NOTES ON THE AFFINITIES OF THE MEMBERS OF THE BLANDINGII SECTION OF THE CRAYFISH GENUS PROCAMBARUS

(Decapoda, Astacidae)

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The last comprehensive work in which the relationships of the members of the Blandingii Section were treated was that of Ortmann (1905). Subsequent studies involving segments of the Section include those of Hobbs (1942b, 1958c), Williams (1954), Villalobos (1953, 1955, 1959), and Penn (1956a). Ortmann (1905: 101-102) included 15 species in the Blandingii Section, assigning: *spiculifer, versutus, pubescens, angustatus,* and *lecontei* to his "Group of *C. spiculifer*"; *acherontis,*[1] *blandingii, hayi,* and *fallax* to his "Group of *C. blandingii*", *clarkii* and *troglodytes* to his "Group of *C. clarki*"; and *evermanni, barbatus, weigmanni,* and *alleni* to his "Group of *C. alleni*". Of these, *barbatus* was removed to the Barbatus Section and *acherontis* to the Acherontis Section by Hobbs (1942b: 35 and 91), and *weigmanni* was declared a *nomen nudum* by Villalobos (1950: 383). Since 1905, some 42 species and subspecies assignable to the Blandingii Section have been described, and are listed following the diagnoses of the several groups below.

Before entering into a discussion of the inter-relationships of the members of the Blandingii Section, it seems advisable to discuss briefly the position of the Section within the genus, and to do so, it will be helpful to consider the probable characteristics of the ancestral procambarid and to emphasize certain morphological features which have not been thoroughly considered, although Villalobos has mentioned and illustrated some of them beautifully for the Mexican crayfishes.

The Ancestral Procambarid

Although certain non-secondary-sexual characteristics have been found to be of taxonomic importance, evidence exists which indicates that many, if not most of them, might often better be associated with environmental factors than with phylogeny. It is not implied that such characteristics have *no* phylogenetic significance. For example, such features as spination, which is frequently strongly developed in crayfishes living in open water and obsolete in burrowing forms, can only be useful when used in combination with other characters which are not so affected. On the other hand, all of the members of the Spiculifer Group (see below) possess two or more lateral spines on the carapace, a characteristic which is shared only by the members of the Pilosimanus Group of the Mexicanus Section, distant relatives at best of the members of the Spiculifer Group—the first pleopods of the males of the two groups are morphologically far removed. It is maintained that within each group the presence of multiple spines *is* of phylogenetic significance, and it is at least possible that in the advanced Pilosimanus Group the two spines represent a primitive retention, but all students of the crayfish will agree that there are many other species of crayfishes with only a single spine (or without any) which are more closely related to members of the Spiculifer Group than is any member of the Pilosimanus Group.

In contrast to those characteristics which appear to be influenced by environmental factors are the secondary sexual ones which seem not to have been strongly influenced in their form by other than genetic factors—suffice it to say that no particular secondary sexual characteristic may be associated with any particular type of environment. These secondary sexual characteristics associated with the female will undoubtedly provide, when adequately studied, additional evidence upon which an understanding of the phylogeny of the group is ultimately to be realized. Presently, no comparative studies have been made of them. Therefore, our present understanding is based primarily on the secondary sexual characteristics of the

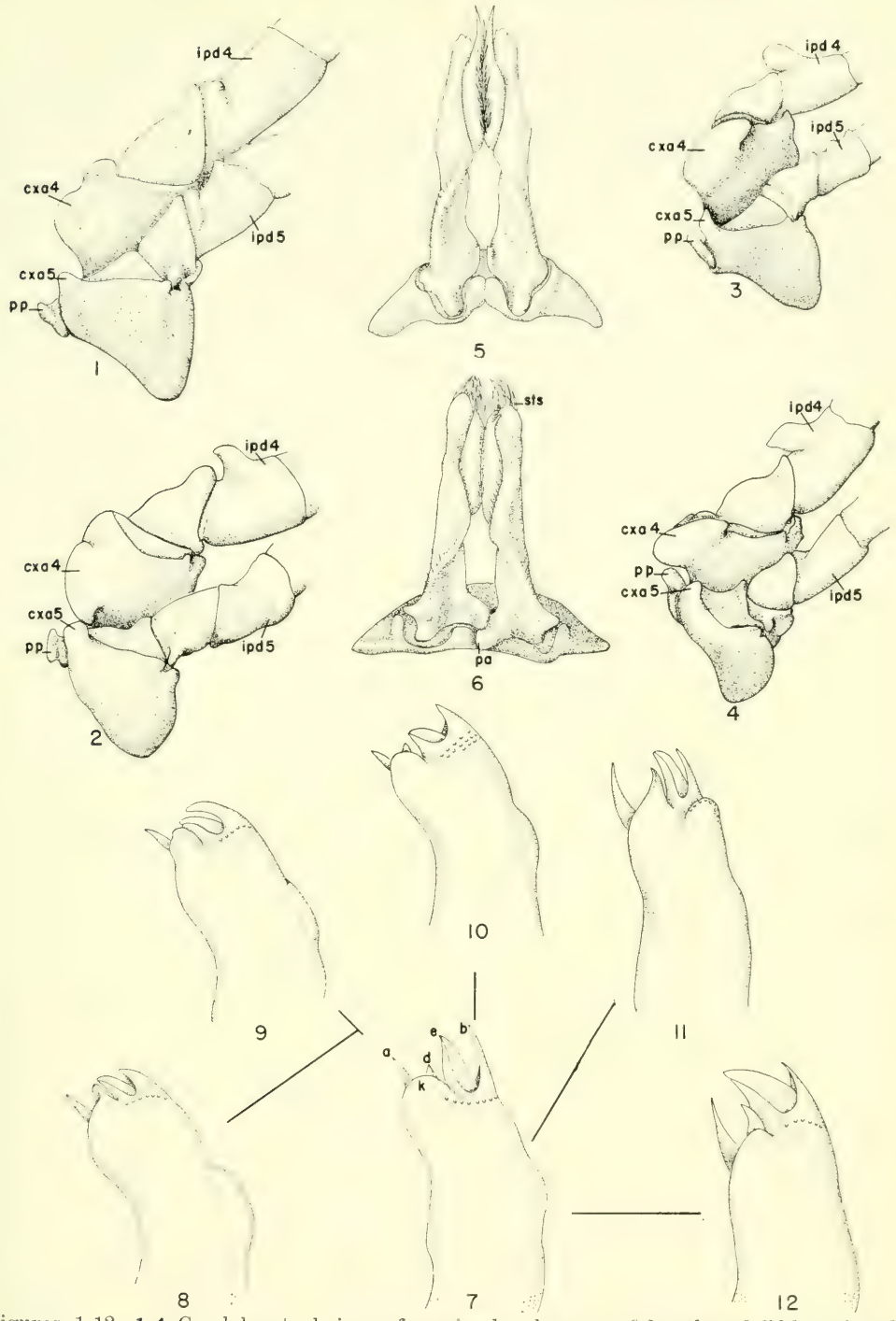
[1] This designation was based on *acherontis* Faxon (not Lönnberg) which is a synonym of *lucifugus lucifugus* (Hobbs).

male augmented by such characteristics as spination, body proportions, color, etc.

Ortmann (1905: 93-96) outlined what he considered to have been the primitive facies of the genus *Cambarus* [equivalent to the subfamilies Cambarinae (Hobbs 1942a) and Cambarellinae (Laguarda 1961)]. These features may be summarized as follows: (1) *General shape of the carapace* ". . . seems to be more or less ovate, generally depressed". (2) *Areola* ". . . rather broad and short". (3) *Rostrum* ". . . rather long . . . with more or less parallel margins, with a marginal spine on each side, and a rather long acumen". (4) *Copulatory hooks of the male* were considered by Ortmann but no concrete generalization was made; it does seem apparent that he considered an increase in number of hooks a more advanced condition. (5) *Chelae*—"Among the more primitive species the shape of the chelae seems to be more or less subcylindrical, and rather elongated." (6) Ortman discussed the *"Sexual Organs"* (= first pleopods) of the male, and emphasized their importance in that their study "gives us a standard by which to judge the other characters that are of systematic value, and as we shall presently see, there is hardly another structure that has the same value for revealing the affinities within the genus, that is to say, the characters generally develop independently in different groups, being clearly subject to parallelism, presumably under the influence of similar external conditions." He did not characterize the generalized pleopod but stated, "The most primitive sexual organs are found in species of the first section [Section of *C. digueti*], where there is only one tooth at the end of the outer part." (Ortmann, loc. cit., p. 98).

Hobbs (1940c) depicted a hypothetical generalized pleopod, and while stating that *"Cambarus pubescens, Cambarus lucifugus,* and *Cambarus pallidus* may be cited as species which most nearly approximate the hypothetical pleopod in their structure", he indicated that the pleopod of *Cambarus digueti* "most nearly approaches that of the prototype appendage . . ." The latter statement is not at all in line with my present views, and in making it, I was most certainly influenced by Ortmann's contention that the Section of *C. digueti* represents the most primitive of the cambarids. In discussing the evolutionary history of the Pictus Group Hobbs (1958c) treated four characteristics and the conclusions were similar to those of Ortmann. "A *broad, short areola* (not more than four times as long as broad, and its length not exceeding thirty per cent of the total length of the carapace) in contrast to a narrow long one is here deemed more generalized" . . . "a *rostrum with subparallel or convex margins and bearing a pair of marginal spines* . . . is a more generalized type than one in which the margins converge or are lacking spines altogether" . . . *"the first pleopod of the first form male terminating in four distinct elements* is considered to be more primitive than one terminating in fewer elements" . . . and a *"color pattern . . . which includes a U-shaped 'saddle' on the thoracic portion of the carapace* is considered to be more generalized than one that has only portions of the saddle." The above generalizations are maintained here.

Hooks on the ischiopodites of the pereiopods of the males are employed in amplexus in holding the females. They occur in a variety of forms with their apices either simple or bituberculate, and they may or may not be opposed by a tubercular prominence on the corresponding coxa. Not only is there variation in form of the hook but variations also occur in their presence or absence on the second through the fifth pereiopods. Among the nearctic and oriental crayfishes the following combinations of hooks are present: (1) only on the third—*Procambarus, Orconectes,* and *Cambarus;* (2) only on the fourth—*Procambarus* and *Paracambarus;* (3) on the second and third—*Cambaroides* and *Cambarellus;* (4) on the third and fourth—*Procambarus, Troglocambarus, Orconectes* and *Cambarus dissitus* Penn (1955); (5) on the third and fourth and occasionally on the fifth—*Procambarus latipleurum* Hobbs (1942b); (6) absent—*Pacifastacus.* It is at least possible that the primitive stock from which the cambaroids, cambarellids, and cambarids were derived exhibited serially homologous hooks on the ischiopodites of the second through fifth pereiopods of the males and that the derived condition has been reached through the loss of hooks with two main lines having developed: (1) retention of hooks on the second and third—*Cambaroides* and *Cambarellus,* and (2) retention



Figures 1-12. **1-4.** Caudalventral views of proximal podomeres of fourth and fifth periopods of first form males. **1.** *P. gracilis.* **2.** *P. pictus.* **3.** *P. latipleurum.* **4.** *P. riojae.* **5-6** Caudal view of the first pleopods of first form males. Pleopods in the normal resting position. **5.** Symmetrical pleopods of *P. gracilis.* **6.** Asymmetrical pleopods of *P. pictus.* **7-12.** Lateral views of hypothetical pleopods of first form males. **7.** Generalized Procambarid. **8.** Proclarkii. **9.** Proplanirostris. **10.** Propictus. **11.** Problandingii. **12.** Prospiculifer. Abbreviations—a, mesial process; b, cephalic process; cxa4 and cxa5, coxal apophyses of fourth and fifth pereiopods; d, caudal process; e, central projection; ipd4 and ipd5, ischiopodites of fourth and fifth pereiopods; k, caudal knob; pa, proximal apophysis of first pleopod; pp, penis papilla.

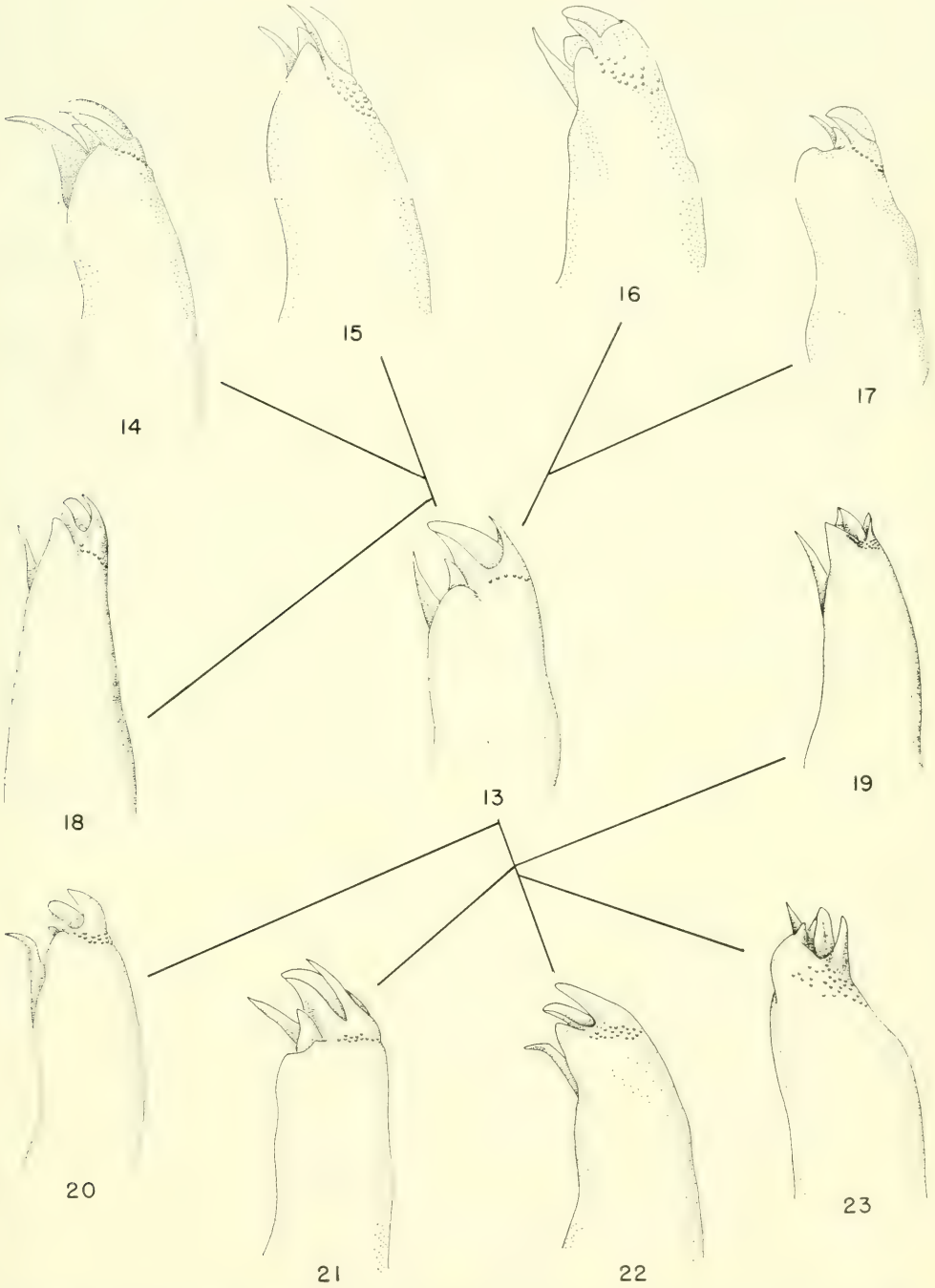
of hooks on the third and fourth. Adhering to the second derived condition are many members of the genus *Procambarus,* a few members of *Orconectes,* one member of the genus *Cambarus,* and the monotypic *Troglocambarus.* Deviating from the second derived condition are (a) those which retained hooks only on the third pereiopods —some members of *Procambarus,* most members of *Orconectes,* and all but one member of *Cambarus;* and (b) those which retained hooks only on the fourth pereiopods—some Mexican members of *Procambarus* and the two species (also Mexican) of *Paracambarus.* The possession of hooks on the fifth pereiopod of some members of *P. latipleurum* is considered to be an atavistic tendency. Following this explanation, one must conclude that the absence of such hooks in *Pacifastacus* (as well as in the European Astacines) must be explained as a loss from primitive stock, or that hooks appeared in the ancestral stock after the Astacines had been separated from it, or that there was an independent origin, presumably from marine ancestors, of the two stocks of holarctic crayfishes. In light of the absence of cyclic dimorphism in the adult males of the Astacinae (including *Pacifastacus*) and its occurrence in the remaining subfamilies (Cambaroidinae, Cambarinae, and Cambarellinae) one of the latter two alternatives seems more probable.

Heretofore not considered are the apophyses which occur on the coxae of the third, fourth, and fifth pereiopods of the male, particularly those of the fourth and fifth. These are most prominently developed in *Paracambarus, Cambarellus, Troglocambarus,* and most members of *Procambarus* but are poorly developed or absent in most members of the genera *Orconectes* and *Cambarus.* There is scarcely a trace of them in *Cambaroides.* What is believed to be the generalized condition of the fourth and fifth pereiopods is depicted in Figure 2 where the apophysis on the fourth pereiopod is a vertically expanded prominence, flattened in the longitudinal axis of the body, projecting ventrally from the caudomesial rim of the coxa. The evolutionary trends are believed to have been in two directions: (1) a shifting of the apophysis on the fourth from the vertical to the horizontal axis (Figs. 3, 4) and (2) a reduction of the apophysis to form a globular prominence on the fourth coxa and a tuberculiform projection on the fourth (Fig. 1)—this tendency culminating in the absence of one or both apophyses.

Not previously taken into account also are the articulations of the first pleopods (of the male) and the subterminal setae that are present on many of them. The first pleopods may be *symmetrical* (Fig. 5), or *asymmetrical* (Fig. 6). If symmetrical, the *bases* of the two pleopods, when viewed ventrally, lie in essentially the same horizontal plane, and have similar configurations. If asymmetrical, the base of one of the pleopods (the left in all specimens examined) lies in a plane posterior to the other, and frequently their proximomesial apophyses overlap. The distinct asymmetrical condition appears only in the genera *Procambarus* (where it is a characteristic of the majority of the species), *Paracambarus,* and *Troglocambarus.* The symmetrical arrangement is considered to be more primitive.

The presence of terminal setae on the pleopods of holarctic crayfishes must be assumed to be a derived condition; however, in the genus *Procambarus* a row of them across the anterolateral surface at the base of the terminal elements must be viewed as a generalized feature; likewise in both paracambarids, and *Troglocambarus.* The major trends from the generalized setiferous condition are: (1) an elevation of the part of the pleopod bearing the row to form a knob—Blandingii Group—and the shifting of this knob caudally along the lateral surface of the appendage (Figs. 44, 45); (2) a duplication of the row to form several rows or a cluster (Figs. 13, 21, 15); and (3) a reduction in the number of setae culminating in a total loss of them (Gracilis and Mexicanus sections and certain members of other sections).

To summarize, the ancestral Procambarid is considered to have had the following characteristics: (1) carapace subovate, somewhat depressed, and bearing several lateral spines on each side of its carapace; (2) areola not more than four times as long as broad, and its length not exceeding 30 per cent of the total length of the carapace; (3) rostrum with subparallel or convex margins and with marginal spines delimiting the base of an acumen about one-third the total length of the rostrum; (4)



Figures 13-23. Lateral view of terminal portions of first pleopods of first form males. **13.** Hypothetical Prospiculifer. **14.** *P. raneyi.* **15.** *P. spiculifer.* **16.** *P. ouachitae.* **17.** *P. suttkusi.* **18.** *P. versutus.* **19.** *P. penni.* **20.** *P. vioscai.* **21.** *P. echinatus.* **22.** *P. natchitochae.* **23.** *P. dupratzi.* [dark semicircles represent positions of subterminal setae.]

color pattern with a U-shaped "saddle" on the thoracic portion; (5) chelae that are elongate, subovate, and slightly depressed; (6) simple hooks on the ischiopodites of the third and fourth pereiopods; (7) coxae of the third, fourth, and fifth pereiopods provided with apophyses—that on the fourth elongate in the vertical axis, and that on the fifth smaller and compressed in the longitudinal axis of the body; (8) symmetrical first pleopods bearing a row of terminal setae on the cephalolateral surface of the appendage at the base of the terminal elements; tip terminating in four distinct parts disposed as illustrated in Figure 7 and with a *caudal knob* (k) at the base of the *caudal process* (d).

The Composition of the Genus Procambarus

As presently understood, the genus *Procambarus* consists of some 108 species and subspecies which have been assigned to *Sections, Groups,* and *Subgroups.* Hagen (1870), in the first monograph of the American Astacidae, initiated the practice of employing infrageneric categories, "Groups", for the purpose of expressing relationships between certain species. Ortmann (1905) proposed a supergroup category which he designated the "Section". Subsequent authors have found it convenient to continue to utilize both categories, and Hobbs (1942b), Penn (1953a), and Villalobos (1955) employed a third one, "Subgroup". (The latter is not utilized in the proposed groupings in this study.)

While there has been some rearrangement of the groupings and shuffling of species within them from time to time, it does not seem appropriate here to summarize such changes. With full acknowledgment of the contributions of those authors listed in *References Cited,* the infrageneric categories herein recognized within the genus *Procambarus* are summarized in Table 1. Following each, the number of species and

Table 1.
Subdivisions of the Blandingii Section of the Genus Procambarus [1]

Sections	Groups
Blandingii (55) Ortmann 1905: 98	Spiculifer (10) Ortmann 1905: 100 Pictus (10) Hobbs 1942b: 129 **Seminolae (6) Hobbs 1942b: 142 **Lucifugus (3) Hobbs 1942b: 134 Blandingii (10) Ortmann 1905: 100 **Planirostris (7) Penn 1953a: 75 Clarkii (5) Ortmann 1905: 100 Disjunct members (4)
Tenuis (1) Here designated.	
Riojae (6) Villalobos 1955: 94	Riojae (3) Villalobos 1955: 96 Erichsoni (3) Villalobos 1955: 130
Digueti (2) Ortman 1905: 98	
Advena (8) Hobbs 1942b: 73	Advena (4) Hobbs 1942b: 73 Rogersi (4) Hobbs 1942b: 88
Acherontis (1) Hobbs 1942b: 91	
Hinei (2) Penn 1953c: 67	
Barbatus (12) Hobbs 1942b: 33	Barbatus (7) Hobbs 1942b: 35 Alleni (3) Ortmann 1905: 100 Disjunct members (2)
*Gracilis (5) Ortmann 1905: 98	
Mexicanus (16) Villalobos 1955: 159	Mexicanus (8) Villalobos 1955: 160 Pilosimanus (4) Villalobos 1955: 160 Cubensis (4) Here designated.

[1] Following each category the number of species and subspecies assigned to it is enclosed in parentheses, and this is followed by the author of the category.
* Originally proposed as a group.
** Originally proposed as a subgroup.

subspecies assigned to it is enclosed in parentheses.

As is indicated in Table 1, more than half of the species and subspecies within the genus are placed within the Blandingii Section, the most heterogeneous, but which nevertheless appears to contain the most generalized members. The characteristics of the Section and the inter-relationships of the groups within it are discussed below. Excluding introductions by man (see Penn, 1954), the range of the Section extends from southern New England, east of the Appalachian mountains to Florida, northwest along the southern Great Lakes to Minnesota, and south into Veracruz, Mexico.

The Tenuis Section, represented by a single species, *Procambarus tenuis* Hobbs (1950: 194), is undoubtedly one of the most disjunct of the genus. Its range is restricted to eastern Oklahoma and western Arkansas. Although its affinities are questionable, it seems probable that it is more closely allied to the members of the Blandingii Section than to the other species.

The Riojae Section, restricted to the Gulf slopes in Hidalgo, Puebla, and Veracruz, Mexico, consists of two distinct groups. The more generalized Riojae Group shows, in the first pleopods of *P. riojae* (Villalobos 1944a: 162) and *P. Hoffmani* (Villalobos 1944a: 169), distinct affinities with members of the generalized Spiculifer and Pictus groups of the Blandingii Section, while the third member, *P. hortonhobbsi* Villalobos (1950: 402), possesses a pleopod which is quite similar to those of the three members of the Erichsoni Group. *P. contrerasi* (Creaser 1931: 1) is probably the most divergent member of the Section.

The Digueti Section, comprising only two species that themselves are not strikingly similar, is restricted to streams of the Pacific slope in Jalisco and Michoacan, Mexico. These two morphologically and geographically disjunct species *P. digueti* (Bouvier 1897: 225) and *P. bouvieri* (Ortmann 1909: 159) are perhaps best linked to the other sections through the Simulans Section.

The seven members of the Advena Section, confined to the coastal plain of Georgia and Florida, constitute a closely allied morphological and ecological assemblage. In both respects, the Section represents, as a whole, the most specialized segment of the genus. Except for *P. pygmaeus* Hobbs (1942b: 83), all of its members are primary burrowers, very probably deriving early from a stock not greatly unlike *P. spiculifer* (LeConte 1856: 401), a member of the Blandingii Section.

The monotypic Acherontis Section is restricted to subterranean waters in peninsular Florida, and while not obviously related to any other particular species, exhibits certain characteristics of the Spiculifer Group of the Blandingii Section.

The Hinei Section, comprising two species found in lentic and sluggish lotic habitats in the coastal areas of Louisiana and Texas, like the Acherontis Section is morphologically somewhat disjunct. It is probably best linked to the other sections through the Pictus Group of the Blandingii Section.

There seems to be little reason to question the origins of the three remaining Sections, Barbatus, Simulans, and Mexicanus, from a common stock. The three sections are allopatric, occupying respectively the coastal plain from South Carolina to Alabama; Alabama to Wisconsin southwest to Tamaulipas, Mexico and Veracruz to Honduras, Cuba and the Isle of Pines. While obvious similarities occur between the first pleopods of the members of these three sections, it is decidedly difficult to link them with the remaining sections, except as pointed out above, possibly with the Digueti Section. At present, our best clue is seen in *P. rathbunae* (Hobbs 1940a: 414) and the supposedly disjunct *P. alleni* (Faxon 1884: 110), the pleopods of which resemble respectively those of *P. shermani* Hobbs (1942b: 61), a disjunct member of the Barbatus Section which approaches the Blandingii Section, and *P. bivittatus* Hobbs (1942b: 96) a member of the Blandingii Section.

The foregoing treatment is so brief as to seem almost useless; however, a fuller documented manuscript on the Sections of the genus exclusive of the Blandingii Section is in progress, and the evidence upon which the above statements of relationships are made will be presented therein. If, for the present, these statements be granted, it be-

Key to Sections of *Procambarus*

1	Hooks present on ischiopodites of fourth pereiopods only, occasionally with a rudimentary hook on that of third	2
1′	Hooks present on ischiopodites of third, third and fourth, or third, fourth, and fifth pereiopods; hook on third always well developed	3
2(1)	First pleopod with subterminal setae, mesial process decidedly the most conspicuous terminal element; apophysis on coxa of fourth pereiopod not prominent	Barbatus Section
2′	First pleopod without subterminal setae, mesial process never the most conspicuous terminal element; apophysis on coxa of fourth pereiopod strongly developed and expanded horizontally	Riojae Section
3(1′)	Hooks on ischiopodites of third and fourth pereiopods bituberculate	Acherontis Section
3′	Hooks on ischiopodites of third, third and fouth, or third, fourth and fifth pereiopods, but never those on third and fourth (both) bituberculate	4
4(3′)	First pleopods asymmetrical (fig. 6)	5
4′	First pleopods symmetrical (fig. 5)	9
5(4)	First pleopods extend forward between bases of second pereiopods	6
5′	First pleopods extend forward between bases of third pereiopods	8
6(5)	Hooks present on ischiopodites of third and fourth pereiopods	*P. shermani* (Barbatus Section)
6′	Hooks present on ischiopodites of third pereiopods only	7
7(6′)	Cephalic process of first pleopod forming a rounded plate across cephalic side of tip	*P. bouvieri* (Digueti Section)
7′	Cephalic process present or absent but never forming a rounded plate across cephalic side of tip	Advena Section
8(5′)	Cephalic process of first pleopod arising *distinctly* from mesial side of appendage; palm of chela often barbate; two lateral spines never present on each side of carapace	Barbatus Section
8′	Cephalic process of first pleopod seldom arising *distinctly* from mesial side of appendage (only in *P. suttkusi* and occasionally in *P. ouachitae*, both of which possess two lateral spines on each side of carapace); one of two lateral spines may be present on each side of carapace; palm of chela never barbate	Blandingii Section
9(4′)	Hooks present on ischiopodites of third and fourth pereiopods	10
9′	Hooks present on ischiopodites of third pereiopods only	11
10(9)	Dactyl of chela longer than inner margin of palm	Tenuis Section
10′	Dactyl of chela much shorter than inner margin of palm	Hinei Section
11(9′)	Cephalic process of first pleopod spiniform, directed distally and although sometimes small, always clearly recognizable; prominent caudal process corneous and distally somewhat lamellate	Gracilis Section
11′	Cephalic process of first pleopod never spiniform, either broad and corneous, acute, vestigal or absent; caudal process mostly absent, if present never lamellate	12
12(11′)	Caudal process present; cephalic process a transversely broad corneous element	Digueti Section
12′	Caudal process absent; cephalic process usually absent (small and acute in *P. acanthophorus*)	Mexicanus Section

comes apparent that the Blandingii Section has served as a focal point, suggesting both diversity of its members and the probable generalized nature of at least some of them.

BLANDINGII SECTION (*Ortmann* 1905: 98)

Diagnosis.—(Based on the first form male.) Palm of chela never barbate. Hooks present on ischiopodites of third and fourth pereiopods and occasionally also on fifth. Coxae of fourth pereiopods with prominent vertically disposed apophyses (Fig. 2). First pleopods asymmetrical (except in *P. jaculus*,[2] a member of the Planirostris Group) and reach the coxopodites of the third pereiopod when the abdomen is flexed; subterminal setae present except in the disjunct *bivittatus* and *lewisi;* pleopod terminating in three or four distinct parts (cephalic or caudal processes may be lacking); cephalic process never *arising distinctly* from mesial face of appendage except in *suttkusi* and sometimes in *ouachitae* (both of which have two lateral spines on each side of carapace).

Relationships.—The inter-relationships of the several groups of this Section are depicted in Figures 7 through 12 in which five secondary prototype appendages radiate from the prototype of the Blandingii Section. The secondary prototype appendages (Figs. 8 through 12) are reproduced again in the following plates where the relationships of the members of each group are indicated by lines diverging from the prototype. It will be noted that the Pictus, Seminolae, and Lucifugus groups are postulated to have arisen from the same prototype (Figs. 25-43).

[2] There is only one first form male of this species known, and one of the pleopods had been removed before it was determined whether or not they are symmetrical. In a recent examination of this specimen, the pleopods appear to be symmetrical.

Key to the Groups and Disjunct Members of the Blandingii Section

1	Albinistic, eyes reduced	Lucifugus Group
1′	Pigmented, eyes well developed	2
2(1′)	Two lateral spines present on each side of carapace	Spiculifer Group
2′	A single lateral spine present or absent on each side of carapace	3
3(2′)	Cephalic surface of first pleopod always bearing a prominent angular or tuberculiform shoulder some distance proximal to tip (figs. 59-63)	Clarkii Group
3′	Cephalic surface of first pleopod entire or bearing a distinct hump, but never is the latter angular or tuberculiform	4
4(3′)	Subterminal setae present	5
4′	Subterminal setae absent	10
5(4)	Tip of cephalic process of first pleopod lying in a plane caudal to terminal third of main shaft of pleopod (fig. 57)	*P. toltecae*
5′	Tip of cephalic process of first pleopod lying cephalic to caudal surface of distal third of main shaft of pleopod	6
6(5′)	Caudal process of first pleopod in the form of a corneous longitudinal ridge along caudodistal surface of appendage (fig. 64)	*P. gonopodocristatus*
6′	Caudal process of first pleopod variable in form; if present, never in the form of a corneous longitudinal ridge	7
7(6′)	Subterminal setae of first pleopod borne on a knob on cephalodistal or laterodistal surface	Blandingii Group
7′	Subterminal setae of first pleopod never borne on a distinct knob	8
8(7′)	Cephalic process arising from cephalic side of central projection; caudal process prominent, compressed laterally, arising distinctly from caudolateral surface of pleopod; caudal knob never well defined (figs. 66-72)	Planirostris Group
8′	Cephalic process arising from cephalic or lateral side of central projection; caudal process seldom prominent (sometimes absent) and arising distinctly mesial to caudal knob except in *P. lepidodactylus* which possesses a laterally situated cephalic process (fig. 33)	9
9(8′)	Areola 4.7 to 9.0 times as long as broad (if less than 5.0 then caudal process of first pleopod always lacking) and constituting 28 to 35.5 percent of entire length of carapace (mostly greater than 30 percent)	Seminolae Group
9′	Areola 2.5 to 5.2 times as long as broad (if greater than 4.9 then caudal process of first pleopod always present) and constituting 25 to 30.5 percent of entire length of carapace (mostly less than 30 percent)	Pictus Group
10(4′)	Cephalic process of first pleopod cephalic to base of central projection (fig. 56)	*P. bivittatus*
10′	Cephalic process of first pleopod lateral to base of central projection (fig. 55)	*P. lewisi*

Spiculifer Group (*Ortmann* 1905: 100)[3]

(Figures 14-23)

Diagnosis.—Rostrum with marginal spines. Areola two to five times as long as broad and constituting 23-29 percent of entire length of carapace. Two or more lateral spines present on each side of carapace. First pleopod of first form male terminating in three or four distinct parts (cephalic process sometimes absent); subterminal setae in anterolateral rows or clusters, dense or relatively sparse, but never arising from the surface of a knob; corneous caudal process always present but caudal knob sometimes absent; cephalic surface of pleopod always lacking a prominent angular or tuberculiform shoulder some distance proximal to tip. Female with a tuberculate sternum immediately cephalic to annulus ventralis; tubercles frequently projecting over ventral face of annulus.

[3] A detailed study of the Spiculifer Group is presently being conducted by Dr. George H. Penn, Jr. He has read this section of the manuscript and has kindly added several range extensions.

Species and Ranges

P. dupratzi Penn (1953b: 1) Trinity, Red, Neches, Sabine, and Calcasieu drainages (La. and Tex.).

P. echinatus Hobbs (1956: 117) Salkehatchie and Edisto drainages (S.C.).

P. natchitochae Penn (1953b: 5) Red, Calcasieu, and Bayou Teche drainages (La. and Tex.).

P. ouachitae Penn (1956b: 109) Ouachita and Arkansas drainages (Ark.).

P. penni Hobbs (1951: 273) Pearl and Pascagoula drainages (La. and Miss.).

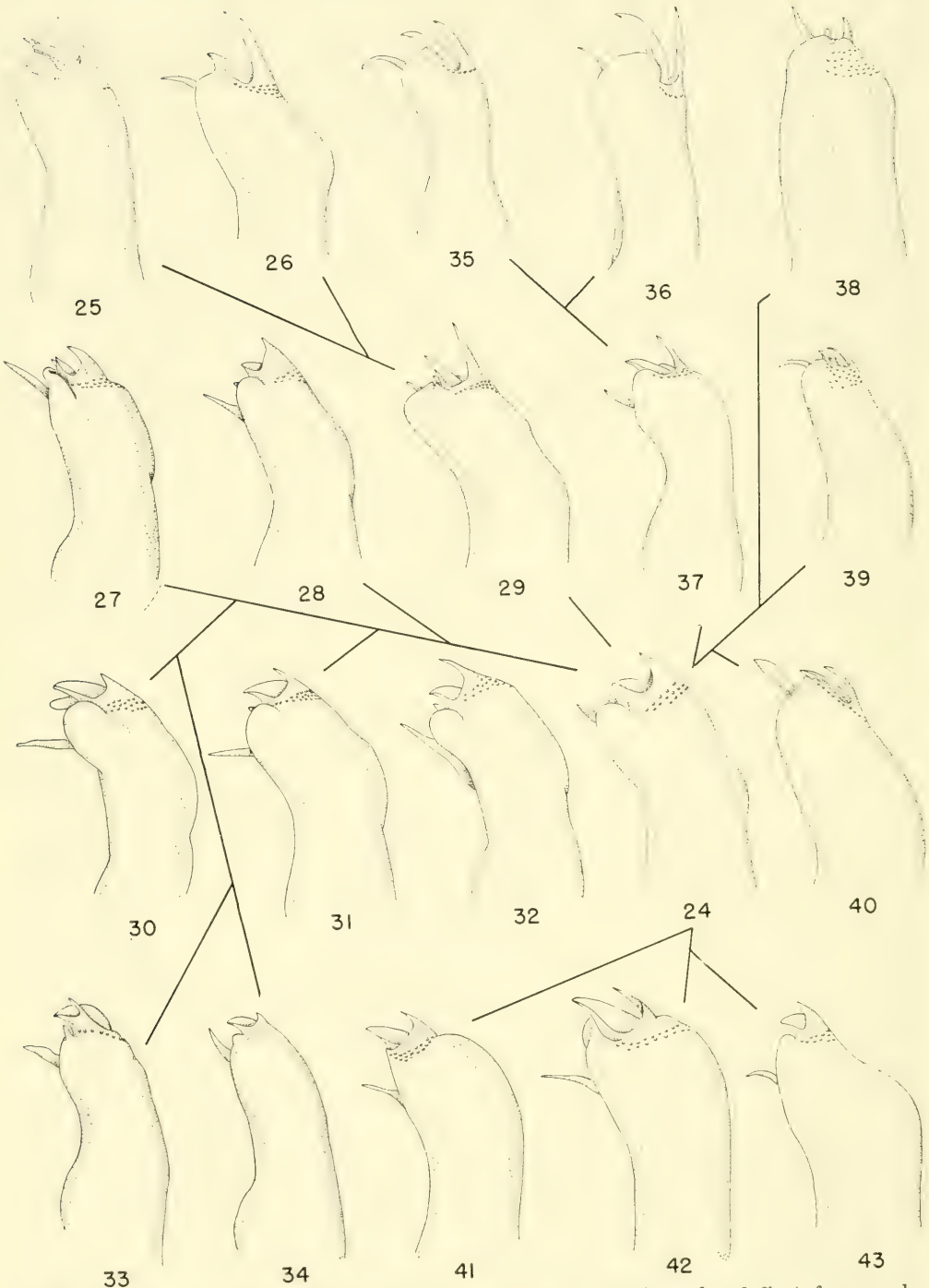
P. raneyi Hobbs (1953b: 412) Upper Savannah and Ocmulgee drainages (Ga. and S.C.).

P. spiculifer (LeConte 1856: 401) Savannah Drainage (S.C.) to Escatawpa Drainage (S.E. Ala.).

P. suttkusi Hobbs (1953a: 173) Choctawhatchee Drainage (Ala. and Fla.).

P. versutus (Hagen 1870: 51) Chattahoochee Drainage (Ga. and Fla.) to Escatawpa Drainage (S.E. Miss.).

P. vioscai Penn (1946: 27) Red Drainage to Tombigbee Drainage (La. and Miss.).



Figures 24-43. Lateral view of terminal portions of first pleopods of first form males. **24.** *Hypothetical Propictus.* **25.** *P. youngi.* **26.** *P. hirsutus.* **27.** *P. litosternum.* **28.** *P. chacei.* **29.** *P. pubescens.* **30.** *P. epicyrtus.* **31.** *P. enoplosternum.* **32.** *P. pictus.* **33.** *P. lepidodactylus.* **34.** *P. angustatus.* **35.** *P. ancylus.* **36.** *P. seminolae.* **37.** *P. lunzi.* **38.** *P. pycnogonopodus.* **39.** *P. leonensis.* **40.** *P. fallax.* **41.** *P. lucifugus lucifugus.* **42.** *P. lucifugus alachua.* **43.** *P. pallidus.* [Dark semicircles represent positions of subterminal setae.]

As a group the range extends from the Salkehatchie and Edisto systems in South Carolina to the Trinity and Red systems in Texas and Arkansas.

Habits.—All of the members of the Spiculifer Group frequent lotic habitats where they may be found among vegetation and debris, under logs or stones, or in shallow burrows in the banks of the streams. [Further details may be found in Hobbs (1942b, 1953b) and Penn (1946, 1953b, 1956a, 1956b)].

Relationships.—There is no reason to question the close affinities of the crayfishes assigned to the Spiculifer Group, and there are a number of reasons for postulating that, as a group, these crayfishes closely approximate, in their anatomy, the ancestral procambarid stock. All of the members are so similar except in certain of their secondary sexual characteristics that a discussion of their relationships must be based largely on the first pleopods of the male. The diagnostic feature of sharing two or more lateral spines on each side of the carapace occurs elsewhere only in certain members of the Mexicanus Section.

Procambarus vioscai (Fig. 20) retains more nearly than do any of the other species the primitive facies of the pleopod of the postulated Prospiculifer stock (Fig. 13). Its caudal process arises from the mesial base of the caudal knob, and the other terminal elements are disposed much as they are in the prototype. With a straightening of the terminal portion of the appendage, *dupratzi* (Fig. 23) has also remained little altered. In *penni* (Fig. 19) and *natchitochae* (Fig. 22) the caudal knob has been imperceptibly fused with the caudal process, and the former has approached *dupratzi* in the straightening of the terminal elements. In *echinatus* (Fig. 21), the caudal knob has been almost completely suppressed, and the cephalic process has been shifted laterally to arise primarily from the lateral base of the central projection. In *versutus* (Fig. 18), the entire distal portion of the appendage has been attenuated, and in many populations there is hardly a trace of the caudal knob, although the caudal process remains distinct. In *suttkusi* (Fig. 17), the emphasis of change is seen in the tremendously enlarged and caudally removed caudal knob leaving the caudal process at the caudolateral base of the central projection; too, the cephalic process has been shifted to a mesial position (not visible in Fig. 17) to arise at the mesial base of the central projection close to the cephalic base of the mesial process, thus departing markedly from the prototype appendage. The most striking deviations from the postulated ancestral appendage are seen in *spiculifer* (Fig. 15), some specimens of *ouachitae* (Fig. 16), and *raneyi* (Fig. 14) in which the cephalic process is lacking. The former two have retained the caudal knob which is absent in the latter. In *ouachitae,* the caudal process is strongly developed and arises from a generalized caudal knob, and in some specimens (Penn 1956b: 116) the cephalic process is present, arising on the cephalomesial side of the central projection, thereby approaching the disposition of this process in *suttkusi.* In *spiculifer* the caudal knob is elongated and bears a comparatively small caudal process.

With reference to the pleopods, the more generalized forms, *vioscai, penni, natchitochae, dupratzi,* and *echinatus* occupy the western and eastermost portion of the range of the group, while the more divergent members are found in the eastern half and *ouachitae* near the westernmost limit of the range.

One of the most striking features of the females of the Spiculifer Group is the tuberculate sternum immediately cephalic to the annulus ventralis. Among the generalized members it is most prominent in *dupratzi* and *echinatus* but is also well developed in *penni* and *vioscai* and to a lesser degree in *natchitochae.* Among the more divergent species, *versutus* and *suttkusi* exhibit this feature to an extent surpassing that of any other member of the group. In *raneyi* it is prominent as it is also in some populations of *spiculifer.*

Pictus Group (*Hobbs* 1942b: 129)

(Figures 2, 6, 25-34)

Diagnosis. — Rostrum with marginal spines. Areola 2.5 to 5.2 times longer than broad (if greater than 4.9 then caudal process of first pleopod always present) and constituting 25 to 30.5 percent of entire length of carapace. A single lateral spine present on each side of carapace. First pleopod of first form male terminating in three or four distinct parts (caudal process some-

times absent, but if so, areola never more than 3.5 times longer than wide); subterminal setae in rows or clusters on cephalolateral surface of appendage (very sparse in *youngi,* and their disposition is not known in *angustatus*); caudal knob well developed, or clearly evident, except in *lepidodactylus;* cephalic surface of pleopod lacking a prominent angular or tuberculiform shoulder some distance proximal to tip although some of the more generalized species exhibit a hump in the corresponding position. Female with or without a tuberculate sternum immediately cephalic to annulus ventralis.

Species and Ranges

P. angustatus (LeConte 1856: 401) Known only from the type specimen which was reported to have been collected *"Habitat in Georgia inferiore, in aquae purae rivalos que inter colloculos arenosus* [sand-hills] *currunt."*

P. chacei Hobbs (1958a: 5) Wateree, Congaree, Edisto, and Savannah drainages (S.C.) and from isolated localities in the Ogeechee and Ocmulgee drainages (Ga.).

P. enoplosternum Hobbs (1947a: 5) Ohoopee Drainage (tributary of the Altamaha River) (Ga.).

P. epicyrtus Hobbs (1958b: 1) A single stream tributary of the Ogeechee River in Screven Co., Ga.

P. hirsutus Hobbs (1958a: 160) Edisto, Salkehatchie, and Savannah drainages (S.C.).

P. lepidodactylus Hobbs (1947b: 25) Pee Dee, Black, and Wateree drainages in the lower piedmont and coastal plain of S.C. and extreme southeastern N.C.

P. litosternum Hobbs (1947a: 9) Canoochee, Ogeechee, and Newport drainages (Ga.).

P. pictus (Hobbs 1940a: 419) Black Creek drainage (tributary of the St. Johns River) in Clay Co., Fla.

P. pubescens (Faxon (1884: 109) Savannah and Ogeechee drainages, and a single locality in the Altamaha drainage (Ga.).

P. youngi Hobbs (1942b: 131) St. Marks River, Leon Co., and from a tributary of the Chipola River and Wetappo Creek, Gulf Co. (Fla.).

Habits.—"The ecological requirements of all of them seem to be satisfied in streams (mostly sand-bottomed) of the lower piedmont and coastal plain. The size of the stream, as well as the condition of the water, whether clear, silt-laden, or coffee-colored, appear to have no effect on the subgroup [=Group] as a whole. Whether or not certain species may be limited by these factors remains to be demonstrated. There seems to be little doubt that a lotic habitat is necessary. These species occur abundantly in beds of *Vallisneria* and other aquatic plants. They are also found in litter and roots along the undercut banks of streams." (Hobbs 1958c: 76).

Relationships.—The intra-group relationships of the members of the Pictus Subgroup [equivalent to Group here] have been discussed in some detail by Hobbs (1958c), and there seems little reason to modify conclusions set forth therein. These are depicted in Figures 24 through 34. The inter-group relationships are mentioned above.

Seminolae Group (Here designated as a Group)[4]
(Figures 35-40)

Diagnosis.—Rostrum with or without marginal spines, margins often entire. Areola 4.7 to 9.0 times as long as broad (if less than 5.0 then caudal process of first pleopod always lacking) and constituting 28 to 35.5 percent of entire length of carapace (mostly greater than 30 percent). A single lateral spine or tubercle on carapace present or absent. First pleopod of first form male terminating in three of four parts (caudal process always reduced or absent); subterminal setae in a row or cluster at, or near, base of cephalic process and central projection; caudal knob greatly swollen or almost imperceptibly fused with shaft of appendage; cephalic surface of pleopod lacking a prominent angular or tuberculiform shoulder some distance proximal to tip. Female with or without a tuberculate sternum immediately cephalic to annulus ventralis.

4 Previously treated as the Seminolae Subgroup of the Pictus Group (Hobbs 1942b: 142; Hobbs 1958c) and the Fallax Subgroup of the Blandingii Group (Hobbs 1942b: 111); united here as the Seminolae Group.

Species and Ranges

P. ancylus Hobbs (1958b: 164) "From Columbus and Bladen counties, North Carolina, in the lowermost portions of the piedmont and in the coastal plain to the Santee River system in South Carolina." (Hobbs 1958c: 80).

P. fallax (Hagen 1870: 45) From the Suwannee and St. Mary drainages (Ga.) south to DeSoto, Highlands, and Palm Beach counties, Fla.

P. leonensis Hobbs (1942b: 114) Between the Apalachicola and Suwannee rivers (Fla.).

P. lunzi (Hobbs 1940b: 3) Hampton and Beaufort counties, S.C.

P. pycnogonopodus Hobbs (1942b: 117) Between the Apalachicola and Choctawhatchee rivers (Fla.).

P. seminolae Hobbs (1942b: 142) Coastal plain from the Altamaha River (Ga.) south to Marion County, Fla.

Habits.—The members of the Seminolae Group have habits markedly similar to those of the Clarkii Group, frequenting swamps, ponds, lakes, roadside ditches, springs, and streams. Not infrequently, they also dig simple burrows—even when standing water is available. *Procambarus fallax* is particularly abundant among the roots of floating mats of water hyacinths. (See Hobbs 1942b: 113-119, 145.)

Relationships.—Two previously recognized subgroups of the Blandingii Section are here united, for while *fallax* (Fig. 40), *leonensis* (Fig. 39), and *pycnogonopodus* (Fig. 38) appear to be more closely allied to one another than either is to *ancylus* (Fig. 35), *lunzi* (Fig. 37), and *seminolae* (Fig. 36), I now believe that all of them have arisen from a common ancestor. Previously, my opinion was that *evermanni* (Fig. 72) represented a possible link between the Fallax Subgroup and the Clarkii Subgroup; however, in light of the discovery of the several other species of which the Planirostris Group is composed, the relationships of *evermanni* seem clearer and it is highly unlikely that *fallax* and its obvious relatives should be linked closely with it, but rather to *lunzi*.

This Group is confined to the coastal plain from the Choctawhatchee Drainage in Florida to the lakes region in southeastern North Carolina. Here, the ranges of only two of them, *fallax* and *seminolae*, overlap —in extreme southern Georgia and northern Florida.

On the basis of the first pleopods, the most generalized members of the Group appear to be *lunzi* and *ancylus*, with *leonensis* and *fallax* not far removed. The greatest divergence is seen in the accentuated terminal elements of *seminolae* and the reduced ones in *pycnogonopodus*. In the structure of the areola, *seminolae*, in contrast, has both the broadest and shortest, approaching that of the generalized members of the Pictus Group. Conspicuous in this Group is the tendency toward a reduction of the caudal process of the first pleopod. Only in *fallax* and *leonensis* is there a vestige of it remaining.

Hobbs (1958c: 88) discussed the possible origin of *ancylus, lunzi,* and *seminolae,* and the addition of the other three species to the Group does not alter his conclusions. In this discussion *P.* sp. D is *ancylus.*

Lucifugus Group (Here designated as a Group)[5]
(Figures 41-43)

Diagnosis.—Albinistic, eyes reduced. Rostrum with marginal spines. Areola 10 to 36 times as long as broad and constituting 37 to 43 percent of entire length of carapace. Lateral surface of carapace strongly tuberculate with a row of them along caudal margin of cervical groove, occasionally one somewhat larger than the others—corresponding to the lateral spine of other crayfishes. First pleopod of first form male terminating in four distinct parts although caudal process is not evident in lateral aspect; subterminal setae arising from cephalolateral base of the terminal elements in the form of an arc consisting of two or more rows; cephalic surface lacking a prominent angular or tuberculiform shoulder some distance proximal to tip. Female with or without a tuberculate sternum immediately cephalic to annulus ventralis.

Species and Ranges

P. lucifugus alachua (Hobbs 1940a: 402) Western part of Alachua County, Fla. [Intergrades between the two subspecies occur in Marion Co., Fla.]

P. lucifugus lucifugus (Hobbs 1940a: 398) Citrus and Hernando counties, Fla.

[5] Previously treated as the Lucifugus Subgroup of the Pictus Group (Hobbs 1942b: 134; Hobbs 1958c).

P. pallidus (Hobbs 1940a: 154) North-Western part of Alachua Co. to Leon Co., Fla.

Habits.—These three crayfishes are confined to subterranean waters where they are found in caves and sinkholes wandering about over muddy or rock-littered bottoms of pools. While the animals appear to avoid bright light, they are often found in large numbers in diffuse light in sinkholes or at the mouths of caves.

Relationships.—The members of the Lucifugus Group have their closest affinities with the generalized members of the Pictus Group. As was shown by Hobbs (1958c), a common ancestry of the two seems almost certain. Of the three, *lucifugus alachua* (Fig. 42) is probably the most generalized —the first pleopod of the male resembles that of the primitive members of the Pictus Group more closely than do those of typical *lucifugus* (Fig. 41) and *pallidus* (Fig 43). The areola is slightly shorter and distinctly broader than in the latter two, and it is only one of the three that has retained (?) pigment in the eyes. A discussion of the origin of the Group may be found in Hobbs (1958c).

Blandingii Group (Ortmann 1905: 100) (Figures 44-54)

Diagnosis.—Rostrum with or without marginal spines or tubercles, but if without, then margins always interrupted near apex except in *viae-viridis* and *caballeroi*. Areola four to twenty times as long as broad and constituting 25 to 38 percent of entire length of carapace (30 to 38 percent excluding *lecontei*). A single lateral spine present or absent on each side of carapace. Apophysis on coxa of fourth pereiopod somewhat reduced in *viae-viridis*, otherwise typical of the Section. First pleopod of first form male terminating in four distinct parts; subterminal setae always arising from the surface of a knob (not always clearly distinct in *verrucosus*); cephalic surface of pleopod always lacking a prominent angular or tuberculiform shoulder some distance proximal to tip. Female with or without a tuberculate sternum immediately cephalic to annulus ventralis, but only in *caballeroi* do the tubercles approximate the sizes characteristic of certain members of the Spiculifer Group *(e.g., versutus and suttkusi).*

Species and Ranges

P. acutissimus (Girard 1852:91) Tombigbee, Alabama, and Choctawhatchee drainages (Ala. and Miss.).

P. blandingii acutus (Girard 1852: 91) Florida to Texas and Minnesota to Ohio. [The ranges of the subspecies of *blandingii* are not accurately determined.]

P. blandingii blandingii (Harlan 1830: 464) Coastal plain and piedmont from Massachusetts to Georgia. [See note under *blandingii acutus* above.]

P. blandingii cuevachicae (Hobbs 1941: 1) Puebla and San Luis Potosi, Mexico.

P. caballeroi Villalobos (1944b: 175) Villa Juárez, Puebla, Mexico.

P. hayi (Faxon 1884: 108) Tallahatchie and Tombigbee drainages (Miss.)

P. lecontei (Hagen 1870: 145) Pascagoula, Escatawpa, and Chickasaw drainages (Miss. and Ala.).

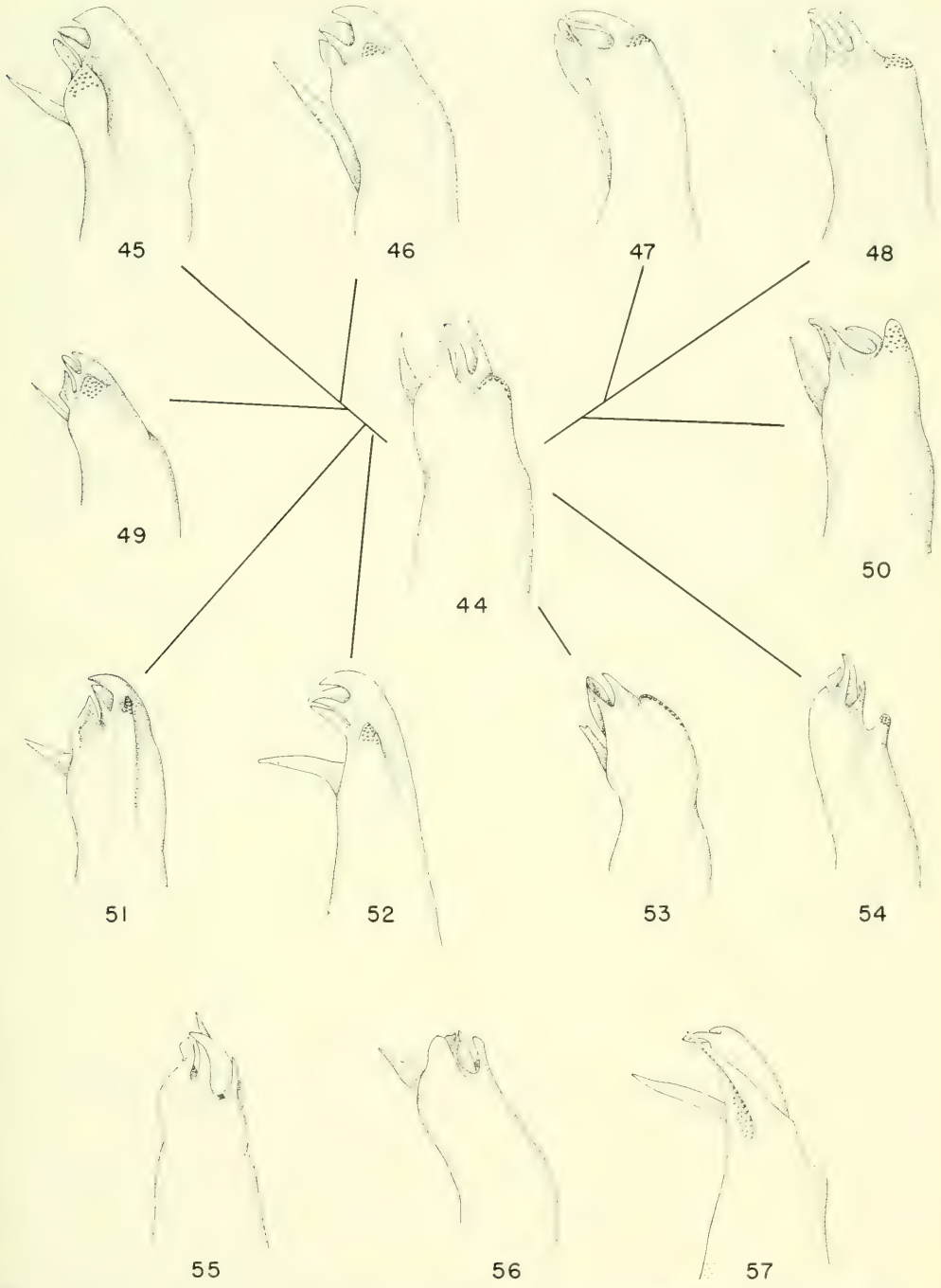
P. lophotus Hobbs and Walton (1960: 123) Alabama drainage in Lowndes, Montgomery and Wilcox counties, Ala.

P. verrucosus Hobbs (1952b: 212) Chattahoochee and Tallapoosa drainages (Ala.).

P. viae-viridis (Faxon 1914: 370) Southeastern Arkansas and northeastern Louisiana, western Tennessee, northern Mississippi and northwestern Alabama.

Habits.—The members of the Blandingii Group, with the possible exception of *lecontei,* occur in all types of epigean lotic and lentic habitats, and frequently they are found in simple burrows. *Procambarus lecontei* has been found only in sand and silt bottom streams.

Relationships.—The characteristics which unite this assemblage of crayfishes are a pleopod (1) terminating in four parts which, for the most part, are similarly disposed and (2) bearing a setiferous knob along the distal cephalic (or lateral) surface of the appendage. The most generalized pleopod is probably that of *blandingii blandingii* (Fig. 48) with the setiferous knob situated on the cephalic surface at the base of the cephalic process. In *blandingii acutus* (Fig. 50) the terminal elements and the setiferous knob are similarly disposed but the latter is much accentuated. In *blandingii cuevachicae* (Fig. 47), the knob has shifted caudally on the lateral side of the



Figures 44-57. Lateral view of terminal portions of first pleopods of first form males. **44**. Hypothetical Problandingii. **45**. *P. hayi*. **46**. *P. lophotus*. **47**. *P. blandingii cuevachicae*. **48**. *P. blandingii blandingii*. **49**. *P. caballeroi*. **50**. *P. blandingii acutus*. **51**. *P. acutissimus*. **52**. *P. lecontei*. **53**. *P. verrucosus*. **54**. *P. viae-viridis*. **55**. *P. lewisi*. **56**. *P. bivittatus*. **57**. *P. toltecae*. [Dark semicircles represent positions of subterminal setae.]

appendage, a tendency which is slightly more accentuated in *lophotus* (Fig. 46), caballeroi (Fig. 49), *acutissimus* (Fig. 51), and *lecontei* (Fig. 52), and reaches the extreme in *hayi* (Fig. 45) where it lies in a caudolateral position at the base of the caudal process. Accompanying the shifting of the setiferous knob is a tendency of the cephalic process to form a hood-like element over the central projection; the extreme of this condition is seen in *lecontei,* although it is clearly evident in *lophotus, acutissimus,* and *hayi.* The two most divergent members of the group are *verrucosus* (Fig. 53) and *viae-viridis* (Fig. 54). In the former, the setiferous knob is not so well defined as in the other members of the group, and the terminal setae are dispersed along a longitudinal ridge rather than in a cluster. In *viae-viridis,* not only is the setiferous knob much withdrawn from the terminal elements, but the mesial process is also displaced cephalically so as to lie only slightly cephalomesial to the cephalic process (in Fig. 54 it may be seen lying between the cephalic process and the central projection).

In the rostrum and the areola, *lecontei* is the most generalized. It is the only member of the group in which the areola constitutes less than 30 percent of the entire length of the carapace and is less than 7 times as long as broad. In this connection, it is worthy of note that this is the only species which is known to occur only in lotic habitats—approaching both ecologically and morphologically the members of the Spiculifer and Pictus groups.

The ranges of only two members of the group, *caballeroi* and *blandingii cuevachicae,* do not extend into the Mississippi-Alabama-Georgia area, and the ranges of five of them (*hayi, lophotus, acutissimus, lecontei,* and *verrucosus)* are limited to this region. It seems, therefore, highly possible that the Problandingii stock took its origin in this region.

Planirostris Group (Here designated as a Group)[6]
(Figures 65-72)

Diagnosis--Rostrum with or without marginal spines or tubercles, margins usually entire. Areola 30 to 37.5 percent of entire length of carapace and from 3.7 to 24 times longer than broad. A single lateral spine or tubercle present or absent on each side of carapace. First pleopod of first form male terminating in three or four distinct parts (cephalic process lacking in *mancus*); subterminal setae linearly arranged except in *evermanni* and *jaculus* in which they are more irregularly arranged—never, however, arising from a distinct knob; caudal process corneous, compressed laterally and always well developed; caudal knob; if recognizable, always imperceptibly fused with caudal process; cephalic surface of pleopod lacking a prominent angular or tuberculiform shoulder some distance proximal to tip, although a weak shoulder present in *pearsei plumimanus* and a rounded prominence in *planirostris, hybus, mancus,* and *jaculus.* Female with, or more usually without, a tuberculate sternum immediately cephalic to annulus ventralis.

Species and Ranges

P. evermanni (Faxon 1890: 620) Okaloosa County, Fla. west to Jackson County, Miss.

P. hybus Hobbs and Walton (1957: 39) Green County, Ala. and Kemper, Lowndes, and Noxubee counties, Miss.

P. jaculus Hobbs and Walton (1957: 48) Known only from the type locality, one mi. W. of Scott-Rankin County line on U.S. Hwy. 80, Rankin County, Miss.

P. mancus Hobbs and Walton (1957: 44) Known only from the type locality, five mi. S. of Meridian, Lauderdale County, Miss.

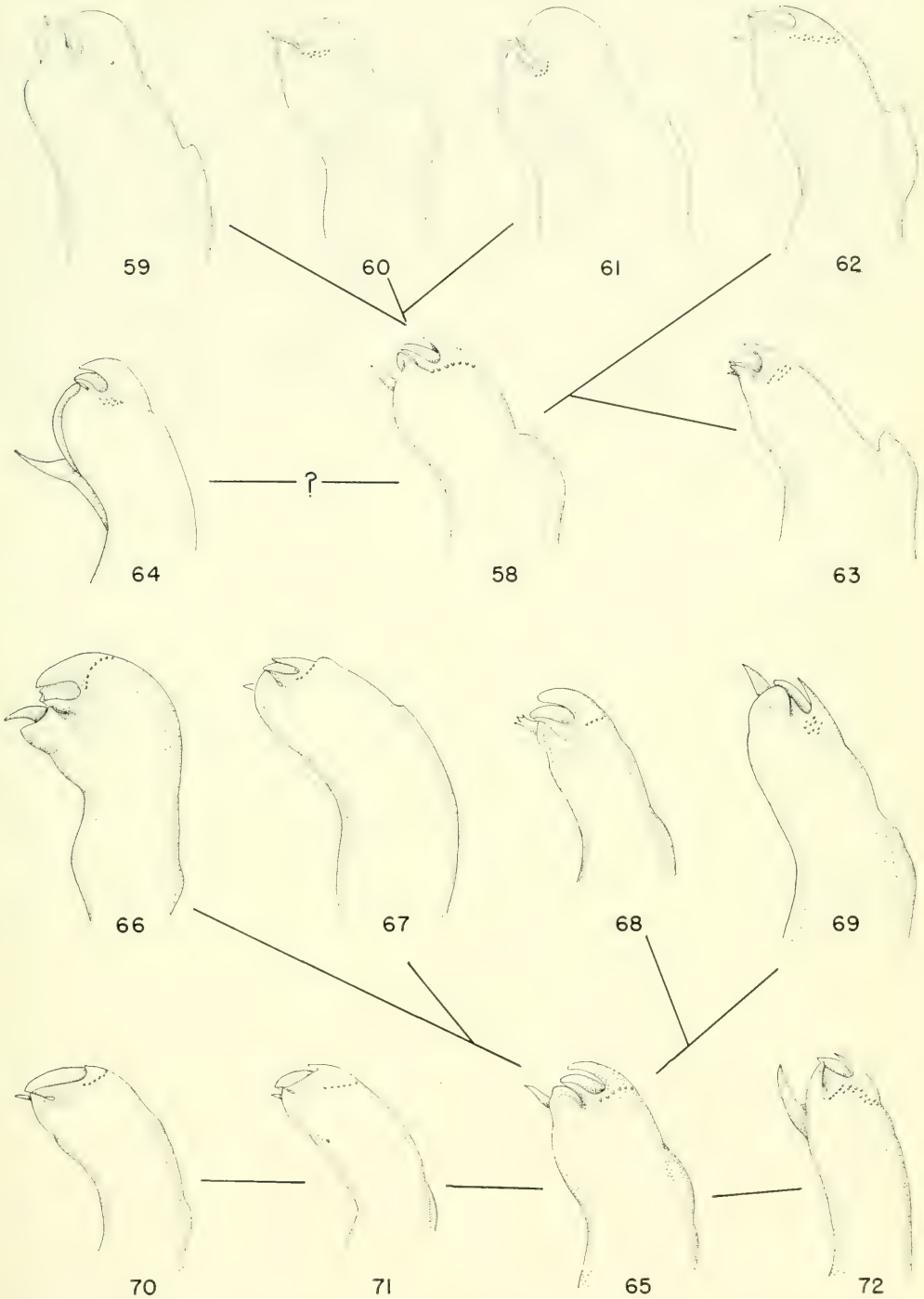
P. pearsei pearsei (Creaser 1934: 1) Johnson and Pitt counties, N.C. south to Horry County, S.C.

P. pearsei plumimanus Hobbs and Walton (1958: 8) Craven and Duplin counties, N.C.

P. planirostris Penn (1953a: 71) Florida parishes of southeastern Louisiana and Perry and Pearl River counties, Miss.

Habits.—For the most part, the members of the Planirostris Group are secondary burrowers, frequenting temporary bodies of water and burrowing during dry seasons. They occur in shallow ponds, roadside ditches, swamps, and sluggish streams. Penn (1956a: 412) summarized the habits and life history of *planirostris,* and these observations are in

[6] Originally proposed as the monotypic Planirostris Subgroup of the Blandingii Section (Penn 1953a: 75).



Figures 58-72. Lateral view of terminal portions of first pleopods of first form males. **58.** Hypothetical Proclarkii. **59.** *P. clarkii.* **60.** *P. okaloosae.* **61.** *P. troglodytes.* **62.** *P. paeninsulanus.* **63.** *P. howellae.* **64.** *P. gonopodocristatus.* **65.** Hypthetical Proplanirostris. **66.** *P. pearsei pearsei.* **67.** *P. pearsei plumimanus.* **68.** *P. hybus.* **69.** *P. jaculus.* **70.** *P. mancus.* **71.** *P. planirostris.* **72.** *P. evermanni.* [Dark semicircles represent positions of subterminal setae.]

accord with the few data available for the other species.

Relationships.—The generalized members of the Planirostris Group have much in common with those of the Clarkii Group. Hobbs and Walton (1957) originally assigned *jaculus* to what they called the Clarkii Subgroup, and Penn (1953a), in discussing the affinities of *planirostris,* indicated the close relationships existing between it and the members of the same subgroup.

As to intra-group relationships, the most generalized species are probably *hybus* (Fig. 68), *planirostris* (Fig. 71), *jaculus* (Fig. 69), and *evermanni* (Fig. 72) and with *pearsei plumimanus* (Fig. 67) not far removed. The specialized members are *mancus* (Fig. 70) in which the cephalic process of the first pleopod is lacking, and *pearsei pearsei* (Fig. 66) in which the entire group of terminal elements is strongly recurved.

The generalized species are found in the Mississippi-Alabama coastal plain, as are all of the members except the two subspecies of *pearsei,* which are widely separated from the other members. There is a gap in the range of the Group which extends from western Alabama almost to the North Carolina-South Carolina line. Apparently vicariating for the Planirostris Group in most of this region are members of the Barbatus Section. Insofar as is known, the ranges of none of the species of the Planirostris Group overlap.

Clarkii Group (Ortmann 1905: 100) (Figures 58-63)

Diagnosis.—Rostrum with marginal spines or tubercles except in some older animals; in them, margins always interrupted near apex. Areola six to an infinite number of times as long as broad (usually obliterated in *clarkii*) and constituting 23 to 38 percent of entire length of carapace (excluding some specimens of *paeninsulanus,* 31 to 38 percent). A single lateral spine present or absent on each side of carapace. First pleopod of first form male terminating in four distinct parts; subterminal setae sparse *(clarkii)* or abudant but never arising from the surface of a knob; cephalic surface of pleopod always bearing a prominent angular or tuberculiform shoulder some distance proximal to tip (shoulder on right pleopod frequently bent caudally to lie against mesial surface of appendange); corneous caudal process present, but a distinct caudal knob always absent. Female with or without a tuberculate sternum immediately cephalic to annulus ventralis.

Species and Ranges

P. clarkii (Girard 1852: 91) From eastern Ala. to western Tex. and up the Mississippi Valley to Dunklin County, Mo. and Hickman County, Ky. [Introductions: Calif., Fla., Nev., Va., Hawaii, and Japan.]

P. howellae Hobbs (1952a: 167) Tributaries of the Altamaha River in Bibb, Emanuel, and Telfair counties, Ga.

P. okaloosae Hobbs (1942b: 100) Between the Yellow and Perdido rivers in Ala. and Fla.

P. paeninsulanus (Faxon 1914: 369) From the Choctawhatchee River to the Atlantic Ocean, and from southern Ga. to Hillsborough County, Fla.

P. troglodytes (LeConte 1856: 400) North of the Altamaha River in Ga. and S.C. (piedmont and coastal plain).

Habits.—Like the members of the Blandingii Group, these crayfishes occur in lotic and lentic habitats, and are frequently found in burrows. *Procambarus clarkii* is also known to inhabit brackish water. Both *clarkii* and *paeninsulanus* have been observed walking across land some distance from a body of water. Penn (1943:3) gives an excellent summary of the habits of *clarkii* in his study of its life history. Also see Hobbs (1924b: 103, 106).

Relationships. — As noted above, the Clarkii Group consists of five allopatric species which, as a group, occupy an almost unbroken range from Texas to South Carolina. In addition to similarities in their habits and body conformation, the first pleopod of the male has an angular prominence on its cephalic margin — the only members of the Blandingii Section which possess an angular shoulder or hump. An examination of the accompanying figures will disclose the presence of *rounded* prominences in members of the Pictus and Planirostris groups but here the humps are neither so prominent nor are they distinctly angular.

It seems probable that the most generalized member of the group is *paeninsulanus,* for not only is the first pleopod of the male

more similar to that of the generalized appendages in the other groups, but also in this species is found the broadest, shortest areola. On the basis of the same characteristics, *howellae* (Fig. 63) is more closely related to *paeninsulanus* (Fig. 62) than are the other three. The close affinities of *clarkii* (Fig. 59), *okaloosae* (Fig. 60), and *troglodytes* (Fig. 61) are seen primarily in the expanded cephalic process which reaches the extreme condition in *troglodytes.* In this Group, therefore, the generalized members are found in the Alabama-Georgia-Florida area, and the more divergent members at the western and eastern limits of the range of the Group.

The Disjunct Members of the Blandingii Section

(Figures 55-57, 64)

Four species which seem properly associated with the members of the Blandingii Section are not, on the basis of present definitions, readily assignable to one of the above seven groups, nor are they closely related to one another. Rather than erect four additional monotypic groups, they are here grouped as disjunct members of the Section.

Species and Ranges

P. bivittatus Hobbs (1942b: 96) Escambia Drainage (Fla.) and Pearl Drainage (La.)

P. lewisi Hobbs and Walton (1959: 39) Lowndes, Montgomery, and Macon counties, Ala.

P. gonopodocristatus Villalobos (1958: 279) Known only from two localities in the State of Veracruz, Mexico.

P. toltecae Hobbs (1943: 198) Vicinity of Tamazunchale, San Luis Potosi, Mexico.

Procambarus bivittatus (Fig. 56) has its closest affinities with the members of the Pictus and Blandingii Groups but is not readily assignable to either. There are no subterminal setae on the first pleopod, and the caudal knob, bearing the caudal process on its cephalodistal surface, sets it apart from both groups. In the elongation of the caudal knob, it approaches *P. alleni* (Faxon 1884: 110) and it also has bituberculate hooks on the ischiopodites of the fourth pereiopod, another characteristic which is shared with *alleni.*

Procambarus lewisi (Fig. 55) is most closely related to the members of the Planirostris Group but, like *bivittatus,* lacks subterminal setae on the first pleopod. Furthermore, the cephalic process lies at the lateral base of the central projection, whereas in the Planirostris Group this process occupies a cephalic position but shows a tendency to migrate toward a mesial position. Also, its range lies on the eastern boundary of the range of the Group. It might well be considered a disjunct member of the Planirostris Group.

Procambarus gonopodocristatus (Fig. 64) is almost certainly allied to the members of the Clarkii Group. Neglecting the absence of the cephalic angular shoulder and the greatly expanded (elongated) ridge-like caudal process, its other characteristics are those of this Group (*c.f.* Figs. 64 and 58-63). Supporting this view are the obliterated areola, the somewhat flattened ventral face of the annulus ventralis, and the arrrangement of the subterminal setae. All of these are characteristic of *clarkii.* There seems to be little doubt that *gonopodocristatus* had a common origin with the members of the Clarkii Group.

Procambarus toltecae (Fig. 57), because of its twisted first pleopod, is difficult to place in the above scheme of classification. That portion which corresponds to the lateral surface of the pleopods of other members of the Section has been displaced caudomesially so that the cephalic process lies in the position usually occupied by the caudal process, and the latter is situated caudomesially. If it could be imagined that the displaced elements were shifted to the usual position, then the pleopod would assume the appearance of that somewhat typical of the members of the Blandingii Section. Probably *toltecae* is most closely related to the members of the Blandingii and Pictus groups although there is a distinct shoulder on the cephalic surface of the appendage. As pointed out above, however, although the members of the Clarkii Group have the best developed shoulder, it is by no means restricted to these crayfishes. It is likely that *toltecae* was derived from a stock that also gave rise to the modern members of the Pictus and Blandingii groups.

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