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NEW SPECIES AND RELATIONSHIPS OF THE  
MEMBERS OF THE GENUS *FALLICAMBARUS*

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In an attempt to obtain additional specimens of *Fallicambarus strawni* (Reimer, 1966:11), Jean E. Pugh, my wife Georgia, and I spent several days in the southwestern part of Arkansas, in April 1973, collecting burrowing crayfishes. Due to recent heavy rains, the task of digging for them was made somewhat less arduous than it otherwise might have been, and, as a result, not only was a good series of this crayfish secured from four localities, but also members of two undescribed species of the genus were obtained.

Upon comparing the undescribed forms with specimens of other members of the genus, it became apparent that *Fallicambarus* as now defined comprises two rather distinct species groups for which subgeneric designations are here proposed. Among the morphological features that deserve mention are the undivided, uniformly calcified telson (Fig. 3h) in *F. strawni* and *F. byersi* (Hobbs, 1941:118). To my knowledge, such a telson is known elsewhere only in certain crayfishes occurring in the Southern Hemisphere (e.g., members of the genera *Engaeus* and *Parastacus*). In *F. strawni* (Fig. 3h), *F. byersi*, and in other members of the genus, the mesial ramus of the uropod is devoid of lateral, and frequently of median, spines; in contrast, that of *F. macneesei* (Black, 1967:173) (Fig. 3f) rivals in its spination the corresponding ramus in *Procambarus (Acucauda) fitzpatricki* Hobbs (1971:461) and *Procambarus (Girardiella) hagenianus* (Faxon, 1884:141).

Another similarity to certain crayfishes of the Southern Hemisphere exists in at least two members of the genus *Fallicambarus*. In them, the cephalic lobe of the pleuron of

the second abdominal segment is reduced to the extent that it fails to overlap the pleuron of the first segment (Fig. 3*b, c*). In most crayfishes, this overlap is typical (Fig. 3*a*).

Of unusual interest to me was finding that in some of the members of this genus the ischium of the first pereopod possesses a recurved, or at least angular, prominence on the proximal postaxial lateral surface that articulates with an elevated knoblike condyle on the corresponding distolateral surface of the coxa. This prominence (Fig. 3*d*), here designated the *sufflamen*, serves as a brake in the backward elevation of the cheliped. In some members of the genus, not only is the sufflamen absent, but also the distolateral knob on the corresponding coxa is small and deflected distally (Fig. 3*e*). The presence or absence of the sufflamen in the several members of the genus is noted below.

Following are diagnoses of the genus *Fallicambarus* and of proposed subgenera, descriptions of two new species, notes on *F. strawni*, and a discussion of relationships within the genus and its probable common origin with *Procambarus* (*Tenuicambarus*) *tenuis* Hobbs (1950:194). Figure 4 depicts my concept of the relationships of these crayfishes and provides a key for recognizing the members of the genus *Fallicambarus*.

*Acknowledgments*: Special thanks are extended to Dr. Pugh and to my wife for their invaluable assistance in collecting the specimens on which most of this manuscript is based. I am also grateful to Fenner A. Chace, Jr., and to Margaret A. Daniel for their critical reading of the manuscript.

#### Genus *Fallicambarus*

*Fallicambarus* Hobbs, 1969:111.

*Diagnosis*: Adults with rostrum devoid of marginal spines. Mesial margin of palm of chela with row of fewer than 12 tubercles; opposable margin of dactyl usually with prominent excision. Areola linear or obliterated. Antennal scale more than twice as long as broad. First pleopods of first form male symmetrical and terminating in two or three distinct parts (mesial process, central projection and, occasionally, cephalic process; caudal element always absent) bent caudally or caudomesially at angle of 90 degrees or more to main shaft or forming broad arc; central projection corneous, blade-like or tapering (but flattened laterally) and lacking, except in *F. byersi*, subapical notch; non-corneous mesial process never bulbiform but often appearing twisted and usually

with eminence on cephalic (morphological) border slightly distal to base; cephalic process, when present, small, at least partially corneous, situated mesially at base of mesial process, and directed caudally or caudadistally (modified from Hobbs, 1969:111).

*Type-species*: *Cambarus strawni* Reimer, 1966:11.

*Gender*: Masculine.

#### Subgenus *Fallicambarus*

*Diagnosis*: First pleopod of male with proximomesial spur. Cheliped lacking sufflamen except in *F. macneesei*; chela with tubercles over most of dorsal surface, and lateral margin of palm and basal portion of immovable finger rounded or subserrate. Second pereiopod with mesial surface of chela and that of carpus lacking dense mats of plumose setae. Ischium of third or third and fourth pereiopods with hooks. Coxa of fourth pereiopod with conspicuously large boss. Abdomen narrowly joined to thorax except in *F. macneesei* and *F. dissitus*. Antennal scale very narrow except in *F. macneesei*.

*List of Species*: *Fallicambarus (F.) dissitus* (Penn, 1955:73); *F. (F.) jeanae*, new species; *F. (F.) macneesei* (Black, 1967:173); *F. (F.) spectrum*, new species; *F. (F.) strawni*.

#### Subgenus *Creaserinus*, new subgenus

*Diagnosis*: First pleopod of male lacking proximomesial spur. Cheliped with sufflamen; chela with tubercles on dorsal surface largely limited to mesial two rows, and lateral margin of palm and basal portion of immovable finger costate. Second pereiopod with mesial surface of chela and part of that of carpus bearing dense mats of plumose setae except in *F. byersi*. Ischium of only third pereiopod with hooks. Coxa of fourth pereiopod with boss not conspicuously large. Abdomen broadly joined to thorax except in *F. byersi* and *F. oryktes*. Antennal scale comparatively broad except in *F. byersi* and *F. oryktes*.

*Type-species*: *Astacus fodiens* Cottle, 1863:217.

*Gender*: Masculine.

*List of Species*: *Fallicambarus (Creaserinus) byersi* (Hobbs, 1941:118); *F. (C.) fodiens*; *F. (C.) hedgpethi* (Hobbs, 1948:224); *F. (C.) hortoni* Hobbs and Fitzpatrick, 1970:829; *F. (C.) oryktes* (Penn and Marlow, 1959:197); and *F. (C.) uhleri* (Faxon, 1884:116).

*Etymology*: Named in honor of Dr. Edwin P. Creaser whose contribution to our knowledge of American crayfishes is invaluable.

#### **Fallicambarus (Fallicambarus) jeanae**, new species

##### Figure 1

*Diagnosis*: Mesial ramus of uropod without distolateral spine; telson with transverse suture but lacking lateral spines; abdomen conspicuously narrower than cephalothorax; width of palm of chela of first pereiopod usually no less than 1.7 times length of its mesial margin, its color

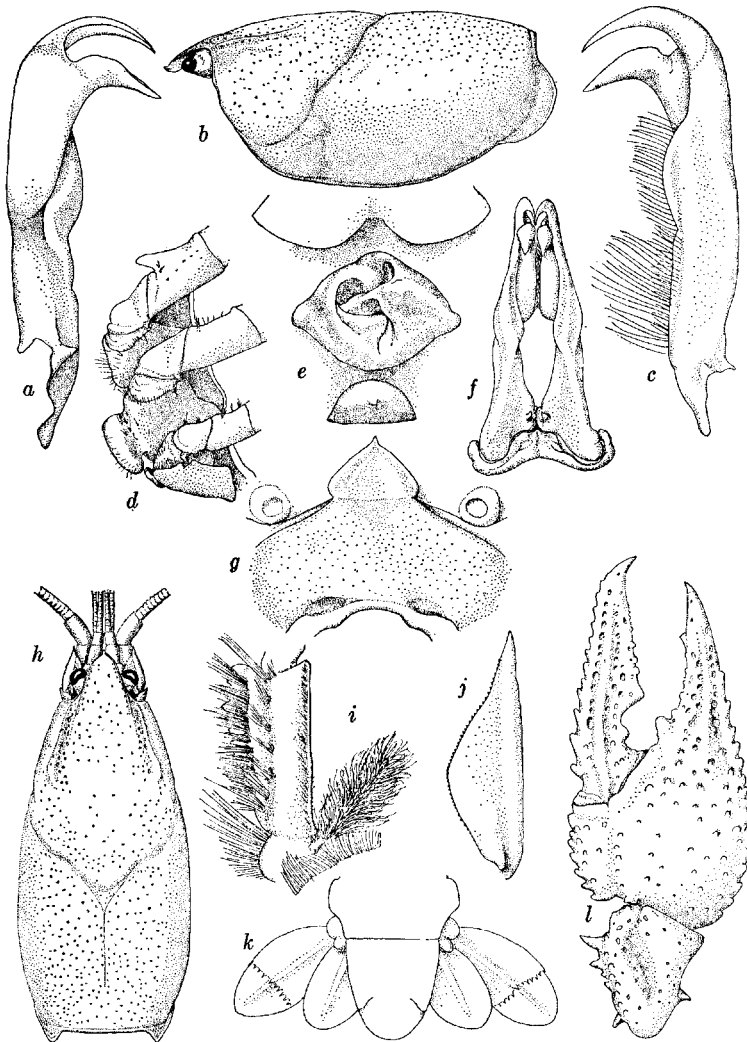


FIG. 1. *Fallicambarus (Fallicambarus) jeanae*, new species (pubescence removed from all structures illustrated except *c*, *d*, and *i*, and all depicting holotype except *e*, *f*, and *i*). *a*, Mesial view of first pleopod; *b*, Lateral view of carapace; *c*, Lateral view of first pleopod; *d*, Basal podomeres of third, fourth, and fifth pereiopods; *e*, Annulus ventralis of allotype; *f*, Caudal view of first pleopods of paratypic male, form I; *g*, Epistome; *h*, Dorsal view of carapace; *i*, Basal podomeres of third maxilliped of paratypic male, form I; *j*, Antennal scale; *k*, Dorsal view of telson and uropods; *l*, Dorsal view of distal podomeres of cheliped.

yellowish tan with bluish-brown tubercles. Male with hook on ischium of third pereopod only; first pleopod without cephalic process, and central projection strongly recurved with apex reaching, or almost reaching, level of cephalic base of projection and almost to level of arc of mesial process.

*Holotypic Male, Form I:* Body subovate, compressed (Fig. 1*b, h*). Abdomen much narrower than cephalothorax (11.0 and 16.2 mm); greatest width of carapace slightly greater than depth at caudodorsal margin of cervical groove (16.2 and 15.9 mm). Arcola linear over much of its length; length 39.0 percent of entire length of carapace (44.4 percent of postorbital length). Rostrum with convergent moderately thickened margins, lacking marginal spines or tubercles and contracting rather suddenly near apex to form short subtriangular acumen; upturned tip almost reaching distal end of penultimate podomere of antennular peduncle; dorsal surface of rostrum concave with submarginal setiferous punctations and scattered ones between. Subrostral ridges well developed and evident in dorsal aspect almost to midlength of rostrum. Postorbital ridge strong, grooved laterally and truncate cephalically. Suborbital angle obsolete. Branchiostegal spine vestigial, represented by slight obtuse prominence at junction of cervical groove and cephalolateral margin of carapace. Cervical spine or tubercle absent. Carapace punctate dorsally and laterally with few weak tubercles on extreme cephaloventral portion of branchiostegite.

Abdomen distinctly shorter than carapace (30.4 and 35.1 mm); pleura very short and rounded, only that of sixth segment with angular caudoventral margin; pleuron of first abdominal segment slightly overlapped by cephalic lobe of that of second. Cephalic section of telson (Fig. 1*k*) without spines but with dense setal tufts in caudolateral corners; entire telson and uropods setose dorsally. Proximal podomere of uropod (Fig. 1*k*) without spines. Both rami narrow, studded with dense short stiff setae and with conspicuous strong median rib, rib on mesial ramus extending almost to distal margin but lacking distal spine; distolateral spine absent; median rib on proximal lobe of lateral ramus terminating in spine; rib on distal lobe merging with flattened distal portion and not reaching distal margin.

Cephalomedian lobe of epistome (Fig. 1*g*) subtriangular with margins elevated (ventrally) and with transverse groove at base; main body comparatively long and lacking fovea. Ventral surface of proximal podomere of antennule lacking spine. Antennal peduncle without spines, flagellum reaching third abdominal tergum. Antennal scale (Fig. 1*j*) about 3.1 times longer than broad and with mesiodistal margin of lamellar area sloping distolaterally almost from midlength to distolateral spine; row of setae on mesial margin of scale continuing onto base of corneous tip of spine; spine reaching distal end of penultimate podomere of antennular peduncle. Ventral surface of ischium of third maxilliped (Fig. 1*i*)

with setae abraded, but, in other specimens, with submedian row of long stiff setae and submarginal lateral row of short finer ones.

Right chela (Fig. 1*l*) about twice as long as broad, strongly depressed; mesial margin of palm with row of 7 tubercles subtended dorsolaterally by row of 5 smaller ones; dorsal surface of palm with scattered squamous tubercles; lateral margin of chela with serrate row of tubercles extending almost from base to midlength of fixed finger; ventral surface with few scattered tubercles, large one opposite base of dactyl with other smaller ones proximal to it. Opposable margin of fixed finger with row of 6 tubercles along proximal three-fifths, proximalmost much larger than others in series; single large tubercle on lower level immediately distal to distal member of row; dorsal surface of finger with prominent submedian longitudinal ridge flanked by large deep punctations; proximally, ridge merging into flattened distal third of finger; distal half of lateral margin with row of 5 setiferous punctations; ventral surface with submedian ridge flanked by setiferous punctations. Opposable margin of dactyl with prominent tubercle in proximal excavation and with 7 tubercles, decreasing in size distally, between distal margin of excavation and base of distal fourth of finger; dorsal surface with submedian longitudinal ridge flanked in proximal fourth of finger by tubercles and distally by large deep punctations, ridge merging with flattened surface of finger in distal third of latter; mesial surface with serrate row of tubercles decreasing in size distally; ventral surface as in fixed finger but with few tubercles flanking ridge proximolaterally.

Carpus of cheliped with sinuous furrow and scattered punctations dorsally; dorsomesial surface tuberculate; mesial surface with row of 4 tubercles increasing in size distally, distalmost spikelike and directed mesiodistally; ventromesial surface with several small tubercles, ventrodistal margin with large tubercle on lateral condyle and another near median line; lateral surface punctate. Merus with dorsal surface tuberculate, tubercles increasing in size distally and three subdistal ones acute with corneous tips; mesial and lateral surfaces sparsely punctate; ventral surface with lateral row of 8 small tubercles and mesial one of 12 slightly larger ones increasing in size distally; ventral distolateral margin without spine. Mesioventral margin of basioischial podomere with single rounded tubercle slightly distal to fracture suture.

Chela of second pereopod with marginal rows of setae on palm, and carpus with dorsal row of long setae; mesial surfaces of both without tuft of plumose setae.

Ischium of third pereopod with simple hook extending proximally over basioischial articulation (Fig. 1*d*), not opposed by tubercle on basis. Coxa of fourth pereopod with massive caudomesial boss compressed laterally, thus directed almost in longitudinal plane of body; mesial and lateral surfaces of boss setiferous. Coxa of fifth pereopod lacking caudomesial boss but with setiferous ventral membrane.

First pleopods (Fig. 1*a, c, f*) reaching coxa of third pereopods, held

TABLE 1.—Measurements (mm) of *Fallicambarus (F.) jeanae*

|                            | Holotype | Allotype |
|----------------------------|----------|----------|
| Carapace:                  |          |          |
| Entire length              | 35.1     | 34.3     |
| Postorbital length         | 30.8     | 30.2     |
| Width                      | 16.2     | 16.4     |
| Height                     | 15.9     | 16.3     |
| Areola:                    |          |          |
| Width                      | —        | —        |
| Length                     | 13.7     | 13.1     |
| Rostrum:                   |          |          |
| Width                      | 5.0      | 5.0      |
| Length                     | 5.5      | 5.0      |
| Chela:                     |          |          |
| Length, palm mesial margin | 7.9      | 6.5      |
| Palm width                 | 13.7     | 11.4     |
| Length, lateral margin     | 25.8     | 21.2     |
| Dactyl length              | 19.1     | 15.1     |
| Abdomen:                   |          |          |
| Width                      | 11.0     | 11.0     |
| Length                     | 30.4     | 30.6     |

deep within sternum, and largely hidden by setae extending caudally and mesially from ventral margins of sternum and mesial surface of boss on fourth pereopod; proximomesial spur well developed; terminal elements subparallel and curved throughout their length; mesial process somewhat grooved and acute distally; central projection tapering from base and recurved with apex almost reaching same level as cephalic base of projection; cephalic process absent.

The second form male is unknown.

*Allotypic Female:* Excluding secondary sexual characteristics, differing from holotype in following respects: rudiment of branchiostegal spine slightly more prominent; left chela with row of 8 tubercles on mesial margin of palm; second tubercle from base in row on opposable margin of fixed finger of chela larger than first, ridge on dorsal surface of finger less prominent; opposable margin of dactyl of chela with row of only 5 tubercles distal to excavation; merus of chela with ventromesial row of only 10 tubercles on right chela and ventrolateral row of only 6 on left. (See measurements.)

Annulus ventralis (Fig. 1e) subrhomboidal, 1.3 times broader than long, moderately deeply embedded in sternum, and immovable, although broad fissure present between it and adjacent cephalic sternal plate.

Cephalomedian area excavate with trough curving dextrally, concavity limited caudosinistrally by prominent sloping tongue; sinus originating in trough on cephalic side of tongue, curving around dextral base of latter and extending sinistrally slightly across median line, there turning caudally in sinuous course and ending on caudal wall, not reaching caudal margin. Sternite between fifth pereopods broadly oval cephalically, about twice as broad as long, elevated ventrally, and with submedian prominence.

*Color Notes:* Dominant color of carapace pale mauve; rostral margins, postorbital ridges, and paired subtriangular areas caudal to postorbital ridges dark brown; latter joining along cervical groove and in caudal gastric area where almost black; caudal margin of carapace dark brown. First abdominal tergum dark brown, remaining ones pale yellowish tan with paired dorsolateral cream splotches and each edged caudally with vermilion. Telson and uropods cream with pale tan suffusion basally. Antennule and antenna with dark yellowish-brown peduncles; flagella with each article yellowish tan basally and dark brown distally; lateral margin of antennal scale almost black. Cheliped mostly yellowish tan dorsally with dark bluish-brown tubercles and bluish-brown suffusion on dorsal margin of merus, dorsomesial surface of carpus, and dorsomesial part of dactyl. Ventral surface of cheliped yellowish cream. Remaining pereopods with coloration similar to that of cheliped but lacking dark brown tubercles.

*Type-locality:* A seepage area, 1.8 miles east of the Clark County line, Hot Springs County, Arkansas, on State Route 84. The crayfish were dug from complex (highly branching) burrows with two or three openings to the surface. The soil was basically a sandy clay with shallow pockets rich in organic material and some gravel. The area supported a moderate growth of grasses and sedges, and nearby was a stand of trees including members of the genera *Acer*, *Juniperus*, and *Pinus*. This crayfish is known only from the type-locality.

*Disposition of types:* The holotypic male, form I (no. 144672) and the allotypic female (no. 144673) are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes consisting of 4 ♂ I, 1 ♀, 3 juvenile ♂, and 2 juvenile ♀. All of the specimens were collected on 21 April 1973.

*Variations:* The apex of rostrum reaches between the midlength and the distal extremity of the penultimate podomere of the antennular peduncle. The branchiostegal spine is absent or very small. The cephalomedian lobe of the epistome ranges from subtriangular to suboval. The antennal scale is highly variable both in width and in the contour of the mesial margin and cannot always be distinguished from that of the species described below. The mesial margin of the palm of the chela of the first pereopod bears 6 to 8 tubercles, and there are 5 or 6 tubercles in the row immediately dorsolateral to it; the opposable margin of the fixed finger bears 4 to 7 tubercles, and that of the dactyl, 5 to 8. The mesial surface



of the carpus supports 1 to 3 tubercles. The ventral surface of the merus has a lateral row of 6 to 9 tubercles and a mesial one of 11 to 13; the ischium may lack or possess as many as 3 small tubercles on its ventro-mesial margin. The mesial process of the right first pleopod of the holotype is somewhat flared distally and bears paired subapical angles.

*Relationships:* See the section on Affinities below.

*Etymology:* This crayfish is named in honor of my friend and former student, Dr. Jean E. Pugh, who, in company with my wife and me, assisted in collecting the specimens on which this description is based.

**Fallicambarus (Fallicambarus) spectrum**, new species

Figure 2

*Diagnosis:* Mesial ramus of uropod without distolateral spine; telson with transverse suture and with or without paired lateral spines; abdomen conspicuously narrower than cephalothorax; width of palm of chela of first pereiopod usually no more than 1.6 times length of its mesial margin, its color grayish blue with dark blue tubercles. Male with hook on ischium of third pereiopod only; first pleopod without cephalic process, and central projection strongly recurved with apex extending proximal to level of cephalic base of projection as well as proximal to that of "distal" margin of arc of mesial process.

*Holotypic Male, Form 1:* Body subovate, compressed (Fig. 2*b, h*). Abdomen narrower than cephalothorax (9.8 and 14.3 mm); greatest width of carapace subequal to depth at caudodorsal margin of cervical groove (14.3 and 14.4 mm). Areola linear along most of its length; length 39.3 percent of entire length of carapace (44.3 percent of post-orbital length). Rostrum with convergent moderately thickened margins, lacking marginal spines or tubercles, ending rather suddenly at base of short triangular acumen, latter limited only by prolongation of subrostral ridges; upturned tip reaching midlength of penultimate podomere of antennular peduncle; dorsal surface of rostrum deeply concave with submarginal setiferous punctations and few scattered between. Subrostral ridges well developed and evident to tip of rostrum. Postorbital ridges strong, grooved laterally and gently merging with carapace cephalically. Suborbital angle absent. Branchiostegal spine small but with corneous acute tip. Cervical spine absent. Carapace punctate dorsally and laterally with few weak tubercles cephalolaterally, few moderately large ones on ventral flank of upturned cephalolateral portion of cervical groove.

Abdomen shorter than carapace (28.8 and 30.8 mm); pleura very short and rounded, only that of sixth segment with subangular caudoventral margin; pleuron of first abdominal segment not overlapped by cephalic lobe of that of second. Cephalic section of telson (Fig. 2*k*) with caudo-lateral angle produced in acute spine; entire telson and uropods setose dorsally. Proximal podomere of uropod (Fig. 2*k*) without spines; both rami similar to those in *F. jeanae*.

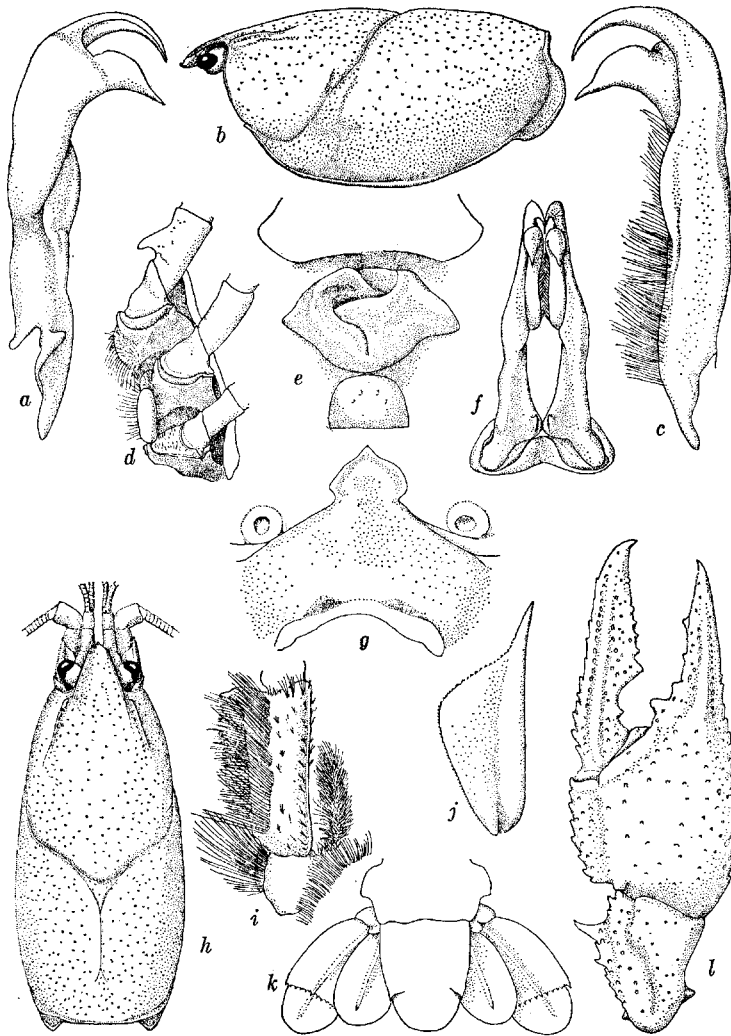


FIG. 2. *Fallicambarus (Fallicambarus) spectrum*, new species (pubescence removed from all structures illustrated except *c*, *d*, and *i*, and all depicting holotype except *e*, *f*, and *i*). *a*, Mesial view of first pleopod; *b*, Lateral view of carapace; *c*, Lateral view of first pleopod; *d*, Basal podomeres of third, fourth, and fifth pereopods; *e*, Annulus ventralis of allotype; *f*, Caudal view of first pleopods of paratypic male, form I; *g*, Epistome; *h*, Dorsal view of carapace; *i*, Basal podomeres of third maxilliped of paratypic male, form I; *j*, Antennal scale; *k*, Dorsal view of telson and uropods; *l*, Dorsal view of distal podomeres of cheliped.

Cephalomedian lobe of epistome (Fig. 2g) subcordiform with margins slightly thickened and elevated ventrally; main body long and lacking fovea. Ventral surface of proximal podomere of antennule with vestigial spine (tubercle) near midlength. Antennal peduncle without spines, flagellum reaching third abdominal tergum. Antennal scale (Fig. 2j) about 2.8 times longer than wide; mesiodistal margin of lamellar area with base of distolateral slope originating distinctly distal to midlength; row of setae on mesial margin of scale continuing onto base of corneous tip of spine; spine reaching slightly beyond midlength of penultimate podomere of antennular peduncle. Third maxilliped (Fig. 2i) with ischium bearing submedian longitudinal row of long stiff setae, submarginal lateral row of shorter finer ones, and few additional short, some plumose, setae between rows.

Right chela (Fig. 2l) slightly more than twice as long as broad, distinctly depressed; mesial margin of palm with row of 7 tubercles subtended dorsolaterally by row of 6 smaller ones; dorsal surface of palm with scattered squamous tubercles; lateral margin of chela with serrate row of tubercles extending almost from base to level of second tubercle on opposable margin of fixed finger; ventral surface of palm also with squamous tubercles and 1 prominent tubercle opposite base of dactyl. Opposable margin of fixed finger bearing row of 3 tubercles, proximalmost largest, along proximal half and single large tubercle on lower level at base of distal third; dorsal surface of finger with broad submedian longitudinal ridge flanked by setiferous punctations; distal three-fifths of lateral margin with row of 5 setiferous punctations; ventral surface with weak submedian ridge flanked by setiferous punctations. Opposable margin of dactyl with moderately large tubercle in proximal excavation, latter followed distally by row of 7 tubercles, decreasing in size distally, and reaching distal fifth of finger; dorsal surface with submedian longitudinal ridge flanked proximally by tubercles, and, along most of its length, by setiferous punctations; mesial surface with serrate row of tubercles decreasing in size distally; ventral surface similar to that of fixed finger but with cluster of small tubercles at lateral base.

Carpus of cheliped with sinuous furrow and punctations dorsally; dorsomesial surface tuberculate; mesial surface also tuberculate with 2 tubercles distinctly larger than others, distalmost heavier and acute; ventromesial surface with few small tubercles; ventrodistal margin with large tubercle on lateral condyle and another submedian in position; lateral surface punctate. Merus tuberculate dorsally with tubercles increasing in size distally; 2 subdistal members with corneous tips; mesial and lateral surfaces punctate; ventral surface with lateral row of 13 small rounded tubercles and mesial row of 14 of which several more distal ones subacute with corneous tips. Distolateral articular knob without spine. Mesoventral margin of basioischial podomere with 3 small tubercles distal to fracture suture.

Chela of second pereopod with marginal rows of setae on palm, and

carpus with dorsal row of long setae, but mesial surfaces of both lacking tuft of plumose setae.

Ischium of third pereopod with simple hook extending proximally to distal extremity of basis (Fig. 2*d*), not opposed by tubercle on latter. Coxa of fourth pereopod with very large laterally compressed boss directed almost in longitudinal plane of body; mesial and lateral surfaces of boss setiferous. Coxa of fifth pereopod without boss but with setiferous ventral membrane.

First pleopod (Fig. 2*a, c, f*) reaching coxa of third pereopod, situated deep in sternum, and largely concealed by setae borne on margins of sternum and bosses of fourth pereopods; proximomesial spur prominent; terminal elements subparallel and curved throughout their length; mesial process somewhat flattened distally but acute; central projection tapering from base with apex directed proximally, surpassing level of cephalic base of projection and "distal" margin of arc of mesial process; cephalic process absent.

The second form male is unknown.

*Allotypic Female:* Excluding secondary sexual characteristics, differing from holotype in following respects: left rostral margin merging with subrostral ridge; tubercle on ventral surface of proximal podomere of antennular peduncle virtually obsolete; antennal scale distinctly narrower with cephalomesial margin sloping almost to midlength before turning proximolaterally, and spine on right member almost reaching base of ultimate podomere; chela about twice as long as broad; opposable margins of both fingers of chela with row of 5 tubercles, second from base largest; ventral surface of merus with mesial row of 12 (right with 8) tubercles and lateral row of 7; ischium with no tubercle on right and only 1 on left.

Annulus ventralis (Fig. 2*e*) subrhomboidal, about 1.7 times broader than long, deeply embedded in sternum, and immovable. Cephalomedian area excavate with trough curving strongly dextrally; prominent tongue extending almost horizontally from sinistral wall of concavity; sinus originating at cephalic base of tongue following it caudodextrally across median line, then turning sharply caudosinistrally to median line, there extending caudally and terminating before reaching caudal extremity of annulus. Sternite between fifth pereopods subrectangular; about 1.5 times as broad as long, elevated ventrally, but lacking submedian prominence.

First pleopod uniramous but well developed with distinct protopodite. (See measurements.)

*Color Notes:* Dominant color of carapace pale mauve gray; rostral margin and postorbital ridges almost black; paired subtriangular reddish-brown markings extending caudally from caudal extremity of postorbital ridges, their basal portions coalescing in median posterior gastric region, slightly overlapping cervical groove, and filling cephalic triangular vestige of areola. Hepatic region with pale reddish-tan suffusion; caudal margin of carapace edged with black. First abdominal tergum reddish brown

TABLE 2.—Measurements (mm) of *Fallicambarus (F.) spectrum*

|                            | Holotype | Allotype |
|----------------------------|----------|----------|
| Carapace:                  |          |          |
| Entire length              | 30.8     | 32.1     |
| Postorbital length         | 27.3     | 28.2     |
| Width                      | 14.3     | 14.0     |
| Height                     | 14.4     | 14.4     |
| Areola:                    |          |          |
| Width                      | —        | —        |
| Length                     | 12.1     | 12.8     |
| Rostrum:                   |          |          |
| Width                      | 4.4      | 4.4      |
| Length                     | 5.0      | 5.1      |
| Chela:                     |          |          |
| Length, palm mesial margin | 6.6      | 6.6      |
| Palm width                 | 10.0     | 9.3      |
| Length, lateral margin     | 21.9     | 18.5     |
| Dactyl length              | 14.7     | 12.5     |
| Abdomen:                   |          |          |
| Width                      | 9.8      | 8.4      |
| Length                     | 28.8     | 28.5     |

with succeeding terga progressively fading to uniformly reddish-tan telson and uropods; tergum also fading laterally, and pleuron concolorous with telson. Peduncle of antennule and antenna dark mauve gray, flagella with each article pale tan proximally, becoming dark gray distally; antennal scale with lateral thickened portion almost black. Chelipeds grayish blue dorsally with dark blue tubercles; ventral surface cream; remaining pereopods similar to cheliped but lacking dark blue tubercles.

*Type-locality and Range:* Complex burrows in roadside ditch, 2 miles east of Daisy, Pike County, Arkansas, on U.S. Hwy. 70. In addition to the grasses and sedges in the ditch, members of the genus *Pinus* and *Cornus florida* were abundant nearby.

The only other locality in which this species is known to occur is 1 mile east of Amity, Clark County, Arkansas, on St. Rte. 84 where the crayfish were also found in complex burrows. There, a first form male and a female were taken from the same burrow on 21 April 1973. The dominant trees there were members of the genus *Pinus* and *Liquidamber styraciflua*.

*Disposition of types:* The holotypic male, form I (no. 144674) and the allotypic female (no. 144675) are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes consisting

of 2 ♂ I, 3 ♀, and 1 juvenile ♀. Those specimens (1 ♂ I, 4 ♀, 1 juvenile ♂ and 2 juvenile ♀) from Clark County are not included in the type-series. The specimens from both localities were collected on 21 April 1973.

*Variations:* The rostrum is unique in the holotype in that the rostral ridges end abruptly at the base of the acumen instead of fusing with the subrostral ridges and continuing to the apex; the same occurs on the right side of the rostrum of the allotype; in all other specimens, however, the corresponding ridges fuse, and the subrostral ridge is sometimes evident, in dorsal aspect, only along the basal one-fourth or half of the rostrum. In only one specimen does the apex of the rostrum reach the distal end of the ultimate podomere of the antennular peduncle. The branchiostegal spine, always small, is absent in some specimens. Whereas in all of the specimens from the type-locality the pleuron of the second abdominal segment does not overlap that of the first, in only one of those from Clark County does it not overlap. The cephalic lobe of the epistome varies from subcordiform to subtriangular. The telson may lack lateral spines (possibly due to abrasion) or may have a pair of immovable spines and/or a pair of more mesial movable ones. The tubercles on the ventral surface of the proximal podomere of the antennular peduncle are either vestigial or absent. The antennal scale varies considerably in length and width, reaching various levels of the penultimate podomere of the antennular peduncle—as wide as in the holotype to narrower with the distomesial slope angling from midlength to the base of the distal third of the scale. The mesial margin of the palm of the chela bears a row of 6 to 9 (usually 7, and 9 only on 2 largest specimens from Clark County) tubercles subtended dorsolaterally by another row of 3 to 5. The number of tubercles on the opposable margin of the immovable finger varies from 4 to 7, and on that of the dactyl, 4 to 9. The number of tubercles in the ventrolateral row on the merus of the cheliped ranges from 4 to 13, and in the ventromesial row, 8 to 15. The number of tubercles on the ventromesial margin of the ischium of the cheliped ranges from 0 to 4. (See measurements.)

*Relationships:* See the section on Affinities below.

*Etymology:* Spectrum L.—apparition; so named because of the ghost-like appearance resulting from the predominantly pale cephalothorax, especially the branchiostegites.

*Fallicambarus* (*Fallicambarus*) *strawni* (Reimer)

Figure 3c, e, h

*Cambarus strawni* Reimer, 1966:11, figs. 9–18.

*Fallicambarus strawni*.—Hobbs, 1969:111, figs. 2f, 13j, 20i.

*Color Notes:* Dominant color of carapace pinkish cream overlain by markings of various shades of gray and vermilion; most of dorsum of cephalic region pink, fading laterally to buff with lavender suffusion; rostrum and postorbital ridges very dark gray; caudal gastric area and

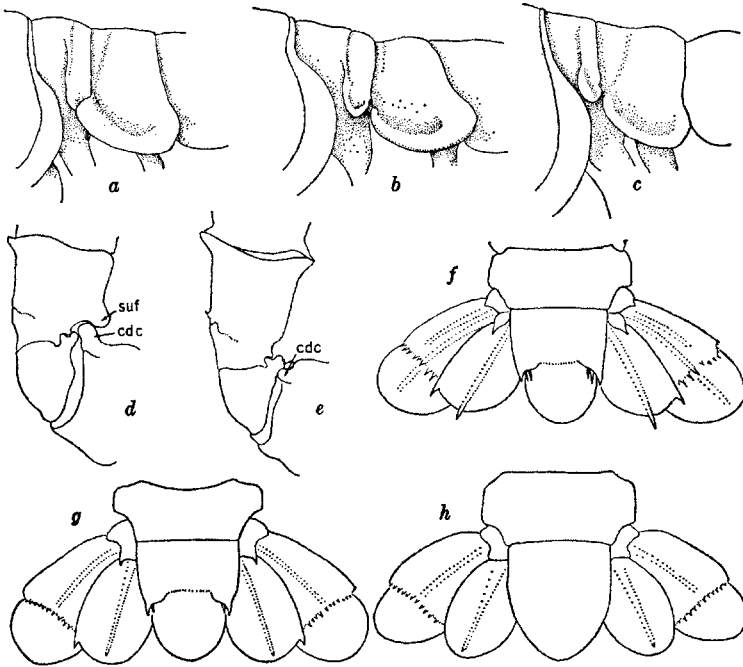


FIG. 3. Variations in *Fallicambarus*. a, Lateral view of caudal carapace and cephalic abdominal region of *F. (F.) macneesei*; b, Same of *F. (C.) byersi*; c, Same of *F. (F.) strawni*; d, Lateral view of coxa, basis and ischium of cheliped of *F. (C.) uhleri* (cdc, condyle on coxa; suf, sufflamen); e, Same of *F. (F.) strawni*; f, Dorsal view of caudal abdominal region of *F. (F.) macneesei*; g, Same of *F. (C.) fodiens*; h, Same of *F. (F.) strawni*.

cervical groove pale gray; cephalic triangle of areola dark gray, and linear portion and caudal triangle vermilion; paired pale gray longitudinal stripes flanking linear areola; remainder of branchiostegites, excluding dark bluish-gray caudal margin, very pale cream tan. Tergum of first abdominal segment and cephalic part of that of second maroon; terga of other segments yellowish tan, with vermilion splotches dorsally, fading caudally to telson, and all pleura lighter tan toward ventrolateral margin. Telson largely translucent but with vermilion to brick-red splotches cephalically, laterally, and along caudal margin. Uropod similarly translucent, but peduncle reddish tan; lateral ramus with reddish splotches lateral to median rib and over entire distal section; mesial ramus with red pigment largely restricted to median rib and distal third. Exposed parts of peduncles of antennules and antennae mostly bluish gray, and

flagella with each article buff proximally becoming dark gray distally; antennal scale margined in very dark bluish gray. Chelipeds basically tan with dense reticulations of intense dark grayish blue dominating dorsum of distal half of merus, that of carpus, and most of that of chela, lateral portion of propodus fading to pinkish cream; all tubercles, except for corneous extremities of some, very dark blue, almost black. Remaining pereopods similar in color to that of cheliped although with more red and less blue pigment on fifth. Ventral surface of body and pereopods cream, latter with blue pigment concentrated around more distal articulations.

*Range and Specimens Examined:* No specimens of this species have been reported to have been collected since the original description appeared. Reimer (op. cit.) recorded it from 2.7 miles northwest of Dierks, Howard County, Arkansas, on U.S. Hwy. 70, the type-locality, and from 4 miles west of Umpire, also in Howard County.

Additional collections were made in the following localities in Arkansas by Hobbs, et al., during April 1973: (1) Type-locality—2 ♂ I, 1 ♂ II, 1 ♀, 1 juvenile ♂, 1 juvenile ♀, April 21; (2) Seepage area on road shoulders, 0.1 mile east of the junction of U.S. Hwys. 59 and 70 on latter, Sevier County—4 ♂ I, 4 ♂ II, 13 ♀, 2 juvenile ♂, 5 juvenile ♀, April 20; (3) Seepage area 5.0 miles northeast of the junction of U.S. Hwys. 59 and 70 on latter, Sevier County—1 ♂ I, April 20; (4) Roadside ditch, 0.9 mile northeast of Pike-Howard County line, Pike County—1 ♂ I, 1 ♀, April 21.

*Life History Notes.*—First form males have been collected in April and June. No ovigerous females have been obtained, but the female specimen from Pike County was brought into the laboratory where she laid yellowish-orange eggs on May 17, most of which became detached. Believing those remaining on the abdomen to be infertile, I failed to note the date on which two of them hatched—probably in early June. The two young appeared to be devoid of body pigment when they became free from the mother; only the dark alimentary canal, pigment in the eye, and later the yellowish coloration of the hepatopancreas contrasted with the otherwise whitish translucent body. Unfortunately, neither of the young survived the third molt.

#### THE AFFINITIES OF THE MEMBERS OF THE GENUS *Fallicambarus*

In discussing the phylogeny of the genus *Cambarus* and related genera, Hobbs (1969:123) indicated several adaptive modifications in the cambaroid stock that enabled *Fallicambarus* derivatives from it to become independent of open bodies of water. He also discussed (p. 124) those secondary sexual features he considered to be primitive and commented on their subsequent modifications.

In comparing these crayfishes with those belonging to related genera, one is impressed by the similarities existing between *Fallicambarus macneesei* and *Procambarus (Tenuicambarus) tenuis*, likenesses that are far



too numerous to assume that they have resulted from convergence in two independently evolving stocks. Among the characters that they share in common are: (1) a somewhat compressed cephalothorax; (2) an abdomen broadly attached to the cephalothorax, not conspicuously narrower cephalically than the caudal thoracic region; (3) a divided telson with one or more spines in the caudolateral corners of the cephalic section; (4) a moderately broad antennal scale; (5) a cheliped with a well-developed sufflamen on the ischium; (6) a chela with the palm subovate in cross section, subserrate laterally, and possessing a dactyl with a very weak excision on the opposable margin; (7) a second pereiopod in which the mesial surface of the palm and distal portion of the carpus lack mats of plumose setae; (8) hooks on the ischia of the third and fourth pereiopods of the male; (9) a conspicuous boss on the coxa of the fourth pereiopod of the male; (10) a male first pleopod with three terminal elements and a proximomesial spur; (11) a rather broad mesial ramus of the uropod bearing a distolateral spine; and (12) an annulus ventralis with two comparatively simple, interlocking lobes.

These characteristics are considered here to be those of the ancestors of *P. tenuis* and of the *Fallicambarus* stock which existed during the middle Tertiary along the western flank of the early Cenozoic Mississippi embayment. Among the descendants from this stock, *F. macneesei* is the only member of the genus that exhibits all of these features, and thus links its congeners with the disjunct *Procambarus tenuis*, the only species assigned to the subgenus *Tenuicambarus*. Closely allied to *F. macneesei*, but having lost or modified certain of the primitive features, is *F. dissitus* in which the abdomen and the antennal scale are somewhat narrower; the cheliped has lost the sufflamen; the chela is more depressed, and the excision on the opposable margin of the dactyl is strong; the cephalic process of the first pleopod is lacking, and the annulus ventralis is strongly asymmetrical.

*Fallicambarus jeanae*, *F. spectrum*, and *F. strawni* are, in general, more similar to *F. dissitus* than to *F. macneesei*. All three species have a somewhat laterally inflated carapace; the abdomen is distinctly narrow basally; the telson of *F. jeanae* (Fig. 1k) and *F. spectrum* (Fig. 2k) retain the transverse suture on the telson, but in *F. strawni* (Fig. 3h) there is no trace of it; the antennal scale is quite narrow; the cheliped of the three lack the sufflamen (Fig. 3e); the palm of the chela is strongly depressed and broad, especially so in *F. jeanae* and *F. spectrum*, and is subserrate laterally; the excision on the dactyl of the chela is conspicuous in the three; the mesial surface of the propodus and distal part of the carpus of the second pereiopod have few to no setae; hooks are limited to the third pereiopod, and the coxa of the fourth bears a conspicuously large boss in *F. jeanae* and *F. spectrum*; there is no trace of a cephalic process on the first pleopod of the male in the latter two species or in *F. dissitus*, but it is distinct in *F. strawni*; the distolateral spine is lacking from the slender mesial ramus of the uropod in all three, and the entire

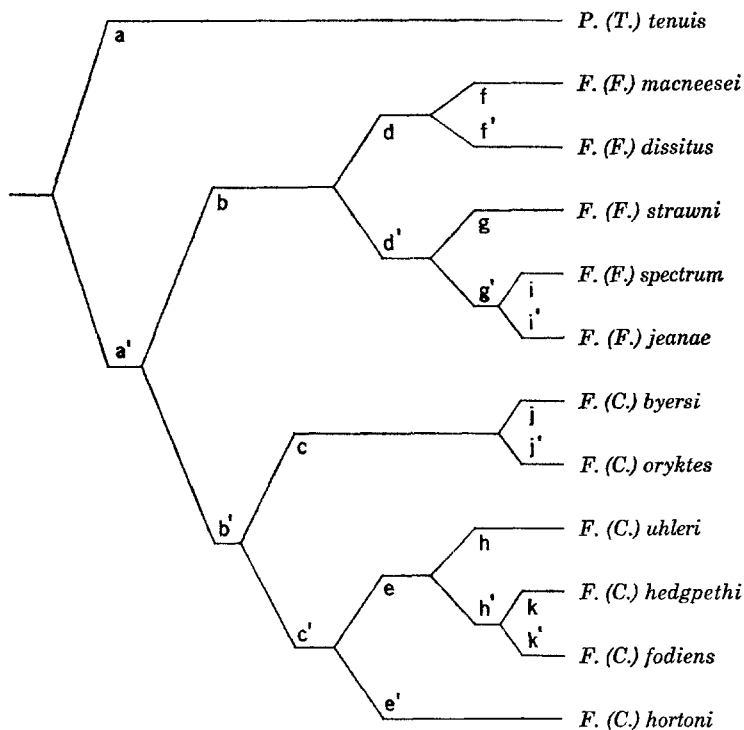


FIG. 4. Interrelationships of the members of *Fallicambarus* and their common origin with *Procambarus (Tenuicambarus) tenuis*.

"tail fan" is comparatively small; finally, the annuli ventrales are much more complexly sculptured than in *F. macneesei* and *F. dissitus*. In most respects, *F. strawni* appears to have diverged from the postulated primitive mien to an extent almost as great as *F. jeanae* and *F. spectrum*. With a larger series of specimens from throughout the ranges of the latter two, *F. spectrum* may prove to be a subspecies of *F. jeanae*.

The remaining species of the genus, those assigned to the subgenus *Creaserinus*, have diverged in several respects from the primitive facies. All of them possess a more inflated cephalothorax; a strongly depressed chela, the dactyl of which bears a deep excision on its opposable surface; hooks on the ischia of only the third pair of pereopods; a comparatively small boss on the coxa of the fourth pereopod; and only two terminal elements on the first pleopod. The abdomen is broad at its base except in *F. byersi* and *F. oryktes*; the telson is provided with a transverse suture (Fig. 3g) except in *F. byersi* (similar to Fig. 3h); the antennal scale is broad except in *F. byersi* and *F. oryktes*; the mesial surface of the

propodus and mesiodistal surface of the carpus of the second pereopod bear conspicuous mats of plumose setae except in *F. byersi*; and the mesial ramus of the uropod is provided with a distolateral spine except in *F. byersi* and *F. oryktes*.

Obviously, *F. byersi* and *F. oryktes* are more closely allied than is either to the remaining species of the subgenus. Most of the characters that set them apart are features of one or more members of the typical subgenus, and ones that are considered to be advanced rather than primitive, suggesting convergence in the two stocks.

Figure 4 depicts the interrelationships of members of the genus *Fallicambarus*.

EXPLANATION OF FIGURE 4 AND KEY TO SPECIES

- a First pleopod of male with terminal elements bent caudally at angle much less than 90°; annulus ventralis movable, not fused to sternum ..... *P. (T.) tenuis*
- a' First pleopod of male with terminal elements bent caudally at no less than 90°; annulus ventralis fused to sternum ..... b
- b First pleopod of male with proximomesial spur; coxa of fourth pereopod with large caudomesial boss; dorsal surface of chela with tubercles other than in two mesial rows and with rounded or serrate lateral surface; sufflamen present or absent ..... d
- b' First pleopod of male lacking proximomesial spur; coxa of fourth pereopod with moderate caudomesial boss; dorsal surface of chela with tubercles largely limited to two mesial rows, never in lateral half, and with costate lateral surface; sufflamen present ..... c
- c Abdomen conspicuously narrower than cephalothorax; antennal scale greatly reduced, almost blade-like; mesial ramus of uropod without distolateral spine ..... j
- c' Abdomen not conspicuously narrower than cephalothorax; antennal scale comparatively broad; mesial ramus of uropod with distolateral spine ..... e
- d Mesial ramus of uropod with distinct distolateral spine; male with hooks on ischia of third and fourth pereopods; abdomen not conspicuously narrower than thorax; sufflamen present or absent ... f
- d' Mesial ramus of uropod without distolateral spine; male with hook on ischium of third pereopod only; abdomen conspicuously narrower than thorax; sufflamen absent ..... g
- e First pleopod of male with central projection subtruncate, broad distally, and directed caudally ..... *F. (C.) hortonii*
- e' First pleopod of male with central projection somewhat tapering and directed caudoproximally ..... h
- f First pleopod of male with cephalic process, central projection not inclined laterally and never overlapping that of corresponding pleopod; mesial ramus of uropod with distomedian spine projecting beyond margin; chela with sufflamen ..... *F. (F.) macneesei*
- f' First pleopod of male without cephalic process, central projection inclined laterally and frequently overlapping that of corresponding pleopod; mesial ramus of uropod with distomedian spine never reaching margin; chela without sufflamen ..... *F. (F.) dissitus*
- g First pleopod of male with cephalic process; telson lacking transverse suture ..... *F. (F.) strawni*
- g' First pleopod of male without cephalic process; telson with transverse suture ..... i

- h Areola usually constituting less than 39 percent of entire length of carapace; rostrum subplane dorsally and only moderately deflexed anteriorly; proximolateral  $\frac{1}{2}$  of postaxial surface of ischium of third maxilliped with many hirsute punctations mesial to lateral row ..... *F. (C.) uhleri*
- h' Areola usually constituting more than 39 percent of entire length of carapace; rostrum concave dorsally and strongly deflexed anteriorly; proximolateral  $\frac{1}{2}$  of postaxial surface of ischium of third maxilliped with few, if any, hirsute punctations mesial to lateral row ..... k
- i First pleopod of male with apex of central projection over-reaching level of cephalic base of projection; width of chela usually no more than 1.6 times length of mesial margin of palm, its color grayish blue with dark blue tubercles ..... *F. (F.) spectrum*
- i' First pleopod of male with apex of central projection almost reaching level of cephalic base of projection; width of chela usually no less than 1.7 times length of mesial margin of palm, its color yellowish tan with bluish black tubercles .... *F. (F.) jeanae*
- j First pleopod of male with distal half of shaft strongly inclined caudally; ventral surface of propodus of chela with longitudinal row of long stiff setae near lateral margin, lacking row of tubercles at base of dactyl; mesial surface of palm of chela of second pereopod without plumose setae ..... *F. (C.) byersi*
- j' First pleopod of male with distal half of shaft not strongly inclined caudally; ventral surface of chela without conspicuous stiff setae but with row of tubercles on propodus opposite base of dactyl; mesial surface of palm of chela of second pereopod with dense mat of plumose setae ..... *F. (C.) oryktes*
- k Hump on mesial process of first pleopod obscuring part of central projection in lateral aspect; central projection with subapical notch (often abraded in middle to late internolt stages); opposable margin of fixed finger of chela with only 1 tubercle markedly larger than others ..... *F. (C.) hedgpathi*
- k' Hump on mesial process of first pleopod never obscuring part of central projection in lateral aspect; central projection lacking subapical notch; opposable margin of fixed finger with 2 major tubercles ..... *F. (C.) fodiens*

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