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*Cambarus striatus* (Decapoda: Cambaridae)

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# Taxonomy, ecology and phylogeny of the subgenus *Depressicambarus*, with the description of a new species from Florida and redescriptions of *Cambarus graysoni*, *Cambarus latimanus* and *Cambarus striatus* (Decapoda: Cambaridae)

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**ABSTRACT:** Bouchard, Raymond William, Taxonomy, ecology and phylogeny of the subgenus *Depressicambarus*, with the description of a new species from Florida and redescriptions of *Cambarus graysoni*, *Cambarus latimanus* and *Cambarus striatus* (Decapoda: Cambaridae). *Bulletin Alabama Museum of Natural History*, Number 3, 34 pages, 14 figures, 4 tables, 1977. A study of the subgenus *Depressicambarus* is presented to further the understanding of this widely distributed group of crayfishes in the southeastern United States. The definition of the subgenus is emended to include recent information. In addition to diagnoses of the 11 present members of *Depressicambarus*, relationships and phylogeny are discussed, nomenclatorial changes are proposed, one new species is described and three are redescribed. *Cambarus pyronotus*, a new species of primary burrowing crayfish from Torreya State Park in Liberty County, Florida, is described and illustrated. *Cambarus graysoni*, *C. latimanus* and *C. striatus* are redescribed and illustrated. *Cambarus jordani* and *C. floridanus* are synonymized with *C. latimanus* and *C. striatus*, respectively. Color notes, life history notes, and ecological data are presented for the four described species.

## Introduction

With the exception of the monotypic subgenera *Veticambarus* and *Exilicambarus*, the eight other nominal subgenera of *Cambarus* are fraught with taxonomic problems. One of the most imposing groups is *Depressicambarus*, a widespread subgenus of epigeal and burrowing crayfishes ranging from North Carolina to the Florida panhandle and westward to Mississippi and Kentucky. Most of the problems associated with this subgenus are related to the burrowing activities and variability of the taxonomic features of many of its members. Because of the arduous task of collecting burrowers, they are poorly represented in museum collections. In addition, many populations of morphologically similar crayfish (especially burrowers) often exhibit seemingly significant variations from one another, compounding the problem of analysis of morphological characters. This latter problem was noted early by students of crayfishes. As stated by Kingsley (1899): "The discrimination of the species is

not easy . . . difficulties which surround the systematic arrangement of these forms can be seen from the fact that the late William Stimpson, our most accurate student of the Crustacea, would not touch the crayfish, remarking that either we had only one species of *Cambarus* [=Cambarinae and Cambarellinae] in our country, or each mud puddle has its own species."

This study of the subgenus *Depressicambarus*, including several proposed nomenclatorial changes and the description of a new species, should provide a better understanding of this widely distributed group and hopefully will serve as a basis for assessing newly discovered populations belonging to *Depressicambarus*. While this work attempts to define the relationships and morphological limits of the known members of the subgenus, complete analysis is not possible until additional specimens of *Cambarus latimanus* from Alabama, *C. striatus* from Alabama and Mississippi and *C. reduncus* from North Carolina are collected and the descriptions of new species are

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published. This paper includes an emended diagnosis of the subgenus *Depressicambarus*, diagnoses of and a key to the species, mensural data and drawings of variation in the gonopods. Because the original descriptions of *C. latimanus*, *C. graysoni* and *C. striatus* were brief, re-descriptions and drawings of the three species are included, and a new species from Florida is described. All measurements are from adult specimens, with juveniles tending to possess shorter areolae that would increase range values of morphometric data involving this structure. Morphometric data in parentheses refer to single measurements lying outside the clustered range for the species.

Although I originally had no thought of examining the entire subgenus, the broad subject encompassed in this paper was precipitated by a study of the Tennessee fauna. Here members of *Depressicambarus*, exhibiting three different color patterns (see color notes under *Cambarus graysoni* and *C. striatus*), are found together in central Tennessee. One of these color morphs is easily recognizable as a dominant epigeic species of the Nashville Basin (Bouchard, 1974) referred to in the literature as *C. striatus*. After morphological analysis, the remaining two color forms were determined to be color morphs of the same species, closely related to *C. striatus*. The most surprising aspect of this study was the discovery that this latter species is conspecific with the type-specimens of *C. striatus*, and the species identified as *C. striatus* for more than thirty years is actually Faxon's (1914) *C. graysoni*. A consistent character (epistomal zygoma) for separating *C. graysoni* from *C. striatus* was known (see Bouchard, 1973), so additional research leading to this presentation centered around defining the variability within *striatus* and finding characters to separate it from other morphologically similar species.

A brief recounting of the taxonomic histories of *C. latimanus*, *C. striatus* and *C. graysoni* is helpful in revealing factors that may have contributed to our confusion in identifying *C. striatus*. *Cambarus striatus* was described from Nashville, Tennessee, by Hay (1902) as *C. latimanus striatus*. His designation of *striatus* as a subspecies of *latimanus* was in keeping with the taxonomic interpretation in astacology at that time. Populations of crayfishes that did not differ greatly in morphology from certain nominal species were designated as subspecies of that species.

Ortmann (1931) believed *C. striatus* to be "more closely related to *C. bartoni* than to *latimanus*" and in keeping with contemporary taxonomic principles designated *striatus* a subspecies of *bartonii*. He also stated that Faxon's "*graysoni* . . . is very likely the same as *striatus*" [Faxon (1914) had described *C. graysoni* from Grayson County, Kentucky, considering it "related to *C. ortmani*"]. Rhoades (1944), in his study of Kentucky crayfishes, supposedly followed Ortmann in regarding *striatus* as a subspecies of *bartonii*: "*Cambarus bartoni striatus* is represented by several local varieties and races which intergrade into each other to a greater or lesser degree. I have not seen my way clear to create new subspecies and,

furthermore, I have followed Ortmann in uniting *Cambarus graysoni* with *C. b. striatus*. . . ." I do not interpret Ortmann (1931) as definitely uniting *graysoni* with *striatus* (see above). Rhoades (1944) himself is the first to state definitely that *C. graysoni* is a junior synonym of *C. striatus* as follows: "*Cambarus graysoni* is . . . a local variety of *striatus* equivalent to the others listed here." Of special interest is another statement by Rhoades (1944) concerning specimens related to *C. striatus*: "I possess four collections of mostly small individuals of a variety from the lower Green River drainage which is probably a distinct species." Rhoades (1944) noted some differences in this probable new species but "did not describe this form because of the lack of mature specimens." My examination of those specimens, which were deposited in the United States National Museum, shows them to be *C. striatus*.

For later astacologists, another factor obscuring the identity of *C. striatus* was that *C. graysoni* is the most common member of the subgenus *Depressicambarus* collected in epigeic waters near Nashville, Tennessee (the type-locality for *C. striatus*). Since these two species are morphologically very similar, collections of *graysoni* in this area were assumed to represent *C. striatus* but have proven to be inseparable from topotypic *C. graysoni*.

When close relatives of *C. striatus* were examined in the course of this study, no mensural or meristic character could be found to distinguish *C. floridanus* populations from *C. striatus*. The red color attributed to *C. floridanus* (Hobbs and Hart, 1959; Hobbs, 1969) also proved to be an inadequate character. The color pattern of live topotypic material (kindly supplied by Horton H. Hobbs, Jr.) is not drastically different from *C. striatus* (see color notes for *C. striatus*). Therefore, without a difference between *C. floridanus* and *C. striatus*, the former is here regarded as a synonym of *C. striatus*. The bright orange-red colored populations of *C. floridanus* in Torreya State Park, Liberty County, Florida (Hobbs, 1942; Hobbs and Hart, 1959), are distinct enough to be considered a separate species which is described herein.

A morphologically close ally of *C. striatus* is *C. latimanus*. They are both considered valid species, although certain individuals cannot be clearly assigned to either species (see relationships). The crayfishes are distinct and easily separable in syntopic populations where *C. striatus* generally prefers a burrowing habitat and exhibits a larger branchial chamber reflected in its longer and narrower areola. *Cambarus latimanus* dominates the open stream and displays a comparatively shorter and wider areola. The most consistent character to separate all populations of *C. striatus* from *C. latimanus* appears to be the ratio of areola length to width, although the range of measurements from occasional individuals and certain populations of each overlaps.

An examination of *C. latimanus* material revealed considerable variation in a number of characters but most importantly in spination. Among populations of *C. latimanus*, the range of variation in the development of spines on the rostrum and cephalothorax, a character

thought to be highly variable in many members of the genus *Cambarus* (Bouchard, 1976b), suggests that *C. jordani* is a form of *C. latimanus*. In those populations of *C. latimanus* in which the juveniles possess rostral spines, (Fig. 2b) these spines usually become reduced with maturity. An adult population may possess rostral margins that blend indiscernably with the acumen, margins that are well inflated above the acumen, or margins with tubercles representing remnants of the juvenile spines (Fig. 2a).

The description of *C. jordani* (Faxon, 1884) from the Etowah River near Rome, Floyd County, Georgia, was based upon a single juvenile male which had well-developed rostral spines (cf. Faxon, 1885: plate 3, figure 3). Specimens assignable to *C. jordani* from localities near the type-locality do not differ from *C. latimanus*. The only distinctive character in *C. jordani*, spines or tubercles on the rostrum, is not uncommon in members of *C. latimanus*. The variation in rostral spination among populations of *C. latimanus* encompasses populations considered to be *C. jordani*, and the latter should, therefore, be considered a synonym of *C. latimanus*.

#### Acknowledgements

I should like to extend a special appreciation to Dr. Horton H. Hobbs, Jr., Smithsonian Institution, who discussed many aspects of this study with me, reviewed the manuscript, graciously recommended that I describe the new species herein and very importantly collected live topotypic material of *Cambarus floridanus* for me. To my wife Judith I am, as always, indebted for her assistance in the field, review of the manuscript, and rendering of the numerous drawings that contribute greatly to this paper. To Drs. Joseph F. Fitzpatrick, Jr., (University of South Alabama) and Joe B. Black (McNeese State University), who made their Mississippi collections of *Depressicambarus* available to me and to the former who kindly reviewed the manuscript, I owe thanks. I wish to also acknowledge Dr. Herbert W. Levi, Museum of Comparative Zoology, Harvard University, for loan of type-specimens of *C. graysoni*. I am grateful to the Smithsonian Institution for awarding me a Smithsonian Postdoctoral Fellowship that permitted me to examine the large holdings at the Smithsonian Institution thus making this study possible. In addition, a research grant,

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#### Diagnosis of the Subgenus *Depressicambarus*

*Cambarus (Depressicambarus)* Hobbs, 1969:102. Type-species: *Astacus latimanus* Le Conte, 1856:402. Eyes variable in size and pigmented. Rostrum with or without tubercles or small spines (spination most evident on juveniles), margins variable in thickness. Areola width variable, obliterated to 2.9 times longer than broad and constituting 29.8 to 45.7 percent of total length of carapace (38.2 - 50.7 percent of postorbital carapace length); bearing as many as 7 shallow punctations across narrowest part. Postorbital and cervical spines rare except in *C. englishi*, *C. halli*, *C. obstipus* and some populations of *C. latimanus*. Suborbital angle obsolete to moderately well developed except in *C. cymatilis*, *C. graysoni* and some populations of *C. halli* in which well developed. Branchiostegal spines present. Chela broadly subtriangular, strongly depressed (less so in *C. halli*, *C. englishi* and some populations of *C. sphenoides*) with mesial margin of palm comparatively short and bearing two major rows of tubercles, small squamous tubercles and/or punctations studding dorsal surface; lateral margin of fixed finger strongly costate and punctate; fingers never widely gaping but with well-defined longitudinal ridges dorsally, proximal opposable margin of dactyl never deeply concave; conspicuous tuft of setae never present at mesial base of fixed finger, lateral base flattened. First form male with first pleopods almost contiguous at base and with distal portion of shaft almost straight, never inclined caudad; terminal elements consisting of (i) blade-like, broad or tapering central projection recurved at angle of approximately 90 to 155 degrees to main shaft, subapical notch present or absent, (ii) mesial process tumescent, caudally directed, and sometimes exceeding tip of central projection caudally, contracted apical portion sometimes with two or more projections, (iii) caudal knob typically vestigial or absent (well developed in some populations of *C. striatus*, rarely so in *C. latimanus*) (See Fig. 12a, d, j). Hook on ischium of third pereopod simple, overreaching basioischial articulation and generally not opposed by tubercle on basis.

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Key to the Species of the Subgenus *Depressicambarus*

1. Propodus of chela with opposable margin bearing conspicuous gap between second and third tubercles from base (Fig. 1j).....*cymatilis*  
Propodus of chela with opposable margin lacking conspicuous gap between second and third tubercles from base (Fig. 4i).....2
2. Epigtomal zygoma gently bent (Fig. 2c).....*graysoni*  
Epigtomal zygoma moderately well to strongly arched (Fig. 2d-f).....LL3
3. First pleopod of first form male aciculate (Fig. 3h).....*reduncus*  
First pleopod of first form male not aciculate (Fig. 3c).....4
4. Abdominal pleura with moderately sharp caudoventral angles (Fig. 1b).....*englishi*  
Abdominal pleura with broad caudoventral angles (Fig. 1a).....5
5. Antennal scale moderately narrow with steeply declivous mesial margin (Fig. 1c).....*catagius*  
Antennal scale moderately broad to broad with declivous to angulate mesial margin (Fig. 1e).....6
6. Dactyl of chela with opposable margin bearing 8 or 9 fairly evenly sized tubercles (Fig. 1i).....*obstipus*  
Dactyl of chela with opposable margin bearing 4 or 5 dominant basal tubercles, first, fourth or fifth; first and fourth or first and fifth largest (Fig. 4i).....7
7. Areola densely punctate (Fig. 1f).....*halli*  
Areola moderately to sparsely punctate or obliterated (Fig. 1g).....8
8. Suborbital angle obsolete (Fig. 9b); proximolateral portion of telson with caudolateral corners bearing single immovable spine (rarely movable spine also present).....*pyronotus*  
Suborbital angle poorly to moderately well developed (Fig. 10b); proximolateral portion of telson with caudolateral corners bearing single movable and immovable spines.....9
9. Epigtomal zygoma strongly arched (cf. Fig. 2f); fingers of chela with opposable margins bearing double or triple row of denticles (cf. Fig. 1k, l).....*sphenoides*  
Epigtomal zygoma moderately well arched (Fig. 2d, e); fingers of chela with opposable margins bearing double row of denticles only (Fig. 1l).....10
10. Areola narrow, length 10 or more times greater than width, or obliterated (occasional individuals from above the Fall Line, especially the Tallapoosa River system, range as low as 9.1 times) (Figs. 10i, 11i).....*striatus*  
Areola broader, length less than ten times greater than width (populations from below the Fall Line in Georgia and Alabama, and upper Savannah and Santee River systems, South Carolina, with proportions up to 11.8 and 12.3 times, respectively) (Fig. 5l).....*latimanus*

***Cambarus (Depressicambarus) catagius***  
**Hobbs and Perkins, 1967**

DIAGNOSIS.—Rostrum excavate dorsally with slightly concave, subparallel margins devoid of marginal spines or tubercles. Areola narrow and long, 14.4 to 32.0 times longer than broad, comprising 37.0 to 40.1 percent of total length of carapace [(43.6) 44.4 - 47.3 percent of post-orbital carapace length], with no punctations or as many as 2 across narrowest part. Carapace vaulted; cervical spines reduced to small, rounded tubercles. Suborbital angle weakly developed and rounded. Antennal scale moderately narrow; margin of lamellar portion steeply declivous (Fig. 1c). Cephalic portion of epistome of medium width; epigtomal zygoma moderately well arched (cf. Fig. 2d, e). Chela with opposable margin of dactyl bearing 4 dominant tubercles, first or fourth largest (fourth primarily), sometimes subequal in size; opposable margin of propodus with 3 dominant tubercles increasing in size distally, third largest; opposable margins of both fingers with double row of denticles (cf. Fig. 1l). First pleopod of first form male with central projection lacking subapical notch or bearing very shallow one and recurved at angle of approximately 115 to 120 degrees. Annulus ventralis situated deep in sternum, suboval in outline; caudal wall conspicuously thickened and elevated above cephalic portion, latter bearing shallow sinus flanked by low ridges.

RANGE.—*Cambarus catagius* is known from only Greensboro, Guilford County, North Carolina. Greensboro is in the Piedmont province and the Cape Fear River basin.

***Cambarus (Depressicambarus) cymatilis***  
**Hobbs, 1970**

DIAGNOSIS.—Rostrum excavate dorsally with slightly concave, subparallel margins devoid of spines or tubercles. Areola long, comprising 41.7 to 44.8 percent of total length of carapace (48.1 - 50.4 percent of postorbital carapace length) and obliterated to narrow with space for no more than 1 punctation in narrowest part. Carapace vaulted; cervical spines reduced to small rounded tubercles. Suborbital angle well developed and acute. Antennal scale narrow; margin of lamellar portion steeply declivous. Cephalic portion of epistome narrow; epigtomal zygoma moderately well arched. Chela with opposable margin of dactyl bearing 2 dominant tubercles, distal one larger; corresponding margin of propodus with 3 dominant tubercles, proximal 2 increasing in size distally followed by large gap between second and third (Fig. 1j); opposable margins of both with single row of evenly spaced denticles (Fig. 1m). Central projection of first pleopod of first form male short, with well-defined subapical notch and recurved at angle of approximately 95 to 105 degrees. Annulus ventralis situated deep in sternum, suboval in outline; caudal wall conspicuously thick-

ened and elevated above cephalic portion, latter bearing shallow sinus flanked by low ridges.

**RANGE.**—This primary burrowing crayfish has been collected from the Coosa River basin in the Ridge and Valley province. Within this drainage *C. cymatilis* is known from Murray County, Georgia, and Bradley County, Tennessee.

***Cambarus (Depressicambarus) englishi*  
Hobbs and Hall, 1972**

**DIAGNOSIS.**—Rostrum of adults lacking or possessing tubercles, but if absent, base of acumen generally delimited by conspicuous angles; that of juveniles with spines or tubercles decreasing in size with maturity; margins concave and subparallel; surface excavate. Areola moderately long, 33.2 to 38.0 percent of total length of carapace (41.3 - 46.7 percent of postorbital carapace length); 3.4 to 4.9 times longer than broad (as low as 3.3 in some juveniles) and bearing 4 to 6 punctations across narrowest part. Carapace depressed; cervical spines small and acute. Suborbital angle weakly to moderately well developed and rounded to obsolete. Antennal scale somewhat broad; margin of lamellar portion angulate (*cf.* Fig. 5*h*) to declivous. Cephalic portion of epistome of medium width; epistomal zygoma moderately well arched. Chela with opposable margin of dactyl bearing 4 or 5 dominant tubercles, first and fourth or first and fifth largest; corresponding margin of propodus with 3 or 4 dominant tubercles, third or fourth largest; opposable margins of both with single or double row of crowded denticles. Central projection of first pleopod of first form male tapering, lacking subapical notch and recurved at angle of approximately 105 to 115 degrees; element long. Annulus ventralis situated moderately deep in sternum, subquadrangular in outline; caudal wall elevated; cephalic portion bearing shallow sinus flanked by low ridges. Cephalic portion of annulus ventralis sometimes equal in height to caudal wall.

**RANGE.**—*Cambarus englishi* occurs in that portion of the Tallapoosa River system which drains the Piedmont province in Georgia and Alabama. This crayfish has been collected from Haralson County, Georgia, and Clay, Cleburne and Tallapoosa counties, Alabama.

***Cambarus (Depressicambarus) graysoni*  
Faxon, 1914**

**DIAGNOSIS.**—Body and eyes with pigment. Rostrum usually without tubercles. Areola 9.0 to 15.1 times longer than broad and constituting 37.1 to 41.1 (43.9) percent of total length of carapace [(43.2) 44.2 - 49.2 percent of postorbital carapace length] with 2 to 4 punctations across narrowest part. Cervical spines reduced to small, rounded tubercles or absent; hepatic spines absent; branchiostegal spines present; suborbital angle well developed, acute, sometimes terminating in small spine or tubercle; postorbital ridge moderately strong, rounded cephalically. Antennal scale moderately broad to wide;

margin of lamellar portion angulate. Cephalic portion of epistome comparatively wide; epistomal zygoma with anterior margin gently bent. Chela with 2 rows of 8 or less tubercles on mesial surface of palm; opposable margin of dactyl with proximal 4 tubercles prominent—first, fourth or first and fourth largest; corresponding margin of propodus with proximal 3 or 4 tubercles dominant in size, third or fourth largest; opposable margins of both with irregular double to quadruple row of denticles, increasing to triple and quadruple row with age; lateral margin costate and lateral base of fixed finger impressed above, less so below. Hook on ischium of third pereopod of male overreaching basioischial articulation and not opposed by tubercle on basis. First pleopod of first form male with central projection corneous, bladeliike, lacking subapical notch, recurved at angle of approximately 115 to 140 degrees; mesial process tumescent, tapering to subacute tip, and directed caudally at angle of approximately 90 degrees to shaft of appendage. First pleopod of second form male noncorneous; central projection rounded distally; mesial process tapering to subacute tip. Annulus ventralis asymmetrical, subquadrangular, with caudal portion somewhat movable; cephalic half bearing longitudinal median trough between subparallel ridges, and caudal half with sinuate sinus and elevated caudal wall. First pleopod of female uniramous and reaching beyond midlength of annulus when abdomen flexed.

The following description of *C. graysoni* is based upon topotypes collected from Bear Creek, Grayson Springs, Grayson County, Kentucky. After comparing a second form male and a female from the syntypic series (3 males, form II; 1 female) with topotypes, I concluded that, without a doubt, they represent the same species.

**TOPOTYPIC MALE, FORM I (USNM 144571).**—Body subovate, slightly depressed (Fig. 4*b*). Abdomen narrower than thorax (15.3 and 18.0 mm). Greatest width of carapace greater than depth at caudodorsal margin of cervical groove (18.0 and 12.6 mm). Areola 10.6 times longer than broad with 2 punctations across narrowest part; length of areola 38.5 percent of total length of carapace (44.2 percent of postorbital carapace length). Rostrum excavate dorsally with subparallel, thickened margins devoid of marginal spines or tubercles. Acumen set off from basal portion of rostrum with concave, oblique margins, not swollen; small upturned tubercle at tip broken; upper surface with submarginal punctations and others scattered between. Postorbital ridges moderately strong, shallowly grooved dorsolaterally and rounded cephalically. Suborbital angle strong; branchiostegal spine small. Cervical spines or tubercles absent; hepatic area and lateral portion of branchiostegite tuberculate; dorsal portion of carapace punctate.

Abdomen longer than carapace (36.1 and 33.0 mm); pleura of moderate length with caudoventral extremity broadly angular. Cephalic section of telson with single movable and immovable spines in each caudolateral corner; separated from caudal section by paired oblique excisions. Basal podomere of uropod with spines extending over mesial and lateral rami. Lateral ramus of uropod

with median ridge terminating in acute spine at transverse flexure; additional small ridge lateral to median one; proximal portion with row of small spines distally and movable spine submarginally at caudolateral corner. Mesial ramus of uropod with median ridge terminating distally in premarginal acute spine. Caudal margin of tail fan with plumose setae; dorsal surface lightly setiferous.

Cephalic lobe of epistome (Fig. 4k) pentagonal with slightly upturned cephalolateral margins and with small cephalomedian projection; ventral surface convex. Basal portion of epistome with deep median fovea and pair of obliquely disposed slitlike fossae immediately cephalic and subparallel to thickened, gently bent anterior margin of epistomal zygoma; lateral extremities lacking tubercles. Proximal segment of antennule with small spine on ventral surface at base of distal third. Antennae broken. Antennal scale (Fig. 4d) moderately broad, broadest slightly distal to midlength; thickened lateral portion terminating in acute, corneous-tipped spine projecting forward beyond tip of rostrum; lamellar area with mesial margin broadly angulate, crenulate and edged with long, plumose setae.

Left chela (Fig. 4i) approximately 2 times longer than broad (23.2 and 11.4 mm), depressed, although more inflated proximolaterally; mesial margin of palm with 2 rows of 6 tubercles each in primary and secondary rows, and several smaller tubercles on dorsal surface over mesial half of palm; distoventral surface of palm with 2 large, swollen tubercles at base of dactyl, mesial one with very small, rounded, corneous tip. Lateral surface of propodus costate with row of punctations rendering proximolateral margin of fixed finger irregular in dorsal aspect. Fixed finger with proximolateral base impressed dorsally, less so ventrally; dorsal and ventral surfaces with distinct submedian ridges flanked by setiferous punctations; opposable surface with row of 5 tubercles along proximal three-fifths of finger, fourth largest, decreasing in size proximally; additional small tubercle present on lower level at base of distal two-fifths, and double row of minute denticles extending proximally from corneous tip of finger to fourth tubercle from base, interrupted by fifth. Dorsal and ventral surfaces of dactyl with median longitudinal ridges, flanked by setiferous punctations; opposable margin with row of 6 tubercles, first largest; mesial margin of dactyl tuberculate along nearly proximal two-thirds and punctate distally; row of minute denticles extending from corneous tip to third tubercle, interrupted by fourth.

Carpus longer than broad with deep oblique furrow dorsally; mesial surface with large procurved spine near midlength and with smaller one located caudally and one ventrally; distoventral margin with strong spiniform tubercle; dorsomesial surface with 3 small, rounded tubercles; podomere otherwise punctate.

Dorsodistal surface of merus with 3 rounded tubercles; ventral surface with lateral row of 4 tubercles, some corneous-tipped, and mesial row of 9 corneous-tipped, acute

tubercles; both rows decreasing in size proximally. Ischium with row of 4 small tubercles on mesial margin.

Hook on ischium of third pereopod only (Fig. 4h); hook simple, overreaching basioischial articulation and not opposed by tubercle on basis. Coxa of fourth pereopod with prominent caudomesial boss; fifth pereopod without prominence. For measurements see Table 1.

Table 1. Measurements (mm) of *Cambarus (Depressicambarus) graysoni*

	Topotypic Male, Form I	Topotypic Female	Topotypic Male, Form II
Carapace			
Height	12.6	15.8	11.3
Width	18.0	24.6	17.2
Total length of carapace	33.0	44.4	31.9
Postorbital carapace length	28.7	38.5	27.3
Areola			
Width	1.2	1.5	1.1
Length	12.7	17.4	12.1
Rostrum			
Width	4.5	5.9	4.4
Length	4.3	5.9	4.6
Chela			
Length, mesial margin of palm	7.0	8.8	5.7
Width, palm	11.4	14.7	19.7
Length, lateral margin	23.2	30.1	19.7
Length, dactyl	14.7	19.0	12.2

First pleopods (Fig. 4e, f, g) reaching caudal portion of coxae of third pereopods when abdomen flexed. See "Diagnosis" for description.

TOPOTYPIC FEMALE (USNM 144571).—Differing from topotypic male, form I, in following respects: tip of acumen terminating in small, rounded, corneous tubercle. Primary row of tubercles on mesial margin of palm consisting of 7 tubercles, secondary row of 5. Carpus with 2 tubercles caudal to large procurved spine on mesial surface; dorsomesial surface with 5 and 4 small, rounded tubercles on right and left, respectively. Ventral surface of merus of right cheliped with 5 tubercles on lateral margin and 11 on mesial margin of left. Ischia of chelipeds with row of 3 tubercles on each. Opposable margin of right propodus with 7 tubercles. Opposable margin of dactyl with 5 tubercles on both left and right chelipeds; row of minute denticles extending from corneous tip to second tubercle, interrupted by third and fourth tubercles from base. Cervical spines consisting of small, rounded tubercle with setal tuft.

Annulus ventralis (Fig. 4j) subquadrangular, broader than long and situated moderately deep in sternum with cephalic portion fused to sternum and caudal half movable. Annulus ventralis divided by sinus into C-shaped and triangular portions, latter with basal tongue projecting into concavity of "C." Cephalic half with sinus broadening into median longitudinal trough flanked by subparallel, longitudinal ridges; caudal portion elevated and nearly bisected by shallow sinus. Postannular sclerite subconical and approximately two-thirds width of annulus.

**TOPOTYPIC MALE, FORM II (USNM 147861).**—Differing from topotypic male, form I, in following respects: tip of acumen terminating in small, upturned, corneous tubercle. Areola with 3 punctations across narrowest part. Opposable margin of propodus with 7 tubercles on both right and left chelae. Opposable margin of dactyl with 5 tubercles on each chela. Carpus with 2 tubercles proximal to large procurved spine on mesial surface of left cheliped and 6 small, rounded tubercles on dorso-mesial surface of both left and right. Upper surface of merus with 2 spines on each cheliped; ventral margin with 11 and 10 tubercles in mesial row of right and left chelipeds, respectively. Suborbital angle terminating in small spine. Cervical spines reduced to small, rounded tubercle with setal tuft.

Hook on ischium of third pereopod much reduced, not reaching basioischial articulation, and not opposing tubercle on basis; boss on coxa of fourth pereopod somewhat smaller and less sharply defined. First pleopod of uniform texture and reaching caudal portion of coxa of third pereopod when abdomen flexed. See "Diagnosis" for description.

**COLOR NOTES.**—Cephalothorax and abdomen mottled or concolorous brown, green-brown to green. Abdomen with or without pair of submedian and paired lateral, narrow, broken, dark brown stripes extending onto dorsolateral part of thorax as very small sinistral and dextral horns. Occasional individuals with blue or red color patterns. Young crayfish well mottled, color pattern becoming concolorous with maturity and abdominal stripes less discernible. Gastric region with paired, lighter, vermiculated areas marking attachment of mandibular muscles. Branchiostegites and hepatic areas mottled to concolorous brown, green-brown to green dorsally, fading to white ventrad. Pleural regions of abdomen with distinct ventral, broad, mottled, cream to yellow colored margin, often most evident on first abdominal segment as cream through yellow colored spot on each side; spots especially striking in populations from Green River system in Kentucky and Tennessee. Ventral aspects of cephalothorax and abdomen white, occasionally tinged with blue.

Rostral margins yellow, tan or brown. Postorbital ridges light brown or same color as cephalothorax. Tubercles, spines and articular condyles yellow through cream. Lateral margin of antennal scale darker than lamellar portion. Antennae generally dark green or brown.

Chelae brown, green-brown, green to green-blue dorsally with lighter proximolateral area; white ventrally. Distal ends of fingers red, orange, yellow or cream, fading with age or if living in turbid waters. Pereiopods same general color as cephalothorax but lighter dorso-laterally; white ventrolaterally. Distal podomeres darker dorsally than proximal ones.

**TYPE-LOCALITY.**—Bear Creek (Green River System), at Grayson Springs, Grayson County, Kentucky (Faxon, 1914). On 11 May 1973 a collection from the type-locality revealed the following crayfish associates: *Cambarus (Erebicambarus) tenebrosus* and *Orconectes putnami*.

**DISPOSITION OF TYPES.**—The syntypes, consisting of 1♂II and 3♀ were collected by F. W. Putnam on 24 October 1874 and deposited in the Museum of Comparative Zoology, Harvard College, (MCZ 3593). Two series of topotypes consisting of 2♂I, 5♂II, 10♀, 19 juv.♂ and 12 juv.♀ are in the National Museum of Natural History, Smithsonian Institution.

**RANGE.**—This crayfish is a common inhabitant of streams primarily draining limestone deposits of the Highland Rim and Nashville Basin sections (Bouchard, 1974) and occurs at the western edge of the Cumberland Plateau (Bouchard, 1976b) in Kentucky, Tennessee and Alabama. In valleys at the western edge of the Cumberland Plateau, *C. graysoni* has primarily penetrated streams draining Mississippian limestone deposits. The streams here have notched headward into the predominantly Pennsylvanian sandstone cap exposing the underlying Mississippian limestones.

**VARIATIONS.**—The most significant variations exhibited by *C. graysoni* are in the gonopod of the first form male and on the rostrum. The central projection of the first form male gonopod varies in its length relative to the cephalocaudal diameter of the shaft of the appendage (see Fig. 3d, e), being generally longer in populations south of the Green River system. In most populations of *C. graysoni*, the rostrum is unadorned, although it is not uncommon for very small juveniles to exhibit small spines on the cephalic ends of the margins. These spines are usually lost with maturity, but in some populations remnants are retained in the form of tubercles. These rostral tubercles are especially noticeable in populations from the Caney Fork (Cumberland) River system, Tennessee.

**SIZE.**—The largest specimen available is a female from Smith County, Tennessee, with a carapace length of 68.6 mm (postorbital carapace length 59.7 mm).

#### *Cambarus (Depressicambarus) halli* Hobbs, 1968

**DIAGNOSIS.**—Rostrum with or without tubercles on adults, but if absent, base of acumen delimited by conspicuous angles; juveniles with spines or tubercles decreasing in size with maturity; margins nearly straight and slightly converging, excavate dorsally. Areola short, 28.9 to 35.1 percent of total length of carapace [39.3 - 42.5 (43.3) percent of postorbital carapace length], and 2.9 to 4.5 times longer than broad, moderately to densely punctate, with space for 5 to 7 punctations across narrowest part. Carapace subovate; cervical spines small and acute. Suborbital angle moderately to well developed and obtuse to rounded. Antennal scale of medium breadth and lamellar portion with declivous margin (Fig. 1e). Cephalic portion of epistome of medium width; epistomal zygoma moderately well arched. Opposable margin of dactyl of chela with proximal 4 or 5 tubercles prominent—first, fourth or fifth or first and fourth or first and fifth largest; corresponding margin of propodus with proximal 3 or 4 tubercles dominant in size, third or

fourth largest; opposable margins of both with single or double row of crowded denticles. Central projection of first pleopod of first form male moderately long, bearing subapical notch and recurved at angle of approximately 120 to 130 degrees. Annulus ventralis situated moderately deep in sternum; subquadrangular in outline; caudal wall elevated; cephalic portion bearing shallow sinus flanked by low ridges.

RANGE.—*Cambarus halli* is known from only that portion of the Tallapoosa River system draining the Piedmont province in Alabama and Georgia. This crayfish has been collected from Carroll and Haralson counties, Georgia, and Chambers, Clay, Cleburne, Lee, Randolph and Tallapoosa counties, Alabama.

***Cambarus (Depressicambarus) latimanus***  
(LeConte, 1856)

*Cambarus jordani*, 1884:119.

DIAGNOSIS.—Body and eyes with pigment. Rostrum with or without tubercles in adults; juveniles often with spines or tubercles, decreasing in size with maturity; sometimes low carina; margins subparallel to acuminate. Areola variable, 3.4 to 12.3 times longer than broad and constituting 29.8 to 38.9 percent of total length of carapace (38.2-45.8 percent of postorbital carapace length) with 2 to 5 punctations across narrowest part. Cervical spines variable, prominent or reduced to small, rounded tubercles or absent; hepatic spines absent; branchiostegal spine present; suborbital angle moderately well developed and rounded to acute, sometimes with small spine or tubercle; postorbital ridge somewhat strong, rounded cephalically or terminating in acute spine or tubercle. Antennal scale moderately broad to wide; margin of lamellar portion angulate. Cephalic portion of epistome comparatively wide; epistomal zygoma moderately well arched. Chela with 2 rows of 8 or fewer tubercles on mesial surface of palm; opposable margin of dactyl with proximal 4 or 5 tubercles prominent—first, fourth or fifth or first and fourth or first and fifth largest; corresponding margin of propodus with proximal 3 or 4 (rarely 5) tubercles dominant in size, third, fourth or fifth largest; opposable margins of both with irregular double row of denticles; lateral margin costate and lateral base of fixed finger impressed above, less so below. Hook on ischium of third pereopod of male overreaching basioischial articulation and not opposed by tubercle on basis. Central projection of first pleopod of first form male corneous, bladelike, with or without subapical notch, recurved at angle of 100 to 145 degrees; mesial process tumescent, tapering to subacute tip, and directed caudolaterally at angle of approximately 90 degrees to shaft of appendage (Fig. 5e, f, g). First pleopod of second form male noncorneous; central projection rounded distally; mesial process tapering to subacute tip. Annulus ventralis asymmetrical, subquadrangular, with caudal portion somewhat movable; cephalic half bearing longitudinal median trough between prominent or reduced subparallel longitudinal ridges, and caudal half with

sinuate sinus and elevated caudal wall. First pleopod of female uniramous and reaching at least to midlength of annulus when abdomen flexed.

According to Hobbs (1974), there are only two individuals of *C. latimanus* that can be considered type-specimens. These are a dry second form male at the Museum of Comparative Zoology, Harvard University, and a dry female (Faxon, 1914) at the Academy of Natural Sciences of Philadelphia. Taking thorough, descriptive notes and figures from such specimens would not be possible and would probably damage them. Therefore, the following descriptions are based upon topotypes collected in Athens, Clarke County, Georgia.

TOPOTYPIC MALE, FORM I (USNM 146435).—Body subovate, slightly depressed (Fig. 5b). Abdomen narrower than thorax (14.8 and 17.1 mm). Greatest width of carapace greater than depth at caudodorsal margin of cervical groove (17.1 and 12.6 mm). Areola 5.8 times longer than broad with 2 punctations across narrowest part; length of areola 35.4 percent of entire length of carapace (42.8 percent of postorbital carapace length). Rostrum excavate dorsally with subparallel, thickened margins devoid of marginal spines or tubercles and elevated well above acetabulum; upper surface with submarginal punctations and others scattered between. Acetabulum set off from proximal portion of rostrum with concave, oblique margins, not swollen, and terminating in corneous, acute, upturned tubercle. Postorbital ridges moderately strong, with a somewhat deep groove dorsolaterally and rounded cephalically. Suborbital angle acute; branchiostegal spine large. Cervical spines reduced to single small, rounded tubercle on each side; hepatic area and lateral portion of branchiostegite tuberculate; dorsal surface of carapace punctate.

Abdomen longer than carapace (33.5 and 31.1 mm); pleura of moderate length with caudoventral extremity broadly angular. Cephalic section of telson with single movable and immovable spines in each caudolateral corner, separated from caudal section by paired oblique excisions. Basal podomere of uropod with spines extending over mesial and lateral rami. Lateral ramus of uropod with median ridge terminating in acute spine at transverse flexure; additional small ridge lateral to median one; proximal portion with row of small spines distally and movable spine (missing on right side) located submarginally at caudolateral corner. Mesial ramus of uropod with median ridge terminating distally in pre-marginal acute spine; lateral margin terminating in acute spine. Caudal margin of tail fan with plumose setae; dorsal surface lightly setiferous.

Cephalic lobe of epistome (Fig. 5k) pentagonal with slightly upturned cephalolateral margins and with small cephalomedian projection; ventral surface convex. Basal portion of epistome with deep median fovea and pair of obliquely disposed slitlike fossae immediately cephalic and subparallel to thickened, moderately well-arched epistomal zygoma; lateral extremities without tubercles. Proximal segment of antennule with small acute spine on ventral surface at base of distal third. Antennae bro-

ken. Antennal scale (Fig. 5h) moderately broad, broadest slightly distal to midlength; thickened lateral portion terminating in acute, corneous-tipped spine projecting forward beyond tip of rostrum; lamellar area with broadly angulate mesial margin, crenulate and edged with long, plumose setae.

Left chela (Fig. 5i) approximately 2 times longer than broad (22.1 and 11.4 mm), depressed, although more inflated proximolaterally; mesial margin of palm with 2 rows of 6 tubercles each in primary and secondary rows, and squamous tubercles over dorsal surface of palm; distoventral surface of palm with 2 large, swollen tubercles at base of dactyl, with small, rounded, corneous, acute tip. Lateral surface of propodus costate with row of punctations rendering proximolateral margin of fixed finger irregular in dorsal aspect. Fixed finger with proximolateral base impressed dorsally, less so ventrally; dorsal and ventral surfaces with distinct submedian ridges flanked by setiferous punctations; opposable surface with row of 6 tubercles along proximal three-fifths of finger, fourth largest, decreasing in size proximally; additional small tubercle on lower level at base of distal third broken; double row of minute denticles extending proximally from corneous tip of finger to fifth tubercle, interrupted by sixth from base. Dorsal and ventral surfaces of dactyl with median longitudinal ridges, flanked by setiferous punctations; opposable margin with row of 8 tubercles, first and fourth largest; mesial margin of dactyl tuberculate along nearly proximal three-fifths and punctate distally; double row of minute denticles extending from corneous tip to fourth tubercle from base, broken by fifth and sixth.

Carpus longer than broad with deep oblique furrow dorsally; mesial surface with large procurved spine near midlength and small ones located proximally, proximolateral and ventral to large spine; distoventral margin with strong subspiniform tubercle and additional smaller one proximodorsally; dorsomesial surface with 10 rounded tubercles; podomere otherwise punctate.

Dorsodistal surface of merus with 2 subacute tubercles; ventral surface with lateral row of 5 tubercles decreasing in size proximally, some corneous-tipped, and mesial row of 11 corneous-tipped, acute tubercles. Ischium with row of 4 small tubercles on mesial margin.

Hook on ischium of third pereopod only (Fig. 5d); hook simple, overreaching basioischial articulation and not opposed by tubercle on basis. Coxa of fourth pereopod with prominent caudomesial boss, fifth pereopod without prominence. For measurements see Table 2.

First pleopods (Fig. 5e, f, g) reaching caudal portion of coxae of third pereopods when abdomen flexed. See "Diagnosis" for description.

**TOPOTYPIC FEMALE (USNM 116986).**—Differing from topotypic male, form I, in following respects: margins of rostrum less swollen. Areola with 3 punctations across narrowest part. Cervical spines consisting of slightly larger rounded tubercles. First chelipeds missing.

Annulus ventralis (Fig. 5j) subquadrangular, broader than long and situated moderately deep in sternum with

Table 2. Measurements (mm) of *Cambarus (Depressicambarus) latimanus*

	Topotypic Male, Form I	Topotypic Female	Topotypic Male, Form II
Carapace			
Height	12.6	12.5	11.2
Width	17.1	17.0	15.6
Total length of carapace	31.1	31.7	30.2
Postorbital carapace length	25.7	26.8	25.0
Areola			
Width	1.9	2.2	1.7
Length	11.0	11.5	10.6
Rostrum			
Width	3.5	3.8	3.5
Length	5.4	4.9	5.2
Chela			
Length, mesial margin of palm	6.7	*	6.5
Width, palm	11.4	*	10.7
Length, lateral margin	22.1	*	21.9
Length, dactyl	13.7	*	13.6
* no chelae			

cephalic portion fused to sternum and caudal half movable. Annulus ventralis divided by sinus into C-shaped and triangular portions, latter with basal tongue projecting into concavity of "C." Cephalic half with sinus broadening into median longitudinal trough flanked by subparallel, longitudinal ridges; caudal portion elevated and nearly bisected by shallow sinus. Postannular sclerite subconical and approximately half width of annulus.

**TOPOTYPIC MALE, FORM II (USNM 118442).**—Differing from topotypic male, form I, in following respects: margins of rostrum less swollen. Areola with 3 punctations across narrowest part. Cephalic portion of epistome with anterior edges rounded. Chelae with 5 and 4 tubercles in secondary row on mesial surface of palm of right and left ones, respectively. Propodus of each cheliped with 9 tubercles along opposable margin and additional smaller one on lower level, third largest on right propodus; row of denticles extending from corneous tip to third tubercle from base on right (fourth on left), interrupted by fourth tubercle (fifth on left). Opposable margin of dactyl of each chela with 9 tubercles; denticles extending from corneous tip to third tubercle from base on right dactyl, interrupted by fourth and fifth tubercles (fifth on left). Carpus with 2 tubercles located proximad to large procurved spine on mesial surface, lacking distoventral tubercle on left carpus and ventrally disposed one on right; ventral margin with 2 tubercles situated proximodorsad to large one on distoventral margin. Merus with 3 tubercles on dorsodistal surface of each cheliped; mesial row on ventral surface with 10 tubercles on both left and right chelipeds. Ischium of right with row of 5 small tubercles.

Hook on ischium of third pereopod much reduced, not reaching basioischial articulation and not opposing tubercle on basis; boss on coxa of fourth pereopod somewhat smaller and less sharply defined. First pleopods of uniform texture and reaching caudal portion of coxae of third pereopods when abdomen flexed.

**COLOR NOTES.**—*Cambarus latimanus* exhibiting dimorphic color pattern. Cephalothorax and abdomen mottled to concolorous, usually brown, green-brown or green. Abdomen with (i) pair of complete, moderately broad, submedian, and narrower, broken, lateral, dark brown stripes or, (ii) pair of submedian and lateral narrow, broken stripes. Abdominal stripes extending onto thorax as sinistral and dextral horns, darker in color morph with solid stripes and often extending length of branchiostegites. Abdominal stripes, especially narrow, broken ones, often less discernible on mature specimens. Gastric region with paired, lighter, vermiculated areas marking attachment of mandibular muscles. Branchiostegites and hepatic areas mottled to concolorous brown, green-brown or green dorsally, fading to white ventrad. Caudal margins of abdominal terga sometimes bearing inconspicuous, narrow, red border. Pleural regions of abdomen with obvious ventral, light, mottled margin sometimes terminating dorsally on first abdominal segment as conspicuous, single, large spot on each side, varying from cream through yellow. Ventral aspects of cephalothorax and abdomen white, occasionally tinged with blue. Young crayfish more mottled than adults, becoming more concolorous with age.

Rostral margins yellow, tan or brown. Postorbital ridges yellow, light-brown, or same color as cephalothorax. Tubercles, spines and articular condyles yellow through cream. Lateral margin of antennal scale darker than lamellar portion. Antennae generally dark-green or brown.

Chelae brown, green-brown or green dorsally with lighter proximolateral area; white ventrally. Distal ends of fingers red, orange, yellow or cream, fading with age or if living in turbid waters. Pereiopods same general color as chelae dorsolaterally, only lighter; white ventrolaterally. Distal podomeres darker dorsally than proximal ones.

**TYPE-LOCALITY.**—"Georgia superiore" (LeConte, 1856). The type-locality was restricted by Hagen (1870) to Athens, Georgia, based upon an examination of a female type-specimen on deposit at the Academy of Natural Sciences of Philadelphia and more than a dozen specimens deposited at the Museum of Comparative Zoology, Harvard College, and collected by LeConte from Athens.

**DISPOSITION OF TYPES.**—According to Hobbs (1974) the only extant specimens that can be regarded as types are syntypes consisting of 1♂ I (MCZ 3378) at the Museum of Comparative Zoology, Harvard University, and a single female (ANSP 329) at the Academy of Natural Sciences, Philadelphia. At the National Museum of Natural History there are 59 specimens that probably represent topotypic material from Athens, Clarke County, Georgia.

**RANGE.**—This crayfish is common in the Piedmont and Coastal Plain provinces from the Pamlico River drainage in North Carolina to the Altamaha River system in Georgia and from the Apalachicola River basin westward to the Escambia and upper Alabama rivers and their tributary systems in Florida and Alabama. *Cam-*

*barus latimanus* is conspicuously absent from the Pee Dee River drainage of North Carolina and South Carolina. [Curiously, only in the Pee Dee River system does *C. acuminatus* (*sens. lat.*) possess prominent abdominal stripes typical of *C. latimanus* (Hobbs, personal communication).] *Cambarus latimanus* also occurs at the southern end of the Blue Ridge province in Georgia and southeastern Tennessee as well as in the Coosa River basin draining the Ridge and Valley province in Tennessee, Georgia and Alabama and the eastern edge of the Cumberland Plateau in Georgia and Alabama where limestone exposures are present (Bouchard, 1976b). Besides those aforementioned drainages of the Atlantic and Gulf of Mexico, *C. latimanus* has crossed into the Tennessee River system of Georgia and Tennessee. Here the species occurs downstream in the Ocoee (Tennessee) River drainage to the Little Frog Mountains in Polk County, Tennessee. This species has also been collected from a single locality in the French Broad River system (Blue Ridge province) in Transylvania County, North Carolina, and may represent an introduction since it is the only record from the Tennessee River system outside the Ocoee River basin.

**VARIATIONS.**—The most notable variations exhibited by this species other than an expected range in meristics are seen in the suborbital angle, rostrum, relation of areola width to length, annulus ventralis, morphology of the first form male gonopod and development of spination on the body. The suborbital angle varies from rounded to acute and may possess a small spine or tubercle. The cephalic extremities of the rostral margins often bear small, acute spines on juveniles (Fig. 2b) which become reduced with maturity. Adults display all grades of development of the rostral margins from tubercles (Fig. 2a) to margins that merge imperceptibly with the acumen. The margins of the rostrum also vary from subparallel to acuminate. The areola is typically less than 10 times as long as broad in populations of *C. latimanus* above the Fall Line except for occasional populations in the Savannah and Santee River drainages in South Carolina where the areola may be as much as 12.3 times as long as broad. Below the Fall Line in Alabama and Georgia it may attain a length of 11.8 times. The annulus ventralis varies in its development of the cephalic ridges bordering the anterior trough, from well developed to indiscernible. The trough itself ranges in width from narrow to moderately wide. The caudal wall ranges from broadly rounded to angulate. The gonopod of the first form male varies in the angle of the central projection to the shaft of the appendage from approximately 100 to 145 degrees (Figs. 6, 7, 8). The length of the central projection is also variable with populations north of the Pee Dee River drainage in North Carolina usually exhibiting a longer one (Fig. 6c-j). The central projection may or may not bear a subapical notch with an array of notch development when present (Figs. 6, 7, 8). The mesial process exhibits one to several distal projections (Figs. 6, 7, 8), a common feature in many members of the genus *Cambarus*. Over most of the range, no ap-

parent caudal element is exhibited in populations of *C. latimanus* except in the Apalachicola and Coosa River systems (Figs. 7e, g, o). The spination of the body and appendages varies from acute spines to rounded tubercles depending on the populations and the amount of abrasion of these structures.

**SIZE.**—The largest specimen available is a female from Orange County, North Carolina, with a carapace length of 64.0 mm (postorbital carapace length 54.0 mm).

**LIFE HISTORY NOTES.**—Of the numerous collections of *C. latimanus* that have been made, only three specimens are females with eggs (or young). This probably indicates that the female retreats to a burrow to lay eggs. Two of these ovigerous females were collected from under a large, flat rock which partly rested upon the shore in a tributary of the Tallapoosa River in Cleburne County, Alabama, on 22 April 1973. The third ovigerous female was collected from a tributary (Brier Creek?) of the Neuse River in Wake County, North Carolina, on 16 April 1977.

#### *Cambarus (Depressicambarus) obstipus* Hall, 1959

**DIAGNOSIS.**—Rostrum with or without tubercles in adults, but if absent, base of acumen delimited by conspicuous angles; juveniles with spines or tubercles, decreasing in size with maturity; excavate dorsally with margins concave and subparallel to subacuminate. Areola comparatively long, (33.7) 35.4 to 39.6 percent of total length of carapace (34.0-47.0 percent of post orbital carapace length) and 6.5 to 11.1 times longer than broad, moderately punctate with space for 2 to 4 (modal number 3) punctations across narrowest part. Carapace subovate; cervical spines small and acute. Suborbital angle moderately well developed and rounded. Antennal scale of medium breadth, lamellar portion possessing angulate to declivous margin. Cephalic portion of epistome wide; epistomal zygoma moderately well to strongly arched. Chela with opposable margin of dactyl bearing 8 or 9 fairly evenly sized tubercles, first and/or fourth or first and/or fifth sometimes slightly larger; propodus with proximal 4, 5 or 6 tubercles large, fourth, fifth or sixth largest; opposable margins of both with single or double row of crowded tentacles. First pleopod of first form male with central projection short, tapering, bearing shallow subapical notch and recurved at angle of approximately 90 to 100 degrees. Annulus ventralis situated moderately deep in sternum, subquadrangular in outline; caudal wall elevated; cephalic portion elevated equal to or greater in height than caudal wall.

**RANGE.**—*Cambarus obstipus* has been collected from the Black Warrior River system where it drains the predominantly Pennsylvanian sandstone and shale deposits of the Cumberland Plateau in Blount, Cullman, Fayette, Jefferson, Tuscaloosa, Walker and Winston counties, Alabama (Bouchard, 1976b). An additional locality in Marion County, Alabama (one specimen from the Butta-hatchee River), probably represents an introduction, and it is unknown if a population is established.

#### *Cambarus (Depressicambarus) pyronotus*, new species

**DIAGNOSIS.**—Body and eyes with pigment. Rostrum without tubercles or spines. Areola 18.3 to 26.0 times longer than broad and constituting (37.8) 39.0 to 40.3 percent of total length of carapace (43.8 - 46.2 percent of postorbital carapace length) with 1 punctation in narrowest part. Cervical and hepatic spines absent; suborbital angle obsolete; postorbital ridge somewhat strong, rounded cephalically. Antennal scale moderately broad to wide; margin of lamellar portion angulate. Cephalic portion of epistome comparatively narrow; epistomal zygoma moderately well arched. Chela with 2 rows of 4 to 6 tubercles on mesial surface of palm; opposable margin of dactyl with proximal 4 tubercles prominent, first and/or fourth largest; corresponding margin of propodus with proximal 3 tubercles dominant in size, third largest; opposable margins of both with irregular double row of denticles; lateral margin costate; lateral base of fixed finger impressed above, less so below. Hook on ischium of third pereopod of male overreaching basioischial articulation and probably not typically opposed by tubercle on basis (see "Holotypic male, form I"). First pleopod of first form male with central projection corneous, bladelike, bearing very shallow subapical notch, recurved at angle of approximately 115 degrees; mesial process tumescent, tapering to subacute tip and directed caudolaterally at angle of approximately 90 degrees to shaft of appendage. First pleopod of second form male noncorneous; central projection rounded ventrodorsally; mesial process tapering to subacute tip. Annulus ventralis asymmetrical, subquadrangular, with caudal portion somewhat movable; cephalic half bearing longitudinal median trough between subparallel, longitudinal ridges; caudal half with sinuate sinus and elevated caudal wall. First pleopod of female uniramous and reaching midlength of annulus when abdomen flexed.

**HOLOTYPE MALE, FORM I.**—Body subovate, slightly vaulted (Fig. 9b). Abdomen narrowed than thorax (10.2 and 13.9 mm). Greatest width of carapace greater than depth at caudodorsal margin of cervical groove (13.9 and 12.2 mm). Areola 18.7 times as long as broad with 1 punctation across narrowest part; length of areola 39.0 percent of total length of carapace (44.6 percent of postorbital carapace length). Rostrum excavate dorsally with swollen, subparallel, slightly concave, thickened margins devoid of marginal spines or tubercles. Acumen set off from proximal portion of rostrum, oblique margins concave, not swollen and terminating in corneous, acute, upturned tubercle; upper surface of rostrum with submarginal punctations and others scattered between. Postorbital ridges moderately strong, grooved dorsolaterally and rounded cephalically. Suborbital angle absent; branchiostegal spine small. Cervical spines consisting of row of 3 small, rounded tubercles on each side; hepatic area and lateral portions of branchiostegites tuberculate; dorsal surface of carapace punctate.

Abdomen shorter than carapace (25.6 and 28.7 mm); pleura of moderate length with caudoventral extremity

broadly angular. Cephalic section of telson with single immovable spine in each caudolateral corner, separated from caudal section by paired oblique excisions. Basal podomere of left uropod with spine extending over mesial ramus. Lateral ramus of uropod with median ridge terminating in acute spine at transverse flexure; additional small ridge lateral to median one; proximal portion with row of small spines distally and movable spine submarginally at caudolateral corner. Mesial ramus of uropod with median ridge terminating distally in pre-marginal acute spine; additional acute spine at distolateral margin. Caudal margin of tail fan with plumose setae; dorsal surface lightly setiferous.

Cephalic lobe of epistome (Fig. 9k) triangular with slightly upturned cephalolateral margins; ventral surface convex. Basal portion of epistome with deep median fovea and pair of obliquely disposed slitlike fossae immediately cephalic and subparallel to thickened, moderately well-arched epistomal zygoma; lateral extremities without tubercles. Proximal segment of antennule with small, acute spine on ventral surface at base of distal fourth. Antennae broken. Antennal scale (Fig. 9h) moderately broad, broadest slightly distal to midlength; thickened lateral portion terminating in acute, corneous-tipped spine projecting forward to level of tip of rostrum; lamellar area with angulate mesial margin, crenulate and edged with long, plumose setae.

Both chelae regenerated. Hook on ischium of third pereopod only (Fig. 9d); hook simple, overreaching basioischial articulation and opposed by small, rounded tubercle on right (lacking on left). Coxa of fourth pereopod with prominent caudomesial boss, fifth pereopod without prominence. For measurements see Table 3.

Table 3. Measurements (mm) of *Cambarus*  
(*Depressicambarus*) *pyronotus*

	Holotype	Allotype	Morphotype
Carapace			
Height	12.2	13.9	11.6
Width	13.9	15.7	12.7
Total length of carapace	28.7	32.1	27.5
Postorbital carapace length	25.1	28.0	23.8
Areola			
Width	0.6	0.7	0.6
Length	11.2	12.8	11.0
Rostrum			
Width	3.1	3.6	3.3
Length	3.6	4.1	3.7
Chela			
Length, mesial margin of palm *		6.9	5.1
Width, palm		10.6	8.2
Length, lateral margin		22.9	16.5
Length, dactyle		15.2	10.8

\* chelae regenerated

First pleopods (Fig. 9e, f, g) reaching caudal portion of coxae of third pereopods when abdomen flexed. See "Diagnosis" for description.

ALLOTYPE.—Differing from holotype in following respects: rostrum broader and cephalic portion of epistome

terminating in small cephalomedian projection. Single dominant cervical tubercle on each side.

Right chela (Fig. 9l) approximately 2 times longer than broad (22.9 and 10.6 mm), depressed, although more inflated proximolaterally; mesial margin of palm with 2 rows of tubercles, 6 and 4 in primary and secondary rows, respectively; small, squamous tubercles over mesial half of palm; distoventral surface of palm with 2 large, swollen tubercles at base of dactyl, mesial one with small, corneous, acute tip. Lateral surface of propodus costate with row of punctations rendering proximolateral margin of fixed finger irregular in dorsal aspect. Fixer finger with proximolateral base impressed dorsally, less so ventrally; dorsal and ventral surfaces with distinct submedian ridges flanked by setiferous punctations; opposable surface with row of 5 and 6 tubercles on right and left chelae, respectively, third largest, decreasing in size proximally; additional small tubercle present on lower level at base of distal two-fifths, and double row of minute denticles extending proximally from corneous tip of finger to third tubercle, interrupted by fourth to sixth tubercles from base on right chela (fourth and fifth on left). Dorsal and ventral surfaces of dactyl with median longitudinal ridges, flanked by setiferous punctations; opposable margin with row of 7 tubercles on each chela, fourth largest; mesial margin of dactyl tuberculate along nearly proximal half and punctate distally; double row of minute denticles extending from corneous tip to fourth tubercle from base, interrupted by sixth and seventh tubercles on both chelae.

Carpus longer than broad with deep oblique furrow dorsally; mesial surface with large, corneous-tipped procurved spine near midlength with 5 smaller, rounded ones nearby on each cheliped; distoventral margin with corneous-tipped tubercle and additional one proximodorsally; dorsomesial surface with 9 and 7 small, rounded tubercles on left and right chelipeds, respectively.

Merus with 3 tubercles dorsodistally on right cheliped (2 on left); ventral surface with lateral row of 6 and 8 tubercles on right and left chelipeds, respectively, decreasing in size proximally, and mesial row of 11 tubercles on right cheliped (10 on left). Ischium with row of 3 very small tubercles on mesial margin of each cheliped.

Annulus ventralis (Fig. 9j) subquadrangular, broader than long, and situated deep in sternum with cephalic portion pushed to sternum and caudal half movable. Cephalic half bearing median longitudinal trough flanked by low subparallel, longitudinal ridges; caudal half bearing high caudal wall and divided by sinistral, sinuate sinus. First pleopods uniramous and extending to cephalic half of annulus when abdomen flexed. Postannular sclerite subconical with flattened caudal surface and approximately three-fifths width of annulus.

MORPHOTYPIC MALE, FORM II.—Differing from holotype in following respects: rostrum broader with sharply delimited acumen and single cervical tubercle conspicuously larger than others. Cephalic portion of epistome with cephalomedian projection. Proximal segment of antennule lacking spine on ventral surface.

Right cheliped (left regenerated) differing from allotype (those of holotype regenerated) as follows: mesial margin of palm with secondary row of 6 tubercles. Opposable margin of dactyl with 6 tubercles; row of denticles extending from distal end to second tubercle from base, interrupted by third through sixth. Dorsal surface of carpus with 3 small, rounded tubercles. Ischium with row of 4 small tubercles on mesial margin.

Hook on ischium of third pereopod much reduced, not reaching basioischial articulation and not opposing tubercle on basis; boss on coxa of fourth pereopod somewhat smaller and less sharply defined. First pleopods of uniform texture and reaching caudal portion of coxae of third pereopods when abdomen flexed. See "Diagnosis" for description.

COLOR NOTES.—I have not seen live or freshly preserved specimens, but Hobbs (1942) indicates the species to be a "distinct orange-red."

TYPE-LOCALITY.—This species was dug from burrows along a tributary of the Apalachicola River south of Indian Ridge, Torreya State Park, Liberty County, Florida. The first permanent creek south of Indian Ridge is Beaver Dam Creek. This stream, some 4 to 10 feet wide and less than a foot deep, flows over a mostly sandy substrate, although scattered brush and leaf litter are present as well as a few scattered rocks immediately downstream from a trickling water fall. The shore consists of moss near the water, especially above and downstream from the waterfall, while the surrounding area, as described by Hubbell (1939) is as follows: "'Camp Torreya' is a deep ravine situated about one mile south of Rock Bluff Landing—one of many cutting back into the sandy uplands which border the Apalachicola River valley on the east. Moist and cool, these ravines contain an interesting assemblage of plants and animals which comprise southern species, northern relicts, and a number of endemics of very limited distribution. The steep slopes and bottoms of the ravines are covered with dense forest in which beech, magnolia, red oak, hickories and sweet gums are dominant, and ironwood, wild plum, slippery elm, holly, spruce pine and other trees are also common. The undergrowth is composed largely of stinking cedar or savron (*Tumion taxifolium*, formerly *Torreya*), a coniferous shrub or small tree confined to the Apalachicola ravines, as is also the less common Florida yew (*Taxus floridana*). A characteristic member of the ground flora is the needle palm (*Rhapidophyllum hystrix*), growing side-by-side with such northern types as bloodroot, Trillium, hepatica, and toothwort. The sandy soil is thickly carpeted with dead leaves and humus, and brush heaps and decaying logs are numerous."

DISPOSITION OF TYPES.—The holotypic male, form I (no. 146761), the allotype (no. 146762) and the morphotypic male, form II (no. 146763) are deposited in the National Museum of Natural History, Smithsonian Institution. Paratypes consisting of 7♀, 7 juv. and 5 juv.♀ are in the National Museum of Natural History.

RANGE AND SPECIMENS EXAMINED.—This new species of crayfish is known from only Torreya State Park in Liberty County, Florida. The species has been collected from burrows in the following localities: (i) ravine in northern part of Torreya State Park, 17 March 1939, J. S. Rogers, et al., 2 juv.♂ and 2 juv.♀, (ii) Rock Bluff, deep ravine in Torreya State Park, 13 December 1939, L. Berner and H. H. Hobbs, Jr., 1 juv.♂ and 1 fragment, (iii) ravine south of Indian Lodge in Torreya State Park, 8 April 1941, H. H. H., 1♂ II, 1♀, 4 juv.♂ and 2 juv.♀, (iv) stream south of Indian Ridge, Torreya State Park, 28 November 1941, H. H. H., 1♂ I, 7♀ and 1 juv.♀.

VARIATION.—The most notable variation exhibited by this species concerns the caudolateral corners of the proximal portion of the telson. Two of the 21 specimens examined possessed a single movable spine on each side of the telson, absent in all others.

SIZE.—The largest specimen available is a female with a total carapace length of 33.0 mm (postorbital carapace length 28.9 mm). The only first form male available has corresponding lengths of 28.8 and 25.1 mm. Females with eggs or young have not been collected to date.

ECOLOGICAL NOTES.—Hobbs (1942) noted that "From a ravine in the northern part of Torreya State Park where *latimanus* occurs I have several specimens which were taken from complex burrows . . . [and] were a distinct orange-red." A description of the burrows in Torreya is presented by Hobbs (1942) as follows and is applicable to *C. pyronotus* as well as *C. latimanus* (Hobbs, personal communication): "The rill and brook occupying this ravine . . . empties into the Apalachicola River. . . . Also along this stream are many complex burrows which extend downward and beneath its banks. Because there is such an entwined mass of roots in this soil, digging into these burrows is a laborious job that seldom yields any specimens."

Collected with *C. pyronotus* at Torreya State Park were *Cambarus* (*Lacunicambarus*) *diogenes* Girard (1852) and *C. (D.) latimanus*.

ETYMOLOGY.—*Pyr* (Gr.), fire, in combination with *notos* (Gr.), back; so named because of the orange-red color exhibited by the species at the type-locality.

#### *Cambarus* (*Depressicambarus*) *reduncus* Hobbs, 1956

DIAGNOSIS.—Rostrum excavate dorsally with nearly straight and subparallel to subacuminate margins devoid of marginal spines or tubercles. Areola 6.6 to 28.4 times longer than broad and constituting 36.4 to 42.1 percent of total length of carapace [(40.0) 43.2-47.8 percent of postorbital carapace length]. Carapace subovate to somewhat vaulted; cervical spines lacking or reduced to small rounded tubercles. Suborbital angle obsolete to weakly developed and rounded. Antennal scale narrow; margin of lamellar portion angulate to steeply declivous. Cephalic portion of epistome of medium width; epistomal

zygoma moderately well arched. Chela with opposable margin of dactyl bearing 4 prominent basal tubercles, first and fourth largest; propodus with 3 or 4 major basal tubercles, third or fourth largest; opposable margins with irregular double row of denticles. First pleopod of first form male with central projection long, aciculate, well separated from mesial process and inclined at angle of approximately 130 to 140 degrees. (Fig. 3*h*). First pleopod of second form male with conspicuous wide gap between central projection and mesial process (Fig. 3*i*). Annulus ventralis situated deep in sternum; suboval to subquadrangular in outline; caudal wall conspicuously thickened and elevated above cephalic portion, latter bearing sinus flanked by low ridges; sinus deep and often very wide, greater than one-third width of cephalic portion.

REMARKS.—In Catawba County, North Carolina, there are populations of a crayfish that probably represent variants of this species. The carapace is more vaulted and the areola is obliterated or nearly so constituting 41.5 to 42.6 percent of the total length of the carapace (46.4-48.4 percent of postorbital carapace length). The color pattern is blue (Hobbs, personal communication) rather than typical grayish olive to brown (Hobbs, 1956). In other regards, especially the distinctive gonopod of the first form male, there appears to be little significant difference between these populations and others of *C. reduncus*. Because the areola width is narrower than in any other known population, I have not included the areola measurements of these populations with those of typical *C. reduncus* in the "Diagnosis." When more populations of *C. reduncus* are sampled the gap between the two sets of data may not remain. These morphological differences possibly reflect the more fossorial behavior of the variant populations much in the same manner as in some primary burrowing populations of *C. striatus* which sometimes also exhibit a blue color pattern.

RANGE.—This species of crayfish has been collected in the Piedmont province from the Cape Fear River drainage in North Carolina southward to the Santee River basin in South Carolina.

***Cambarus (Depressicambarus) sphenoides*  
Hobbs, 1968**

DIAGNOSIS.—Rostrum lacking tubercles or spines in adults; small juveniles occasionally with small spines or tubercles; margins subparallel to subacuminate; surface excavate to comparatively flat and often with low carina. Areola 32.8 to 39.3 per cent of total length of carapace [(41.6) 42.4-45.6 (46.5) percent of postorbital carapace length], 5.0 to 9.2 times longer than broad with space for 2 to 5 punctations across narrowest part. Carapace subovate; cervical spines reduced to small rounded tubercles. Suborbital angle poorly to moderately well developed, rounded to acute, sometimes exhibiting small tubercle. Antennal scale moderately broad to wide; margin of lamellar portion angulate to declivous. Cephalic portion of epistome comparatively wide; epistomal zygoma strongly arched. Chela with dorsal surface of palm

bearing numerous small squamous tubercles; opposable margin of dactyl with basal 4 or 5 tubercles prominent, first, fourth or fifth or first and fourth or first and fifth largest; opposable margin of propodus with basal 3 tubercles conspicuous, third largest; opposable margins of fingers with irregular double or triple rows of denticles, increasing to triple row with age. First pleopod of first form male with subapical notch on central projection; element moderately long, tapering little and inclined at angle of approximately 115 to 130 degrees (Fig. 3*j*). Annulus ventralis situated moderately deep in sternum; subquadrangular in outline; caudal wall elevated; cephalic portion bearing shallow sinus flanked by low ridges.

RANGE.—*Cambarus sphenoides* is endemic to the Cumberland Plateau from Marion County, Tennessee, northward to Jackson County, Kentucky, in the Tennessee, Cumberland and Kentucky (one locality) River systems.

***Cambarus (Depressicambarus) striatus* Hay, 1902**

*Cambarus floridanus* Hobbs, 1941:114.

DIAGNOSIS.—Body and eyes with pigment. Rostrum without spines or tubercles; sometimes with low carina. Areola obliterated to 9.1 times longer than broad and constituting 33.9 to 43.6 (45.7) percent of total length of carapace [41.6-49.7 (50.7) percent of postorbital carapace length] usually with 1 or 2 punctations across narrowest part. Cervical spine reduced to small, rounded tubercle or absent; hepatic spines absent; branchiostegal spine present; suborbital angle weakly to moderately well developed, rounded to obtuse; postorbital ridge somewhat strong, rounded cephalically. Antennal scale moderately broad to wide; margin of lamellar portion angulate. Cephalic portion of epistome comparatively wide; epistomal zygoma moderately well arched. Chela with 2 rows of 8 or fewer tubercles on mesial surface of palm; opposable margin of dactyl with proximal 4 or 5 tubercles prominent—first, fourth or fifth or first and fourth or first and fifth largest; corresponding margin of propodus with proximal 3 or 4 (rarely 5) tubercles dominant in size, third, fourth or fifth largest; opposable margins of both with irregular double row of denticles; lateral margin costate and lateral base of fixed finger impressed above, less so below. Hook on ischium of third pereopod of male overreaching basioischial articulation and not opposed by tubercle on basis. First pleopod of first form male with central projection corneous, bladeliike, with or without subapical notch and recurved at angle of 95 to 155 degrees (Figs. 12-14); mesial process tumescent, tapering to one to several subacute to acute tips, generally directed caudally at angle of approximately 90 degrees to shaft of appendage (Figs. 12*d*, *r*). First pleopod of second form male noncorneous; central projection rounded distally; mesial process tapering to subacute tip. Annulus ventralis asymmetrical, subquadrangular, with caudal portion somewhat movable; cephalic half bearing longitudinal median trough usually between subparallel, longitudinal ridges, and caudal half with sinuate sinus and elevated caudal wall. First pleopod of

female uniramous and reaching at least midlength of annulus ventralis when abdomen flexed.

**SYNTYPIC MALE, FORM I (USNM 25109).**—Body subovate, slightly depressed (Fig. 10*b*). Abdomen narrower than thorax (15.5 and 18.3 mm). Greatest width of carapace greater than depth at caudodorsal margin of cervical groove (18.3 and 13.7 mm). Areola 38.0 times longer than road with 1 punctation across narrowest part; length of areola 43.6 percent of entire length of carapace (49.5 percent of postorbital carapace length). Rostrum excavate dorsally with subparallel, thickened margins devoid of marginal spines or tubercles; upper surface with several submarginal punctations with few scattered between. Acumen set off from proximal portion of rostrum with concave oblique margins, latter not swollen, and terminating in small upturned tubercle at tip. Postorbital ridges moderately strong with moderately deep groove dorsolaterally and rounded cephalically. Suborbital angle weak; branchiostegal spine small. Cervical tubercles bituberculate; hepatic area and lateral portion of branchiostegites tuberculate; dorsal portion of carapace punctate.

Abdomen shorter than carapace (33.1 and 34.9 mm); pleura of moderate length with caudoventral extremity broadly angular. Cephalic section of telson with single movable and immovable spines in each caudolateral corner; separated from caudal section by paired oblique excisions. Basal podomere of uropod with spine extending over mesial and lateral rami. Lateral ramus of uropod with median ridge terminating in acute spine at transverse flexure; additional small ridge lateral to median one; proximal portion with row of small spines distally and movable spine submarginally at caudolateral corner. Mesial ramus of uropod with median ridge terminating distally in premarginal acute spine. Caudal margin of tail fan with plumose setae; dorsal surface lightly setiferous.

Cephalic lobe of epistome (Fig. 10*j*) pentagonal with slightly upturned cephalolateral margins and bearing cephalomedian projection; ventral surface convex. Basal portion of epistome with deep median fovea and pair of obliquely disposed slitlike fossae immediately cephalic and subparallel to thickened, moderately well-arched epistomal zygoma; lateral extremities with single tubercle on each side. Proximal segment of antennule with small spine on ventral surface at base of distal third. Antennae broken. Antennal scale (Fig. 10*h*) moderately broad, broadest slightly distal to midlength; thickened lateral portion terminating in acute, corneous-tipped spine projecting forward beyond tip of rostrum; lamellar area with mesial margin broadly angulate, crenulate and edged with long, plumose setae.

Right chela (Fig. 10*l*) approximately 2 times longer than broad (24.4 and 11.6 mm), depressed, although more inflated proximolaterally; mesial margin of palm with 2 rows of 6 and 5 tubercles in primary and secondary rows, respectively; several smaller squamous tubercles on dorsal surface over slightly less than half of mesial portion of palm; distoventral surface of palm with

2 large, swollen tubercles at base of dactyl. Lateral surface of propodus costate with row of punctations rendering proximolateral margin of fixed finger irregular in dorsal aspect. Propodus with proximolateral base of finger impressed dorsally, less so ventrally; dorsal and ventral surfaces with distinct submedian ridges flanked by setiferous punctations; opposable margin with row of 6 tubercles along proximal two-thirds of finger, fourth largest, basal 4 decreasing in size proximally; additional small tubercle present on lower level near base of distal third; double row of minute denticles extending proximally from corneous tip of finger to fifth tubercle from base, interrupted by sixth. Dorsal and ventral surfaces of dactyl with median longitudinal ridges, flanked by setiferous punctations; opposable margin with row of 8 tubercles, first and fourth largest, second and third slightly smaller; double row of minute denticles extending from corneous tip to sixth tubercle from base, interrupted by seventh and eighth; mesial margin of dactyl tuberculate along proximal two-thirds and punctate distally.

Carpus longer than broad with deep oblique furrow dorsally; mesial surface with large procurved spine near midlength and smaller ones located proximally and proximoventrally with additional small tubercle near base of spine; distoventral margin with large subacute tubercle; dorsomesial surface with 5 small, rounded tubercles; podomere otherwise punctate.

Dorsodistal surface of merus with 4 rounded tubercles; ventral surface with lateral row of 5, decreasing in size proximally, and mesial row of 11 tubercles, some corneous-tipped. Ischium with row of 3 very small tubercles on mesial margin.

Hook on ischium of third pereopod only (Fig. 10*d*); hook simple, overreaching basioischial articulation and not opposed by tubercle on basis. Coxa of fourth pereopod with prominent caudomesial boss, fifth pereopod without prominence. For measurements see Table 4.

Table 4. Measurements (mm) of *Cambarus* (*Depressicambarus*) *striatus*

	Syntypic Male, Form I	Syntypic Female	Syntypic Male, Form II
Carapace			
Height	13.7	13.4	12.7
Width	18.3	17.5	16.0
Total length of carapace	34.9*	**	31.2
Postorbital carapace length	30.7	29.2	27.3
Areola			
Width	0.4	0.5	0.4
Length	15.2	13.8	13.4
Rostrum			
Width	4.1*	4.0	3.6
Length	4.2*	**	3.9
Chela			
Length, mesial margin of palm	7.3	6.9	5.9
Width, palm	11.6	10.6	10.2
Length, lateral margin	24.4	22.2	19.6
Length, dactyl	15.8	13.9	12.7

\* rostrum damaged (see Fig. 10*i*)

\*\* tip of acumen missing

First pleopods (Fig. 10e, f, g) reaching caudal portion of coxae of third pereopods when abdomen flexed. See "Diagnosis" for description.

**SYNTYPIC FEMALE (USNM 25019).**—Differing from syntypic male, form I, in following respects: cervical spine consisting of low, rounded tubercle and bearing several setae. Areola open but lacking punctations across narrowest part. Left chela (right missing) with 3 tubercles in secondary row on mesial surface of palm. Dorsomesial tubercles of left carpus consisting of single very small proximal and proximoventrally disposed ones. Opposable margin of propodus with row of minute denticles extending from corneous tip proximally to fourth tubercle, interrupted by fifth. Opposable margin of dactyl with row of minute denticles extending from corneous tip proximally to fifth tubercle from base, interrupted by sixth and seventh.

Annulus ventralis (Fig. 10k) subquadrangular, broader than long, and situated moderately deep in sternum with cephalic portion fused to sternum and caudal half movable. Annulus ventralis divided by sinus into C-shaped and triangular portions, latter with basal tongue projecting into concavity of "C." Cephalic half with sinus broadening into median longitudinal trough flanked by low, subparallel, longitudinal ridges; caudal portion elevated and nearly bisected by shallow sinus. Postannular sclerite subconical and approximately three-fifths width of annulus.

**SYNTYPIC MALE, FORM II (USNM 25019).**—Differing from syntypic male, form I, in following respects: rostrum with median carina present on acumen. Areola narrow and open but lacking punctations across narrowest part. Cervical spines consisting of single low, rounded tubercle on each side bearing several setae. Cephalic portion of epistome with cephalomedian projection. Chelae with 5 tubercles in primary row on mesial surface of palm; 6 tubercles in secondary row of right. Opposable margin of propodus of right chela with row of denticles extending from corneous tip proximally to sixth tubercle. Opposable margin of dactyl of right chela with 9 tubercles; row of denticles extending from corneous tip proximally to fourth tubercle from base, interrupted by fifth, sixth and seventh on each chela.

Hook on ischium of third pereopod much reduced, not reaching basioischial articulation, and not opposing tubercle on basis; boss on coxa of fourth pereopod somewhat smaller and less sharply defined. First pleopods of uniform texture and reaching caudal portion of coxae of third pereopods when abdomen flexed. See "Diagnosis" for description.

**COLOR NOTES.**—*Cambarus striatus* exhibiting dimorphic color pattern. Cephalothorax and abdomen mottled to concolorous, usually brown, green-brown or green. Abdomen with (i) pair of complete, moderately broad, submedian, and narrower, broken, lateral, dark brown stripes or, (ii) pair of submedian and lateral narrow, broken stripes. Abdominal stripes extending onto thorax as sinistral and dextral horns, darker in color morph

with solid stripes and usually extending length of branchiostegites. Populations known with blue, blue-gray or dark red-brown coloration. Abdominal stripes, especially narrow, broken ones, often less discernible on mature specimens. Gastric region with paired, lighter, vermiculated areas marking attachment of mandibular muscles. Branchiostegites and hepatic areas mottled to concolorous brown, green-brown or brown dorsally, fading to white ventrad. Pleural regions of abdomen bearing inconspicuous ventral, narrow, light, mottled margin sometimes terminating dorsally on first abdominal segment as distinct single large spot on each side, varying from cream through yellow. Ventral aspects of cephalothorax and abdomen white, occasionally tinged with blue. Young crayfish more mottled than adults, becoming more concolorous with maturity.

Rostral margins yellow, cream, tan or brown. Post-orbital ridges yellow, light-brown or same color as cephalothorax. Tubercles and spines yellow through cream. Articular condyles of chelae red, yellow or cream. Lateral margin of antennal scale darker than lamellar portion. Antennae generally dark green or brown.

Chelae colored as cephalothorax with lighter proximolateral area, white ventrally. Distal ends of fingers red, orange, yellow or cream, fading with age or if living in turbid waters. Pereiopods same general color as chelae dorsolaterally, only lighter; white ventrolaterally. Distal podomeres darker dorsally than proximal ones.

Specimens from Leon County, Florida (type-locality, *C. floridanus*), more colorful with chelae exhibiting blue fingers and orange tubercles. Postorbital ridges orange; margins of rostrum and articular condyles of chela reddish-orange. Caudal margin of abdominal terga, distal edge of transverse flexure of outer ramus of uropod and lateral edge of telson margined with red. Tail fan blue. Pereiopods with blue tips and orange articulations. Abdominal pleura with white ventral margins.

Additional color notes are provided by Hay (1902), and Hobbs and Hart (1959) furnish the following color notes from specimens collected from southwestern Georgia and adjacent portions of Florida: "purplish-red dorsally fading to pinkish-lavender along the lower lateral margins of the carapace. The chelipeds are also purplish-red with dark tubercles."

**TYPE-LOCALITY.**—Reported as "near Nashville, Tennessee," by Hay (1902). The exact locality cannot be defined but was surely a part of the Cumberland River system and probably in Davidson County, Tennessee. There apparently were no crayfish associates collected with *C. striatus* at the type-locality.

**DISPOSITION OF TYPES.**—The syntypes, consisting of 1 ♂ I, 3 ♀ II, 4 ♀ (USNM 25019) and 1 ♂ I, 1 ♂ II and 3 ♀ (MCZ 7348), were collected by E. B. Williamson and deposited in the National Museum of Natural History, Smithsonian Institution, and Museum of Comparative Zoology, Harvard College, respectively.

**RANGE.**—This crayfish is widespread above and below the Fall Line east and south of the Mississippi and Ohio

ivers. It is known to occur in the following geomorphic regions above the Fall Line: Highland Rim, Cumberland Plateau, Nashville Basin, Shawnee Hills, Ridge and Valley, Blue Ridge and Piedmont. Below the Fall Line *C. striatus* inhabits waters in the Gulf (including the Mississippi Embayment but minus the Mississippi Alluvial Plain) and Atlantic Coastal plains. In the Mississippi River drainage, this species is known from the Green River system, Kentucky, downstream to the Homochitto River system in Mississippi. *Cambarus striatus* occurs upstream in the Cumberland River system onto the Cumberland Plateau in Tennessee and Kentucky and in the Tennessee River basin to Jefferson and Knox counties, Tennessee. This species is also known from the Pearl River drainage eastward to and including the entire Mobile Bay basin (*i.e.*, Tombigbee, Black Warrior, Coosa and Tallapoosa River systems) and from the Gulf drainages east of Mobile Bay to the Ochlockonee River basin. In the Atlantic drainages, *C. striatus* has been collected from the Altamaha River system.

**VARIATIONS.**—The most outstanding variations exhibited by this species are in the gonopod of the first form male, the length-width ratio of the areola, annulus ventralis and in the rostrum. Most populations of *C. striatus* lack a subapical notch on the first form male gonopod, although certain populations in the Pearl, Coosa, Altamaha, lower Cumberland and upper Tennessee River system exhibit a well-defined notch (Fig. 13*m, s, t*). The central projection of the first form male gonopod also varies in its angle to the shaft of the appendage (Figs. 12, 13, 14). In many populations a well-developed caudal shoulder can be observed on the gonopod of the first form male, and the mesial process offers a great deal of variation in the number of apical projections (Figs. 12, 13, 14). The areola varies in its length and width usually relative to the fossorial behavior of the population, narrower in the burrowing members. The width of the areola varies from obliterated to 9.1 times the length. The annulus ventralis varies in its development of the cephalic ridges bordering the anterior trough, from well developed to indiscernible. The trough itself ranges in width from narrow to moderately wide. The rostrum of *C. striatus* also varies from subparallel to a more acuminate condition in some populations. Compare Figs. 10 and 11.

**SIZE.**—The largest specimen available is a female from Murray County, Georgia, with a carapace length of 60.1 mm (postorbital carapace length 52.8 mm).

**LIFE HISTORY NOTES.**—Only a single female with eggs or young has been collected. The female, carrying 5 eggs, was taken from Rickwood Cavern in Blount County, Alabama, on 11 March 1966. This species appears to occupy burrows during the period of egg laying.

### Ecology

Crayfishes of the subgenus *Depressicambarus* occur in a wide range of epigean waters as well as in the sub-

surface water table as burrowers. The invasion of the subsurface water table has contributed greatly to their radiation and speciation. The epigean species [*C. englishi*, *C. graysoni* (in part), *C. halli*, *C. latimanus* (in part), *C. obstipus*, *C. sphenoides* (in part) and *C. striatus* (in part)] occupy lotic and lentic habitats ranging from small to large streams, springs and ponds where they can be found under rocks, in leaf litter, roots of riparian trees and in mats or dense growths of algae and aquatic vascular plants. While most epigean species occur primarily in pool areas, *C. obstipus* is also commonly found in riffles. *Cambarus englishi* is more likely to inhabit riffle areas, including those in large streams, than the other species and exhibits morphological characteristics that may be advantageous to locomotion in fast flowing waters by reducing resistance to water flow. The dorsoventrally flattened carapace and sharply angulate abdominal pleura (moderately sharp caudoventral angles in *C. englishi*) are especially distinct in some of its relatives of the cambaroid line (within the subfamily Cambarinae, after Hobbs, 1969), *Barbicambarus cornutus* (Faxon, 1884), *C. (Erebicambarus) hubbsi* Creaser (1931) and *C. (E.) rusticiformis* Rhoades (1944), all three of which commonly inhabit areas of streams with a rapid or moderately rapid flow. Since these three species live in regions dominated by the genus *Orconectes* (Bouchard, 1976 a) and *C. englishi* lives in a river system that possesses three close relatives—*C. halli*, *C. latimanus* and *C. striatus*, the above characters possibly assist in exploiting an available habitat. The flattened body is probably the more important of the two characters for an existence in fast flowing waters. That such modifications are not limited to inhabitants of swiftly flowing water is evidenced by members of the subgenus *Hobbsastacus* (Bouchard, in press) of the genus *Pacifastacus* which also exhibit sharply angulate abdominal pleura, and at least *P. fortis* and *P. connectens* (Faxon, 1914) occur primarily in pool areas of streams. It also should be noted that members of the genus *Orconectes* occur in riffle areas of streams and do not exhibit either of the above characters.

Most species of *Depressicambarus* are well adapted to a burrowing existence and are divisible into three overlapping categories as defined by Hobbs (1942). The primary burrowers are those that are restricted to burrows. This group includes *C. catagius*, *C. cymatilis*, *C. pyronotus* and certain populations of *C. reduncus* and *C. striatus*. The secondary burrowers generally occupy burrows but at times occur in open waters (slightly modified from Hobbs, 1942) and include *C. reduncus* (in part) and *C. striatus* (in part). Those species that are abundant in open waters but burrow either in periods of seasonal low water levels, to lay eggs or because of the paucity of epigean habitats constitute the tertiary burrowers (modified from Hobbs, 1942). These include *C. graysoni* (in part), *C. latimanus* (in part), *C. sphenoides* (in part) and *C. striatus* (in part). Although *C. obstipus* has never been collected from a burrow, its moderately narrow areola and broad, flat chelae, similar to those of fossorial species, indicate an adaptation to burrow.

*Cambarus latimanus* adults are most common as burrowers below the Fall Line, probably due to the lack of well-indurated rocks to provide cover. *Cambarus striatus* adults, on the other hand, are more frequently found in surface waters in the Tennessee River basin from the Hiwassee River system (Tennessee) downstream to Hardin County, Tennessee, and in the Mobile Bay drainage above the Fall Line in Tennessee, Georgia and Alabama.

### Relationships

The subgenus *Depressicambarus* appears to be a distinct group of closely related crayfishes within the genus *Cambarus* the members of which generally exhibit a broadly subtriangular, depressed chela bearing two major rows of tubercles along the mesial margin of the palm. Based upon morphological and color pattern similarities within the subgenus, it is further divisible as termed here into the *halli* and *latimanus* groups. In the *halli* group, *C. halli*, *C. englishi* and *C. obstipus* are distinctly more closely related to one another than to any other member of the subgenus and display more plesiomorphic characters. The *latimanus* group, exhibiting more apomorphic characters, includes *C. latimanus*, *C. striatus*, *C. sphenoides*, *C. graysoni*, *C. pyronotus*, *C. catagius*, *C. cymatilis* and *C. reduncus*. Members of this group display a wider array of morphological variation than do those of the *halli* group; this is in part due to their utilization of and adaptation to diverse habitats. Convergent evolution in the burrowing members of the *latimanus* group has obscured many morphological characters that would provide a clearer understanding of relationships within this group.

The *halli* group generally possesses rostral tubercles (often reduced or lacking in adults, but if absent, base of the acumen is usually delimited by conspicuous angles) and well-developed cervical spines and displays a bright-green color pattern with red, reddish-orange or reddish-brown postorbital ridges and margins of the rostrum. The chelae exhibit red, reddish-orange or reddish-brown articular condyles and a pale-white coloration on approximately the distal half of the fingers. The ventral and caudal margins of the abdominal pleura and caudal edge of the terga (except the sixth) are white, that of the first tergum broader and more conspicuous. Some populations of *C. obstipus* display a more subdued coloration of the dimorphic, striped, abdominal patterns typical of *C. latimanus*, *C. sphenoides* and *C. striatus* (see color notes in the sections on *C. latimanus* and *C. striatus*).

Within the *halli* group, *C. halli* is morphologically more similar to *C. englishi*, and the three species are separable utilizing the following characters. The central projection of the gonopod of *C. obstipus* is distinctive, being short and bearing a shallow subapical notch (Fig. 3g). The moderately long central projection of the first form male gonopod of *C. halli* possesses a distinct subapical notch (Fig. 3f); the longer one of *C. englishi* lacks a notch (Fig. 3c). The most rheophilic *C. englishi* exhibits a more dorsoventrally flattened carapace and possesses abdominal pleura that are less broadly angulate

(Fig. 1b) than in any other member of the subgenus (Fig. 1a). In *C. obstipus* the opposable margin of the dactyl on the chela is distinct from the rest of the subgenus in possessing a row of 8 or 9 fairly evenly sized tubercles (Fig. 1i). All other species in *Depressicambarus* bear 2 to 5 dominant basal tubercles on the opposable margin of the dactyl.

Of the three, *Cambarus obstipus* possesses the narrowest, least punctate areola: 6.5 to 11.1 times longer than broad with space for 2 to 4 punctations (modal number 3) across the narrowest part. In *C. halli* the areola is 2.9 to 4.5 times as long as broad with 5 to 7 punctations (Fig. 1f) and in *C. englishi* 3.4 to 4.9 times as long with 4 to 6 punctations (Fig. 1h). *Cambarus halli* has a shorter areola [28.9-35.1 percent of the total length of the carapace or 39.3 to 42.5 (43.3) percent of the postorbital carapace length] than does *C. englishi* (33.2-38.0 percent and 41.3-46.7 percent). In addition, *C. halli* possesses straighter rostral margins (concave in *C. englishi*) and lacks an elevated cephalic portion on the annulus ventralis which is typical of *C. obstipus* and present in populations of *C. englishi* that are syntopic with *C. halli*. Syntopic populations of *C. halli* and *C. englishi* exhibit some character displacement in the areola (length, width and number of punctations), rostrum and annulus ventralis and are much easier to separate into their respective species than allotopic populations which show a broader overlap in these characters.

Members of the *latimanus* group are morphologically more diverse with only one species sharing some of the distinctive characters of the *halli* group. Certain populations of *C. latimanus* bear moderately well-developed cervical spines or rostral tubercles and/or have a short, broad areola similar to that in *C. halli*. These two characters—spination and the length-width ratio of the areola—are the only consistent morphological characters that will separate *C. latimanus* from its close ally *C. striatus*. The small rostral spines found on the young of *C. latimanus* are lacking in *C. striatus*. The areola of *C. latimanus* is normally wider than that of *C. striatus* which generally is 10 or more times longer than broad. Exceptions for both species occur, however. This ratio may be as low as 9.1 for *C. striatus*, especially in the Tallapoosa River system, Alabama and Georgia, above the Fall Line. Populations of *C. latimanus* with individuals that exhibit an areola greater than 10 times as long as broad (up to 12.3) are found below the Fall Line in Alabama and Georgia and in the upper Savannah and Santee River drainages in South Carolina.

*Cambarus sphenoides* is morphologically similar to *C. latimanus* and *C. striatus*, sharing with them a dimorphic striped color pattern (see color notes for *C. latimanus* and *C. striatus*). *Cambarus sphenoides* may be separated from these two species using a combination of the following characters. While *C. latimanus* and *C. striatus* have a moderately well-arched epistomal zygoma (Fig. 2d, e), it is more strongly arched in *C. sphenoides* (cf. Fig. 2f). Both *C. latimanus* and *C. striatus* have a double row of denticles along the opposable margins of the fingers,

while *C. sphenoides* has a double or triple row (increasing to triple row with age). In addition, *C. sphenoides* differs from *C. striatus* in exhibiting a broader areola, 5.0 to 9.2 times longer than broad (Fig. 1g) (9.1 to obliterated in *C. striatus*, Figs. 10i, 11i), and often more convergent rostral margins with an intervening surface that is comparatively flat and often bearing a low carina (Fig. 1g). The rostrum of *C. striatus* has subparallel margins with a deeply excavate surface (Figs. 10i, 11i).

*Cambarus graysoni* bears a close resemblance to *C. sphenoides* and *C. striatus* and has long been confused with the latter. *Cambarus graysoni* with a gently bent epistomal zygoma (Fig. 4k) differs from *C. striatus* and all other members of the subgenus *Depressicambarus* which possess one that is at least moderately well arched (Fig. 2d, e, f). *Cambarus graysoni* is further distinguished from *C. sphenoides* by the lack of a subapical notch on the central projection of the gonopod (Fig. 3d, e). In addition, the areola of *C. graysoni* is 9.0 to 15.1 times longer than broad (5.0-9.2 times in *C. sphenoides*) and the rostrum bears subparallel margins and a concave surface (often subacuminate with a comparatively flat surface in *C. sphenoides*).

*Cambarus pyronotus* is more closely related to *C. striatus* than to any other species but differs from *C. striatus* in the following characters. It bears an obsolete suborbital angle which is usually moderately well to weakly developed in *C. striatus*. The opposable margin of the propodus bears 3 dominant tubercles proximally in *C. pyronotus* and generally 4 in *C. striatus* (Figs. 9l, 10l, and 11l). The caudolateral corners of the proximal portion of the telson of *C. pyronotus* lack a movable spine (2 of the 21 specimens examined actually do possess a movable spine on each side) while the telson of *C. striatus* generally bears both a movable and an immovable spine in each corner, rarely only the immovable spine. In addition, *C. pyronotus* is a bright, orange-red color not found in *C. striatus*.

Two morphologically similar relatives of *C. cymatilis* are *C. catagius* and *C. reduncus*, all three of which are burrowers. In *C. cymatilis* the opposable margins of the fingers of the chela are distinct with the dactyl bearing 2 dominant basal tubercles (3-5 in other members of the subgenus, except *C. obstipus* usually with 8 or 9 fairly evenly sized ones Fig. 1i), the distal one largest, and the propodus with 3 dominant basal tubercles, the proximal 2 of which increase in size distally, followed by a large gap between the second and third (Fig. 1j) (no such large gap exists in any other nominal member of the subgenus, Figs. 4i, 5i, 9l, 10l, 11l). A narrow to moderately narrow, steeply declivous antennal scale (Fig. 1c, d) is shared by all three although *C. reduncus* also exhibits one that varies from steeply declivous to angulate. In addition, the weakly developed suborbital angle, often obsolete, of *C. reduncus* is in contrast to the well-developed and acute suborbital angle in *C. cymatilis* and the moderately well developed and rounded one in *C. catagius*. All three species display a suboval and deeply situated annulus ventralis with a conspicuously thickened caudal wall. The

very wide cephalic trough is a distinguishing feature of the annulus ventralis of some populations of *C. reduncus*. The first form male gonopod of *C. cymatilis* bears a short central projection with a well-defined subapical notch (Fig. 3b) and differs from that of *C. catagius* which bears a central projection of moderate length with a subapical notch that is poorly defined or lacking (Fig. 3a). In *C. reduncus* the long, aciculate central projection (Fig. 3h) of the male gonopod is unique among the members of the genus. The gonopod of the nonreproductive male is also distinctive, bearing a wide gap between the central projection and mesial process (Fig. 3i). The latter feature also serves to separate the second form male of this species from any other member of the subgenus.

### Phylogeny

The two most likely sites of origin of the subgenus *Depressicambarus* are the Cumberland Plateau section and the Piedmont province. Hobbs (1969) proposed that the subgenus probably originated on the slopes of the Cumberland Plateau. An equally viable hypothesis is that the ancestral stock of the subgenus arose on the southern end of the Piedmont. These regions are not too far removed from one another, and outliers of the Cumberland Plateau actually lie in close proximity to the Piedmont province in Alabama. It is in these regions that members of the subgenus exhibiting the most plesiomorphic characters are found. These members, *C. englishi*, *C. halli* and *C. obstipus*, constitute a distinctive unit (*halli* group) within the subgenus. *Cambarus englishi* and *C. halli* are endemic to the Tallapoosa River system (Piedmont province) in Georgia and Alabama as is *C. obstipus* to the Black Warrior River system (Cumberland Plateau section) in Alabama. The Tallapoosa drainage seems to have undergone two occupations by the *halli* group, first by *C. halli* and later by *C. englishi*.

The *halli* group may have moved northward along the strikes of the Piedmont, Ridge and Valley and Cumberland Plateau, although no member of this group is presently known outside the southern portions of the Piedmont and Cumberland Plateau. Based upon the present distribution of other crayfishes within these physiographic regions, movement along the dispersal corridors seems to be a probable avenue of migration (Bouchard, 1976a). Movements among the Piedmont, Ridge and Valley and Cumberland Plateau seem certain based upon present distributions of the *halli* group. This migration was facilitated by (i) the close proximity of the three regions in the southern parts of their ranges, (ii) the lower elevation of the eastern escarpment of the Cumberland Plateau toward its southern end before it is overlapped by Coastal Plain deposits and (iii) the presence of the Coosa River system which not only drains the Ridge and Valley but also the eastern and western flanks of the Cumberland Plateau and Piedmont, respectively.

The members of the *latimanus* group display a wider variation in morphological characters, many of which are more advanced than those of the *halli* group. Within the former group the closest relative to the more plesio-

morphic *halli* group is *C. latimanus* with some populations displaying the more primitive short, broad areola and well-developed spination on the body typical of *C. halli*. The *latimanus* group (*C. catagius*, *C. cymatilis*, *C. graysoni*, *C. latimanus*, *C. pyronotus*, *C. reduncus*, *C. sphenoides* and *C. striatus*) probably also arose on the Piedmont province, but further to the northeast than the *halli* group in the Georgia-South Carolina area, and utilized several corridors of migration.

The *latimanus* group moved northeast following the strike of the Piedmont as well as southwest onto the Ridge and Valley province. From here it probably moved southwest and northeast, following exposures of the Ridge and Valley and westward through Walden Gorge, gaining access here to the predominantly Mississippian limestone streams of the Highland Rim section. This Tennessee River corridor through the Cumberland Plateau has been utilized by a number of crayfishes [*C. girardianus*, *Orconectes forceps*, *O. erichsonianus* and *O. spinosus* (*sens. lat.*)], distributions of which predominantly occur in limestone areas on both sides of the Cumberland Plateau. The *latimanus* group also entered the Cumberland Plateau either along the eastern escarpment of the region where it borders the Ridge and Valley or along the Sequatchie Valley. In addition, streams draining the Blue Ridge province in the Tennessee and Georgia area were penetrated by this group from the Ridge and Valley. Migrations into the Coastal Plain province probably initially occurred from the Piedmont and Ridge and Valley. From here they spread along the Coastal Plain.

*Cambarus pyronotus* probably represents a recently derived species having been isolated from *striatus* stock that migrated along the Apalachicola River drainage into the Torreya Ravine area. Torreya Ravine is a unique area in that it supports an assemblage of plants and animals representing southern species, northern relicts that were isolated in the area after the last glacial egression and some endemics of limited distribution (Hubbell, 1939).

The ancestral stock of the subgenus *Depressicambarus* probably exhibited the following characteristics, many of which are presently found in *C. halli* and in the chela of some populations of *C. sphenoides* north of the Obey and Emory River systems in Tennessee and Kentucky: (i) eyes large, (ii) carapace subovate, (iii) rostrum with straight, subparallel margins bearing distal rostral tubercles, (iv) suborbital angle acute, (v) antennal scale with mesial margin of lamellar portion angulate (Fig. 11h), (vi) postorbital ridge with cephalic spine, (vii) cervical spine present, (viii) areola short (29-35 percent of total length of carapace or 39-43 percent of postorbital carapace length), broad (less than 4.5 times longer than broad) and densely punctate (5-7 punctations across narrowest part), (ix) chela subovate and subrectangular with squamous tubercles over dorsal surface of palm and with two primary rows of larger ones along mesial margin of moderately long palm; opposable margins of fingers with triple row of crowded denticles, (x) annulus ventralis subquadrate and situated moderately deep in sternum; caudal wall elevated; cephalic portion elevated, at least equal in

height to caudal wall and divided by median trough extending caudally as sinuate sinus that divides caudal wall, (xi) first form male gonopod with central projection short, corneous, bladelike, directed caudally, bearing subapical notch and inclined at angle of approximately 90 degrees to main shaft of appendage; mesial process caudally directed and tumescent; caudal element conspicuous; (xii) color bright green with dark saddle at caudal end of cephalothorax; margins of rostrum and postorbital ridges red; chelae with at least distal half of fingers pale white and articular condyles red; abdominal segments with caudal margins of terga (except sixth) and ventral and caudal margins of pleura white, that of first tergum broader and more conspicuous. This species probably was most common under rocks in pool areas of small to medium-sized streams.

Evolutionary trends in the epigeal members of the subgenus *Depressicambarus* have involved the following changes: (i) reduction of spination on rostrum, postorbital ridges and cervical spines, (ii) mesial margin of antennal scale becoming declivous, (iii) lengthening and narrowing of areola with reduction in number of punctations, (iv) chela becoming more subtriangular and flattened; reduction in number of squamous tubercles over surface and shortening of mesial margin of palm; opposable margins of fingers with reduction in number of rows of crowded denticles; lateral margin of propodus becoming more impressed, (v) annulus ventralis with elevated cephalic portion reduced to ridges bordering cephalic trough and lower in height than caudal wall, (vi) first form male gonopod with central projection becoming longer, reduction in subapical notch and inclining toward angle of more than 90 degrees to main shaft of appendage, (vii) color pattern more subdued greens and browns with margins of rostrum and articular condyles yellow, if light colored; chelae with distal tips of fingers red, orange, yellow or cream; abdominal segments retaining only lighter ventral pleural margins.

The burrowing species of the subgenus, especially the more fossorial primary burrowers, exhibit further changes in morphology as follows: (i) reduction in size of eyes, (ii) vaulting of carapace, (iii) narrowing of rostrum, (iv) postorbital ridges becoming reduced, (v) antennal scale narrower and with more steeply declivous mesial margin (Fig. 3b), (vi) suborbital angle further reduced, (vii) areola narrower and longer, (viii) chela broader and more depressed with reduction in number of tubercles and rows of denticles along opposable margins of fingers, (ix) deepening of sternum, (x) annulus ventralis becoming suboval with conspicuously thickened caudal wall, (xi) abdomen reduced in width, (xii) color variable, red, blue or subdued browns or greens.

#### Addendum

In view of the paucity of information concerning life history aspects of *C. latimanus* and *C. striatus* additional information has been obtained subsequent to the submission of this paper and is added as follows: A single female with young of *C. striatus* was collected under a

rock approximately a half meter from shore in a tributary of Spring Creek (Coosa River system) off Alabama State Highway 35, Cherokee County, Alabama, R10E-T8S-S21NE, on 9 October 1977. A copulating pair of *C. latimanus* was observed in midstream under a bridge crossing a tributary of Talladega Creek (Coosa River system) at Talladega County Road 9, Talladega County, Alabama, R6E-T20S-S3NE, on 2 November 1974.

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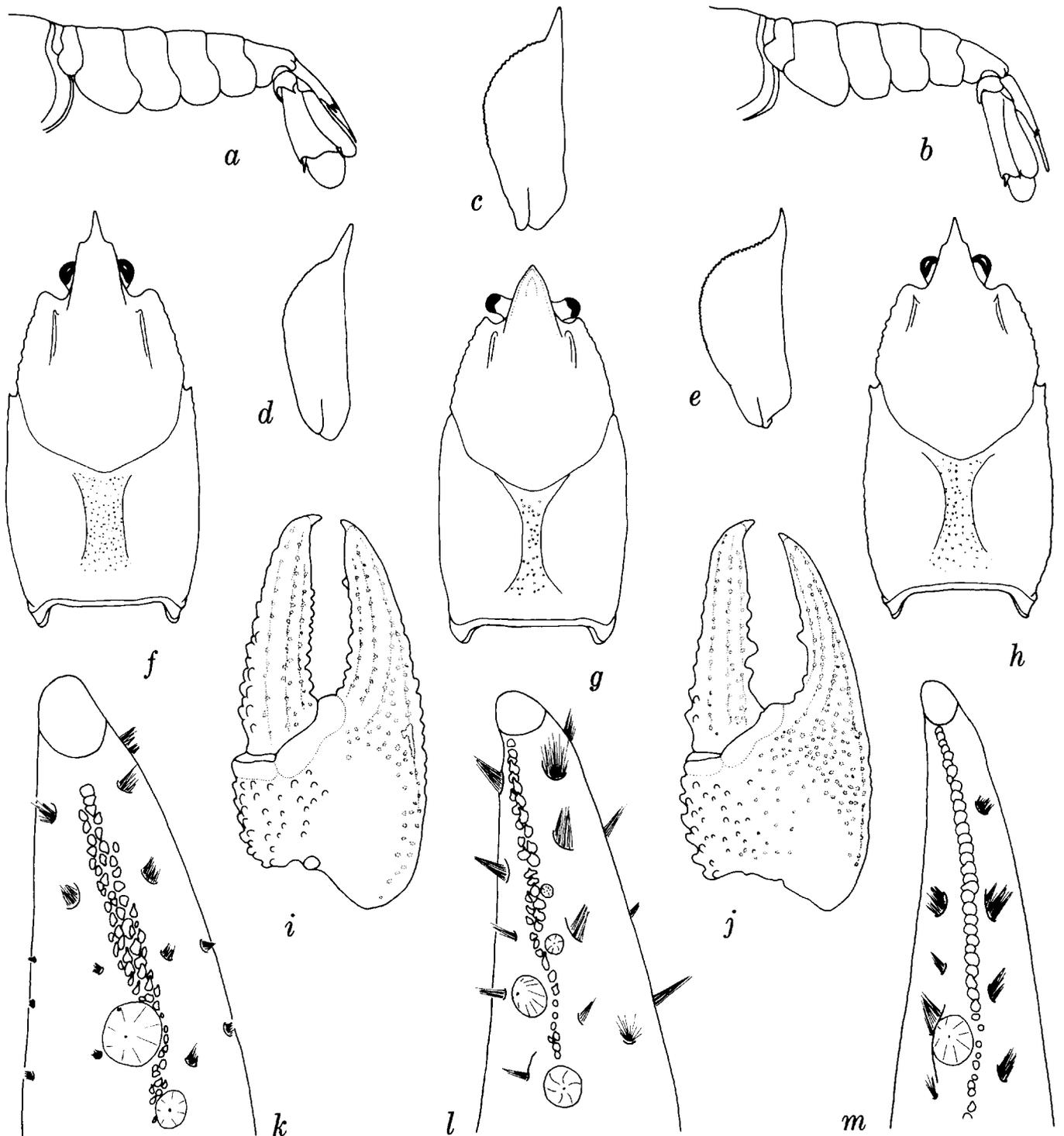


Fig. 1. a, *C. halli*, Lateral view of abdomen; b, *C. englishi*, Lateral view of abdomen; c, *C. cymatilis* Antennal scale; d, *C. catagius*, Antennal scale; e, *C. halli*, Antennal scale; f, *C. halli*, Dorsal view of carapace; g, *C. sphenoides*, Dorsal view of carapace; h, *C. englishi*, Dorsal view of carapace; i, *C. obstipus*, Dorsal view of chela; j, *C. cymatilis*, Dorsal view of chela; k, *C. graysoni*, Opposable margin of distal end of propodus; l, *C. latimanus*, Opposable margin of distal end of propodus; m, *C. cymatilis*, Opposable margin of distal end of propodus.

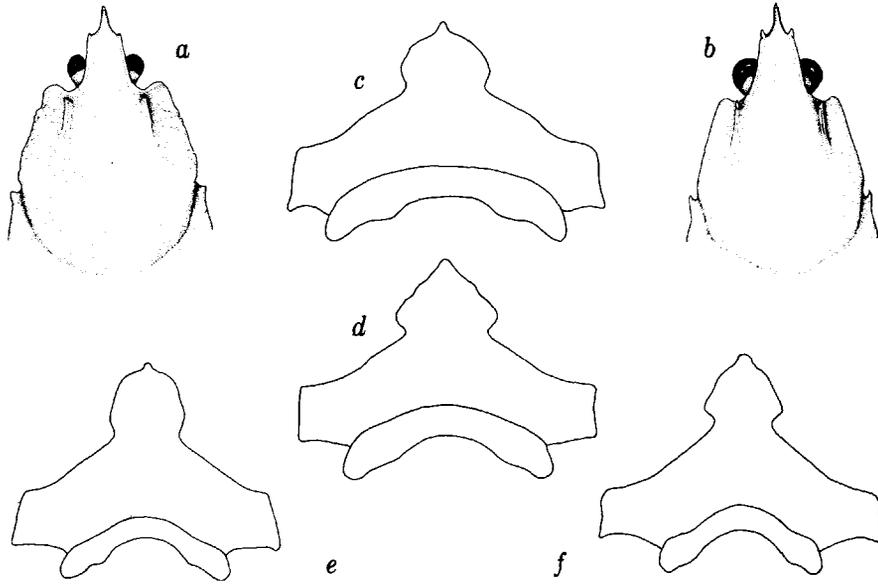


Fig. 2. a, *C. latimanus*, Dorsal view of carapace; b, *C. latimanus*, Juvenile, Dorsal view of carapace; c, *C. graysoni*, Epistome with gently bent epistomal zygoma; d, *C. striatus*, Epistome with moderately well-arched epistomal zygoma; e, *C. striatus*, Epistome with moderately well-arched epistomal zygoma; f, *C. obstipus*, Epistome with well-arched epistomal zygoma.

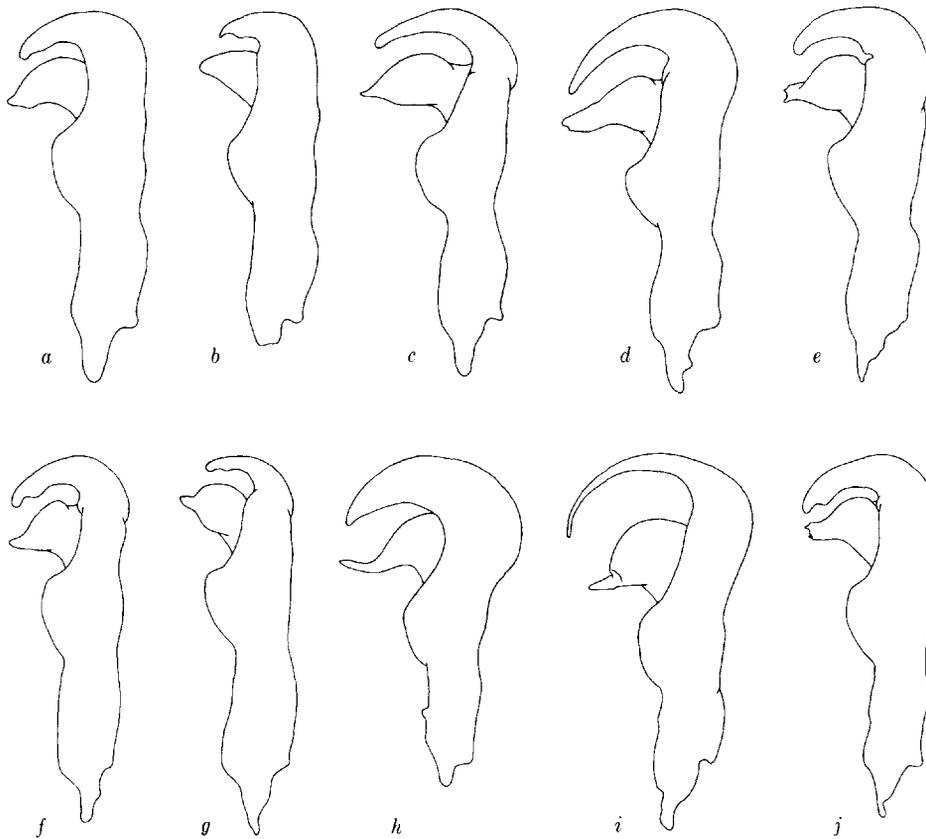


Fig. 3. Lateral view of left first pleopod of eight species of *Depressicambarus*. a-g, i-j, Male, form I; h, Male, form II: a, *C. catagius*, Guilford Co., N.C.; b, *C. cymatilis*, Murray Co., Ga.; c, *C. englishi*, Haralson Co., Ga.; d, *C. graysoni*, Lincoln Co., Tn.; e, *C. graysoni*, Grayson Co., Ky.; f, *C. halli*, Haralson Co., Ga.; g, *C. obstipus*, Lawrence Co., Al.; h, *C. reduncus*, Chatham Co., N.C.; i, *C. reduncus*, Fairfield Co., S.C.; j, *C. sphenoides*, Cumberland Co., Tn.

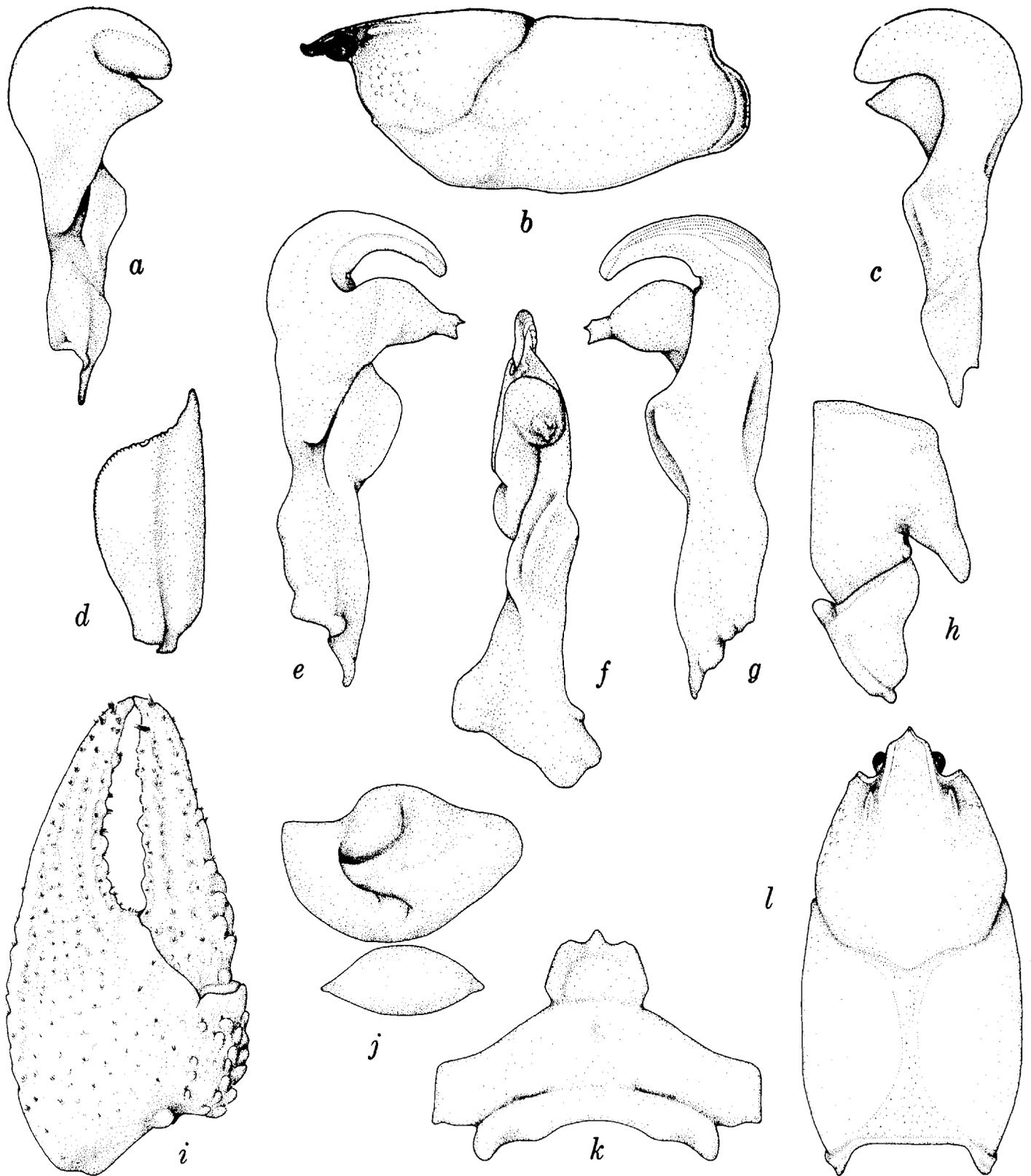


Fig. 4. *Cambarus graysoni*. a, Mesial view of first pleopod of topotypic male, form II; b, Lateral view of carapace of topotypic male, form I; c, Lateral view of first pleopod of topotypic male, form II; d, Antennal scale of topotypic male, form I; e, Mesial view of first pleopod of topotypic male, form I; f, Caudal view of first pleopod of topotypic male, form I; g, Lateral view of first pleopod of topotypic male, form I; h, Basipodite and ischiopodite of third pereiopod of topotypic male, form I; i, Dorsal view of chela, Lincoln Co., Tn.; j, Annulus ventralis of topotypic female; k, Epistome of topotypic male, form I; l, Dorsal view of carapace of topotypic male, form I.

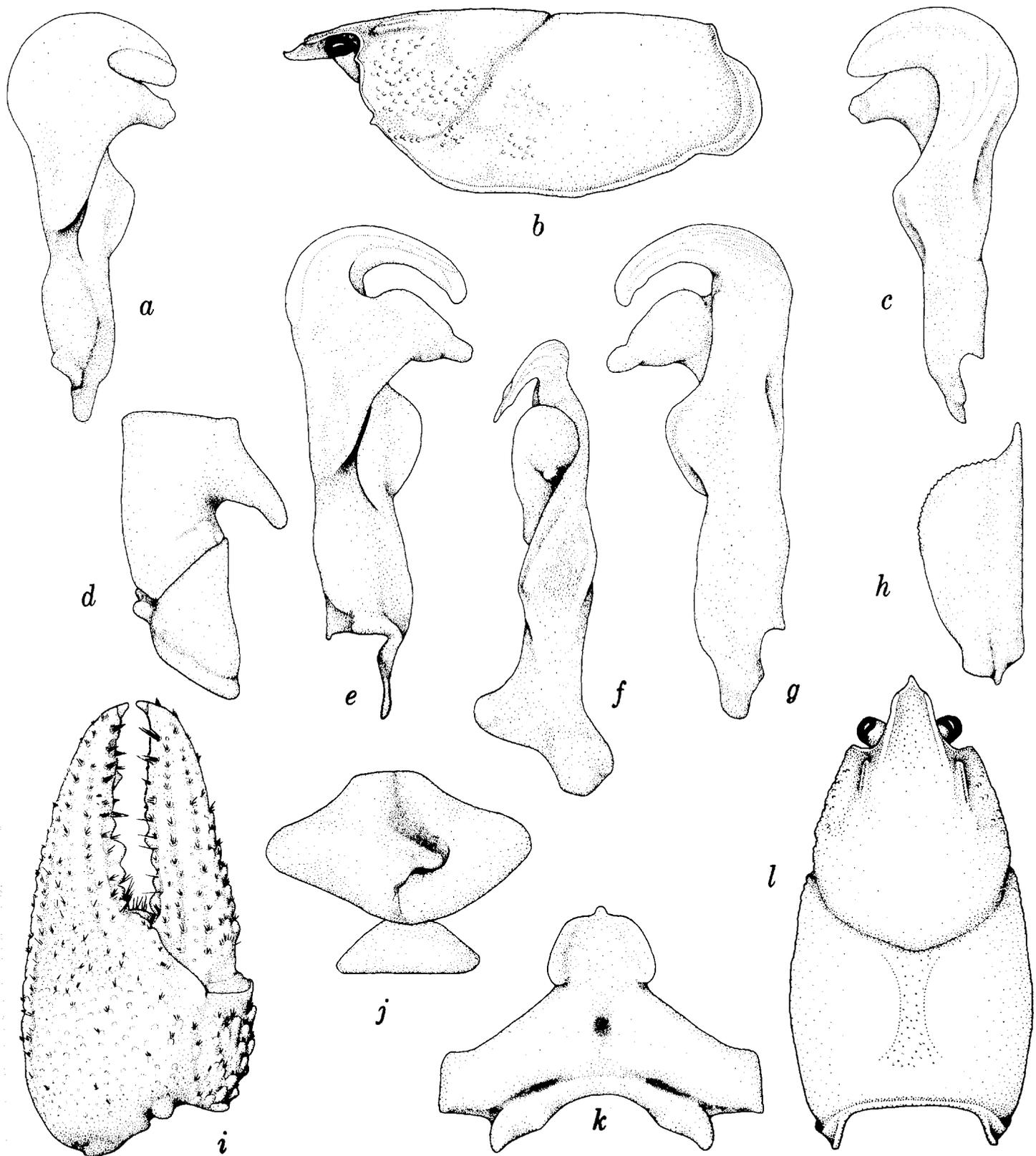


Fig. 5. *Cambarus latimanus*. a, Mesial view of first pleopod of topotypic male, form II; b, Lateral view of carapace of topotypic male, form I; c, Lateral view of first pleopod of topotypic male, form II; d, Basipodite and ischiopodite of topotypic male, form I; e, Mesial view of first pleopod of topotypic male, form I; f, Caudal view of first pleopod of topotypic male, form I; g, Lateral view of first pleopod of topotypic male, form I; h, Antennal scale of topotypic male, form I; i, Dorsal view of chela, topotypic male, form I; j, Annulus ventralis of topotypic female; k, Epistome of topotypic male, form I; l, Dorsal view of carapace of topotypic male, form I.

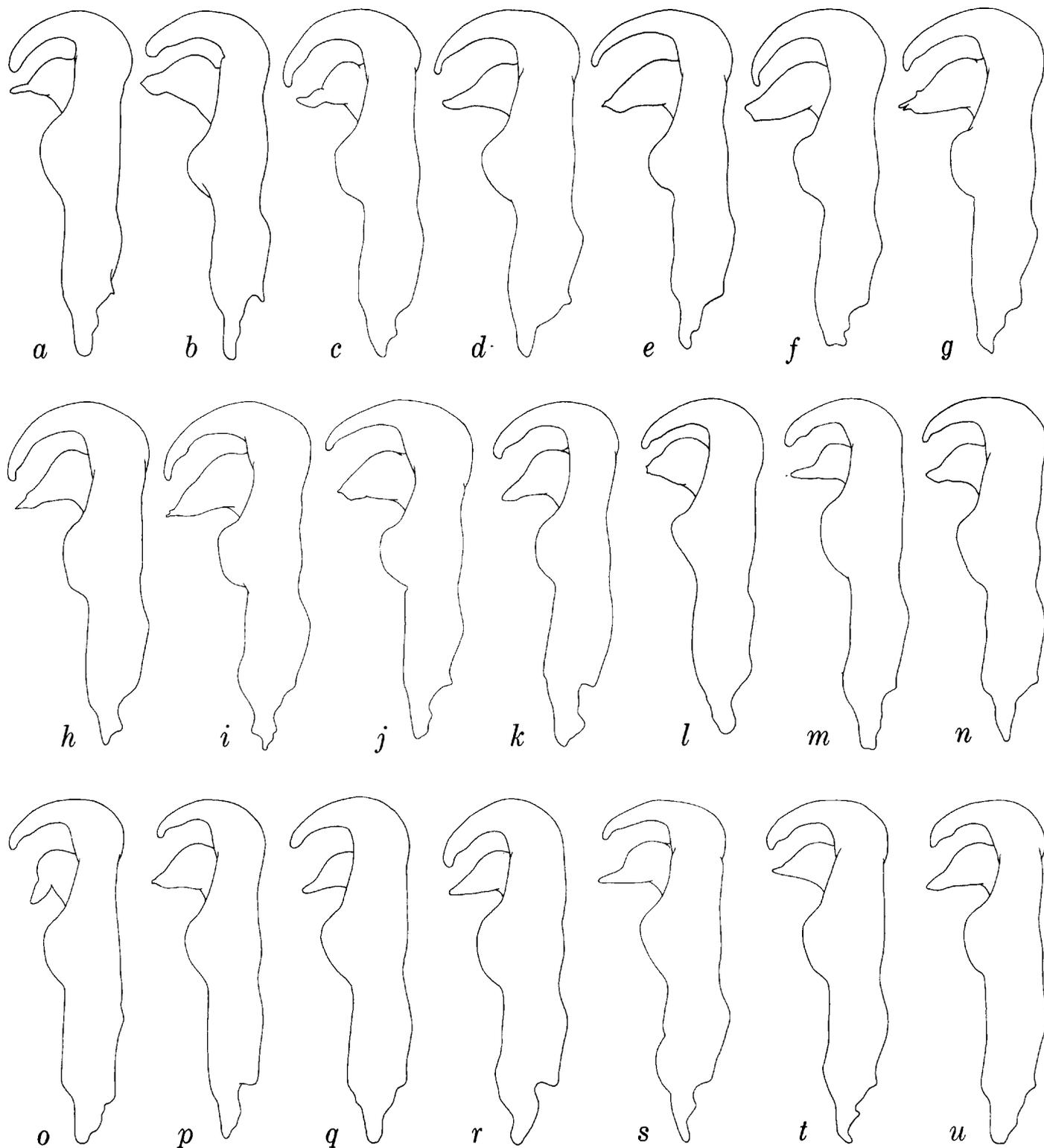


Fig. 6. *C. latimanus*. Lateral view of left first pleopod, male, form I. *a-b*, Polk Co., Tn.; *c-d*, Craven Co., N.C.; *e-g*, Durham Co., N.C.; *h*, Halifax Co., N.C.; *i*, Onslow Co., N.C.; *j*, Orange Co., N.C.; *k*, Aiken Co., S.C.; *l*, Anderson Co., S.C.; *m*, Chester Co., S.C.; *n*, Fairfield Co., S.C.; *o*, Greenville Co., S.C.; *p*, Oconee Co., S.C.; *q*, Pickens Co., S.C.; *r-u*, Richland Co., S.C.

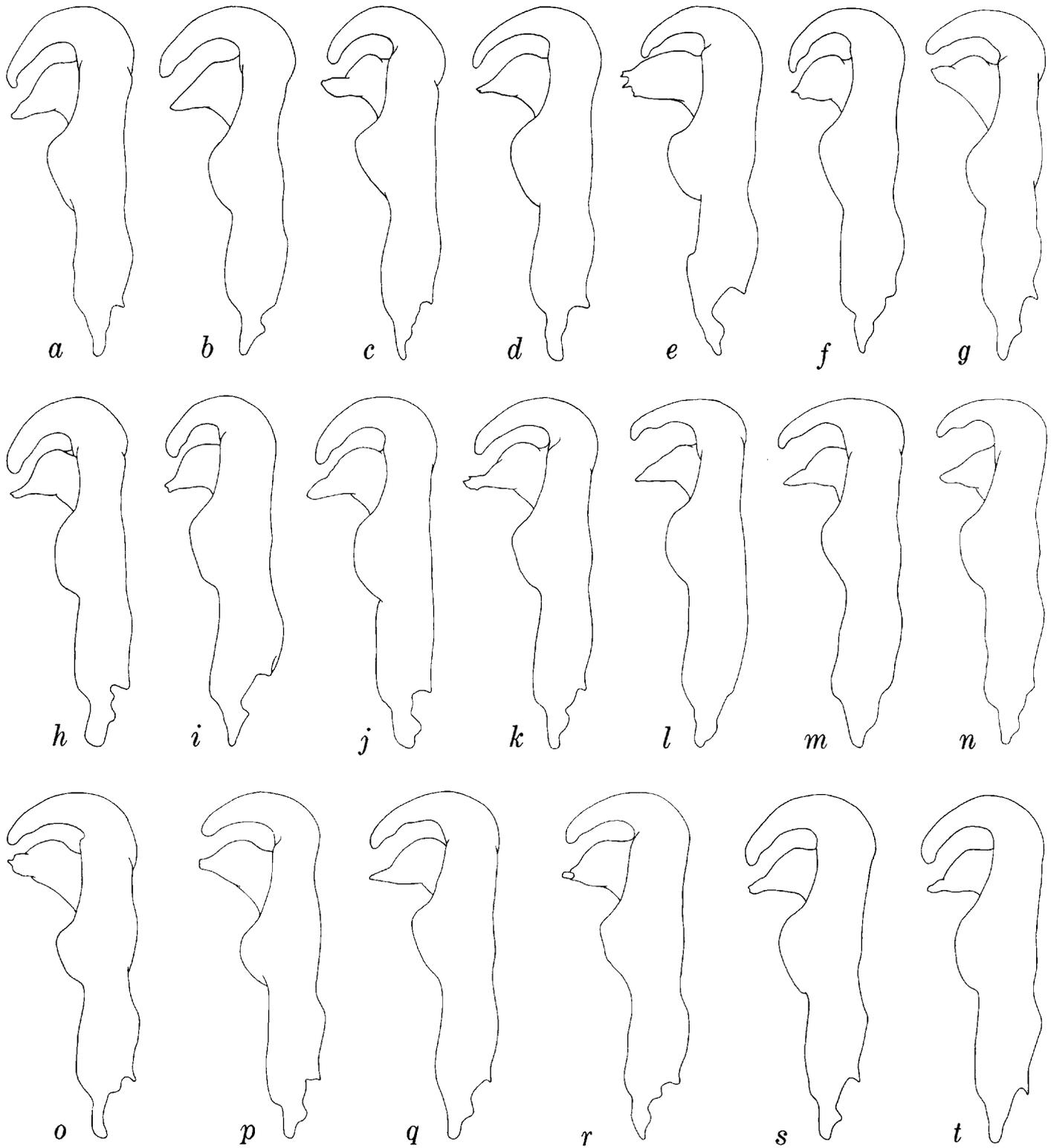


Fig. 7. *C. latimanus*. Lateral view of left first pleopod, male, form I. *a-b*, Lee Co., AL; *c*, St. Clair Co., AL; *d*, Shelby Co., AL; *e*, Talladega Co., AL; *f*, Tallapoosa Co., AL; *g*, Bartow Co., Ga.; *h*, Bibb Co., Ga.; *i*, Carroll Co., Ga.; *j*, Chattooga Co., Ga.; *k*, Douglas Co., Ga.; *l*, Elbert Co., Ga.; *m*, Hancock Co., Ga.; *n*, Madison-Franklin cos., Ga.; *o*, Pickens Co., Ga.; *p*, Polk Co., Ga.; *q*, Richmond Co., Ga.; *r*, Walton Co., Ga.; *s-t*, Liberty Co., FL.

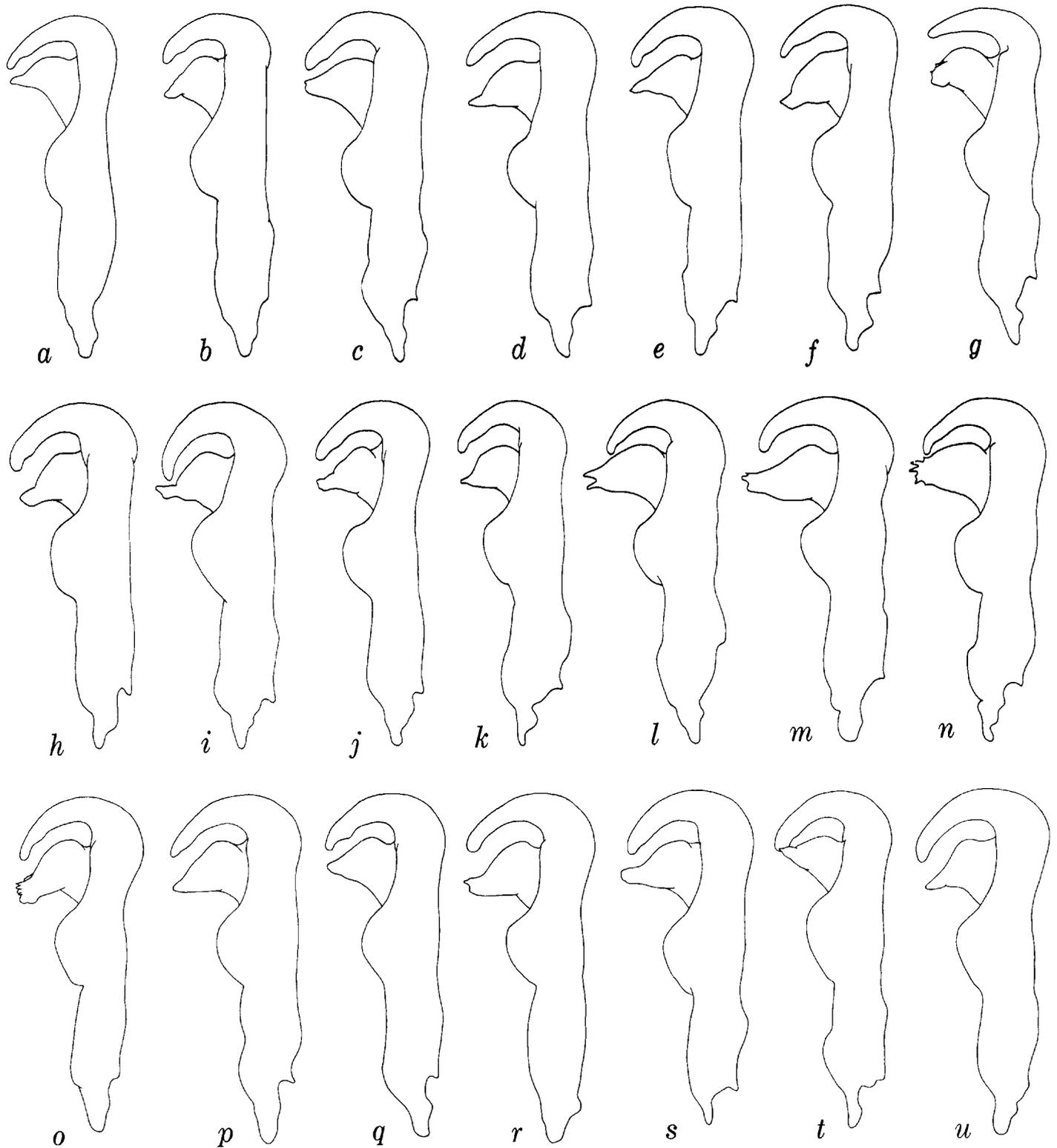


Fig. 8. *C. latimanus*. Lateral view of left first pleopod, male, form I. *a-g*, Calhoun Co., Al.; *h*, Chambers Co., Al.; *i*, Cherokee Co., Al.; *j*, Chilton Co., Al.; *k-o*, Clay Co., Al.; *p-r*, Cleburne Co., Al.; *s-t*, Coosa Co., Al.; *u*, Lee Co., Al.

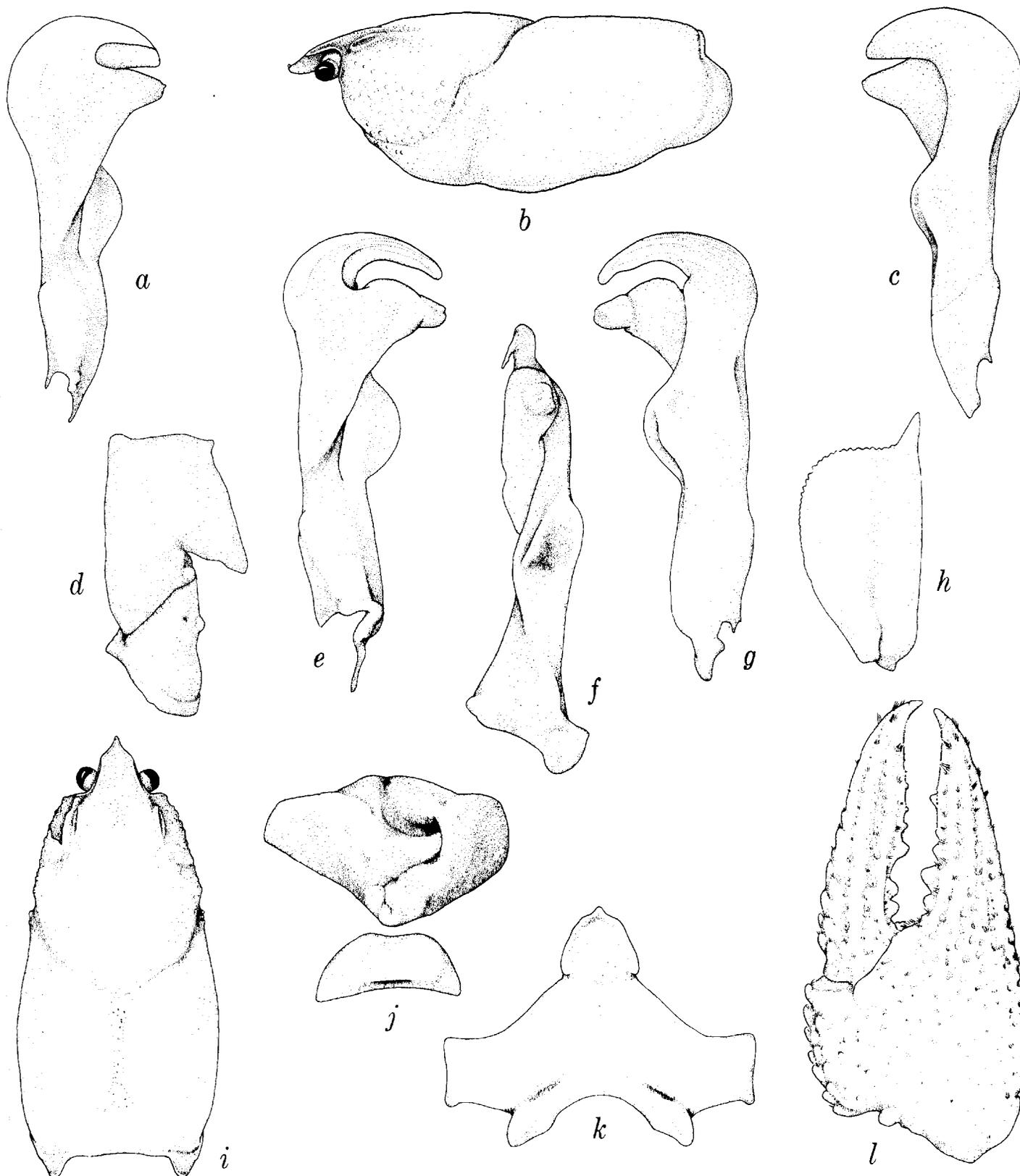


Fig. 9. *Cambarus pyronotus*, new species. *a*, Mesial view of first pleopod of morphotypic male; *b*, Lateral view of carapace of holotype; *c*, Lateral view of first pleopod of morphotypic male; *d*, Basipodite and ischiopodite of third pereiopod of holotype; *e*, Mesial view of first pleopod of holotype; *f*, Caudal view of first pleopod of holotype; *g*, Lateral view of first pleopod of holotype; *h*, Antennal scale of paratype female; *i*, Dorsal view of carapace of holotype; *j*, Annulus ventralis of allotype; *k*, Epistome of morphotypic male; *l*, Dorsal view of chela of morphotypic male.

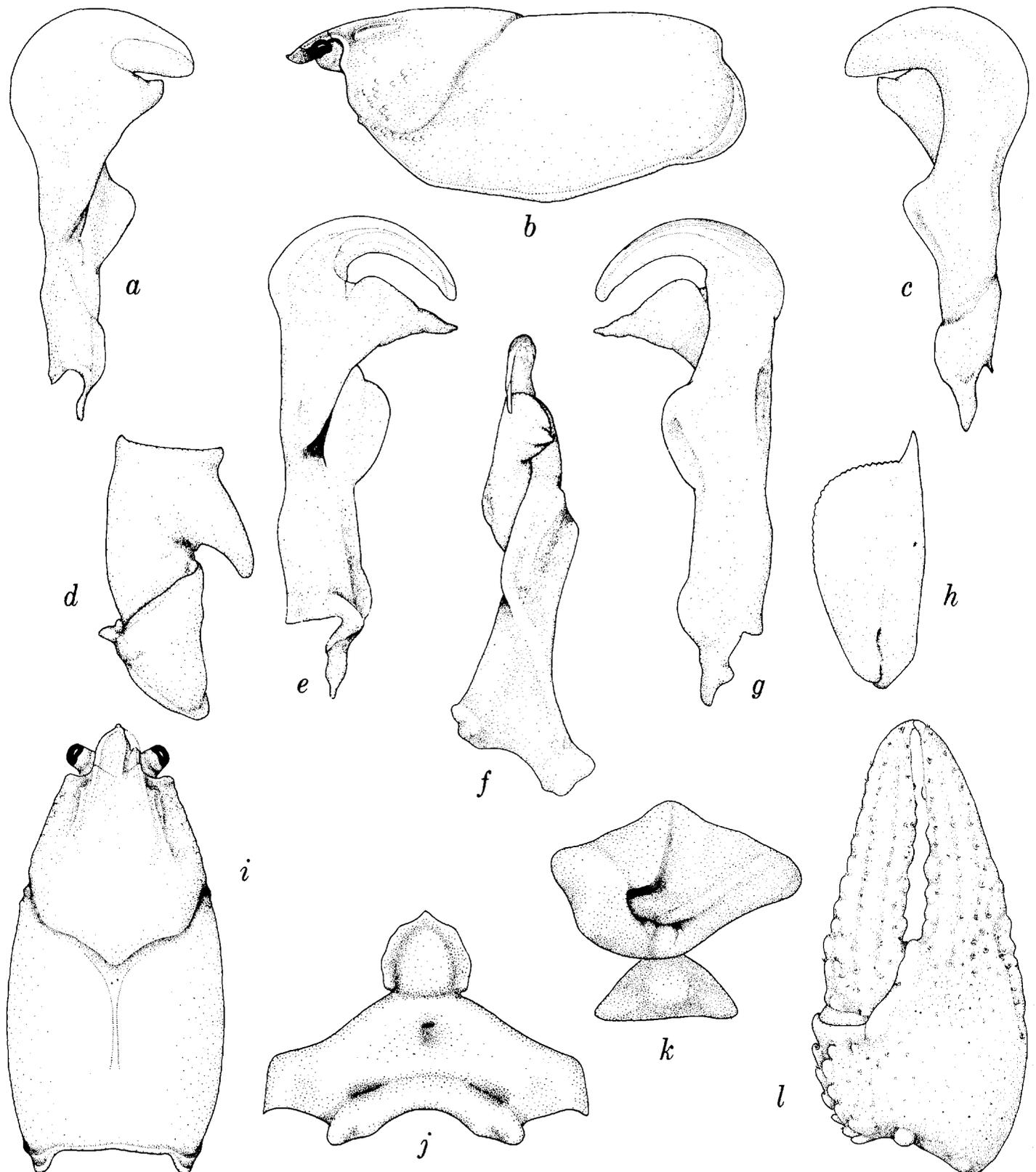


Fig. 10. *Cambarus striatus*. *a*, Mesial view of first pleopod of totypic male, form II; *b*, Lateral view of carapace of totypic male, form I; *c*, Lateral view of first pleopod of totypic male, form II; *d*, Basipodite and ischiopodite of third pereopod of totypic male, form I; *e*, Mesial view of first pleopod of totypic male, form I; *f*, Caudal view of first pleopod of totypic male, form I; *g*, Lateral view of first pleopod of totypic male, form I; *h*, Antennal scale of totypic male, form II; *i*, Dorsal view of carapace of totypic male, form I; *j*, Epistome of totypic male, form I; *k*, Annulus ventralis of totypic female; *l*, Dorsal view of chela of totypic male, form I.

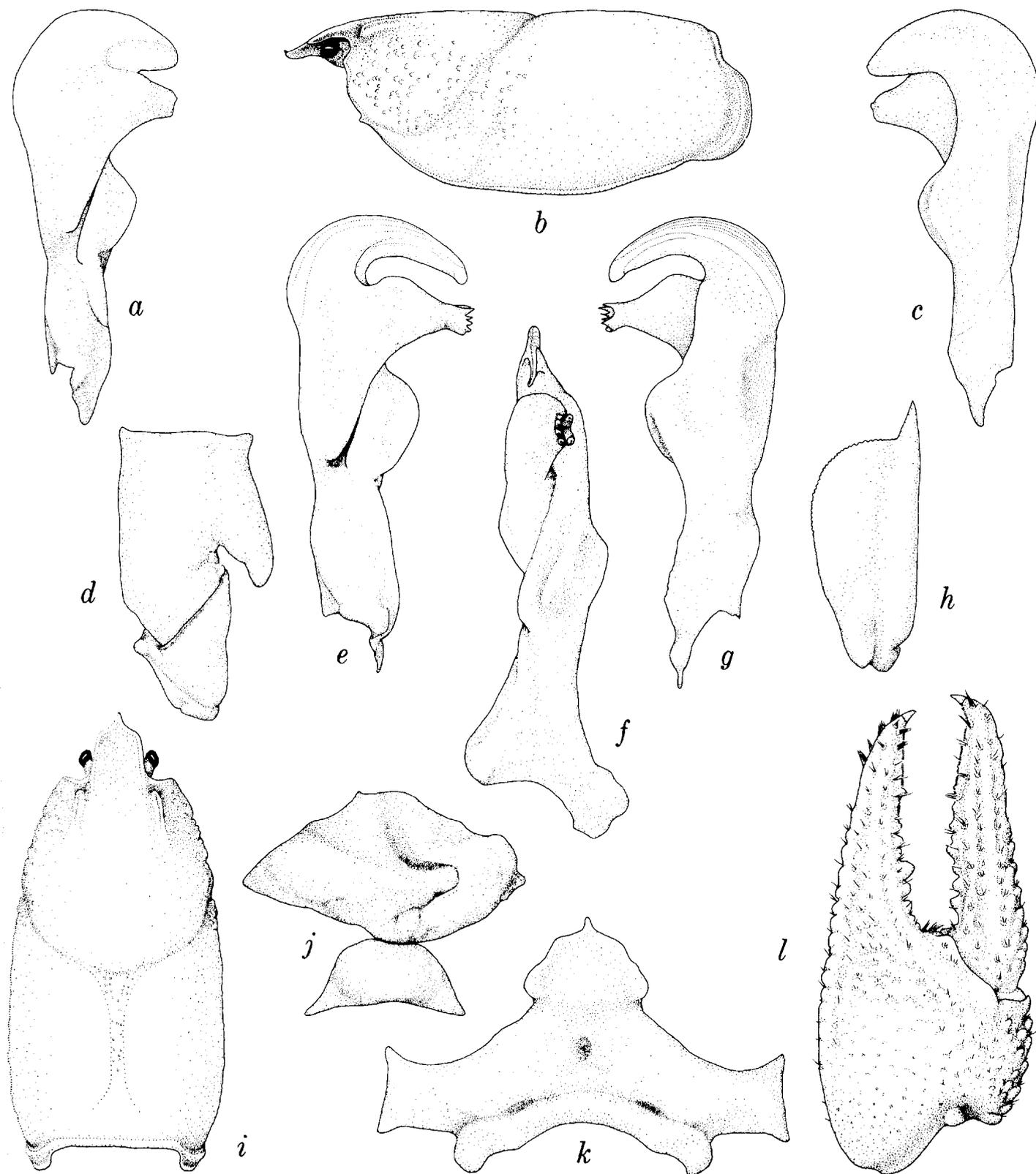


Fig. 11. *Cambarus striatus*. Bradley Co., Tn. (Mobile R. dr.). a, Mesial view of first pleopod of male, form II; b, Lateral view of carapace of male, form I; c, Lateral view of first pleopod of male, form II; d, Basipodite and ischiopodite of third pereiopod of male, form I; e, Mesial view of first pleopod of male, form I; f, Caudal view of first pleopod of male, form I; g, Lateral view of first pleopod of male, form I; h, Antennal scale of male, form II; i, Dorsal view of carapace of male, form I; j, Annulus ventralis of female; k, Epistome of male, form I; l, Dorsal view of chela of male, form I.

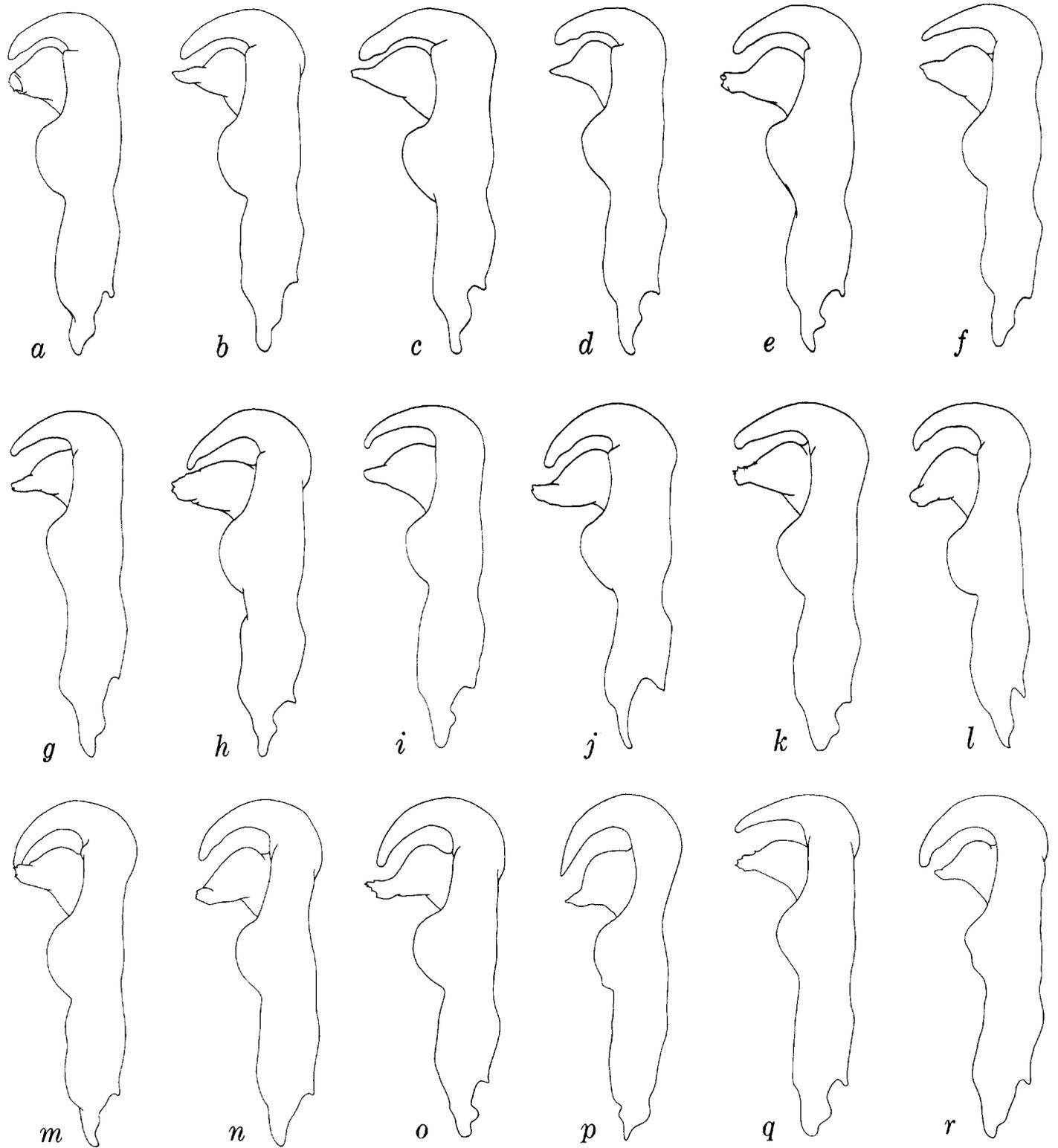


Fig. 12 *C. striatus*. Lateral view of left first pleopod, male, form I. *a*, Blount Co., Al.; *b*, Cullman Co., Al.; *c-d*, DeKalb Co., Al.; *e*, Etowah Co., Al.; *f-g*, Fayette Co., Al.; *h*, Hardin Co., Tn.; *i*, Henry Co., Al.; *j-k*, Jefferson Co., Al.; *l-n*, Lee Co., Al.; *o-p*, Macon Co., Al.; *q*, Madison Co., Al.; *r*, Marion Co., Al.

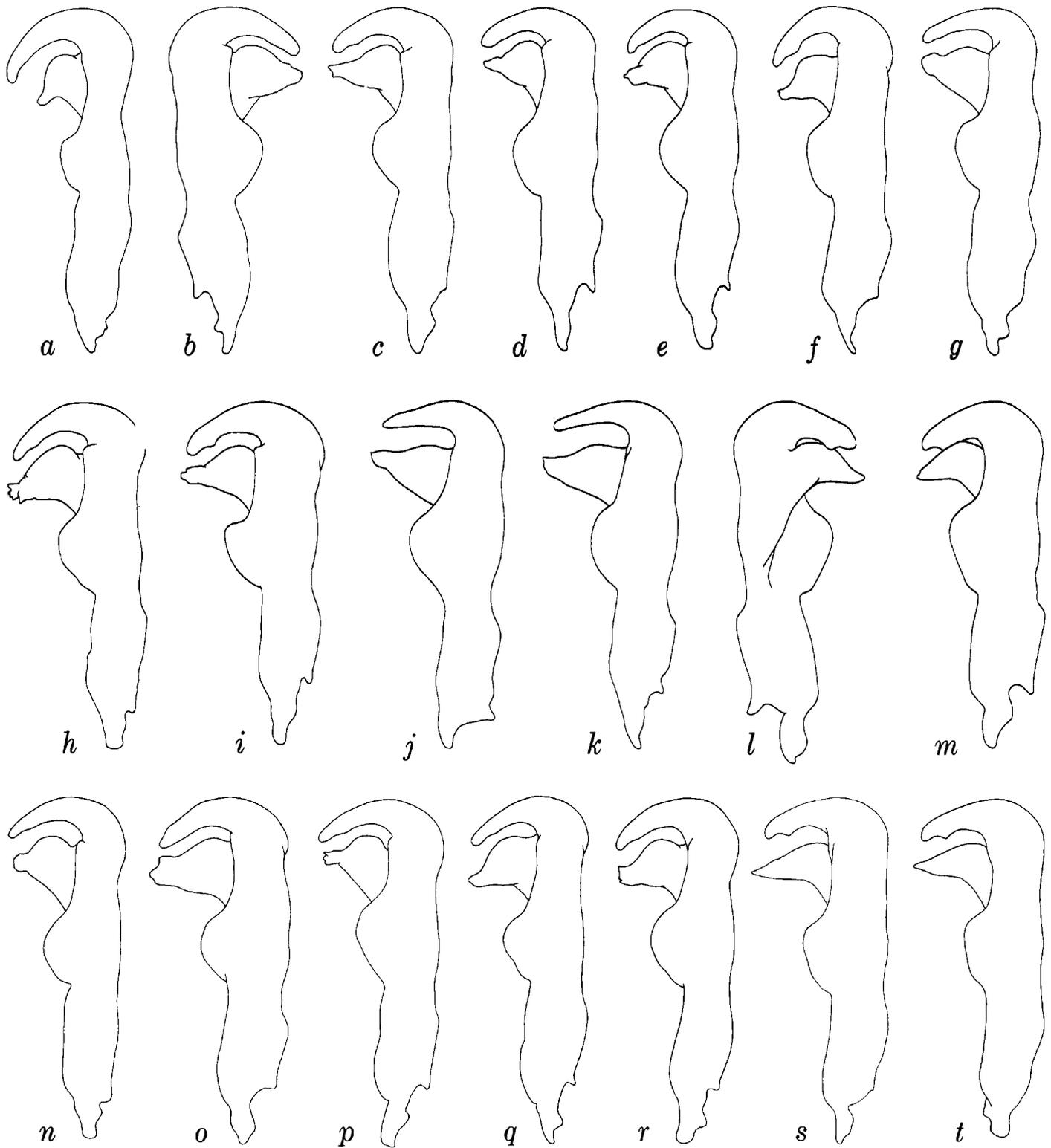


Fig. 13. *C. striatus*. *a, c-k, m-t*, Lateral view (*l*, Mesial view) of left first pleopod (*b*, right first pleopod), male, form I. *a*, Marion Co., Al.; *b-e*, Marshall Co., Al.; *f*, Randolph Co., Al.; *g*, Sumter Co., Al.; *h*, Franklin Co., Al.; *i-k*, Tuscaloosa Co., Al.; *l-m*, Dawson Co., Ga.; *n-o*, Gordon Co., Ga.; *p*, Harris Co., Ga.; *q*, Walker Co., Ga.; *r*, Whitfield Co., Ga.; *s-t*, Wilkinson Co., Ga.

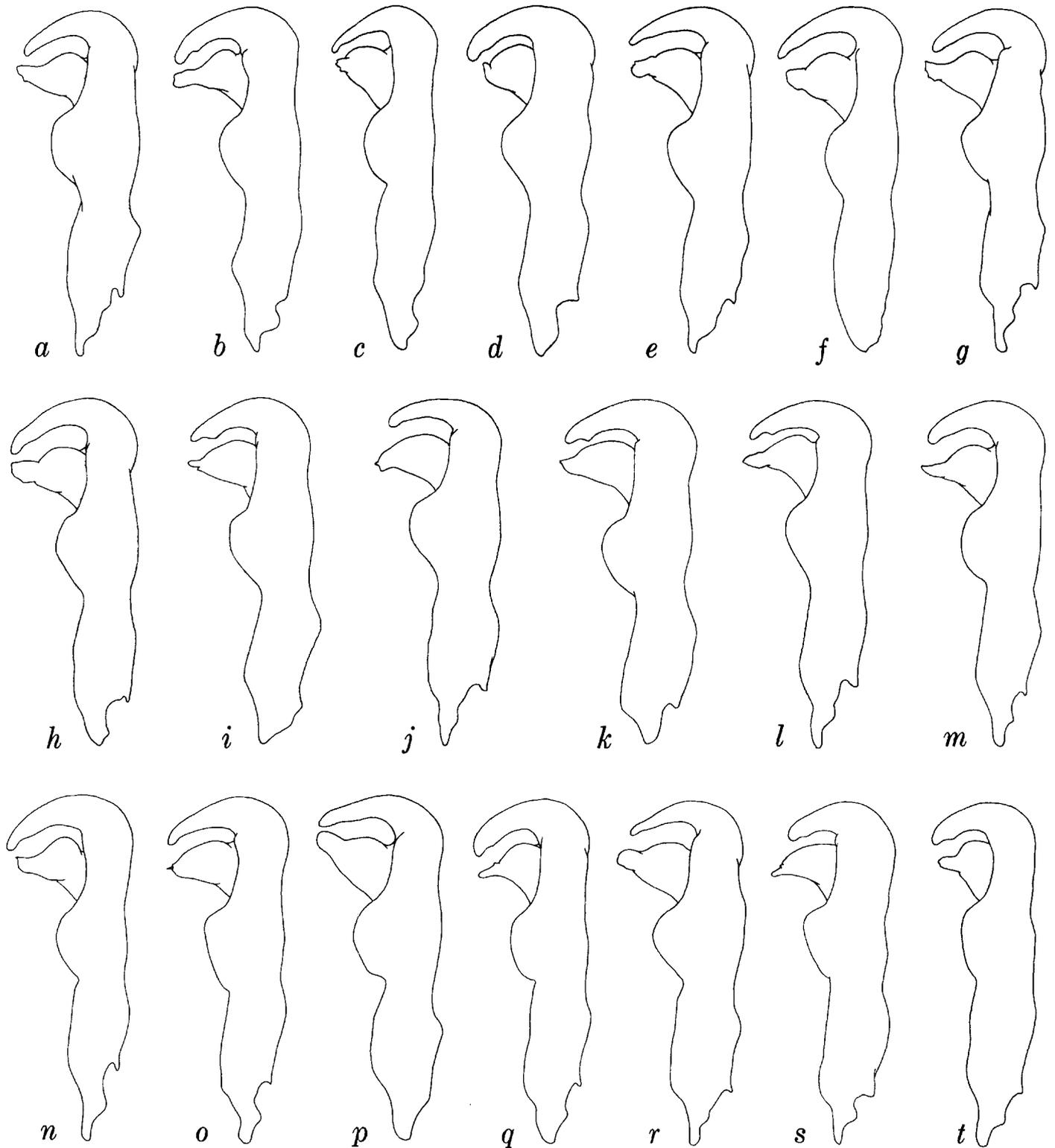


Fig. 14. *C. striatus*. Lateral view of left first pleopod, male, form I. *a*, Bledsoe Co., Tn.; *b*, Cheat-ham Co., Tn.; *c*, Coffee Co., Tn.; *d*, Davidson Co., Tn.; *e*, Hardin Co., Tn.; *f-h*, Henderson Co., Tn.; *i*, Knox Co., Tn.; *j*, Lincoln Co., Tn.; *k*, Loudon Co., Tn.; *l*, Montgomery Co., Tn.; *m*, Rhea Co., Tn.; *n*, Rutherford Co., Tn.; *o*, Scott Co., Tn.; *p*, Lafayette Co., Ms.; *q*, Lowndes Co., Ms.; *r*, Monroe Co., Ms.; *s-t*, Winston Co., Ms.