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A New Crayfish from Alabama Caves with Notes on the Origin of the Genera *Orconectes* and *Cambarus* (Decapoda: Astacidae)

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The discovery of the new species described herein represents, from a phylogenetic standpoint, one of the most significant finds in the history of crayfish studies in the United States. With the knowledge of the occurrence of this remarkable crayfish in caves in northern Alabama, the initial postulate of Ortmann (1905a, p. 107) that the genus *Orconectes* (=Ortmann's subgenus *Faxonius*) was derived from a stock of the genus *Procambarus* (=Ortmann's subgenus *Cambarus*) now becomes more firmly fixed. In addition, there is more concrete evidence for postulating the places of origin for the *Orconectes* and *Cambarus* stocks, and, indirectly, for limiting the possible time of their origins.

I should like to express my appreciation to Mr. W. S. Peck, who collected the first specimens of this new species, and to Mr. and Mrs. John E. Cooper, who have added a third locality and a number of specimens from the type-locality. All three of them have generously donated specimens to the Smithsonian and have furnished me with data on the three localities from which the crayfishes were collected.

Genus *Procambarus* Ortmann

Procambarus Ortmann, 1905b, p. 437.

DIAGNOSIS.—First pleopod of first form male symmetrical or asymmetrical and terminating in from two to five distinct parts, which may be truncate, platelike, or spiniform; shoulder present or absent on cephalic surface; if pleopods terminate in two parts, shoulder always present some distance proximal to base of central projection. Hooks present on ischia of third or fourth pereiopods, or both. Third maxillipeds not conspicuously elongate and with row of teeth on mesial margin of ischium. (Slightly modified from Hobbs, 1942, p. 342).

Procambarus pecki, new species

DIAGNOSIS.—Albinistic, eyes reduced and without pigment; rostrum with subparallel or slightly convergent margins and with marginal spines at base of acumen; postorbital ridges terminating cephalically in spines; areola 5.2 to 6.4 times longer than broad with three or four punctations across narrowest part and constituting 38.3 to 43.2 percent of total length of carapace; one to three cervical spines present on each side of carapace. Simple hooks present on ischia of third pereiopods of male. First pleopods of first form male symmetrical, reaching coxae of third pereiopods, with distinct shoulder on cephalic surface proximal to base of central projection; mesial process heavy, noncorneous, extending anterodistally considerably beyond apex of central projection and somewhat enveloping base of latter, distal end rounded; central projection slender, corneous, acute, and directed cephalodistally at angle of approximately 55 degrees to main shaft of appendage. Annulus ventralis somewhat globose but with shallow longitudinal median trough and very short, caudally situated, arclike sinus; proannular plate absent.

HOLOTYPIC MALE, FORM I.—Albinistic, eyes reduced. Body subcylindrical, only slightly depressed. Abdomen narrower than thorax (7.8 and 8.8 mm in widest parts, respectively). Carapace wider than high in region of caudodorsal margin of cervical groove (8.8 and 7.3 mm); carapace widest slightly cephalic to midlength of areola.

Areola (fig. 3) moderately broad, 6.4 times longer than wide, with three or four punctations across narrowest part. Cephalic section of carapace 1.4 times longer than areola; length of areola 41.7 percent of entire length of carapace. Rostrum with nonthickened elevated convergent margins interrupted at base of acumen by long marginal spines reaching midlength of penultimate podomere of peduncle of antennule; acumen long and terminating apically in acute corneous spine reaching base of flagellum of antenna and beyond distal podo-

mere of peduncle of antennule; upper surface concave with scattered punctations and shallow fovea at base; rows of setiferous punctations mesial and lateral to margins, lateral row terminating cephalically at base of acumen and mesial row continuing onto acumen. Subrostral ridges moderately well developed and evident in dorsal aspect for short distance at base of rostrum. Postorbital ridges weak, each with shallow, setiferous, dorsolateral groove, and terminating cephalically in corneous, acute, long spine. Suborbital angle obsolete. Branchiostegal spine moderately well developed and acute. Surface of carapace punctate dorsally and granulate laterally, three prominent cervical spines on left and two on right.

Abdomen longer than carapace (25.9 and 20.9 mm). Cephalic section of telson with single long spine in each caudolateral corner.

Epistome (fig. 6) broader than long, broadly rounded with very weak cephalomedian projection. Antennule of usual form with spine on ventral surface of basal segment distinctly distal to midlength. Antennae extending caudad beyond end of telson by distance almost equivalent to length of telson. Antennal scale (fig. 9) 2.6 times longer than broad with greatest width distal to midlength; lamellar area distinctly broader than thickened lateral portion, latter bearing long spine distally.

Right chela (fig. 12) elongate, subovate in cross section, and with palm slightly inflated; palm almost entirely tuberculate, tubercles along mesial and lateral surfaces elevated; remainder, except that on ventral surface just proximal to dactyl, mostly squamous; all with setae extending distally; tubercles forming two or three irregular rows along mesial surface of palm with 9 to 14 tubercles in each row. Opposable margin of immovable finger with row of eight small tubercles dorsally, extending from base to midlength of finger, single large tubercle ventrally near midlength, and longitudinal row of minute denticles (no more than three abreast) along almost entire length; dorsal and ventral surfaces of immovable finger with median longitudinal ridge, flanked, particularly dorsally, by setiferous punctations; lateral margin of finger tuberculate proximally and punctate distally. Opposable margin of dactyl with single large tubercle ventrally at base of distal three-fourths of finger and longitudinal row of minute denticles along almost entire length; dorsal and ventral surfaces as on immovable finger and mesial surface similar to lateral surface of immovable finger except basal tubercles slightly more conspicuous.

Carpus longer than broad (4.9 and 2.2 mm) with shallow oblique furrow on dorsal surface; dorsal surface mostly punctate; mesial surface with prominent acute tubercle distal to midlength and three or four smaller ones proximal or ventral to large one; ventral surface

with spine on mesiodistal margin and prominent tubercle lateral to it articulating with socket on ventral surface of propodus; lateral surface tuberculate.

Dorsal surface of merus with crowded small tubercles and single prominent spine near distal margin; lateral and mesial surfaces tuberculate dorsally and ventrally and punctate between; ventral surface tuberculate with lateral and mesial tubercles arranged in irregular rows of approximately 20 tubercles, distal tubercle of both rows very strong and sharp. Ischium with ventromesial margin irregular, bearing approximately 10 small tubercles, otherwise with setiferous punctations.

Hooks (figs. 8, 11) on ischia of third pereiopods only; hooks simple and projecting proximally beyond distal margin of basis. Caudomesial surfaces of coxae of fourth pereiopods (fig. 11) with very prominent tuberosities provided with long setae.

First pleopods (figs. 1, 5, 10, 11) symmetrical and extending cephalad to coxae of third pereiopods when abdomen is flexed. See diagnosis for description.

Allotypic female.—Excluding secondary sexual characters, differing from holotype in following respects: cephalic section of telson with two long spines in each caudolateral corner; opposable margins of fingers of chelae with single row of minute denticles, and opposable margin of dactyl with six small tubercles in proximal row instead of eight; tubercles on cheliped less well developed than in holotype.

Annulus ventralis (fig. 7) pigmented[1] (purplish tan), broader than long with slightly upturned (ventrally) lateral margins; broad shallow trough along median line with lateral areas very slightly inflated. Sinus semicircular and situated at extreme caudal portion of annulus, convexity of sinus extending cephalosinistrally. Sternal sclerite immediately caudal to annulus distinctly broader than long and without conspicuous ornamentation. Proannular plate absent. Sternal plate anterior to annulus unadorned but wings tipped with pigment similar to that coloring annulus. (See "Measurements").

Morphotypic male, form II.—Differs from holotype in following respects: spines and tubercles generally smaller, particularly more dorsal pair of cervical spines; cephalic section of telson with two spines in each caudolateral corner; opposable margin of immovable finger with upper row of tubercles reduced to two; upper opposable margin of dactyl with two tubercles between and at corresponding level of those on immovable finger; denticles on opposable margins of fingers more similar to those in allotype. Spines and tubercles elsewhere on cheliped reduced in size and numbers. Hooks on ischia of

[1] Probably a result of preservation; Mrs. Cooper has indicated she observed no pigment in any of the living individuals.

third pereiopods well developed but not so long as in holotype; protuberances on coxae of fourth pereiopods almost as well developed as in holotype.

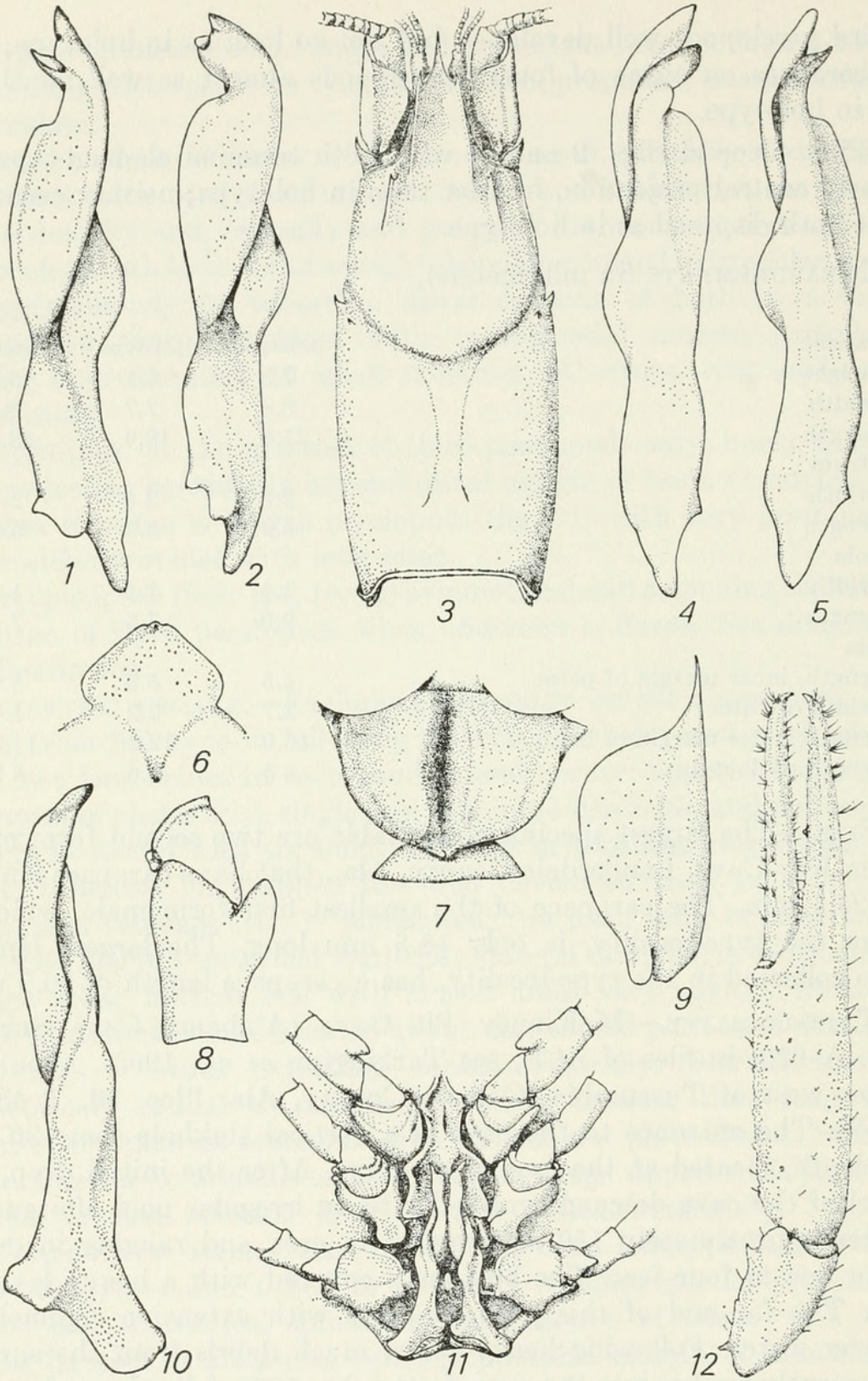
First pleopod (figs. 2 and 4) with both terminal elements, particularly central projection, heavier than in holotype; neither corneous, but both disposed as in holotype.

MEASUREMENTS (in millimeters).—

	holotype	allotype	morphotype
carapace			
height	7.3	6.1	6.3
width	8.8	7.7	8.0
length	21.6	18.9	18.8
rostrum			
width	2.6	2.5	2.4
length	6.2	5.5	5.0
areola			
width	1.4	1.4	1.4
length	9.0	7.6	7.4
chela			
length, inner margin of palm	6.5	5.5	5.0
width of palm	2.7	2.2	1.4
length, outer margin of hand	16.0	12.2	11.2
length of dactyl	8.5	6.6	5.3

SIZE.—The largest specimens available are two second form males from Key Cave, Lauderdale County, Ala., that have carapace lengths of 24.5 mm. The carapace of the smallest first form male, which is from the type-locality, is only 18.5 mm long. The largest female, also collected in the type-locality, has a carapace length of 20.9 mm.

TYPE-LOCALITY.—McKinney Pit Cave (Alabama Cave Survey, No. A–620, in files of ACS; see Tarkington et al., 1965), about 2.5 miles west of Tuscumbia, Colbert County, Ala. (Sec. 10, T 4S, R 12W). The entrance to the cave is a vertical sinkhole some 30 feet in depth, located at the foot of a ravine. After the initial drop, the level of the cave descends gradually to an irregular pool of standing water approximately 150 square feet in area and ranging in depth from one to four feet. The bottom is covered with a heavy layer of silt. The far end of this pool connects with extensive channels of deeper water. Following heavy rains, much debris from the surface apparently washes into the cave. In October 1966, following a drought, the pool originally visited had disappeared completely, and the water level in the cave had dropped at least four feet below that observed on two previous visits. (The foregoing is extracted from notes provided by Mr. and Mrs. Cooper; additional information concerning the cave and its fauna presently is being prepared for publication by them.)



FIGURES 1–12.—*Procambarus pecki:* 1, mesial view of first pleopod of first form male; 2, mesial view of first pleopod of second form male; 3, dorsal view of carapace of first form male; 4, lateral view of first pleopod of second form male; 5, lateral view of first pleopod of first form male; 6, epistome of first form male; 7, annulus ventralis of female; 8, basis and ischium of third pereiopod of first form male; 9, antennal scale of first form male; 10, caudal view of first pleopod of first form male; 11, bases of third, fourth, and fifth pereiopods and first pleopods of first form male; 12, distal podomeres of cheliped of first form male.

DISPOSITION OF TYPES.—The holotypic male, form I, the allotypic female, and the morphotypic male, form II, are deposited in the United States National Museum (nos. 117684, 117685, and 117686, respectively.) Of the paratypes, one male, form I, one male, form II, and a female are in the Museum of Comparative Zoology, a similar series in the Department of Zoology, Tulane University, and two males, form I, one male, form II, and six females are in the United States National Museum.

RANGE.—*Procambarus pecki* is known from two localities other than the type-locality. Four of the 18 specimens available were collected in Cave Spring Cave,[2] nine miles southeast of Decatur, Morgan County, Ala. (ACS No. 53) (Sec. 4. T 6S, R 3W), and two of them from Key Cave (ACS No. 99) just above the northern bank of the Tennessee River, about eight miles southwest of Florence, Lauderdale County, Ala. (Sec. 35, T 3S, R 12W). The type-locality and Cave Spring Cave are south of the Tennessee River whereas Key Cave lies on its north bank.

VARIATIONS.—In general, the specimens from Cave Spring Cave, Morgan County, have weaker spines than those from the type-locality, but for all other variations noted, specimens from one or the other locality exhibit the extreme ranges. The marginal rostral spines may reach the midlength of the ultimate podomere of the antennule; the cervical spines vary from one to three on each side, but in none of the specimens are there fewer than two on at least one side. The proximal section of the lateral ramus of the uropod bears from 7 to 13 spines along its distal margin. The chelipeds exhibit considerable variation in prominence and numbers of tubercles and spines. The annulus ventralis and the wings of the sternal plate immediately cephalic to it may or may not be pigmented.

LIFE HISTORY NOTES.—First form males were collected on Dec. 22, 1965, Apr. 16, 1966, and July 9, 1966. No ovigerous females, or females with young, or even young free in the water have been observed.

RELATIONSHIPS.—*Procambarus pecki* seems equally closely related to the troglobitic members of the genus *Orconectes* and to the members of the Mexicanus Section of the genus *Procambarus*, and there are good reasons for assigning it to either of the two. Almost certainly it has had a common origin with both of the groups mentioned, and, while it resembles *O. p. pellucidus* (Tellkampf, 1844, p. 583) as strongly as it does any other species, at least some of the similarities almost certainly are due to convergence in response to a spelean environ-

[2] This is the type-locality of *Cambarus jonesi* Hobbs and Barr (1960, p. 19), listed by them as "12.1 miles northwest of Valhermosa." Mrs. Cooper has called my attention to the fact that we erred in quoting Dr. Jones' description of this cave, as his was that of another "Cave Spring Cave" in Madison County, Ala.

ment. The first pleopod of the male bears a close resemblance to *P. mexicanus* (Erichson, 1846, p. 99) and its allies, and, since the current definition of the genus *Procambarus* need not be modified to include this species, I am assigning it somewhat arbitrarily to *Procambarus*. In so doing, consideration has been given to this combination of morphological features in a crayfish situated in a geographic area that seems to be crucial from a phylogenetic standpoint (see below). Suffice it to say that, regardless of the genus to which it it assigned, the unique first pleopod of the male and annulus ventralis of the female will serve to distinguish it from any other described crayfish.

PHYLOGENETIC CONSIDERATIONS (figs. 13–21).—There is nothing extraordinary about certain species of closely related genera sharing characteristics of both genera; in fact, the existence of such species provides the best morphological evidence, in the absence of a fossil record, for conclusions that the genera share common ancestry. In the case of the crayfish genera *Orconectes* and *Procambarus*, several able students (Ortmann, 1905a; Rhoades, 1962; and Fitzpatrick, in press) have suggested that the former assemblage of species has had a common origin not too remote from *Procambarus*, and most, if not all, present workers would concede a derivation of *Orconectes* from some *Procambarus* stock. Largely on the presence of hooks on the ischia of the third and fourth pereiopods, Faxon (1885, p. 18) referred *O. p. pellucidus* [=*Cambarus pellucidus*] to his Group I, which encompassed a large segment of the present genus *Procambarus*. Ortmann (1905a, p. 107) was aware of the *Procambarus*-like traits of *O. pellucidus* but argued that it should be included in the genus *Orconectes* [=his subgenus *Faxonius*].

Although no one has so stated, Hobbs (1942, p. 342) and Villalobos (1955, p. 46) realized the difficulty of defining the genus *Procambarus* in such a way as to include *P. mexicanus* and most of its close relatives. Without the statements "if pleopods terminate in two parts, shoulder always present" in the diagnosis of *Procambarus* and "Never is a strongly developed shoulder present on the cephalic margin near the tip of the appendage" in the diagnosis of *Orconectes*, all but one member of the Mexicanus Group would have to be included in the genus *Orconectes*. As is implied, the key generic differences between members of the two genera exist in the first pleopod of the male. All but one member of the genus *Orconectes*, *O. p. australis* (Rhoades, 1941, p. 142), possess a first pleopod ending in two parts, whereas few species of *Procambarus* have such a pleopod. Most members of the latter have at least three terminal elements on their first pleopod, and the majority, four or five. For this and other reasons, Hobbs (1962, p. 278) postulated that the pleopod of the ancestral form of the genus *Procambarus* terminated in four distinct parts.

None of the students of crayfishes, to my knowledge, have questioned the primitiveness of the Limosus Section of the genus *Orconectes*, as originally pointed out by Ortmann (1905a, p. 108), and none since have denied that that assemblage embraces or has close affinities with the troglobitic species ranging from Indiana to Alabama. (There is disagreement concerning the taxonomic treatment of the epigean and spelean members of the section (Rhoades, 1944; Hobbs, 1948; Creaser, 1962), and Creaser has taken issue with the generic nomenclature that was proposed by Hobbs (1942), but this is of little consequence in the context of the present discussion.)

A comparison of the troglobitic members of the genus *Orconectes* with members of the genus *Procambarus* demonstrates that these troglobites possess a distinctly advanced first pleopod of the male that is approached most closely in the genus *Procambarus* by the species of the Mexicanus Group. Only one species of this group, *P. acanthophorus* Villalobos (1948, p. 175), can be claimed on the basis of the pleopod to be more generalized, for it is the only member of the group in which the first pleopod terminates in three rather than two parts (a small cephalic process is present.)

Were the first pleopods considered alone in assessing the primitiveness of the Mexicanus Group among its relatives in the genus *Procambarus*, one would be almost forced to conclude that the group is an advanced one within the genus (see Hobbs, 1962, p. 276). There is, however, additional evidence that the group is indeed an advanced segment of it: (1) the males are provided with ischiopodal hooks only on the third pereiopods; (2) the majority of the species have comparatively long narrow areolae, usually denoting a broad ecological tolerance; (3) most members have few spines, often associated with a secondary burrowing (advanced) habit; (4) there is a unique sternal modification (here designated the proannular plate) immediately anterior to the annulus ventralis of the females that is encountered elsewhere in the family only in the members of the Cubensis Group; and (5) the comparatively long, slender chelipeds of the males most definitely are not of a primitive type. If the members of the Mexicanus Group thus are to be considered as close relatives of the primitive *Orconectes*, one might well conclude that *Orconectes* has been derived not from the more primitive but from an advanced segment of the genus *Procambarus*. One must not conclude, however, that it was from the Mexicanus Section of the genus that the primitive *Orconectes* was derived, for a few primitive characteristics are retained in the troglobitic *Orconectes*, some that do not exist in the Mexicanus stock: (1) multiple cervical spines in most of them; (2) a rudimentary caudal process on the first pleopod of the male in *O. pellucidus australis;* (3) hooks on the ischia of the third and fourth pereiopods; and (4)

the absence of a proannular plate in the females. It does seem probable, nevertheless, that the primitive *Orconectes* did have a more recent common ancestry with the members of the Mexicanus Section than with other segments of the genus *Procambarus* and that *Procambarus pecki* also shares in this ancestry.

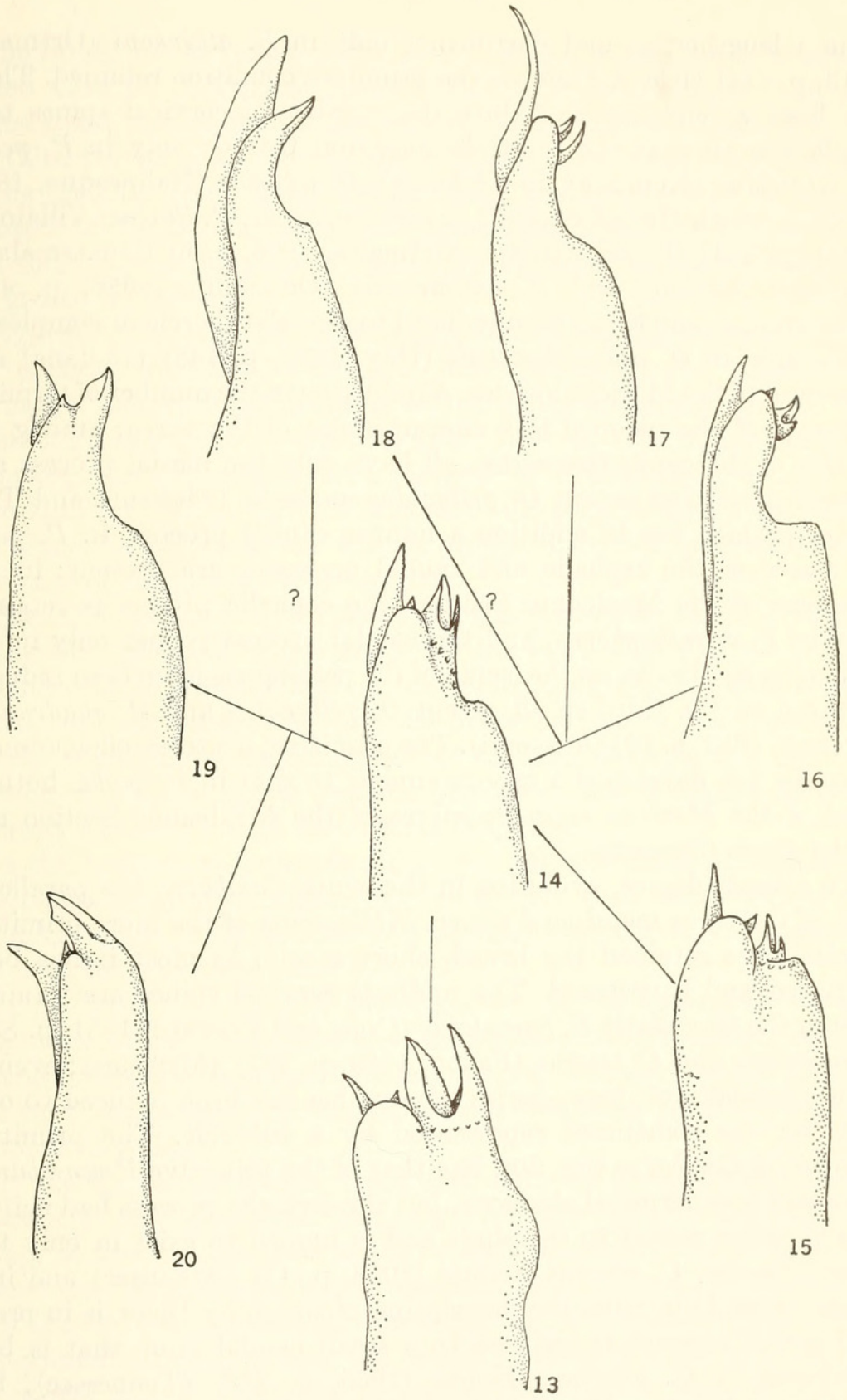
It is postulated here that the ancestral stock from which originated *P. pecki*, the Mexicanus and Cubensis Groups of the genus *Procambarus*, and the genus *Orconectes* possessed, among others, the following characteristics: (1) a long rostrum with prominent marginal spines and acumen; (2) a broad and short areola; (3) multiple (more than one) cervical spines on each side; (4) subcylindrical to subovate chelae with elongate and entirely tuberculate palms; (5) symmetrical first pleopods in the first form male with four short terminal elements, the cephalic process reduced, and with a shoulder distinctly proximally removed from the base of the central projection on the cephalic surfaces of the appendages (fig. 14); (6) hooks on the ischia of the third and fourth pereiopods in the male; and (7) an inflated, oval annulus ventralis without a median depression, and with a short arclike sinus on the caudal declivity.

In *Procambarus pecki*, the primitive characteristics of the stock are maintained in the rostrum, cervical spines, and chelae. The areola has become elongated; the first pleopod has lost both the cephalic and caudal processes; hooks are present on the ischia of only the third pereiopods; and the annulus ventralis has developed a prominent median longitudinal depression.

Utilizing a combination of the most primitive characters represented in the members of the Mexicanus Section, it is postulated that the stock moving into Mexico, and subsequently into Cuba, retained the primitive condition of the rostrum, areola, cervical spines, and chelae, and modified the first pleopods as depicted in figure 14. It lost, however, hooks on the ischia of the fourth pereiopods, and the females developed a prominent sternal plate, a proannular plate, immediately cephalic to the annulus ventralis.

Again, combining the most primitive characteristics represented in the Limosus Section of the genus *Orconectes*, their ancestors retained the primitive rostrum, areola, cervical spines, hooks on the ischia of the pereiopods, and annulus ventralis. The major alterations were in the chelae, in which the uniform tuberculate condition was reduced largely to two rows along the upper inner margin of the palm, and in the first pleopod, in which the cephalic process was lost completely and the caudal process reduced to a rudimentary spine (fig. 19).

To a considerable degree, along with divergence, parallel evolution has progressed in the evolution of *P. pecki*, the primitive *Orconectes*, and the Mexicanus stocks. In general, in all three the areola has under-



FIGURES 13–20.—First pleopods of first form males: 13, generalized *Procambarus* (see Hobbs, 1962, p. 275); 14, hypothetical ancestor of stocks and species indicated; 15, hypothetical ancestor of the barbatus and gracilis sections of *Procambarus*; 16, hypothetical ancestor of the Mexicanus Section of *Procambarus*; 17, *Procambarus alleni* (Faxon); 18, *Procambarus pecki*; 19, hypothetical ancestor of *Orconectes* and *Faxonella*; 20, hypothetical ancestor of *Cambarus*.

gone a lengthening and narrowing; only in *P. atkinsoni* (Ortmann, 1913, p. 414) (Isle of Pines) is the primitive condition retained. There has been a tendency to reduce the number of cervical spines to a single one so that the multiple condition persists only in *P. pecki*, *O. pellucidus* (Kentucky to Alabama), *O. limosus* (Rafinesque, 1817, p. 42) (eastern United States), *P. acanthophorus*, *P. llamasi* Villalobos (1954, p. 364), *P. pilosimanus* (Ortmann, 1906, p. 6) (Guatemala to southern Mexico), and *P. williamsoni* (Ortmann, 1905b, p. 439) (Guatemala), and it has been reduced to a small tubercle or completely obliterated in *O. pellucidus testii* (Hay, 1891, p. 148) (Indiana) and in several of the Mexican species. A reduction in the number of terminal elements of the pleopod is a characteristic of the three; among the species of the genus *Orconectes*, all have only the mesial process and central projection except *O. pellucidus australis* (Alabama and Tennessee), which has in addition a minute caudal process; in *P. pecki* no traces of the cephalic and caudal processes are present; in the members of the Mexicanus Section, the cephalic process is retained only in *P. acanthophorus*, and the caudal process proper only in the Cuban forms. Hooks on the ischia of the pereiopods have been reduced to those on the third in all except *O. pellucidus* and *O. quadruncus* (Creaser, 1933, p. 10) (Missouri). The primitive, ovate, swollen annulus ventralis has developed a groove similar to that in *P. pecki*, both in most of the Mexican representatives of the Mexicanus Section and in the genus *Orconectes*.

To a lesser degree, evolution in the genus *Cambarus* has paralleled that of the three mentioned above. While some of the more primitive species have retained the broad, short areola, in most it has been narrowed and lengthened. The multiple cervical spines are retained only in the troglobitic *C. hamulatus* (Cope and Packard, 1881, p. 881) (Tennessee) and *C. setosus* (Faxon, 1889, p. 237) (Missouri); even in some specimens of these species the number has been reduced to one, and the one sometimes represented by a tubercle. The primitive pleopod of *Cambarus* (fig. 20), like that of the primitive *Procambarus*, possessed four terminal elements, but the cephalic process had shifted to a position mesial to the shaft and is known to exist in only two extant species, *C. strawni* Reimer (1966, p. 11) (Arkansas) and in a species from Louisiana, the description of which by Black is in press. The caudal element is reduced to a small caudal knob that is best developed in *C. pristinus* Hobbs (1965, p. 268) (Tennessee), but vestiges of it occur in several other species of the genus; in most, however, it is absent. Most species of the genus may be characterized by possessing a first pleopod with only two terminal elements (mesial process and central projection) that are directed approximately at a right angle to the shaft of the appendage. The primitive condition

of the hooks on the ischia of the third and fourth pereiopods is maintained only in *C. dissitus* Penn (1955, p. 73) (Louisiana) and the undescribed species mentioned above; all others have them only on the third pereiopods. The annulus ventralis in all species has elements of the median longitudinal trough; thus, the same trends that were pointed out for *Orconectes* and the Mexicanus Section of *Procambarus* and that were attained in *P. pecki* are apparent in the evolution of the genus *Cambarus*.

Figures 13 through 20 depict a hypothesis relating the ancestry of the genera *Orconectes*, *Faxonella*, and *Cambarus*, the Mexicanus, Barbatus, and Gracilis Sections of the genus *Procambarus*, and the disjunct *P. pecki* and *P. alleni* (Faxon, 1884, p. 110). Figure 13, representing the generalized first pleopod of *Procambarus* is redrawn from Hobbs (1962, p. 275); references to the original figure will enable the reader to associate the species groups discussed here with other segments of the genus *Procambarus*.

The chief pre- or early-Miocene changes postulated in the evolution of the first pleopod of the males of this stock (fig. 14) are (1) the accentuation of the shoulder on the cephalic surface, (2) a narrowing of the cephalic-caudal plane in the distal portion of the appendage, (3) the beginning of an elongation of the caudal knob, and (4) a reduction in the size of the cephalic process and its becoming more intimately associated with the central projection.

In the Mexicanus-Cubensis stock (fig. 16), the distal portion of the appendage became elongate and slenderer, thus accentuating the shoulder; the cephalic process and central projection were reduced in size, and the subapical setae lost.

In *P. alleni* (fig. 17), the distal portion of the appendage became even more attenuate than in the Mexicanus-Cubensis stock, and the central projection disproportionately smaller than the cephalic process. The subapical setae were retained and extend along the margin of the rounded shoulder.

In the Barbatus-Gracilis stock (fig. 15), the distal portion of the appendage was shortened, bringing the terminal elements and the subapical setae to the level of the cephalic shoulder. The subterminal setae were subsequently lost in the members of the Gracilis Section.

In the *Orconectes-Faxonella* stock (fig. 19), the cephalic process and subterminal setae were lost, the caudal element reduced to a vestige, the mesial process shortened to project little farther than the central projection, and the latter somewhat broadened in the cephalic-caudal plane.

The *Cambarus* stock (fig. 20) lost the cephalic shoulder and subapical setae, markedly reduced the caudal element to a small knob, shifted the cephalic process to a mesial position at the morpholog-

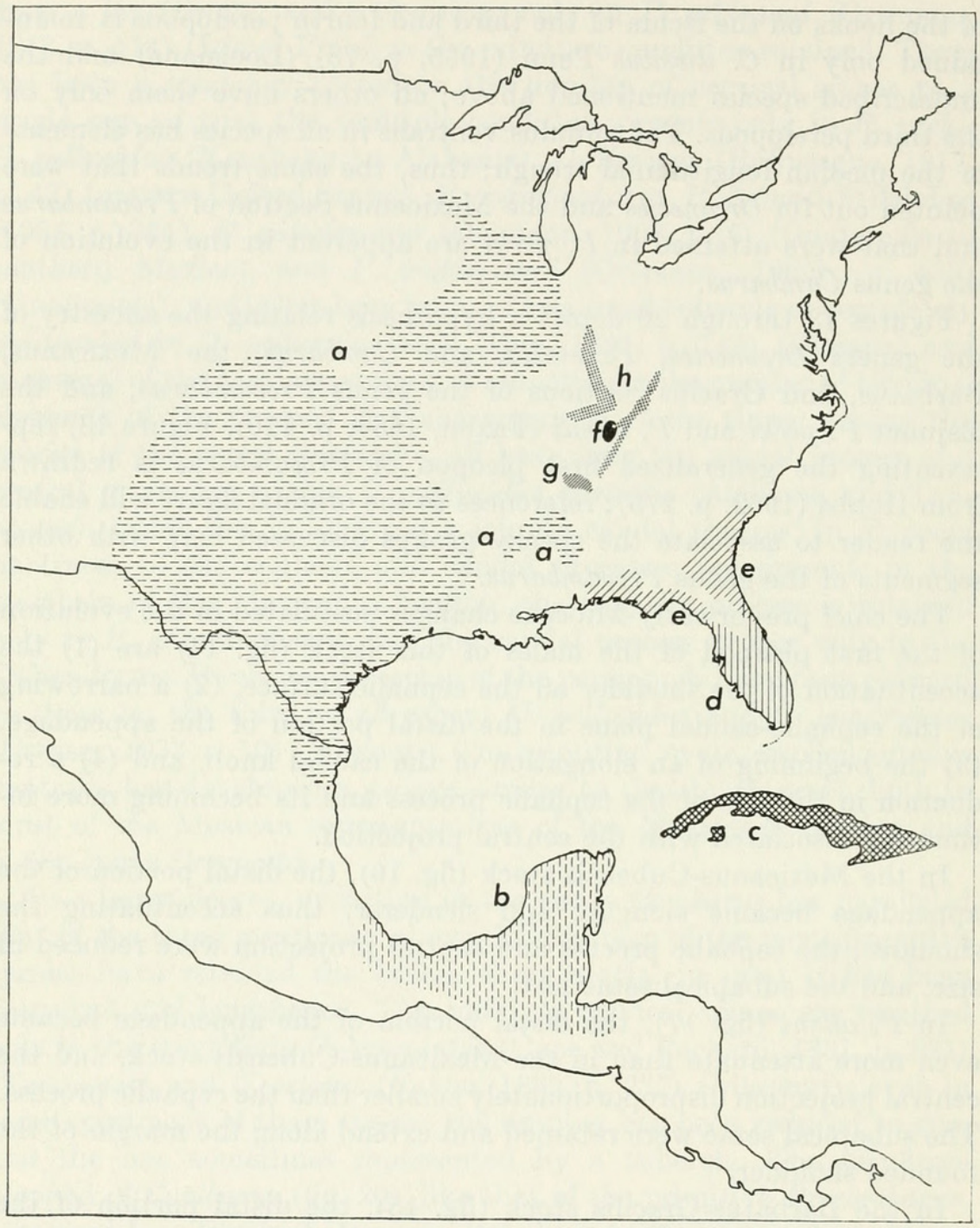


FIGURE 21.—Ranges of *Procambarus pecki* and its allies: *a*, Gracilis Section; *b* and *c*, Mexicanus Section (*b*, Mexicanus Group; *c*, Cubensis Group); d, *Procambarus alleni; e*, Barbatus Section; *f*, primitive *Cambarus* (*C. pristinus* and *C. obeyensis*); *g*, *Procambarus pecki*; *h*, troglobitic *Orconectes*.

ical cephalic base of the mesial process, and initiated a subparallel recurving of the latter and central projection.

In the evolution of *P. pecki* (fig. 18), the shoulder was retained, and the distal portion of the appendage became very slender; the subapical setae, the cephalic process, and caudal elements were lost, and the two remaining apical processes assumed positions similar to those in *P. alleni* and the Mexicanus-Cubensis stock.

A consideration as to the range and time of the existence of the ancestral stock from which these crayfishes have been derived has resulted in the hypothesis that the ancestral precursors occupied an area of the southeastern United States that extended northward from Alabama and encompassed the Cumberland Plateau. Because of the presence of *O. pellucidus australis* in the subterranean refugia of the Cumberland Plateau and the contiguous limestone areas south to Alabama, of the primitive *Cambarus pristinus* and *C. obeyensis* Hobbs and Shoup (1947, p. 138), both occupying limited ranges on the Plateau, and of *P. pecki* in northern Alabama, it seems probable that the centers of origin for *Orconectes*, *Cambarus*, and the Mexicanus Section of the genus *Procambarus* existed in the area of northern Alabama northward through the limestone belt of Tennessee onto the Cumberland Plateau.

This differs slightly from the postulate proposed by Ortmann (1905a, plate 3) that the center of origin for the genus *Orconectes* (=his subgenus *Faxonius*) was situated somewhat more to the west and did not embrace the Cumberland Plateau.

In the area of the Cumberland Plateau, much of the primary divergence in the genera *Orconectes* and *Cambarus* occurred with stocks radiating from this center: in *Orconectes* principally to the north and west, and in *Cambarus*, for the most part, to the east and south, although two or three stocks of the latter moved westward and reached the Ozark-Ouichita region relatively early. *Procambarus pecki* probably remains in the area of its ancestral home but its closest relatives moved southwestward into Mexico and to Cuba.

Villalobos (1955) has discussed the origin of the Mexicanus Group, and Hobbs and Villalobos (1964) have considered the origin of the Cubensis Group. Their conclusions are that, inasmuch as the Mexicanus Group occupies an area south of the Cordillera Volcánica Transversal, which arose no later than the late Tertiary and probably during the upper Miocene, the arrival of the ancestral stock of this group in the area to the south of these mountains must have occurred sometime prior to the end of that era. They also joined other earlier students of Antillean zoogeography in postulating a tertiary land bridge between Cuba and the Central American-Mexican region across which members of this stock reached Cuba. In light of recent studies (including Kendall and Schwartz (1964) on the ability of cambarine crayfishes to tolerate higher salinities than has been supposed, a land bridge seems less a necessity than before. Regardless, however, of the means by which the crayfishes reached Cuba, the time of their arrival on the island must have been prior to the Pleistocene and probably as early as the Miocene.

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