENDIX 2. List of specimens of *Faxonius eupunctus* measured and analyzed for morphological variation along with a list of additional collections examined. The collection lots from CMNH and INHS below are referenced using their museum accession numbers.

MISSOURI: *Oregon County:* **(1).** Eleven Point River below Spring Creek confluence, 5.6 km NNW Greer, 36.81365, -91.38359 (WGS84), 17-Jan-1986, coll: WL Pflieger and S Carnett, INHS-13707, 4 MI, 8 F. **(2).** Eleven Point River south of McCormack Lake, 4.7 km N Greer, 36.81162, -91.34844 (WGS84), 13-May-1986, coll: WL Pflieger, INHS-12361, 1 F. **(3).** Eleven Point River at Hwy-19 bridge, 3.3 km NNE Greer, 36.794236, -91.333258 (WGS84), 23-Aug-2011, coll: E Imhoff, H Ladd, J Brittain and S Olson, CMNH-38776, 9 F. **(4).** Eleven Point River at Greer Access, 3 mi NE Greer, 36.79243, -91.33068 (WGS84), 11-Jun-1972, coll: PW Smith, DM Smith, INHS-4752, 3 MII, 4 F. **(5).** Type Locality: Eleven Point River at U.S. Forest Service Riverton East River Access, 0.2 km NE Riverton, 36.649369, -91.200013 (WGS84), 17-Sep-1984, coll: WL Pflieger, INHS-13206, 8 MI, 3 MII, 8 F; 12-Aug-1948, coll: Leonard and Williams, USNM-129200, 1 MI (Holotype), USNM-1437738, 1 F (Allotype), USNM-1437739, 1 MII (Morphotype); 19-May-2014, coll: C Ames, M Mabery, C Knerr and L Bachmann, CMNH-38786, 3 MI, 3 MII, 3 F. **(6).** Eleven Point River 300 m downstream of Riverton Access boat ramp, 0.2 km SSE Riverton, 36.6466, -91.20067 (WGS84), 28-Nov-1979, coll: L Trial, INHS-12284, 1 MI. **(7).** Eleven Point River at Narrows boat ramp, 2.5 km ESE Billmore, 36.55089, -91.19151 (WGS84), 17-Aug-1987, coll: WL Pflieger and JM Siebels, INHS-12857, 1 F. ARKANSAS: *Randolph County:* **(8).** Eleven Point River 2 km upstream of Diles Creek confluence, 4.7 km NNW Dalton, 36.4599, -91.1629 (WGS84), 16-Aug-2005, coll: BK Wagner and K Irwin, INHS-10508, 1 MI. **(9).** Eleven Point River at Woody's Run, 5.1 km NW Dalton, 36.45509, -91.18069 (WGS84), 03-Aug-2011, coll: BK Wagner, CMNH-38783, 1 MII. **(10).** Eleven Point River 0.7 km downstream of Diles Creek confluence, 4.4 km NW Dalton, 36.45033, -91.17533 (WGS84), 01-Aug-2005, coll: BK Wagner and K Irwin, INHS-10591, 2 MI, 2 MII, 1 F. **(11).** Eleven Point River above Dalton, 2.3 km NNW Dalton, 36.441419, -91.146882 (WGS84), 21-May-2014, coll: C Ames, M Mabery, CMNH-38785, 3 MII, 3 F. **(12).** Eleven Point River above Dalton, 2.1 km N Dalton, 36.43988, -91.14478 (WGS84), 04-Aug-2011, coll: BK Wagner, CMNH-38784, 2 MII, 1 F. **(13).** Eleven Point River immediately below Dalton boat ramp, 0.2 km ENE Dalton, 36.4218, -91.1391 (WGS84), ??-Jul-2012, coll: M Nolen, E Imhoff, CMNH-38787, 3 MII, 1 F, 1 Fjuv. ***Additional Collections (examined but not measured):*** ARKANSAS: *Randolph County:* **(14).** Eleven Point River upstream of Hwy-62 boat ramp, 1.0 km NW Birdell, 36.251094, -91.085014 (WGS84), ??-???-2011, coll: MDC Crayfish Crew, CMNH-38773, 1 M$_{juv}$, 1 F$_{juv}$. **(15).** Eleven Point River north Dalton, 2.3 km N Dalton, 36.441419, -91.146882 (WGS84), 21-May-2012, coll: MDC Crayfish Crew, CMNH-38789, 3 MI, 3 MII. **(16).** Eleven Point River downstream of Dalton boat ramp, 0.2 km E Dalton, 36.421044, -91.139249 (WGS84), 14-Apr-2017, coll: JW Fetzner Jr., BK Wagner and D Filipek, CMNH-38780, 1 MI. MISSOURI: *Oregon County:* **(17).** Eleven Point River at Morgan Spring confluence, 3.0 km E Billmore, 36.558379, -91.181767 (WGS84), ??-???-2011, coll: MDC Crayfish Crew, CMNH-38772, 1 MI, 1 F. **(18).** Barren Fork 150 m upstream of Eleven Point River confluence, 14.4 km W Greer, 36.779695, -91.51464 (WGS84), ??-???-2011, coll: MDC Crayfish Crew, CMNH-38774, 1 MII, 1 F. **(19).** Eleven Point River at Hwy-19 bridge, 3.2 km NNE Greer, 36.79393, -91.33407 (WGS84), 23-Aug-2011, coll: MDC Crayfish Crew, CMNH-38776, 5 MII, 10 F; 36.79393, -91.33407 (WGS84), 16-Apr-2017, coll: JW Fetzner Jr., CMNH-38779, 5 MI, 1 MII, 1 F; 2017-01-11, coll: D Swedberg and T Boersig, CMNH-38796, 2 MI, 1 MII, 2 F. **(20).** Spring Creek near confluence with Eleven Point River, 5.6 km NNW Greer, 36.812959, -91.384324 (WGS84), 11-Aug-2011, coll: E Imhoff, H Ladd, J Brittain, S Olson and L Johnson, CMNH-38777, 1 MI, 1 MII, 1 F. **(21).** Eleven Point River at Cane Bluff boat access, 5.5 km WNW Greer, 36.7956, -91.40537 (WGS84), 23-Aug-2011, coll: E Imhoff, H Ladd, J Brittain and S Olson, CMNH-38778, 5 MII, 5 F. **(22).** Eleven Point River at U.S. Forest Service Riverton East River Access, 0.2 km NE Riverton, 36.649574, -91.199852 (WGS84), 16-Apr-2017, coll: JW Fetzner Jr., CMNH-38781, 1 F; 25-Aug-2011, coll: MDC Crayfish Crew, CMNH-38788, 2 MI, 4 MII.