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Procambarus (*Girardiella*) *holifieldi*, a new species of crayfish (Decapoda: Cambaridae) from Alabama with a revision of the Hagenianus Group in the subgenus *Girardiella*

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Abstract

Procambarus (*Girardiella*) *holifieldi*, new species, is a primary burrowing crayfish from a low-lying field in Perry County, Alabama. It belongs to the Hagenianus Group in the subgenus *Girardiella*. The new species is morphologically most similar to *Procambarus* (*Girardiella*) *barbiger*. They differ in the size and shape of the caudal processes. *Procambarus barbiger* has a beard along the mesial margin of the palm of the chela, while the new species lacks the beard. In addition to the description of the new species, the Hagenianus Group is reviewed and new synonymies are provided. We demonstrate that a cephalic process is indeed present in the Hagenianus Group.

Key words: *Procambarus*, *Girardiella*, Hagenianus Group, Gracilis Group, new species, crayfish

Introduction

This study describes a new species of crayfish from Alabama belonging to the Hagenianus Group in the crayfish subgenus *Girardiella* in the genus *Procambarus* and provides a review and discussion of all of the species in the group. All known species within the subgenus are primary burrowers, which means that they never use permanent water such as a stream or lake and spend most of their life underground in excavated complex burrows. Individuals may sometimes leave their burrows in search of a mate or food, which is most common during and after periods of heavy rains.

Procambarus gracilis (Bundy, 1876) from Illinois was the first species described belonging to the now-recognized subgenus *Girardiella*. It is now the nominal species for the Gracilis Group in the subgenus. Faxon (1884) described *Procambarus hagenianus* based on a specimen mislabeled as being from Charleston, South Carolina, and it now is the nominal species for the Hagenianus Group in the subgenus. In the same paper Faxon also described another Gracilis Group species, *P. simulans*, from Texas. Faxon (1914) was the first to correctly illustrate *P. hagenianus* and provided additional taxonomic data, including observations on variation and color (pages 366–367, plate1), and correct locations for the above species in Mississippi and Alabama. The first comprehensive study on the Hagenianus Group was by Lyle (1938), which was presented as an abstract of his dissertation (Lyle, 1937). In the abstract, Lyle provided names for 4 subspecies of *P. hagenianus*, all of which were later designated as *nomina nuda* by Hobbs (1972a), because the names were published without an accompanying description for the taxa. Lyle also proposed the name *Girardiella* as a subgenus for these taxa. Hobbs (1942) put the *Girardiella* group into the genus *Procambarus* when he elevated most of the subgenera of *Cambarus* to generic rank. Penn (1953) described *P. tulanei*, a Gracilis Group species, from Louisiana.

In a study of species in the Hagenianus Group, Reimer (1969) described *P. hagenianus* as having "chelae….with or without a beard." He also indicated that it had a "cephalic process greatly reduced to flattened, plate-like structure in close connection with mesial surface of central projection." Hobbs (1972a) accepted Lyle's

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name *Girardiella* as a subgenus in *Procambarus* and provided a description of the subgenus. He also, for the first time, indicated that all known *Girardiella* species had a cephalic process, except for *P. hagenianus*. Hobbs (1972b), in a key to North American crayfishes, indicated again that the cephalic process was absent in *P. hagenianus*. He also indicated that *P. hagenianus* had a median spine on the inner ramus of the uropod that projected beyond the distal margin of the ramus. Reimer (1975), in his description of *P. curdi*, mentioned that one of the differences between *P. curdi* and *P. hagenianus* was the lack of a cephalic process in *P. hagenianus*. Thus, in his paper he followed Hobbs (1972a) rather than what he reported in his dissertation (Reimer, 1969), that *P. hagenianus* had a reduced to flattened cephalic process.

Fitzpatrick (1978a) published the seminal work on the taxonomy of the Hagenianus Group. He also followed Hobbs (1972a), and indicated that the Hagenianus Group could be separated from the Gracilis Group based on the absence of the cephalic process and the presence of the large spine on the inner ramus of the uropod that extended beyond the distal margin of the ramus. In this paper he described the following new species: *P. barbiger, P. cometes, P. connus* (misspelled as *connos* in the abstract), and *P. pogum.* He also described a new subspecies for *P. hagenianus*, *P. hagenianus vesticeps*. He indicated that the main difference between the two subspecies was that *P. h. vesticeps* had a beard of dense long setation on the inner margins of the palm of the chelae, whereas *P. h. hagenianus* did not. Fitzpatrick for the most part accepted the taxa Lyle (1938) described in his dissertation; however, he also described *P. cometes* and *P. connus*, which were not recognized by Lyle. Fitzpatrick also included a key to the known Hagenianus Group species for both males and females.

Since Fitzpatrick (1978a), numerous other *Girardiella* species have been described, all of which belong to the Gracilis Group. These include: *P. liberorum* Fitzpatrick (1978b), Arkansas; *P. reimeri* Hobbs (1979), Arkansas; *P. parasimulans* Hobbs and Robison (1982), Arkansas; *P. ferrugineus* and *P. regalis* Hobbs and Robison (1988), Arkansas (with a key to Gracilis Group species); *P. nigrocinctus* (Reimer 1969; species F) and *P. kensleyi* (Reimer 1969; species F, in part) Hobbs (1990), Texas; *P. ceruleus* Fitzpatrick and Wicksten 1998, Texas; *P. machardyi* Walls 2006, Louisiana. Walls (2006) also provided a key to all known species of the *Girardiella*, essentially using distinguishing characters for the Hagenianus Group species from Fitzpatrick's (1978a) key.

In the current paper a new species, *Procambarus* (*Girardiella*) *holifieldi*, is described and assigned to the Hagenianus Group. This is the first description of a new species for the Hagenianus Group since Fitzpatrick (1978a). The presence and absence of the cephalic process was an important character separating the Gracilis Group from the Hagenianus Group. We discuss the presence of the cephalic process in the Hagenianus Group. In addition, the Hagenianus Group is revised based on morphological characters of the nominal taxa in the group. The two species groups can still be separated by differences in length of the median spine on the mesial ramus of the uropod. As result of the revision of the Hagenianus Group three species are synonymized, and four taxa are recognized as valid.

Materials and methods

The primary types, paratypes and other specimens of *P. barbiger, P. cometes, P. connus*, *P. hagenianus hagenianus*, *P. hagenianus vesticeps* and *P. pogum* were studied and photographed. The study was hampered by the paucity of fresh or live specimens, because all of the organisms are primary burrowers and are very difficult to collect. Few recent collections of the species exist. The largest series of the taxa are specimens collected by Lyle (1938) which are all housed in the National Museum of Natural History (USNM) in Washington, D.C. The holotype and allotype of *Procambarus hagenianus* are at the Museum of Comparative Zoology (MCZ) at Harvard University, Boston, MA.

Most specimens of *P. holifieldi*, new species, were found walking in the vicinity of their burrows at the type locality at night after or during heavy rains. Two of the paratypes were collected by excavating burrows with a shovel.

Measurements of crayfish structures were to the nearest 0.1 mm using a Mitutoyo Absolute Digimatic dial caliper. A Wild stereo dissecting microscope was used to make measurements and to photograph the smaller structures such as the gonopods. Photographs were taken with a Canon 5D Mark III. The photographs were edited in Adobe Photoshop CC2014 and Lightroom 5, and were used to make all of the figures. Photomicrographs were taken through either a Wild or Meiji Stereomicroscope. For most of the photomicrographs, the software program Helicon Focus (Helicon Soft, Ltd) was used through a process called photo stacking to give the photographs a great depth of field.

The following abbreviations are used in subsequent sections: AL, for areola length; AW, for areola width; CP, for central projection; CaP, for caudal process; CeP, for cephalic process; F, for female; INHS, for Illinois Natural History Survey, Champaign, IL; Juv, for juvenile; MI, for form I male; MII, for form II male; MCZ, for Museum of Comparative Zoology, Harvard University, Cambridge, MA; MMNS, for Mississippi Museum of Natural Science, Jackson, MS; MP, for mesial process; PCL, for postorbital carapace length; RL, for rostral length; RW, for rostral width; TCL, for total carapace length; USFS, for United States Forest Service; USNM, for National Museum of Natural History, Washington, DC.

Specimens Examined. ***Procambarus* (*Girardiella*) *barbiger*:** **MMNS538**, 1 MII, 2 Fe: MS, Scott County, Bienville National Forest; **MMNS557**, 1 MI: MS, Newton County, just east of junction of US 80 and I–20; **MMNS559**, 3 Fe: MS, Newton County, just east of jct SR 80 and I–20; **MMNS560**, 1 Fe, 1 juv: MS, Newton County, just east of junction of US 80 and I–20; **MMNS569**, 3 MII, 3 Fe, 1 juv: MS, Scott County, Bienville National Forest; **MMNS573**, 1 MII, 5 Fe, 5 juv: MS, Scott County, Bienville National Forest; **MMNS604**, 1 MII, 1 Fe: MS, Scott County, Singleton Prairie about 5.6 miles NE junction SR35 and I–20, S of Forrest; **MMNS625**, 1 MI: MS, Smith County, Bienville National Forest, 1.4 miles north of Clear Springs; **MMNS660**, 1 MI, 1 Fe: MS, Jasper, about 4.5 miles southeast of Garlandville; **MMNS734**, 1 MI, 1 Fe: MS, Scott County, Bienville National Forest, 1.6 miles WSW of junction SR35 and I–20; **MMNS739**, 1 MII, 1 Fe: MS, Rankin County, north side Oak Ridge Road, 0.4 miles east of junction Oak Ridge and Wade Patrick roads; **MMNS749**, 1 Fe: MS, Jasper County, about 4.5 miles southeast of Garlandville; **MMNS1502**, 1 MI: MS, Scott County, yard of Forest Service Office, SR35; **MMNS1503**, 1 Fe: MS, Scott County, Bienville National Forest, prairie along Forest Service road 551-A; **MMNS1506**, 1 MI: MS, Scott County, Bienville National Forest, about 5.1 miles northeast of junction I–20 and SR 481; **MMNS1611**, 1 MII: MS, Jasper County, about 2.3 miles south of Garlandville; **MMNS1637** 1 MII: MS, Scott County, Bienville National Forest, north side of Walk Hill; **MMNS1974**, 1 Fe: MS, Scott County, prairie adjacent to Forest Service sign, Bienville District 70; **MMNS1934**, 1 Fe: MS, Rankin County, back lot of 416 Shenandoah Road, west of Grant's Ferry Road; **MMNS2299**, 1 MI: MS, Rankin County, damp grassland on SR 471, 0.8 miles south of junction SR 43 and SR 471; **MMNS2427**, 1 MI: MS, Rankin County, 1287 East Deer Ridge Road, Brandon; **MMNS2689**, 2 MI: MS, Rankin County, Barefoot Spring Road; **USFS-CL001**. 2 MI, 1 Fe: MS, Perry, roadside ditch along Hwy 29, Desoto National Forest; **USNM146258**, **Holotype**, MI: MS, Scott County, Forest; **USNM314825**, **Paratype**, 1 Fe: MS, Scott County, Forest; **USNM146259**, **Allotype**, F: MS, Scott County, Forest; **USNM220592**, 4 MI, 9 Fe: MS, Scott County, Forest.

***Procambarus* (*Girardiella*) *cometes*:** **USNM131280**, **Paratype**, 1 MII: MS, Oktibbeha County, Starkville, Luxury Mobile Homes trailer park; **USNM220542**, **Paratype**, 1 MI: MS, Lowndes County, 6.6 miles E Of Old State Route 12 (Starkville) on US Highway 82; **USNM130263**, **Paratype** 3 Fe: MS, Oktibbeha County, Starkville, dug from burrows at trailer court; **USNM146260**, **Allotype**, 1 Fe: MS, Oktibbeha County, Starkville, Luxury Mobile Homes trailer park; **USNM220543**, 1 Fe: MS, Oktibbeha County, field behind Luxury Mobile Homes trailer park, just outside Starkville city limits; **USNM146275**, **Paratype**, 1 MI, 3 Fe: MS, Oktibbeha County, flooded area, 8.8 miles SW On Route 12, from junction Route 25 State Route 25; **USNM130234**, **Paratype**, 1 MI: MS, Oktibbeha County, Starkville, Luxury Mobile Homes trailer park; **USNM129942**, **Paratype**, 1 Fe; MS, Oktibbeha County, Starkville, Luxury Mobile Homes trailer park; **USNM130227**, **Holotype**, 1 MI: MS, Oktibbeha County, Starkville, Luxury Mobile Homes trailer park.

***Procambarus* (*Girardiella*) *connus*:** **USNM146262**, **Allotype**, 1 Fe: MS, Carroll County, Carrollton; **USNM220371**, **Paratype**, 14 MI: MS, Carroll County, Carrollton; **USNM146264**, **Paratype**, 13 MI: MS, Carroll County, Carrollton; **USNM146263**, **Paratype**, 1 MII: MS, Carroll County, Carrollton; **USNM146269**, **Paratype**, 15 MI: MS, Carroll County, Carrollton; [Note: **USNM146261**, **Holotype**, 1MI: at time of study was missing].

***Procambarus* (*Girardiella*) *hagenianus hagenianus*:** **MMNS589**, 1 Fe: MS, Rankin County, Pelahatchie; **MMNS596**, 1 Fe: MS, Rankin, Yates pasture at west Pelahatchie city limits on US 80; **MMNS597**, 1 MII, 1 Fe: MS, Rankin, prairie remnant on north side of I–20 at wesstbound entry ramp, Pelahatchie; **MMNS600**, 1 MII, 10 Fe: MS, Rankin, Pelahatchie, at wesstbound entry ramp on I–20; **MMNS605**, 1 Fe: MS, Rankin, Yates pasture at west Pelahatchie city limits on US 80; **MMNS620**, 2 Fe: MS, Rankin, Yates pasture on north side of I–20; **MMNS620**, 3 MI, MS Rankin, Yates pasture on north side of I–20; **MMNS621**, 1 MI: MS, Rankin, Yates pasture on north side of I–20; **MMNS622**, 1 Fe: MS, Rankin County, Yates pasture on north side of I–20; **MMNS827**, 1 MI: MS, Rankin County, Yates pasture, west of Pelahatchie City limits, north side of US 80; **MMNS830**, 1 Fe: MS,

Rankin County, prairie on north side of I–20 at Pelahatchie; **MMNS832**, 1 MI: MS, Rankin County, Yates pasture, west Pelahatchie city limits on US 80; **MMNS1530**, 1 MI: MS, Rankin County, wooded prairie remnant at Pelahatchie along I–20, west of westbound entry ramp; **MMNS1531**, 2 MI, 2 MII, 4 Fe: MS, Rankin County, Yates pasture at west Pelahatchie city limits on US 80, north side of road; **MMNS1532**, 1 Fe: MS, Rankin County, Yates pasture at west Pelahatchie city limits on US 80, north side of road; **MMNS1533**, 5 Fe, 1 juv: MS, Rankin County, wooded slope in burrows; **MMNS1534**, 1 MI, 1 Fe: MS, Rankin County, Yates pasture, west of Pelahatchie city limits, on US 80; **MMNS1620**, 1 MII: MS, Rankin County, prairie remnant at Pelahatchie, north of westbound entry ramp to I–20; **MMNS2394**, 3 MI, 2 Fe: MS, Rankin County, Yates pasture at western city limits of Pelahatchie on US 80; **MMNS2429**, 1 MI, 2 Fe: MS, Rankin County, Yates pasture at western city limits of Pelahatchie on US80; **MMNS2433**, 1 Fe: MS, Rankin, Yates pasture at western city limits on US 80; **MMNS2781**, 1 MI, 2 Fe: MS, Rankin County, Yates pasture at western city limits on US 80; **USNM20820**, 1 MI, 1 Fe: MS, Oktibbeha County, just SW of city limits of Starkville on State Route 25; **USNM208209**, 1 MI, 2 Fe: MS, Oktibbeha County, 5 miles S of Starkville, burrow in open meadow; **USNM208433**, 3 MII, 2 Fe, 1 M juv: MS, Oktibbeha County, Bluff Lake Road from State College, at entrance to refuge; **USNM208198**, 8 MI, 2 MII, 5 Fe: MS, Lowndes County, 4.5 miles W of Columbus; **USNM208197**, 3 MII, 10 Fe: MS, from burrow near Chiltons; **USNM208761**, 1 M juv, 1 Fe juv: MS, Chickasaw County; 3.7 miles N, of S junction State Route 32 and State Route 15; **USNM208420**, 1 Fe: MS, Oktibbeha County, Agricultural College, Catalpa Creek under log close to ditch; **USNM208419**, 1 Fe: MS, Oktibbeha County, in field on campus of Mississippi State University, Catalpa Creek; **USNM208211**, 5 MI, 1 Fe: MS, Oktibbeha County, State University; **USNM130232**, 2 MI: MS, Oktibbeha County, burrows along N end of Country Club Lake: **USNM208201**, 1 Fe: MS, Oktibbeha County, south farm unit of MSU property, burrows; **USNM208210**, 6 Fe: MS, Oktibbeha County, Agricultural College; **USNM208200**, 1 MI, 9 Fe: MS, Oktibbeha County, from dairy pond; **USNM208202**, 1 MI, 2 Fe: MS, Oktibbeha County, south farm unit of MSU property; **USNM208212**, 2 Fe juv: MS, Oktibbeha County, in field on MSU campus, Catalpa Creek; **USNM208199**, 17 Fe: MS, Oktibbeha County, State College; **USNM208421**, 1 Fe: MS, Oktibbeha County, in field on MSU campus, Catalpa Creek; **USNM208203**, 1 Fe: MS, Oktibbeha County, oat field (dry); **USNM146279**, 1 MI, 1MII, 11 Fe: MS, Lowndes County, Mayhew; **USNM146280**, 10 MI, 4 MII, 5 Fe: MS, Kemper County, 6 miles E of Macon; **USNM146620**, 1 MI, 1 MII, 1 Fe: MS, Lowndes County, 4.5 miles W of Columbus; **USNM146278**, 2 MI, 1 MII, 16 Fe: MS, Hinds County, Jackson; **USNM146281**, 31 MI, 3 MII: MS, Oktibbeha County, About 10 miles W of Columbus, in open field; **USNM145345**, 1 MI, 1 Fe juv: AL, Sumter County, Jones Creek, 2.8 miles N of junction of US 11 and Route 39 on Route 39.

***Procambarus* (*Girardiella*) *hagenianus vesticeps*: USFS-SA288**, 1 Fe: MS, Monroe County, burrows along roadside Hwy 8, west of Aberdeen; **USFS-SA329**, 2 MI, 2 Fe: MS, a Chickasaw County, roadside burrows, north side of Hwy 8, 1.4 km east of US Alt 45 crossing; **USFS-M031**, 1 MI: MS, Pontotoc County, in yard of Henderson property, south side of Hwy 76/228, 6.5 km ESE of Thaxton; **USFS-M071**, 1 MI: MS, Pontotoc County, in yard of Henderson property, south side of Hwy 76/228, 6.5 km ESE of Thaxton; **USNM69441**, 7 MI, 1 MII: MS, Chickasaw County, Okalona; **USNM208037**, 1 MII, 6 Fe: MS, Monroe County, Muldon, from wells dug on Evans place; **USNM146277**, 1 MI, 1 Fe: MS, Monroe County, Muldon; **USNM208036**, 1 M juv: MS, Monroe County, slough at junction State Route 8 and State Route 25; **USNM146274**, 1 Fe: MS, Pontotoc County, near Hurricane, near Thaxton; **USNM146265**, **Holotype**, 1 MI: MS, Chickasaw County, Egypt, from burrows in pasture; **USNM146268**, **Paratype**, 1 MI: MS, Chickasaw County, Egypt, from burrows in pasture; **USNM220593**, 6 MI, 2 MII, 5 Fe, 1 M juv, 1 Fe juv: MS, Chickasaw County, pasture in Egypt; **USNM146267**, **Paratype**, 1 MII: MS, Chickasaw County, Egypt, from burrows in pasture; **USNM146266**, **Allotype**, 1 Fe: MS, Chickasaw County, Egypt, from burrows in pasture; **USNM129567**, 1 MI, 1 MII, 1 Fe: MS.

***Procambarus (Girardiella) pogum:* USNM129790**, 1 MII, 1 Fe: MS, Chickasaw County, burrows in roadside ditch 0.4 miles E of Houlka Creek on State Route 8; **USNM208205**, 1 Fe: MS, Oktibbeha County, field on MSU campus, Catalpa Creek, burrows; **USNM208214**, 1 Fe: MS, Oktibbeha County, Rock Hill; **USNM208208**, 1 Fe juv: MS, Oktibbeha County, in field on MSU campus, Catalpa Creek, burrow; **USNM146272**, **Paratype**, 1 MII: MS, Chickasaw County, Houston; **USNM208213**, 1 Fe: MS, Oktibbeha County, in field on MSU Campus, Catalpa Creek, burrow; **USNM283973**, 2 MI, 3 MII, 8 Fe: MS, Chickasaw County, Houston; **USNM220594**, 2 MII, 3 Fe: MS, Oktibbeha County, Sand Creek; **USNM146270**, **Holotype**, 1 MI: Chickasaw County, Houston; **USNM208206**, 2 Fe: MS, Oktibbeha County, dairy pool; **USNM208215**, 1 Fe: MS, Oktibbeha County, in field on MSU campus, Catalpa Creek, burrow; **USNM146271**, **Allotype**, 1 Fe: MS, Chickasaw County, Houston.

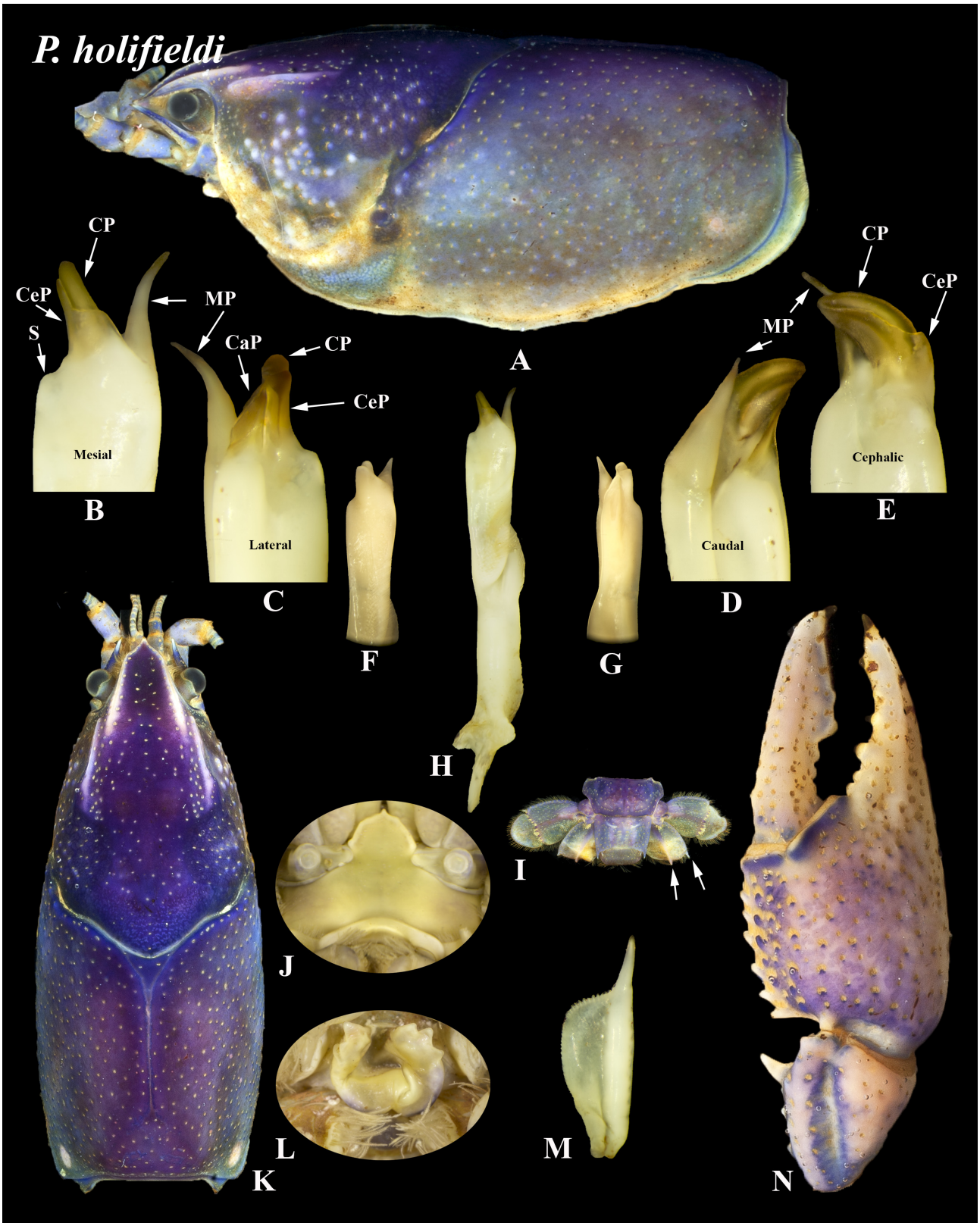

FIGURE 1. *Procambarus* (*Girardiella*) *holifieldi* **n.sp.**: A. lateral view of carapace; B–E, respectively, mesial, lateral, caudal and cephalic view of terminal end of left gonopod of form I male; F–G, mesial and lateral view of terminal end of left gonopod of form II male; H, mesial view of entire left gonopod of form I male; I, dorsal view of tail fan; J, epistome; K, dorsal view of carapace; L, annulus ventralis; M, antennal scale; N, dorsal view of right chela and carpus of form I male; A–D, H–K, M–N from holotype; F–G from morphotype; L from allotype. CP = central projection, CaP = caudal process, MP = mesial process, S = Shoulder, CeP = Cephalic Process.

Systematics

Procambarus (*Girardiella*) *holifieldi* Schuster, Taylor and Adams, new species

(Figure 1–2, Table 1)

TABLE 1. Measurements (mm) of type specimens of *Procambarus holifieldi*, new species

	Holotype	Allotype	Morphotype
Carapace			
Height	12.9	15.5	12.7
Width	12.4	16.1	12.3
Total length of carapace (TCL)	29.4	35.1	28.2
Postorbital carapace length (PCL)	26.2	31.5	24.7
Areola Length	12.0	14.2	11.7
Eye Diameter	1.5	1.8	1.6
Rostrum			
Width	4.1	5.1	3.6
Length	4.1	5.9	4.4
Chela			
Length, mesial margin palm	7.7	8.4	5.9
Width, palm	9.6	10.4	8.9
Length, lateral margin	20.0	21.8	19.0
Length, dactyl	12.0	13.4	12.1

Diagnosis. The following was generated from 23 adults including 6 form I males, 6 form II males and 11 females; the data are pooled except for sexually related structures: Body pigmented; eyes well developed, average eye diameter for adults 1.6 mm; mean carapace height 13.4 mm, mean carapace width 12.8 mm, mean total carapace length (TCL) 29.6 mm, mean postorbital carapace length (PCL) 25.9 mm; mean width of second abdominal segment (widest segment) 9.9 mm; rostral margins widest at base, mean width 3.9 mm, mean length 4.5 mm, average RW/RL ratio 86.6%, margins gradually converge from base to acumen, smoothly rounding apically to form short acumen, no rostral spines or tubercles, no subrostral spines; branchiostegal sclerites meet mid-dorsally; areola obliterated, linear, average AL/PCL ratio 46.8%, average AL/TCL ratio 41%; no cervical spines; suborbital angle obsolete, margins almost straight or with slight curve; postorbital ridges low, with no anterior spines or distinct tubercles; branchiostegal spine may be absent or present as small tubercle or spine; antennal scale mean length 3.8 mm, mean width 1.4 mm, 2.7 times longer than wide, widest at distal 2/3 of scale, mesial margin with mesial row of dense setation; mesial margin of palm without setiferous mat or beard, mean mesial margin length 7.1 mm, mean palm width 9.1 mm; mesial margin of palm with two rows of tubercles, 5–7 tubercles in first row, 2–6 in second row, scattered tubercles on mesial third of palm; dactyl of chela mean length 11.7 mm, with large excision at the base, 2–3 tubercles in area of excision, 2–5 tubercles distal to excision area, dactyl terminating distally with large acute tubercle; propodus of chela mean length 19.1 mm, with 3–6 tubercles in excision area, 3–5 tubercles distal to excision area, distal tubercles almost evenly spaced with small denticles between tubercles, propodus ending distally with large spur; third maxilliped of males in ventral view covered with dense setation on ventral and lateral surfaces of all segments, in females setation less dense on lateral surfaces; margins of sternum between pereiopods of both sexes outlined with dense, long setation, in form I males setation more dense, setae longer; ischia of third pereiopods of form I males with large hook; hook overreaching basioischial joint, hook not

opposed by tubercle on basis; coxae of third, fourth and fifth pereiopods without prominences or bosses, fourth may be slightly enlarged; inner ramus of uropods with two conspicuous spines projecting well beyond margin; form I male pleopods symmetrical, distal extremity of first pleopods with the following structures: 1) central projection, prominent, crescent shaped, from caudal view broadly rounded and directed laterally; 2) cephalic process hood-like, in cephalic view extends over the base of the central projection; 3) caudal process, sharply pointed apically, flat blade-like; 4) mesial process not heavily sclerotized, tapering to point apically, in caudal view broadly rounded, directed laterally, extends to or slightly beyond central projection; gonopod elements all present in form II males, greatly reduced in size and distinct in structure, in mesial and lateral views distinct shoulder just proximal to terminal elements; annulus ventralis of females mean width 1.7 mm, moveable, circular in outline with deep trough mesially, and sigmoid deep sinus, anterior third of annulus on both sides of trough with 3–5 large tubercles, tubercles reduced in size and number (0–2) in smaller individuals.

FIGURE 2. *Procambarus* (*Girardiella*) *holifieldi* **n.sp.**: Holotype, Perry County, AL.

Description of the holotype male, form I. Cephalothorax (Figure 1A & K) TCL 29.4 mm and PCL 26.2 mm; subovate, greatly compressed laterally; maximum width slightly less than maximum height (12.4 and 12.9 mm). Abdomen narrower than cephalothorax (9.5 and 12.4 mm). Areola 12.0 mm long, obliterated, linear (Figure 1K). Cephalic portion of cephalothorax 1.7 times longer than areola; areola comprising 45.8% of PCL (40.8% of TCL). Surface of carapace punctate dorsally (Figure 1K), laterally covered with small rounded tubercles (Figure 1A). Rostrum (Figure 1K) broadest at base (4.1 mm), 4.1 mm long; sides gradually converging to acumen; margins distinctly thickened; anteriorly rounded without tubercles or spines; acumen small; distinct subrostral ridge without spines. Postorbital ridge (Figure 1A) weak with no tubercle or spine anteriorly. Suborbital angle (Fig. 1A) obtuse, margins slightly rounded; branchiostegal spine weak consisting of a small tubercle. Cervical spine absent. Margins of sternum of cephalothorax lined with long flexible plumose setae, the first gonopods may be partially obscured as they lay in between the pereiopods.

Abdomen only slight longer than PCL (26.9 and 26.2 mm). Cephalic part of telson with two spines in each caudolateral corner; inner spines moveable (Figure 1I). Cephalic lobe of the epistome (Figure 1J) somewhat rounded with thickened edges; main body of epistome rectangular in broad outline, zygoma strongly arched. Antennal scale 3.9 mm long and 1.3 mm at widest point; lateral edge with row of erect spine-like setae; mesial margin with row of long, flexible setae (Figure 1M).

Third maxilliped well developed; ventral and lateral sides of basal segments covered with long flexible plumose setae; distal segments also with long setae, but not as dense. Right chela (Figure 1N) total length 19.9 mm, dactyl length (12.0 mm) about 60 % of total length; dactyl and propodus each with very weak dorsomedian ridges. Palm width greater than palm length (9.6 and 7.7 mm); no plumose beard of setae along palm mesial margin; mesial margin of palm with a row of 6 tubercles, a second row of 6 tubercles and scattered tubercles on dorsal surface of palm. Opposable margin of dactyl with distinctly rounded basal excision; with 3 round tubercles in the excision area, and 2 large rounded tubercles distal to excision. Propodus with 3 large tubercles in excision area and 3 equally distributed tubercles distal to excision area, tubercles almost evenly spaced with small denticles in between and to base of terminal spur. Carpus of cheliped with curved dorsal furrow; one large dorsomesial spine and a number of small rounded tubercles along mesial margin. Hook on ischium of third pereiopod only. Coxae of third, fourth or fifth without prominences or bosses, but coxa of fourth somewhat enlarged caudomesially.

First Form pleopods symmetrical at base with long proximomedian lobe (Figure 1H); terminal elements as described in "Diagnosis" (Figure 1B, C, D, E and H).

Description of allotype female. Differs from male holotype in the following: Cephalothorax TCL 35.0 mm and PCL 31.5 mm; maximum width slightly less than maximum height (16.1 and 15.5 mm). Abdomen narrower than cephalothorax (12.1 and 16.1 mm). Areola 14.2 mm long, obliterated, linear. Branchiostegal spine small but distinct. Cephalic portion of cephalothorax 1.7 times longer than areola; areola comprising 45.1% of PCL (40.6% of TCL). Rostrum widest at base (5.1 mm), 5.9 mm long. Margins of sternum of cephalothorax lined with long flexible plumose setae, not as dense as in holotype. Abdomen subequal to TCL. Antennal scale 4.1 mm long, 1.5 mm at widest point. Ventral segments of third maxilliped covered with long flexible plumose setae, lateral margins with row of long setae but not as dense or as long as in holotype. Right chela total length 21.8 mm, dactyl length (13.4 mm) 61.5% of total length; palm width greater than palm length (10.4 and 8.4 mm). Opposable margin of dactyl with distinctly rounded excision at base, with 2 round tubercles in excision area and three tubercles distal to excision with denticles in between to terminal spur. Opposable margin of propodus with 3 large tubercles within excision area and 5 almost equally spaced distal to excision, with small denticles in between to terminal spur. No hook on ischium of third pereiopod. Annulus ventralis (Figure 1L) as described in "Diagnosis."

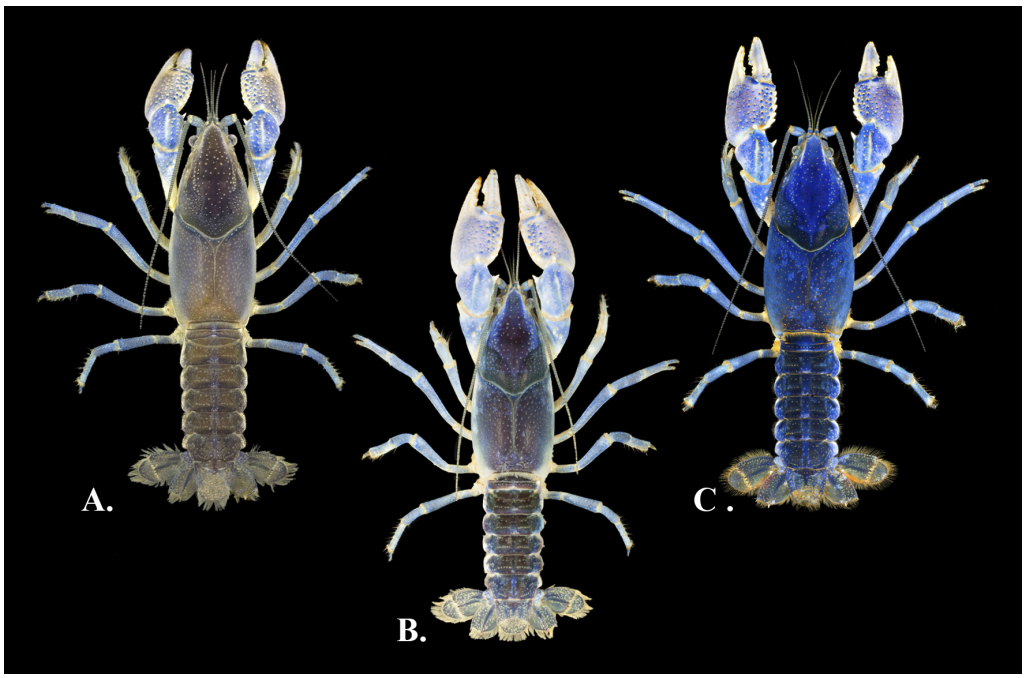

FIGURE 3. *Procambarus* (*Girardiella*) *holifieldi* **n.sp.**: A–C, color variations, Perry County, AL.

Description of the morphotype male, form II. Differs from male holotype in the following: Cephalothorax TCL 28.2 mm and PCL 24.7 mm; maximum width slightly less than maximum height (12.3 and 12.7 mm). Abdomen narrower than cephalothorax (9.2 and 12.3 mm). Areola 11.7 mm long, obliterated, linear. Branchiostegal spine small but distinct. Cephalic portion of cephalothorax 1.4 times longer than areola; areola comprising 47.4 % of PCL (41.5 percent of TCL). Rostrum widest at base (3.62 mm), 4.35 mm long. Margins of sternum of cephalothorax lined with long flexible plumose setae, not as dense as in holotype. Abdomen somewhat shorter in length than TCL (23.8 and 28.2 mm). Antennal scale 3.9 mm long, 1.4 mm at widest point. Right chela total length 19.0 mm, dactyl length (12.1 mm) about 63.7 % of total length; palm width greater than palm length (8.9 and 6.6 mm); Opposable margin of dactyl with distinctly rounded excision at base; with 3 round tubercles in excision area and 2 tubercles distal to excision with denticles in between to terminal spur. Opposable margin of propodus with 3 large tubercles within excision area and 4 almost equally spaced distal to excision, with small denticles in between to terminal spur. Hook on ischium of third pereiopod, much smaller than on holotype. Gonopod length 8.8 mm, all four terminal elements present and identifiable, description of placement similar to holotype terminal elements, but greatly reduced from holotype (Figure 1F & G).

Color. (Figures 2 and 3). Dorsum of the carapace is deep royal blue, all appendages from dorsal view usually a lighter blue. Punctations on body and legs stand out with lighter blue to straw color. Basal segments of cheliped light blue, chelae blue basally turning to purple distally, fingers lighter blue to tan with larger tubercles white to yellowish tan, tubercles on mesial surface of palm white, all other tubercles on palm royal blue to purple, main spine on carpus white. Antennal and antennule segments blue, antennal scales blue ending distally with white to cream colored spine, eye stalks blue-green, eye black, rostrum and postocular ridges outlined in cream to white. Abdominal segments dorsally dark blue to almost black with lateral margins of pleura royal blue. Cephalic areas of telson and uropods royal blue, more distal areas lighter blue changing to golden brown, spines on lateral ramus of uropod tan, large spines on mesial ramus of uropod blue at base, pink or reddish at tip. Venter of body and all legs straw to white in color. Most setae on the body golden-straw to brown in color.

Variation in color and color pattern in *P. holifieldi* was less than in other Hagenianus Group taxa, however, only one population of *P. holifieldi* was examined. In this species, the greatest color variation occurs in the abdomen and carapace, where some individuals have some brown color bleeding through the blue base color, whereas other individuals are predominantly blue. There is some variation in the intensity of the blue base color from royal blue to indigo to purple. There is also some variation in the color of the chelae from light cream to blue or purple.

Disposition of types. The holotype, allotype, and morphotype are deposited in the Illinois Natural History Survey Crustacean Collection, Champaign, IL (catalogue numbers, respectively, as INHS 14888, INHS 14890, and INHS 14889), respectively. The following collection of paratypes have been deposited at the Illinois Natural History Survey Crustacean Collection, Champaign, IL (catalogue number INHS 14891). The following paratypes have been deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (catalogue numbers USNM 1283165 and USNM 1283166).

Size. The largest specimen in this study was a female having a TCL of 37.7 mm (PCL 32.8 mm). The largest first form male had a TCL of 32.7 mm (PCL 29.1 mm). The smallest first form male had a TCL of 29.3 mm (PCL 25.2 mm). No ovigerous females or females carrying young were collected.

Type locality. Burrows along power line right of way on private property, 2.2 Km SE of junction State Route 5 and County Road 38, Perry County, Alabama (32.5435N; -87.3298W). The burrows were in the Bogue Chitto drainage, a tributary of the Cahaba River in the Alabama River drainage.

Range and specimens examined. *Procambarus holifieldi* is currently known only from the immediate area of the type locality. All known specimens were from collections made on three different dates from this location. Undoubtedly, this species will be collected from other locations within Perry County.

A total of 23 adults was examined for this study. The collection dates, collectors, and disposition of specimens are as follows: April 12, 2009, J. Holifield and M. Buntin, paratypes UNSM 1283166 3MI, 2F, 1 juv M, 3 juv F; April 15, 2009, M. Buntin, USNM 1283165 3 MII, 2F; February 10, 2010, M. Buntin, J. Holifield, G.A. Schuster, C.A. Taylor, paratypes INHS 14891 1MII, 1F; January 28, 2011, J. Holifield, holotype INHS 14888, allotype INHS 14890, morphotype INHS 14889, paratypes USNM 1283166, 2MI, 1MII, 5F.

Etymology. Named in honor of Jesse Holifield, from the Alabama Biodiversity Center in Marion, AL. Mr. Holifield has been an ardent collector of crayfishes in Perry County and was responsible for making this new species known to us. He collected most of the specimens used in this study.

Habitat and life-history notes. *Procambarus holifieldi* is a primary burrower. The habitat is a field spanning the width of a power line easement. Soils in the southwestern part of Perry County are from the Vaiden-Okolona-Sucarnoochee Soil Unit (Harris, 1998). The site is located on the Blackland Prairie. Soils in this area are mostly Sucarnoochee soils, which are characterized as somewhat poorly drained. Seasonally high water table ranges from 15 to 45 cm below the surface from January to April (Harris, 1998). This soil is known for flooding, wetness and very slow permeability. Numerous burrows were seen along this right of way. Several burrows were excavated by the authors and found to be fairly complex in structure with a main channel leading from a mud chimney at the surface. The main channel may have several side channels that open to the surface. During periods of soil saturation the ground water is just a few centimeters below the soil surface. No additional life history information is known for this species.

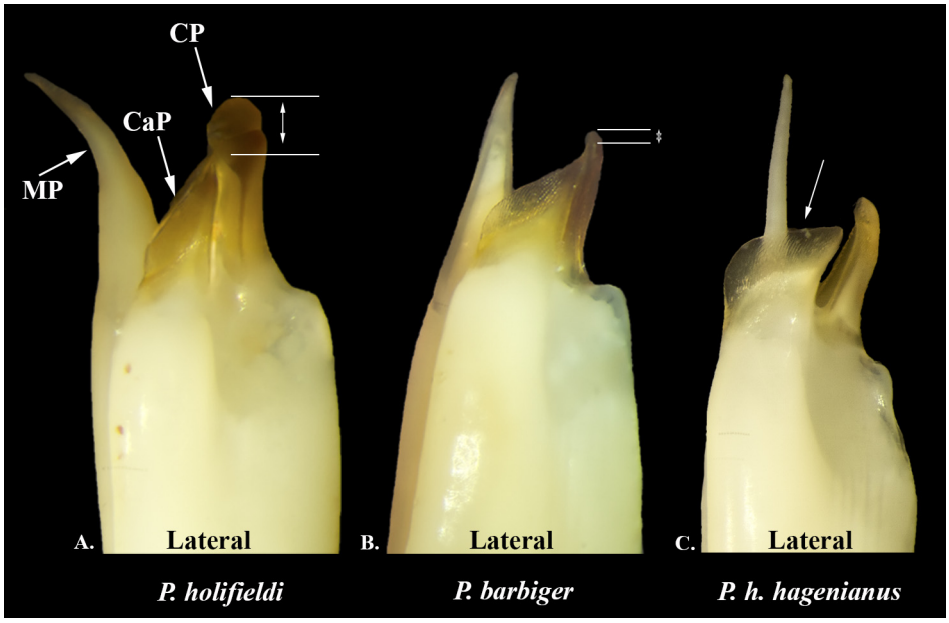

FIGURE 4. Morphological differences between *Procambarus* (*Girardiella*) *holifieldi* **n.sp.**, *Procambarus barbiger* and *Procambarus hagenianus hagenianus* in the elements of the form I male gonopod in lateral view, respectively, in A–C. CP = central projection, CaP = caudal process, MP = mesial process.

Crayfish Associates. *Fallicambarus fodiens* and an unidentifiable *Procambarus* sp. were also collected at the type locality.

Variation. Variation found within the 23 adult specimens examined is minimal for most characters. Characters that were consistent include the following: 1) Females with first pleopod present but reduced in size; 2) Areola linear and obliterated in all individuals; 3) Inner ramus of uropods with large spines extending beyond margin; 4) Numerous small round tubercles cover the lateral hepatic and branchiostegal surfaces of the carapace, dorsally carapace is smooth except for large punctations scattered throughout; 5) Distinct excision at base of dactyl.

Characters for which some variation was noted include the following: 1) Length of palm of chela ranges from 70.2–88.1% of width; 2) Length of dactyl of chela ranges from 59.0–63.7% of length; 3) Mesial row of tubercles on palm of chela ranges from 5–7, second row ranges from 2–6; 4) Number of tubercles on opposable surface of dactyl in excision area ranges from 2–3, last tubercle usually the largest, number of tubercles distal to excision area ranges from 2–5 with minute denticles in between, tubercles usually progressively smaller distally; 5) Number of tubercles in excision area of propodus ranges from 3–6, distal to excision area 3–5, usually progressively smaller distally with small denticles in between; 6) Usually one large spine on dorsal surface of carpus, some specimens with 1 large spine and 1–2 smaller spines; 7) Setae of third maxilliped in both first and second form males very long and dense and cover lateral and dorsal surfaces of all basal segments, slightly less dense on more distal segments, in females dorsal setation as in males, but lateral setation less dense and setae much shorter so lateral surfaces of segments visible; 8) Width of annulus ventralis of female ranges from 1.7 to 2.8 mm with mean of 2.2 mm, number of tubercles on ventral surface of annulus seems to vary and increases with size and maturity of female.

Relationships. Based on the shape of the caudal process, this species seems to be most closely related to *P. barbiger*. Both species have a distinctly triangle-shaped caudal process (Figure 4A & B), best seen in lateral view; it comes to a sharp point distally, as opposed to all other Hagenianus Group taxa (Figure 4C) where the caudal process in lateral view is subrhomboidal with the distal edge linear. There are a number of morphological differences between *P. holifieldi* and *P. barbiger* (Figure 4A & B). The caudal process in *P. holifieldi* is in the form of an acute triangle that is distinctly shorter than the central projection (Figure 4A). In *P. barbiger* the caudal process is in the form of an obtuse triangle and is subequal in length to the central projection (Figure 4B). The central projection in *P. holifieldi* is very wide and distinctly twisted in lateral view (Figure 4A), while in *P. barbiger* it is narrower, mostly straight and only curves near the distal end (Figure 4B). Lastly, *P. holifieldi* lacks the beard on the mesial margin of the palm of the chela (Figure 1N), and *P. barbiger* has a thick conspicuous beard (Figure 13M).

Common name. The suggested common or vernacular name for this species is Celestial Crayfish because of the deep blue base color that blends to violet and purple on the chelae, and its ethereal appearance.

Conservation status. Although other collecting has been done for primary burrowers in the vicinity of the type locality in Perry County, no additional populations have been found. It is clear that additional fieldwork needs to be done to better assess the distribution of this species and its current status. However, based on the criteria of the American Fisheries Society as outlined by Taylor et al. (2007) and the system developed by The Nature Conservancy/NatureServe (Master, 1990), we propose that this species, because of its apparent narrow range, be considered Endangered (E) with a G1 global ranking. Assuming that additional populations of *P. holifieldi* will be found in Perry Co., the species would rank as Vulnerable by the International Union for the Conservation of Nature (IUCN) under Criteria D2.

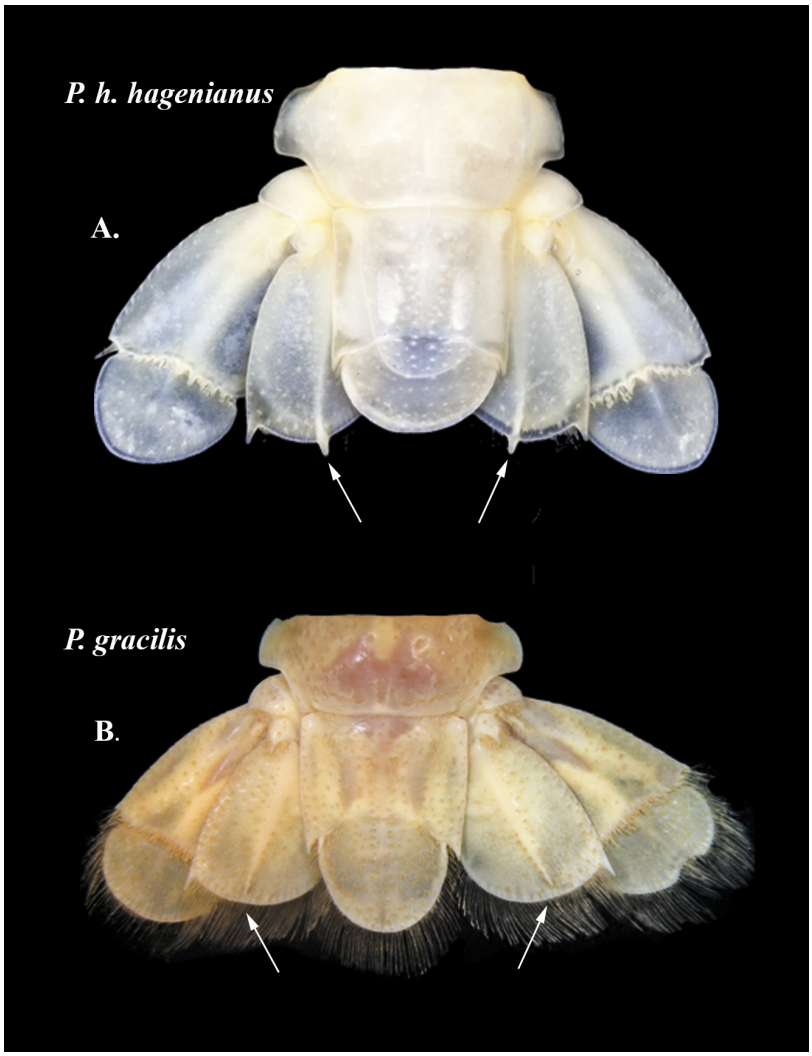

FIGURE 5. Tail fans of *Procambarus hagenianus hagenianus* and *Procambarus gracilis*, respectively A–B.

Distinguishing the species groups: The Case of the Missing Cephalic Process. The subgenus *Girardiella* was divided into two species groups: the Gracilis Group and the Hagenianus Group based on two morphological characters (Hobbs, 1972a). First, the cephalic process is present in Gracilis Group, whereas Hobbs (1972a) indicated that it is absent in the Hagenianus Group. Second, the median spine on the mesial ramus of the uropod extends beyond the edge of the ramus margin (Figure 5A) in the Hagenianus Group but does not extend beyond the margin in Gracilis Group (Figure 5B).

The presence of the cephalic process on the gonopod of Gracilis Group species has never been in contention. However, in the Hagenianus Group there has been some confusion whether the cephalic process was present or not. Reimer (1969), in his dissertation, indicated that in *P. hagenianus* the "*cephalic process (was) greatly reduced to flattened, (a) plate-like structure in close connection with mesial surface of central projection*." However, Hobbs (1972a) in his description of the subgenus *Girardiella* stated that the cephalic process was absent in *P. hagenianus*. Since the publication of this statement by Hobbs, every researcher working on this subgenus, including Reimer (1975), has directly or parenthetically agreed with the conclusion of Hobbs. Fitzpatrick (1978a) followed Hobbs (1972a); however, like Reimer (1969) he recognized the presence of a morphological feature laying against the central projection and indicated that the Hagenianus Group had what he called an "*enveloping fold*" that lays against the central projection. Fitzpatrick also indicated in his key that this "fold" is absent in *P. cometes*. After examining all of the Hagenianus Group taxa, including type specimens, we found the structure in all of them. As such, we believe Fitzpatrick (1978a) was in error when he stated that it was absent in *P. cometes*.

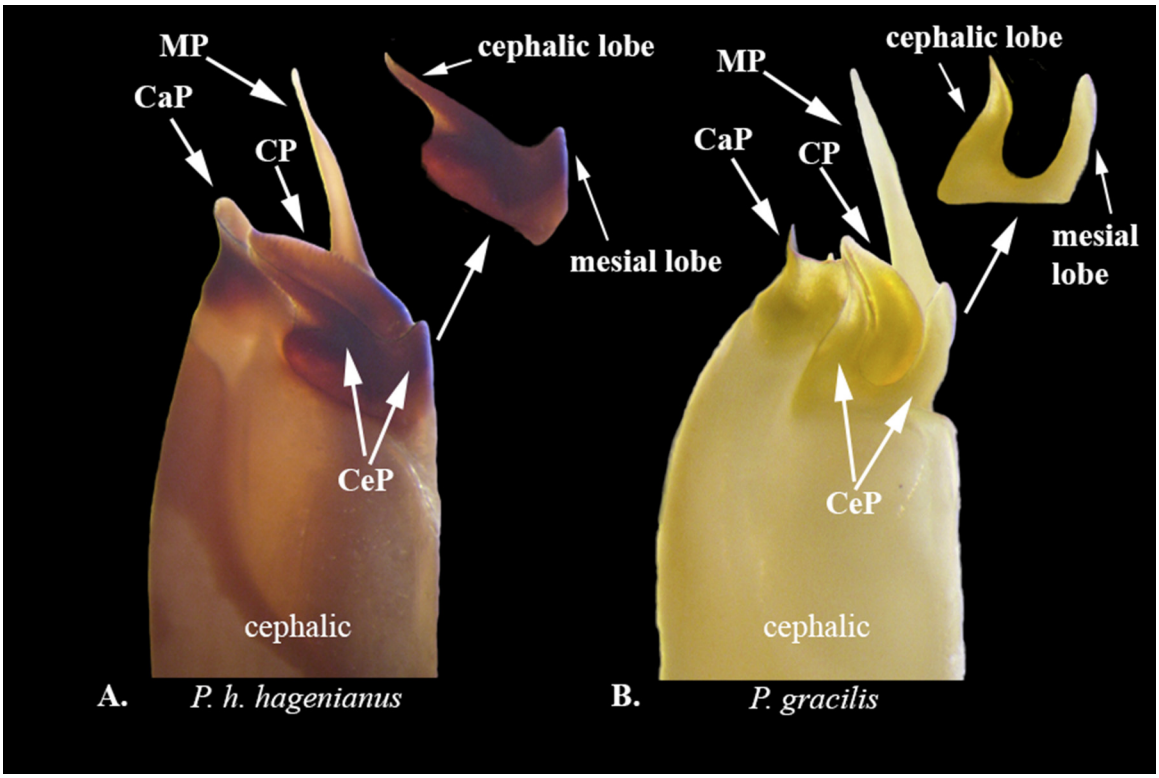

FIGURE 6. Terminal elements of form I male gonopod in cephalic view for *Procambarus hagenianus hagenianus* and *Procambarus gracilis* with inset on details of cephalic processes. CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process.

After closely examining the gonopods of all of the recognized taxa of the Hagenianus Group we believe that Reimer's (1969) observation and description of a true cephalic process in *P. hagenianus* was correct, and the work of subsequent researchers was in error. Figures 6A and 6B show the presence of the cephalic process in the cephalic view of the gonopod of *P. hagenianus* in comparison to the same structure in *P. gracilis*, the nominal species of the Gracilis Group. The presence of the cephalic process in the Hagenianus Group is exactly as Reimer

(1969) described it – "*a plate-like structure in close connection with the mesial surface of the central projection.*" This structure is synonymous with Fitzpatrick's (1978a) enveloping fold. The cephalic process in the Gracilis Group is distinctly U-shaped (Figure 6B, inset) with two large lobes, a large mesial lobe that extends around the base of the central projection and has an elongated free distal margin, and a cephalic lobe that wraps under the central projection. The cephalic process in the Hagenianus Group has a much-reduced mesial lobe that tightly wraps around the base of the central projection, and only the very tip of the distal margin may be somewhat free. The cephalic lobe is well developed (Figure 6A, inset) and is wrapped around the central projection. These structures in the two species groups represent the same morphological structure, the cephalic process. The cephalic process can be seen in all of the Hagenianus Group taxa (Figs. 7–10), however it is best seen in the mesial and cephalic views of the gonopod (Figs. 7 and 10).

The presence and absence of the cephalic process was an important character separating the Gracilis Group from the Hagenianus Group. Our hypothesis that Hagenianus Group members do possess a cephalic process, albeit much smaller, does not preclude the diagnosis of the two groups. The two species groups can still be separated by differences in length of the median spine on the mesial ramus of the uropod (Figs. 5A and B).

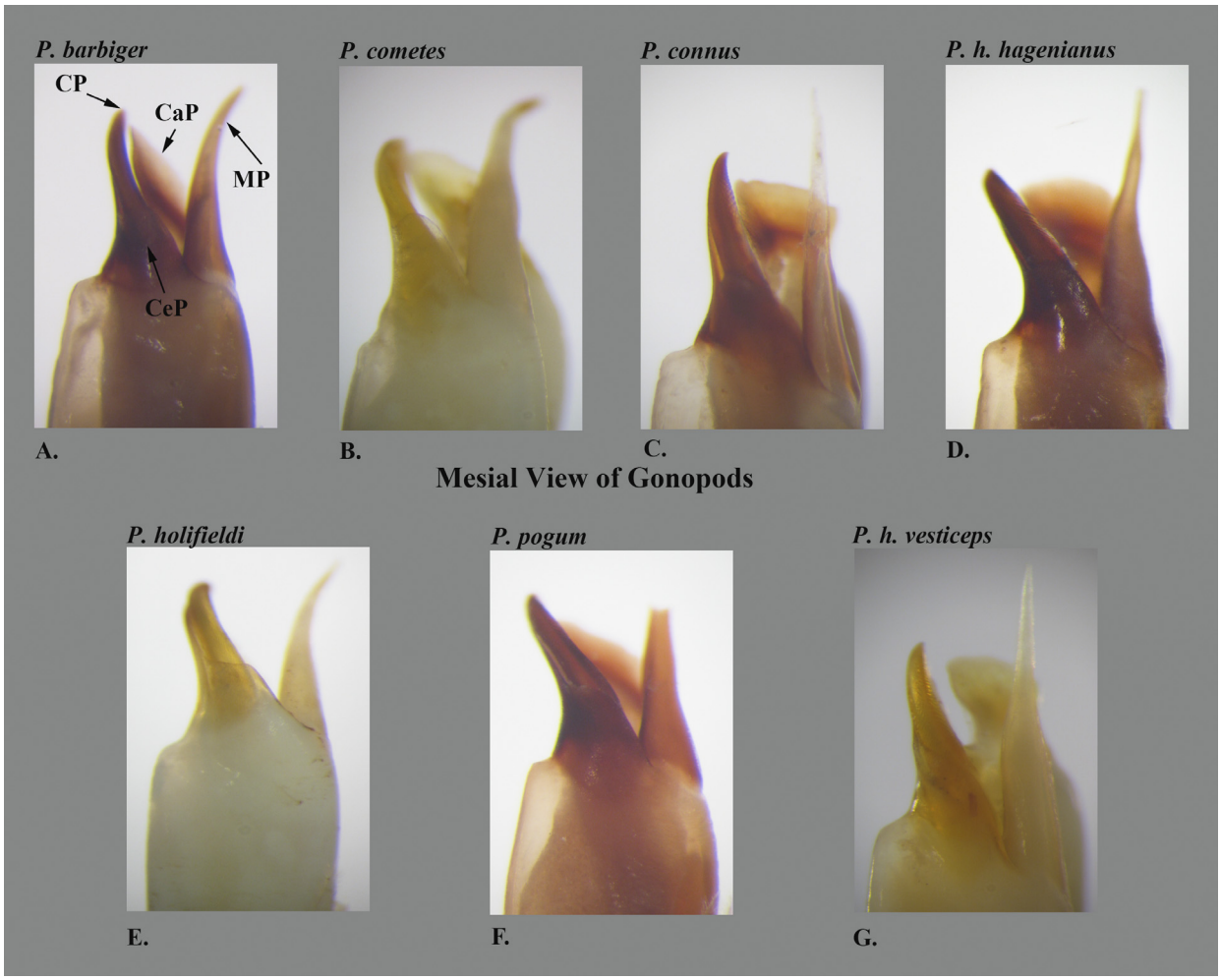

FIGURE 7. A–G respectively, terminal elements of form I male gonopod in mesial view for *Procambarus barbiger*, *Procambarus cometes*, *Procambarus connus*, *Procambarus hagenianus hagenianus*, *Procambarus holifieldi*, *Procambarus pogum* and *Procambarus hagenianus vesticeps*. CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process.

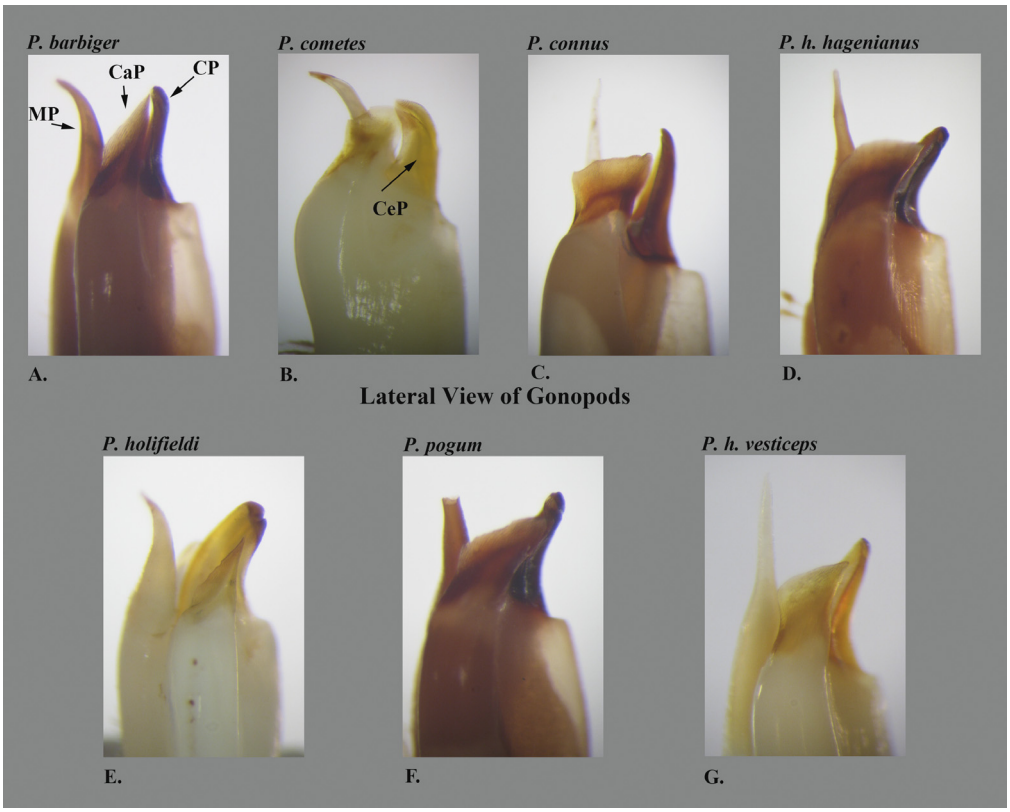

FIGURE 8. A–G respectively, terminal elements of form I male gonopod in lateral view for *Procambarus barbiger*, *Procambarus cometes*, *Procambarus connus*, *Procambarus hagenianus hagenianus*, *Procambarus holifieldi*, *Procambarus pogum* and *Procambarus hagenianus vesticeps*. CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process.

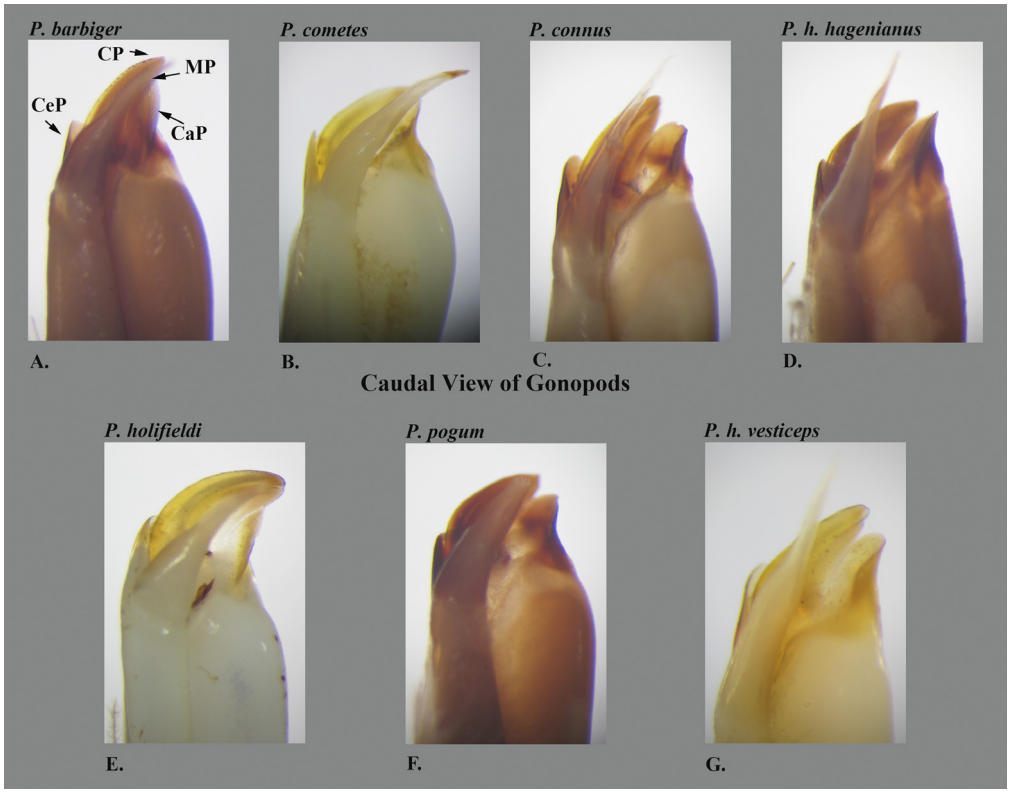

FIGURE 9. A–G respectively, terminal elements of form I male gonopod in caudal view for *Procambarus barbiger*, *Procambarus cometes*, *Procambarus connus*, *Procambarus hagenianus hagenianus*, *Procambarus holifieldi*, *Procambarus pogum* and *Procambarus hagenianus vesticeps*. CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process.

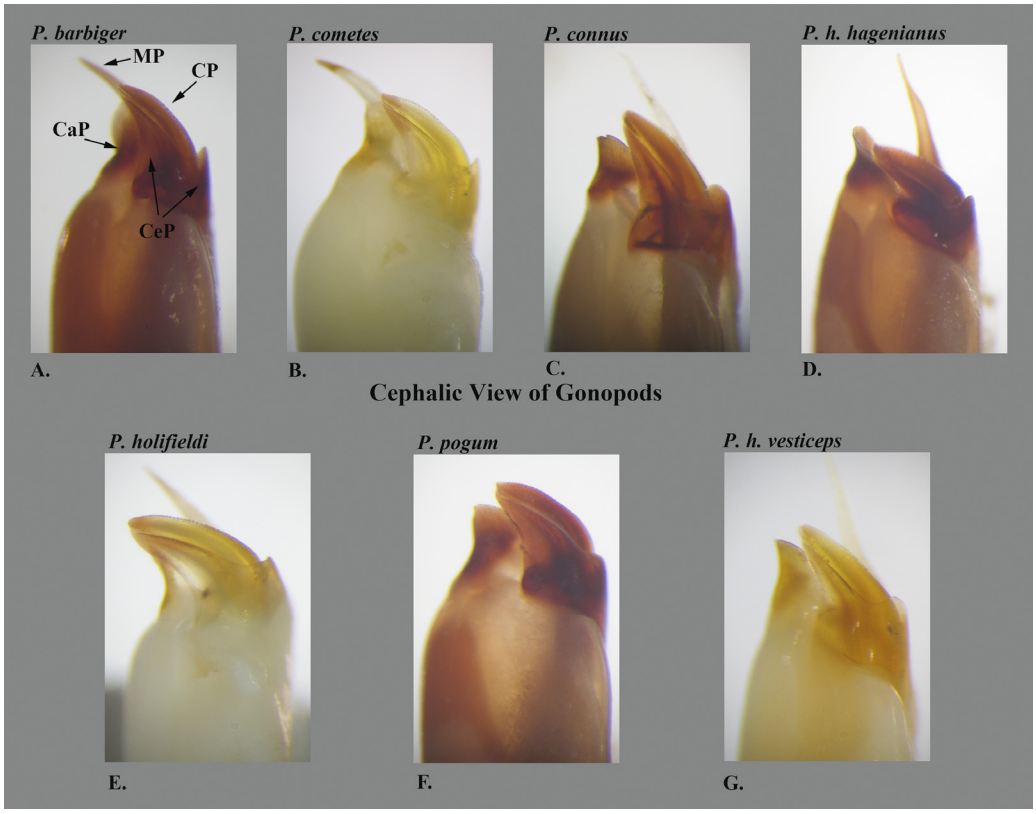

FIGURE 10. A–G respectively, terminal elements of form I male gonopod in cephalic view for *Procambarus barbiger*, *Procambarus cometes*, *Procambarus connus*, *Procambarus hagenianus hagenianus*, *Procambarus holifieldi*, *Procambarus pogum* and *Procambarus hagenianus vesticeps*. CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process.

Other Taxonomic Issues within the Hagenianus Group. The seminal work on the Hagenianus Group is that of Fitzpatrick (1978a). In it Fitzpatrick re-described *P. hagenianus hagenianus* (Figure 11) and described a new subspecies, *P. hagenianus vesticeps* (Figure 12), and four new species: *P. barbiger* (Figure 13), *P. cometes* (Figure 14), *P. connus* (Figure 15) and *P. pogum* (Figure 16). All of the taxa have a beard of thick long setae on the inner margin of the palm of the chelae and, in some, on the margin of the dactyl as well. Fitzpatrick for the most part accepted, but renamed, the taxa that Lyle (1938) recognized (Table 2). He described two additional taxa and included a key to both males and females for all known taxa of the Hagenianus Group.

TABLE 2. Hagenianus Group taxa names proposed by Lyle 1938 and those in current use after Fitzpatrick 1978a. Names sharing a row represent the same taxon.

Fitzpatrick 1978a	**Lyle 1938**
Procambarus hagenianus hagenianus	*Cambarus hagenianus hagenianus*
Procambarus hagenianus vesticeps	*Cambarus hagenianus evansi* (nomina nudum)
Procambarus barbiger	*Cambarus hagenianus forestae* (nomina nudum)
Procambarus pogum	*Cambarus hagenianus carri* (nomina nudum)
Procambarus cometes	Did not recognize
Procambarus connus	Did not recognize

While examining Fitzpatrick's (1978a) study of the Hagenianus Group in order to determine how the new species, *P. holifieldi*, relates to the known taxa, a number of critically important discrepancies and errors were noted (Table 3). These led us to question his findings and conclusions. The first error is in couplet 3' of the key (Fitzpatrick, 1978a; p. 95), where it is indicated that taxa beyond this couplet lack the long setae on the margin of the dactyl of the chelae. If one follows that couplet through the key, it will eventually lead to *P. barbiger*, which does have long setae along the margin of the dactyl. In the holotype of *P. barbiger* (Figure 17A) these setae are present but reduced, while in other types (Figure 17B) they are long and easy to see.

TABLE 3. Summary of taxonomic errors in Fitzpatrick (1978a).

	Taxonomic Issues
1	Use of "*enveloping fold* " which is really the cephalic process
2	It is indicated "*dactyl lacking long tufts of setae*" which includes *P. barbiger*, however, this species has long tufts of setae on the at the base of the dactyl along its margin
3	"*Caudal process subperpendicular to axis of shaft of gonopod*;" character is confusing; apical and other views of the gonopods of *P. h. hagenianus*, *P. h. vesticeps*, *P. cometes*, *P. connus* and *P. pogum* show the position of the caudal process, central projection and axis of the gonopod to be very similar in all
4	"*Trough of annulus broad and descending precipitously cephalically towards sternites*;" this character is quite variable and may depend on the maturity of the female
5	"*Postannular sclerite conical*;" character variable and some specimens of all species have conical postannular sclerite
6	For *P. cometes* it is stated that "*mesial process of first pleopod is subequal to central projection*;" this is true for the holotype but for paratypes of USNM146275 this character is incorrect
7	"*Antennal scale setae arising in tufts*" in some species; this is incorrect, this character does not exist in these crayfishes nor in any other known species

In couplet 4' and 5 (Fitzpatrick, 1978a; p. 96) it is stated that for *P. pogum* and *P. cometes* "form I male lacking enveloping fold." This is incorrect (see Figure 10B & 10F); the enveloping fold is in actuality the cephalic process and is present in all Hagenianus Group taxa. In addition, in couplet 5 it is stated for *P. cometes*, that the "mesial process of the first pleopod (is) subequal to (the) central projection in length." This is true for the holotype, but not true for Form I male paratypes (USNM 130227 and 146275). Therefore, it is not clear if this character is variable for this species or if the designated paratypes are not *P. cometes* specimens.

In couplet 6 (Fitzpatrick, 1978a; p. 96) it is stated for *P. h. vesticeps*, that the "*caudal process of the first pleopod (is) subperpendicular to main axis of shaft of pleopod*." This is directly contradicted in the text on p. 87 where it is stated: "*only in P. h. hagenianus, however, is the distal margin (of the caudal process) subperpendicular to the main axis of the shaft*." Figure 9 shows in caudal view that the position of the caudal process in relationship to the central projection and the shaft of the pleopod in *P. h. hagenianus*, *P. h. vesticeps*, *P. cometes*, *P. connus* and *P. pogum* are the same with only slight variation. This is also borne out in the apical view (Figure 18) of the gonopods of these taxa. The slight variation seen in these figures are due to individual differences or slight differences in the perspective of the camera.

In couplets 8 and 11 (Fitzpatrick, 1978a; p. 96), it is indicated that *P. connus*, *P. pogum*, *P. cometes* and *P. h. vesticeps* all possess "*setae of lamellar portion of antennal scale arising in tufts from tubercular eminences*." This was illustrated in Figure 34, p. 71 of the text. Simply put, this character does not exist. In cambarid crayfishes the mesial lamellar margin of the antennal scale has a single row of setal cups that each bear a single non-branched seta. Figure 19 shows photos of the antennal scales of all of the Hagenianus Group taxa. The character described by Fitzpatrick is found in none of these taxa and has never been reported in any cambarid species.

In couplet 10 (Fitzpatrick, 1978a; p. 96), female *P. pogum* and *P. cometes* are separated by the width and cephalic descent of the trough of the annulus ventralis in the females. In the Hagenianus Group, annulus morphology varies greatly with the sexual maturity of the female. Once the females reach sexual maturity, annuli among the taxa, with the exception of *P. holifieldi*, are very difficult to distinguish (Figure 20). Some sexually mature females in some or all of the taxa, such as in *P. holifieldi* (Figure 20D), may develop large tubercles on the ridges of the annulus. The utility of these tubercles in the taxonomy of these taxa is unknown since most specimens examined during this study do not have them. In addition, Fitzpatrick used the conical shape of the postannular sclerite as a distinguishing character. We found that the postannular sclerite is quite variable and can be conical in all of the taxa.

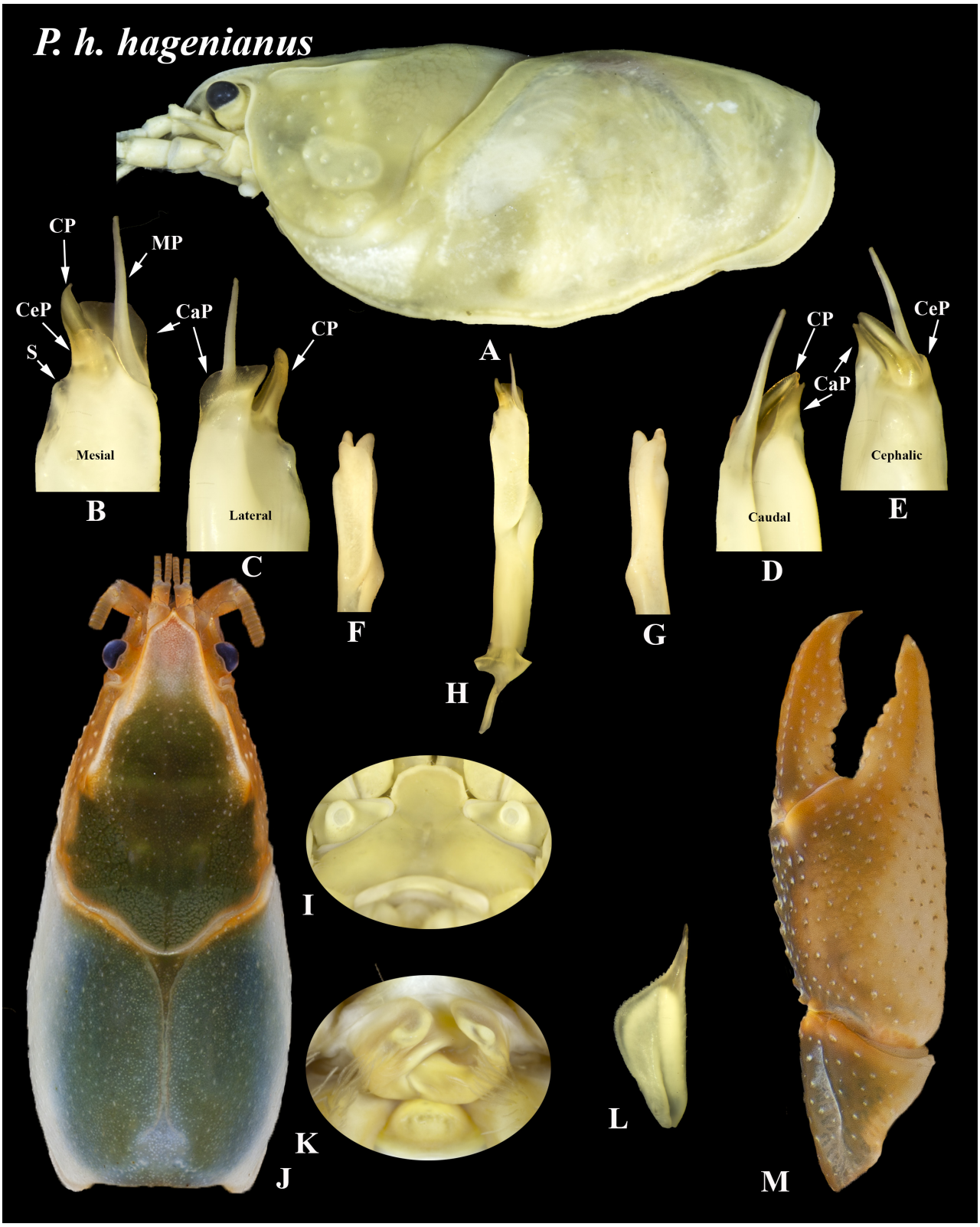

FIGURE 11. *Procambarus* (*Girardiella*) *hagenianus hagenianus*: A. lateral view of carapace; B–E, respectively mesial, lateral, caudal and cephalic view of terminal end of left gonopod of form I male; F–G, mesial and lateral view of terminal end of left gonopod of form II male; H, mesial view of entire left gonopod of form I male; I, epistome; J, dorsal view of carapace; K, annulus ventralis; L, antennal scale; M, dorsal view of right chela and carpus of form I male; A–E, H–J, L–M from Perry County, AL (INHS 11691); F–G and K from Rankin County, MS (MMNS 01531). CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process; s = shoulder.

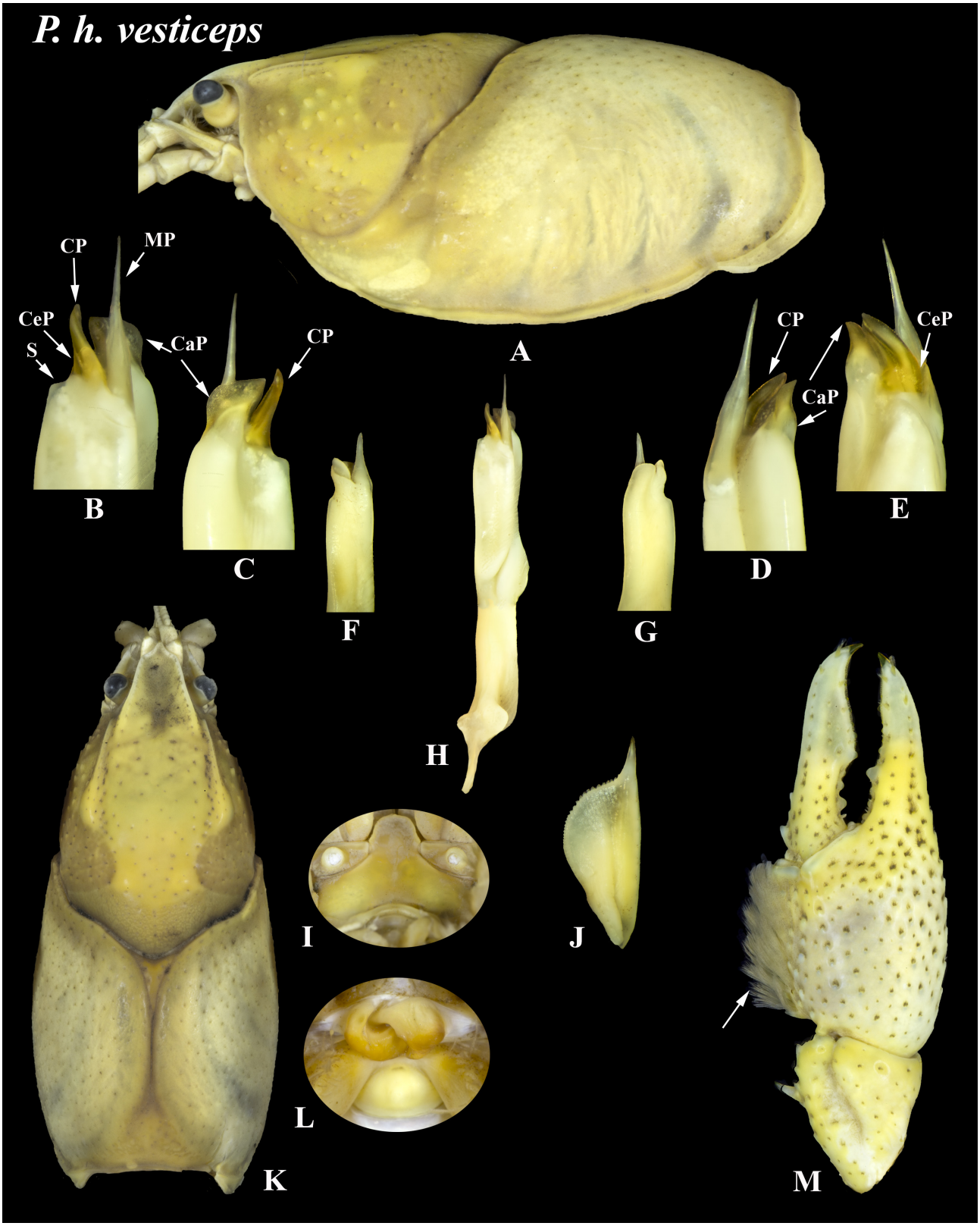

FIGURE 12. *Procambarus* (*Girardiella*) *hagenianus vesticeps*: A. lateral view of carapace; B–E, respectively mesial, lateral, caudal and cephalic view of terminal end of left gonopod of form I male; F–G, mesial and lateral view of terminal end of left gonopod of form II male; H, mesial view of entire left gonopod of form I male; I, epistome; J, dorsal view of carapace; K, annulus ventralis; L, antennal scale; M, dorsal view of right chela and carpus of form I male; A–E, H–J, L–M from Chickasaw County, MS (USFS SA329–01); F–G from Chickasaw County, MS (USFS SA329–02) and K from Pontotoc County, MS (USFS SA501). CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process; s = shoulder.

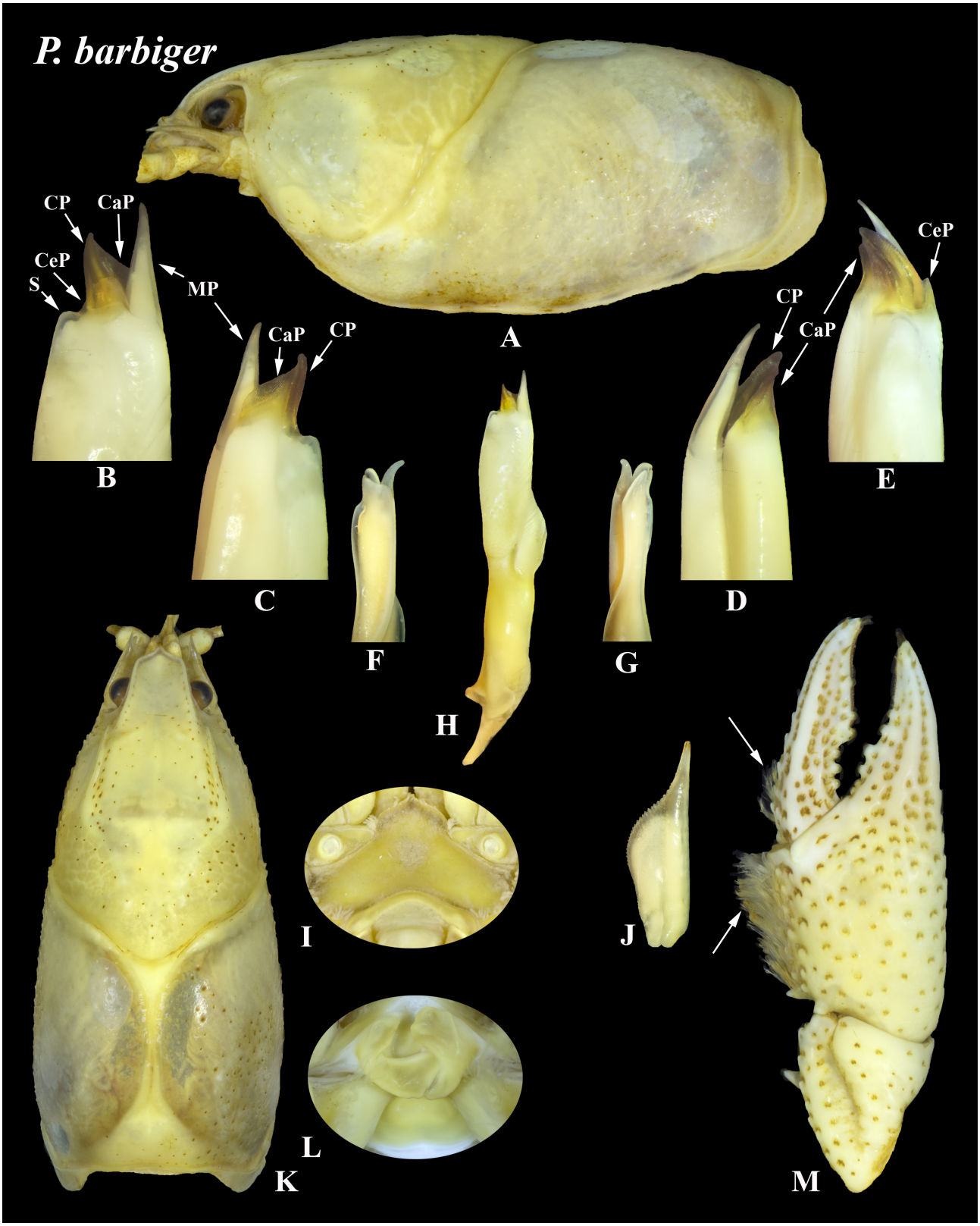

FIGURE 13. *Procambarus* (*Girardiella*) *barbiger*: A. lateral view of carapace; B–E, respectively mesial, lateral, caudal and cephalic view of terminal end of left gonopod of form I male; F–G, mesial and lateral view of terminal end of left gonopod of form II male; H, mesial view of entire left gonopod of form I male; I, epistome; J, dorsal view of carapace; K, annulus ventralis; L, antennal scale; M, dorsal view of right chela and carpus of form I male; A–E, H–J, L–M from Rankin County, MS (MMNS 00739); F–G from Jasper County, MS (MMNS 01611) and K from Rankin County, MS (MMNS 00739). CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process; s = shoulder.

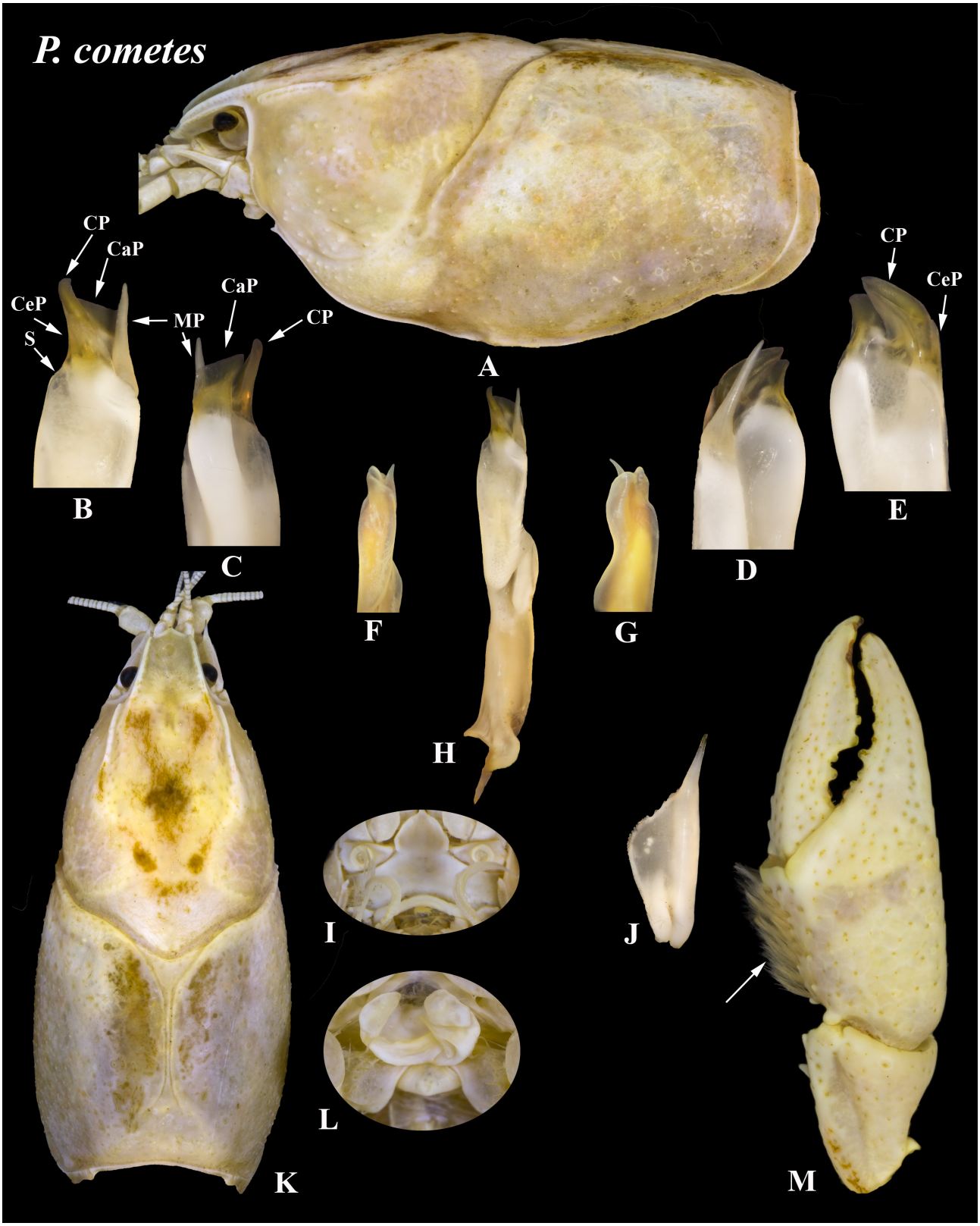

FIGURE 14. *Procambarus* (*Girardiella*) *cometes*: A. lateral view of carapace; B–E, respectively mesial, lateral, caudal and cephalic view of terminal end of left gonopod of form I male; F–G, mesial and lateral view of terminal end of left gonopod of form II male; H, mesial view of entire left gonopod of form I male; I, epistome; J, dorsal view of carapace; K, annulus ventralis; L, antennal scale; M, dorsal view of right chela and carpus of form I male; A–E, H–J, L–M from Oktibbeha County, MS (USNM 130227); F–G from Oktibbeha County, MS (USNM 131280) and K from Oktibbeha County, MS (USNM 146260). CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process; s = shoulder.

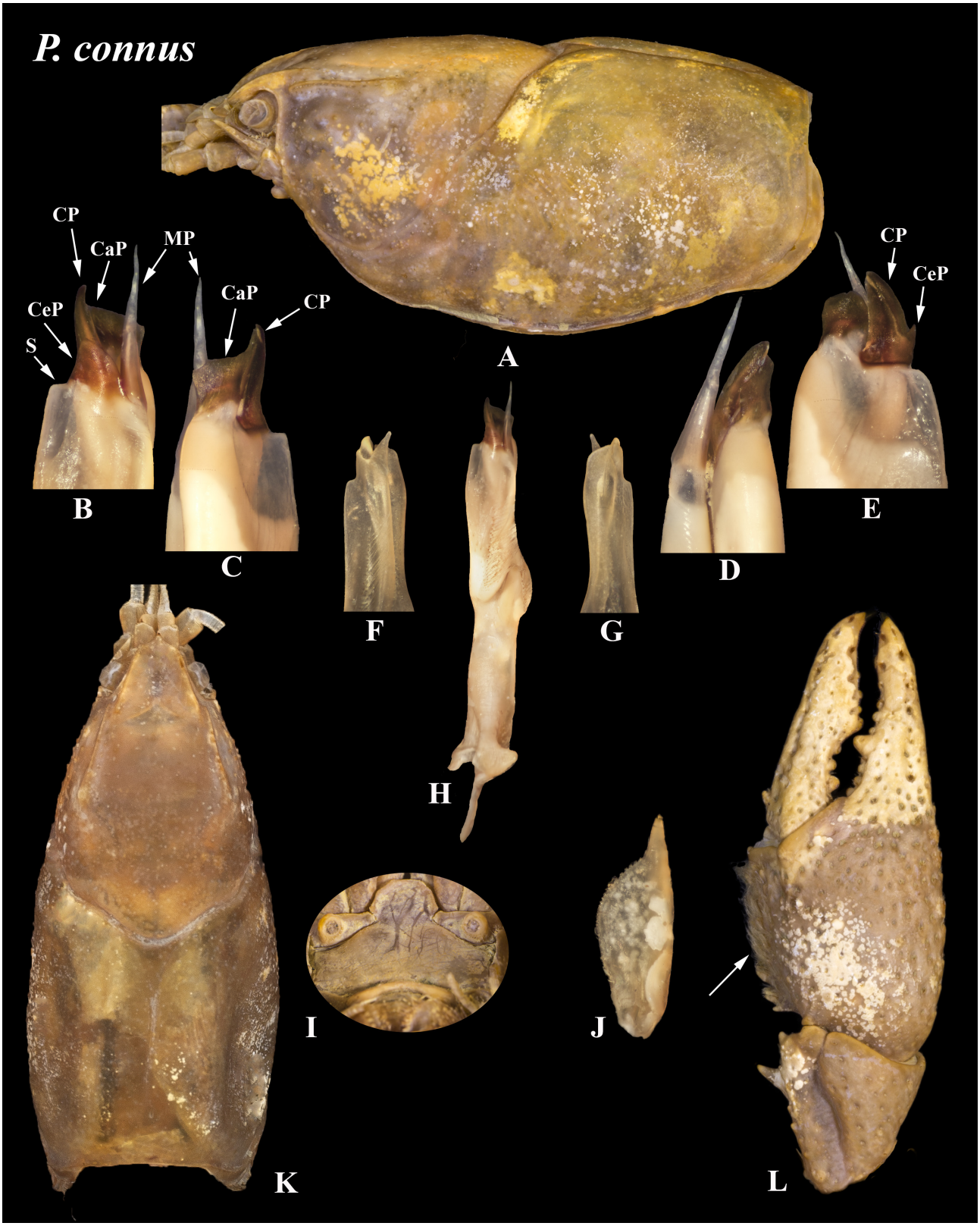

FIGURE 15. *Procambarus* (*Girardiella*) *connus*: A. lateral view of carapace; B–E, respectively mesial, lateral, caudal and cephalic view of terminal end of left gonopod of form I male; F–G, mesial and lateral view of terminal end of left gonopod of form II male; H, mesial view of entire left gonopod of form I male; I, epistome; J, dorsal view of carapace; K, annulus ventralis; L, antennal scale; M, dorsal view of right chela and carpus of form I male; A–E, H–J, L–M from Carroll County, MS (USNM 146269); F–G from Carroll County, MS (USNM146263) and K (Not Available). CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process; s = shoulder.

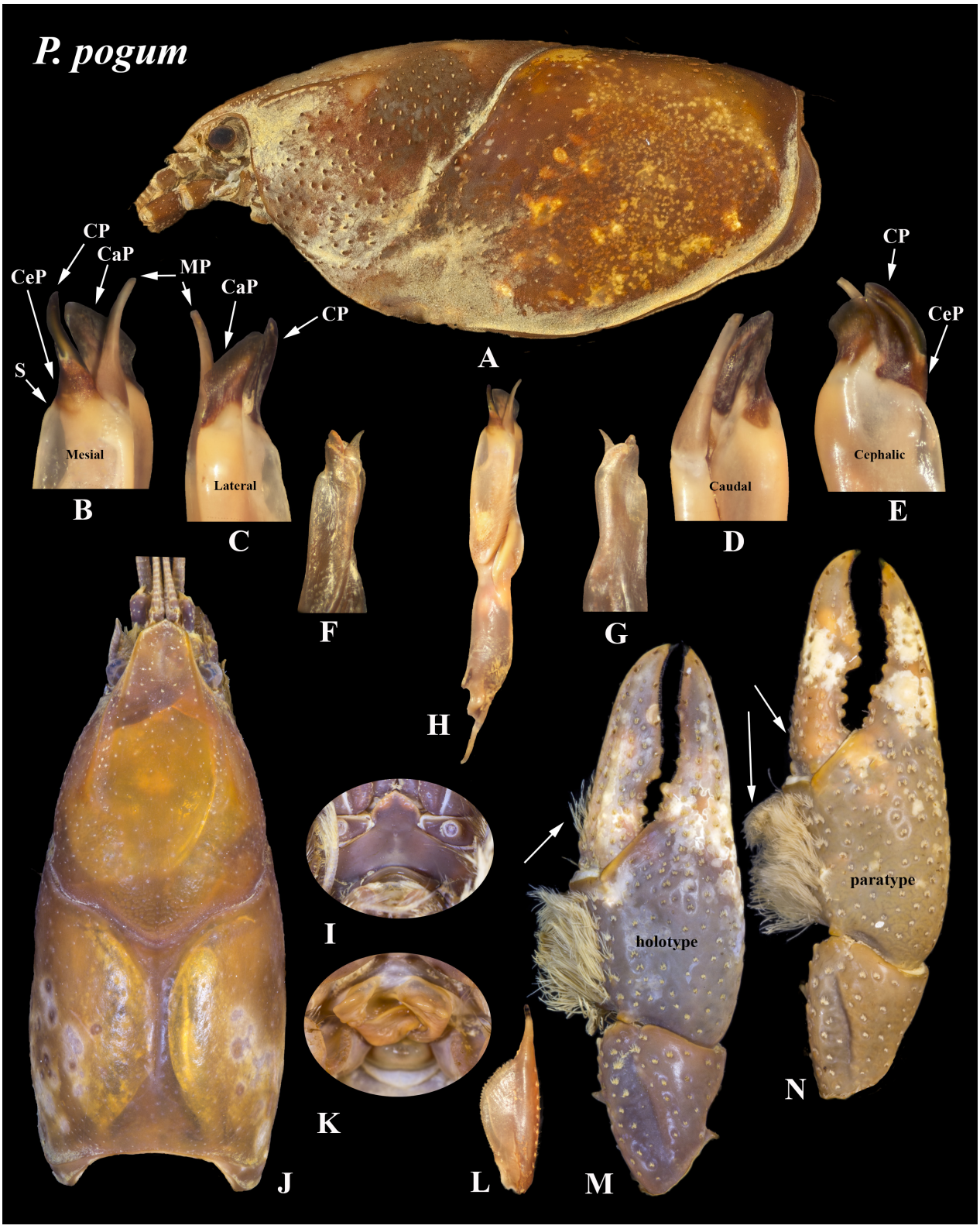

FIGURE 16. *Procambarus* (*Girardiella*) *pogum*: A. lateral view of carapace; B–E, respectively mesial, lateral, caudal and cephalic view of terminal end of left gonopod of form I male; F–G, mesial and lateral view of terminal end of left gonopod of form II male; H, mesial view of entire left gonopod of form I male; I, epistome; J, dorsal view of carapace; K, annulus ventralis; L, antennal scale; M, dorsal view of right chela and carpus of form I male; A–E, H–J, and L–M from Houston County, MS (USNM 146270); F–G from Chickasaw County, MS (USNM 146272); K from Chickasaw County, MS (USNM 146271) and N from Chickasaw County, MS (USNM 220594). CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process; s = shoulder.

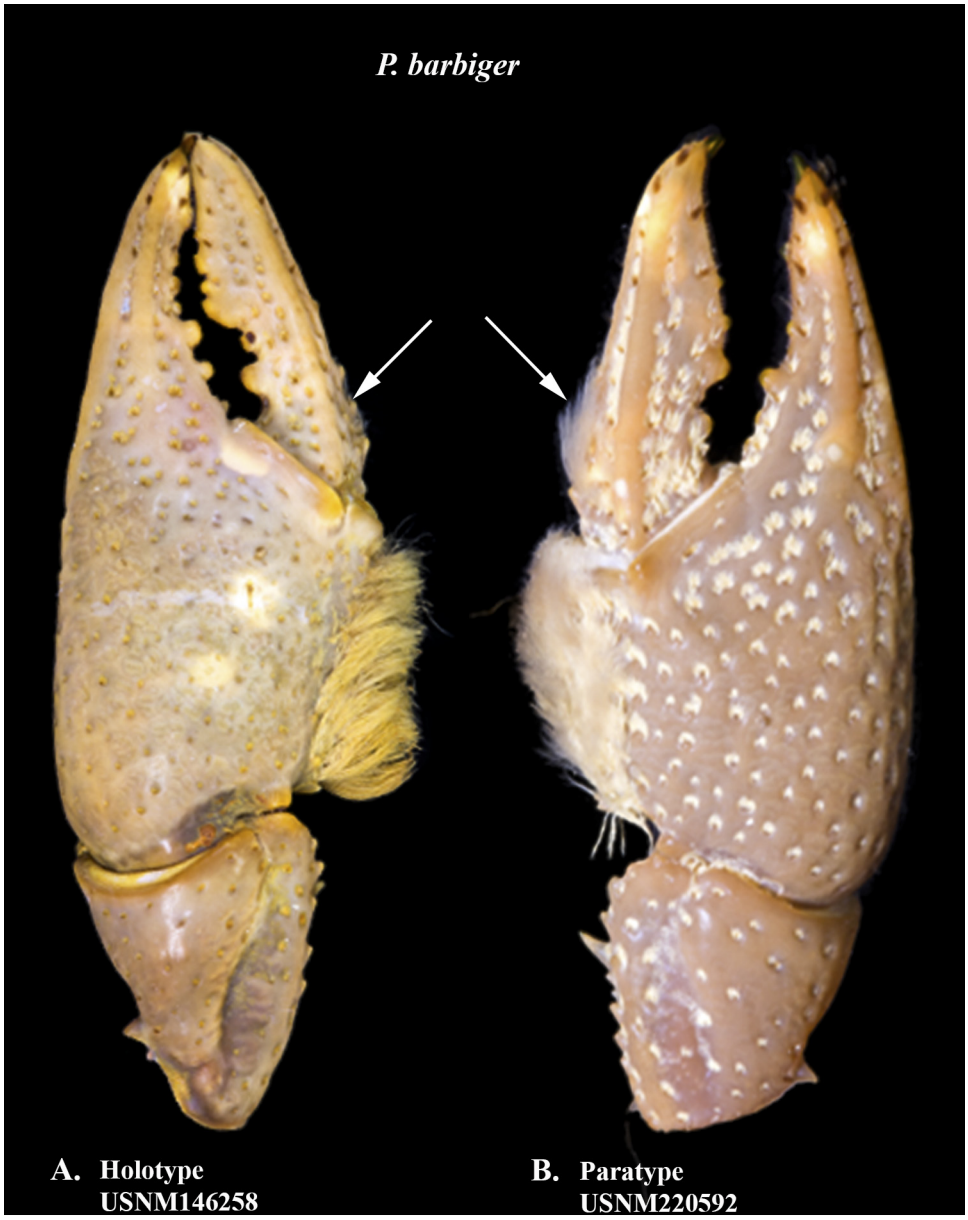

FIGURE 17. Chelae of *Procambarus* (*Girardiella*) *barbiger* showing beard development on base of dactyl margin; A. holotype (USNM 146258); B. paratype (USNM 220592).

Fitzpatrick (1978a) established the subspecies *P. h. vesticeps* on the basis of a setal beard along the mesial margin of the palm of the chelae (Figure 12M). In the examination of the type material (USNM 69441 and 44746) it became apparent that there was some variation in the density of the beard and the length of the setae in *P. h. vesticeps*. Figure 21A and 21B each show a series of chelae of three paratypes from two different populations. Each shows that the density of setae of the chela on the left is far less than the density of setae of the chelae to right. Figure 22 shows variation of this character in *P. h. hagenianus*. The variation ranges from having no setae Figure 22A and 22B along the mesial margin and top of the palm to having few (Figure 16C) to having an abundance of setae (Figure 22D). However, the setae, when present in *P. h. hagenianus*, are relatively short and seem to be relegated to an area just distal to each tubercle on the chela. They are also arranged in a fan-like formation. In the observed *P. h. hagenianus* specimens, the setae never are as long as they are in specimens of *P. h. vesticeps*. For the most part in *P. h. vesticeps*, *P. cometes, P. connus,* and *P. pogum*, setae are restricted to Form I males, although there is a series of female paratypes of *P. cometes* that have well developed beards (USNM 146275). Fitzpatrick (1978a) separated *P. pogum* from *P. h. vesticeps* based on the presence of long dense setation at the base of the dactyl in *P. pogum*. It is not clear why Fitzpatrick gave *P. pogum* species-level recognition based on setation of the dactyl yet gave *P. h. vesticeps* subspecies status based on setation of the palm.

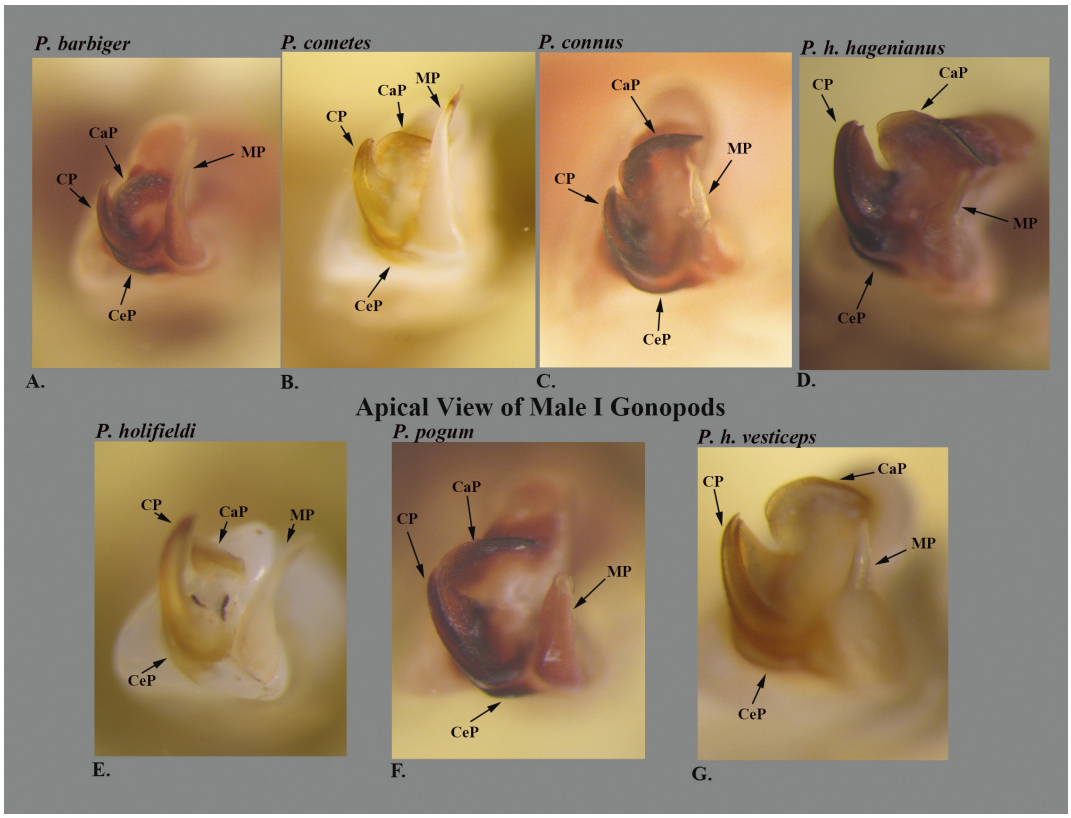

FIGURE 18. A–G respectively, terminal elements of form I male gonopod in apical view for *Procambarus barbiger*, *Procambarus cometes*, *Procambarus connus*, *Procambarus hagenianus hagenianus*, *Procambarus holifieldi*, *Procambarus pogum* and *Procambarus hagenianus vesticeps*. CP = central projection, CaP = caudal process, CeP = cephalic process; MP = mesial process.

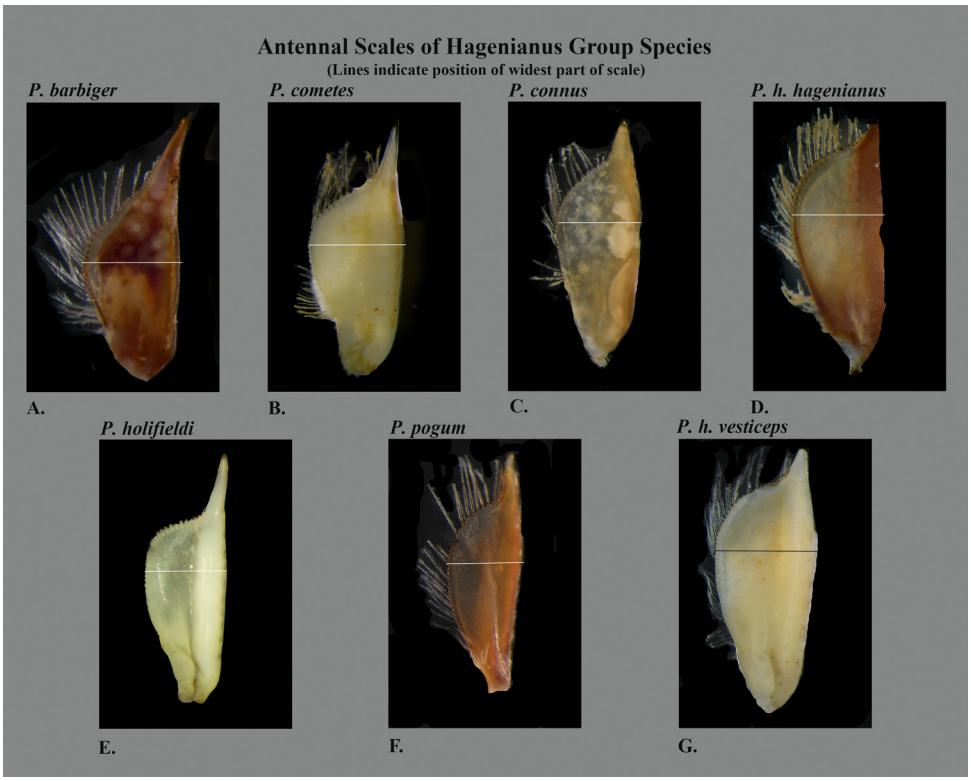

FIGURE 19. A–G respectively, dorsal view of antennal scales for *Procambarus barbiger*, *Procambarus cometes*, *Procambarus connus*, *Procambarus hagenianus hagenianus*, *Procambarus holifieldi*, *Procambarus pogum* and *Procambarus hagenianus vesticeps*. Lines indicate position of widest part of scale.

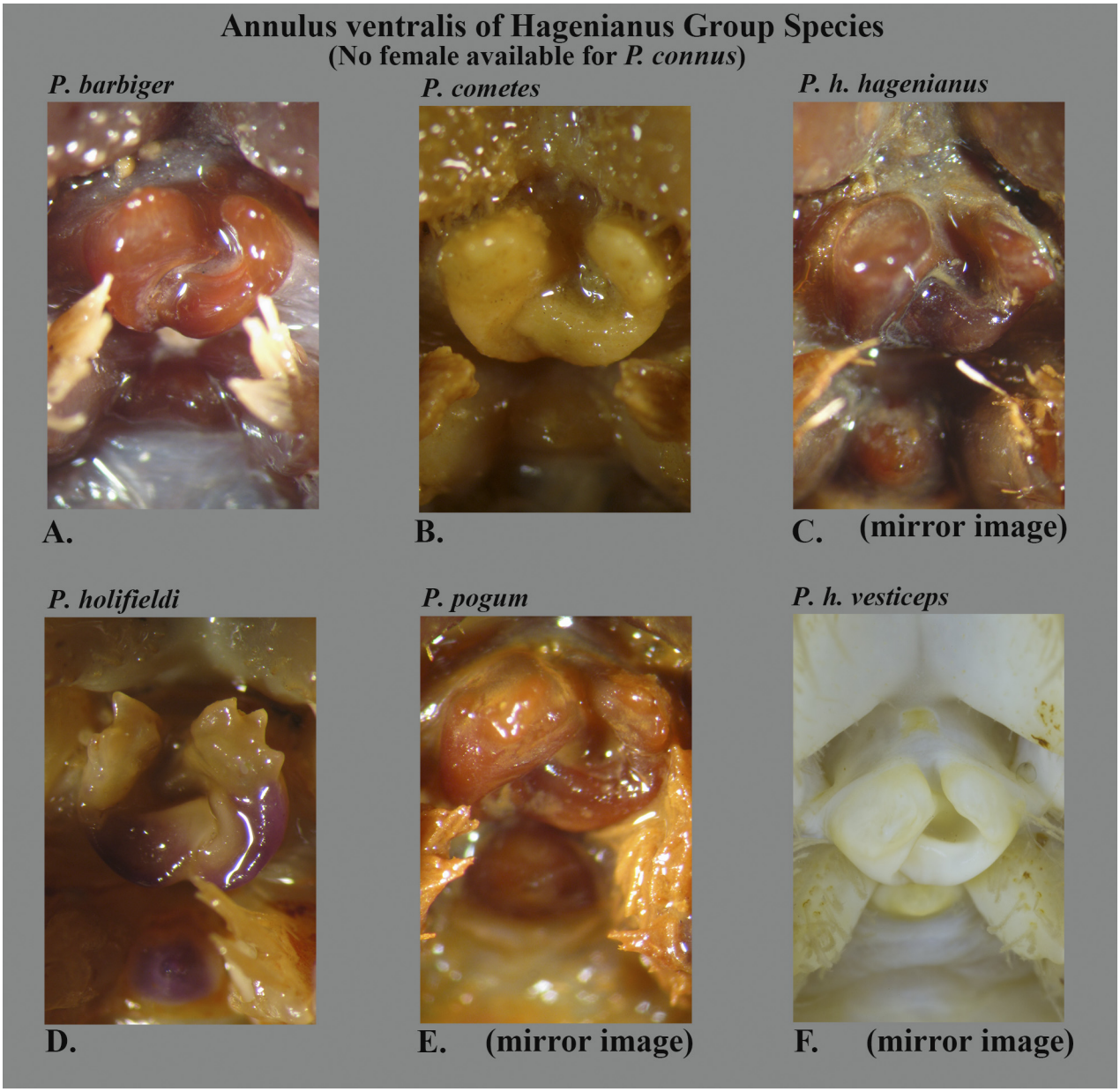

FIGURE 20. A–F respectively, annulus ventralis for *Procambarus barbiger*, *Procambarus cometes*, *Procambarus hagenianus hagenianus*, *Procambarus holifieldi*, *Procambarus pogum* and *Procambarus hagenianus vesticeps*. No female available for *P. connus*. Figures C, E and F are mirror images of the original structure to make for easier comparison.

Color Patterns in the Hagenianus Group. The Hagenianus Group species undoubtedly are some of the most colorful crayfish species known (Figures 3 and 23–25). Lyle (1937) commented on this and provided color descriptions for all of the taxa he recognized. Fitzpatrick (1978a) provided color notes for all of the taxa in his paper, with the exception of *P. connus* for which he had not seen live individuals. Both Lyle's and Fitzpatrick's notes indicate that all of the taxa have vivid colors and quite a bit of variation. Figure 23 shows, for example, variation in color pattern and intensity in *P. barbiger*. Colors of individuals range from mostly yellow, brown or royal blue, to a mixture of these colors. The color variation noted in *P. holifieldi* (Figure 3) does not seem as great as that in *P. barbiger*, but only one population of *P. holifieldi* is known. Figure 24 shows color variation within *P. h. vesticeps*, while Figure 25 shows variation in the color pattern of *P. h. hagenianus* populations, from Hale and Perry counties, AL.

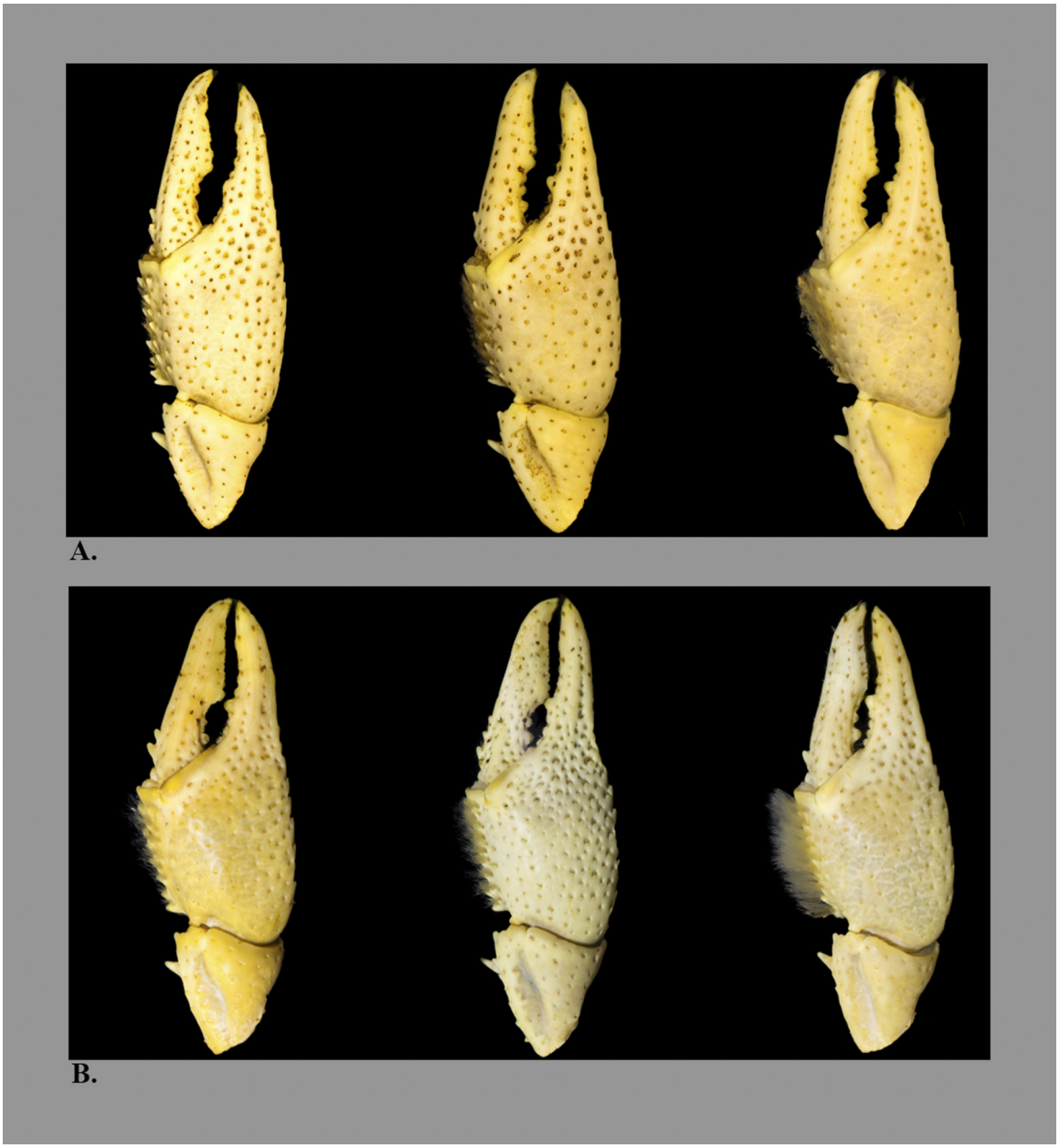

FIGURE 21. Variation of the beard on margin of chelae in *P. hagenianus vesticeps*; A. Three individual paratypes from Chickasaw County, MS (USNM 69441); B. Three individual paratypes from Monroe County, MS (USNM 44746).

Discussion

Crayfish workers have long separated the Hagenianus Group and Gracilis Group of the *Procambarus* subgenus *Girardiella* based on two characters: presence or absence of the cephalic process of the Form I gonopod and the presence or absence of a long median spine extending beyond the distal margin of the mesial lobe of the uropods. It has been shown here that Reimer (1969) was correct in that *P. hagenianus*, as well as all Hagenianus Group taxa, indeed possess a cephalic process. The two groups can still be separated based on the long median spine on mesial lobe of the uropods (Figure 5A and 5B) and the development of the mesial lobe of the cephalic process. In the Gracilis Group the mesial lobe is well developed and elongated with the distal margin set free (Figure 6B). In the Hagenianus Group the mesial lobe is much reduced and wraps itself closely to the base of the central projection so that the distal margin does not extend freely (Figure 6A).

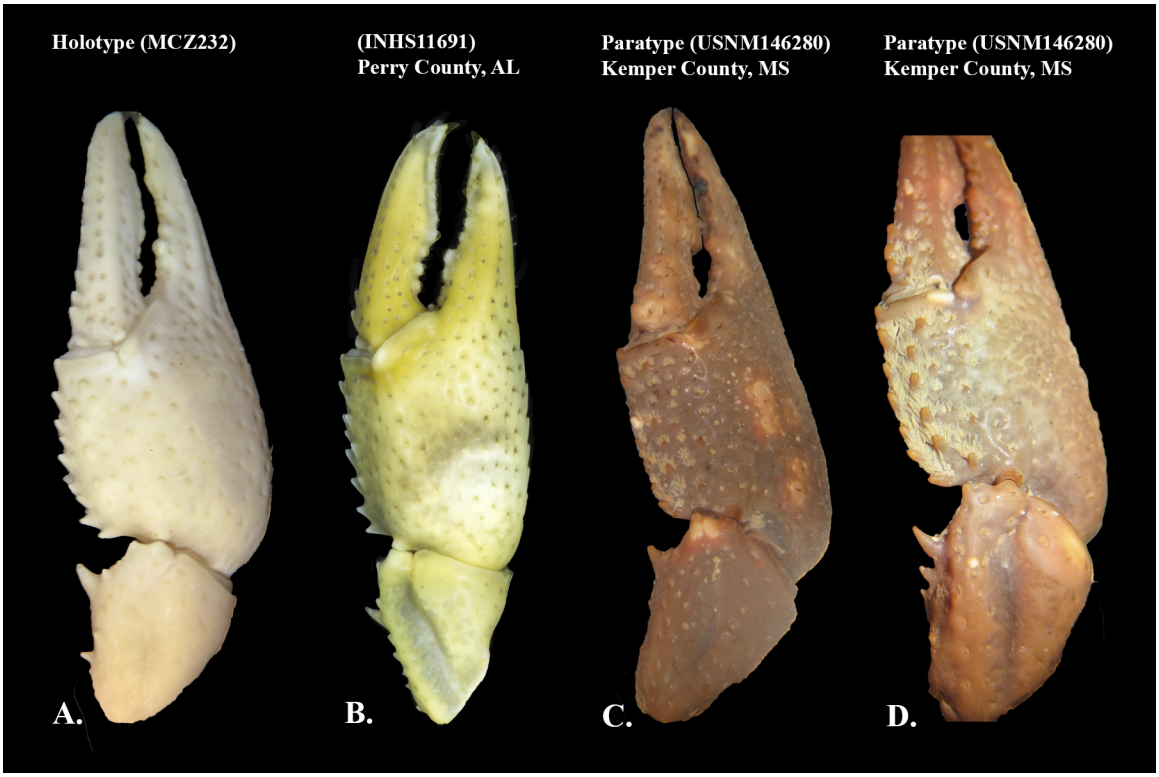

FIGURE 22. Variation of the beard on margin of chelae of *P. hagenianus hagenianus*; A. Holotype (MCZ 232); B. Individual from Perry County, AL (INHS 11691); C. Paratype, Kemper County, MS (USNM146 280); D. Paratype, Kemper County, MS (USNM 146280).

TABLE 4. Hagenianus Group species recognized and their synonyms.

***Procambarus* (*Girardiella*) *hagenianus hagenianus* (Faxon 1884)**
Cambarus advena Hagen 1870
Cambarus carolinus Hagen 1870
Cambarus hagenianus Faxon 1884
***Procambarus* (*Girardiella*) *hagenianus vesticeps* Fitzpatrick 1978**
Cambarus (*Girardiella*) *hagenianus evansi* Lyle 1938 (nomen nudum)
Procambarus cometes Fitzpatrick 1978
Procambarus connus Fitzpatrick 1978
Procambarus connos Fitzpatrick 1978 (misspelling)
Procambarus pogum Fitzpatrick 1978
Cambarus (*Girardiella*) *hagenianus carri* Lyle 1938 (nomen nudum)
***Procambarus* (*Girardiella*) *barbiger* Fitzpatrick 1978**
Cambarus (*Girardiella*) *hagenianus forestae* Lyle 1938 (nomen nudum)
Cambarus (*Girardiella*) *hagenianus forrestae* Fitzpatrick 1978 (misspelling)
***Procambarus* (*Girardiella*) *holifieldi* Schuster, Taylor, Adams 2015**

From examining the gonopod morphology of all taxa in the Hagenianus Group, it was determined that there were two species subgroups within the Hagenianus Group. The first consists of *P. barbiger* and *P. holifieldi*. The second group consists of *P. hagenianus hagenianus* and *P. hagenianus vesticeps*. These are separated from all of the other taxa based primarily on the shape of the caudal process. In the mesial view (Figure 4A and 4B), the caudal process of *P. barbiger* and *P. holifieldi* appears triangular in shape, coming to a distinct point distally, whereas in the other group it appears subrhomboidal with a linear distal margin (Figure 4C). In addition, species in the latter group possess a caudal process that is continuously curved in, which can be seen in caudal (Figure 9B–C and 9F–G) and apical views (Figure 18).

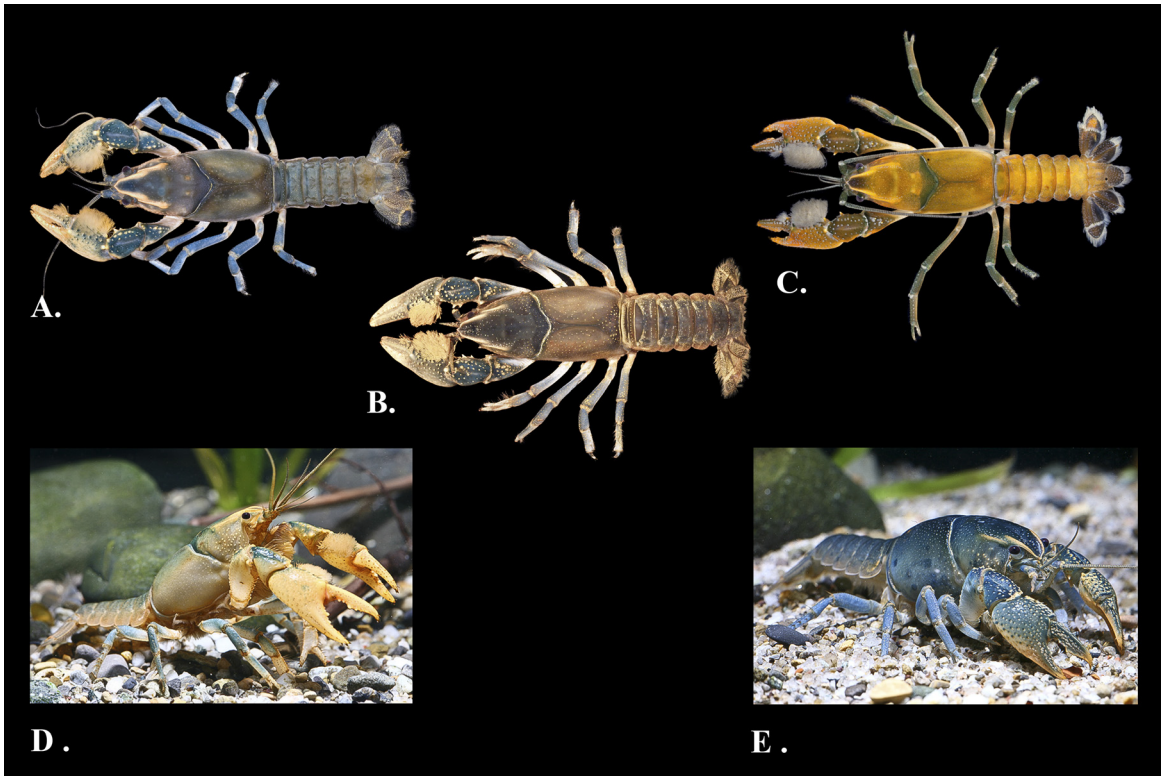

FIGURE 23. Variation in color pattern in *P. barbiger*; A. USFS CL001-01, M1, Perry Co., MS, C. Lukhaup photo; B. USFS CL-001-02, M1, Perry Co., MS, C. Lukhaup photo; C. Scott Co., MS; D. USFS CL001, Perry Co., MS, C. Lukhaup photo; E. USFS CL001-03, F, Perry Co., MS, C. Lukhaup photo.

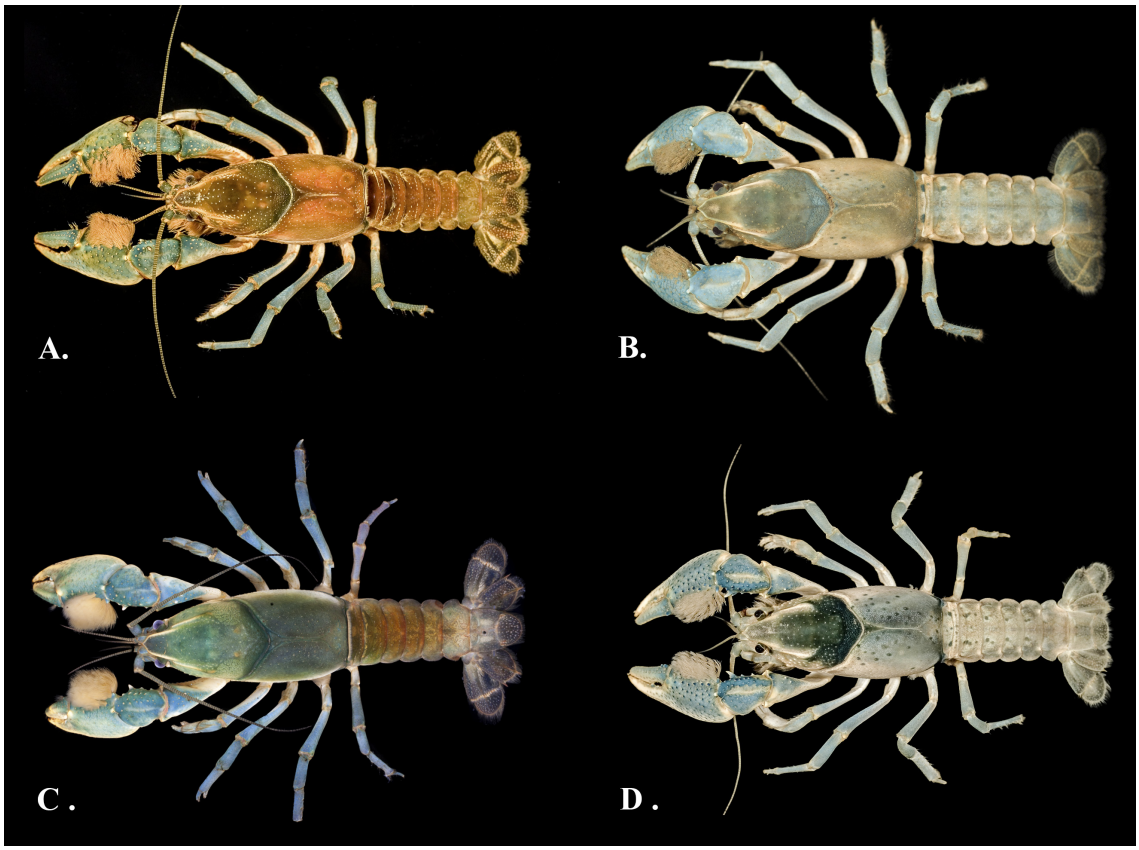

FIGURE 24. Variation in color pattern in *P. h. vesticeps*; A. USFS M031-01, M1, Pontotoc Co., MS; B. USFS SA329-02, M2, Chickasaw Co., MS; C. Oktibbeha Co., Starkville, MS, swimming pool; D. USFS SA329-01, M1, Chickasaw Co., MS

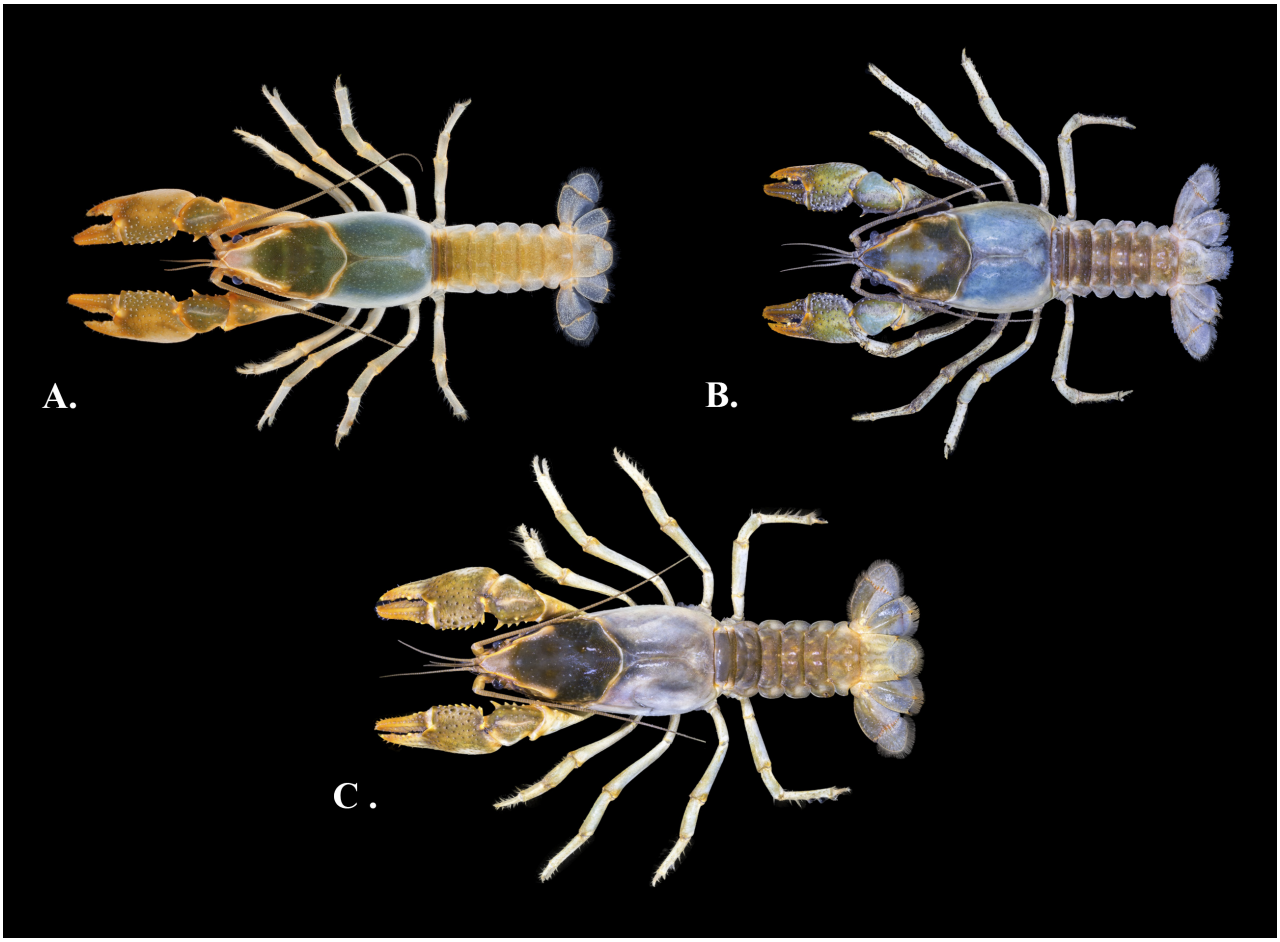

FIGURE 25. Variation in color pattern of *P. h. hagenianus*, A. Perry Co., AL; B. and C. Hale Co., AL

The numerous errors and uncertainties in existing taxonomy led us to revise the Hagenianus group. Although *P. barbiger* and *P. holifieldi* both have triangle-shaped caudal processes they can be separated by the length of the caudal processes and size and robustness of the central projections (Figure 4A and 4B). However, finding species limits among *P. h. vesticeps*, *P. cometes*, *P. connus* and *P. pogum* using Fitzpatrick's (1978a) descriptions and key is very problematic. Given the number of errors in the paper and the lack of definitive characters to separate these taxa from one another, it became very difficult to continue to recognize the validity of *P. cometes*, *P. connus* and *P. pogum*. To address the uncertainties, we assign an alternative taxonomic arrangement to the Hagenianus Group (Table 4).

Although there is some variation in the setation of the mesial margin of the chelae in both *P. h. hagenianus* and *P. h. vesticeps* we feel that the two subspecies should be retained. In *P. h. hagenianus*, the setae are either completely absent (Figure 22A and B) or are short and arranged in fan-shaped bundles along the distal margins of each tubercle on the surface of the chela (Figure 22C and D). In *P. h. vesticeps*, the setae are much longer, and even in individuals where they are sparse, they still retain the appearance of a thinned beard. Fitzpatrick himself commented that there seem to be areas in Mississippi where the two subspecies intergrade. The remaining species present much more of a taxonomic issue. It is not clear why Fitzpatrick chose to list *P. cometes*, *P. connus* and *P. pogum* as full species. The errors in the descriptions and in the key (see above) virtually eliminate any character that can reliably be used to separate these three taxa from each other or from *P. h. vesticeps*. We have found that all of the setal and secondary sex characters Fitzpatrick presented in his key and paper are without diagnostic taxonomic value. In addition, one of them (antennal scale setal character) is nonexistent. It is for these reasons, and the overall similarity of the three taxa, that we synonymize these three taxa with *P. h. vesticeps*.

The taxa belonging to the Hagenianus Group have an extremely interesting range of color variations. Blue seems to be the predominant theme among these taxa as indicated by photos presented here and by the notes of Lyle and Fitzpatrick. However, both Lyle and Fitzpatrick noted red forms of *P. h. hagenianus* and *P. h. vesticeps*. We do not have photos of distinctly red individuals, but in both of the subspecies a reddish brown color is evident in some of the individuals. Unfortunately, few color photos exist for these taxa. There may be more color variations in these taxa than in any other cambarid crayfishes. The taxonomic utility or the biological importance, if any, of these color forms or phases is not known.

Two additional issues have compounded the uncertainty surrounding Hagenianus Group, and they are worth mentioning here. The holotype of *P. connus*, which is housed in the collection of the USNM (#146261), could not be found during the course of this study. It has not been loaned out and may have just been misplaced in the collection, or it may be lost. This may present a problem for future workers. In addition, the type locality for *P. connus* is given as Carrollton, Caroll County, MS, but the exact location is unknown.

Key to the Form I Males of the Hagenianus Group of *Procambarus* (*Girardiella*) Lyle, 1938

1a. Without long median spine that overlaps the distal margin of the mesial lobe of the uropods (Figure 5b)... . . . . **Gracilis Group species**

1b. With long median spine that overlaps the distal margin of the mesial lobe of the uropods (Figure 5a). . . . . **Hagenianus Group species** 2

2a. Caudal process in lateral view rhomboidal in outline, distally with an elongated straight edge (Figure 4C) . . . . . ***Procambarus hagenianus***...3

2b. Caudal process in lateral view triangular in outline, distally coming to a sharp point (Figure 4A&B) 4

3a. Lateral margin of palm of chelae without a beard of dense long setation, sometimes with short hairs in pits anterior to tubercles (Figure 22A–D). . . . . ***Procambarus hagenianus hagenianus***

3b. Lateral margin of palm with a beard of dense setation, sometimes less dense but with long setae (Figure 21A&B) . . . . . ***Procambarus hagenianus vesticeps***

4a. Caudal process in lateral view an acute triangle, distinctly shorter than the central projection (Figure 4A); lateral margin of palm of chelae without a beard of dense setation (Figure 1N).. . . . . ***Procambarus holifieldi***

4b. Caudal process in lateral view an obtuse triangle, subequal in length to the central projection (Figure 4B); lateral margin of palm of chelae with a beard of dense setation (Figure 13M).. . . . . ***Procambarus barbiger***

Distribution of Hagenianus Group Taxa

Procambarus barbiger is found in south-central Mississippi in the headwaters of the Pearl and Pascagoula river drainages in Jasper, Newton, Rankin, Scott and Smith counties. *Procambarus hagenianus hagenianus* is known in Mississippi from the western tributaries of the upper Tombigbee River in Chickasaw, Kemper, Lowndes, and Oktibbeha counties and from disjunct populations in Rankin and Hinds counties, near Jackson, and in Alabama from the Tombigbee River drainage in Hale and Sumter counties and the Alabama River drainage in Perry County. *Procambarus hagenianus vesticeps* is found in Mississippi in the western tributaries of the Upper Tombigbee River drainage in Chickasaw, Monroe, Pontotoc and Oktibbeha counties, and in the Yazoo River drainage near Carrolton, Carroll County. Fitzpatrick (1978a) thought that the population near Muldon, Monroe County, Mississippi, might represent a hybrid zone for the two subspecies. He indicated that individual Form I males from that population exhibited extreme variation in the development of the beard on the margin of the palm of the chelae. Some individuals had very few long setae, reminiscent of *P. h. hagenianus*, whereas others had a dense beard more typical of *P. h. vesticeps. Procambarus holifieldi* is currently known only from the type locality in Perry County, Alabama, in the Alabama River drainage.

Conclusion

A new species of crayfish belonging to the Hagenianus Group of the subgenus *Girardiella* in the genus *Procambarus* was described. It is most closely related to *Procambarus barbiger*, and can be separated from it by

size and shape of the caudal process of the form I male gonopod. Much of the past literature has indicated that the species in the Hagenianus Group lack a cephalic process as one of the terminal elements of the form I male gonopod. This study has shown that this process does, in fact, exist in these species. The two species groups (Hagenianus Group and Gracilis Group) can still be separated from one another by the shape and development of the lobes of the cephalic process, and by the presence or absence of a long median spine that overlaps the distal margin of the mesial lobe of the uropods. A review of the Hagenianus Group species indicated that there are a number of important discrepancies and errors in the past taxonomy of the group. In addition, we have found significant overlapping variation among four taxa, and therefore, have synonymized three described species (*P. cometes*, *P. connus* and *P. pogum*) with *P. hagenianus vesticeps*. This leaves four taxa in this group (*P. hagenianus hagenianus, P. hagenianus vesticeps*, *P. barbiger* and *P. holifieldi*).

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