

***Cambarus (Cambarus) davidi*, a new species of crayfish
(Decapoda: Cambaridae) from North Carolina**

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Abstract.—*Cambarus (Cambarus) davidi* is a new species of crayfish from the eastern Piedmont Plateau of North Carolina, where it is restricted to intermittent streams, seepage areas, springs, and burrows. Although the ranges of the two species appear to be broadly disjunct, *C. (C.) davidi* is most closely related to the ecologically more tolerant *Cambarus (C.) bartonii* (s.l.), and especially resembles some members of the controversial subspecies *C. (C.) b. cavatus*. *Cambarus (C.) davidi* is distinguished by a suite of characters that includes a vaulted carapace; a deeply excavate, ladlelike rostrum; a very narrow, sparsely punctate areola; and an obtuse to nearly obsolete suborbital angle that almost always bears a small tubercle.

On 18 August 1993, David G. Cooper collected several specimens of a *Cambarus* from under large rocks in a shallow, intermittent tributary of the Neuse River, Wake County, North Carolina. In the field they appeared to be aberrant individuals of the burrowing species, *Cambarus (Depressicambarus) reduncus* Hobbs, 1956, which is not uncommon in such habitats in the upper Neuse River watershed. In the laboratory, however, I was surprised to discover that the specimens belonged to the subgenus *Cambarus*, and to some species previously unknown from the Neuse River basin, whose crayfish fauna is well documented (Cooper & Ashton 1985, Cooper & Braswell 1995, Cooper & Cooper 1995). Since that time, many additional specimens from the Neuse and Cape Fear river basins have either been collected or have been recognized in prior collections. They belong to an undescribed species of *Cambarus* that seems to have its closest affinities with congeners that occur in the Tennessee and Ohio river drainages.

Abbreviations used in the text are as follows: j, juvenile; NC, North Carolina State

highway; NCSM, North Carolina State Museum of Natural Sciences, Raleigh; PCL, postorbital carapace length; R, river; SR, state secondary (county) road; TCL, total carapace length; US, United States highway; USGS, United States Geological Survey; and UTM, Universal Transverse Mercator coordinates.

Cambarus (Cambarus) davidi,
new species
Fig. 1, Table 1

Diagnosis.—Body and eyes pigmented, eye small (\bar{X} adult diam 1.7 mm, $n = 30$). Carapace vaulted, thoracic section averaging 1.3 times wider than deep ($n = 52$). Rostrum acarinate; margins elevated, subparallel, caudally thickened, strongly to moderately constricted at base of acumen, lacking marginal spines or tubercles; floor (dorsal surface) of rostrum deeply concave, ladlelike; acumen 24.5 to 49.1% ($\bar{X} = 33.6\%$, $n = 52$) length of rostrum, latter 13.0 to 19.3% ($\bar{X} = 16.2\%$, $n = 52$) of TCL. Areola 5.2 to 14.5 ($\bar{X} = 8.1$, $n = 76$) times longer than wide, constituting 35.4 to

41.8% ($\bar{X} = 37.6\%$, $n = 76$) of TCL and 42.2 to 47.3% ($\bar{X} = 44.1\%$, $n = 45$) of PCL; areola sparsely punctate, with 2 ($n = 22$) to 3 ($n = 64$) punctations across narrowest part. Cervical spines reduced to multiple tubercles. Branchiostegal spine reduced to small tubercle; hepatic and surrounding regions of carapace crowded with tubercles. Suborbital angle obtuse to nearly obsolete, almost always bearing small tubercle; postorbital ridge short, cephalic margin rounded and usually devoid of tubercle. Antennal scale 2.0 to 3.6 ($\bar{X} = 2.5$, $n = 50$) times as long as broad, widest just distal to midlength, lateral margin thickened and with long distal spine.

Palm of chela of cheliped 1.5 to 1.8 ($\bar{X} = 1.6$, $n = 51$) times wider than deep, width 1.3 to 1.7 ($\bar{X} = 1.5$, $n = 51$) times length of mesial margin; dorsolateral margin costate distally, without impression; mesial margin of palm with 2, rarely 3, rows of tubercles: mesial row of 6 to 8 (usually 7) large, generally adpressed tubercles, subtended dorsally by row of 1 to 5 (usually 4 or 5) smaller tubercles. Fixed finger of chela costate laterally, with well defined longitudinal ridges dorsally and ventrally; opposable surface of finger with row of 4 to 11 (usually 5 or 6) tubercles in addition to subconical tubercle; dactyl 1.7 to 2.6 ($\bar{X} = 2.0$, $n = 51$) times as long as mesial margin of palm, with strong longitudinal ridge dorsally, weaker ridge ventrally; mesial margin with prominent tubercles; opposable surface with row of 6 to 14 (usually 7 to 9) tubercles. Carpus of cheliped generally lacking dorsomesial tubercles; merus with prominent multiple dorsodistal tubercles and often row of small squamous tubercles along dorsal ridge.

Hook on ischium of third pereopod of males, that of form I male (Fig. 1K) uniramous, overreaching basioischial articulation and opposed by tubercle on basis; coxa of fourth pereopod of males with vertically disposed, caudomesial boss.

In situ gonopods (Fig. 1G) symmetrical, with abutted or slightly separated, tubercle-

like proximomesial apophyses; proximolateral portion of gonopod set off from rest of shaft by weak groove; in lateral aspect (Fig. 1B), central projection curved over 90° to plane of shaft, untapered, with proximally directed subapical notch; mesial process inflated, symmetrically tapered, slightly constricted at base of caudal third, with subacute, caudally directed apex extending slightly farther caudally than apex of central projection; caudal process reduced to swelling at caudodistal margin of shaft; in mesial aspect (Fig. 1C), distal portion of gonopod with essentially flat surface, few setae at midlength.

Annulus ventralis of allotypic female (Fig. 1H) 1.3 times broader than long, generally symmetrical and subrhomboidal; cephalic margin convex and fused to sternum, caudal margin subangular, free and capable of slight movement; cephalic half of annulus depressed, sloping, with narrow median trough, flanked each side by low, poorly defined ridge; ridges diverging caudally, sinistral ridge continuing obliquely and terminating before joining caudosinistral wall, dextral ridge curving caudodextrally to merge with upper arm of heavy, C-shaped caudodextral wall; transverse tongue prominent, originating from sinistral wall near caudal midline, continuing cephalically and slightly obliquely before turning dextrally and plunging into fossa beneath dextral wall; sinus dissecting caudal wall near midline.

Measurements of type specimens provided in Table 1.

Description of holotypic male, form I.—Body and eyes pigmented, eye 1.8 mm diam. Cephalothorax (Fig. 1A, D) subcylindrical, thoracic section 1.2 times wider than deep. Areola 9.2 times longer than wide, constituting 39.3% of TCL (45.1% of PCL), sparsely punctate, with 3 punctations across narrowest part. Rostrum acarinate, with slightly thickened caudal margins moderately converging to base of acumen, where moderately constricted; margins of acumen slightly concave and converging to

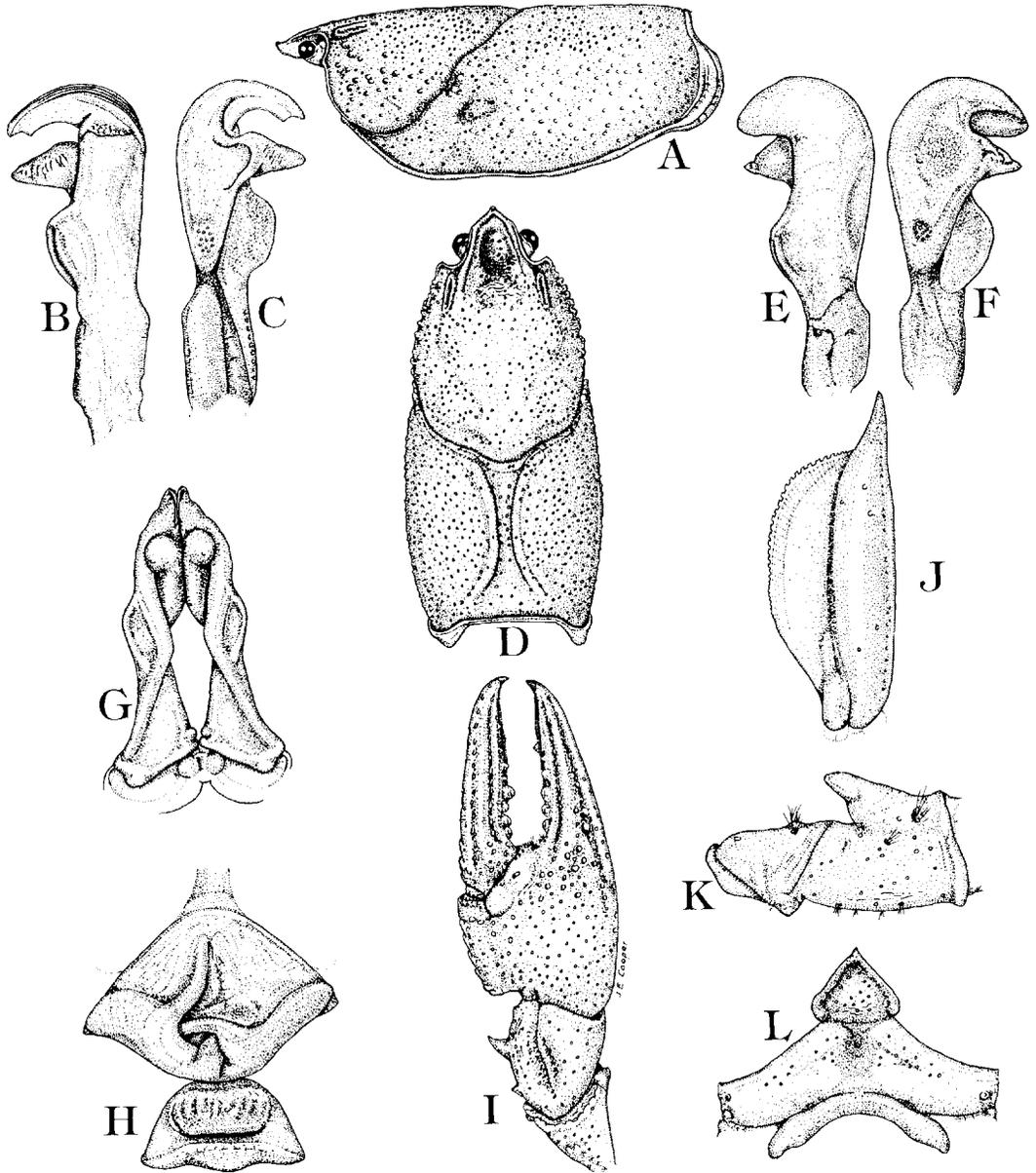


Fig. 1. *Cambarus (Cambarus) davidi*, new species (all from holotypic male, form I, except E, F, from morphotypic male, form II, and H, from allotypic female): A, lateral aspect of carapace; B, E, lateral aspect of gonopod (first pleopod); C, F, mesial aspect of gonopod; D, dorsal aspect of carapace; G, caudal aspect of in situ gonopods; H, annulus ventralis and postannular sclerite; I, dorsal aspect of distal podomeres of right cheliped; J, antennal scale; K, hook on ischium of third pereiopod; L, epistome.

dorsally directed apical tubercle, which reaching just beyond midlength of penultimate podomere of antennular peduncle; acumen comprising 30.2% of rostrum length, latter constituting 14.2% of TCL;

floor of rostrum excavate, ladlelike, moderately punctate, and ascending caudally into broad dorsomedian depression of carapace; subrostral ridge strong, visible to base of acumen in dorsal aspect.

Table 1.—Measurements (mm) of types of *Cambarus (Cambarus) davidi*, new species.

	Holotypic male	Allotypic female	Morphotypic male
Carapace			
Total length	30.3	36.5	30.7
Postorbital length	26.4	31.6	26.6
Length cephalic section	18.4	22.4	19.0
Width	15.7	18.4	15.3
Depth	12.6	15.1	12.2
Length rostrum	4.3	5.6	4.9
Length acumen	1.3	2.2	1.2
Length areola	11.9	14.1	11.7
Width areola	1.3	2.1	1.9
Antennal scale			
Length	4.5	5.4	5.2
Width	1.8	2.1	1.8
Abdomen			
Length	29.6	37.7	30.6
Width	13.6	16.4	12.2
Cheliped			
Length lateral margin chela	24.4	26.7	23.8
Length mesial margin palm	7.3	8.8	7.5
Width palm	11.5	13.4	11.1
Depth palm	6.8	7.8	6.7
Length dactyl	15.5	16.3	15.2
Length carpus	10.0	11.1	9.5
Width carpus	7.2	8.0	6.7
Length dorsal margin merus	12.0	13.8	12.2
Depth merus	7.1	8.5	6.9
Gondopod length	8.4	N/A	8.0

Postorbital ridge strong, groove essentially lateral, cephalic margin with vestigial tubercle. Branchiostegal spine reduced to tubercle; suborbital angle obtuse, without tubercle. Thoracic section of carapace dorsally and dorsolaterally punctate, laterally with large, scattered granules; cephalic section 1.5 times longer than areola and constituting 60.7% of TCL, laterally crowded with large tubercles and with row of small tubercles along ventral margin of cephalic section of cervical groove; gastric region mostly glabrous. Cervical spine region on right with 4 large and 3 smaller tubercles (2 large and 2 smaller on left). Abdomen slightly narrower and shorter than cephalothorax. Proximal podomere of uropod without spine or tubercle on lateral lobe,

with prominent caudomedian spine on mesial lobe; mesial ramus of uropod with median keel bearing strong caudal spine, tip of which reaching caudal margin of ramus, caudolateral margin with small spine; lateral ramus with submedian keel bearing terminal spine at transverse flexure, latter with total of 17 fixed spines along margin and 1 long, movable sublateral spine. Telson with 1 long stationary and 1 long articulated spine in each caudolateral corner of cephalic section; caudal margin domelike.

Epistome (Fig. 1L) with symmetrical, subtriangular cephalic lobe bearing short cephalomedian projection; margins of lobe uninterrupted, moderately thickened, lateral apices thicker than rest; floor (ventral surface) of lobe punctate and slightly convex, concave along lateral margins; transverse basal sulcus complete; central depression of body broad, moderately deep, with cephalomedian fovea; lamellae punctate, lateral margins subtruncate, with 2 large subacute tubercles and 1 small rounded tubercle in right caudolateral corner (1 large subacute and 1 small rounded tubercle on left); zygoma moderately arched, pits elongate. Antennal peduncle with small cephalolateral tubercle on basis, small ventral tubercle on ischium; antennular peduncle with small, laterally displaced subdistal spine on ventral surface of basal podomere. Antennal scale (Fig. 1J) 2.5 times longer than wide, broadest just distal to midlength; lateral margin thickened, terminating in long distal spine, tip of which reaching distal margin of penultimate podomere of antennular peduncle; lamella ca. 1.3 times as wide as thickened lateral margin; distal margin of lamella subtransverse for most of width, then sloping to widest point; mesial margin subparallel to lateral margin for most of length.

Third maxilliped with tip of endopodite reaching about midlength of penultimate podomere of antennal peduncle; exopodite hirsute, tip reaching base of distal two-thirds of merus of endopodite; cephalolateral corner of ischium slightly produced,

not spinelike; ventrolateral ridge flanked mesially by row of punctations bearing moderately long setae; lateral half of ischium with punctations bearing short setae, punctations most abundant on proximal third; mesial half with long stiff setae largely obscuring mesial margin, latter with 27 denticles on right. Right mandible with incisor ridge bearing 7 denticles (6 on left).

Right chela (Fig. 11) 2.1 times longer than wide; palm 1.7 times broader than deep, width 1.6 times length of mesial margin; latter 29.9% of chela length, 47.1% of dactyl length. Dorsal surface of palm punctate; distolateral margin of palm and lateral margin of fixed finger costate, area at juncture of palm and finger with aggregation of large punctations creating slight impression; lateral margin of palm rounded and with row of large punctations. Ventral surface of palm less punctate than dorsal, distolateral area with moderate depression and aggregation of large punctations; lateral eminence of articular ridge with distal tubercle, none proximal to ridge. Mesial margin of right palm with mesial row of 7 adpressed tubercles, proximal 3 of which with elevated distal margins (same on left), mesial row subtended dorsally by row of 4 smaller tubercles (5 on left) and ventrally by 1 small, squamous distal tubercle (3 on left).

Fingers gaping in proximal three-fourths of length, greatest width of gape about four-fifths width of base of fixed finger; opposable base of fixed finger with tuft of short setae; both fingers slightly curved distoventrally in lateral aspect, dactyl very slightly bowed in dorsal aspect. Mesial margin of right dactyl bearing row of 4 prominent and 4 weaker tubercles on proximal half, distal half of margin punctate; dorsal surface of dactyl with low, rounded longitudinal ridge, flanked mesially by punctate groove, laterally by row of large, spaced punctations; ventral surface with similar longitudinal ridge; opposable surface with 8 tubercles, fourth from base very large and slightly displaced ventrally (7 tubercles on left, third

from base largest); denticles in 2 or 3 rows from near tip of finger to sixth tubercle from base, single row from there. Fixed finger with very strong dorsomedian ridge flanked mesially by deep punctate groove and second narrower ridge, laterally by deep punctate groove; lateral margin with irregular row of large punctations; ventral surface with very strong longitudinal ridge, flanked both sides by row of large punctations; opposable margin with subconical tubercle ventral to denticles at base of distal third of finger, and 5 tubercles proximal to subconical one, third from base more prominent than others (4 tubercles on left finger, third from base very large); denticles in 2 or 3 rows from tip of finger to subconical tubercle, single row from there.

Carpus (Fig. 11) 1.4 times as long as wide, 1.4 times as long as mesial margin of palm; carpus dorsally with long, deep, slightly oblique sulcus, lateral and mesial to which surface punctate; mesial margin with large distal spine and prominent proximal tubercle; ventral surface with stout, rounded tubercle at lateral articular condyle, similar distomedian tubercle, and 1 small tubercle proximomesial to latter. Right merus 1.7 times longer than deep; dorsal surface with 3 prominent and 2 smaller subdistal tubercles (2 prominent and 1 smaller on left), and small squamous tubercles along much of dorsomedian ridge; ventrolateral ridge with 2 small acute tubercles and 1 minuscule tubercle near articular condyle (1 small acute tubercle and minuscule distal tubercle on left); ventromesial ridge with 10 spiniform tubercles, distalmost one somewhat larger than others; ischium with 3 small ventral tubercles (4 on left).

Palm and fingers of chela of second pereopod hirsute. Ventral margins of pleura subtruncate or slightly rounded, caudovertral corners slightly angular, caudal margins rounded; terga very punctate, except articular cephalic portions glabrous. Sternites between third and fourth coxae with very dense, matted setae, covering distal ends of in situ gonopods.

Gonopods (Fig. 1B, C, G) as described in "Diagnosis." Length of gonopod 27.7% of TCL (31.8% of PCL).

Description of allotypic female.—Except for secondary sexual characters, differing from holotypic male in following respects: Areola 6.7 times wider than long, constituting 38.6% of TCL (44.6% of PCL). Acumen comprising 39.3% of rostrum length, latter constituting 15.3% of TCL. Suborbital angle nearly obsolete, with small tubercle. Cervical spine region on both sides of carapace with 3 prominent tubercles, largest of those on right side subacute. Caudolateral corner of cephalic section of telson with 2 spines on right, 3 on left. Cephalic lobe of epistome subcordiform; lamellae with single tubercle each caudolateral corner; zygoma strongly arched. Antennal peduncle lacking tubercle on basis; antennal scale 2.6 times longer than wide, lamella about 1.5 times as wide as thickened lateral margin. Incisor ridge of right mandible bearing 8 denticles. Right chela 2.0 times longer than wide, palm length 33.0% of chela length, 54.0% of dactyl length. Opposable surface of right dactyl with 10 tubercles (9 on left); opposable surface of both fixed fingers with 6 tubercles in addition to subconical one, fourth from base largest. Carpus of cheliped 1.3 times as long as mesial margin of palm; merus 1.6 times longer than deep, dorsal surface with 2 prominent and 2 smaller subdistal tubercles (same on left); ventrolateral ridge with 5 small tubercles (same on left), ventromesial ridge with 8 spiniform tubercles (9 on left).

Annulus ventralis (Fig. 1H) as described in "Diagnosis." In addition, first pleopods short, reaching caudal margin of annulus when abdomen flexed; annulus about 3 times wider than postannular sclerite, which elongate, ventrally domed, punctate.

Description of morphotypic male, form II.—Differing from holotypic male in following respects: Thoracic section of carapace 1.3 times wider than deep. Areola 6.2 times as long as wide, constituting 38.1% of TCL (44.0% of PCL). Margins of ros-

trum less constricted at base of acumen, converging at ca. 45°, acumen comprising 24.5% of rostrum length, latter constituting 16.0% of TCL. Suborbital angle obtuse and with very small tubercle. Cephalic section of carapace 1.6 times longer than areola and constituting 61.9% of TCL. Cervical region on both sides of carapace with 3 prominent and 1 moderate tubercle, ventralmost of which on right side subacute. Transverse flexure of lateral ramus of right uropod with 16 spines in addition to sublateral one. Lateral corners of lamellae of epistome with 1 moderate tubercle on right, 2 on left; zygoma strongly arched. Antennal scale 2.9 times wider than long, lamella ca. 1.5 times width of thickened lateral margin, distal margin moderately declivous. Length of palm of cheliped 31.5% of chela length, 49.3% of dactyl length. Mesial margin of palm with mesial row of 6 adpressed tubercles, subtended dorsally on right palm by row of 3 moderate tubercles (4 on left) and ventrally by 4 small squamous tubercles (2 on left). Opposable surface of dactyl with 9 tubercles on right, 8 on left, basalmost largest. Opposable surface of fixed finger with 6 tubercles on right in addition to subconical one, 7 on left, third from base largest. Carpus 1.3 times as long as palm. Merus 1.8 times longer than deep; dorsal surface of right merus with patch of 5 prominent subdistal tubercles and 5 smaller tubercles proximal to them (2 moderate and 6 smaller on left); ventrolateral ridge on right with 2 subacute and 2 other tubercles (2 small, and 1 minuscule articular tubercle, on left); ventromesial ridge on right with 10 small tubercles (9 on left).

Hook on ischium of third pereopod weak, not overreaching basioischial articulation, opposed by tubercle on basis; boss on coxa of fourth pereopod moderately developed.

Gonopod (Fig. 1E, F) length 26.1% of TCL. In situ gonopods with weak, separated proximomesial apophyses; mesial process noncorneous, bulbous, distal surface creased near extruded tip; in lateral aspect,

gonopod with weak juvenile suture; central projection noncorneous, curved 90° to shaft, tapered to subacute tip; mesial process tapered, triangular in outline, tip directed caudally and inclined slightly distolaterally. Setae on sternites between third and fourth coxae not dense.

Color notes.—Adult ground color usually dark olivaceous, sometimes light brown with orange or tan overtones. Cephalic section of carapace often lighter in color than thoracic section. Hepatic region with orangish midlateral streak just cephalic to cervical groove. Margins of rostrum outlined in tan; antennal scale pale orangish-tan with dark lateral margin, antennal flagellae green. Most tubercles, spines, and granules of carapace and chelipeds tan to orangish. Dorsal surface of cheliped greenish or olivaceous; articular ridges of chela pinkish or orangish, ventral surface of chela pale grayish-tan. Lateral surface of entire propodus (palm and fixed finger) strikingly colored, varying from pinkish-tan to creamy orange or yellow. Tips of fingers of chelipeds pale orange or orangish-tan, color not subtended by black band. Proximal podomeres of other pereopods pale tan to light brown with darker mottling, distal podomeres greenish or bluish, fingers of chelae of second and third pereopods pale blue. Cephaloventral structures bluish-gray, except epistomal zygoma almost white. Annulus ventralis usually pale, mottled with orange in one female.

Cephalicmost tergite of abdomen with transverse dark brown or black rectangular band. Lighter colored adults and all juveniles with dark, diagonal blotch each side of caudal margin of thoracic section of carapace, blotches extending onto dorsolateral surfaces of two adjacent tergites as short, curved markings. Series of short, dark bars producing interrupted dorsolateral stripe each side of abdomen. Other dorsal surfaces of abdomen with scattered dark spotting. Ventrolateral pleura of abdomen with pale pink cephalic area and narrow oblique or V-shaped black bar dorsal to it, series of

these bars producing zigzag lateral stripe each side of abdomen. Juveniles generally paler than adults, color patterns in most respects similar but more vivid.

Type locality.—North Carolina, Wake County, small intermittent stream entering cove along western shore of Falls Lake (impoundment of Neuse River), ca. 1.4 air km NW of western end of NC 98 bridge & ca. 2.6 air km W of Stony Hill (Bayleaf 7.5' USGS quadrangle, UTM zone 17, 3984850/712190).

The shallow stream, which lies at the bottom of a steep ravine in a hardwood forest, is seasonally intermittent and has a maximum width of about 1.2 m. All specimens from this locality were found in the mud of shallow residual pools under large rocks when water levels were very low.

Disposition of types.—The holotypic male, allotypic female, and morphotypic male are in the crustacean collection of the NCSM (catalogue numbers NCSM C-4413, C-4414, and C-2656, respectively), as are paratypes consisting of 2 ♂ I, 15 ♂ II, 6 j ♂, 18 ♀, and 5 j ♀.

Range and specimens examined.—Apparently limited to the upper Neuse and Cape Fear river basins in the eastern Piedmont Plateau of North Carolina. Voucher specimens ($n = 107$), all in the crustacean collection at NCSM (catalogue numbers in parentheses), have been collected at the following localities.

Neuse River Basin: Durham Co.; upper trib Little R near Durham, 1 ♂ II (C-4742), 13 Feb 1995, coll. T. Cuffney. Orange Co.; small intermittent stream in headwaters West Fork Eno R at SR 1358, 2.4 air km E of Carr, 3 j ♀ (C-3425), 25 Jul 1995, coll. M.A. Hartman, M.E. Savacool. Wake Co.; seep entering small trib New Light Crk along SR 1918, 0.3 km SW of jct SR 1909, ca. 7.4 air km NNE of Bayleaf, 2 j ♂ (C-44), 18 Feb 1976, coll. A.L. Braswell (ALB), N. Murdock; type locality, 1 ♂ II (C-2656), 1 j ♂ (C-2657), 4 Jul 1994, coll. D.G. Cooper (DGC), JEC, 1 j ♂, 3 ♀ (C-2779), 1 j ♀ (C-2780), 3 j ♂ (C-2781), 18

Aug 1993, coll. DGC, JEC, 1 ♂ I (C-4413), 8 ♂ II, 6 j♂, 6 ♀, 7 j♀ (C-3795), 14 Jun 1997, coll. DGC, 1 ♀ (C-4553), 20 Jun 1998, coll. DGC; spring on small trib Lower Barton Crk between SR 1005 & SR 1844, SW of Bayleaf, 2 j♀ (C-3055), 6 Apr 1996, coll. S. Yirka, DGC, 1 j♂, 1 ♀, 2 j♀ (C-3293), 4 Jul 1996, coll. D. DeOliveira (DD), DGC; spring on S shore Lower Barton Crk, W of SR 1005, ca. 1.6 km NNW of center of Bayleaf, 1 ♂ II (C-3333), 11 Aug 1996, coll. DGC; small spring entering Falls Lake, ca. 0.8 km N of entrance of Lower Barton Crk into lake, 2 ♂ II, 1 ♀, 3 j♀ (C-5151), 11 Apr 1999, coll. DGC; "Raleigh," 2 ♀ (C-3143), 28 Nov 1924, coll. C.S. Brimley, W.B. Mabee; small intermittent stream entering lake at Schenck Forest, Raleigh, 1 ♂ II (C-3471), 25 Oct 1996, coll. DGC, 1 ♀ (C-3603), 4 Apr 1997, coll. DGC; small trib to Richland Crk near SW side of Reedy Creek Rd, Schenck Forest, Raleigh, 2 ♀ (C-5077), 10 Apr 1999, coll. DGC; small stream E of Jeffrey Dr off Lake Wheeler Rd, SE of Lake Wheeler, Raleigh, 3 ♀, 5 j♀ (C-3717), 20 May 1997, coll. DD, DGC, 1 ♂ II, 5 j♂, 4 j♀ (C-3766), 1 ♀ (C-4414), 24 May 1997, coll. DGC; Crabtree Crk below Duraleigh Rd, Raleigh, 1 j♀ (C-4591), 30 Aug 1998, coll. D.A. Jackan.

Cape Fear River Basin: Alamance Co.; spring on trib Toms Crk, Scott farm off SR 1612, 0.8 km NW of Union Ridge, 1 ♂ I, 1 ♀ in amplexus (C-45), 2 Mar 1976, coll. F.D. Scott (FDS); burrow at 403 Glen Raven Rd, Burlington, 1 ♂ II (C-3618), 25 Jun 1993, coll. C. McGrath (CM). Caswell Co.; Benton Branch between SR 1103 and 1105, S of SR 1100, ca. 1.9 air km SW of town of Stoneycreek, 1 ♂ II, 1 j♂, 1 ♀ (C-789), 14 May 1975, coll. FDS, JEC. Chatham Co.; small, intermittent upper trib New Hope Crk at SR 1716, 6.6 km NNE of jct US 64, ca. 10.4 air km ENE of center of Bynum, 1 j♂ (C-3026), 1 Apr 1986, coll. D.R. Lenat (DRL), T. MacPherson, 1 j♀ (C-3106), 15 Oct 1992, coll. CM, 1 j♀ (C-3748), 1 Feb 1993, coll. CM, 1 ♂ I (C-

4464), 13 Feb 1998, coll. DRL, D. Penrose (DP); upper trib Robeson Crk at US 64, Pittsboro, 1 ♀ (C-4316), 6 Mar 1997, coll. DP. Harnett Co.; upper trib Kenneth Crk at SR 1447, NE of Rawls, 2 ♂ II, 1 j♂ (C-2963), 28 Aug 1991, coll. N. Medlin (NM), DP. Rockingham Co.; spring on small trib Benaja Crk, ca. 0.3 air km ESE of jct SR 2426 and 2427, 1 ♂ II, 1 j♂, 2 ♀, 2 j♀ (C-3104), 1 ♂ II (C-3105), 3 Jun 1976, coll. M.R. Cooper, JEC; drainage ditch in floodplain Haw R, Camp Guilrock, ca. 19.2 air km SE of Monroeton, 1 ♀ (C-4843), Mar 1998, coll. A.B. Somers & students; Little Troublesome Crk at SR 2600, ca. 1.1 air km W of Williamsburg, 1 ♀ (C-4912), 6 Apr 1998, coll. B. Tracy, NM, L. Eaton, DP.

Variations.—In addition to those addressed in the "Diagnosis," the following variations have been recorded. The margins of the rostrum are usually abruptly or at least moderately constricted at the base of the acumen, but in seven specimens the margins, while increasing in convergence, are not notably constricted. The number of prominent cervical tubercles varies from one to six (usually three to five), and in some specimens at least one of these tubercles is spiniform. In three individuals, the usual small tubercle on the suborbital angle is absent, and in several the angle itself is subacute. Nearly all specimens have a minuscule tubercle or very weak spine on both the basis and ischium of the antennal peduncle, but five lack a tubercle on the ischium and two lack a tubercle on the basis. The width of the lamella of the antennal scale ranges from approximately 1.1 to 2.0 ($\bar{X} = 1.4$) times the width of the thickened lateral margin. The distal margin of the lamella is usually either subtransverse or moderately sloping for much of its width, but in three females it is strongly declivous from the base of the distolateral spine to the mesial margin.

Most individuals have two spines in each caudolateral corner of the cephalic section of the telson, but seven of them have two spines in one corner and three in the other,

and two have two spines in one corner and one in the other. The lateral lobe of the proximal podomere of the uropod normally lacks a spine or tubercle, but 12 specimens have a very small spine or acute tubercle on this lobe. The spine on the mesial lobe of this podomere varies in size from very small to moderate, and is absent in one animal.

The chela of form I males is longer than that of mature form II males and females, averaging 81% of TCL. In form II males the average is 71.6% and in females it is 70.8%. The largest tubercle on the opposable surface of the fixed finger varies from the third to the fifth from the base, but in most specimens the fourth tubercle is much larger than the others. The largest tubercle on the comparable surface of the dactyl varies from the first to the fifth, but in most it is the fourth, and the largest tubercle is almost always offset toward the ventral surface. The dorsal surface of the merus bears from one to eight prominent subdistal tubercles, with the usual number being three or four. Most specimens have from two to four weaker tubercles just proximal to the more prominent ones, and many have squamous to subsquamous tubercles along at least part of the dorsal ridge. The number of tubercles on the ventrolateral ridge of the merus ranges from two to five (usually three), and the distalmost is very small or vestigial. The number of tubercles on the ventromesial ridge ranges from six to eleven (usually nine or ten), and the distalmost is seldom much larger than the largest of the others.

In 17 adult females the width of the annulus ranges from 1.2 to 1.8 (\bar{X} = 1.5) times its length, and the cephalomedian trough varies from moderately wide to nearly obliterated. The thick, C-shaped wall of the annulus, beneath which lies the deepest part of the fossa, is dextral in 22 females, sinistral in eight others.

The floor (dorsal surface) of the rostrum of juveniles and some subadults, while notably excavate, is often less ladlelike than

it is in larger, mature animals. Also in these smaller individuals, the setae on the opposable surface of the fixed finger of the cheliped are far longer and more dense than they are in adults, often filling the space between the fingers and obscuring the tubercles on both.

Size.—The largest specimens collected are two females measuring 50.7 and 50.0 mm TCL (44.4 and 44.5 mm PCL), both from the Haw River subdrainage of the Cape Fear River basin. The next largest specimen is a form I male, which measures 42.5 mm TCL (37.3 mm PCL). The largest form II male measures 33.4 mm TCL (28.7 mm PCL).

Life history notes.—A form I male was collected at the type locality on 14 June 1997, one was taken in Chatham County on 13 February 1998, and one was found in amplexus with a female in Alamance County on 2 March 1976. No females with attached ova or young have yet been seen, but one measuring 32.5 mm TCL, taken on 4 April 1997, had all cement glands highly developed.

Crayfish associates.—Seldom have other crayfishes been found in the same habitats with *C. (C.) davidi*. At a few localities, however, a number of specimens of *Cambarus (Depressicambarus) latimanus* (LeConte, 1856), and of at least one of the species in the complex subsumed under *Cambarus (Puncticambarus) acuminatus* Faxon, 1884, have been found. At two sites, juvenile *C. (D.) reduncus* were collected. While juvenile *Cambarus (Lacunicambarus) digenes* Girard, 1852, have been taken from under cover near the mouth of the stream at the type locality, and chimneyed burrows of this species may be seasonally abundant along the nearby shoreline of Falls Lake, this burrowing species has not been found with *C. (C.) davidi*.

Relationships.—It appears to me that *C. (C.) davidi* has its strongest affinities with *Cambarus (Cambarus) bartonii* (Fabricius, 1798). Students of American crayfishes, however, have long been cognizant of the

taxonomic perplexities presented by the broadly distributed and highly variable populations currently assigned to this species. Two subspecies have been described, *Cambarus (Cambarus) bartonii cavatus* Hay, 1902, and *Cambarus (Cambarus) bartonii carinirostris* Hay, 1914, but opinions anent their validity have for years fluctuated (see Faxon 1914, Ortmann 1931, Hobbs 1972, 1989, Bouchard 1976, Thoma & Jezerinac 1982, Jezerinac 1985, Fitzpatrick 1983, Jezerinac & Thoma 1984, Jezerinac et al. 1995, Cooper 2000). The status of *C. (C.) b. cavatus* remains controversial, but *C. (C.) b. carinirostris* has been elevated to species status (Thoma & Jezerinac 1999). Although it is still difficult at this time to establish precise diagnostic parameters for these taxa throughout their ranges (whatever those ranges might be), current diagnoses must be used in assessing the relationships of *C. (C.) davidi*.

In his brief description of *C. b. cavatus*, whose type locality is the Powell River (Tennessee-Ohio river drainage) near Tazewell, Claiborne County, Tennessee, Hay (1902:435) emphasized its "deeply excavated rostrum," an areola that is "narrower and more thickly punctate than in *C. bartoni bartoni*," and a carapace that is "more nearly cylindrical." Except for the "more thickly punctate" areola, a number of the characters displayed by *C. (C.) davidi* indicate a possible relationship with the progenitors of "topotypic" *C. (C.) b. cavatus*, although their similarities could just as well be a result of convergence. In Ohio and West Virginia, this putative subspecies apparently lacks the deeply excavated rostrum, and displays other characters that differ from those of the "typical" form (Jezerinac 1985, Jezerinac et al. 1995).

The combination of a narrow (but not obliterated), sparsely punctate areola, a ladlelike rostrum, and a vaulted, unflattened carapace will serve to separate *C. (C.) davidi* from all other members of the subgenus except some *C. (C.) b. cavatus*, and some upland southern populations currently as-

signed to *C. (C.) b. bartonii* (s.l.). *Cambarus (C.) davidi* differs from *C. (C.) b. cavatus* and most populations of *C. (C.) b. bartonii* (s.l.) in its obtuse to nearly obsolete suborbital angle, the shape of its antennal scale, and the presence of multiple tubercles on the dorsal surface of the merus of the cheliped. In some montane populations of *C. (C.) b. bartonii* (s.l.) the carapace is relatively vaulted and the rostrum is deeply excavate and somewhat ladlelike. These populations, however, characteristically have areolae that are broader and have more punctations across the narrowest part than does the areola of *C. (C.) davidi*. Also, in nearly all *C. (C.) bartonii* (s.l.) the lamella of the antennal scale is much narrower than it is in *C. (C.) davidi*, and its distal margin is usually quite declivous from the base of the lateral spine to the mesial margin. In addition, *C. (C.) bartonii* (s.l.) seldom displays prominent multiple tubercles on the dorsal surface of the merus.

Roger F. Thoma, whose knowledge of subgenus *Cambarus* is extensive, has suggested that a comparison of *C. (C.) davidi* with the burrower, *Cambarus (Cambarus) ortmanni* Williamson, 1907, would be useful. That species differs from *C. (C.) davidi* in many ways, including the following: Areola of *C. (C.) ortmanni* generally obliterated or nearly so, constituting 41.0 to 44.0% of TCL; suborbital angle obsolete and lacking tubercle; cephalothorax markedly longer than abdomen; subdistal spine on mesial margin of carpus of cheliped thick and knoblike rather than long and acute; cervical region of carapace lacking strong, multiple tubercles; ventrolateral ridge of merus of cheliped usually lacking tubercles; and annulus ventralis and form I male gonopod quite different in configuration.

Remarks.—Current evidence indicates that the range of *C. (C.) davidi*, limited to parts of the eastern Piedmont Plateau in two endemic North Carolina river basins, is disjunct from that of other members of the subgenus. The nearest known North Caro-

lina populations of *C. (C.) bartonii* (s.l.) are in the mountains and eastern foothills. Whether or not *C. (C.) davidi* is indeed allopatric, however, will only be revealed by more extensive field work throughout the Piedmont Plateau. Specimens of subgenus *Cambarus* from seeps and burrows in the Dan River subdrainage of the Roanoke River basin resemble *C. (C.) davidi* in many respects, differ in others. The sample size of available adult specimens is far too small for accurate assignment of the Roanoke material at this time.

Cambarus (C.) davidi has yet to be found in the Tar-Pamlico River basin, whose crayfish fauna is as well known as that of the Neuse and is nearly identical (Cooper & Braswell 1995). Unfortunately, almost no sampling has been done in appropriate habitats within the Tar-Pamlico basin.

Etymology.—I take great pleasure in naming this species for my son, David George Cooper, an avid naturalist who brought the species to my attention and who spent many hours tromping in mud and muck to collect quite a few of the existing specimens.

Suggested vernacular name: Carolina ladle crayfish.

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