THE OHIO JOURNAL OF SCIENCE

Vol. 67 MAY, 1967 No. 3

THE PROPINQUUS GROUP OF THE CRAWFISH GENUS *ORCONECTES* (DECAPODA: ASTACIDAE)[1, 2]

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ABSTRACT

Nine species and subspecies assigned to the Propinquus Group, Propinquus Section, of the crawfish genus *Orconectes* are evaluated on the basis of 1226 specimens examined. Eleven characters are analyzed statistically and 12 more qualitatively, principally by determination of comparative frequencies. *O. jeffersoni* is judged specifically distinct from *O. propinquus* and the conspecific *O. s. sanborni* and *O. s. erismophorous.* All other taxa of the Group are distinct species. A new species from Iowa is diagnosed, but not described. Two distinct subgroups, Propinquus and Sanborni, are proposed and diagnosed. A lectotype and paralectotypes were designated for *Cambarus obscurus* Hagen and for *Cambarus sanborni* Faxon. Standard taxonomic characters in crawfishes are discussed briefly with particular reference to the Propinquus Group.

Less than one hundred years ago, only 55 known species and subspecies of crawfish were recognized on the North American continent (Hagen, 1870), and all were believed to belong to two genera, one of which was endemic. Almost nothing was known concerning their interrelations and evolution. Today approximately 350 species and subspecies are assigned to eight genera and three subfamilies, of which all genera and two subfamilies are endemic. Most of the additional knowledge was contributed near the turn of the century and subsequent to 1930. Hobbs (1940, *et seq.*), among others, has demonstrated that the conclusions of earlier writers, especially of A. E. Ortmann, require re-evaluation and often revision because of the rapid increase of available data.

Except for members of the Genus *Cambarus*, the several taxa assigned to the Propinquus Group of the Genus *Orconectes* are the most difficult of the crawfishes to assess by the procedures of classical taxonomy. The remarkable homogeneity of morphology, particularly the gross appearance of the first pleopod of the first form male, in the several populations has led to questions of assignment and relationships. Many of the species and subspecies descriptions have been based on semi-quantitative comparative lengths, shapes, and such characters; for example, a species may have been defined or diagnosed by having the terminal elements of the first pleopod of the male shorter than another species, without comparative ratios being stated. The undesirabilities of such practices are obvious.

Hobbs (1948a) demonstrated that the infrageneric "Sections" of the genus

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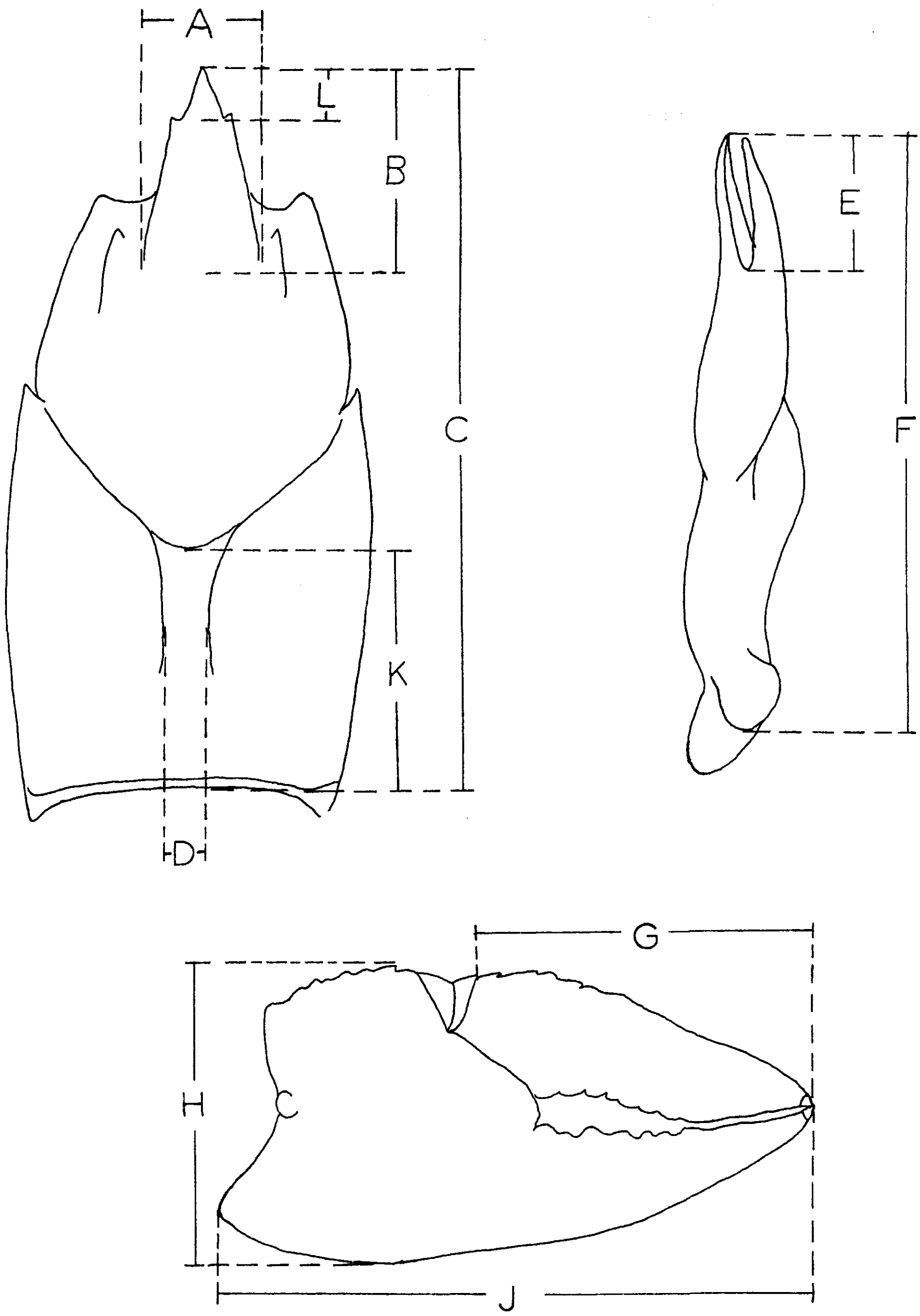


FIGURE 1. Techniques of measurement: A. rostrum width; B. rostrum length; C. carapace length; D. areola width; E. central projection length; F. pleopod length; G. dactyl length; H. palm width; J. Chela length; K. areola length; L. acumen length.

Orconectes are not as distinct as one would wish for an orderly association of the several species into supraspecific and subgeneric categories. Among other recent discussions with differing opinions are Rhoades (1944a, 1959, 1962a), Creaser (1933b; 1962), and Fitzpatrick (1963). The genus *Procambarus* has fared a little better than *Orconectes*, with Hobbs (1942b, *et seq.*), Villalobos (1946, *et seq.*), and Penn (1953, *et seq.*) agreeing in principle on the groupings of the species of the genus. In his most recent paper, however, Hobbs (1962) revised his earlier groupings because of newly available information. The relationships of the members of the genus *Cambarus* are as much of an enigma as are those of *Orconectes*. Morphological similarities are so pronounced that many years of intense study will be necessary before these genera can be organized to the degree of orderliness found in *Procambarus*.

FIGURE 2. Recent distribution of the Propinquus Group. Vertical: *O. s. sanborni;* horizontal: *O. obscurus;* lower left to upper right: *O. propinquus;* upper left to lower right: *O. erichsonianus;* perpendicular cross-hatching: *O. illinoisensis;* diagonal cross-hatching: *O. virginiensis;* stipple: *O. jeffersoni;* dashes: *O. s. erismophorus;* wavy: *O.* sp. A.

Penn (1957) resolved the question of relationship between *Orconectes palmeri* (Faxon), *O. p. longimanus* (Faxon), and *O. p. creolanus* (Creaser) (Virilis Section, Palmeri Group) by the application of statistical procedures to the analysis of variation of taxonomic characters. The present study was initiated using similar techniques on a larger group of animals, having the promise of accurate quantitative definition of variation in the several species and subspecies.

MATERIALS AND METHODS

The specimens used in this study came from three primary sources: the personal collections of Horton H. Hobbs, Jr. (HHH), the collections of the United States National Museum (USNM), and the personal collections of Rudolph Prins (RP). The Hobbs collections are now incorporated into the collections of the United States National Museum. Unless otherwise specified, all data were accumulated from one of these sources. The large geographic area occupied by the Propinquus Group made extensive field collection impracticable.

Field collections were made, however, in northwestern Georgia, northern Alabama, eastern Tennessee, and extreme southeastern Kentucky in the spring of 1962. These collections are now at the United States National Museum as numbers 114091–114242, inclusive. In the fall of 1963 collections were made in northwestern Illinois; in the summer of 1964 collections were made in eastern Iowa. These latter two collections are retained in the personal collections of the writer. Only mature (as indicated by size) specimens were used in data accumulation because of the absence of information concerning ontogenetic variation. Full locality data may be obtained from a dissertation entitled "Studies in the Propinquus Section of the Crawfish Genus *Orconectes*," submitted to the University of Virginia in June, 1964.

Measurements were made, with micrometer calipers, of the length of the cephalothorax, the length and width of the rostrum, the length of the acumen, the length and width of the areola, the length of the outer margin of the palm, the width of the palm, the length of the dactyl, and, in males, the length of the pleopod. An ocular micrometer mounted in a stereoscopic microscope was used to measure the length of the central projection and the length of the mesial process in males.

Qualitative characters were recorded for the nature and existence of spinose or tuberculate ornamentation as exemplified by marginal spines on the rostrum, lateral spines on the carapace, postorbital spines, spines on the mesial surface of the carpus, and ornamentation of the lower latero- and lower mesiodistal margins of the carpus. Notes on the presence or absence of a median carina on the rostrum, location of hooks on the ischiopodites of the pereiopods of males, shape of the margins of the rostrum, and counts of the punctations in the narrowest part of the areola were made. Initially, records were kept of ornamentation of the merus, number of tubercles along the opposable margins of both fingers, and number of and rows of tubercles on the inner margin of the palm, but these recordings were discontinued early in the study when it became evident that no significant information would be revealed by these data.

Statistical analyses were made for each characteristic in the three categories: males, Form I; males, Form II; and females. When no dimorphism was evidenced, data were combined for presentation. For those species which occupy a wide geographic range or for which previous writers have suggested geographic variations, the characters were examined for clinal variation. I found no clines in the material with which I worked. To allow comparison of different-sized animals, ratios were calculated to relate each character to some standard length or measurement (for details *cf.* Penn, 1957; Fitzpatrick, 1963).

Data are presented in graph form, following the method of Hubbs and Hubbs (1953) for presenting the results of statistical analyses. Statistical differences were determined by Student's *t* test or the coefficient-of-difference equation. Significant qualitative characters are reported by the use of histograms or in tabular form. Because the length of the cephalothorax was chosen as the standard length in crawfishes, this character is reported in the three categories. Only the range and mean of the character are graphed (fig. 3), because statistical analyses

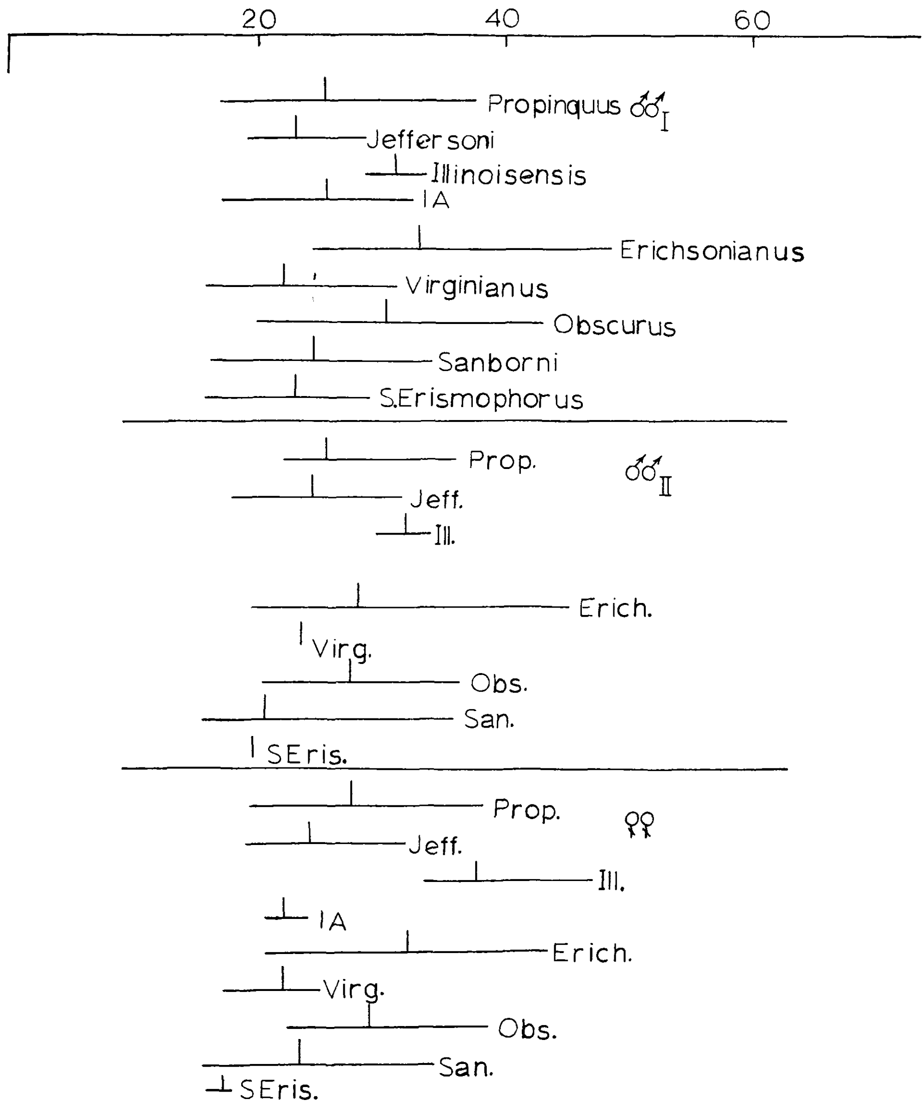


FIGURE 3. Carapace length in mm: horizontal line represents actual range of specimens examined; vertical line represents arithmetic mean. Species names abbreviated for second form males and females.

of this character are meaningless, and the maximum sizes examined are reported (table 1).

Following statistical analyses, characteristics which are less liable to precise definition (e.g., distribution, history, etc.) were considered, and an attempt was made to understand the taxonomic and evolutionary relationships. In my revision of the nomenclature, I have attempted to use the taxonomic heirarchy to describe the evolutionary, as well as the morphological, relationships between the several taxa studied.

TABLE I
Size ranges of Propinquus Group crawfishes (all measurements: length of cephalothorax in mm)

Species	Max. ♂♂ I	Min. ♂♂ I	Max. ♂♂ II	Max. ♀♀
O. propinquus	37.0	17.1	36.2	38.4
O. erichsonianus	48.8	24.3	45.6	43.7
O. illinoisensis	31.6*	—	29.6*	33.5*
O. jeffersoni	29.6	19.0	31.6	32.2
O. s. sanborni	34.0	16.1	36.0	34.5
O. s. erismophorus	29.2	17.6	19.8*	16.3
O. obscurus	42.9	20.5	36.6	38.9
O. virginiensis	31.2	15.6	23.4*	25.2

*Only one specimen examined.

TAXONOMIC CHARACTERS, THEIR VALIDITY AND APPLICATION

As is the case with most systematic studies, taxonomists have selected certain morphological characteristics of crawfishes which are used to distinguish the several taxa, one from the other. Ideally, such taxonomic characters are also characters of evolutionary significance, but this is not always the case. In ideal situations, taxonomic characters will reflect the evolutionary history of the organism. This method of the selection of characters has been discussed by Mayr, Simpson, and others (*cf.* especially Mayr, Linsley, and Usinger, 1953; and Simpson, 1961). Likewise, taxonomic characters are selected for their relative stability in a given taxon. It follows that the precise limits of variability of each character should be known before it may be fully utilized.

In crawfishes, the specific, infraspecific, and supraspecific taxonomic characters used have been modified repeatedly. Likewise, evolutionary characters have been proposed, rejected, and sometimes reproposed as additional studies have revealed more insight and more data have been accumulated. The following paragraphs are an attempt to review the more significant characters, to evaluate the reliability of each, and to evaluate their reflection of the evolutionary history of the species of the Propinquus Group.

Among the earliest characters found to be useful to the taxonomist, and certainly one of the most prominently visible, is the rostrum. The general configuration of this structure, and its ornamentation, are frequently used to characterize a particular species of crawfish, especially among those species groups which have similar external genitalia. In the Propinquus Section, however, the rostrum is so remarkably similar in most species that only one who is familiar with all the members of the Section can use this character, and even then, only in conjunction with other characters. The rostrum lacks evolutionary stability and often can not be used in supraspecific or evolutionary studies. This is due, in a large part, to the probable convergence of rostral forms dependent apparently upon the ecological habits and requirements of the individual species. This is discussed in some detail by Hobbs (1958: 82–83). The presence or absence of a median carina on the rostrum is frequently a significant character, but its degree of development is often variable (Crocker, 1957: 37), and in some instances (e.g., *O. virginiensis*), it is so variable as to be almost useless. The length and shape of the acumen is usually quite variable when many specimens are examined. In part, I attribute this to the exposed location of this structure and therefore to its frequent injury.

Another conspicuous structure of the dorsal region of the carapace is the areola. Its configuration varies from long to short, and from narrow to broad. As with the rostrum, the areola is subject to little interspecific variation in the Propinquus Section. Because the crawfishes with which the members of the Section are associated have combinations of rostral configuration and areola morphology different from members of the Propinquus Section, these characters may be used in certain regions to identify an individual as a member of the Propinquus Section. Usually this combination cannot be used to make a specific determination. In groups of crawfishes other than those in the Propinquus Section, the morphology of the areola is often useful as a key character. The length of the areola in any given species seems to be relatively stable when expressed as per cent length of the carapace. The width of the areola in the Propinquus Group is so variable intraspecifically that it must be eliminated from consideration as a key character. Also the areola is as subject to ecologic canalization as is the rostrum (Hobbs, 1958: 82), thus offering the same problems as previously outlined.

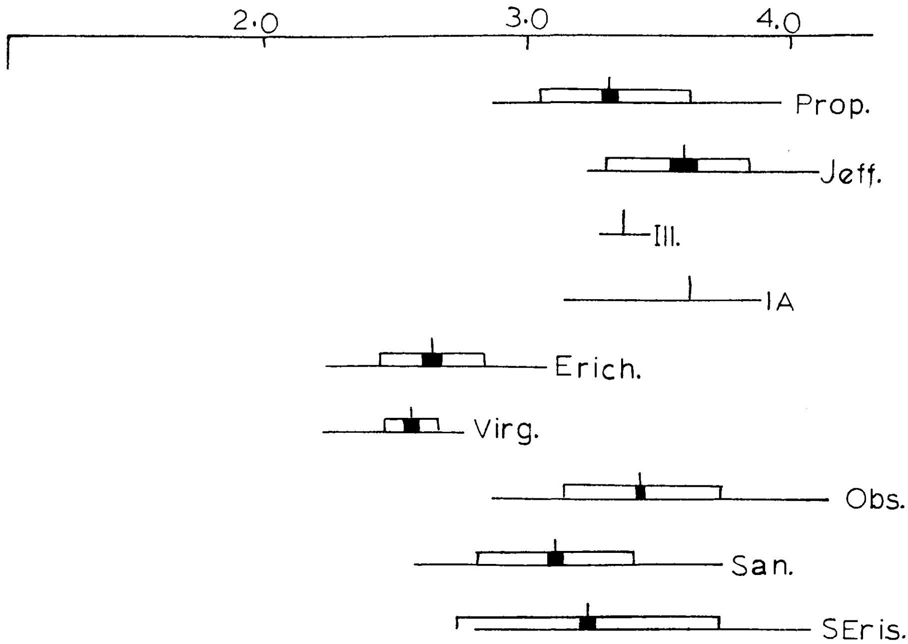


FIGURE 4. Rostrum length: solid bar represents 1.5 standard deviations; open bar represents 2 standard errors. Other symbols same as Figure 3. Species names abbreviated.

The contours and ornamentation of the cheliped, the modified and enlarged first pereiopod, have long been used as taxonomic characters. A specialist is required to evaluate these characters correctly, however. In some instances, certain features of the chela are distinctive and can be used to distinguish a species. In the Propinquus Group, and to some degree the Propinquus Section, the contours and ornamentation of the hand and carpus are sufficiently stable and unique to permit Group (and Section) recognition. The cheliped is the most useful field character in distinguishing between the sexes, other than the gonopod and annulus ventralis. This is complicated, however, by reproductive dimorphism evident in male Cambarinae, which dimorphism is reflected in the cheliped morphology. Other difficulties arise when one attempts to use the cheliped as a

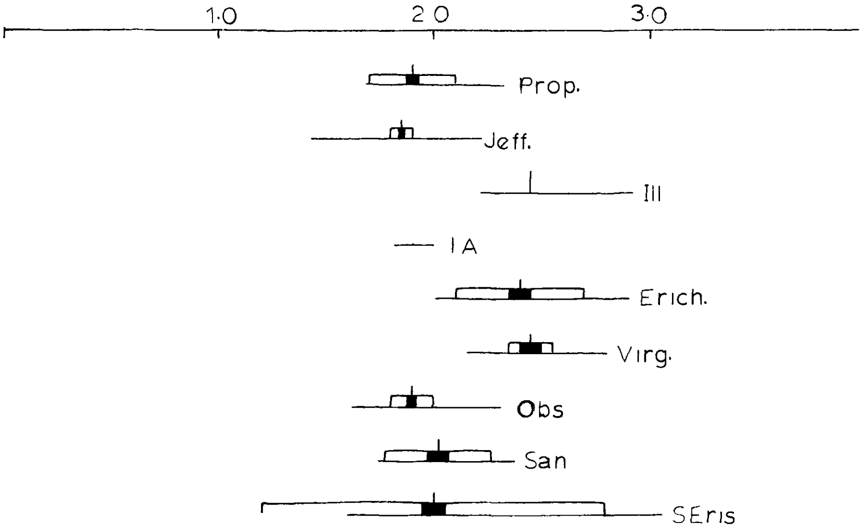


FIGURE 5. Rostrum width: Symbols same as Figure 4. Species names abbreviated.

taxonomic character. The chela is used for defense, offense, mating, and food getting; therefore, it is continually subject to injury, and frequently to loss. When lost, the cheliped is regenerated, usually in a modified form. If the cheliped is lost early in life, the modifications are often subtle, and I do not have confidence that I can always recognize a regenerated cheliped. In the Propinquus Group, all species have similar chelipeds.

The male members of the Propinquus Group all bear single simple hooks only on the ischiopodites of the third pereiopods, with extremely rare exceptions among individuals, but definitely not within species.

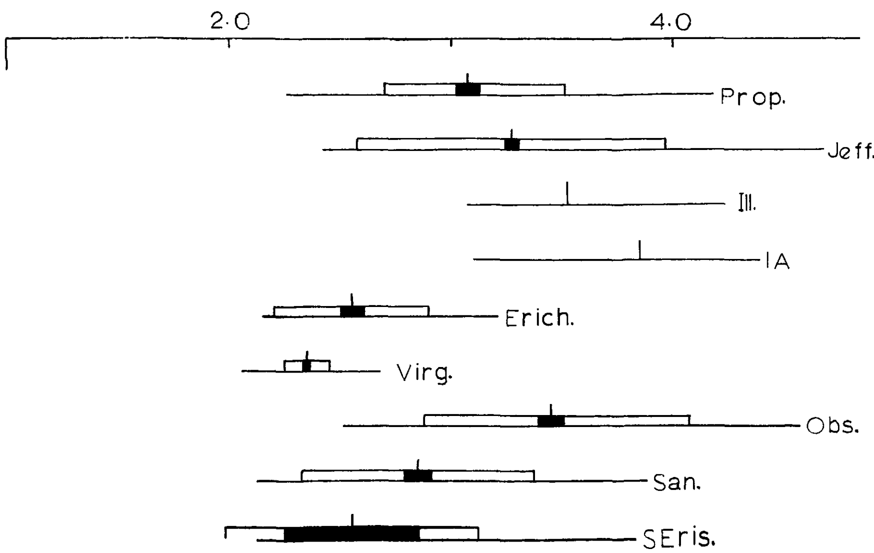


FIGURE 6. Acumen length: Symbols same as Figure 4. Species names abbreviated.

Structures utilized in amplexus have been found to be the most useful characters for both taxonomic and evolutionary studies. The first pleopod of the male astacid is modified into a rolled, cannula-like structure to facilitate spermatophore transfer at mating, and in the Cambarinae, Cambarellinae, and Cambaroidinae, it is specifically unique and subject to reproductive dimorphism. In the reproductively active male (Form I) Cambarinae, the tips of the appendages bear distinct spiniform, setiform, or plate-like distal projections, at least one of which is corneous. In immature, subadult, and non-breeding males (Form II), the projections are less distinct, more blunt, and usually non-corneous, and in this condition it is usually similar in closely related species, making accurate identification difficult. Despite shortcomings, the first pleopod of the male is the most useful taxonomic and evolutionary character yet discovered. It is usually stable and, insofar as is known, is little affected by ecological factors (Hobbs, 1958: 83–84). In the Genus *Orconectes*, the curvature of the two rami, the length of the central projection when expressed as per cent length of the pleopod, and ornamentation are distinctive, seemingly evolutionarily significant, and easily recognized. The

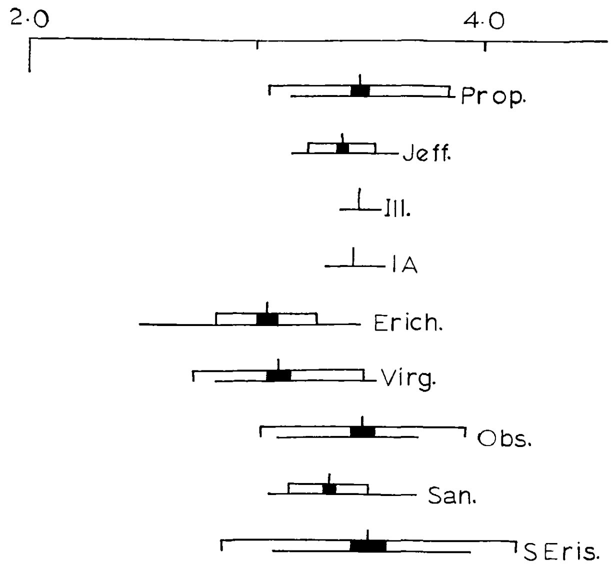


FIGURE 7. Areola length: Symbols same as Figure 4. Species names abbreviated.

pleopod can be used to identify a specimen as belonging to a species assigned to the Propinquus Section, or one of the Groups of the Section, with reasonable accuracy. In some species, the first pleopod, especially of the Form I male, bears a shoulder on the cephalic surface. The degree of development and location of this shoulder are frequently useful in the identification of species, but too little is known of homologies of this structure to permit other than limited use as an evolutionary character at the present time.

The Cambarinae female possesses a distinct *receptaculum seminis* on the midline of the sternum between the fourth and fifth pereiopods, called the *annulus ventralis*, which structure seemingly reflects evolutionary relationships and is usually unique in the adult of each species. In juvenile specimens, the *annulus ventralis* is less likely to be unique, inversely related to age. As with the pleopod, it seems to be unaffected by the habits of the animal. Unfortunately, this structure has been little utilized for taxonomic distinction. Little is said of it in most publications, exclusive of species descriptions. This is due in part to the facts that it is difficult to draw if one is not a skilled artist, almost impossible to photograph adequately, and difficult to describe. In recent years the artistic skills of the taxonomists Villalobos and Hobbs have added much to our knowledge of the *annulus ventralis*, especially of the genus *Procambarus*.

Often much significance is attached to the presence of spinose ornamentations, or to their replacement by tubercles. In the Propinquus Section, spines are definitely more prominent on younger animals and tubercles more frequent on older ones. This is not an absolute correlation, but the data accumulated in this study appear to make this observation valid. The use of ornamentation as a taxonomic character has more validity if used in absolute relationships, such as those which are always present or always absent, or as a part of a meristic or pattern study. Ornamentation is usually in a prominent location, subject to

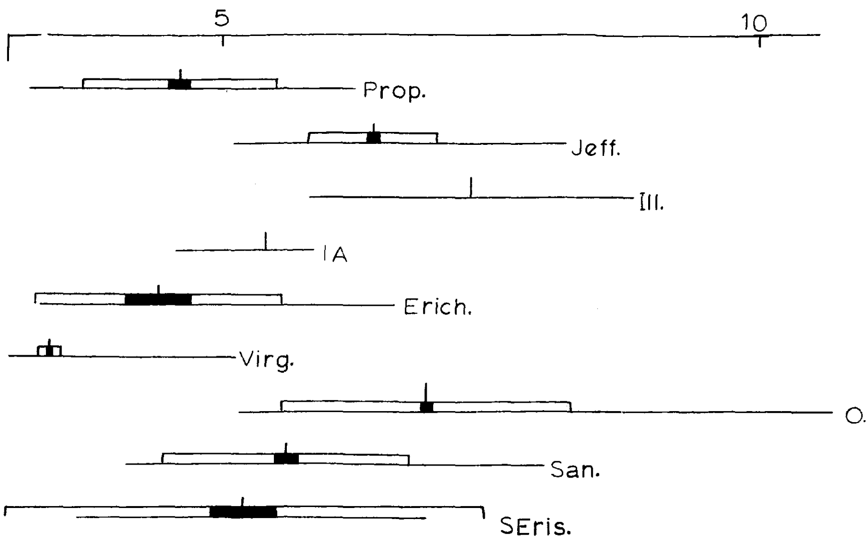


FIGURE 8. Areola width: Symbols same as Figure 4. Species names abbreviated.

injury, and subject to a reflection of the specific environmental stresses experienced by the individual animal. For example, I have found that animals which have been collected from rapidly flowing or tumbling water with small rocks and gravel on the bottom are more prone to have spines missing or badly worn than animals taken from quieter waters. Thus, the use of this characteristic would require a thorough knowledge of both the age and the microhabitat of each animal. The only conclusion that I can infer about the evolutionary significance of spines in the Genus *Orconectes* is that rostral, lateral, and cheliped spines are more primitive than tubercles, which are more primitive than a complete absence of ornamentation. In making these observations, I rely heavily on a knowledge of other, apparently "primitive" species. The pattern of ornamentation and armature of the carpus of the species of the Propinquus Group are similar and can be used to assign a specimen to this Group. Among the loci examined for ornamentation, the absence of spines at a specific locus in very young animals is indicative that ornamentation will never occur in that locus in adult animals.

HISTORICAL STATEMENT

Although an astacine crawfish (*Cancer astacus*) was known to Linnaeus (1758: 631), there was a lapse of time until Fabricius (1798) described the first American astacine, *Astacus Bartonii* (=*Cambarus bartonii bartonii*). Erichson

(1846) observed the distinction of North American forms and proposed a new subgenus, *Cambarus*, for these crawfishes. Erichson's (1846) *Cambarus* was neglected by zoologists until Hagen (1870) recognized the validity of the genus. The notable exception to this was Charles Girard who (1852) reaffirmed *Cambarus*, elevated it to generic rank, and was the first to recognize the importance of the first abdominal appendage of the male as a taxonomic character.

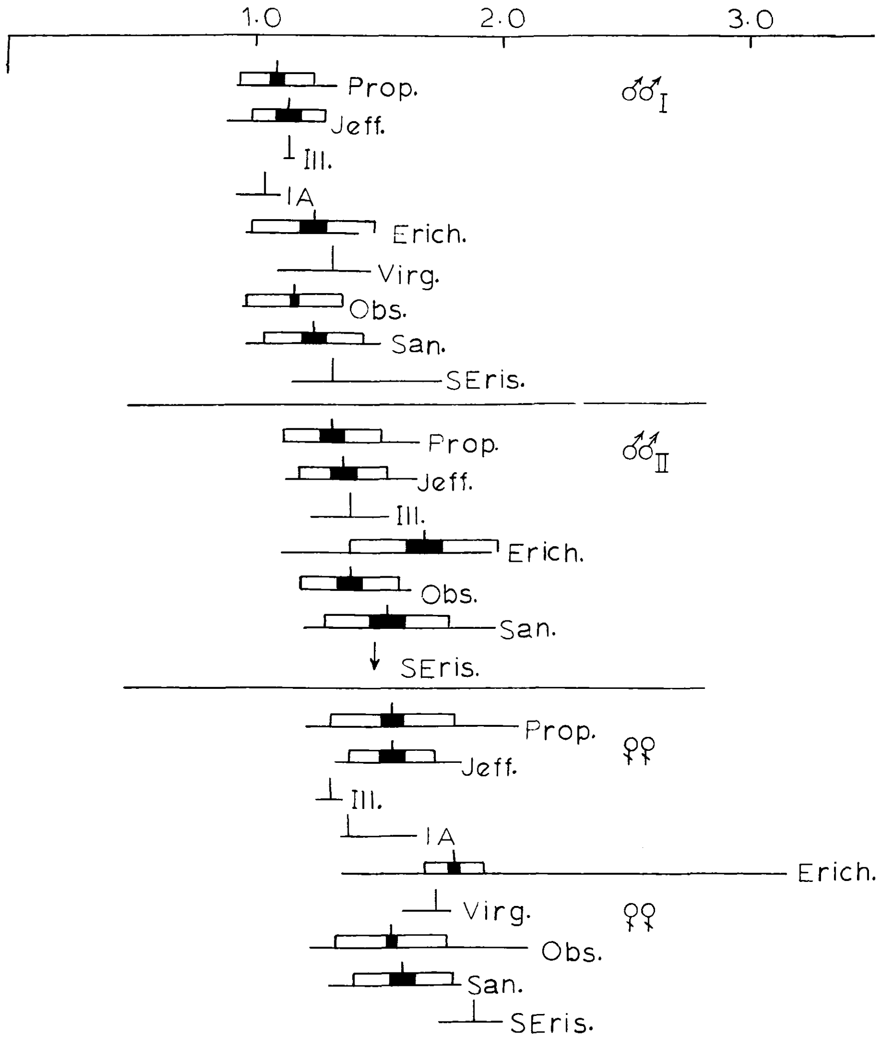


FIGURE 9. Chela length: Symbols same as Figure 4. Species names abbreviated.

The first major work devoted entirely to North American crawfishes was the monograph of Hagen (1870). He relied heavily on the peculiarities of the first pleopod of the male to identify the several species of *Cambarus* and was meticulous in pointing out the dimorphism of the males. The first extensive attempts at subgeneric organization were made by Walter Faxon who, in a series of papers (1885 to 1914), combined species of *Cambarus* into several groups based primarily on the hooks of the ischiopodites of the males. Ortmann (1905b; 1906a) proposed a series of subgenera based primarily on the morphology of the first pleopod of Form I males. This basic concept is still in use today with only minor modifications.

Creaser (1933a) was the first to recognize that the subgenera of Ortmann (1905b) were in part generic entities; he elevated the subgenus *Faxonius* to generic status. Hobbs (1942a) determined the need for more precise distinction between the several groups, elevated Ortmann's (1905b; 1906a) subgenera to generic rank, evoked the rule of priority to establish certain names, and established a new sub-

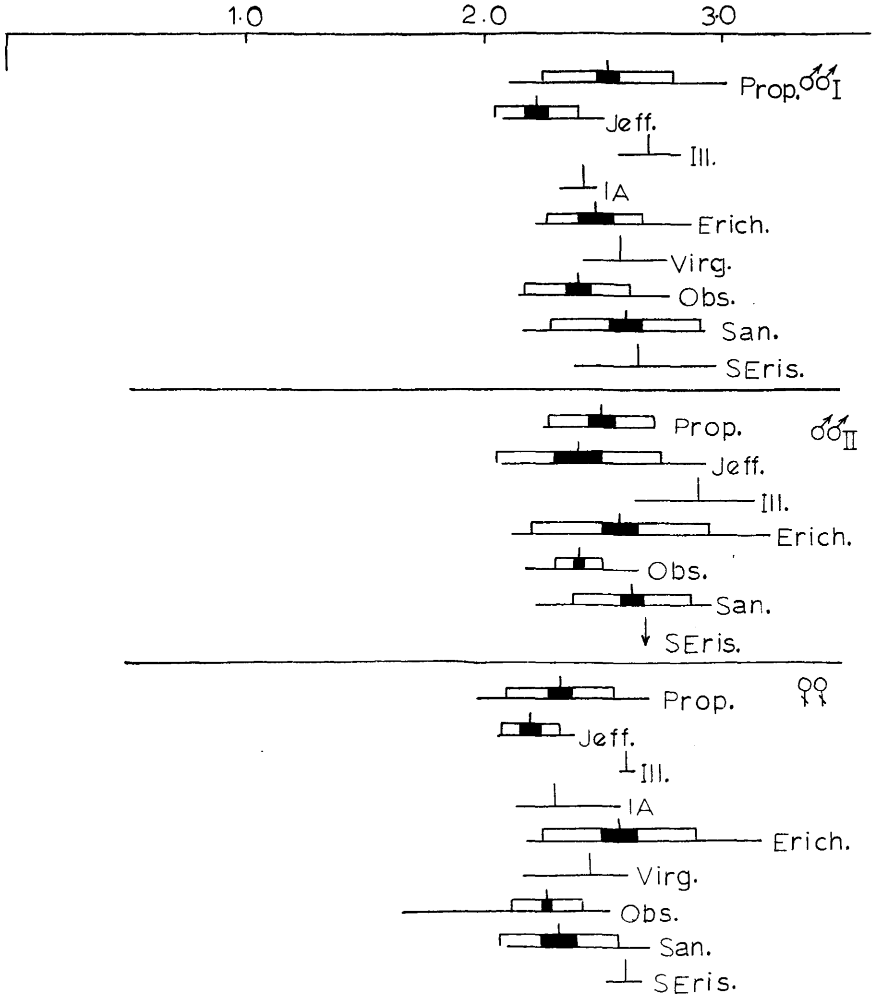


FIGURE 10. Palm width: Symbols same as Figure 4. Species names abbreviated.

family of the Astacidae, the Cambarinae. The new subfamily was distinguished by its branchial apparatus and included all of the species of *Cambarus* and *Faxonius* of previous writers. These species were assigned to one of the following genera: *Procambarus* Ortmann (=*Procambarus* and *Cambarus* of Ortmann), *Paracambarus* Ortmann, *Cambarellus* Ortmann, *Orconectes* Cope (=*Faxonius* of Ortmann and Creaser), *Cambarus* Erichson *sensu stricto* (=*Bartonius* of Ortmann), and the newly-discovered monotypic genus *Troglocambarus* Hobbs. Since that time only two significant changes have been made in the nomenclature of the Cambarinae. LaGuarda (1961) observed that the branchial apparatus of *Cambarellus* was unique and proposed a new monotypic subfamily Cambarellinae. Fitzpatrick (1963) elevated the subgenus *Faxonella* Creaser (1933b) of the genus *Orconectes* to generic rank. Creaser (1962) published a defense of *Faxonius* as a generic name and proposed a different arrangement for classification of the Cambarinae. Among other proposals, he suggested that within *Orconectes* (*sens.* Hobbs) there

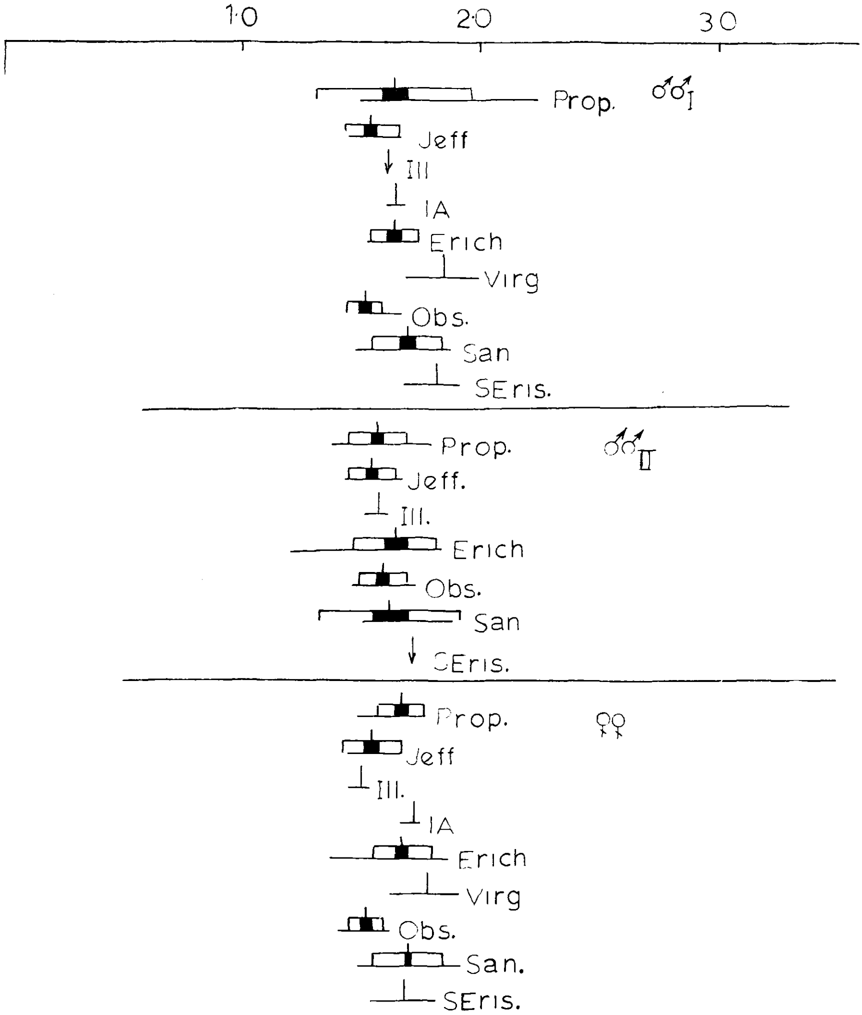


FIGURE 11. Dactyl length: Symbols same as Figure 4. Species names abbreviated.

are three "distinct natural groups, either genera or subgenera": *Faxonella* Creaser, 1933b, *Faxonius* Ortmann, 1905b, and *Orconectes* Cope, 1872 (restricted to *inermis*, *pellucidus*, and *lancifer*). With the exception of Fitzpatrick's (1963) recognition of *Faxonella* as a distinct genus, Creaser's proposal seems to have been accepted only by the author at the present time. I believe that a much better understanding of the relationships between the several groups of the genus *Orconectes* (*sens*. Hobbs) is necessary before further division of the genus can be accepted. Thus, the Cambarinae remain much the same as designated by Hobbs (1942a). The number of genera remains at six—*Cambarellus* being removed to another subfamily, but *Faxonella* being accorded generic status.

THE GENUS *Orconectes*

Astacus limosus was the first crawfish now assigned to the genus *Orconectes* to be described (Rafinesque, 1817). Cope (1872) erected the genus *Orconectes*, on the basis of troglobitic adaptations, to contain his new species *O. inermis*. The genus was rejected by most workers and *inermis*, at best, was received with doubt. The status of *inermis* and the relationships of the closely-related *A. pellucidus* Tellkampf (1844) were detailed by Hobbs (1942a: 351–352), and the priority of *Orconectes* Cope, 1872, over *Faxonius* Ortmann, 1905, was established (p. 352). Rhoades (1959) indicated that he believed *inermis* to be a distinct geographic race, but conspecific with Tellkampf's (1844) *pellucidus*; he continued this thesis in his latest paper (1962a). Hobbs and Barr (in manuscript) disagreed, stating that *inermis* is a distinct species, and they said further that the *pellucidus* of Rhoades is composed of two additional species, *pellucidus* and *australis*. Despite the differences of opinion over the specific status of the troglobitic *Orconectes*, all contemporary writers except Creaser (1962) accept the genus as established by Hobbs (1942a).

Because *Faxonius* Ortmann is a junior synonym of *Orconectes* Cope, the first good description of the modern concept of the genus may be drawn from Ortmann's (1905b: 97) definition of *Faxonius*. In the same paper, Ortmann organized certain "supraspecific" categories which he called Groups and Sections, in ascending order. Because of Hobbs' (1942a) revision, these are probably best considered "infrageneric" categories now. According to Ortmann (1905b), *Faxonius* (=*Orconectes*) could be divided into four Sections: Limosus (no Groups), Lancifer (monotypic), Virilis (three Groups), and Propinquus (two Groups). The major changes to this basic scheme of classification have been the addition of one Group to the Propinquus Section (Creaser, 1934a: 2) and a division of the Limosus Section. Rhoades (1944a: 117) proposed a Rafinesqui Group for the Limosus Section, but Hobbs (1948a) questioned its validity. Later Rhoades (1962a) defended his Group on an evolutionary basis, but Hobbs and Barr (in manuscript) again reject the Group, dispute Rhoades' interpretation of the evolution, and propose a different division, erecting a Pellucidus Group to receive the troglobitic forms of the genus.

THE PROPINQUUS SECTION

The Propinquus Section as erected by Ortmann (1905b: 108) was divided into the Propinquus Group (p. 109) and the Rusticus Group (p. 109). Ortmann's (1905b: 108) definition of the Propinquus Section is basically sound, except for his statement regarding the hooks on the ischiopodites. I can only add that the central projection of the pleopod is 15–60 per cent of the total length of the pleopod and, in total length, the pleopod is ⅓ the length of the carapace or longer. The description of the Propinquus Group (p. 109) is basically sound, too, though this study revealed refinements which will be discussed later. His characterization of the Rusticus Group (p. 109) is sound, but it should be added that the central projection of the pleopod is longer than 30 per cent of the total length of the pleopod, and the total length of the pleopod is usually greater than ⅓ of the length of the carapace. Creaser (1934a: 2) added the Hylas Group to the Section, but his description was in need of considerable refinement, and Williams (1954a: 834) provided a more thorough description.

To the best of my knowledge, there has been no complete listing of the species of the Section since Ortmann erected it, so the following listing of the several species and their relationships is offered, based on my understanding of the Propinquus Section.

Propinquus Section Ortmann, 1905b: 108.
  Propinquus Group Ortmann, 1905b: 109.
    Propinquus Subgroup, herein proposed.
      Orconectes propinquus (Girard, 1852: 88).
      Orconectes erichsonianus (Faxon, 1898: 659).
      Orconectes illinoisensis Brown; 1951, 163.
      Orconectes jeffersoni Rhoades, 1944a: 123. (*comb. nov.*)
      Orconectes species A.
    Sanborni Subgroup, herein proposed.
      Orconectes sanborni sanborni (Faxon, 1884: 128). (*comb. nov.*)
      Orconectes sanborni erismophorous Hobbs and Fitzpatrick, 1963: 207. (*comb. nov.*)
      Orconectes obscurus (Hagen, 1870: 69).
      Orconectes virginiensis Hobbs, 1951: 108.
  Rusticus Group Ortmann, 1905b: 109.
      Orconectes rusticus rusticus (Girard, 1852: 88).
      Orconectes rusticus barrensis Rhoades, 1944a: 125.
      Orconectes rusticus mirus (Ortmann, 1931: 81).
      Orconectes rusticus placidus (Hagen, 1870: 65).
      Orconectes forceps (Faxon, 1884a: 133).
      Orconectes juvenilis (Hagen, 1870: 66).
      Orconectes luetus (Creaser, 1933b: 7).
      Orconectes medius (Faxon, 1885b: 121).
      Orconectes neglectus neglectus (Faxon, 1885c: 142).
      Orconectes neglectus chaenodactylus Williams, 1952: 344.
      Orconectes transfugus Fitzpatrick, 1966b.
  Hylas Group Creaser, 1934: 2.
      Orconectes hylas (Faxon, 1889: 632).
      Orconectes eupunctus Williams, 1952: 330.
      Orconectes leptogonopodus leptogonopodus Hobbs, 1948c: 146.
      Orconectes leptogonopodus acares Fitzpatrick, 1965: 87.
      Orconectes marchandi Hobbs, 1948c: 140.
      Orconectes menae (Creaser, 1933b: 5).
      Orconectes nana nana Williams, 1952: 333.
      Orconectes nana macrus Williams, 1952: 337.
      Orconectes ozarkae Williams, 1952: 339.
      Orconectes peruncus (Creaser, 1931: 7).
      Orconectes punctimanus (Creaser, 1933a: 2).
      Orconectes quadruncus (Creaser, 1933a: 10).
      Orconectes williamsi Fitzpatrick, 1966a.

Several regional faunal studies of crawfishes and catalogues have been published. Because these publications have done little more than give locality data, they are cited without comment in the synonymies. One such paper worthy of individual recognition is that of Harris (1903), in which extensive locality and ecological data were compiled, mostly from existing literature, for almost all the then-known species of crawfishes.

PROPINQUUS GROUP ORTMANN, 1905

Definition: Based on the examination of 1226 specimens (409 ♂♂ I; 257 ♂♂ II; 560 ♀♀). Rostrum with margins subparallel, convergent, or sometimes concave, margins usually moderately thickened; rostrum concave above; median carina present or absent, usually consistent in any taxon; rostrum acuminate, marginal spines or tubercles usually present, but degree of development variable in any population; rostrum 25–40% the total length of carapace, 2–3 times longer than wide. Carapace puncate; areola 27–42% length of carapace, 3–8 times longer than wide, 2–7 punctations in irregular longitudinal rows in its narrowest part; postorbital ridges strong, terminating cephalically in spines or spinose tubercles; carapace with a single lateral spine on each side; branchiostegal spine small, but acute; suborbital angle lacking or much reduced (figs. 4–8, 16; table III).

Chela usually somewhat depressed with palm slightly inflated, exhibiting sexual dimorphism in that those of males are usually longer and with slightly different contours, which conditions is more pronounced in first form males; two irregular rows of tubercles along inner margin of palm extending onto dactyl; outer margin of immovable finger strongly keeled; dactyl divisible into length of outer margin of palm 1.5–2.0 times; palm width divisible into outer margin length 2–3 times, with latter two characters exhibiting no marked sexual dimorphism. Carpus with single prominent acute spine on middle third of inner surface, single spine or spinose tubercle on inner distal margin, and usually tuberculate on proximomesial margin; lower laterodistal margin with prominent spine or spinose tubercle; lower mesiodistal margin with a prominent spine or spinose tubercle (except *O. propinquus*) (figs. 19–27G, 9–11, 17; table II).

First pleopod terminating in two *straight, subparallel, subequal rami* (central projection: mesial process ratio 0.9–1.2, avg slightly greater than 1.0 in first form males); *central projection 17–38% of total length of pleopod in males, Form I, and 7–21% in males, Form II;* pleopods symmetrical (*sensu* Hobbs, 1962); *pleopod about ⅓ length of carapace.* Males with hooks on ischiopodites of third pereiopod (one male, Form II, of *O. erichsonianus* was found to have a very weakly developed hook on the fourth pereiopods!) (figs. 19–27A, B, D, E; figs. 12–15).

Annulus ventralis elliptical in outline, widest in transverse axis, *weakly or only moderately sculptured;* sinuous longitudinal sinus always present; transverse trough in cephalic half shallow or, frequently, absent (figs. 19–27F).

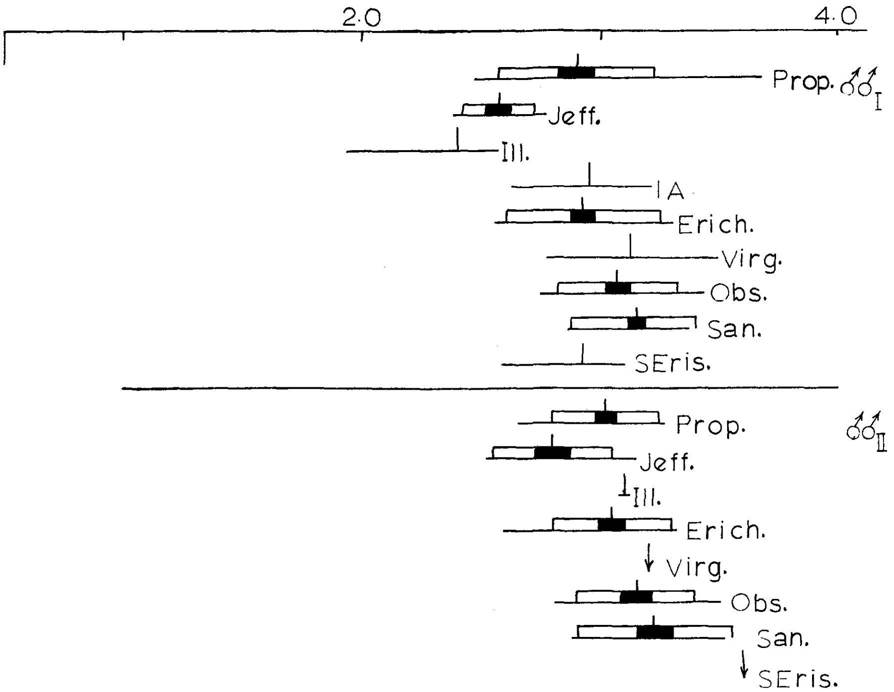


FIGURE 12. Pleopod length: Symbols same as Figure 4. Species names abbreviated.

The several populations of the Propinquus Group have raised differences of opinion concerning their interrelationships and, in some instances, even identity (Faxon, 1884; Faxon, 1885; Turner, 1926; Crocker, 1957). Of the nine species and subspecies currently assigned to the group, three are established on the basis of syntypes (="Cotypes"); another has no types. It seems prudent to take this opportunity to designate appropriate lectotypes. These are designated under species headings at a later point in this paper.

There are two distinct morphological types within the Propinquus Group. These are characterized by the relative average length of the male pleopod and the relative length of the longer ramus of the terminal elements of the pleopod. The dichotomy suggested by the pleopod morphology is reflected in the geographic distribution of the crawfishes exhibiting the two characters. The two types appear to be evolutionarily significant and worthy of distinctive designation. The practice initiated by Hobbs (1942b) for the genus *Procambarus* is adopted and the two types are designated Subgroups of the Propinquus Group.

Propinquus Subgroup, here designated

Diagnosis: First pleopod of male, Form I, with length of central projection greater than 28% of total length of pleopod, of male, Form II, greater than 14% of total length; pleopod length divisible into carapace length an average of greater than 3.0 times in the male, Form I, and 3.2 times in the male, Form II. Occurring generally west of 83rd meridian.

Sanborni Subgroup, here designated

Diagnosis: First pleopod of male, Form I, with length of central projection less than 28% of total length of pleopod, of male, Form II, less than 14% of total length; pleopod length divisible into carapace an average of less than 3.0 times in male, Form I, and in male, Form II, less than 3.2 times. Occurring generally east of the 83rd meridian.

KEY TO THE SPECIES OF THE PROPINQUUS GROUP

1. Rostrum length divisible into carapace length more than 3 times....................... 4
   Rostrum length divisible into carapace length less than 3 times......................... 2
2. Rostrum carinate...*O. virginiensis*
   Rostrum acarinate... 3
3. Areola with 5–7 punctations in its narrowest part..........................*O. virginiensis*
   Areola with 2–5 punctations in its narrowest part..........................*O. erichsonianus*
4. Margins of rostrum concave. Occurring in extreme southern Illinois. Annulus ventralis of female with circular protuberence in anteriomedian portion of trough *O. illinoisensis*
   Margins of rostrum usually not concave. Annulus ventralis without such protuberence in trough. Occurring elsewhere.. 5
5. Rostrum carinate... 9
   Rostrum acarinate... 6
6. Pleopod of male, Form I, with length of central projection greater than 28% of total length of pleopod; of male, Form II, greater than 15%.....................*O. jeffersoni*
   Pleopod of male, Form I, with length of central projection less than 28% of total length of pleopod; of male, Form II, less than 15%.. 7
7. Pleopod of male, Form I, with distinct, strong shoulder on cephalic margin at level of base of central projection. Mesial process slightly expanded at tip..........*O. obscurus*
   Pleopod of male, Form I, lacking such a shoulder; or if shoulder present, then weak and poorly developed. Mesial process not truncate at tip.............................. 8
8. Mesial process of first pleopod of male, Form I, with a distinct caudal eminence *O. s. erismorphorous*
   Mesial process of first pleopod of male, Form I, lacking caudal eminence *O. s. sanborni*
9. Annulus ventralis of female wider than long, weakly sculptured. Mesial process of male, Form I, usually acute distally, never rounded...........................*O. propinquus*
   Annulus ventralis of female about as long as wide, moderately to weakly sculptured. Mesial process of male, Form I, spatulate, tip rounded.....................*O.* species A

Orconectes propinquus (Girard, 1852)

Cambarus propinquus Girard, 1852, Proc. Acad. Nat. Sci. Philadelphia, 6: 88.

Cambarus propinquus: Hagen, 1870: 7, 31, 58, 67–69, 70, 71, 82, 97, 99, 101–102, 106–109, Pl. I, Pl. III; Smith, 1874: 638; Forbes, 1876: 4, 19; Bundy, 1877: 177, 178, 179, 181; Faxon, 1884a: 129, 131, 140, 144, 147; Faxon, 1884b: 43; Faxon, 1885a: 5, 6, 7, 8, 11, 14, 44, 47, 71, 85, 86, 89, 91, 92, 93, 94, 95, 124, 162, 164–174; Faxon, 1885b: 360; Faxon, 1885c: 142; Underwood, 1886: 371; Packard, 1886: 126; Faxon, 1889: 629, 630; Hay, 1891: 148, 149; Faxon, 1894: 332; Bouvier, 1897: 225, 226; Faxon, 1898: 651–652, 659–660; Williamson, 1899: 47; Hay, 1899: 960, 962; Harris, 1901a: 50; Harris, 1901b: 685, 688; Williamson, 1901: 1, 2, 4; Ortmann, 1902: 278; Hay, 1902a: 235 (?) (probably *O. juvenilis*, *fide* Ortmann, 1931: 66); Hay, 1902b: 439; Harris, 1903: 59, 61, 116, 119–120, 123, 138, 139, 140, 145, 146, 147, 148, 149, 150, 151, 152, 153, 154, 155, 156, 157, 166, Pl. V; Ortmann, 1905a: 387–389, 392, 400–403, 405; Ortmann, 1905b: 95, 109, 115–117, 128, 129, 132; Hay, 1905: 225, 226; Ortmann, 1906b: 349, 350, 351, 358–365, 366, 367, 368, 369, 370, 374, 380, 397, 410–413, 430, 431, 433–447, 464, 465, 476–477, 492, 499, 501, 502, 503, 505, 506, 507, 508, 509, 510, 512, Pl. XXXIX, Pl. XLII; Adams, 1907: 897, 898, 899; Hankinson, 1907: 233; Pearl and Clawson, 1907: 3; Shull, 1909: 298, 209; Pearse, 1910a: 10, 11, 15, 16–17, Pl. II; Pearse, 1910b: 74; Fowler, 1911: 565, 566; Ortmann, 1913: 338, 339; Graenicher, 1912; Faxon, 1914: 373, 374, 378, 417; Hay, 1919: 232, 234, 235; Turner, 1926: 146, 154, 156, 158, 160, 161, 162, 165, 166, 172, 174, 179, 181, 182, 183, 192; Engle, 1927: 87, 88, 89, 90, 94, 95, 97, 91, Fig. 1; Newcombe, 1929: 284, 285; Ortmann, 1931: 63, 64, 65, 66, 70, 88; Creaser, 1931b: 259, 266, 267, Fig. 33, Map 5; Creaser, 1932: 324, 325, 329, 334, 336; Turner, 1935b: 270, 272; van Deventer, 1937: 6, 8, 10–12, 14–19, 21, 22, 25, 28, 30–34, 36–38, 40, 41, 42, 45; Fleming, 1939: 304, 305; Rhoades, 1941: 98; Tack, 1941: 420, 425, 431, 444; Penn, 1943: 2, 9, 13; Rhoades, 1944a: 112, 132, 119; Park, 1945: 305; Villalobos, 1946: 215; Scudamore, 1948: 229, 230, 231, 232; Stephens, 1952: 251, 253, 255; Lewis, 1955: 146; Slack, 1955: 38; Crocker, 1957: 7, 35; McManus, 1960: 428.

Astacus propinquus: Hagen, 1870: 61.

Cambarus (Faxonius) propinquus: Ortmann, 1905b: 112; Anonymous, 1926: 90.

Faxonius propinquus: Creaser, 1933a: 1, 3, 6, 9; Creaser, 1934a: 364; Creaser, 1934b: 581, 583–585; Creaser, 1926: 1–2 (by implication).

Cambarus propinquus propinquus: by implication in each citation of *C. propinquus sanborni* (*q. v.*).

Orconectes propinquus propinquus: Hobbs, 1942a: 350–352 (by implication); Rhoades, 1944a: 124; Hobbs, 1948a: 17, 19, 20; Hobbs, 1948b: 139, 142, 144, 145, Fig. 5, Fig. 15; Hobbs, 1951: 125; Williams, 1952: 333; Smith, 1953: 79; Brown, 1956: 166; Crocker, 1957: 3, 4, 5, 7, 13, 18, 19, 24, 28, 35–39, 45–50, 51–56, 58, 60–62, 64, 67, 74–80, 83, 86–88; Black, 1958: 193, 198; Larimore, et al., 1959: 380; McManus, 1960: 420, 421, 426, 427; Hobbs and Fitzpatrick, 1962: 207.

Orconectes (Orconectes) propinquus: Hobbs in Edmondson, 1959: 891, 894.

Orconectes propinquus: Hobbs, 1951: 125, 127; Pennack, 1953: 453, 464, 465; Williams, 1954a: 816, 819, 833, 834, 837, 912, 913, 915, 972; Eberly, 1955: 282; Slack, 1955: 37; Penn, 1957: 236; McManus, 1960: 421, 425, 426, 427, 428; Weins and Armitage, 1961: 40; Rhoades, 1962b: 81, 82, 84, 88, 94; Hobbs and Fitzpatrick, 1962: 207; Black, 1963: 594.

Types: Not extant. ("Destroyed in Chicago Fire of 1871." *fide* Faxon, 1914: 417).

Type locality: Lake Ontario, 4 miles off Oswego, Oswego County, New York. (Ortmann, 1906b: 363, restricted the type locality to Oswego, Oswego Co., N. Y., stating in a footnote: "This is the first locality given by Girard, and consequently in the type locality." Although Ortmann did not correctly designate the locality, his intention is clear and must be accepted as a proper restriction of the type locality under the ICZN. The modification here given is to be considered persuant to the regulation set forth in Article 72, Recommendation E, ICZN.)

Range: Great Lakes Drainage of the United States and Canada, northern Hudson River Drainage, Rock River Drainage in Illinois and Wisconsin (fig. 2).

Diagnosis: Based on a study of 484 specimens (211 ♂♂ I; 79 ♂♂ II; 194 ♀♀). Eyes normal; carapace pigmented. Rostrum with marginal spines (58.4%) or tubercles (37.3%), rarely with only a strong shoulder at level of base of acumen (4.3%), concave above, median carina usually present (97.6%), but rarely absent (2.4%); margins usually converging (85.7%), occasionally concave (12.0%) and rarely subparallel (2.3%), with margins moderately thickened; rostrum length divisible into carapace length 2.88–3.95 (avg 3.32) times; rostrum 1.50–2.33 (avg 1.89) times longer than wide; rostrum 2.25–4.18 (avg 3.07) times longer than acumen. Areola 31.6–38.2% (avg 34.6%) total length of carapace, 3.20–6.20 (avg 4.60) times longer than wide, with 2–5 punctations in its narrowest part; postorbital ridges strong, terminating cephalically in spines (57.6%) or tubercles (42.4%). Length of first pleopod of male, Form I, divisible into carapace length 2.48–3.68 (avg 2.90) times, and of male, Form II, 2.66–3.37 (avg 3.02) times; pleopod of male, Form I, with central projection 22.2–26.8% (avg 30.4%) of total length of pleopod, and of Form II, 13.0–20.3% (avg 16.6%); central projection: mesial process ratio for males, Form I, 0.96–1.13 (avg 1.03), and of Form II, 0.94–1.31 (avg 1.07). Annulus ventralis of female usually weakly sculptured, as figured (fig. 19F), variable but always in same basic pattern.

Discussion: Orconectes propinquus has been considered to be conspecific with *sanborni*, *erismophorous*, and *jeffersoni*. The data which I have been able to accumulate indicate, however, that the two former taxa are significantly different from *propinquus* and no evidence of intergradation has been observed. *O. jeffersoni* is more like *propinquus*, but differs from it in many characteristics, noteworthy among which is the annulus ventralis. Like *sanborni*, *jeffersoni* shows no evidence of intergradation with *propinquus*.

O. propinquus is the widest ranging of the species of the Propinquus Group and, as might be expected from such a situation, is also the most variable. Despite considerable interspecific variability, there are no evidences of clines or morphologically distinct geographic races.

In his description of *C. propinquus*, Girard cited three localities for his species but neglected to designate any one as a type locality. Ortmann (1906b: 363) restricted the type locality to Girard's first cited locality: "Lake Ontario, four miles from the shore, opposite to Oswego [New York], found in the stomach of

Lota maculosa." Faxon (1914: 417) selected the second of Girard's cited localities as the type locality; "Garrison Creek, Sacketts Harbor [New York]." Crocker (1957: 36) states: "It appears that the first locality listed by Ortmann is the type locality." Ortmann's selection of a type locality leaves much to be desired. The specimen, which would become the holotype if it existed, was recovered from the stomach of a fish. No comment of its condition or degree of decomposition is given. A crawfish taken from the stomach of a fish could have been eaten at a considerable distance from the place at which the fish was captured; in fact, it could have been taken from a stream and not from the Lake proper. Nevertheless, by the rules of priority which are applicable here (ICZN: 72E), Ortmann's (1906b: 363) restriction of the type locality is proper and is here accepted as the type locality, restricted.

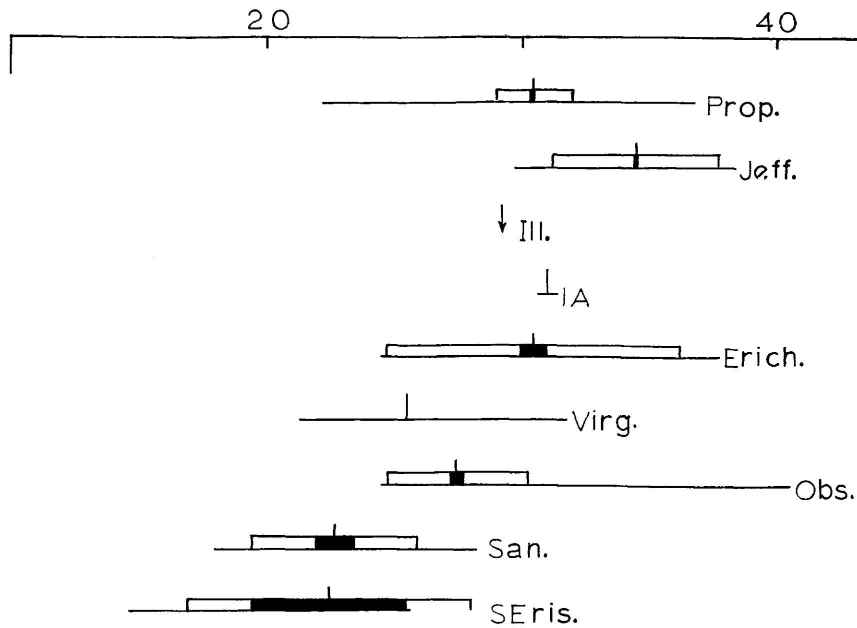


FIGURE 13. Length of central projection of pleopod expressed as per cent total length of pleopod (Males, Form I): Symbols same as Figure 4. Species names abbreviated.

Orconectes erichsonianus (Faxon, 1898)

Cambarus erichsonianus Faxon, 1898, Proc. U. S. Nat. Mus., 29: 659.
Cambarus erichsonianus: Faxon, 1898: 659–660, 693, Pl. LXIV; Hay, 1899: 960, 964; Ortmann, 1902: 278; Harris, 1903: 60, 96, 144, 146, 147, 151, 154, 159, 161; Ortmann, 1905b: 109, 112, 114, 116, 128, 130; Faxon, 1914: 418; Ortmann, 1931: 65, 69, 70, 71, 72, 87, 88, 90; Fleming, 1939: 300, 301, 302, 303, 305.
Cambarus erichsonionus: Fleming, 1939: 299.
Cambarus (*Faxonius*) *erichsonianus:* Ortmann, 1905b: 112.
Faxonius erichsonianus: Creaser, 1933b: 7; Creaser, 1962: 2–3 (by implication).
Orconectes erichsonianus: Hobbs, 1942a: 350–353 (by implication); Hobbs and Fitzpatrick, 1962: 207.

Types: Designated by Faxon: Cotypes [=Syntypes], USNM no. 20787; MCZ no. 4347.

Type locality: Rip Roaring Fork, 5 miles northwest of Greenville, Greene County, Tennessee.

Range: Upper Tennessee River Drainage above Walden Gorge and Elk River Drainage (fig. 2).

Diagnosis: Based on 77 specimens (21 ♂♂ I; 16 ♂♂ II; 40 ♀♀) and the types of USNM. Eyes normal; carapace pigmented. Rostrum with marginal spines (never lacking, but tubercles in 2% of specimens), concave above, median carina absent, margins parallel (converging in 10% of specimens) with margins moderately thickened; rostrum divisible into carapace length 2.26–3.08 (avg 2.66) times; rostrum 1.99–3.50 (avg 2.99) times longer than wide; rostrum 2.15–3.21 (avg 2.56) times longer than acumen. Areola 24.9–34.5% (avg 30.6%) of total length of carapace, 4.66–5.32 (avg 4.88) times longer than wide, with 2–6 punctations in its narrowest part; postorbital ridges strong, terminating cephalically in strong spines. Length of first pleopod of male, Form I, divisible into carapace length 2.56–3.30 (avg 2.95) times, of male, Form II, 2.58–3.33 (avg 3.05) times; first pleopod of male, Form I, with central projection 22.5–37.8% (avg 30.6%) of total length of pleopod, of Form II, 13.8–19.9% (avg 17.0%); central projection: mesial process ratio for males, Form I, 1.03–1.27 (avg 1.11), and for Form II, 1.00–1.87 (avg 1.32). Annulus ventralis moderately sculptured and as figured (fig. 20F).

Discussion: Orconectes erichsonianus is the most disjunct (morphologically) species of the Propinquus Subgroup. On the basis of available data, *erichsonianus* occupies a position intermediate between the two Subgroups of the Propinquus Group, but with a closer morphological affinity with the members of the Propinquus Subgroup. Ortmann (1905b: 109) has commented on the "transitional"

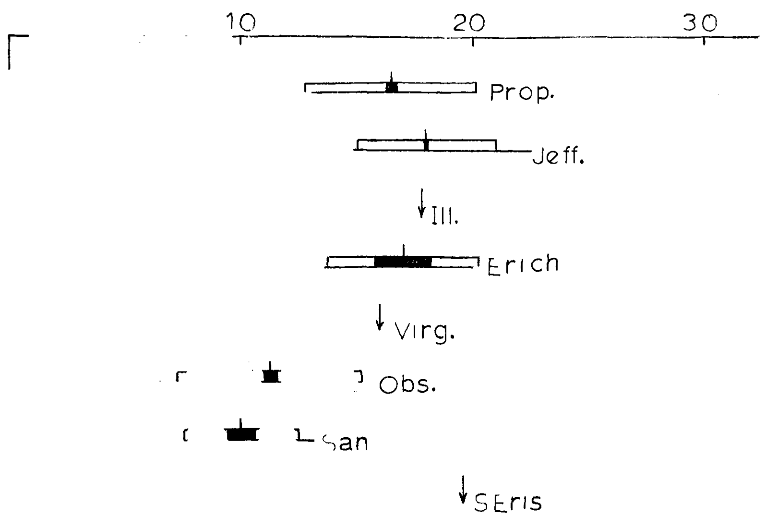


FIGURE 14. Length of central projection of pleopod expressed as per cent total length of pleopod (Males, Form II): Symbols same as Figure 4. Species names abbreviated.

position between the Propinquus Group and Rusticus Group occupied by *erichsonianus*. *O. erichsonianus* probably represents an early divergence from the ancestral stock which gave rise to both the Propinquus and Rusticus Groups, probably occurring shortly after differentiation toward the former began.

Orconectes erichsonianus is easily identified and is the only member of the Propinquus Group found in the Tennessee drainage. The only confusion which might arise would result from the description of *Cambarus spinosus* Bundy (1877). From the verbal description of the first pleopod given by Bundy, one could be led to believe that he was describing *erichsonianus*. The first form male which he described and any other first form males which he had before him, however, are lost. Subsequent recollection in the type locality cited by Bundy has yielded only *Orconectes juvenilis*. I have examined "types" of *C. spinosus* at the USNM (no. 19779) and all of the specimens are clearly *O. juvenilis* (Hagen, 1870). I have not examined other "cotypes" (MCZ 3540, 3541), but I feel certain that my identification of these would not differ from that of the USNM specimens, and I have serious reservations concerning whether or not the designated "cotypes" at either museum were among the specimens before Bundy at the time he described

C. spinosus. Thus, it appears that *spinosus* must be considered at best a *nomen dubium*, or otherwise a subjective synonym of *O. juvenilis*.

There seems to be no need to designate a lectotype for *Orconectes erichsonianus*.

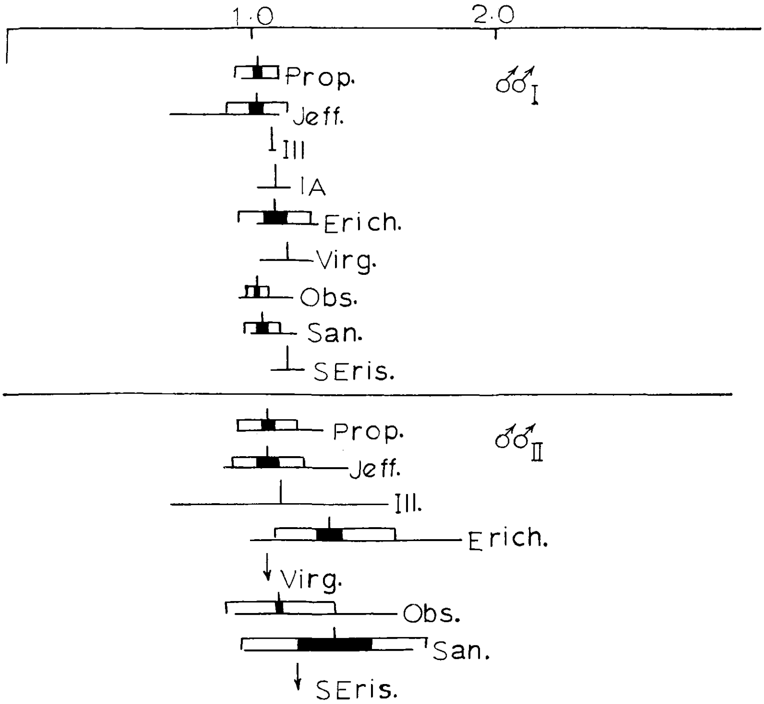


FIGURE 15. Ratio of length of central projection to length of mesial process. Symbols same as Figure 4. Species names abbreviated.

Orconectes illinoisensis Brown, 1956

Orconectes illinoisensis Brown, 1956, Amer. Midl. Nat., 36: 163.
Orconectes illinoisensis: Hobbs and Fitzpatrick, 1962: 207.
Faxonius illinoisensis: Creaser, 1962: 2–3 (by implication).

Types: U.S.N.M. nos. 97997, 97998, 91661 (holo-, allo-, and morphotypes, respectively).

Type locality: Cypress Creek, 3.25 miles south of Mt. Pleasant, Union Co., Illinois.

Range: Alexander, Gallatin, Hardin, Pope and Union Cos., Ill. (fig. 2).

Diagnosis: Based on three paratypic specimens (1 ♂ I; 1 ♂ II; 1 ♀) and the types. Eyes normal; carapace pigmented. Rostrum with marginal spines (66.7%) or tubercles (33.3%), concave above, median carina absent, margins concave (*fide* Brown, 1956, but 5 of my 6 specimens have converging margins) and somewhat thickened; carapace length: rostrum length ratio 3.16–3.56 (avg 3.34); rostrum 2.00–2.15 (avg 2.07) times longer than wide; rostrum 3.07–3.56 (avg 3.27) times longer than acumen. Areola 34.5–34.9% (avg 34.7%) total length of carapace, 6.60–8.80 (avg 7.40) times longer than wide, with 2–4 punctations in its narrowest part; postorbital ridges strong, terminating cephalically in strong spines. Length of first pleopod of male, Form I, divisible into carapace length 2.7 times, of male, Form II, 2.08 times; pleopod of male, Form I, with central projection 29.2% of total length of pleopod, of Form II, 17.8%; central projection: mesial process ratio for male, Form I, 1.09, and for Form II, 1.58. Annulus ventralis of female moderately sculptured and as figured (fig. 21F).

Discussion: Orconectes illinoisensis is poorly represented among the specimens which were available for my examination. My material and the type specimens at the United States National Museum, however, indicate that *illinoisensis* is a distinct species, allied with the other species of the Propinquus Subgroup. The drawings published with the description do not agree with the observations I made on the type specimens. The right chela of the holotype, which was illustrated, appeared to be a malformed regenerate, so I am illustrating the left chela of the holotype (fig. 21G). The figures of the carapace (fig. 21C) and annulus ventralis (fig. 21F) which appear herein are of paratypes, but they have been compared with the types and agree closely. Note that the margins of the rostrum are converging rather than deeply concave, as illustrated by Brown, and that there is a circular protuberence raised ventrally in the anteriomedian portion of the trough of the annulus, absent in Brown's figure. The protuberence occurs in both of the females of *O. illinoisensis* that I have seen and may well be a distinctive feature of the species.

FIG. 16

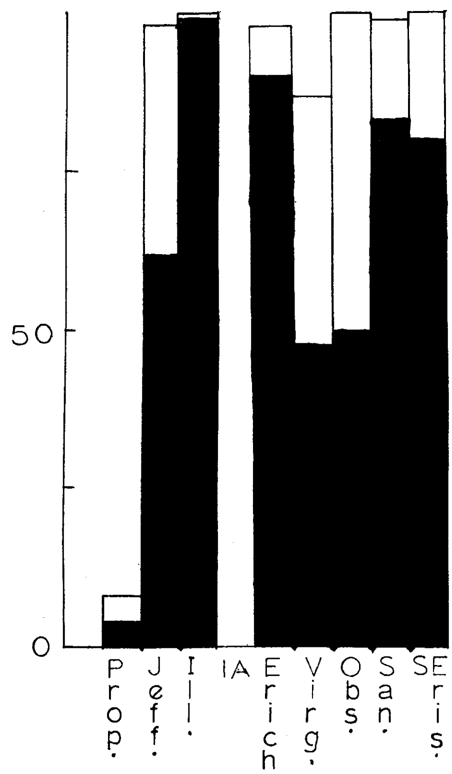


FIG. 17

FIGURE 16. Incidence of median carina on rostrum: Solid bar: strongly developed; open bar: weakly developed. Species names abbreviated.

FIGURE 17. Incidence of spines on lower mesial margin of carpus: Solid bar: spine present; open bar: tubercles present. Species names abbreviated.

Orconectes species A

Cambarus propinquus: Faxon, 1885b, Mem. Mus. Comp. Zool., 10(4): 91. (*in partim*).
Cambarus propinquus: Harris, 1903, Kansas Univ. Sci. Bull., 2(3): 59, 120, 138, 152. (*in partim*).

Range: Des Moines River and streams at Davenport, Iowa. Also in drainages of northeastern Iowa.

Diagnosis: Based on eight specimens (3 ♂♂ I; 3 ♀♀; 2 ♀♀), all at the Museum of Comparative Zoology (nos. 3434, 3704, 12644, 12645). Similar to *Orconectes propinquus* (Girard) in almost all respects, but occurring west of the Mississippi River (which river *propinquus* does not cross) and with annulus ventralis of female being about as wide as long, usually subcircular in outline, and always with margins more raised and sculpturing more prominent than in *propinquus*. Mesial process of pleopod distinctly spatulate (fig. 27).

Discussion: During the period when data were being accumulated for this study, no specimens collected after 1885 were seen. Shortly before this manuscript was submitted for publication, I was able to see several additional specimens from elsewhere in Iowa. These were supplied through the courtesy of Dr. Karl Goellner from the Coe College collections. This new species is included herein because the localities have been mentioned in the literature and comparison of these forms with *O. propinquus* from the Rock River drainage in Illinois make it clear that

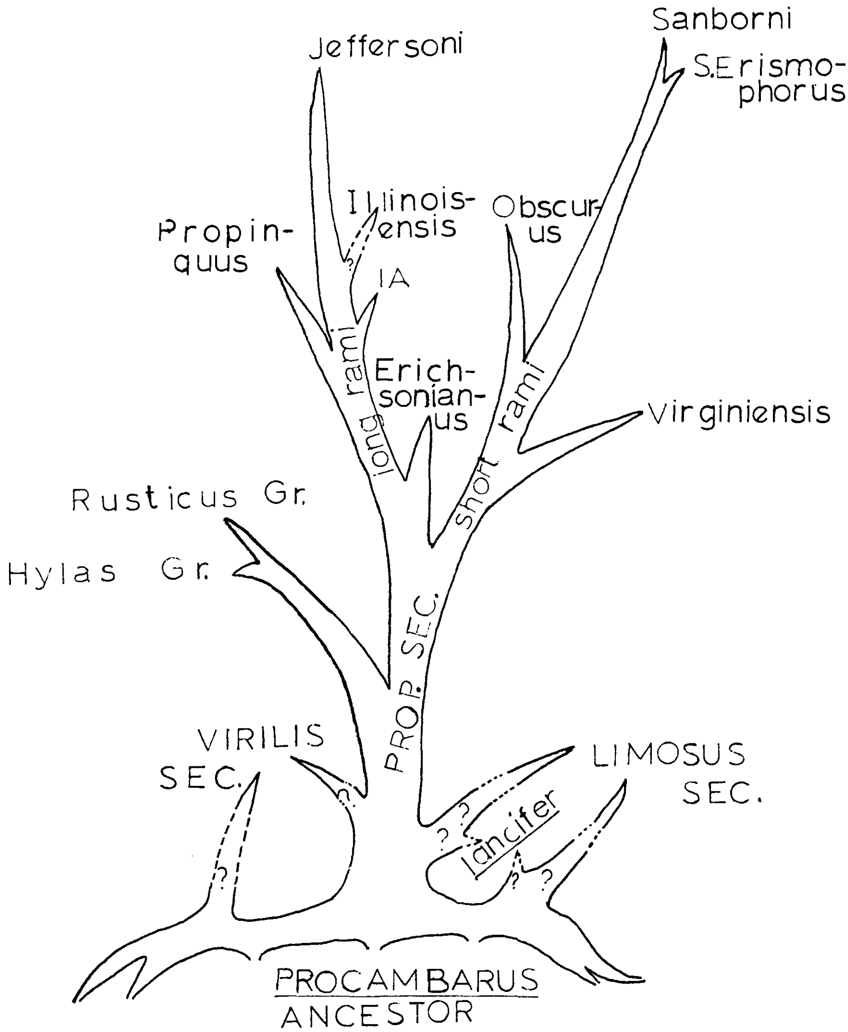


FIGURE 18. Proposed lineages and relationships in the Propinquus Group.

there are distinctive differences between the two. I have found no evidence of intergradation between them. A comparison of figure 19 (*propinquus*) with figure 27 (sp. A) will indicate that the two are easily separable on the basis of the annulus ventralis of the female and the mesial process of the male. Description of this new species is deferred until all available specimens are thoroughly examined and studied.

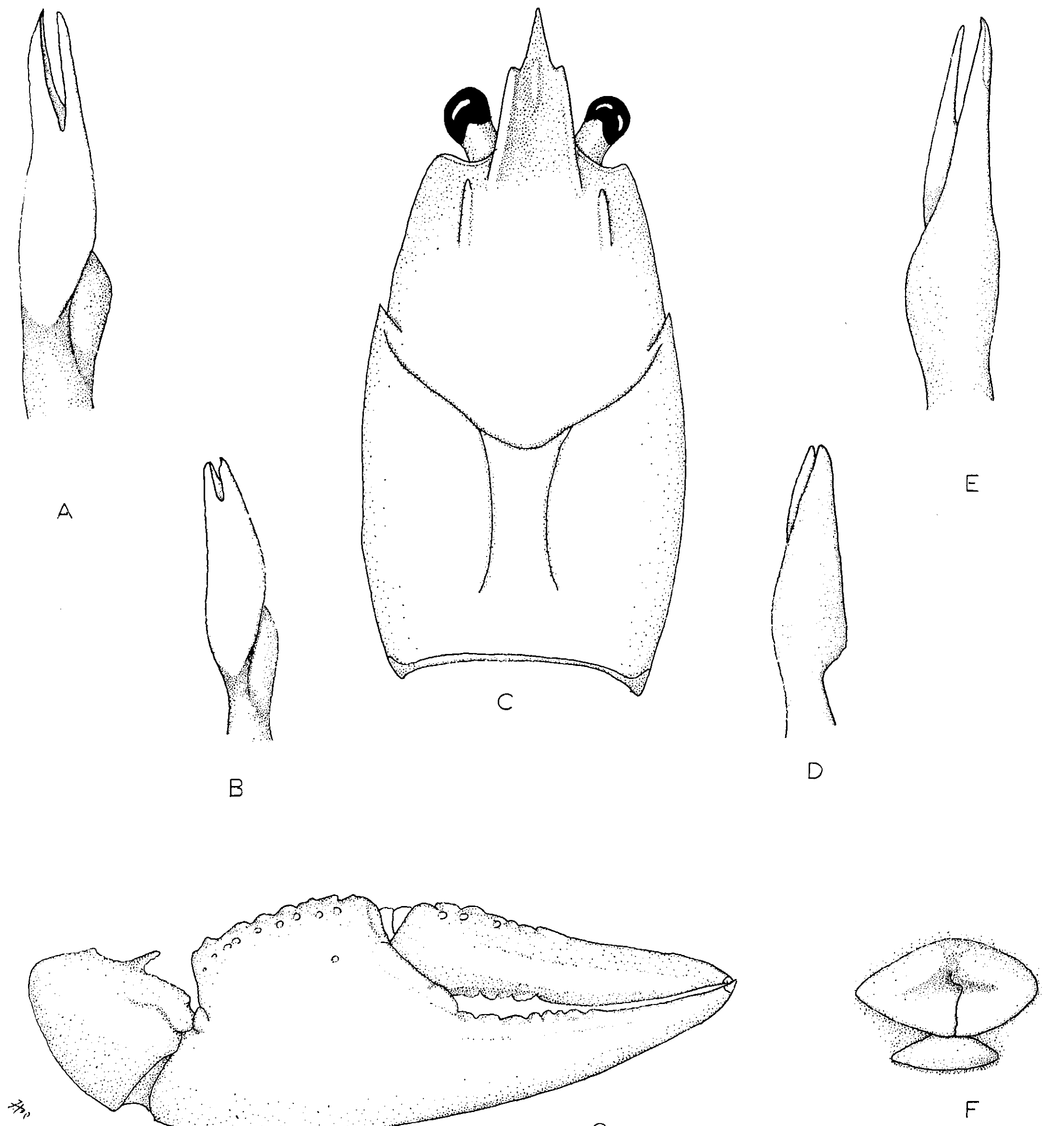


FIGURE 19. Diagnostic features of *Orconectes propinquus* (Girard, 1852): A. Dorsal view of carapace; B. Mesial view of first pleopod of first form male; C. Mesial view of first pleopod of second form male; D. Lateral view of first pleopod of second form male; E. Lateral view of first pleopod of first form male; F. Annulus ventralis of female; G. Upper view of right chela and carpus of first form male.

Orconectes jeffersoni Rhoades, 1944 (*comb. nov.*)

Orconectes propinquus jeffersoni Rhoades, 1944a, Amer. Midl. Nat., 31: 123.
Orconectes propinquus jeffersoni: Hobbs, 1948b: 139; Hobbs, 1951: 125, 127; Brown, 1956: 166; Hobbs and Fitzpatrick, 1962: 207.
Faxonius propinquus jeffersoni: Creaser, 1962: 2–3 (by implication).

Types: U.S.N.M. nos. 81316, 81317, 81318 (holo-, morpho-, and allotypes, respectively).

Type locality: Tributary to Muddy Fork of Beargrass Creek, 1 mile east of Louisville (U.S. Hy. 42 at Hubbard's Lane), Jefferson Co., Kentucky. ("When examined in

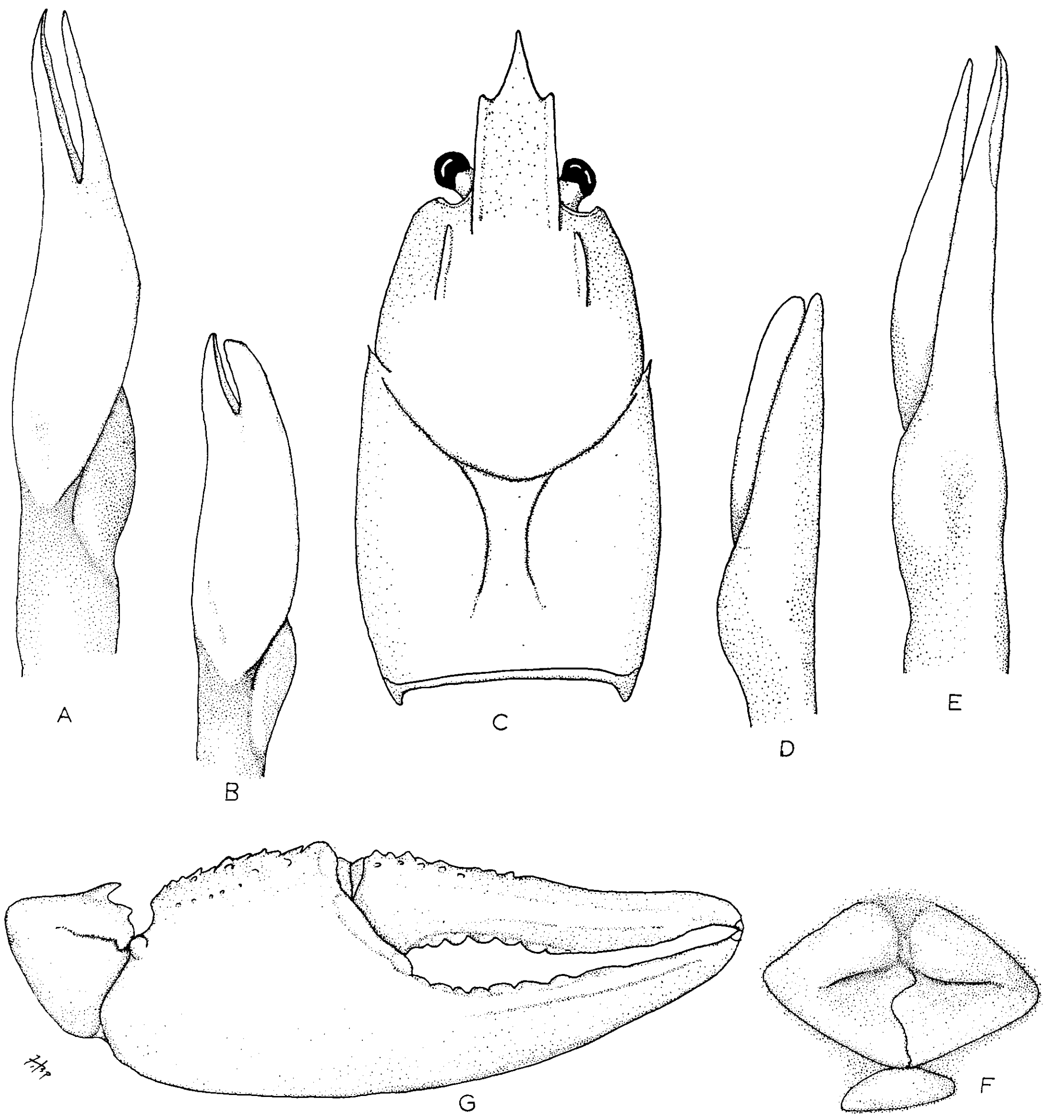


FIGURE 20. Diagnostic features of *Orconectes erichsonianus* (Faxon, 1898): Symbols same as Figure 19.

July, 1963 [and January, 1964] the type locality was devoid of *O. jeffersoni*, as also was the Muddy Fork of Beargrass Creek where the former empties into it; this absence was probably caused by the polluted water in those areas." *fide* Rudolph Prins, personal communications.)

Range: Jefferson and Bullit Cos., Kentucky (fig. 2).

Diagnosis: Based on the examination of 123 specimens, including topotypes and the types (33 ♂♂ I; 38 ♂♂ II; 53 ♀♀). Eyes normal; carapace pigmented. Rostrum with marginal spines (62.0%), tuberculate (29.6%), or with marked shoulders at level of base of acumen (8.4%), concave above, median carina usually absent (98.5%), margins usually converging (73.9%), but sometimes concave (24.6%) and occasionally parallel (1.5%); carapace length: rostrum length ratio 3.24–4.13 (avg 3.60); rostrum 1.34–2.21 (avg 1.86) times longer than wide; rostrum 2.43–4.67 (avg 3.28) times longer than acumen. Areola 31.6–36.3% (avg 33.8%) total length of carapace, 5.1–8.2 (avg 6.4) times longer than wide, with 2–5 punctations in its narrowest part; postorbital ridges strong, terminating cephalically in spines (66.7%) or tubercles (33.3%). Length of first pleopod of male, Form I, divisible into carapace length 2.38–2.79 (avg 2.57) times, of male, Form II, 2.52–3.15 (avg 2.80) times; pleopod of male, Form I, with central projection 29.7–38.4% (avg 34.5%) of total length of pleopod, of Form II, 15.0–22.5% (avg 18.1%); central projection: mesial process ratio for males, Form I, 0.67–1.12 (avg 1.03) and for Form II, 0.89–1.40 (avg 1.08). Annulus ventralis of female moderately sculptured and as figured (fig. 22F).

Discussion: Orconectes jeffersoni was considered by Rhoades (1944a: 123) to be conspecific with *O. propinquus*. I can find no evidence, however, of intergrada-

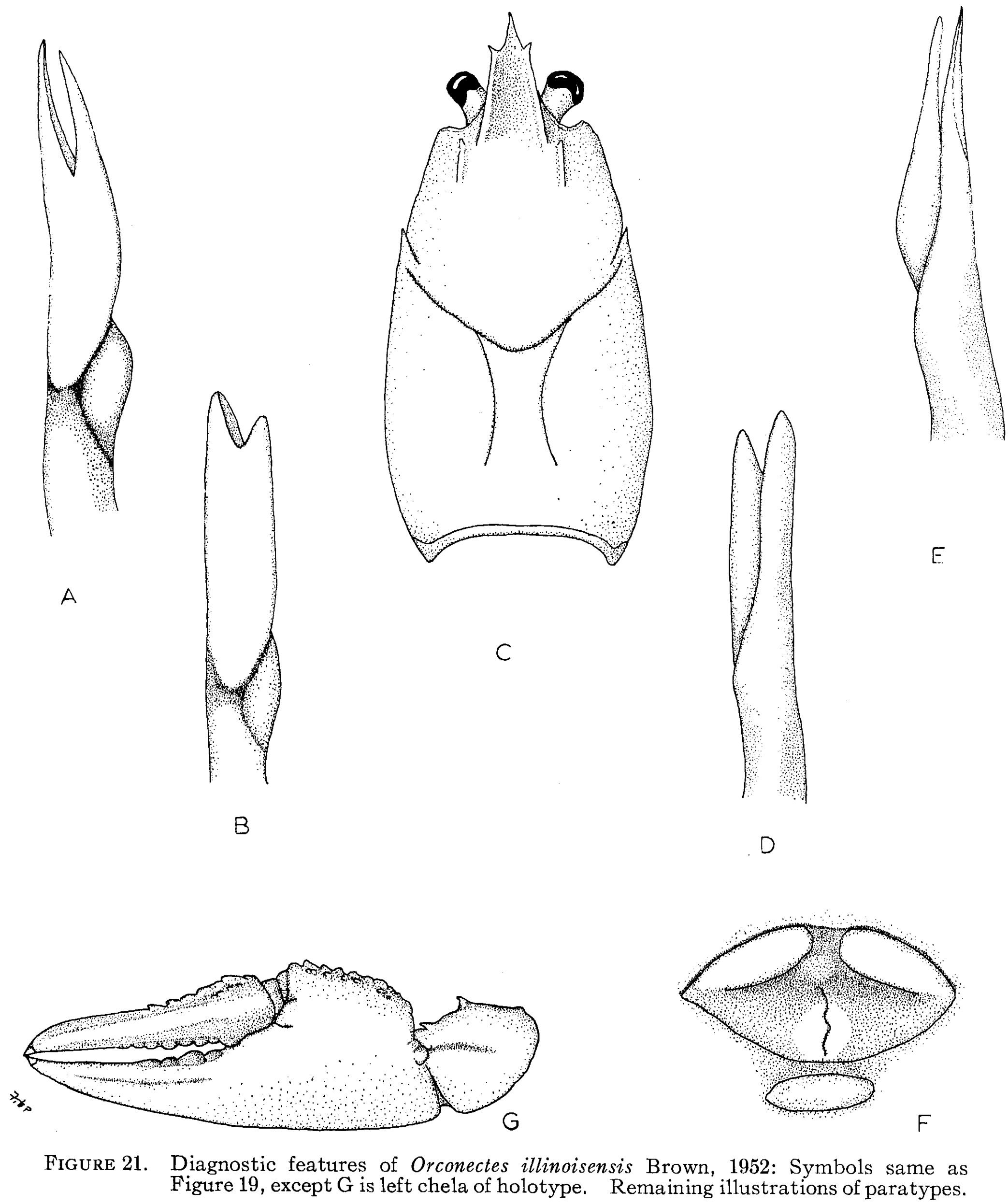


FIGURE 21. Diagnostic features of *Orconectes illinoisensis* Brown, 1952: Symbols same as Figure 19, except G is left chela of holotype. Remaining illustrations of paratypes.

tion between the two taxa, and morphologically the two are distinct. There is no evidence that the two species are more similar (or dissimilar) than other members of the Propinquus Subgroup. Therefore, I consider that the two taxa represent distinct species until contradictory information can be provided. Further, *O. jeffersoni* is confined to tributaries of the south shore of the Ohio River. I can find no evidence that *O. propinquus* has access to the Ohio except possibly through the Wabash River system, which if true, would place a sizable geographic gap between the two alledged subspecies.

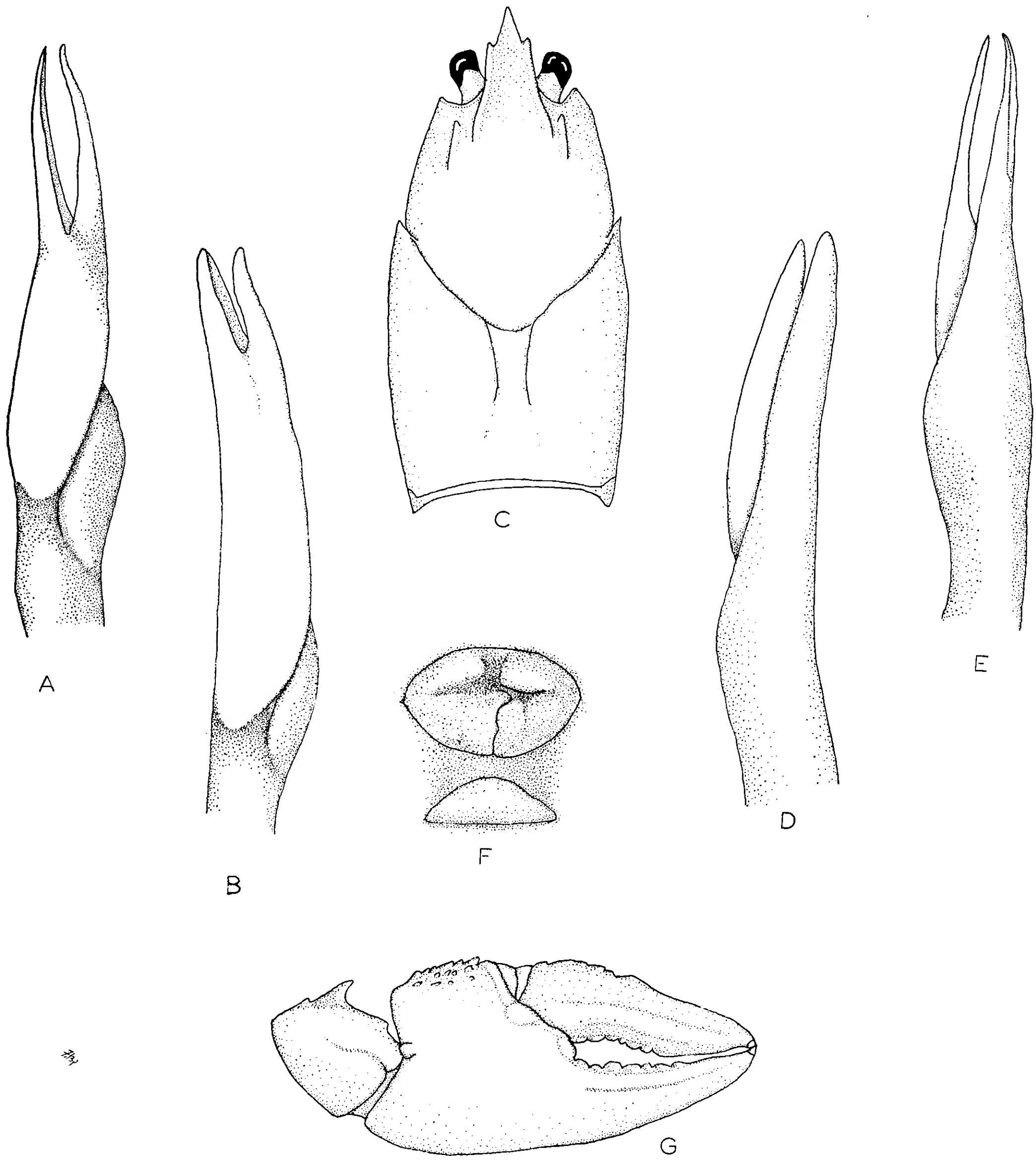


FIGURE 22. Diagnostic features of *Orconectes jeffersoni* Rhoades, 1944: Symbols same as Figure 19.

I have seen specimens of *O. jeffersoni* from the Salt River system in Bullit County, Kentucky (RP-6-2663-1), which differ from the "typical" *jeffersoni* from the tributaries of Beargrass Creek. The Salt River drainage specimens (from Knob Creek and some of its tributaries) bear a very weakly developed shoulder on the first pleopod of Form I males at a locus comparable to that at which a cephalic shoulder is borne by other species in the Propinquus Section. Likewise, the rostra are narrower and the areolae are wider than topotypic *jeffersoni*. In other features, noteworthy among which are the configuration of the annulus of the female and the rami of the first pleopod of the first form male, the specimens

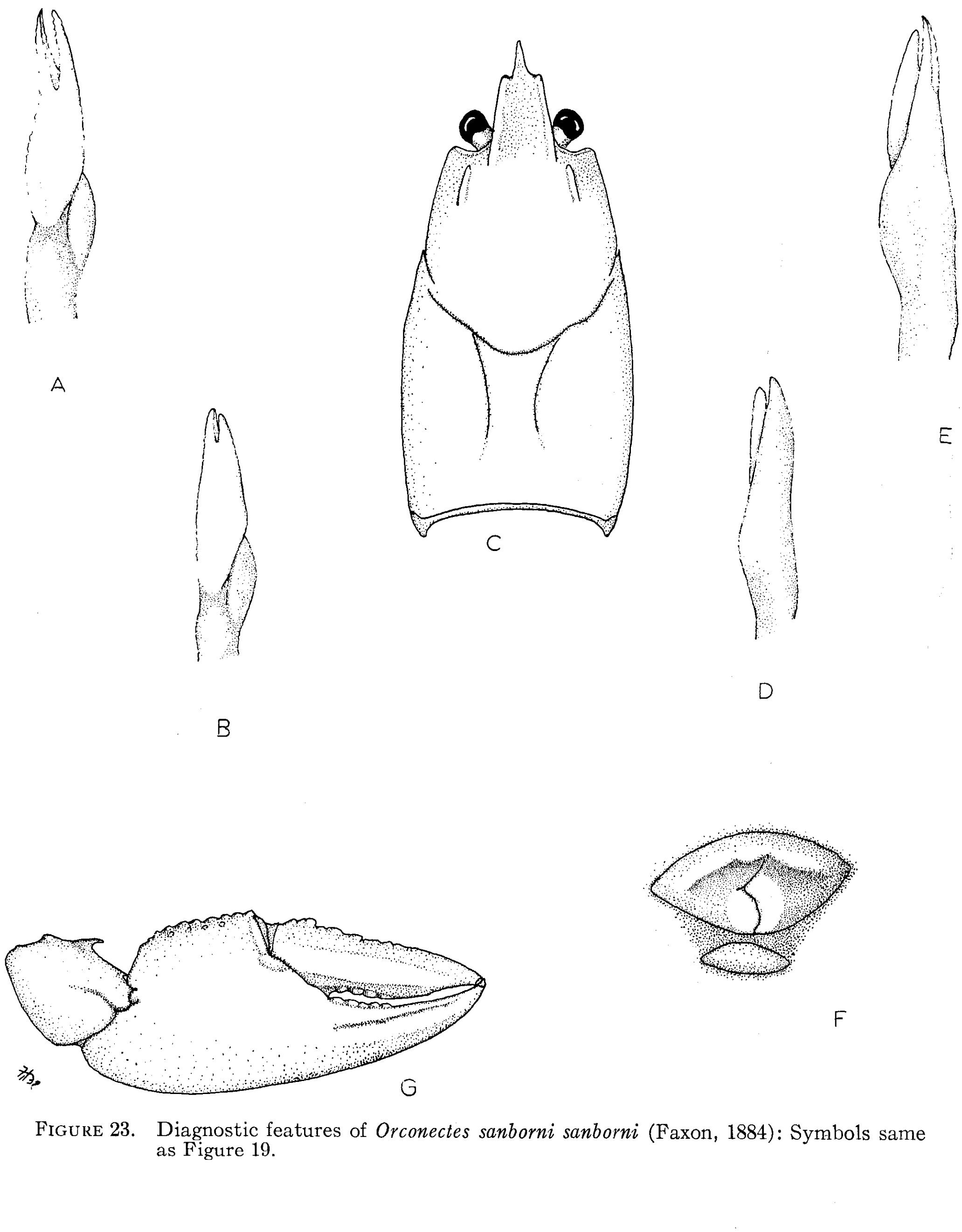


FIGURE 23. Diagnostic features of *Orconectes sanborni sanborni* (Faxon, 1884): Symbols same as Figure 19.

resemble topotypic *jeffersoni*, and I am convinced that they are conspecific populations. Dr. Rudolph Prins informs me (personal communication) that he has subsequently collected other specimens from the same areas which agree with the above-mentioned collection.

Orconectes sanborni sanborni

(Faxon, 1884a) (*comb. nov.*)

Cambarus sanborni Faxon, 1884, Proc. Amer. Acad. Arts and Sci., 20: 128.
Cambarus sanborni: Faxon, 1884: 128–130, 147; 1885b: 91–94, 162, 168, 170, 174, Pl. 5, Pl. 10; Underwood, 1886: 372; Ortmann, 1906b: 365, 368, 438, 499, 506, 507, 512.
Cambarus propinquus sanborni: Faxon, 1885b: 91, 92, 162, 174, Pl. IX; Underwood, 1886: 372; Hay, 1895: 498; Osborn and Williamson, 1898: 21; Faxon, 1898: 660; Hay, 1899; 960, 964; Williamson, 1899: 48; Harris, 1903: 59, 120, 121, 138, 139, 146, 154, Pl. V; Ortmann, 1905b: 128, 132; Hay, 1905: 228; Ortmann, 1906b: 350, 365–369, 374, 413, 433–447, 476–477, 492, 505, 507, Pl. XLII; Ortmann, 1913: 334, 335, 339, 356; Faxon, 1914: 374, 417, 418; Turner, 1926: 146, 154, 160, 161, 162, 163, 166, 170, 175, 179, 180, 181–182, 183, Pl. XIX, Pl. XX; Ortmann, 1931: 65, 67, 132; Turner, 1935a: 868, 870, 875; van Deventer, 1937: 12; Fleming, 1939: 305a, 306a, 307, 319a, 320a, Pl. XIV; Rhoades, 1944b: 95; Hobbs, 1948a: 14, 18.
Cambarus obscurus sanborni: Ortmann, 1906b: 437.
Orconectes propinquus sanborni: Hobbs, 1942a: 350–352 (by implication); Rhoades, 1944a: 111, 112, 113, 115, 124, 125; Rhoades, 1944b: 95, 96; Hobbs, 1948b: 139; Hobbs, 1951: 125, 127; Crocker, 1957: 75, 76, 79, 84; Meredith and Schwartz, 1960: 5; Rhoades, 1962a: 27–33; Rhoades, 1962b: 84, 94; Hobbs and Fitzpatrick, 1962: 207, 212.
Faxonius propinquus sanborni: Creaser, 1962: 2–3 (by implication).

Types: Cotypes [=syntypes] M.C.Z. nos. 3587, 3692. *Lectotype*, here designated: *ex* MCZ no. 3692; *paralectotypes*, here designated: MCZ nos. 3692 (from which the lectotype was selected), 3587. MCZ no. 3587 (Carter Co., Ky.), mentioned in the original description, was later designated *paratypes* by the author (Faxon, 1914: 418).

No distinctive number has been assigned to the lectotype by the Museum of Comparative Zoology. At this writing, the Museum is without a curator of its crustacean collection. Dr. Herbert Levi, Associate Curator of Arachnology, who is temporarily in charge of the crustaceans informs me (personal communication) that he intends to defer the numbering of specimens until a new Curator of Crustacea can be appointed. At the earliest opportunity following the assignment of a definite number to this specimen, the number will be published. The lectotype has been separated, however, placed in a separate container, and appropriately labeled.

Type locality: Oberlin, Lorain Co., Ohio.

Range: East of the eighty-first meridian and south of the terminal moraine of the Wisconsin Glacier in tributaries of the Ohio River. Erratic occurrence in the Lake Erie drainage in Ohio from between the Sandusky and Huron Rivers to, but not including, the Grand River (fig. 2).

Diagnosis: Based on 229 specimens (63 ♂♂ I; 76 ♂♂ II, 90 ♀♀) and the lectotype. Eyes normal; carapace pigmented. Rostrum with marginal spines (83.1%), occasionally with tubercles (16.1%), and rarely (0.8%) with only well-developed shoulders at level of base of acumen, concave above, median carina absent, margins predominantly converging (98.4%), but sometimes parallel (1.6%); carapace length: rostrum length ratio 3.24–41.3 (avg 3.60); rostrum 1.34–2.21 (avg 1.86) times longer than wide; rostrum 2.43–4.67 (avg 3.28) times longer than acumen. Areola 31.6–36.3% (avg 33.8%) of total length of carapace, 5.1–8.2 (avg 6.4) times longer than wide, with 1–5 punctations in its narrowest part; postorbital ridges strong, terminating cephalically in spines (88.7%), but sometimes in tubercles (11.3%). Length of first pleopod of male, Form I, divisible into carapace length 2.87–3.38 (avg 3.15) times, of male, Form II, 2.91–3.53 (avg 3.23 times); pleopod of male, Form I, with central projection 18.0–28.2% (avg 22.6%) of total length of pleopod, of Form II, 7.5–13.3% (avg 9.9%) its length; central projection: mesial process ratio for males, Form I, 1.00–1.19 (avg 1.06), and for Form II, 0.99–1.67 (avg 1.35). Annulus ventralis of female moderately sculptured and as figured (fig. 23F).

Discussion: Statistical analyses of variation indicate that *Orconectes sanborni* is significantly distinct from *O. propinquus*, which species has been considered to be conspecific with *sanborni*. Further, *sanborni* is geographically and morphologically distinct from the other species which I have assigned to the Sanborni Subgroup and there is no apparent gene exchange with populations other than *O. erismophorous*. The recognition of the specific distinction of *sanborni* is not a new concept. Faxon (1884: 128) initially considered *sanborni* to be a distinct species, but later changed his mind and considered it to be conspecific with *propinquus* (1885: 91). Turner (1926: 181–183) suggested that Faxon's original

(1884) thesis was the correct one. Recently, Dr. David Stansbery of the Ohio State Museum (personal communication) has independently arrived at the same conclusion. He indicated that his opinion is based largely on the fact that he has found no evidence of intergradation between *sanborni* and *propinquus* in those areas of the Lake Erie drainage where *sanborni* is found.

Although Turner (1926) recorded *sanborni* from the Lake Erie drainage in Ohio, until recently I had not seen any specimens of this species from the Lake

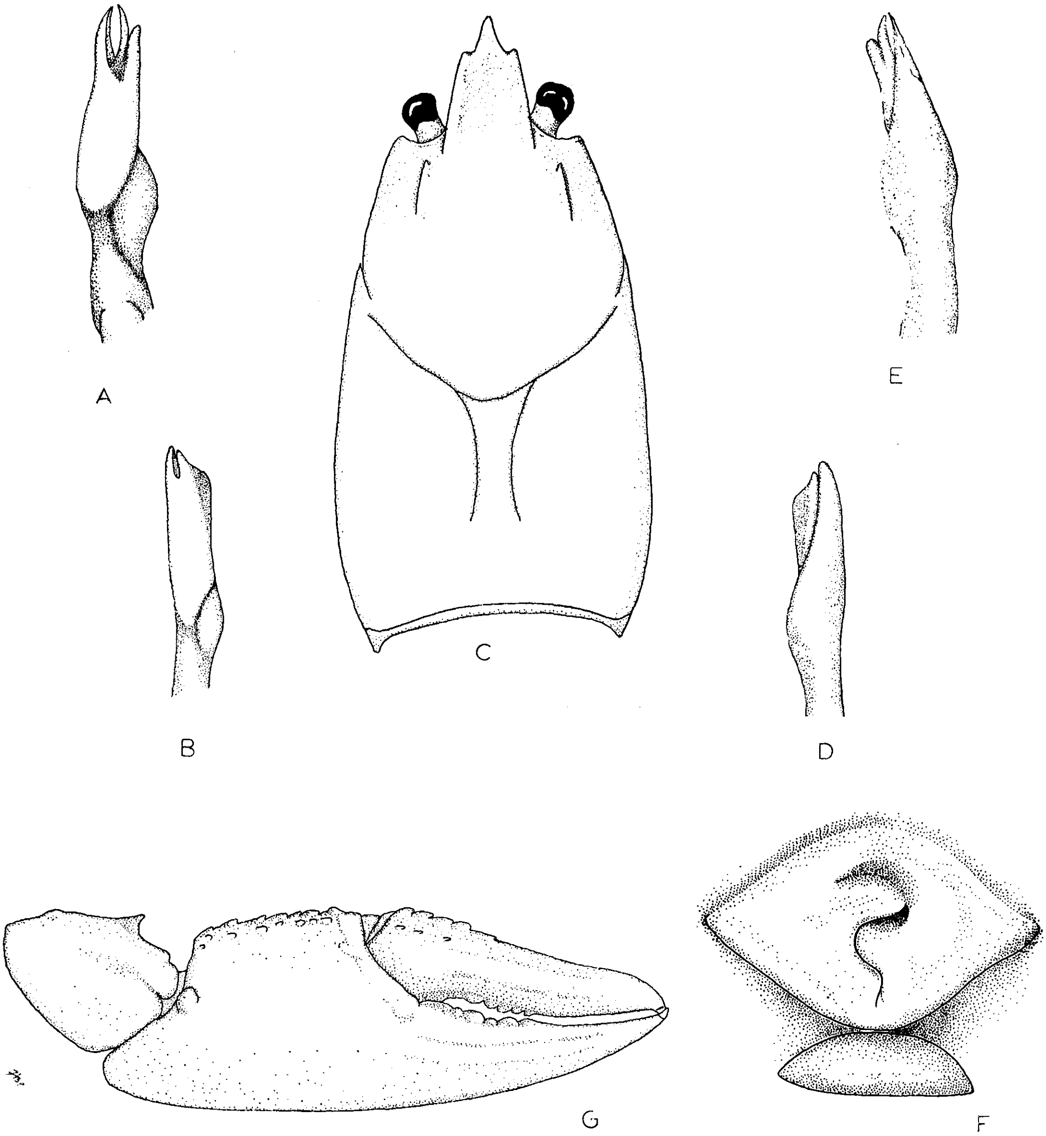


FIGURE 24. Diagnostic features of *Orconectes sanborni erismophorus* Hobbs and Fitzpatrick, 1963: Symbols same as Figure 19. All illustrations of paratypes except F which is of allotype (drawn by Hobbs).

Erie drainage. Dr. Stansbery sent me a collection from the Cuyahoga River which were clearly *sanborni*; he added the notes of the occurrence of this species from that drainage and other Lake Erie drainages which are incorporated in the range notation above (personal communications).

Ortmann (1931: 67) attempted to restrict the type locality of *O. sanborni* to Smoky Creek, Carter Co., Kentucky. This is the first of the localities given by Faxon (1884a) in his description of the species, but Ortmann probably overlooked

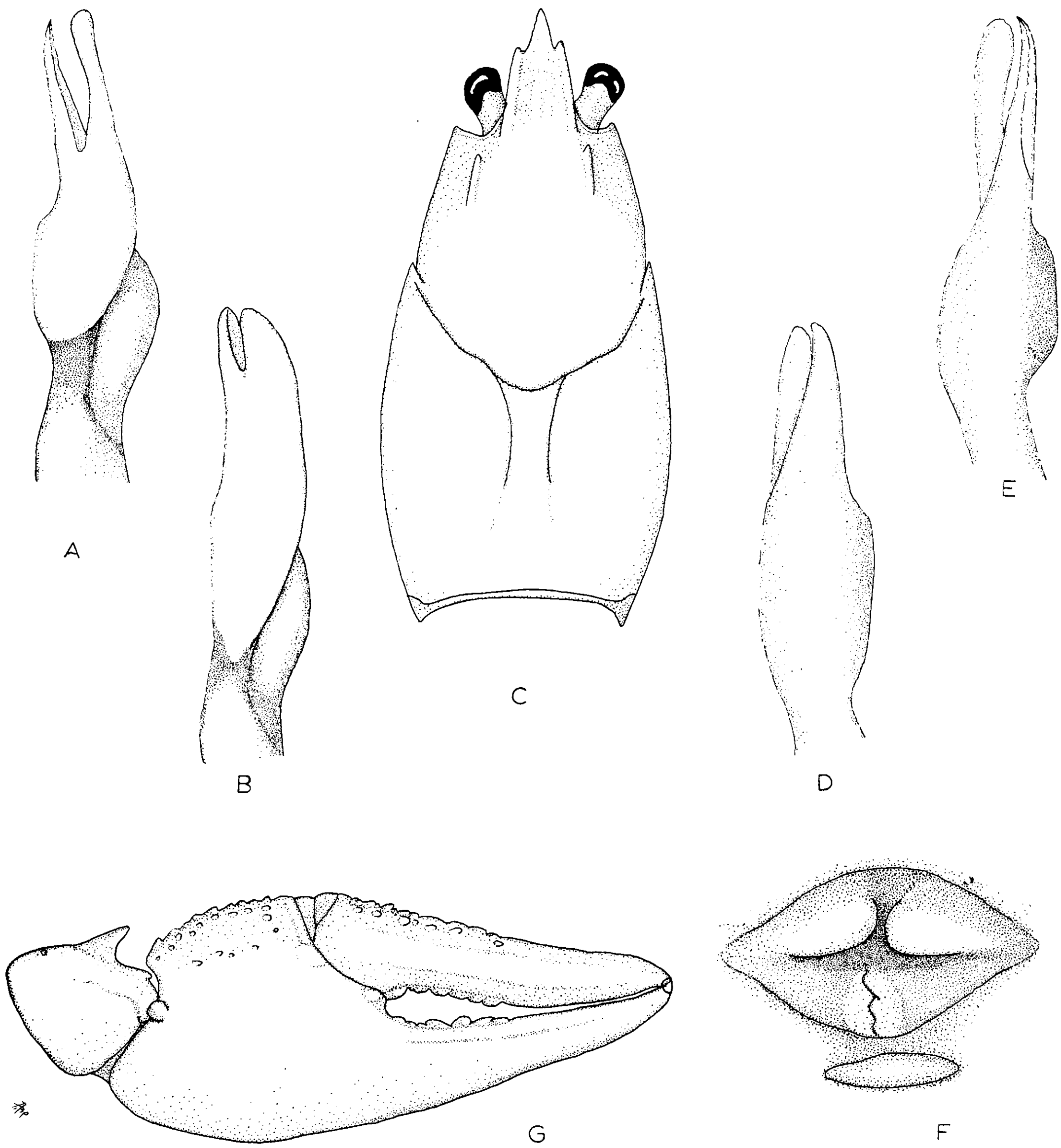


FIGURE 25. Diagnostic features of *Orconectes obscurus* (Hagen, 1870): Symbols same as Figure 19.

the valid restriction of the type locality in a later work of Faxon (1914: 418). Under the provisions of ICZN (72E), Faxon's designation of the type locality for this species is here accepted.

As noted above, no holotype for *Cambarus sanborni* exists. True syntypes do exist, and among them there is a first form male suitable to be designated the lectotype. This specimen is here designated the *lectotype* and can be identified as outlined above. The specimen is incomplete, lacking the left first pleopod, which appears to have been removed *post mortem*. Thus, this is probably the appendage figured by Faxon (1885b Pl. IX, Figs. 10, 10'). Diligent search by the staff of MCZ has failed to discover the missing appendage (*fide* Levi, personal communication). Specimens numbered MCZ 3587 and designed paratypes by the author (Faxon, 1914: 418) are no longer at MCZ (Levi, personal communication).

Measurements of lectotype as follows (in mm)—Carapace: length, 35.8, width, 18.2, height, 13.8; Areola: length, 13.4, width, 2.2; Rostrum: length, 10.4, width, 5.2; Chela: length of inner margin of palm, 10.8, width of palm, 13.8, length of outer margin of hand, 34.6, length of dactyl, 20.7.

Orconectes sanborni erismophorous

Hobbs and Fitzpatrick, 1962 (*comb. nov.*)

Orconectes propinquus erismophorous Hobbs and Fitzpatrick, 1962, Proc. Biol. Soc. Washington, 75: 207.

Types: U.S.N.M. nos. 107597, 107598, 107599 (holo-, allo-, and morphotypes, respectively).
Type locality: Crane's Nest Creek at Pee Wee, Wirt Co., West Virginia.
Range: Little Kanawah drainage of West Virginia.
Diagnosis: Based on 11 paratypic specimens (7 ♂♂ I; 1 ♂ II; 3 ♀♀) and the types. Eyes normal; carapace pigmented. Rostrum with marginal spines (40%) or tubercles (60%), concave above, median carina absent; carapace length: rostrum length ratio 2.83–4.11 (avg 3.24); rostrum 1.36–3.07 (avg 2.01) times longer than wide; rostrum 2.12–3.83 (avg 2.48) times longer than acumen. Areola 30.9–39.4% (avg 35.0%) of total length of carapace, 3.65–6.90 (avg 5.20) times longer than wide, with 2–4 punctations in its narrowest part; postorbotal ridges strong terminating cephalically in spines (72.7%) or tubercles (27.3%). Length of first pleopod of male, Form I, divisible into carapace length 2.58–3.10 (avg. 2.93) times, of male, Form II, 3.60 times; pleopod of male, Form I, with central projection 16.7–25.5% (avg 24.4%) of total length of pleopod, and of Form II, 19.4%; central projection: mesial process ratio 1.09–1.22 (avg 1.14) for males, Form I, and for Form II, 1.20. *Mesial process of first pleopod of male bearing a distinct caudal eminence* (figs. 24A, B, D, E). Annulus ventralis of female moderately sculptured and as figured (fig. 24F).

Discussion: Orconectes sanborni erismophorous is a morphologically distinct group of crawfishes apparently confined to the Little Kanawha drainage system of West Virginia. The existence of morphological forms which are intermediate between *erismophorous* and *sanborni* (Hobbs and Fitzpatrick, 1962: 212) leaves little doubt that *erismophorous* is a geographic race of the surrounding *sanborni*. In addition, I have found other collections from Carter Co., Kentucky (HHH 8–1153–4a), and Scioto County, Ohio (HHH 9–655–7a), in which a small percentage of the "hybrid" form was present and other specimens blended almost imperceptibly into "typical" *sanborni*.

Orconectes obscurus (Hagen, 1870)

Cambarus obscurus Hagen, 1870, Illus. Cat. Mus. Comp. Zool., Harvard Coll., 3: 69.
Cambarus obscurus: Hagen, 1870: 57–58, 69–70, 71, 98, 99, 106, 108, Pl. I, Pl. III; Smith, 1874: 639; Bundy, 1877: 172, 173; Faxon, 1884a: 148; Faxon, 1885b: 8, 93, 114, 116, 172; Underwood, 1886: 372; Faxon, 1898: 652; Hay, 1899: 964; Harris, 1903: 59, 112, 138, 139, 154; Ortmann, 1905a: 387, 388, 389, 391, 392, 400, 401, 402–404, 405–406; Ortmann, 1905b: 109, 115, 128–130, 133; Ortmann, 1906b: 349, 351, 365–368, 374, 376, 380, 387, 388, 393, 410, 412, 413, 415, 433, 434, 436–448, 450, 463–470, 474, 476–485, 488, 492, 495, 499, 501, 505–509, 512; Ortmann, 1907: 714; Adams, 1907: 897, 898, 899; Andrews, 1910: 259; Fowler, 1911: 564, 565; Ortmann, 1913: 333, 334, 335, 336, 339, 356, 366; Turner, 1926: 154, 156, 158, 160, 161, 162, 163, 166, 170, 179, 181; Newcombe, 1959: 268, 275, 276, 277, 284, Fig. 1; Turner, 1935a: 865, 866, 868, 869, 874; Turner, 1935b: 272; van Deventer, 1937: 8, 12, 21, 28, 30, 31, 32, 34, 36, 40, 42, 47, 48, 50; Fleming, 1939: 305.

Astacus obscurus: Hagen, 1870: 5.
Cambarus obscura: Faxon, 1914: 374–375, 418.
Cambarus propinquus obscurus: Faxon, 1885a: 360; Hay, 1899: 960; Ortmann, 1906b: 369; Ortmann, 1931: 65.
Cambarus propinquus obscura: Faxon, 1885b: 86, 90, 92, 162, 165–174; Fowler, 1911: 564.
Cambarus (Faxonius) obscurus: Ortmann, 1905b: 112.
Orconectes obscurus: Hobbs, 1942a: 350–352 (by implication); Hobbs, 1948b: 139; Penn, 1950: 647; Hobbs, 1951: 125–127; Pennak, 1953: 465; Crocker, 1957: 3, 4, 7, 13, 18, 19, 24, 28, 36–39, 46, 47, 51, 52, 53, 55, 58, 64, 67, 75, 76, 78, 83, 84, 86–88; Meredith and Schwartz, 1960: 4, 5, 21, 22, 26, 27, 30, 40, 42, 54; Hobbs and Fitzpatrick, 1962: 207.
Orconectes (Orconectes) obscurus: Hobbs in Edmondson, 1959: 893.

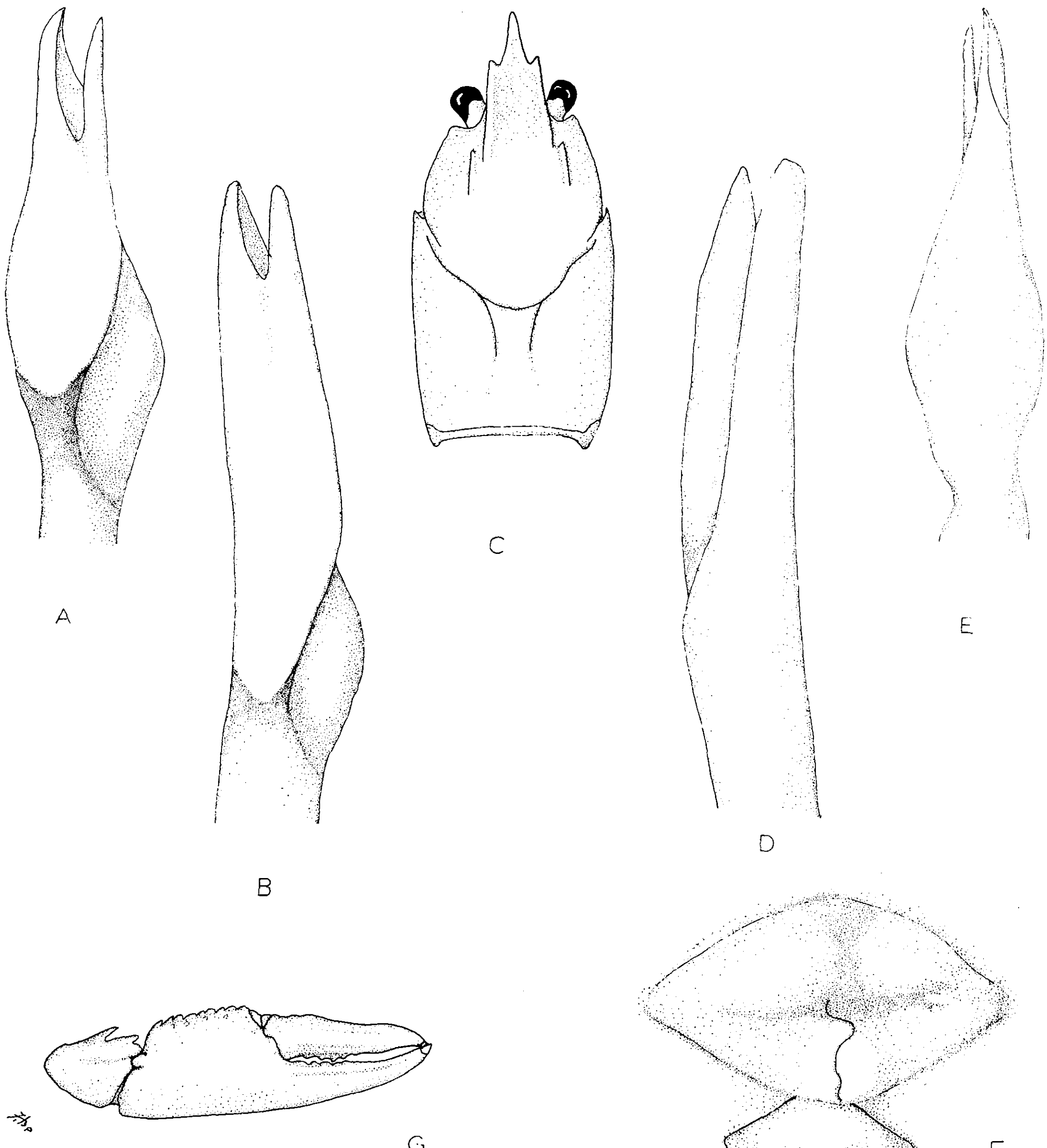


FIGURE 26. Diagnostic features of *Orconectes virginiensis* Hobbs, 1951: Symbols same as Figure 19. All illustrations of paratypes.

Faxonius obscurus: Creaser, 1962: 2–3 (by implication).

Types: Cotypes [=syntypes] M.C.Z. nos. 181, 3353, 3354; U.S.N.M. no. 4971; Mus. Nat. Hist. Philadelphia; Wurzberg Mus.; Australian Mus. *Lectotype*, herein designated, (*ex* MCZ no. 181): *paralectotypes*, herein designated, all other specimens designated "types". (See notes under *Orconectes s. sanborni* above).

Type locality: Genessee River, Rochester, Monroe County, New York.

Range: Ohio River drainage east of the eighty-first meridian; Susquehanna, Potomac, and upper Rappahannock River drainages; miscellaneous Lake Erie and Lake Ontario drainages in extreme western New York, northern Pennsylvania, and extreme northeastern Ohio (fig. 2).

Diagnosis: Based on 278 specimens (66 ♂♂ I; 44 ♂♂ II; 168 ♀♀), the lectotype, and the types at the USNM. Eyes normal; carapace pigmented. Rostrum with marginal spines (70.0%) or tubercles (24.2%) or occasionally with only strong shoulders at level of base of acumen (5.8%), concave above, median carina rarely present (0.8%) and then only weakly developed, margins usually converging (98.4%) but rarely parallel (1.6%); carapce length: rostrum length ratio 2.87–4.17 (avg 3.40); rostrum 1.60–2.32 (avg 1.90) times longer than wide; rostrum 2.52–4.59 (avg 3.40) times longer than acumen. Areola 31.9–37.4% (avg 34.8%) of total length of carapace, 5.15–10.65 (avg. 6.90) times longer than wide, with 2–5 punctations in its narrowest part; postorbital ridges strong terminating cephalically in spines (67.7%) or tubercles 32.3%). Length of first pleopod of male, Form I, divisible into carapace length 2.77–3.43 (avg 3.07) times, of male, Form II, 2.80–3.50 (avg 3.14) times; pleopod of male, Form I, with central projection 24.5–40.5% (avg 27.5%) of total length of pleopod, and of Form II, 5.4–13.5% (avg 11.2%) its length; central projection: mesial process ratio for males, Form I, 0.95–1.16 (avg 1.02), and for Form II, 0.94–1.60 (avg 1.13). *First pleopod of male, Form I, with strong right-angled shoulder on cephalic margin just proximal to base of central projection; mesial process truncate* (figs. 25A, E). Annulus ventralis of female moderately sculptured and as figured (fig. 25F). Annulus most prominently sculptured of any species in Propinquus Group.

Discussion: Orconectes obscurus is a distinct geographic and morphologic entity. The strong cephalic shoulder on the first pleopod of the male (figs. 25A, E) and the annulus ventralis of the female (fig. 25F) are unlike any other found in the Propinquus Group. In bearing a cephalic shoulder, *O. obscurus* is more like the members of the Rusticus Group than the other members of the Propinquus Group; however, the relatively short terminal elements of the first pleopod and comparatively simply sculptured annulus ventralis leave no doubt that *obscurus* is properly placed when associated with the Sanborni Subgroup, Propinquus Group. I have not seen Crocker's collections in which he suggests "hybrids between *obscurus* and *propinquus*" are to be found (1957: 46), but I have seen comparable collections and have had no difficulty in separating adults and assigning them to one of the two species. Immature specimens are not so easily identified, but all immature specimens of the several species of the Propinquus Group are similar to one another and difficult to assign to a definite species if adults are lacking.

O. obscurus should be considered an acarinate species. I have not seen a single specimen with a carinate-like ridge on the rostrum which did not also have other rostral anomalies. This leads me to suspect that the rarely-found carinate condition may be, in this species, an anomalous situation.

Seemingly, *O. obscurus* should be a well-understood and easily distinguished species. The literature, however, has instances in which the relationships of this species are questioned (e.g., Faxon, 1885a: 360; Faxon, 1885b: 86, 90, 92, 162, 165–174; Faxon, 1898: 652; Hay, 1899: 960; Ortmann, 1906b: 369; Fowler, 1911: 564; Ortmann, 1931: 65). Crocker (1957: 46) has even suggested that it hybridizes with *O. propinquus*, which latter species I have assigned to a separate Subgroup! This seems to be the proper time and place to select one specimen from the more than 32 designated syntypes and designate that specimen the lectotype. Accordingly, I designate the male, Form I, selected from MCZ no. 181 as the *lectotype* of *Cambarus obscurus* Hagen (1870). All other specimens labeled "types", wheresoever dispersed, are hereby designated *paralectotypes*. See the comments under *O. s. sanborni* for notes concerning the numbering system applied to this specimen.

Measurements of lectotype as follows (in mm)—Carapace: length, 28.1, width, 13.2, height, 11.4; Areola: length, 9.9, width, 1.8; Rostrum: length, 8.7, width, 4.6;

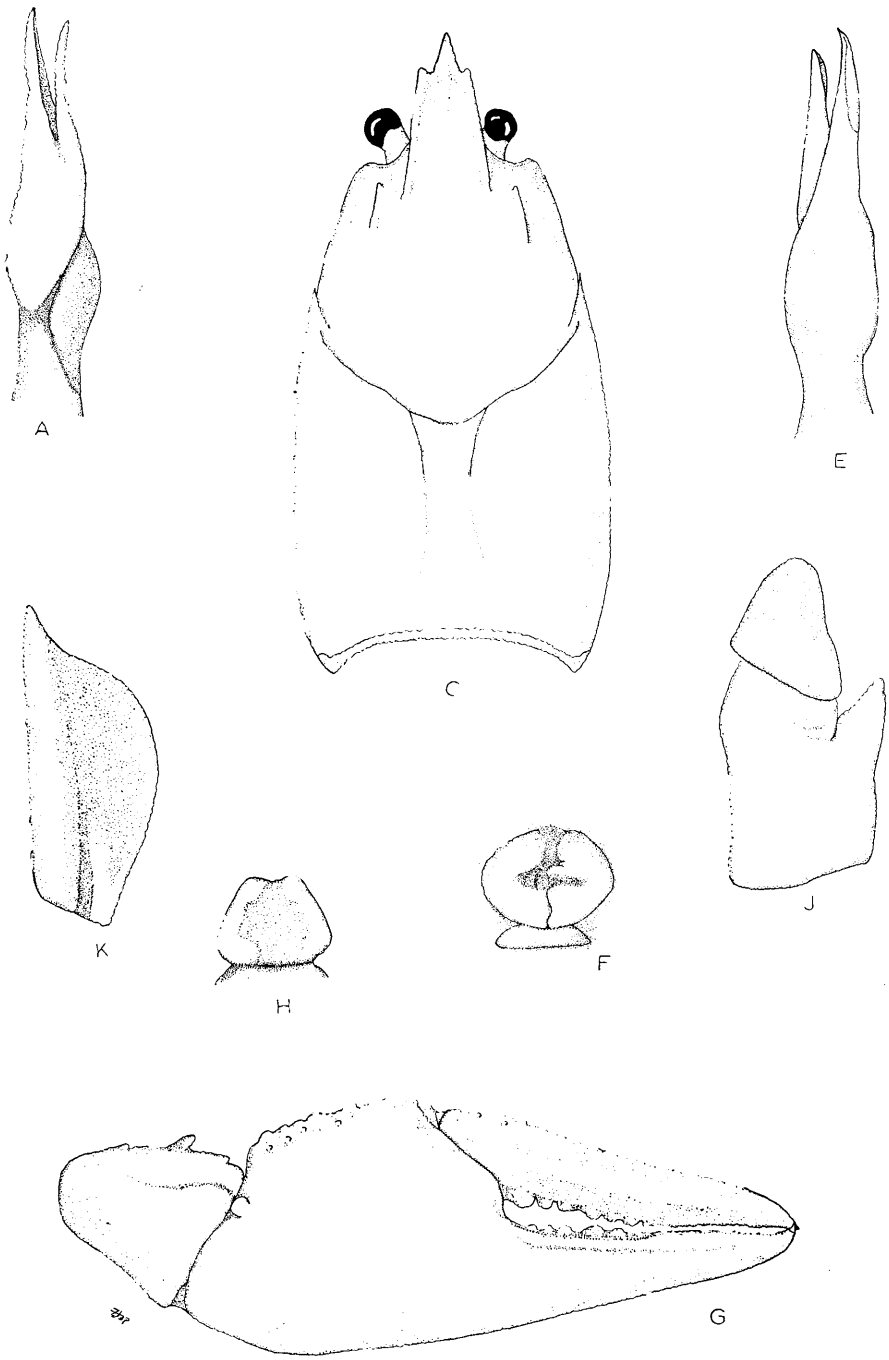


FIGURE 27. Diagnostic features of *Orconectes* species A: Symbols same as Figure 19. H. epistoma of first form male; J. basipodite and ischiopodite of first form male showing hook; K. antennal scale of first form male.

Chela: length of inner margin of palm, 6.0, width of palm, 8.1, length of outer margin of hand, 22.5; length of dactyl, 14.6.

Orconectes virginiensis Hobbs, 1951

Orconectes virginiensis Hobbs, 1951, Virginia Jour. Sci., N. S. 2: 122.
Orconectes virginiensis: Brown, 1956: 167; Hobbs and Fitzpatrick, 1962: 207.

Types: U.S.N.M. nos. 91659, 91660, 91661 (holo-, allo-, and morphotypes, respectively).

Type locality: Rowanty Creek, trib. to Nottaway River, 3.3 miles south of Reams Station on U.S. Highway 301, Dinwiddie Co., Virginia.

Range: Chowan River drainage (fig. 2).

Diagnosis: Based on 17 paratypic specimens (7 ♂♂ I; 1 ♂ II; 9 ♀♀) and the types. Eyes normal; carapace pigmented. Rostrum with marginal spines (92.4%), but occasionally with only strong shoulders at level of base of acumen (7.6%), concave above, median carina present (50%) or absent (50%), margins moderately thickened and usually parallel (66.7%) but sometimes converging (33.3%); carapace length: rostrum length ratio 2.23–2.77 (avg 2.58); rostrum 2.12–2.80 (avg 2.48) times longer than wide; rostrum 2.06–2.67 (avg 2.34) times longer than acumen. Areola 28.2–35.3% (avg 31.0%) of total length of carapace, 2.65–5.01 (avg 3.04) times longer than wide, with *5–7 punctations in narrowest part;* postorbital ridges strong terminating cephalically in spines. Pleopod length of male, Form I, divisible into carapace length 2.79–3.47 (avg 3.13) times, and of male, Form II, 3.21 times; pleopod of male, Form I, with central projection 21.4–31.9% (avg 25.5%) of total length of pleopod, and of Form II, 16.0%; central projection: mesial process ratio 1.04–1.25 (avg 1.16) for males, Form I, and for Form II, 1.08. Annulus ventralis of female weakly sculptured and as figured (fig. 26F).

Discussion: Orconectes virginiensis is geographically isolated from all other members of the Propinquus Section. The annulus ventralis is reminiscent of the simplicity and weak development of the annulus of *O. propinquus*. It is more like the members of the Propinquus Subgroup than those of the Sanborni Subgroup in possessing a carinate rostrum, though only half of the specimens have this character. The proportions of the first pleopod of the male, Form I, and of the male, Form II, however, leave little doubt that *virginiensis* is a member of the Sanborni Subgroup, although it probably retains several primitive characters.

DISCUSSION

Ortmann's original thesis (1905b: 109) concerning the "natural association" of the Propinquus Group appears to be sound, but additional information provided by this and other studies requires that the nomenclature of the species and subspecies of the Group be modified. The overall homogeneity of the Group is emphasized by the statistical study to which the several species and subspecies were subjected, but certain associational relationships not previously suspected were revealed.

Among the twelve statistical and eleven quantitative characters evaluated in this study, only five character differences were significant to the degree that they were usable for the purpose of making distinctions between taxa. These characters are (i) the length of the central projection of the first pleopod of the two forms of the male (figs. 13 and 14), in which calculation of the coefficient of difference indicates that the separation of the species is valid (table IV); (ii) the ratio of length of the pleopod: carapace length (i.e., relative length of the pleopod) is useful for the separation of the species into species groups when one compares arithmetic means of several populations by Student's t test (fig. 12), but because of considerable overlap, this is unreliable for the evaluation of any single specimen or a small series of specimens. Among the qualitative data, differences are principally in frequency of occurrence (figs. 16, 17, Tables II, III), but species differences are obvious in such characters as (iii) median carina of the rostrum (fig. 16), (iv) ornamentation of the lower mesial margin of the carpus (fig. 17), and (v) punctations in the areola (table III).

The evaluation of the statistical data reveals that there are two distinct morphological types in the Propinquus Group. To determine the relationships between the several taxa proposed in this Group, the summations of total observed differences, qualitative and quantitative, are recorded in Table IV. The length

TABLE II

Ornamentation of mesial margin of carpus of Propinquus Group crawfishes (Figures in per cent frequency)

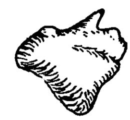
Species				Other
O. propinquus	0	35.5	63.2	1.3
O. erichsonianus	0	100.0	0	0
O. illinoisensis	0	67.7	0	33.3
O. jeffersoni	7.3	56.4	29.1	7.2
O. s. sanborni	0	91.5	8.5	0
O. s. erismophorus	0	90.0	10.0	0
O. obscurus	0	44.3	54.8	0.9
O. virginiensis	6.7	93.3	0	0
O. sp. A	0	50.0	50.0	0

TABLE III

Punctations in narrowest part of areola (all figures in per cent frequency)

Species	1–2	2–3	3–4	4–5	5–6	6–7
O. propinquus	0	10.6	86.3	3.1	0	0
O. erichsonianus	0	4.2	35.4	52.1	8.3	0
O. illinoisensis	0	67.7	33.3	0	0	0
O. jeffersoni	0	46.8	50.6	2.6	0	0
O. s. sanborni	0.8	44.4	47.6	7.2	0	0
O. s. erismophorus	0	54.6	45.4	0	0	0
O. obscurus	0	59.4	38.3	2.3	0	0
O. virginiensis	0	0	0	0	47.1	52.9

TABLE IV

Differences in characters between Propinquus Group crawfishes. Vertically listed species are compared with horizonally listed species. Upper right half, summation of significant quantitative and qualitative differences; lower left half, calculated coefficients of difference for the length of the central projection expressed as per cent total length of pleopod

	propinquus	*erichsonianus*	*jeffersoni*	*Orconectes* *s. sanborni*	*s. erismophorus*	*obscurus*	*virginiensis*
O. propinquus	X	11	13	10	5	8	6
O. erichsonianus	0.046	X	9	7	6	11	7
O. jeffersoni	1.318	0.653	X	9	12	8	5
O. s. sanborni	2.391	1.298	3.711	X	3	12	8
O. s. erismophorus	1.707	1.093	2.073	0.072	X	8	4
O. obscurus	1.020	0.547	1.758	1.717	0.926	X	13
O. virginiensis	1.045	0.680	1.545	0.458	0.421	0.365	X

of the central projection of the first pleopod, when expressed as the per cent length of the total length of the pleopod (the "cleft" or "split" of the pleopod of earlier writers), proved to be even more significant in determining relationships than expected at the beginning of the study, reflecting what has been interpreted to be the initial dichotomy in the evolution of the Propinquus Group. The two distinct evolutionary lines suggested by statistical analyses are also reflected in the geographic distribution of the species.

Since the time of Hagen (1870), the significance of the morphology of the first pleopod of first form males of the Cambarinae has been recognized as a characteristic of prime importance in reflecting species differentiation in these crawfishes. Ortmann (1905b; 1906a) demonstrated that this characteristic was the most useful one available in attempts to determine interspecific relationships. Hobbs (1940; 1942b; 1945; 1958; 1962) has carried the study further, showing that the evolutionary history of Cambarinae crawfishes is reflected by the first pleopod. Ortmann (1905b), as has been noted, placed considerable emphasis on the relative lengths of the terminal elements of species assigned to *Cambarus* (*Faxonius*) (=*Orconectes*, *sensu lato*).

Subsequent workers have agreed with these evaluations and they permit refined evaluations of the evolution of Propinquus Group crawfishes. Apparently there were two major periods of evolution in the Propinquus Group. One of these provided the isolation necessary for the two Subgroups to develop, and it probably occurred during or immediately following Illinoian glaciation. Stout and Lamb (1938), among others, have suggested that, during the Illinoian, a marked east-west division of drainage developed to replace drainages covered by ice, particularly the old Ohio which was impounded near the eighty-fifth meridian. Among the eastern populations, a predisposition toward a secondary shortening of the pleopods existed and these populations developed into the Sanborni Subgroup. The precursors of the Propinquus Subgroup contained the potentialities for a lengthening of the terminal elements and were isolated in the western portion of the original range. At about the same time, a portion of the pro-Propinquus Group stock gained access to the Tennessee River drainage and developed into *O. erichsonianus*. Sometime shortly after the isolation of the pro-Sanborni Subgroup stock, another population gained access to the James or Roanoke Rivers, probably by stream capture from the Kanawha River System. This population diversified and became restricted to the Chowan River system to become *O. virginiensis*.

The second period of speciation is postulated to have been associated with Wisconsin glaciation and to have given rise to most of the species of the Group.

There are specimens of *O. propinquus* from Ashtabula County, Ohio, and Oconito and Oneida Counties, Wisconsin; of *O. jeffersoni* from Bullit County, Kentucky; and of *O. s. sanborni* from Carter County, Kentucky, most southeastern counties of Ohio, and Jackson County, West Virginia; in which the pleopod in some males bears a weakly developed shoulder in a location at or near to that at which a strong shoulder is borne by males of *O. obscurus*. This suggests that the "ancestral type" probably bore a shoulder. This also suggests possible sites at which refuges existed during the advance of the Wisconsin ice sheet.

The possible origin of *O. virginiensis* is discussed in a preceeding paragraph. It is now confined to small coastal drainage between the much larger James and Roanoke systems. It is the only species of the Group (except species A) which is not found in drainages having at least a part of their origin in the central Appalachians. *O. obscurus* probably arose from populations taking refuge in western Pennsylvania. Ortmann (1906b) has discussed this at length. He observed the close association of this species with the Erigan River of the Pliocene. If this relationship has significance, it could mean that *obscurus* arose from a pre-Pleistocene population. *O. s. sanborni* radiated from populations taking refuge in southern Ohio and northwestern West Virginia. *O. s. erismophorous* probably arose as a result of a mutation occurring in ***sanborni*** which has become sufficiently isolated in the Little Kanawha system to allow the distinctive form to develop.

*O. **propinquus*** probably reinvaded the Lakes drainage by moving behind the retreating glacier from refuges in northeastern Ohio and northern Wisconsin. The facts that variations are not regional and that the apparent refuges are two, widely separated, could mean that the populations of ***propinquus*** were in communication all along the marginal lakes of the ice sheet. *O. jeffersoni* represents a refuge population unable to undergo much expansion following the retreat of the glacier, possibly because of competitive exclusion by other Propinquus Section crawfishes to the south, east, and west, and by the Ohio River to the north. Inadequate representatives of *O. illinoisensis* and *O.* species A prevent an accurate assessment of their relationships and evolutionary history. The specimens provided by Dr. Goellner, however, suggest that increased flow of the Mississippi, possibly associated with the retreat of the Wisconsin ice sheet, served to isolate a *propinquus*-like stock from the main population, which stock then gave rise to *O.* species A.

Origins of *O. erichsonianus* are discussed in a preceeding paragraph. *O. erichsonianus* is probably closer to the "ancestral type" than any of the known extant species of the Propinquus Group. Although I have assigned it to the Propinquus Subgroup, it occupies a position somewhat intermediate between the two Subgroups. Likewise, it seems to be more closely allied to certain members of the Rusticus Group than are any of the other species of the Propinquus Group. This leads me to believe that the ancestors of *O. erichsonianus* were isolated from the parental stock before the origin of many of the characters which distinguish the Subgroups of the Propinquus Group, and not long after the isolation of the Rusticus Group progenitors. The proposed lineages are demonstrated in figure 18.

The ancestral stock of the Propinquus Group probably resembled *O. erichsonianus* with these shared characteristics: (i) the pleopod of the male, Form I, had the central projection about 30 per cent of the total length of the pleopod; (ii) the areola was about 30 per cent of the total length of the carapace, four to five times longer than broad, and with two to five punctations in its narrowest part; (iii) the terminal elements of the first pleopod were two subequal rami, which were also subparallel and straight; (iv) the annulus ventralis of the female was moderately sculptured with a tendency toward weak sculpturing. It was unlike *erichsonianus* in that the first pleopod bore a weak shoulder near the base of the central projection. This latter character was probably variable, being more frequent in northern populations than in southern ones. Certainly the shoulder was borne by the progenitors of ***propinquus***, ***sanborni***, and *jeffersoni* until Wisconsin times. The strong development of the shoulder in ***obscurus*** is another suggestion that the progenitors of this species may have been derived as early as were those of *erichsonianus*.

The gross distinctiveness of each taxon of the Group is discussed above in the general discussion of each. The morphometric data, when subjected to statistical analysis, further support these ideas. When one compares *O. sanborni* with *O. **propinquus***, one discerns that there are five statistical differences (in 11 examined characters) and five qualitative differences (in 12 examined characters) between the two species. A similar comparison of ***sanborni*** with *O. jeffersoni* reveals six statistical differences and seven qualitative differences; in a comparison of ***propinquus*** with *jeffersoni*, the results are four statistical and five qualitative differences (table IV). The calculated coefficients of difference for length of the central projection of the first pleopod of the male, Form I, in the same three comparisons are 2.39, 1.32, and 3.71, respectively, indicating the significant joint non-overlaps of 96++%, 91−%, and 96++% (*fide*, Mayr, et al., 1953: 146). The application of Student's t test to the length ratio of the male, Form I, pleopod, indicates, in the same comparisons, that differences between the species for this character are highly significant, all having a probability of considerably less than 0.01 of not being different from one another. Such results, when occurring in an analysis of taxa exhibiting the degree of homogeneity shown by the Propinquus Group, would, to me, be indicative that the three are separate entities, each worthy of specific status. I have examined specimens from the suggested *sanbori-propinquus* (Ortmann, 1906b: 368, 374) and *propinquus-obscurus* (Ortmann, 1906b: 374; Crocker, 1957: 46) areas of intergradation and have had no difficulty in separating mature specimens.

Thus, there are evolutionary, geographic, and morphologic data to support the taxa as listed:

Orconectes propinquus (=*O. p. propinquus*)
Orconectes erichsonianus
Orconectes illinoisensis
Orconectes jeffersoni (=*O. propinquus jeffersoni*)
Orconectes obscurus
Orconectes sanborni sanborni (=*O. propinquus sanborni*)
Orconectes sanborni erismophorous (=*O. propinquus erismophorous*)
Orconectes virginiensis

SUMMARY

1. Eleven taxonomically important characters of the nine species and subspecies of the Propinquus Group of the Propinquus Section of the crawfish genus *Orconectes* were measured, appropriate ratios were calculated, and the ratios were examined statistically.

2. Twelve qualitative or meristic characters, also of taxonomic value, were recorded and also subjected to analysis and evaluation, principally by determination of comparative frequencies.

3. The study was accomplished by the examination of a total of 1226 specimens, including those types available at the United States National Museum, representing *Orconectes propinquus propinquus*. *O. p. erismophorous*, *O. p. jeffersoni*, *O. p. sanborni*, *O. erichsonianus*, *O. illinoisensis*, *O. obscurus*, and *O. virginiensis*.

4. It was determined that *Orconectes jeffersoni* is specifically distinct from *O. propinquus*, as are *O. s. sanborni* and *O. s. erismophorous*, although the latter two are conspecific; appropriate nomenclatorial changes are proposed.

5. A new species of the Propinquus Group. *Orconectes* species A (=*Cambarus p. propinquus*: Faxon, 1885b, *in partim*; Harris, 1903, *in partim*), was recognized and diagnosed, but not described.

6. Two distinct morphological types exist in the Propinquus Group: one (Propinquus Subgroup) with a shorter pleopod and longer central projection and occurring generally west of the 83rd meridian; the other (Sanbornii Subgroup) with a longer pleopod and shorter central projection and occurring generally east of the 83rd meridian. The evolutionary history of the Group apparently is the cause of this divergence.

7. The characteristics most useful in distinguishing between the species are the relative length of the first pleopod, the relative length of the central projection, presence of a carina on the rostrum, ornamentation of the lower mesial margins of the carpus, and punctations in the areola. Of more limited use are the relative sculpturing of the annulus ventralis, presence of a strong cephalic shoulder on the first pleopod, and peculiarities of morphology of the mesial process.

8. A discussion of the value of standard taxonomic characters in crawfishes is included, with reference to their application to the Propinquus Group.

9. A *lectotype* and *paralectotypes* were designated for *Cambarus sanborni* Faxon. A *lectotype* and *paralectotypes* were designated for *Cambarus obscurus* Hagen.

ACKNOWLEDGMENTS

I am indebted most of all to my research supervisor, Dr. Horton H. Hobbs, Jr., Senior Scientist, United States National Museum. He has generously lent his entire collection of *Orconectes*, his time, his advice, and has assisted in field collections. Dr. James Norman Dent, my sponsor at the University of Virginia, was most helpful, frequently exceeding the normal requirements of that capacity to assist me in my work. Dr. Rudolph Prins of Clemson University has lent specimens of *O. jeffersoni* and other species from the vicinity of Jefferson County, Kentucky, and aided in bringing my ecological data from this region up to date. Dr. Perry C. Holt of Virginia Polytechnic Institute collected many of the specimens examined and permitted me to examine them before their incorporation into the Hobbs Collections. Dr. David H. Stansbery of the Ohio State Museum has been very helpful with observations, discussions, and specimens from Ohio.

The staff of United States National Museum has been kind and helpful in my many visits to that institution, and they have been liberal in lending specimens to me. Dr. William Newman of the Museum of Comparative Zoology lent the specimens on which *Orconectes* species A is based and Dr. Herbert Levi of the same institution lent me specimens from the type series from which I selected lectotypes for *C. sanborni* and *C. obscurus*. The Graduate School of Arts and Sciences of the University of Virginia has supported me financially with a Philip Francis duPont Fellowship and a Henry Clay Marchant Fellowship during my tenure at that institution.

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