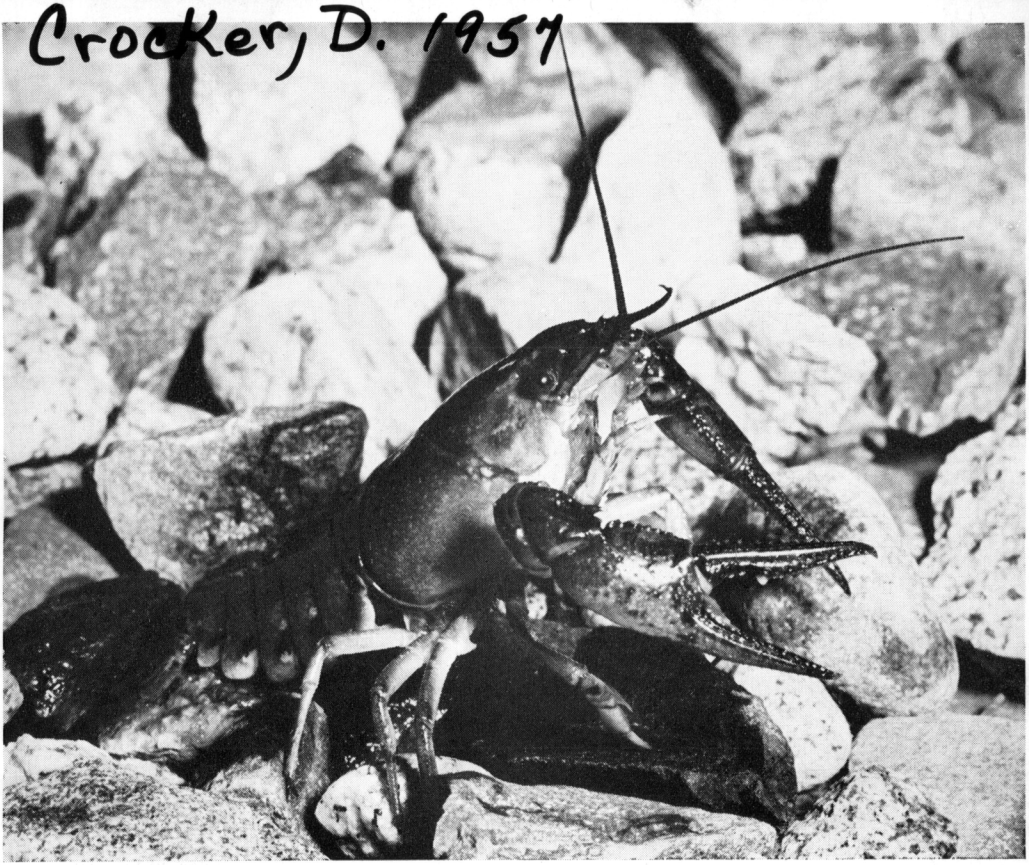

THE CRAYFISHES

of

NEW YORK STATE

(Decapoda, Astacidae)

By

Denton W. Crocker
Temporary Museum Expert

NEW YORK STATE MUSEUM AND SCIENCE SERVICE

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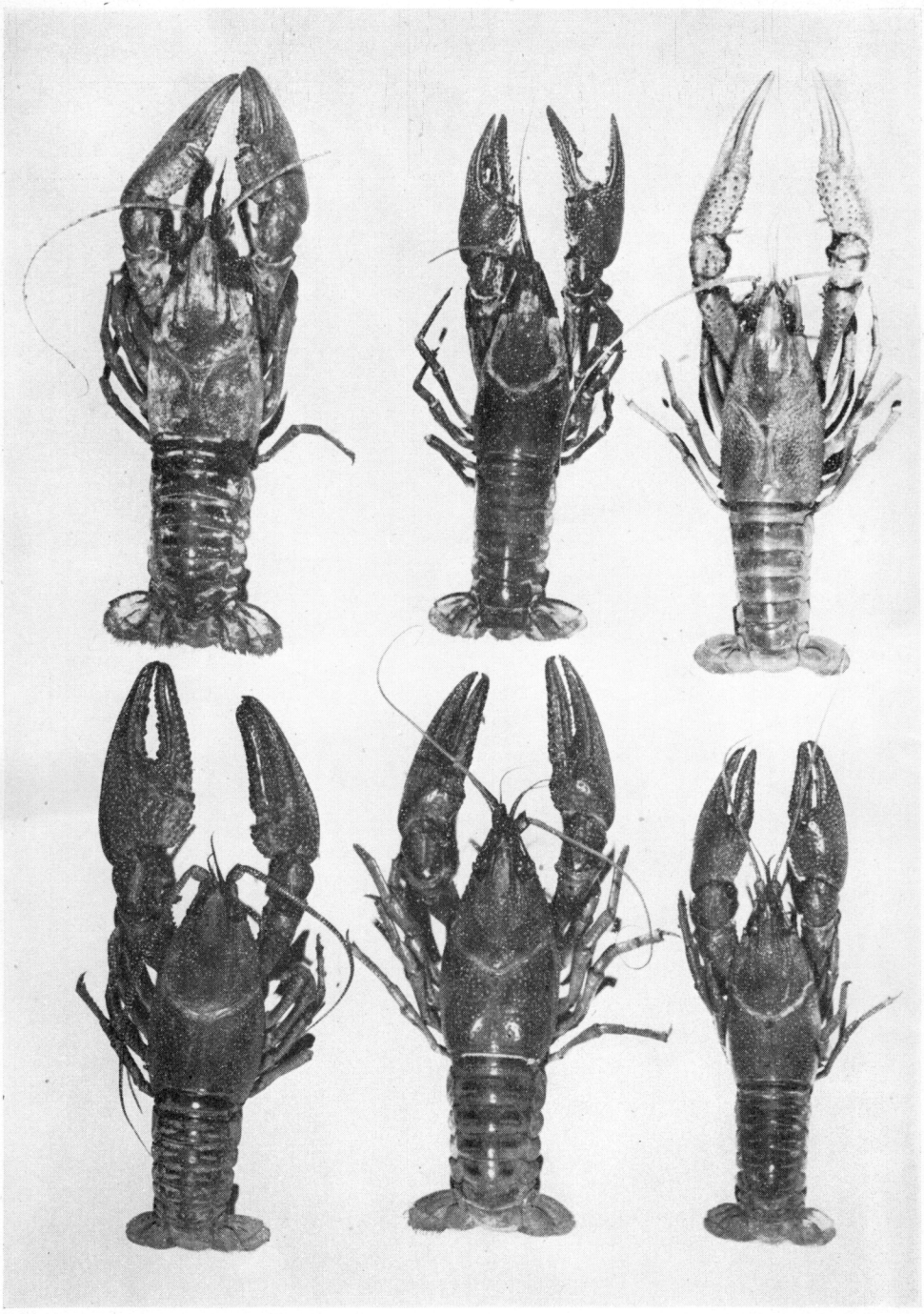


FRONTISPIECE. Dorsal views of form I males of six of the eight known species of New York crayfishes. Upper row from left to right: *Orconectes limosus* (Rafinesque), *Orconectes immunis* (Hagen), and *Procambarus b. blandingi* (Harlan). Lower row: *Cambarus robustus* Girard, *Orconectes virilis* (Hagen), and *Orconectes p. propinquus* (Girard). Collection data for all of these specimens and drawings of their copulatory stylets (except for *O. limosus*) are on plates 2, 3 and 4 and their legends.

INTRODUCTION

Brief Historical Review

The crayfishes (or crawfishes) have long been an object of study by zoologists. Their abundance in many localities and large size (the largest of North American fresh water crustacea) make them excellent animals for zoological study. In fact, Thomas Huxley (1880) wrote a successful textbook of zoology based on this single animal group.

In 1798, Fabricius published the first description of an American crayfish, now known as *Cambarus b. bartoni*. The early published descriptions of our American species by Say (1817), Rafinesque (1817), Girard (1852) and others, were often sketchy and without figures, a characteristic of the times. The first comprehensive systematic work was a *Monograph of the North American Astacidae* (Hagen, 1870). This work was amplified and revised in the several major contributions of Faxon (1885*a*, *b* and *c*, 1890, 1898 and 1914). The taxonomy of crayfishes has undergone many changes culminating, for the present, in the generic revision of Hobbs (1942*a*), who gives a review of taxonomic changes to 1942. Besides these works of larger geographic scope, a number of State surveys have been made.

At present, H. H. Hobbs, Jr. of the University of Virginia is contributing most to crayfish literature and his excellent papers must be included among the basic materials for students of the group.

Studies of life history and ecology are many fewer than those which are primarily taxonomic. Outstanding among the former are the studies of Andrews on breeding behavior (1895, 1904, 1906*a*, and 1910*a*) and on development under laboratory conditions (1907), and the field study by VanDeventer (1937) of the biology of *Cambarus propinquus* (= *Orconectes propinquus*) in Illinois. Ortmann's report of Pennsylvania crayfishes (1906) contains valuable life history information, especially concerning *Orconectes obscurus*. More recent work has been done by Penn (1943), Bovbjerg (1952) and Smith, E. W. (1953).

Although the eight species of crayfishes which occur in New York range beyond the State and have been studied in greater or lesser degree in out-of-State areas, very few studies have been made of these crayfishes within New York State.

Tack (1941) worked out the life history of *Orconectes immunis* at Ithaca. Creaser (1934) reported on the higher Crustacea of the Raquette River system, and Nevin and Townes (1935) include crayfishes in their survey of fish food organisms of the Mohawk-Hudson.

Paulmier (1905) surveyed the higher Crustacea (including marine forms) of New York City and Dekay (1843) gives an account of historical interest of the Crustacea of the State. All other reports of the crayfishes of the State are locality records included in works of larger taxonomic or geographic scope.

Aims of Study

The zoological value of a study of the crayfishes of the State is obvious when the former lack of knowledge is realized. Several adjacent or nearby States to the south, southwest and west have been surveyed: Pennsylvania (Ortmann, 1906); New Jersey (Fowler, 1912); West Virginia (Newcomb, 1929); Ohio (Turner, 1926). These indicate that for several species or subspecies, the present study closes one of the few remaining gaps in our knowledge of their eastern and northern geographic limits.

The present study has the following aims:

1. To determine the number of species or subspecies which occur in New York State
2. To delimit the geographic ranges of the taxonomic forms occurring in New York State
3. To determine the morphological variation of the New York species, both within New York and also compared with these same forms found in other areas
4. To determine, where possible, genetic affinities and pathways of dispersal
5. To add to the often fragmentary knowledge of life histories

Materials and Methods

A major portion of this study was done as a doctoral dissertation at Cornell University (Crocker 1952). However, a considerable quantity of new data has been incorporated and the drawings have been redone.

Most of the crayfishes examined are tabulated in tables 16, 17 and 18 (pages 86-88). In addition, material has been studied at the United States National Museum (USNM) and at the Museum of Comparative Zoology (MCZ) at Harvard.

Crayfishes collected by the several Biological Surveys of the New York State Conservation Department (stream surveys) are deposited in the New York State Museum (NYSM). In 1952 I was employed by the Museum to reorganize these stream survey crayfishes and to make new collections. My report on the present organization of these specimens is an appendix to the quarterly report for October 1, 1952, of the State Zoologist to the Director of the New York State Museum, and is on file at the Museum.

To summarize the report briefly, all this material is now readily available for study. A card file in triplicate, filed by stream survey collection number, by species and by drainage system is available at the Museum as a further aid to the study of these specimens. The new collections which I made in August 1952 are NYSM catalog numbers 6977-7022 inclusive. The stream survey crayfishes are cataloged under the one New York State Museum number 6975. These are referred to in the present paper in the following form:

NYSM (year of survey): stream survey collection number.

The localities plotted on maps (figures 3-7) are all from my personal collections and the collections of the NYSM, with the single exception of the record for *Orconectes virilis* in the Raquette River which is taken from Creaser (1934: 158). The watersheds of New York and their dates of survey are illustrated in figure 2 (page 70).

The drawings of copulatory stylets and seminal receptacles (plates 1-5) were made with a camera lucida. On plate 1, figures 1-4 were drawn with a camera lucida and figures 5 and 6 were obtained by tracing on cellophane, using magnification by the method of Staniland (1953). Pubescence has been omitted from all figures. Receptacles are drawn oriented with the posterior border toward the bottom of the plate.

Collecting has been accomplished largely by seining or by turning stones and collecting by hand. Seining works best in turbid, deep or swift water. Crayfish may also be coaxed readily into a dark colored dip net by prodding with a dark stick.

In sorting specimens to permit tabulation of life history data not all specimens were measured. Therefore, for many specimens, those form II males and females, which were judged by eye to be within 1 mm. of the lower limit of size at sexual maturity (table 2), are reported as male (II?) or female (imm.?). Form II males and females measured and found to be within a few tenths of a millimeter of this value, are similarly reported.

Where "New York" is written, the State and not the city is intended. New York City will always be identified as such.

Acknowledgments

This study would not have been possible without help from many sources. Financial aid during most of my period of graduate study was provided by the people of the United States through the Federal Government under Public Law 16.

Professor Horton H. Hobbs, Jr. of the University of Virginia has been unstintingly generous of his time and materials and has given continued assistance throughout the course of the study.

The loan of Stream Survey crayfishes was obtained from the New York State Museum through the assistance of Dr. Ralph S. Palmer, State Zoologist, who has helped also in many other ways.

The Department of Conservation of Cornell University supplied maps on which the distribution data are plotted, and Professor E. C. Raney of that department has been generous with advice and criticism.

Thanks are due Dr. Waldo L. Schmitt and Dr. Fenner A. Chase, Jr. for many courtesies rendered during my visit to the United States National Museum and for the loan of specimens. Dr. Elisabeth Deichmann of the Museum of Comparative Zoology at Harvard University has very kindly loaned specimens at several different times and has put the museum collections at my disposal during my visits there.

Professor Alfred S. Romer, director of the Museum of Comparative Zoology, for several summers has generously granted me the use of table space in the Museum library, and the library staff has shown considerable patience with my many requests.

Several faculty members and numerous former students at Cornell University have contributed to my crayfish collections. To Royal D. Suttkus (now of the Department of Zoology, Tulane University) go my particular thanks for contributing perhaps as many as 5 percent of my specimens.

I am grateful to Dr. J. Seelye Bixler, president of Colby College, for two grants of money in support of my research. The Science Division of Colby College has given me a small sum of money for the purchase of publications.

I particularly wish to thank Jean-Marie J. Crocker, not only for wifely encouragement and moral support, but also for contributing materially toward the completion of this study with clerical help and assistance in the field.

The cover photograph was taken by Wendell A. Ray.

THE GEOGRAPHIC DISTRIBUTION AND SYSTEMATICS OF CRAYFISHES

Discussion

The relationship of the tribe Astacidea, to which the crayfishes belong, to other groups of the crustacean order Decapoda may be visualized by reference to figure 1. The tribe Astacidea may be separated into four families: the Nephropsidae, including the Norwegian, the European and the American lobsters; the Astacidae, which contains the European, North American and Asian crayfishes; and the Parastacidae and Austroastacidae, which contain the crayfishes of the southern hemisphere. The Nephropsidae are separable from the other three families of the tribe by the condition of the last thoracic segment, which in the Nephropsidae is fused to the carapace. The Parastacidae and Austroastacidae are most readily separated from the Astacidae by the lack in the former two families of sexual appendages (copulatory stylets) in the male.

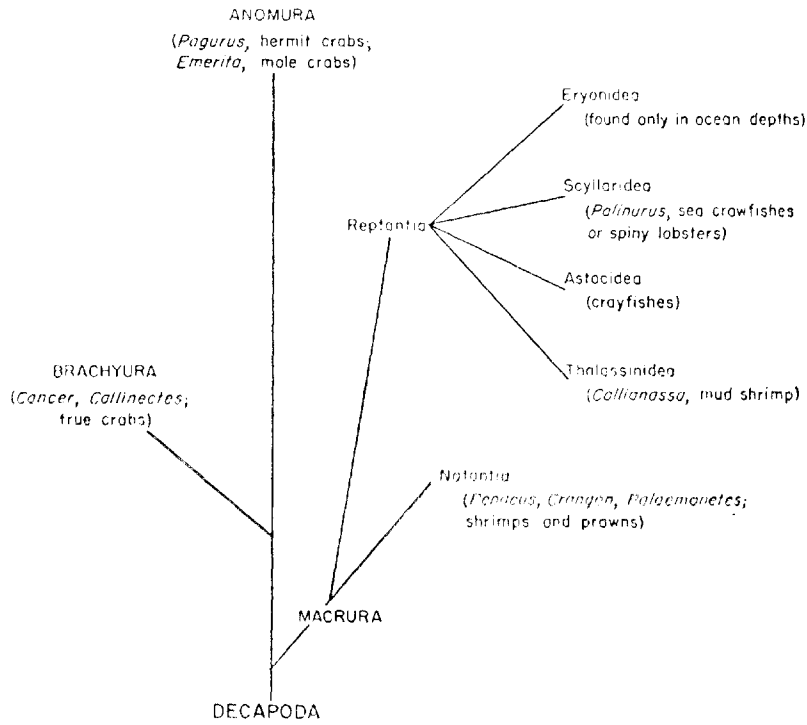


FIGURE 1. The place of crayfishes in the classification of decapod Crustacea (based on correspondence with L. B. Holthuis)

The three families of crayfishes are residents almost exclusively of fresh water (rarely brackish water), and their distributions present a striking picture. For maps of these distributions see Huxley (1880: 309), Calman (1911: 175) and Ortmann (1902: 275). Ortmann's paper contains an analysis of geologic changes which have resulted in the present distributions. These papers were written before the separation of Austroastacidae from Parastacidae by Clark (1936).

In general, the Astacidae are restricted to the Northern Hemisphere, and the Parastacidae and Austroastacidae are restricted to the Southern Hemisphere, with a tropical belt left free of any fresh water Astacidea. This tropical belt covers the area between 10 degrees north latitude and, except for the Parastacidae on New Guinea, 10 degrees south latitude. Of this distribution, Smith and Weldon (1923: 214) state the following:

> It seems reasonable to suppose that the two families of Crayfishes characteristic respectively of the Northern and Southern Hemispheres have been independently derived from marine ancestors, which have subsequently become extinct. Their complete absence in the tropics is striking, and Huxley drew attention to the fact that it is exactly in those regions where the Crayfishes are absent that the other large fresh water Malacostraca are particularly well developed, and *vice versa*. Thus the large freshwater Prawns are typically circumtropical in distribution, while the South African rivers abound with Rivercrabs, which, in general, are found wherever Crayfishes do not occur.

The family Astacidae is made up of two subfamilies. The subfamily Astacinae inhabits North America west of the Rocky Mountains, and Europe and Asia. The subfamily Cambarinae is composed of the crayfishes native to North America east of the Rocky Mountains, but a number of introductions elsewhere have occurred (Penn 1954). The Cambarinae lack gills on the last thoracic somite and are separable from the Astacinae on the basis of this character. New York State crayfishes, then, are members of the crustacean order Decapoda, suborder Reptantia, tribe Astacidea, family Astacidae, subfamily Cambarinae.

The revision of Hobbs (1942*a*) divides the subfamily Cambarinae into the following six genera: *Procambarus, Paracambarus, Troglocambarus, Cambarellus, Orconectes* and *Cambarus,* of which *Paracambarus* and *Troglocambarus* are monotypic. At the time of Hobbs' revision (1942*a*) the subfamily Cambarinae consisted of 96 species,

15 of these containing a total of 47 subspecies; a total of 128 described taxonomic forms. At present there are probably about 200 described species and subspecies. The systematic positions within the subfamily Cambarinae of the eight New York crayfishes is shown in the following list.

Systematic List of New York Crayfishes

Family **Astacidae**

Subfamily Cambarinae

Procambarus Ortmann (1905*b*: 437)
Type: *Cambarus digueti* Bouvier, 1897, subsequent designation by Hobbs (1942*a*: 341)
  Blandingi Section (Ortmann 1905*a*: 98)
    Blandingi Group (Ortmann 1905*a*: 102)
      Blandingi Subgroup (Hobbs 1942*b*: 93-94)
        Procambarus blandingi blandingi (Harlan), 1830
Orconectes Cope (1872: 419)
Type: *Orconectes inermis* Cope, 1872, by monotypy.
  Limosus Section (Ortmann 1905*a*: 108)
        Orconectes limosus (Rafinesque), 1817
  Propinquus Section (Ortmann 1905*a*: 108)
    Propinquus Group (Ortmann 1905*a*: 109)
        Orconectes propinquus propinquus (Girard), 1852
        Orconectes obscurus (Hagen), 1870
  Virilis Section (Ortmann 1905*a*: 109-110)
    Virilis Group (Ortmann 1905*a*: 110)
        Orconectes virilis (Hagen), 1870
        Orconectes immunis (Hagen), 1870
Cambarus Erichson (1846: 88)
Type: *Astacus bartoni* Fabricius, 1798, subsequent designation by Faxon (1898: 644)
  Bartoni Section (Ortmann 1905*a*: 119)
        Cambarus bartoni bartoni (Fabricius), 1798
        Cambarus robustus Girard, 1852

Systematic Characters in the Cambarinae

The copulatory stylets. By far the best indicators of relationships in this subfamily are the copulatory stylets and the disposition of copulatory hooks which occur on the ischia of the male perciopods. These are utilized in the diagnoses of genera (Hobbs 1942*a*) and even of groupings within genera (Ortmann 1905*a*).

The differences in the morphology of the stylets among different species have been homologized through the careful studies of Andrews (1910*b*) and Hobbs (1942*c* and 1945), which are in agreement in principle, although using different nomenclature. Further

studies of stylet anatomy and development have been made by Hart (1952, 1953 and 1956).

Among New York crayfishes there are two major types of copulatory stylet. In discussing these, the terms of orientation used refer to the stylet with its shaft aligned dorso-ventrally, its distal end (excluding flexures of the terminal elements) directed ventrad. Only the form I stylet is considered here (see below for a discussion of the two forms of the male).

One type has four terminal elements and of New York State crayfishes occurs only in *P. b. blandingi*. Plate 4, figure 5 is a lateral view of the right stylet of this species. In the figure, the distal end is toward the top of the plate. The names of the terminal elements, listed in sequence caudad (toward the right of the plate) are: cephalic process, central projection, caudal process and mesial process. The mesial process is so named because it originates proximally on the mesial surface of the stylet. The central projection is composed of two fused parts, the centro-cephalic process and, more caudad, the centro-caudal process. It is always the central projection which contains the duct through which the sexual elements pass.

The other major type of stylet has only two terminal elements, the central projection and the mesial process. The type has two distinct subtypes. In one (plate 2, figure 1) the terminal elements are both short and heavy and are bent caudad at about a 90-degree angle to the main shaft. The central projection is the one at the top of the figure (the more distal element). This subtype is the chief diagnostic character for the genus *Cambarus* (Hobbs 1942*a*: 354) and of New York crayfishes occurs in *C. b. bartoni* and *C. robustus*.

The remaining five New York species possess stylets which terminate in two straight (plate 3, figures 1 and 5) or gently curved (plate 4, figures 1 and 3), short (plate 3, figure 5) or long (plate 4, figure 1) elements. Such a shaped stylet is the chief diagnostic character for the genus *Orconectes* (Hobbs 1942*a*: 350). All of the figured stylets of this last subtype are drawn with the central projection toward the left of the plate and with the mesial process on the right.

The two forms of the male. One of the many complexities confronting the first American crayfish students was the two forms of the male, first noticed according to Hagen (1870: 22) by Louis Agassiz, who did not, however, publish this information. As late as 1870 it was supposed that an individual existed throughout its life either as one form or the other. In 1875 Faxon received a shipment of live crayfishes from Kentucky. One of the males moulted in the laboratory and upon comparing moult with moulted animal he found one to be

of one form and the remaining one of the other. His further observations and published account (Faxon 1884) settled the issue. It is now understood that adult males incapable of reproduction (known technically as form II) are morphologically different from males which are so capable (form I). It is also known that in a given individual the two forms alternate, the time of year and frequency of alternation varying with species. This phenomenon occurs only in the subfamily Cambarinae and in *Cambaroides* of the subfamily Astacinae (Hart 1953).

The major external morphological differences in the form I males are heavier, more corneous and slightly larger copulatory stylets (first pleopods) and larger hooks on those pereiopods which bear them.

Other useful taxonomic characters. The use of form I stylets in keys has the disadvantage of restricting identifications to form I males. Therefore, it is desirable that other morphological features be utilized for separating species. Such features, commonly used in keys and generally used for separating closely related forms, include the following: shape and armature of rostrum, shape of hand and armature of various segments of chela, shape of antennal scale, width of areola, ratio of lengths of anterior and posterior portions of carapace, shape of epistome and shape of seminal receptacle.

The seminal receptacle (annulus ventralis). The seminal receptacle which, among crayfishes, is present only in the Cambarinae, was first reported to function as such by Andrews (1895: 869-870). Hagen (1870) first called attention to the structure and noted its differing shape in the various species of the then inclusive *Cambarus*. Hagen (1870: 20) doubtfully postulated that the seminal receptacle, which he called the annulus ventralis, might function in secreting the cement by means of which the eggs are fastened to the pleopods. The varying shapes of the ridges, sinus, tubercles and fossa of the receptacle are now commonly used to differentiate closely related species of which the females might otherwise, in the present state of crayfish taxonomy, be indistinguishable. However, "As things now stand, an isolated female which does not belong to a species that is very familiar to the taxonomist, generally goes unnamed, and often cannot be determined as to genus." (Hobbs 1942*a*: 340).

Andrews has extensively studied the seminal receptacle and has published on its ontogeny (1906*c*) and its morphology in the adult (1906*b*). He has also pointed out that in *Orconectes limosus, O. virilis, Cambarus b. bartoni* and *Procambarus clarki,* the receptacle

occurs in two forms, one a mirror image of the other, a fact not generally mentioned in taxonomic works, but one that should be remembered by anyone attempting to identify female Cambarinae. In a species such as *C. robustus* there is a ridge of the receptacle which in one of the two forms runs somewhat obliquely to the animal's right

TABLE 1

Crayfishes for which quantitative data are available for the occurrence of left- and right-handed seminal receptacles

SPECIES	LOCALITY	NO. FEMALES EXAMINED	NO. RIGHT HANDED	NO. LEFT HANDED	AUTHORITY
Procambarus clarki[1]	New Orleans, La.	29	16	13	Andrews (1906*b*: 465)
Cambarus b. bartoni	Baltimore Co., Md.	12	8	4	Andrews (1906*b*: 468)
C. robustus	11 localities in vicinity of Ithaca, N. Y.	109	84	25	Author
Orconectes limosus	not given		majority	few	Andrews (1906*b*: 443)
	not given	41	38	3	Andrews (1906*c*: 131)
	two localities in Catatonk Creek, Tioga Co., N. Y.	39	30	9	Author
Orconectes virilis[2]	from Chicago markets	25	4	21	Andrews (1906*b*: 459)
Orconectes immunis[3]	Cornell Univ. Fish Hatchery Ponds, Tompkins Co., N. Y.	137	135	2	Author

[1] Not present in New York State.

[2] After making certain assumptions regarding the homologies of component parts of the seminal receptacles of *Cambarus virilis* (= *Orconectes virilis*) and *C. affinis* (= *O. limosus*), Andrews (1906*b*: 461) says, "On these assumptions a right-handed *C. virilis* would be fundamentally like a left-handed *C. affinis* and in both species these seem to be the rarer form."

[3] Andrews (1906*b*) studied the receptacle of *O. immunis*, but, although he did not report left-handed forms, neither did he specifically state nor even definitely infer that he searched for them. He does say, however, (Andrews 1906*b*: 477), "The inversion of symmetry in the annuli of different individuals may well be general in *Cambarus* [= family Cambarinae]."

and then dips dorsad into a cavity or fossa. This, Andrews (1906*b* and 1906*c*) calls a right-handed seminal receptacle In the left-handed form the ridge runs obliquely to the animal's left and then dips into the fossa. Plate 2, figures 3 and 4 show these two receptacle shapes. Table 1 summarizes the available published information and adds new data concerning the relative abundance of the two shapes in various crayfish species.

The occurrence of the two receptacle forms presents an interesting problem in genetics which, at least as regards rearing a suitable animal in captivity, should not be difficult of solution. Andrews (1907: 68) states of *O. limosus,* "...there would seem to be no obstacle to the establishment of a permanent race of domesticated crayfish bred in captivity." It is also a question whether or not the male acts differently toward the two forms of the receptacle.

Aside from the phenomenon of the two mirror-image forms, however, Andrews suggests other interesting speculations relating to the seminal receptacle. Are the stylets of the male, and the female receptacle closely adjusted to one another in each species or not? If so, how then does it happen that the receptacles in two species such as *C. b. bartoni* and *O. immunis* are so similar when the stylets of the male are so different? Of what survival value is the seminal receptacle, a structure present only in the more advanced of the two subfamilies of the Astacidae, the subfamily Cambarinae, and yet a structure which has been evolved independently in this subfamily and in the marine genus (of the family Nephropsidae) *Homarus*? These questions are not answered in this paper, but are presented to demonstrate how little is yet known of the natural history of crayfishes, even in the relatively well-worked subject of crayfish reproduction.

Key to Adults of Crayfishes Known from New York

The following key is designed to separate mature New York crayfishes without reference to copulatory stylets or to seminal receptacles. The male I stylets are usually the best diagnostic feature of a species and it is preferable that, if form I males are present, their stylets be used in making the identification by comparing them with the stylet figures on plates 2-4.

Form II stylets are less distinctive and the seminal receptacles are in some species confusingly similar. It is for the identification of form II males and females that the key will be most useful. Reference may then be made to the appropriate figures on plates 2-5.

The identification of immature specimens should not be attempted by the nonspecialist. Shapes of various structures, particularly the

rostrum and hand, are different in immature and in mature individuals. The key has not been designed to include immatures. The minimal known carapace lengths of sexually mature individuals are listed in table 2. Because some immature individuals are known to exceed these values, it would be well to add one or two millimeters to each value and to key no specimens smaller than this.

TABLE 2

Minimal carapace lengths in mm. of sexually mature crayfishes in New York

	MALE	FEMALE
Procambarus b. blandingi	31-32(?)	31-32(?)
Orconectes immunis	23.2	23.0
Orconectes virilis	probably similar to *O. immunis*	
Orconectes limosus	23.5 (approx. 19 mm. in Penna.; Ortmann, 1906:477)	22.5
Orconectes p. propinquus	16.2	16.5
Orconectes obscurus	19.9	23.1 (approx. 20 mm. in Penna.; Ortmann, 1906:471)
Cambarus b. bartoni	18.5	(approx. 24 mm. in N. J.; Ortmann, 1906:486)
Cambarus robustus	31.7	31.2

The ratio, length of areola / width of areola, used in the first pair of alternatives (*A* and *AA*) in the key, is based on measurements of the few mature New York specimens of *O. virilis* and *P. b. blandingi* in my personal collections or in NYSM 6976 (stream survey collections). Of the other six species, 30 specimens each were measured (half males and half females). The critical figure (9.6) is the mean of two values: (1) the smallest ratio (11.4) obtained for the three species in the first division of the key, *A*; (2) the largest ratio (7.9) obtained for the five species in the second division, *AA*. The measurement of areola width cannot be made with dividers with sufficient accuracy. It must be made under magnification with an ocular micrometer, or better, with a camera lucida, marking the limits of the narrowest part of the areola on paper and dividing the measurement of this by the power of magnification.

A. The ratio, length of areola/width of areola, greater than 9.6; a narrow areola usually permitting no more than two punctations to occur side-by-side in its narrowest portion.

B. Carapace covered with tubercles of such height that the surface feels definitely granular.
. . . . . *Procambarus b. blandingi.*

BB. Surface of carapace smooth except for low tubercles on lateral surfaces of anterior portion and except for setae.

C. Movable finger (dactyl) of hand with a notch at its base on the inner side. . . . . *Orconectes immunis*

CC. Inner side of movable finger of hand straight.
. . . . . *Orconectes virilis*

AA. The ratio of length to width of areola, less than 9.6; areola relatively broad, permitting at least three punctations to occur in a horizontal row in its narrowest portion.

B. Rostrum with spines (often only tubercles in large specimens) at base of acumen.

C. Lateral surface of carapace ahead of cervical groove with two or more sharp spines.
. . . . . *Orconectes limosus*

CC. Lateral surface of carapace ahead of cervical groove with tubercles only.

D. Rostrum usually with a distinct median carina. Distal margin of ventral surface of carpus of chela usually without either spine or tubercle. . . . . *Orconectes p. propinquus*

DD. Rostrum usually without median carina. Distal margin of ventral surface of carpus of chela with tubercle and usually a spine. . . . . *Orconectes obscurus*

BB. Margins of rostrum not interrupted by spines.

C. Inner margin of palm with a single row of low tubercles; hand inflated, without conspicuous depression near outer margin (plate 1, figure 6). Rostrum tapering acutely to its tip (plate 1, figure 2). Areola with relatively few large punctations, tending to fall into three cephalocaudal rows (plate 1, figure 3). Carapace without lateral spines. Inner border of antennal scale usually directed rather abruptly caudad (plate 1, figure 2).
. . . . . *Cambarus b. bartoni*

CC. Inner margin of palm with two rows of low tubercles; hand with depression, visible both from the dorsal and ventral sides, near its outer margin (plate 1, figure 5). Rostrum tapering less abruptly to its tip (plate 1, figure 1). Areola with smaller more numerous punctations which do not tend toward an arrangement in three rows (plate 1, figure 4). Carapace often with lateral spines. Inner border of antennal scale usually directed mesiad before turning caudad (plate 1, figure 1). . . . . *Cambarus robustus*

PLATE 1

Illustrations of structures used to distinguish between *Cambarus b. bartoni* and *Cambarus robustus.*

Cambarus b. bartoni, male I; carapace length 33.5 mm.; DWC 59; N. Y., Tompkins County, Buttermilk Creek at outlet of Treman Lake; coll. by DWC, Sept. 17, 1950. A copulatory stylet of this specimen is drawn on plate 2, figure 5.

Figure 2. Dorsal view of head region showing rostrum, eye and antennal scale

Figure 3. Areola, showing punctations

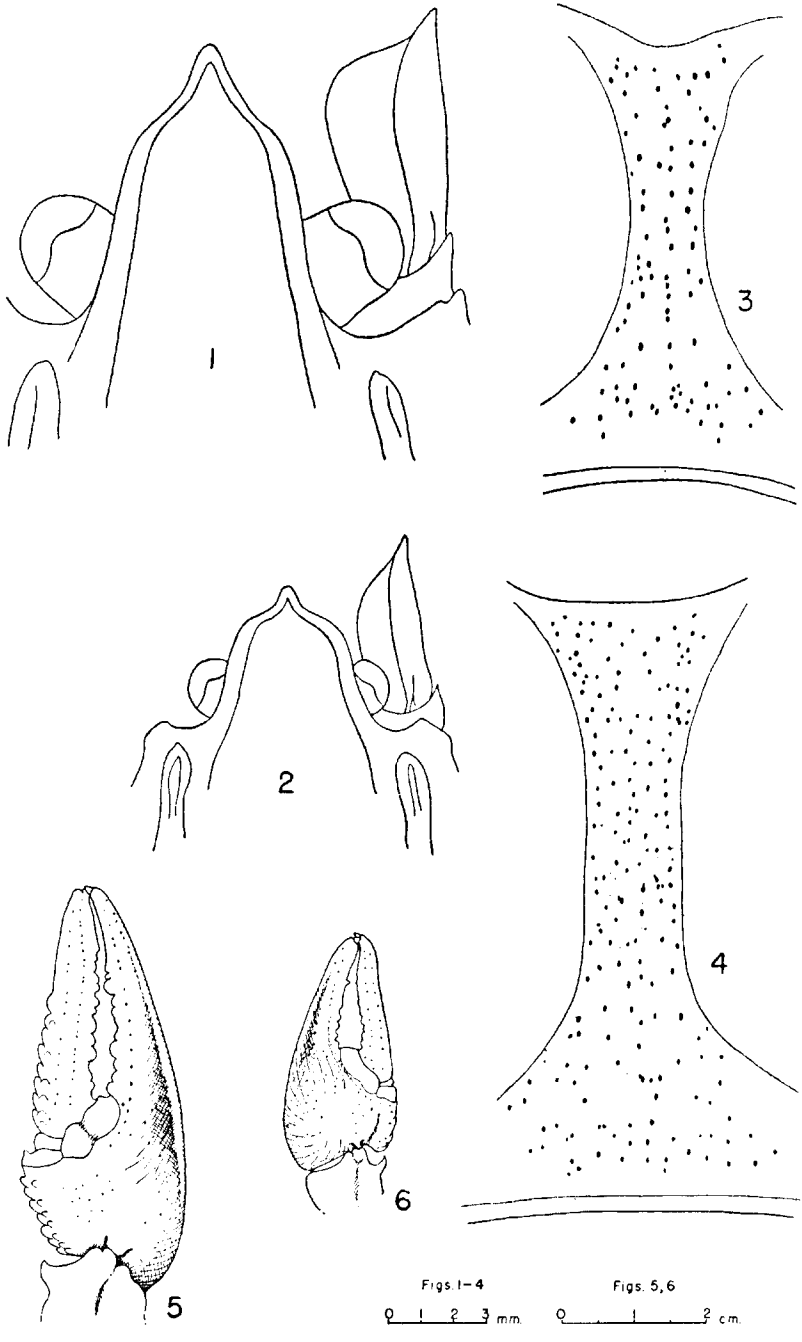
Figure 6. Dorsal view of hand and fingers of left chela

Cambarus robustus, male I; carapace length 50.0 mm.; DWC 12; N. Y., Schuyler County, tributary of Taughannock Creek, 1.4 miles N. W. of Perry City; coll. by R. D. Suttkus, Oct. 8, 1949.

Figure 1. Dorsal view of head region showing rostrum, eye and antennal scale

Figure 4. Areola, showing punctations

Figure 5. Dorsal view of hand and fingers of right chela


1
2
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Figs. 1–4
0 1 2 3 mm.
Figs. 5, 6
0 1 2 cm.

PLATE 2

Copulatory stylets and seminal receptacles of *Cambarus b. bartoni* and *Cambarus robustus*.

Figures 1-4. *Cambarus robustus;* DWC 91; N. Y., Oswego County, Oswego River drainage, Scriba Brook (a tributary of Oneida Lake) at N. Y. State Fish Hatchery dam at Constantia; coll. by R. L. Wigley, May 6, 1951.

Figure 1. Stylet of male I; carapace length 41.5 mm. A photograph of this specimen appears in the frontispiece.

Figure 2. Stylet of male II; carapace length 38.7 mm.

Figure 3. Right-handed seminal receptacle of female; carapace length 41.0 mm.

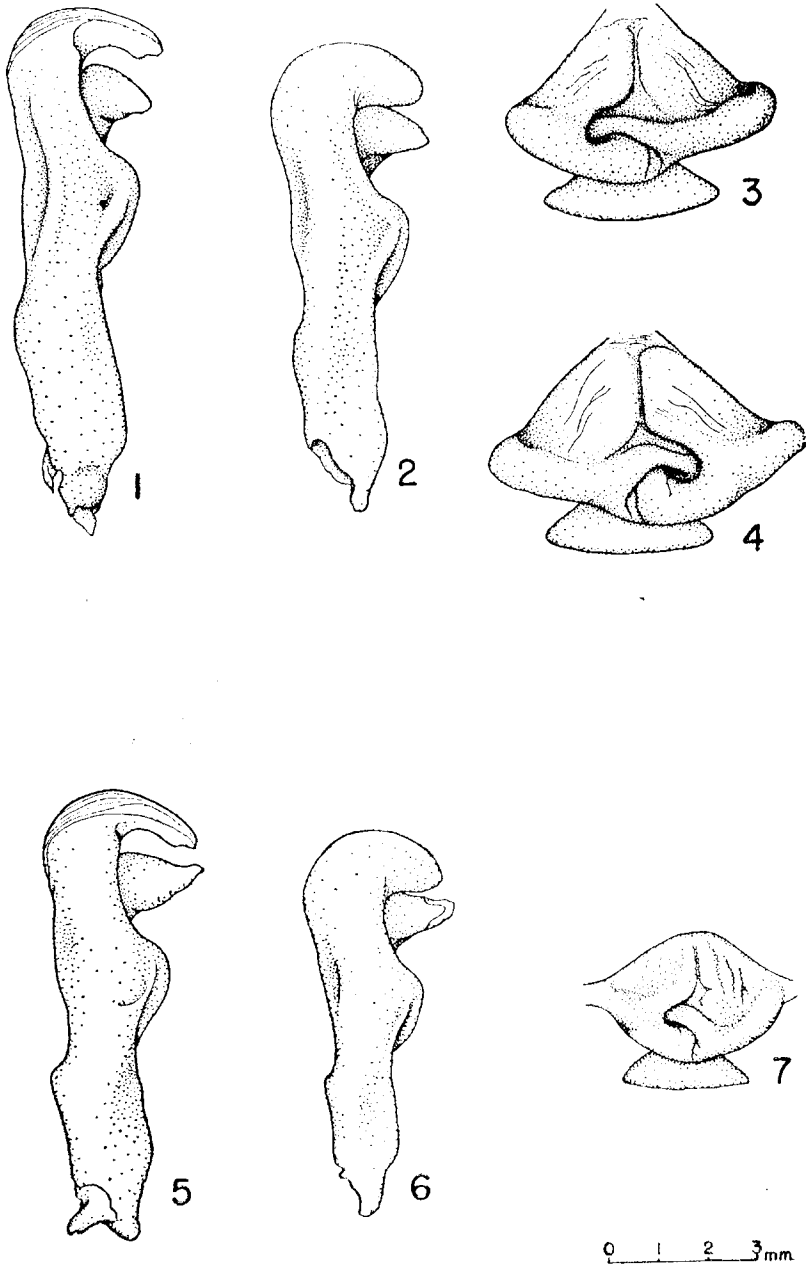
Figure 4. Left-handed seminal receptacle of female; carapace length 41.8 mm.

Figure 5. *Cambarus b. bartoni,* stylet of male I; carapace length 33.5 mm.; DWC 59; N. Y., Tompkins County, Buttermilk Creek at outlet of Treman Lake; coll. by DWC, Sept. 17, 1950. Figures 2, 3 and 6 on plate 1 are drawn from this same specimen.

Figure 6. Same, stylet of male II; carapace length 30.0 mm.; DWC 28; N. Y., Tompkins County, Oswego R. drainage, Fishkill Creek in Robert Treman State Park at Enfield; coll. by DWC, June 5, 1950.

Figure 7. Same, seminal receptacle of female; carapace length 31.7 mm.; DWC 77; same locality as figure 5; coll. by DWC, April 22, 1951.

All stylets are right stylets seen in lateral view.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6
7
0 1 2 3mm

PLATE 3

Copulatory stylets of three New York species of *Orconectes.*

Figure 1. *Orconectes p. propinquus,* male I; carapace length 36.5 mm.; DWC 108; N. Y., Herkimer County, Black River drainage, outlet of Fulton chain of lakes at town of Old Forge; coll. by DWC and J. A. Gustafson, May 19, 1951.

Figure 2. Same, male II; carapace length 27.7 mm.; DWC 33; N. Y., Tompkins County, Oswego River drainage, Fall Creek at McLean; coll. by DWC, June 21, 1950.

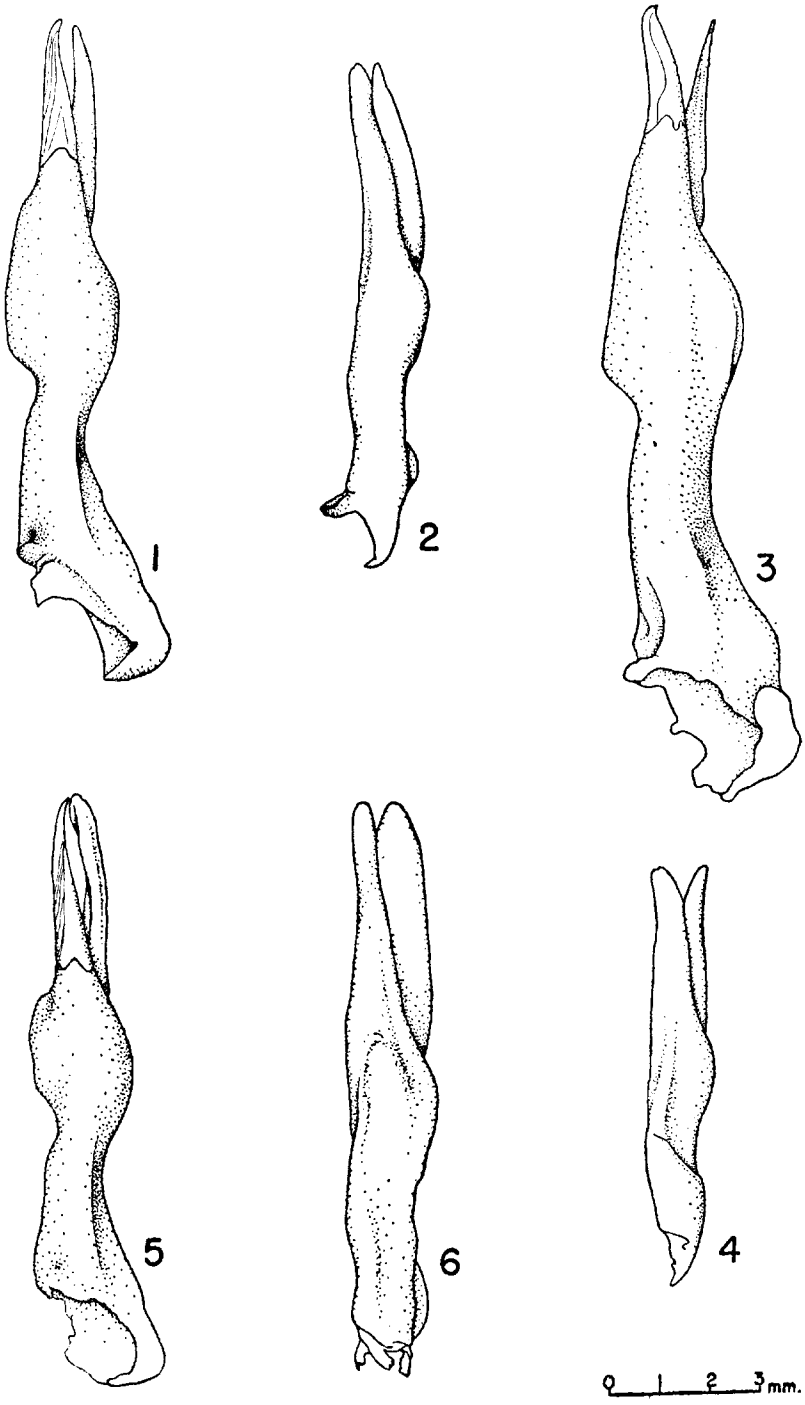
Figure 3. *Orconectes limosus,* male I; carapace length 43.5 mm.; DWC 20; N. Y., Ulster County, Hudson River drainage, Esopus Creek near W. city limits of Kingston; coll. by Theodore Weyhe, Feb. 18, 1950.

Figure 4. Same, male II; carapace length 27.4 mm.; DWC 132; N. Y., Columbia County, Hudson River drainage, Kinderhook Creek between Valatie and Kinderhook; coll. by J. A. Gustafson and Earl Deubler, Jr., June 1, 1951.

Figure 5. *Orconectes obscurus,* male I; carapace length 32.0 mm.; DWC 94; N. Y., Cattaraugus County, tributary of Allegheny River, 5.4 miles W. of town of Allegheny; coll. by C. R. Robins, May 12, 1951.

Figure 6. Same, male II; carapace length 36.6 mm.; DWC 140; N. Y., Chautauqua County, Allegheny River drainage, W. branch of French Creek, 1 mile N. of town of Findley Lake; coll. by John G. New, June 15, 1951.

All are right stylets seen in lateral view. A photograph of the specimen from which the stylet shown in figure 1 was taken appears in the frontispiece along with a photograph of a form I male of *O. limosus* (carapace length 44.7 mm.) from the same collection as figure 3.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0 1 2 3 mm.

PLATE 4

Copulatory stylets of two *Orconectes* species and of *Procambarus b. blandingi.*

Figure 1. *Orconectes virilis,* male I; carapace length 43.9 mm.; DWC 170; N. Y., Saratoga County, Hudson River drainage, stream (probably Kayaderosseras Creek) at bridge on U. S. Route 9, 2.3 miles S. of city limits of Saratoga Springs; coll. by DWC, Aug. 19, 1952.

Figure 2. Same, male II; carapace length 36.5 mm.; same collection as figure 1.

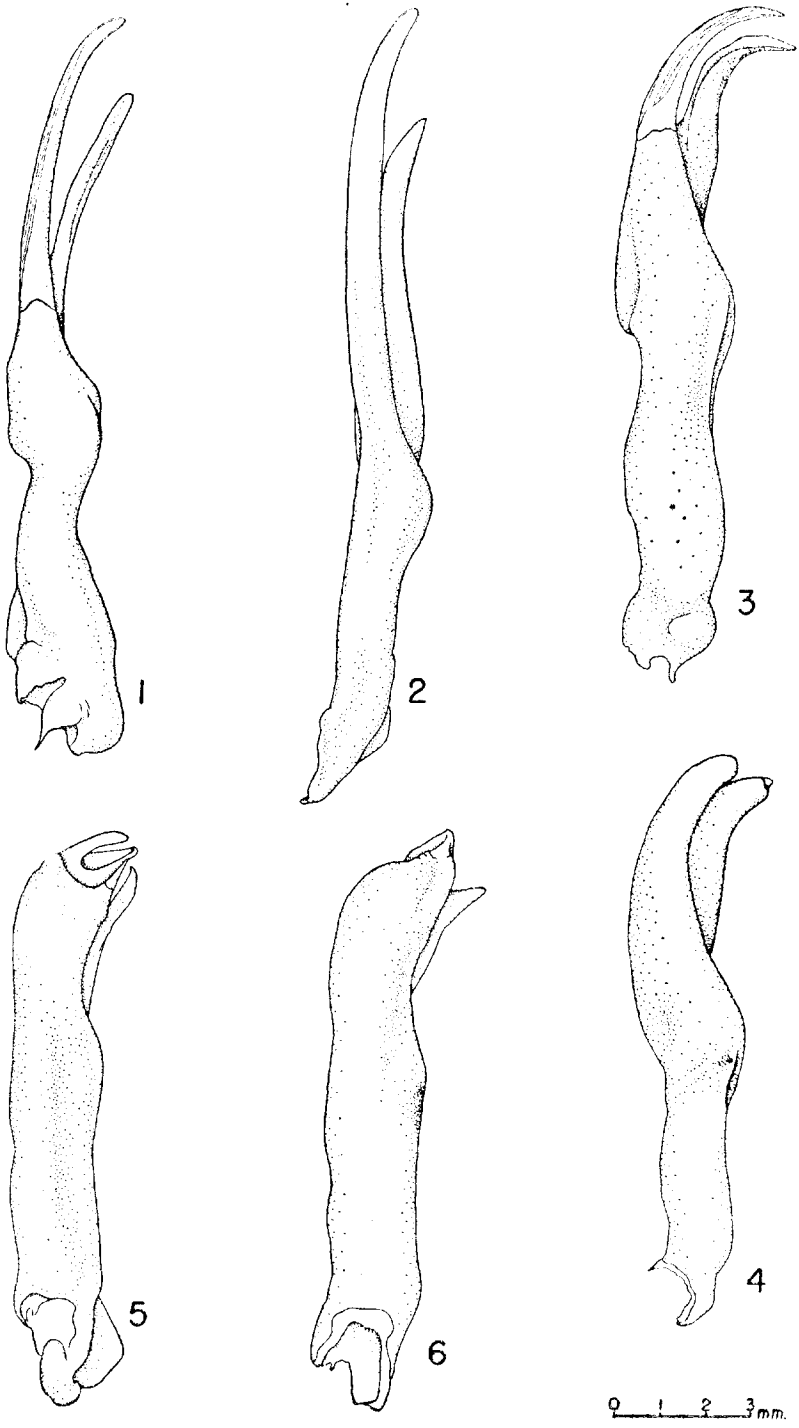
Figure 3. *Orconectes immunis,* male I; carapace length 36.8 mm.; DWC 75*b*; N. Y., Tompkins County, Oswego River drainage, ponds at Cornell University Experimental Fish Hatchery; coll. by Milton Potash and L. C. Cole, April 13, 1951.

Figure 4. Same, male II; carapace length 38.2 mm.; DWC 138; N. Y., Cayuga County, Oswego River drainage, Duck Lake outlet at town of Spring Lake; coll. by E. C. Raney, May 20, 1951.

Figure 5. *Procambarus b. blandingi,* male I; carapace length 42.8 mm.; DWC 173; N. Y., Westchester County, Bronx River at White Plains North Railroad Station; coll. by DWC, Aug. 25, 1952.

Figure 6. Same, male II; carapace length 45.5 mm.; same collection as figure 5.

All are right stylets seen in lateral view. Photographs of the specimens from which the form I stylets were taken appear in the frontispiece.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0 1 2 3mm.

PLATE 5

Seminal receptacles of the New York species of *Orconectes* and *Procambarus*.

Figure 1. *Orconectes p. propinquus;* carapace length 35.6 mm.; DWC 108; N. Y., Herkimer County, Black River drainage, outlet of Fulton chain of lakes at town of Old Forge; coll. by DWC and J. A. Gustafson, May 19, 1951.

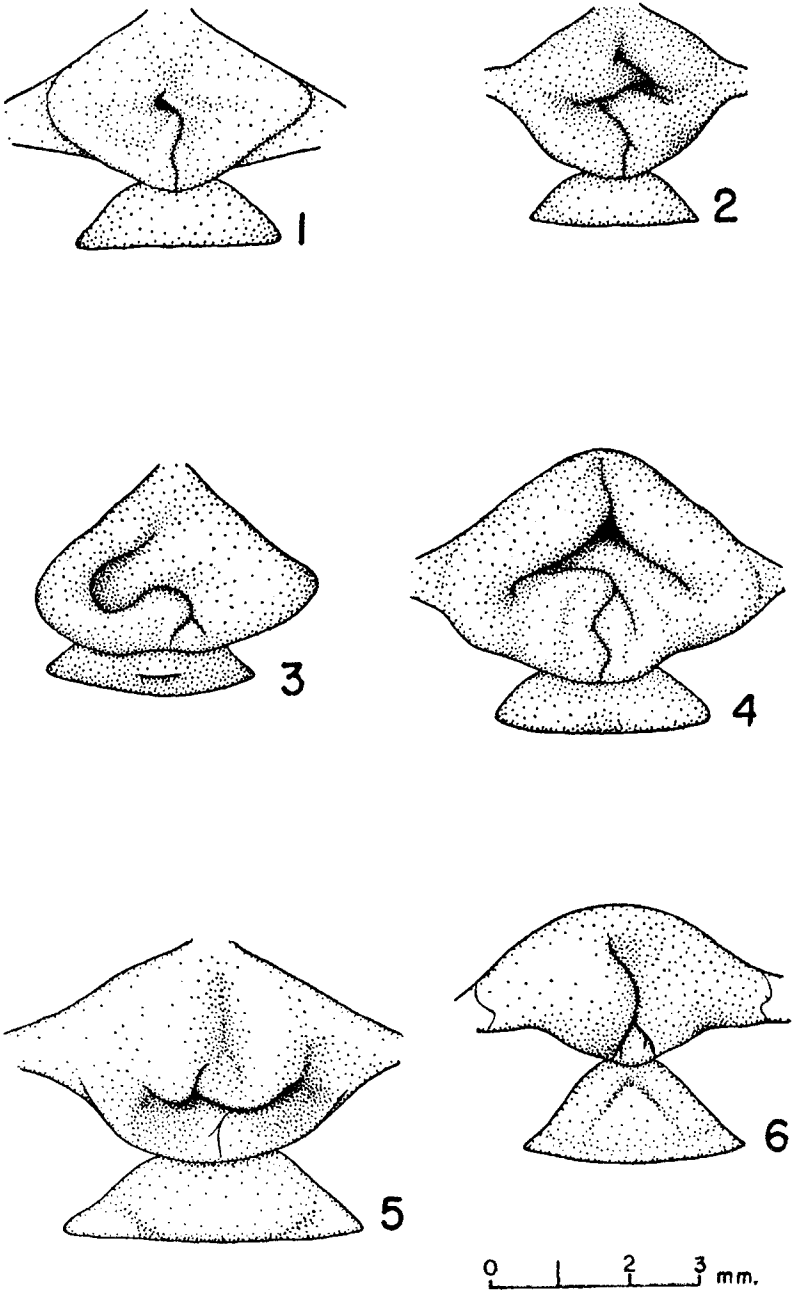
Figure 2. *Orconectes obscurus;* carapace length 28.3 mm.; DWC 140; N. Y., Chautauqua County, Allegheny River drainage, W. branch of French Creek, 1 mile N. of town of Findley Lake; coll. by John G. New, June 15, 1951.

Figure 3. *Orconectes immunis;* carapace length 39.5 mm.; DWC 72 (specimen no. 15); N. Y., Tompkins County, Oswego River drainage, ditch tributary to Cayuga Inlet in Ithaca; coll. by H. Evans and R. D. Suttkus, July 17, 1950.

Figure 4. *Orconectes virilis;* carapace length 38.1 mm.; DWC 170; N. Y., Saratoga County, Hudson River drainage, stream (probably Kayaderosseras Creek) at bridge on U. S. Route 9, 2.3 miles S. of city limits of Saratoga Springs; coll. by DWC, August 19, 1952.

Figure 5. *Orconectes limosus;* carapace length 45.1 mm.; DWC 20; N. Y., Ulster County, Hudson River drainage, Esopus Creek near W. city limits of Kingston; coll. by Theodore Weyhe, Feb. 18, 1950.

Figure 6. *Procambarus b. blandingi;* carapace length 44.6 mm.; DWC 173; N. Y., Westchester County, Bronx River at White Plains North Railroad Station; coll. by DWC, Aug. 25, 1952.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mm.

DESCRIPTIONS

Procambarus blandingi blandingi (Harlan)

(FRONTISPIECE; PLATE 4, FIGURES 5 AND 6; PLATE 5, FIGURE 6)

Astacus blandingi Harlan, 1830: 464-465.
Astacus (Cambarus) blandingi Harlan. Erichson 1846: 98, 99.
Cambarus blandingi Harlan. Hagen 1870: 43-45; pl. I, figs. 63 and 64; pl. III, figs. 140*a*, *b* and *c*.
Cambarus acutus Girard var. B. Hagen, 1870: 36, 37, 39; pl. III, figs. 144*a*, *b* and *c*.
Cambarus acutus Girard. Abbott 1873: 80-84.
Cambarus (Cambarus) blandingi (Harlan). Ortmann 1905*a*: 96-97.
Cambarus (Ortmannicus) blandingi (Harlan). Fowler 1912: 340, 341, pls. 106, 107.
Cambarus blandingi acutus Harlan (in part). Faxon 1914: 367.
Procambarus blandingi blandingi (Harlan). Hobbs 1942*a*: 341, 342.
(not) *Cambarus blandingi* (Harlan). Girard 1852: 91 (authority of Hagen 1870: 45).

Taxonomic remarks: The record of *C. b. acutus* from Fulton County, Md. (Faxon 1914: 367) should be referred to *P. b. blandingi* on the basis of the locality. Hagen (1870: 45) believes that the record of *C. blandingi* from Summerville, S. C., given by Girard (1852: 91), is *C. troglodytes* (=*Procambarus troglodytes*). Harlan (1835) repeats his original description and provides a figure.

It has been pointed out by Hobbs (1942*b*: 94) that many of the references to this species in the literature are unreliable and that the *blandingi* complex is in need of considerable work before the relationships among the various taxonomic forms are clearly understood.

Type: "Acad. Nat. Sci. Philad. (1 male)." Faxon (1914: 413).

Type locality: "Marshes and rivulets, Southern United States [Camden, Kershaw Co., S. C.?]." Faxon (1914: 413). Square brackets are Faxon's.

DESCRIPTION

By touch alone the tuberculated surface of the carapace separates this crayfish from the other New York species.

Male I. The following description is based on the only form I male in NYSM 1936: 3576, from New York, Westchester County, East River drainage, Bronx River. For terminology and method of taking measurements see Hobbs (1942*b*: 24, text figure b). The description is designed so that comparisons may be made between these specimens and the excellent descriptions of the holotype and

paratypes of *P. b. cuevachicae* (Hobbs 1941: 1-4). Because *P. b. blandingi* has not been adequately described, the following description is given in detail:

Carapace evenly tuberculated except on dorsal surface of anterior portion (ahead of cervical groove) where tubercles are lacking. Postorbital tubercles directed somewhat laterad which, together with the mesially directed bases of the postorbital ridges, present a lyre-shaped figure. Areola narrow, bearing a single row of punctations in its narrowest portion. Single, small lateral spine on each side of carapace.

Rostrum elongate and concave, lateral margins sharp. Broad at base, margins slightly convex just distad of base, tapering gradually to a short, but not broad, acumen. Small spines at base of acumen. Margins of acumen densely setose. Rostral surface sparsely punctate at base, non-setose except for a row of setae just inside lateral margins.

Antennal scale bearing a small spine at distal end of lateral border. Very short anterior margin, bending at about a 45-degree angle to form the antero-mesial border which in turn bends near the antero-posterior midpoint of the scale to form a postero-mesial border. The antero-mesial and postero-mesial borders are about equal in length.

Epistome sagittiform, margins slightly elevated, lacking tubercle on median cephalic border, slight depression in midline at base.

Flagellum of right **antenna** reaches to midway on posterior section of telson. Distal third hairlike in thinness.

Right **chela** long and relatively slender. Dorsal and ventral surfaces of propus with few low tubercles. These increase in number and slightly in diameter, but not in height, toward the outer margin. The row of low tubercles on the outer margin is transformed gradually into a row of setiferous punctations on the immovable finger. Toward the inner margin there is a similar increase in number and diameter and a great increase in height. The highest form a row of seven on the exact mesial margin.

Immovable finger (of propus) of right chela with a shallow longitudinal furrow on both dorsal and ventral sides running laterad of the midline and bearing setiferous punctations. A row of 15 tubercles extends from the base of the immovable finger to slightly less than halfway from the tip. This row is situated slightly dorsad of the mesial border. The third tubercle (from the base) is much larger than the others. Slightly ventrad of the mesial border in the distal third of the immovable finger is a row of three tubercles, the most distal being largest. When the fingers are apposed, the proximal enlarged tubercle lies on the dorsal side of the movable finger and the distal enlarged tubercle on the ventral side.

Movable finger (dactyl) of right chela sigmoid, bearing tubercles on basal third, the largest three form a row on the lateral margin. Just dorsal and just ventral to the mesial border is a row of tubercles, the dorsal row containing 21, the ventral row 9. The second tubercle in the ventral row is conspicuously enlarged. The meeting surfaces of both the movable and immovable fingers are flattened and bear, particularly on their distal halves, a dense pile of flattened, bladelike setae.

Carpus of right chela lacking tubercles on lateral border and on lateral halves of dorsal and ventral surfaces except for a single tubercle at a peak of the distal edge on the ventral side about midway between the midline and the lateral margin. Of the tubercles on the remaining surfaces, the two largest are situated, one on the distal edge on the ventral side at the midline, the other on the mesial surface. A shallow, slightly arcuate furrow is present on the dorsal side.

Merus of right chela with mesial and lateral surfaces free of tubercles except on the distal third of the mesial side where they are weakly developed. On the narrow dorsal surface there are 18 tubercles arranged in a single row proximally, but tending toward two rows in the distal half. On the slightly wider ventral surface are two tubercle rows, one mesial and one lateral, with 22 somewhat irregularly aligned tubercles in the former and 14 in the latter. Three small tubercles on the ventral side diverge from the lateral row and follow proximally the lateral arm of the U-shaped distal edge. The end of the arm possesses a well-developed tubercle with a corneous tip.

Anterior section of **telson** with each postero-lateral corner ending in a spine. A second spine occurs on each side mesiad of the corner spine.

Copulatory stylets terminating in four distinct elements (see plate 4, figure 5 drawn from a different specimen), reaching a point just cephalad of caudal border of coxae of third pereiopods when the abdomen is flexed. The cephalic process, central projection and caudal process are corneous. Mesial process not so. All elements are gently curved so that the tips are directed laterad. A conspicuous knob at the base of the cephalic process bears a dense cluster of long setae.

Hooks on ischia of third and fourth pereiopods. Coxae of fourth pereiopods bearing a large, slightly compressed knoblike protuberance.

Measurements: The following measurements in mm. were made on the form I male described above:

Carapace, greatest height – 20.6; greatest width – 22.8; total length – 47.5; length of cephalic section – 31.3
Areola length – 17.1; width – 1.4
Rostrum, width at base – 7.6; length – 11.9
Abdomen length – 42.9

Right chela, length of inner margin of palm – 18.4; width of palm – 14.8; length of outer margin of hand – 51.1; length of movable finger – 29.5

Male II. Plate 4, figure 6 shows a form II stylet from DWC 173 (Bronx River). As compared with the form I stylets, the four terminal elements are not corneous and are shorter, more rounded and softer.

Female. This description is based on the only female in USNM 74,747, from New York, Westchester County, East River drainage, Bronx River. Similar to male I, but chelae proportionately much smaller and less elongate; tubercle count different. Fingers with only a single row of tubercles on the opposable margin of each. Movable finger of hand with conspicuous notch at base of mesial border.

Seminal receptacle (see plate 5, figure 6 drawn from a different specimen) subovate with three tubercles; left, right and caudal. Right tubercle much higher than the other two and curved to the left, creating a deep fossa. Left tubercle gives rise to a ridge which runs to the right on the floor of the fossa and which is largely hidden from view by the overhang of the right tubercle. At the caudal border the sinus originates to left of caudal tubercle. It curves to the right following the caudal edge of the above mentioned ridge and disappears under the overhang of the right tubercle. I am not able to detect its reappearance at the cephalic border of the receptacle. It is very different from the figure given by Hobbs (1941: 3, text fig. 1*G*) for *P. b. cuevachicae*; more similar to, but still different from the figures given by Turner (1926: 195, pl. xx, fig. 25) and Pearse (1910: pl. I, fig. *B*) for *P. b. acutus*.

Orconectes virilis (Hagen)

(Frontispiece; plate 4, figures 1 and 2; plate 5, figure 4)

Cambarus virilis Hagen, 1870: 63-65.
Cambarus debilis Bundy, 1876: 24 (authority of Faxon 1885*b*: 97).
Cambarus couesi Streets, 1877: 803 (authority of Faxon 1885*b*: 97).
Cambarus (Faxonius) virilis Hagen. Ortmann 1905*a*: 107.
Orconectes virilis (Hagen). Hobbs 1942*a*: 352.

Types: "*Types*, M. C. Z., No. 1,151; *paratypes*, M. C. Z., Nos. 194 and 203 (Lake Superior), No. 196 (Quincy, Ill.), No. 3,342 (Lake Winnipeg), No. 3,343 (Red River of the North), No. 3,344 (Saskatchewan River); Mus. Hist. Nat. Paris (Lake Superior); Wurzburg Mus. (Lake Superior); Australian Mus., Sydney." Faxon (1914: 420). I have examined the types and the MCZ paratypes.

Type locality: Lake Superior; designation by Faxon (1914: 420).

Description

The best description of this species is that given by its author, Hagen (1870: 63-64). Because I have seen so few specimens from New York (tables 16, 17 and 18), no account of the extent of its variation can be given.

It is readily separated from *Orconectes immunis*, the crayfish which in New York is most similar to it, by the presence in *O. immunis* of a notch at the inner base of the movable finger. The rostral shape is also different, *O virilis* having straighter sides, a longer acumen and a more shallow excavation in the middle than has *O. immunis*. The shapes of first form stylets should readily separate these two species (plate 4, figures 1 and 3). The male I stylets in *O. virilis* reach just to the caudal border of the bases of the chelae when the abdomen is flexed, while those of *O. immunis* reach only to a point just cephalad of the caudal border of the second pereiopods.

The male II stylets (plate 4, figures 2 and 4) and the seminal receptacles (plate 5, figures 3 and 4) are also different, but less obviously so.

Orconectes immunis (Hagen)

(Frontispiece; plate 4, figures 3 and 4; plate 5, figure 3)

Cambarus immunis Hagen, 1870: 71-73 (in part only, authority of Faxon 1885*b*: 100).
Cambarus signifer Herrick, 1882: 253 (authority of Faxon 1885*b*: 99).
Cambarus immunis spinirostris Faxon, 1885*a*: 146.
Cambarus (*Faxonius*) *immunis* Hagen, Ortmann 1905*a*: 113.
Faxonius immunis immunis (Hagen), Creaser 1933*a*: 13.
Faxonius immunis pedianus Creaser, 1933*a*: 14-16.
Orconectes immunis immunis (Hagen), Hobbs 1942*a*: 352.

Types: "*Types*, M. C. Z., No. 188; *paratypes*, M. C. Z., No. 3,355 (Belleville, Saint Clair Co., Ill.); Mus. Hist. Nat. Paris (Lawn Ridge, Ill., 1 male)." Faxon (1914: 421).

Type locality: Lawn Ridge, Illinois; designated by Faxon (1914: 421).

Taxonomic remarks: I agree with Creaser (1931: 262 and 1933*a*: 13-14) and Ortmann (1931: 93, 94) that *C. i. spinirostris* is but a variant form. See also Rhoades (1944*a*: 132, 133). Williams and Leonard (1952: 1003-1005) present data which indicate that Creaser's *O. i. pedianus* is but one extreme of a clinal variation.

Description

O. immunis is a pond crayfish which is often called the "grass-crab" or "butter-crab" by bait dealers and fishermen. The latter name may be due to its smooth surface which is often slippery, particularly in newly moulted specimens.

The most detailed description of this species is the one given by its author (Hagen 1870: 71-73). The characters which separate it from *O. virilis*, the only New York species likely to be confused with it, are given under the description of *O. virilis*.

Orconectes propinquus propinquus (Girard)

(Frontispiece; plate 3, figures 1 and 2; plate 5, figure 1)

Cambarus propinquus Girard, 1852: 88.
Cambarus (Faxonius) propinquus Girard. Ortmann 1905*a*: 107.
Faxonius propinquus (Girard). Creaser 1933*b*: 4.
Orconectes propinquus propinquus (Girard). Hobbs 1942*a*: 352.

Types: Hagen, in preparing his monograph, borrowed what he called Girard's "types" from William Stimpson (Hagen 1870: 7), and gave figures in his monograph of the first and second form copulatory stylets. It is to be remembered, however, that in 1870 the word "types" did not necessarily have the connotations which it has today. The word merely meant specimens identified by some student of the group, the specimens then being called that person's types of a given species. Whether or not Hagen saw specimens of *O. p. propinquus* which came from a locality listed by Girard, which were used by Girard in writing his original description and which we would now call strictly Girard's types, cannot be known. Hagen does not give localities for the specimens figured.

It is generally believed that Hagen returned the specimens to Stimpson and that they, along with the majority of Girard's material from which a neoholotype might be selected, were destroyed in the great Chicago fire of 1871 (Faxon 1914: 417). At least, at present they cannot be located.

There is a specimen of *O. p. propinquus* in the Academy of Natural Sciences of Philadelphia which has Girard's name on the label followed, however, by a question mark (Hagen 1870: 7; Faxon 1914: 417). This specimen is from Garrison Creek, Sackett's Harbor, N. Y., a locality given by Girard. In view of the fact that Girard's name is followed by a query, that there is a single specimen and that the identity of Garrison Creek is not certain (see below), this is probably not suitable material from which to select a type. Apparently, there are no specimens now in existence of *O. p. propinquus*, which are known with certainty to have been identified as such by Girard, nor have new types been selected.

Type locality: The following three localities are given by Girard (1852:88):

1. "Lake Ontario, four miles from the shore, opposite to Oswego [Oswego Co., N. Y.], found in the stomach of Lota maculosa."
2. "Garrison Creek, Sacketts Harbor [Jefferson Co., N. Y.]."
3. "Four Mile Creek, Oswego [Oswego Co., N. Y.]."

The first locality is listed (as Oswego, Oswego County, N. Y.) as type locality by Ortmann (1906: 363) without selection of new types.

The second locality is given (again without a selection of new type specimens) as the type locality by Faxon (1914: 417) along with locality number 3. After consulting numerous old maps, county histories and gazetteers of Jefferson County, N. Y., I am unable to locate Garrison Creek. It is probable that the stream intended is the one known to the inhabitants of Sacketts Harbor and in the literature as Mill Creek. There is a garrison (Madison Barracks) at its mouth. It is not possible at present, however, to demonstrate conclusively that the two stream names are synonymous.

I have not visited Four Mile Creek nor do I know of existing collections from it. It appears that the first locality as listed by Ortmann is the type locality. This subspecies is described in a comparison between it and *O. obscurus* (given under *O. obscurus*). Hybridization of *O. p. propinquus* is discussed under that heading as a separate section of the study.

Orconectes obscurus (Hagen)

(PLATE 3, FIGURES 5 AND 6; PLATE 5, FIGURE 2)

Cambarus obscurus Hagen, 1870: 69, 70.
Cambarus propinquus var. *obscura* Hagen. Faxon 1885*b*: 92-94.
Cambarus obscurus Hagen. Faxon 1898: 652.
Cambarus (Faxonius) obscurus Hagen. Ortmann 1905*a*: 107.
Orconectes obscurus (Hagen). Hobbs 1942*a*: 352.
Cambarus propinquus Girard. Williamson 1901: 13 (authority of Ortmann 1905*b*: 387, 388).
Cambarus rusticus Girard. Williamson 1901: 13 (authority of Ortmann 1905*b*: 387, 388).

Types: "*Cotypes*, M. C. Z. No. 181, 3,353, 3,354; U. S. N. M. No. 4,971; Mus. Hist. Nat. Paris; Wurzburg Mus.; Australian Mus., Sydney." Subsequent designation by Faxon (1914: 418). I have examined the cotypes in MCZ and USNM.

Type locality: Genessee River, Rochester, Monroe County, N. Y. (Hagen 1870: 70).

DESCRIPTIONS OF *Orconectes p. propinquus* AND *O. obscurus*

Ortmann (1906: 358-362, 365-372) has given detailed descriptions for these two species in Pennsylvania and, because my materials are similar, the descriptions here will be limited to pointing out differences between New York State and Pennsylvania populations. These two species are so close morphologically that comparisons between them will be made wherever there appear to be differences.

The possibility of assigning all specimens to one or the other of these two species is probably limited to localities where they do not occur together for, as discussed under a separate heading below,

hybridization appears to occur between them. None of the discussion of these two species under the present heading of "Descriptions" applies to localities where they occur together (figure 5).

Ortmann found the majority of morphological features to be almost identical in these two species. It is in the features which he found best to show differences that my materials appear to vary from Ortmann's. These features are:

1. Presence or absence of a median keel (carina) on the rostrum
2. Armature of carpus of chela
3. Armature of merus of chela
4. Shape of seminal receptacle
5. Shape of copulatory stylets

Rostral carina. Of the rostrum in *O. p. propinquus*, Ortmann (p. 359) says, "Surface concave, with a more or less distinct, low, longitudinal median keel toward the tip." Of *O. obscurus*, he says (p. 369), "Rostrum similar to that of *C. propinquus*, but always without any trace of a median keel." In New York *O. p. propinquus*, the median carina is indeed usually distinct, but some mature or immature specimens in most large collections show hardly a trace of it and it is only by having the rostrum thoroughly dry and the light source properly directed that it can be made out.

Furthermore, occasional specimens of *O. obscurus*, from widely separated localities, show a relatively broad, slightly raised region in the midline of the rostrum, and considering rostrum alone, they could hardly be separated from specimens of *O. p. propinquus* showing minimal development of the carina. Five of 12 specimens of *O. obscurus* on loan from Dr. H. H. Hobbs, Jr., which were taken in Pendleton County, W. V. (Hobbs' collection 7-3149-3*a*) show a distinct although small median rostral carina.

Presence or absence of rostral carina can not be used as a character for completely separating these two species, even though it will correctly assign to species the majority of individuals.

Armature of carpus of chela. Of the carpus of the chela of *O. p. propinquus* Ortmann (p. 360) says, "Lower surface with a low and broad tubercle in the middle of the anterior margin, which is very rarely subspiniform. . ." Again (p. 364) he says, "The anterior margin is often without any spine, or even tubercle; there is, however, a low tubercle developed in many cases, and in two cases it was spiniform. . ." Of *O. obscurus* he says (p. 370), "The *carpopodite* differs from that of *C. propinquus* in the development of a strong tubercle on the anterior margin of the lower side. This tubercle very rarely

is indistinct (chiefly so in regenerated claws); generally it ends in a distinct, stout, conical spine."

New York *O. obscurus* conform with Ortmann's description given above. In *O. p. propinquus,* however, I have several specimens from widely separated localities, with well-developed spines on the lower distal border of the carpus of each chela and a number of others with spines less well developed, often occurring unilaterally. All degrees of development of the tubercle occur, from none at all to one quite distinct. By far the greatest proportion of specimens, however, have no tubercle or one which is at best barely perceptible.

Of these two species, data on hand show that if a specimen has no tubercle or spine on the lower distal border of the carpus, it is *O. p. propinquus.* The presence of a tubercle, however, does not indicate that the specimen is *O. obscurus.* The character will not give complete separation of these species.

Armature of merus of chela. Of the spines on the lower side of the merus in *O. p. propinquus,* Ortmann (p. 364) says that they are generally represented by only two spines, the distal spine of each row being alone present. He then points out his only localities where additional spines occur.

Of *O. obscurus* Ortmann (p. 370) says, "The *meropodite* differs from that of *C. propinquus* by the constant presence of a series of 4-8 small tubercles, or teeth, behind the distal spine on the inner lower margin. These teeth are never wanting in any of my specimens. The outer lower margin has one or two spines. The lat[t]er number is comparatively rare."

New York *O. obscurus* agree with those of Ortmann. In *O. p. propinquus* however, specimens with a distinct row of low spines on the inner lower margin far outnumber those which show only the single distal-most spine. All degrees of variation occur even in single large collections. I have found as many as four spines in the outer row.

Shape of seminal receptacle (plate 5, figures 1 and 2). Ortmann (p. 361) says of *O. p. propinquus* that its seminal receptacle is flat, slightly depressed in the middle, has no tubercles on the anterior margin and (p. 365) that only slight differences due to age are noticeable. He differentiates the receptacle of *O. obscurus* by its having a "well-marked" depression in the middle and two subconical tubercles in the anterior part (p. 371).

New York *O. p. propinquus* differ from this description in that two tubercles frequently occur near the anterior border of the receptacle. The highest of these tubercles are as high as the lowest tubercle found in *O. obscurus.* However, it is always possible to distinguish

the one species from the other, for in *O. obscurus* the whole receptacle is generally more nearly round and the two tubercles are not only more distinctly conical, but are fused at the midline, which has never been seen to occur in *O. p. propinquus*. The shape of the seminal receptacle is then, at least in New York State material, a character which will give complete separation. Unfortunately the differences are qualitative and no way has as yet been found of expressing them in numbers.

Shape of copulatory stylets (plate 3, figures 1, 2, 5 and 6). The first form copulatory stylets of these species are distinguished by Ortmann (p. 365) as follows, "... there is a tendency in the Pennsylvania specimens [of *O. p. propinquus*] toward the development of a slight notch on the anterior margin in the place where *C. obscurus* has a shoulder... The notch never assumes the shape of the 'shoulder' of *C. obscurus*, and the sexual organs differ in other respects from the lat[t]er species, chiefly in that the tip of the inner part [mesial process] is never blunt or dilated."

Ortmann had only 18 males I of *O. p. propinquus* and of these, seven had a notch. This appears to be more than a tendency toward its formation. I have not kept a record of numbers of New York State specimens with or without a notch on the stylet, but a large proportion have it. This is true throughout the range in New York of this species and in individual collections.

However, these two species are rapidly separated on the basis of this character, for the notch of *O. p. propinquus* is never more than a suggestion of the well-developed, right-angled shoulder on form I stylets of *O. obscurus*. *O. obscurus* males I have never been observed without the shoulder.

The other stylet character which appears to separate completely these species is the shape of the tip of the mesial process both in form I and form II males. In *O. p. propinquus* the mesial process in both forms of the male ends as a relatively sharp point. In *O. obscurus*, on the other hand, the mesial processes in both form I and form II stylets are rounded off at the tip or are even slightly inflated. A few of my males I of *O. obscurus* from the Allegheny River drainage have the distal quarter of the mesial process directed mesiad at about a 45-degree angle. This appears to be an aberrant shape.

O. p. propinquus appears to be a much more variable species than is *O. obscurus*. See the section "Hybridization" for a discussion of possible hybrids between these two species.

Orconectes limosus (Raf.)

(FRONTISPIECE; PLATE 3, FIGURES 3 AND 4; PLATE 5, FIGURE 5)

Astacus limosus Rafinesque. (Nov.) 1817: 42.
Astacus affinis Say. (Dec.) 1817: 168.
Astacus (Cambarus) affinis Say. Erichson 1846: 96.
Cambarus affinis (Say). Girard 1852: 87.
Cambarus pealei Girard, 1852: 87.
Cambarus (Faxonius) limosus (Rafinesque). Ortmann 1905*a*: 107.
Orconectes limosus (Rafinesque). Hobbs 1942*a*: 352.
Astacus bartoni Fabricius. Milne-Edwards 1837: 331.

Types: ". . . types not extant." (Faxon 1914: 417).

Type locality: Designated by Faxon (1914: 417) as: ". . . the muddy banks of the Delaware River, near Philadelphia, Pennsylvania."

Taxonomic remarks: Holthuis (1954) quotes Rafinesque's original description in full.

DESCRIPTION

Ortmann (1906: 352-356) has described *O. limosus* in detail. In the materials I have seen from New York there appear to be no differences. It is readily separated from the other New York State species by the presence of at least two spines on each side on the cephalic section of the carapace. These are present even in young immatures. The divergent tips of the copulatory stylets (plate 3, figures 3 and 4) are a constant character which, in both form I and form II males, separates this from the other New York State species. A relatively dense pubescence, particularly on carapace and claws is typical of specimens up to 30 mm. carapace length. In larger specimens it becomes less noticeable.

Apparent hybridization between this species and *O. p. propinquus* is discussed under the heading "Hybridization" in a separate section.

Cambarus robustus Girard

(FRONTISPIECE; PLATE 1, FIGURES 1, 4 AND 5; PLATE 2, FIGURES 1, 2, 3 AND 4)

Cambarus robustus Girard, 1852: 90.
Cambarus bartoni var. *robusta* Girard. Faxon 1885*c*: 358.
Cambarus bartoni robustus Girard. Faxon 1890: 622.
Cambarus (Bartonius) bartoni robustus Girard. Ortmann 1905*a*: 117.
Cambarus (Bartonius) robustus Girard. Creaser 1931: 260.
Cambarus (Cambarus) robustus (Fabricius). Fowler 1912: 340, 341.
Cambarus bartoni (Fabricius). Williamson 1905: 310 (authority of Ortmann 1906: 388).

Types: "*Type* probably destroyed in the Chicago fire in 1871; *paratype* (?). Acad. Nat. Sci. Philad. (1 male)." (Faxon 1914: 423).

Type locality: Humber River, near Toronto, Canada. Subsequent designation by Faxon (1914: 423) from Girard's first-named locality.

Taxonomic remarks: The current restricted use of *Cambarus* (see Hobbs 1942*a*: 354) makes Ortmann's subgenus *Bartonius* (see synonymy above) identical to it. No subgenera for *Cambarus* (*sensu stricto*) have been proposed.

The opinion of Creaser (indicated in the synonymy above) that *C. robustus* is not a subspecies of *C. bartoni* seems indisputable when the ranges of *C. robustus* and *C. b. bartoni* are compared (figures 6 and 7). The fact that the two can occupy so much territory in common, often the same streams, and still maintain their identity, makes it difficult to conceive of them as subspecies of the same species.

They do, however, have different habitat preferences, which in the case of the mountain stream (headwater) species, *C. b. bartoni*, appear to be rather strict. Assuming *C. b. bartoni* became established first in the New York stream systems which both it and *C. robustus* now occupy together, then perhaps one can view these two taxa as conspecific subspecies living in the same streams, kept fairly well apart by different habitat preferences, but intergrading in those areas where they actually come in contact.

This view does not seem to be supported by the fact that, although 10 percent of localities (29 of 289) from which *Cambarus* was taken produced both *C. robustus* and *C. b. bartoni*, only 14 percent of these 29 (four collections; DWC 35, 92, 95 and 96) contained any specimens which appeared morphologically intermediate. (The single specimen, a female (imm.?), in NYSM 1937: 172 also appears intermediate.) This can be put more strongly by stating that of the 419 specimens of this genus in these 29 collections containing both taxa, only about 2 percent of the individuals (10) appeared intermediate. It seems then that these crayfishes have diverged to the degree that, even when living in the same habitat, they rarely interbreed to produce viable offspring. It is on this basis that I choose, for the moment, to consider these two taxa as belonging to different species. The situation obviously requires detailed study.

I believe that *C. robustus* has its closest affinities with *Cambarus montanus montanus* and its so-called subspecies, *Cambarus montanus acuminatus*, and with *Cambarus bartoni sciotensis* Rhoades.

Of *C. m. montanus*, Faxon (1914: 387) says, "From *Cambarus bartonii montanus* the passage is easy to *C. b. robustus* . . ." Again on p. 388, in speaking of "very nearly typical examples of *C. b. robustus*," from West Virginia, he says, ". . . they show an approach to *C. b. montanus*, from which the form *robustus* is probably derived."

A comparison of some of my New York *C. robustus* with *C. m. montanus* collections at USNM brings out striking similarities. The resemblances are far closer than between *C. robustus* and *C. b. bartoni* and one is practically compelled by the visual evidence to concede a close relationship between *C. m. montanus* and *C. robustus.*

C. robustus is apparently also close to another *C. montanus* subspecies. Faxon (1885*b*: 68), says that specimens of *C. m. acuminatus* from North Carolina approach *C. robustus.*

C. b. sciotensis types have been examined at the United States National Museum and this form may well turn out to be a subspecies of *C. montanus.* Of his subspecies Rhoades (1944*b*: 97) says, "This subspecies is intermediate between *C. m. montanus* of the Appalachians and the *C. b. robustus* of the St. Lawrence drainage."

C. montanus and *C. b. sciotensis* are in need of considerably more taxonomic study before the relationships between them, and of *C. robustus* to them, can be accurately known.

C. robustus is described in a comparison between it and *C. b. bartoni*, given under *C. b. bartoni.*

Cambarus bartoni bartoni (Fab.)

(Plate 1, figures 2, 3 and 6; plate 2, figures 5, 6 and 7)

Astacus bartoni Fabricius, 1798: 407.
Astacus ciliaris Rafinesque, 1817: 42 (authority of Faxon 1914: 423).
Astacus pusillus Rafinesque, 1817: 42 (authority of Faxon 1914: 423).
Astacus affinis Say, Milne-Edwards 1837: 332.
Cambarus bartoni (Fabricius), Girard 1852: 88.
Cambarus (Bartonius) bartoni (Fabricius), Ortmann 1905*a*: 117.
Cambarus (Cambarus) bartoni (Fabricius), Fowler 1912: 340, 341.

Type: "(fragment only), Kiel Museum" (Faxon 1914: 423).

Type locality: "Habitat in America Boreali" (Fabricius 1798: 407).

Taxonomic remarks: Milne-Edwards, in confusing *A. affinis* Say with *A. bartoni* Fabricius was apparently misled by a transposition of the figure numbers for these species in Harlan (1835).

The current restricted use of *Cambarus* (Hobbs 1942*a*: 354) makes Ortmann's subgenus *Bartonius* (and Fowler's new name) identical to it. No subgenera for *Cambarus* (*sensu stricto*) have been proposed.

Faxon's list (1914: 423-425) contains 12 subspecies of *C. bartoni.* Some of these have subsequently been considered full species or removed to other species, but all of the 12 are in need of detailed study before their taxonomic status can be at all certain.

Faxon (1885*b*: 65) says that Professor Smith Barton, the collector, lived in Philadelphia and also (Faxon 1914: 423) suggests that the

type locality is probably Philadelphia, but he does not specifically designate a restricted type locality.

I am unable to explain the inclusion by Fowler (1912: 344) of "*Cambarus acutus* (nec Girard) var. b. Hagen" in his synonymy of *C. bartoni*. Hagen's description (1870: 36-37) and his figure of the antennal scale (plate 3, figure 144*a*) cannot possibly be *C. bartoni* and Hagen himself says that his variety may be *C. blandingi* (Hagen 1870: 37).

Holthuis (1954) reproduces Rafinesque's descriptions of *A. ciliaris* and *A. pusillus*.

Comparison between *Cambarus bartoni bartoni* and *Cambarus robustus*

Ortmann (1906: 377-381, 386-393) gives detailed descriptions for these two species and New York material does not differ. The discussion here is intended to point out the differences between these morphologically similar species. Hybrid individuals probably occur, but are considered elsewhere.

The first character listed in the key is believed to give complete separation. It must be stated, however, that all of my specimens of *C. robustus* have not been checked for the presence of the two rows of tubercles on the inner side of the palm. At first I disregarded this character given by Ortmann, but now believe that I was led astray by the fact that some specimens with regenerated claws were examined and these do not always show it. Subsequent spot checking in numerous collections from a wide range of localties has produced no *C. robustus* with normal claws which lack the two rows (plate 1, figure 5). A regenerated claw can be identified by its greater length of fingers in proportion to palm length and by its being thinner and generally more weakly formed. All of my *C. b. bartoni* have but a single row of tubercles on the inner margin of the palm (plate 1, figure 6).

The depression near the outer margin of the hand in *C. robustus* is always present, even in regenerated claws and in immature specimens. On the dorsal side of *C. b. bartoni* claws there are fewer and larger punctations than in *C. robustus*, and these may sometimes be so closely grouped that they partially fuse. The effect produced is a depression, but the ventral side usually will be fully rounded.

Rostral shapes in the very young of these two species are nearly identical but, as growth proceeds, differences develop resulting typically in the conditions shown on plate 1, figures 1 and 2. Again, however, there appear to be intermediates.

The punctations in the areola are variable in the two species and, although conditions such as are shown in plate 1, figures 3 and 4, leave little cause for doubt, there are other cases where a species determination on the basis of this character alone is hardly possible.

The same may be said for the lateral spine of the carapace. Although all *C. b. bartoni* lack it, not all *C. robustus* possess it and some even lack a tubercle in its place. The newly hatched young of *C. robustus* lack this spine at least up to third stage and its greatest frequency appears to be in individuals between 20 and 30 mm. carapace length.

In plate 1, figures 1 and 2, the shapes of the antennal scale are obviously different, yet measurements of length and width do not show it when a ratio of the two measurements is obtained. Possibly measurements of the angle formed by the cephalic border and the lateral margin will show the difference, but until the range of the variation is shown by measurement, it can hardly be used to give complete separation.

In addition to the characters listed in the key, there are two others which appear to give complete separation. Plate 2, figures 3, 4 and 7, show that where *C. b. bartoni* has the caudal border of the seminal receptacle smoothly rounded, this border, although rounded in *C. robustus*, is less smoothly so. Variants from the figures occur, but I have tested the character by having receptacles of these two species shown me under the microscope. The species were identified previously on the basis of the sum total of their morphology, yet on the basis of receptacle alone the same identifications were made.

Eye size may also be a useful character. The ratio of length of caudal section of carapace to eye diameter in 10 specimens of each species has given complete separation, but many more individuals must be measured before it can be utilized with confidence.

HYBRIDIZATION

Hybridization between *O. p. propinquus* and *O. limosus*

I have two specimens which appear to be intermediate between *O. p. propinquus* and *O. limosus*. This is particularly interesting because *O. limosus* is a rather isolated species both geographically and morphologically.

One of the supposed hybrids is a male I, taken from Catatonk Creek at Candor, Tioga County, N. Y. on May 25, 1951 by Dr. E. C. Raney (DWC 139). The collection contains in addition, specimens of *C. b. bartoni* and one form I male each of *O. p. propinquus* and *O. limosus*. A previous collection from this same locality (DWC 16) produced 40 *O. limosus*.

The features which most indicate the possibility of this specimen being hybrid are rostrum, stylets, armature of merus of chela and spines on lateral surface of carapace ahead of cervical groove.

The rostrum has a low median carina. It is definitely a carina, however, not a broad raised area. I have never before observed this *propinquus* characteristic in *O. limosus*. In contrast, the acumen is long, more like *O. limosus*.

The stylets appear distinctly intermediate. The terminal elements are more divergent and shorter than in *O. p. propinquus*. The mesial process is directed more laterad. All these conditions are an approach to *O. limosus*, but the appearance is no more of one species than the other. Measurements have been made of the length of the free tip of the mesial process (*B*) and of the distance from tip of mesial process to orifice (*A*). Only five specimens each of *O. p. propinquus* and *O. limosus* were measured. The ratios of A/B are as follows:

O. p. propinquus	2.0 – 2.3, mean 2.1
O. limosus	3.0 – 3.1, mean 3.0
Hybrid (?)	2.6

It will be seen that the hybrid (?) is intermediate as are many hybrids on their measurable characters.

The spines of the inner row of the merus of the left chela are rather long as in *O. limosus*. Those of the right chela are shorter and more like *O. p. propinquus*.

There are two spines on the left side of the carapace ahead of the cervical groove. On the right side, no spines are present but there are several reddish-brown spots which probably represent places where some protuberance has broken off or been worn away.

The general appearance of the specimen is as in *O. p. propinquus*, the pubescence of *O. limosus* being absent.

Intensive collecting in this same area on August 29, 1952 has produced one more male I (NYSM 7014) which appears similarly intermediate. Two collections (NYSM 7006 and 7011) from the Unadilla River (Chenango-Otsego Co., Susquehanna R. drainage) contain both these species, but there are no signs of hybridization.

Hybridization between *O. p. propinquus* and *O. obscurus*

The combined descriptions of *O. p. propinquus* and *O. obscurus* show that some of the variations in *O. p. propinquus* tend in the direction of *O. obscurus*. Most of these are found in localities distant from where *O. obscurus* is at present known to occur, and are apparently within the normal range of variation of *O. p. propinquus*, unless perhaps a one-way introgression is occurring. Neither Ortmann (1906) nor Turner (1926) has been able to find hybrids between these species. In fact, I can not find reference to certain hybridization between any crayfish species.

I was unable to find these two species together in the same restricted habitat until 1952 when, knowing the general picture of distribution, I was able to do so in three localities.

Two of these three collections (from localities about 15 miles apart) appear to contain hybrids, for in these collections I am unable to sort out the majority of specimens into one or the other species. Because of this, these two collections are not shown in figure 5. They are:

(1) NYSM 6994 (32 specimens of these two species, including three males I and three females) from New York, Oneida Co., Oswego R. drainage, Fish Creek five miles east of Vienna. This collection also contains *C. robustus*.

(2) NYSM 6996 (109 specimens of these two species; 67 males I and 42 females) from New York, Oneida Co., Mohawk R. drainage, Deans Creek at Westmoreland. This collection also contains *C. robustus* and *O. immunis*.

I am not yet able to show the intermediacy of these supposed hybrids on the basis of measurable characteristics.

Collection NYSM 7022 from Otisco L. outlet, Oswego R. drainage, Onondaga Co., N. Y., contains both species, but none of the specimens appears definitely intermediate. Other recent (1952) collections from this general area inhabited by these two species contain only one or the other species and the majority of specimens sort readily (NYSM 6992, 6993 and 6997).

Hagen (1870: 69) reports a mixed collection of *O. obscurus* and *O. p. propinquus* from Rochester, N. Y. It is not stated whether or not these were from the same restricted locality. I have been able to take only *O. p. propinquus* and *O. immunis* at Rochester (DWC 53, 101), which is unfortunate because Rochester is the type locality for *O. obscurus.*

Hybridization between *C. robustus* and *C. b. bartoni*

In the section "Descriptions," under *C. robustus* it is stated that in collections containing both *C. robustus* and *C. b. bartoni,* about 2 percent of individuals appear morphologically intermediate between these two species. These specimens are intermediate in some or all of the four major distinguishing features: hand, areola, rostrum and antennal scale. See the above mentioned section for a brief discussion of the taxonomic status of these two taxa.

LIFE HISTORIES

Orconectes propinquus propinquus

This species has been carefully studied under field conditions at Urbana, Ill. by Van Deventer (1937). The following outline of its life cycle in Illinois, taken from Van Deventer's work, is presented here as a summary of a life history which, at least in its major events, is typical of New York members of the genus except for *O. immunis*.

Briefly, the life of individuals of *O. p. propinquus* at Urbana, Ill. consists of the following events:

1. The young are hatched in May or June and remain attached to the mother for one or two weeks.

2. Following the second moult they become free swimming and measure about 5 mm., carapace length.

3. They undergo a total of 6 to 10 moults between the time of hatching and the end of the first growing season in late September or early October, and attain a carapace length of 12-27 mm.

4. Sexual maturity in both sexes is attained coincident with a carapace length of about 20 mm. and the majority of the season's young become sexually mature by their first fall after hatching.

5. During the winter no growth takes place.

6. Copulation occurs in late fall and early spring.

7. The eggs are laid in late March or early April and are carried for a period of four to six weeks, depending on temperature. As they are laid, the eggs are fertilized by sperm which has been held in the seminal receptacle.

8. The adult males moult twice during the spring or early summer, changing to form II with the first adult moult, and reverting to form I with the second adult moult.

9. The yearling individuals of both sexes which did not become sexually mature at the end of their first summer of life apparently moult four times during their second year. They attain sexual maturity with the second yearling moult.

10. The adult females undergo a single moult immediately following the shedding of the young in spring.

11. Apparently no growth takes place in connection with the first yearling moult, among either mature males or immature individuals; but marked growth occurs in connection with the second yearling moult in both groups.

12. A similar growth takes place as a result of the single moult among the adult yearling females.

13. The portion of the young of the previous year which reached sexual maturity by the end of their first growing season produce a

brood of young the following spring, attain a maximum size of 35-40 mm. carapace length as a result of the second adult moult of the males and the single adult moult of the females, and die as yearlings.

14. The individuals which failed to attain maturity by the end of their first growing season live over a second year, attain maximum size during their second summer, produce a brood of young in the following spring, and for the most part die as two-year-olds.

15. A very few individuals, among which females predominate, survive over a third year, and produce a brood of young in their third spring.

16. With the possible exception of these last few, the individuals of this species apparently produce only a single brood of young during their lives.

TABLE 3

Seasonal data for *Orconectes p. propinquus* in New York

a. Tabulated from all specimens in D. W. Crocker collections 1-158 and in NYSM 6977-7022 (collected in August 1952)

	APRIL	MAY	JUNE	JULY	AUG.	SEPT.	OCT.
male I	49	107	2	83	203	73	63
male II	–	29	27	8	33	1	8
male imm.	1	27	–	69	53	13	25
female	11	18	51	100	156	68	57
female (with eggs)	6	23	–	–	–	–	–
female (with young)	–	–	9	–	–	–	–
female imm.	7	33	1	83	64	17	16
male (II?)	4	7	1	–	14	–	–
female (imm. ?)	–	10	4	–	12	–	–

b. Adult males in NYSM 6976 (stream survey collections)

	JUNE	JULY	AUG.	SEPT.
male I	5	22	35	3
male II	44	30	4	–

Adult males. The proportions of form I and form II males occurring through the seasons in New York (table 3) indicate the same life cycle which occurs in Illinois. In October, the last month of the year for which I have records, 87 percent of the males are form I; in fact, owing undoubtedly in part to chance in collecting, 98 percent of males are form I in September. Some of the individuals called form II, may really be large immatures, members of the group which reaches sexual maturity in its second summer. The condition in April is similar, the spring moult not having yet taken place. During May

and July, numbers of males are moulting; in May from form I to form II, and in July from form II back to form I again. My earliest record for a soft (freshly moulted) male I is June 21, 1951 (DWC 148). The other male I, recorded in June on the chart of seasonal data, was taken June 21, 1950 (DWC 36) and was very clean and apparently rather freshly moulted. The numbers of immature males decrease through the summer as these, becoming mature, are classed as males I.

Copulation. Dates on which I have observed copulation in New York are:

July 13, 1951 — 5 pairs
Aug. 25, 1950 — 3 pairs
Aug. 28, 1950 — 1 pair
Oct. 19, 1950 — 1 pair

In addition, I have two early records for the capture of females with sperm plugs, July 18, 1949 (DWC 3) and July 28, 1950 (DWC 47). Copulation must begin sometime in July in New York, possibly as soon as the males begin their return to form I. The frequency of finding sperm plugs in females increases until the late fall, when an adult female is only rarely found without one.

Unlike Van Deventer (p. 33) I have no observations of copulation in the spring, although I have watched for it in late March and in April, May and June. Van Deventer (p. 33) in summarizing the literature notes that the duration of the mating season varies widely in different localities. He states, "In more northern latitudes, such as Michigan and Wisconsin, it probably begins in July and August, and lasts until November, but does not occur again in the spring." Data on hand show this also to be true for New York State.

Egg laying. I have seen egg-laying in *O. p. propinquus* once. On April 23, 1950, in Fall Creek, Ithaca, N. Y., a female was noted lying on her back. The abdomen was flexed and the members of the tail fan extended. The chamber so formed was filled with a greyish mucous-like substance. Four eggs were contained in the mass.

Females with eggs. Females with eggs in my personal collection were taken in New York on the following dates:

April 13, 1951 — 1 specimen (DWC 75*a*)
April 23, 1950 — 5 specimens (DWC 21)
May 3, 1950 — 3 specimens (DWC 23)
May 6, 1951 — 3 specimens (DWC 83)
May 13, 1951 — 3 specimens (DWC 102)
May 19, 1951 — 5 specimens (DWC 109)

May 20, 1950 – 1 specimen (DWC 27)
May 20, 1951 – 4 specimens (DWC 135)
May 21, 1950 – 3 specimens (DWC 31)
May 25, 1951 – 1 specimen (DWC 129)

Collection NYSM 1939: 94 contains a female with eggs taken June 2.

The spawning season is apparently about a month later in New York State than it is in Illinois.

Hatching and early moults. A female with eggs was taken from Cascadilla Creek, Ithaca, N. Y., on May 25, 1951 and kept in a dish. Two days later the first of the eggs hatched, but most of the young died. I observed one first stage individual moulting to second stage at 5:30 p.m. on May 30, three days after the first eggs hatched. None of the young reached stage three before dying. The first and second stage individuals correspond closely in manner of attachment to the egg membranes and to the pleopods of the female, with the description of Andrews (1907) for *O. limosus*.

Females with young. I have but one date: June 21, 1950, when eight females with young were taken in one locality and one in another (DWC 33 and 36).

Size at sexual maturity. Although I have not measured all of my 414 males I, I have measured most of those appearing to be under 20 mm. carapace length. I believe that the size below which form I males could be considered exceedingly rare is about the same as the figure of 18 mm. given by Van Deventer (p. 31). The great majority of my males I are over 20 mm., and Van Deventer (p. 30) has reported similarly. My smallest male I is 16.2 mm. Van Deventer (p. 31) found one male I of only 12.6 mm. carapace length.

Minimal size is apparently the same for mature females. I have only eight specimens collected in late fall which are under 20 mm. The smallest female with eggs is 19.1 mm. (DWC 135); smallest female with young 16.5 mm. (DWC 36); smallest females with sperm plug, two specimens 16.4 mm. in carapace length (DWC 7 and 18).

Maximum size. Male I, 38.0 mm. carapace length (DWC 39*b*).
Female, 35.9 mm. carapace length (DWC 102).

There is an interesting phenomenon associated with maximum size which is best documented for, and perhaps occurs only in, males. Van Deventer (1937: 45-46) reasoning from measurements of *O. p. propinquus*, and Ortmann (1906: 471-472) reasoning from field observations of *O. obscurus*, both report an apparent dying-off of old males in the spring. Penn (1943) reports the same phenomenon for the southern *Procambarus clarki*. I, also, have some evidence that

this occurs. Both on April 23 and April 25, 1950, while observing *O. p. propinquus* activities in Fall Creek, Ithaca, N. Y., numbers of dead individuals were noticed lying on the stream bottom. Although some were disintegrating, others appeared to have died recently. None of these latter appeared to be mutilated. The proportions of the two sexes were not recorded. One male I, 25.3 mm. carapace length, was lying on its back still slightly active. Although it showed fairly vigorous activity when placed in a collecting bottle, it died four hours later. Superficially, at least, it appears perfectly normal (DWC 64).

Habitat. *O. p. propinquus* has ecological requirements similar to those of *C. robustus* for, as indicated in tables 4 and 18, each is the most common crayfish associate of the other. Like *C. robustus* it is rare in mountain stream habitats and in still water with a mud or silt bottom, but otherwise it is widespread in distribution in those stream systems which it occupies.

Crayfish associates are listed in table 4.

TABLE 4

Frequency of occurrence of *Orconectes p. propinquus* with other crayfish species in collections made in New York. Tabulated from D. W. Crocker collections 1-158, NYSM 6976 (stream survey collections) and NYSM 6977-7022 (collected in August 1952)

DRAINAGE	*C. b. bartoni*	*C. robustus*	*O. immunis*	*O. limosus*	*O. obscurus*	*O. virilis*
Genesee R.	1	3	1			
Oswego R.	5	28	4		2	
L. Erie-Niagara R.		2	2			1
L. Champlain						1
Grass, St. Regis & Salmon R.	3					
Oswegatchie & Black R.	1	2				
Mohawk-Hudson R.		2	4		1	
Susquehanna R. (East)	1		1	3		
Chemung R.	2		4			
Misc. L. Ontario tribs.		12	13			

Orconectes obscurus

Ortmann (1906: 470-476) has made the most detailed life history observations on *O. obscurus*. Although his data are not as quantitative as are those of Van Deventer (1937) for *O. p. propinquus*, a comparison shows that the life histories of these two species differ only in details. The discussion here will be limited to a presentation of data for New York State, with the addition of data from Ortmann where mine are insufficient, or where his data differ.

TABLE 5

Seasonal data for *Orconectes obscurus* in New York

a. Tabulated from all specimens in D. W. Crocker collections 1-158 and in NYSM 6977-7022 (collected in August 1952)

	MAY	JUNE	JULY	AUG.
male I	46	..	4	72
male II	2	24	21	7
male imm.	23	2	6	66
female	3	19	17	56
female (with eggs)	7	..	..	..
female imm.	29	5	6	58
male (II?)	4	7	8	..
female (imm. ?)	3	5	12	..

b. Adult males in NYSM 6976 (stream survey collections)

	JUNE	JULY	AUG.
male I	4	18	17
male II	41	5	--

Adult males. The apparent sharp drop in males I and increase in males II which appears in table 5*a* in June is due to a limited range of collecting dates. The latest day of collecting in May is May 21, and the two June collections were made June 15. The four June form I males reported in table 5*b* were taken on the first three days of the month. Ortmann found that the first spring moult in the majority of individuals occurred in Pennsylvania in the first half of May. It apparently occurs later in New York State.

Copulation. The earliest date recorded by Ortmann for an observation of copulation is September 5. He records other dates for September, October and November.

Females with eggs. The following are my dates of capture of females with eggs.

May 6, 1951 — 1 specimen (DWC 87)
May 13, 1951 — 4 specimens (DWC 99)
May 19, 1951 — 1 specimen (DWC 111)
May 21, 1951 — 1 specimen (DWC 128)

Collection NYSM 1934: 588 contains a female with eggs taken June 20, from the Erie Barge Canal opposite the entrance of Nine-mile Creek, Mohawk drainage, Oneida County, N. Y.

Ortmann states that he found females with eggs very regularly from the beginning of April to the end of May. His extreme dates are April 6 and May 25.

Females with young. Ortmann gives three dates: May 30, June 5 and June 6.

Size at sexual maturity. My smallest male I measures 19.9 mm. carapace length (NYSM 7015). The smallest female with eggs measures 23.1 mm. carapace length (NYSM 1934: 588). Ortmann's smallest male I is 38 mm. total length and his smallest female with eggs measures 40 mm. total length.

Maximum size.

Male I — 44.0 mm. carapace length (NYSM 1937: 4808)
Male II — 37.3 mm. carapace length (NYSM 1934: 289)
Female — 47.8 mm. carapace length (NYSM 7022)

Ortmann records the maximum size as over 70 mm. total length.

TABLE 6

Frequency of occurrence of *Orconectes obscurus* with other crayfish species in collections made in New York. Tabulated from D. W. Crocker collections 1-158, NYSM 6976 (stream survey collections) and NYSM 6977-7022 (collected in August 1952)

DRAINAGE	*C. k. burtoni*	*C. rusticus*	*O. immunis*	*O. p. propinquus*
Genesee R.	1	4	1	
Oswego R.		2		2
L. Erie-Niagara R.	1	1		
Oswegatchie & Black R.		1		
Mohawk-Hudson R.	1	4	2	1
Allegheny R.	7	17		

Habitat. No differences between the habitat preferences of this species and *O. p. propinquus* have been noted.

Crayfish associates. See table 6.

Orconectes limosus

The best, although a very incomplete, account of the life history of this species is given by Ortmann (1906). The remainder of the literature consists largely of brief mention of habitats. The exceptions are Andrews' studies of copulation (1895), egg-laying (1906*a*) and development of the young (1907). These last are all laboratory studies, but Ortmann (1906) compares his field information with Andrews' and finds few points of difference.

Ortmann concludes from his data that the life histories of *O. limosus* and *O. obscurus*, for which he has better data, agree in every particular, and that there are thus the following general events through the seasons:

1. Mating occurs in the fall.
2. Spawning takes place in the spring.
3. Males of the first form are rare in June and part of July in consequence of a spring moult to form II.
4. First form males appear in numbers in the last half of July and are ready to take part in the fall mating season.

TABLE 7

Seasonal data for *Orconectes limosus* in New York

a. Tabulated from all specimens in D. W. Crocker collections 1-158 and in NYSM 6977-7022 (collected in August 1952)

	FEB.	APRIL	MAY	JUNE	JULY	AUG.	SEPT.	OCT.
male I	4	..	5	1	..	25	1	37
male II	..	..	..	2	..	4	..	..
male imm.	..	..	1	..	..	31	4	18
female	4	1	3	1	1	24	1	35
female imm.	..	..	..	..	..	23	4	4
male (II?)	..	..	..	1	..	1	..	..
female (imm. ?)	..	..	3	..	..	2	..	..

b. Adult males in NYSM 6976 (stream survey collections)

	JUNE	JULY	AUGUST
male I	7	12	9
male II	9	20	5

Adult males. I have too few specimens taken in the critical months of May, June and July (table 7) to determine whether or not the season of moult is the same in Pennsylvania and New York.

Data on hand indicate the same situation as obtains for *O. p. propinquus*. Ortmann records two males I. with quite fresh shells taken on July 10, 1905.

Copulation. Ortmann gives the dates of field observations of copulation as September 4 and 10.

Females with eggs. Ortmann has one record, May 9.

Females with young. A single record from Ortmann, May 30.

Size at sexual maturity. My smallest male I is 23.5 mm. carapace length (NYSM 7000). This same collection has a 22.5 mm. female with sperm plug. Ortmann's minimal sizes for males I are 37 mm. (New Jersey) and 40 mm. (Pennsylvania) total length. Ortmann reports seeing copulation take place in specimens less than 45 mm. total length, and egg-bearing females as small as 40 mm. The data are insufficient but suggest that sexual maturity is attained in *O. limosus* at a slightly larger size than in *O. p. propinquus*.

Maximum size. My largest specimen is a female from Esopus Creek near Kingston, Hudson River drainage (DWC 20), which is 54 mm. in carapace length. Hagen (1870: 61) records a body length of 4.7 inches in very old specimens. Faxon (1914: 372, footnote) reports that the largest specimen of this species in MCZ is 124 mm. total length (MCZ 180).

Habitat. *O. limosus* has been usually described as a river crayfish, preferring slow water and a silt bottom. My personal collections are from only two localities in New York: Catatonk Creek at Candor and Catatonk Creek one mile east of Spencer, both in Tioga County. *O. limosus* appears to be restricted to the wider,

TABLE 8

Frequency of occurrence of *Orconectes limosus* with other crayfish species in collections made in New York. Tabulated from D. W. Crocker collections 1-153, NYSM 6976 (stream survey collections), and NYSM 6977-7022 (collected in August 1952)

DRAINAGE	*C. b. bartoni*	*C. rusticus*	*O. immunis*	*O. p. propinquus*	*P. b. blandingi*
Susquehanna R. (East)	5		1	3	
Lower Hudson R.		1			3
Chemung R.	3		1		

deeper segments of this stream where, consequently, the current is slower and the bottom composed largely of soft silt. The habitats of the 10 localities where this species was taken in August 1952 (table 17) are all characterized, at least in part, by silt.

Crayfish associates are given in table 8.

Orconectes immunis

Forney (1956) discusses raising this species for use as bait, but the only paper published on the life history of this species is the detailed study by Tack (1941). In Ithaca, N. Y., he found the following life history:

1. The eggs hatch about May 15.
2. The young reach 13-29 mm. carapace length by September and may become sexually mature at this time, but most are not sexually mature until late in their second summer.
3. From mid-November until late March or April no moulting occurs.
4. Copulation occurs from mid-July to early October, mostly among yearling individuals.
5. The eggs are laid during late October or early November and are held on the pleopods through the winter.
6. The normal life span of *O. immunis* in the Ithaca region is two years.

TABLE 9

Seasonal data for *Orconectes immunis* in New York

a. Tabulated from all specimens in D. W. Crocker collections 1-158 and in NYSM 6977-7022 (collected in August 1952)

	APRIL	MAY	JUNE	JULY	AUG.
male I	61	3	2	5	9
male II	..	9	3	1	3
male imm.	118	1	2	12	2
female	5	6	4	7	7
female (with eggs)	78	1	..	..	..
female (with young)	..	1	..	..	..
female imm.	142	..	3	17	1
male (II?)	..	3	..	2	1
female (imm. ?)	..	3	..	3	..

b. Adult males in NYSM 6976 (stream survey collections)

	JUNE	JULY	AUG.	SEPT.
male I	5	2	3	7
male II	10	9	2	1

Adult males. The large numbers of immatures appearing in April (table 9) make it plain that the majority of young hatched the previous summer have wintered over as immatures. The criterion used in the present study for separating adults from immature individuals is 23 mm. carapace length.

Tack found the first spring moult of adult males to occur about the middle of April. The second he reports as less pronounced, but it begins in about the last week of June.

Females with eggs. Dates of collection are April 13, 1951 (DWC 75); April 28, 1950 (DWC 39); May 20, 1950 (DWC 27). Tack's earliest fall dates are October 18, 1937, October 23, 1935 and October 24, 1936.

Females with young. The record in table 9 is for May 20, 1950 (DWC 27). Tack gives mid-May as the time of hatching.

Size at sexual maturity. My smallest male I is 23.2 mm. carapace length (DWC 39*b*). The smallest female with eggs is 23.0 mm. (DWC 39*b*). Tack reports but one smaller female with eggs than this: 22 mm. He gives no minimal size for mature males.

TABLE 10

Frequency of occurrence of *Orconectes immunis* with other crayfish species in collections made in New York. Tabulated from D. W. Crocker collections 1-158. NYSM 6976 (stream survey collections) and NYSM 6977-7022 (collected in August 1952)

DRAINAGE	*O. p. propinquus*	*O. virilis*
Genesee R.	1	1
Oswego R.	4	
L. Erie-Niagara R.	2	1
Grass, St. Regis & Salmon R.		1
Mohawk-Hudson R.	4	
Susquehanna R. (Lake)	1	
Chemung R.	4	
Misc. L. Ontario trib's.	13	

Maximum size. The largest specimen on record or seen by me is in NYSM 1939: 1650. It is a female with a carapace length of 48.8 mm., from Glenwood Lake, Ontario County, N. Y.

Food. Analysis of stomach contents, direct observation and preferences shown in feeding tests show (from Tack) that *O. immunis* is largely a vegetarian. Tack does not separate his data for size classes of crayfish.

Crayfish associates are listed in table 10.

Orconectes virilis

No account of the life history of *O. virilis* has been published and what little is known is widely scattered in the literature as brief notes, most of which relate to habitat. Steele (1902) gives some information on the life history in Missouri of a species which she considers to be *O. virilis,* but Creaser (1933*b*: 3) says that *O. virilis* does not occur in Missouri and that she must have had *O. nais.*

Seasonal data. The meager data available for New York are summarized in table 11.

TABLE 11

Seasonal data for *Orconectes virilis* in New York. Tabulated from all specimens in D. W. Crocker collections 1-158, in NYSM 6976 (stream survey collections), and in NYSM 6977-7022 (collected in August 1952)

	MAY	JUNE	JULY	AUG.
male I	1	.	.	7
male II	.	8	2	4
male imm.	.	.	.	23
female	2	.	.	7
female imm.	1	.	.	24
male (II?)	2	.	.	.
female (imm. ?)	.	3	.	.

Copulation. Fasten (1914: 603, table 1) reports two periods of copulation in Wisconsin: April-May and September-October. His data are derived from the cytology of the testis and condition of vasa deferentia.

Egg laying. Creaser (1931: 263) reports that in Michigan the eggs are laid before the last of April. Pearse (1910: 18) gives a record of a female with eggs on April 14 in the same State.

Maximum size. The largest male I seen by Pearse (1910: 17) measured 55 mm. carapace length. Creaser (1932: 326) speaking of *O. virilis* in Wisconsin says, "This species is the largest in the State and frequently attains a size of over eight inches."

Habitat. Pearse (1910: 18) says that this species is found in the lakes and larger streams in Michigan. Creaser (1931: 263) for the same State says it prefers streams with a bottom of stones and is found "... in even the coldest streams where the fish fauna is limited to *Cottus*, the miller's thumb, and *Salvelinus*, the brook trout."

My own two collections of *O. virilis* (DWC 119 and 121) are from the Little Chazy River, near its mouth, Clinton County, and from the Salmon River at Fort Covington, Franklin County. Both habitats are in slow-moving turbid water where the bottom is mud and silt with numerous patches of aquatic plants.

The stream survey collections, of which there are five of this species, carry no habitat data, but I was able to take *O. virilis* in three localities during the August 1952 collecting. These are as follows:

1. NYSM 6978, stream (probably Kayaderosseras Creek) at bridge on rt. U. S. 9, 2.3 miles south of city limits of Saratoga Springs. Scattered boulders, dense silt, slow current and slightly dark water. About 30 feet wide and up to 3 feet deep.
2. NYSM 6985, Lake George outlet in town of Ticonderoga. Bottom of silt, scattered boulders and considerable rubbish.
3. NYSM 7017, east shore and at park at south end of Grand Island, Niagara River. Because of misidentification of these (all immature) specimens in the field, I have no specific habitat data for them; the Grand Island material from several habitats was lumped together as one collection.

Crayfish associates. Three collections contain *O. virilis* with another species: with *O. immunis* in the Niagara and Salmon Rivers and with *O. p. propinquus* in the Niagara River and Lake George outlet.

Cambarus robustus

Discussion. The literature contains practically no information regarding the life history of *C. robustus*. This fact was recognized early in the present study and because *C. robustus* is common in the Ithaca region, the attempt was made to study its life history, particularly by marking methods.

In an intensive study of *O. p. propinquus* in Illinois, Van Deventer (1937) collected and measured in the field large numbers of specimens and then returned them to the stream. He was able to accumulate data which showed the growth rate of this species at all stages of its life. He could also determine length of life, age at sexual maturity and other pertinent facts.

However, in *C. robustus* there is apparently no restricted, at least no single period, during which the eggs are laid and hatched as there is in *O. p. propinquus*. It follows therefore, that, unlike *O. p. propinquus*, graphic plots of frequency distribution of size of *C. robustus*, measured at regular intervals of time, will not show a given year-class as distinct from the remainder of the population. Because of this, *C. robustus* is particularly well suited as a subject of growth study by marking individuals so that they may be subsequently recognized when collected from their natural habitat.

Here, one is led to ask: How can an animal which moults be marked so as to still be recognizable as a marked animal after moulting? I have tried three methods, all apparently unsuccessful. These have been reported upon elsewhere (Crocker 1952), but briefly they are the following: (1) Punching holes in various of the five members of the tail fan, a method used on lobsters with success by Wilder (1948); (2) insertion of bits of metal (tantalum wire, silver sheet, silver wire) into the haemocoele, to be recognized subsequently by means of X-ray; (3) a method used successfully on spiny lobsters by Creaser and Travers (1950), which involves inserting barbed plastic tabs between terga into the abdominal musculature.

TABLE 12

Seasonal data for *Cambarus robustus* in New York

a. Tabulated from all specimens in D. W. Crocker collections 1-158 and in NYSM 6977-7022 (collected in August 1952)

Numbers in parentheses refer to additional adult males, recorded in the field as to form and liberated as marked animals.

	APRIL	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.
male I	18	71	8	6	6(10)	9(13)	24(20)	..
male II	8	36	13	11	14(21)	14(3)	24(13)	2
male imm.	8	59	13	8	11	3	12	..
female	42	148	10	12	17	14	63	2
female (with eggs)	..	..	..	2	..	..	..	..
female (with young)	4	..	..	..	1	..	..	..
female imm.	18	77	11	8	15	2	7	1
male (II?)	..	16	1	..	1	1	9	..
female (imm. ?)	..	15	5	..	4	..	..	..

b. Adult males in NYSM 6976 (stream survey collections)

	JUNE	JULY	AUGUST
male I	25	8	3
male II	12	12	5

Methods one and three failed apparently because of the small size of crayfishes as compared with lobsters and spiny lobsters. Method two may still give results with the use of metal pellets, instead of wire and sheet. These latter either punctured vital organs or worked to the surface much as does a splinter in a finger.

Marking methods attempted for this species having failed up to the present to produce results, life history information must be summarized from field and laboratory observations and data from collections.

Adult males. It is apparent from table 12 that the restriction of form II males to the summer is not the case for *C. robustus* as it is for *O. p. propinquus*. This fact has been pointed out previously by Ortmann (1906: 488). In Pennsylvania, Ortmann found males I in the months of May, July, August, September, October and November, and males II in the months of May through October. I have a field record for a male moulting from form I to form II on September 21, 1950, and records of numerous soft males of both forms in September.

Thus, apparently at all times of the year there are males capable of copulation. Months unsampled are December through March. The data show relatively fewer males I in June, July and August and relatively fewer males II in April, but it is not certain how true a picture this may be.

Copulation. I have but two dates of copulation for this species, occurring under completely natural conditions in the field: October 8, 1949 and October 19, 1950. Two additional dates are May 23 and May 30, 1951, but these specimens were crowded in with a number of others of the same species in a lamprey trap.

One of the pairs from the lamprey trap was placed in boiling water and fixed in position. The positions of male and female correspond to the descriptions of Andrews (1895) for *O. limosus*. The right fifth pereiopod was used by the male to depress his stylets. Particularly well shown by this pair is the function of the hooks on the ischia of the male's third pereiopods. These, one on each side, were hooked over a prominent projection on the coxae of the female's fourth pereiopods to such an extent that the soft membranes dorsad of the projections were deeply impressed.

Although sperm plugs are common in the fall in all the New York State species of *Orconectes* (except *O. virilis* for which data are lacking), I have yet to find a sperm plug in *C. robustus* or in *C. b. bartoni*. All of the adult female *C. robustus* in my personal collection (295 specimens) have been examined for it.

Egg laying. I have seen two females of this species lay eggs, both in captivity. The dates are July 2, 1950, and April 7, 1951. The process is as reported by Andrews (1906*a*) for *O. limosus*. The female lies on her back and secretes a mass of mucous-like material into the chamber formed by the flexed abdomen and extended members of the tail fan. It is into this mass that the nearly black eggs are laid. The mucous disappears in about a day and a half. Each of these females had 30-40 eggs. Carapace lengths were 38.4 and 35.0 mm.

The dates for capture of females with eggs in the field are July 13 (DWC 154) and July 23 (DWC 158), 1951; carapace lengths 35.0 and 31.2 mm. Ortmann (1906: 488) took a female with eggs in Crawford County, Pennsylvania on July 11, 1905; total length 84 mm.; number of eggs 228.

Hatching and early moults. The dates for capture of females with young in the field are April 28 and August 13, 1950, and April 13, 1951. I have a measurement only for the August specimen — 39.2 mm. (DWC 72, specimen 23).

The eggs laid by the female in captivity on April 7, 1951, were first noticed to be hatching on May 24, an interval of over six weeks. The water temperature in the large aquarium in which the animal was kept varied not over two degrees above or below 60 degrees Fahrenheit. On May 25, 13 young were counted and, because they were crawling rather actively over the pleopods of the female, yet were without the five distinct members of the tail fan, they were probably stage two of Andrews (1907: 50). On May 29, only two young remained, the rest were not in evidence, dead or alive, and it is supposed that the mother ate them. Of the two remaining, one was third stage and was preserved. In a slightly shrunken condition it measures 4.7 mm. carapace length. The other, a stage two individual, was kept alive and sometimes between 11 p.m. on May 29 and 10 a.m. on May 30, moulted into third stage. Careful watch was kept on this single individual to detect another moult. Active feeding was first noticed on June 4, when the intestine became visible as a dark line due to its contained food material. The only food available was a rich coating of protozoa-laden algae in the bottom of the dish. On June 28 the animal measured 5.4 mm. carapace length. No cast exoskeleton was found and the animal died on August 4, 1951. It measures 5.6 mm. carapace length.

Immatures under 20 mm. carapace length in my collections or in NYSM collections were taken in May through October.

Moulting. The increment of growth of individuals living under natural conditions has been ascertained in two cases. On September

21, 1950, a male moulting from form I to form II was captured (DWC 65). Its change in carapace length was from 34.8 to 39.3 mm., an increment of 4.5 mm. A female, taken on May 5, 1951, and kept in an aquarium, moulted on May 24, only 19 days later; change in carapace length from 35.1 to 37.6 mm., an increment of 2.5 mm.

A moult by the majority of the adult population in September is indicated by field observation. On September 18, 1950, in Fall Creek at Forest Home, Ithaca, Tompkins County, N. Y., about half of many adult *C. robustus* were soft, yet in this same area on September 30, only one soft animal was seen. Similarly, in Taughannock Creek at Perry City, boundary of Tompkins and Schuyler Counties, N. Y., about 20 *C. robustus* were seen on September 21, 1950. Only two hard individuals were present out of 10-15 large specimens. Both males and females were seen soft, also both males I and males II. Two females were seen half moulted. Yet on October 7, not one soft animal could be found.

TABLE 13

Frequency of occurrence of *Cambarus robustus* with other crayfish species in collections made in New York. Tabulated from D. W. Crocker collections 1-158, NYSM 6976 (stream survey collections), and NYSM 6977-7022 (collected in August 1952)

DRAINAGE	*C. b. bartoni*	*O. immunis*	*O. limosus*	*O. obscurus*	*O. p. propinquus*
Genesee R.	3			4	3
Oswego R.	10	2		2	28
L. Erie-Niagara R.	1			1	2
Oswegatchie & Black R.	4			1	2
Upper Hudson R.	1				
Raquette R.	2				
Mohawk-Hudson R.	1	2		4	2
Lower Hudson R.			1		
Allegheny R.	5			17	
Misc. L. Ontario tribs.	2	1			12

Size at sexual maturity. Of the form I males which I have seen, the smallest measures 31.7 mm. carapace length. This specimen is from Herkimer County, N. Y., at the outlet of Little Moose Lake (DWC 143). Because of the large number of males I (215) which have come under my observation, and because the smallest in all collections have been measured, this value of minimal size is believed to be close to the actual limit. A form I male in NYSM 7021 is so much smaller than this (26.4 mm.) that I consider it abnormal.

The smallest female with eggs (DWC 138) measures 31.2 mm. carapace length and is the smallest normal sexually mature specimen of this species which I have seen or which has been reported.

Maximum size. Male I, 52.4 mm. carapace length (NYSM 1929: 1152).
Male II, 51.8 mm. carapace length (DWC 135).
Female, 55.4 mm. carapace length (DWC 32).

Food. Notes on the food of this species are given by Creaser (1934: 160) who found that in 11 specimens ranging from 42 to 76 mm. total length, the smaller fed largely on insect larvae or naiads, the larger on aquatic plants. The largest three stomachs contained only aquatic plant remains.

Habitat. The ecological requirements for this species are not as restricted as are those of *C. b. bartoni*. It is rarely found in cold mountain streams, the preferred home of *C. b. bartoni*, and it is equally rare in standing water where the bottom is of mud and silt. Otherwise, it has been taken from both ponds and streams of extensive variety. Burrowing habits have not been observed in New York State except for a rather casual digging out of shelters under boulders in streams.

Crayfish associates are listed in table 13.

Cambarus b. bartoni

Other than Williamson's note (1899: 47) of finding a female with young, Ortmann (1906: 486-488), working in Pennsylvania, has contributed the only information on the life history of this subspecies. Owing to its relatively infrequent occurrence near Ithaca, N. Y., I can only present some information which tends to confirm the findings of Ortmann.

Adult males. Ortmann (1906: 487) reports first form males in the months of March through December. He did no collecting in January and February. He gives no quantitative data on the relative frequency of males I and males II. My own data (table 14) show

TABLE 14

Seasonal data for *Cambarus b. bartoni* in New York

a. Tabulated from all specimens in D. W. Crocker collections 1-158 and in NYSM 6977-7022 (collected in August 1952)

	APRIL	MAY	JUNE	JULY	AUG.	SEPT.	OCT.
male I	3	10	1	3	18	4	..
male II	4	11	9	3	13	4	..
male imm.	..	7	2	13	26	..	..
female	9	35	11	3	23	1	1
female (with young)	2	..	..	..	1	..	..
female imm.	..	11	2	8	18	..	..
male (II?)	..	6	1	..	16	1	..
female (imm. ?)	2	..	..	..	13	1	..

b. Adult males in NYSM 6976 (stream survey collections)

	JUNE	JULY	AUG.
male I	4	2	7
male II	25	8	6

that, as in *C. robustus*, there are apparently fewer males I in June and July, but there are fewer specimens of *C. b. bartoni* on which an opinion can be based.

With these small numbers also, a relative infrequency of males II is not apparent. Ortmann (1906: 487) found males II in all months except January and February, in which months he did no collecting.

Males of this subspecies, capable of copulation, are present during at least 10 months of the year.

Copulation. I have not observed copulation in this subspecies. Ortmann (1906: 486) gives only two dates: May 27, 1904, and October 6, 1905.

Females with eggs. Ortmann (1906: 486) found females with eggs in July and August. The number of eggs was between 7 and 133, the smallest number on the smallest individual.

Females with young. My three records are April 1940 (DWC 74), April 22, 1951 (DWC 77) and August 29, 1952 (NYSM 7014). Ortmann (1906: 486-487) reports females with young taken in the months of February, March, August, September and November. The February record is for New Jersey. I have taken immature specimens under 15 mm. carapace length in May, June, July and August.

Size at sexual maturity. The smallest male I which I have seen is 18.5 mm. carapace length (NYSM 6989). The next smallest is 21.4 mm. (DWC 120) and I have a few others close to this. The

smallest male I of *C. b. bartoni* reported by Ortmann (1906: 487) is 49 mm., total length.

The only female with young for which I have a measurement is 28.8 mm. carapace length (DWC 74). Ortmann's smallest female with either eggs or young is 48 mm., total length, which is approximately 7 mm. smaller than my smallest *C. robustus* (a female).

Maximum size. Male I, 36.7 mm., carapace length (DWC 118).
Male II, 36.3 mm., carapace length (DWC 108).
Female, 38.8 mm., carapace length (DWC 108).

Size comparison of *C. b. bartoni* and *C. robustus*. The above data indicate that *C. b. bartoni* is a distinctly smaller species; from 7 to 13 mm. smaller in minimal size at sexual maturity and approximately 16 mm. smaller in maximum size.

TABLE 15

Frequency of occurrence of *Cambarus b. bartoni* with other crayfish species in collections made in New York. Tabulated from D. W. Crocker collections 1-158, NYSM 6976 (stream survey collections) and NYSM 6977-7022 (collected in August 1952)

DRAINAGE	*C. robustus*	*O. immunis*	*O. limosus*	*O. obscurus*	*O. p. propinquus*
Genesee R.	3			1	1
Oswego R.	10				5
L. Erie-Niagara R.	1			1	
Grass, St. Regis & Salmon R.					3
Oswegatchie & Black R.	1				1
Upper Hudson R.	1				
Raquette R.	2				
Mohawk-Hudson R.	1	1		1	
Susquehanna R. (East)		1	5		1
Allegheny R.	5			7	
Chemung R.		2	3		2
Misc. L. Ontario tribs.	2				

Smaller size at sexual maturity may be due either to reaching such maturity at an earlier age in *C. b. bartoni* or to reaching maturity at the same age, but at a smaller size due to a slower growth rate. Both factors may, of course, be in operation. Smaller maximum size may be produced by a slower growth rate, a shorter life, or both.

Habitat. *C. b. bartoni* is typically a mountain stream form, occurring most commonly in cool, fast flowing, well-oxygenated water where there is a bottom of boulders and rubble. If it is found in larger streams, then it is almost invariably at the point of entrance of cold spring water. Burrowing has not been observed in New York State.

Crayfish associates of this species are listed in table 15.

Procambarus b. blandingi

There are six members of the Blandingi subgroup; namely, three subspecies of *P. blandingi* and in addition *P. hayi, P. lecontei* and *P. bivittatus* (Hobbs 1942*b*: 94). Practically nothing is known about the life histories of any of these. Hobbs (1942*b*: 95) reports 37 males I of *P. b. acutus* taken in Florida in May. In the same publication (p. 98) he also states that of 133 specimens of *P. bivittatus* taken in Florida in the months of April, May and October, first form males were taken in May. Penn (1943) has worked out the life history of a member of the same genus, *P. clarki*, but this species is in a different subgroup of the genus and the locality of study is Louisiana. His data may or may not apply to the present species. Penn (1943: 14) places sexual maturity of both males and females of *P. clarki* at 31-32 mm. carapace length.

Seasonal data. The three stream survey collections containing *P. b. blandingi* were all taken in July (NYSM 1936: 2960, 3576 and 3616). They contain two males I, one male II (soft), and two females (one soft). Collection USNM 74747, taken in August from the Bronx River, New York City, contains a male I and a female of *P. b. blandingi*. The female has a sperm plug. Collecting in the Bronx River on August 25, 1952 produced one male I, two males II, six females and one female immature (NYSM 6999).

Habitat. Of its preferred habitats, only slightly more is known. Abbott (1873: 80) describes it as a plant-loving species in New Jersey, frequenting clear running streams where it is to be found resting on aquatic plants, usually near the water surface. Later (Abbott 1886: 167), he decides that this species is not so restricted in habitat. P. R. Uhler, according to Faxon (1885*b*: 23), reports

P. b. blandingi from salt marshes covered twice daily by the tides in company with *Cambarus uhleri*, and characterizes this species as belonging to the lowlands at the mouth of sluggish rivers or near the ocean in muddy and grassy ditches and drains. Uhler also found it in a ditch near Ocean City, Worcester County, Md. in holes six to nine inches deep, and at Goldsborough, N. C. in drains and branches running through cotton fields.

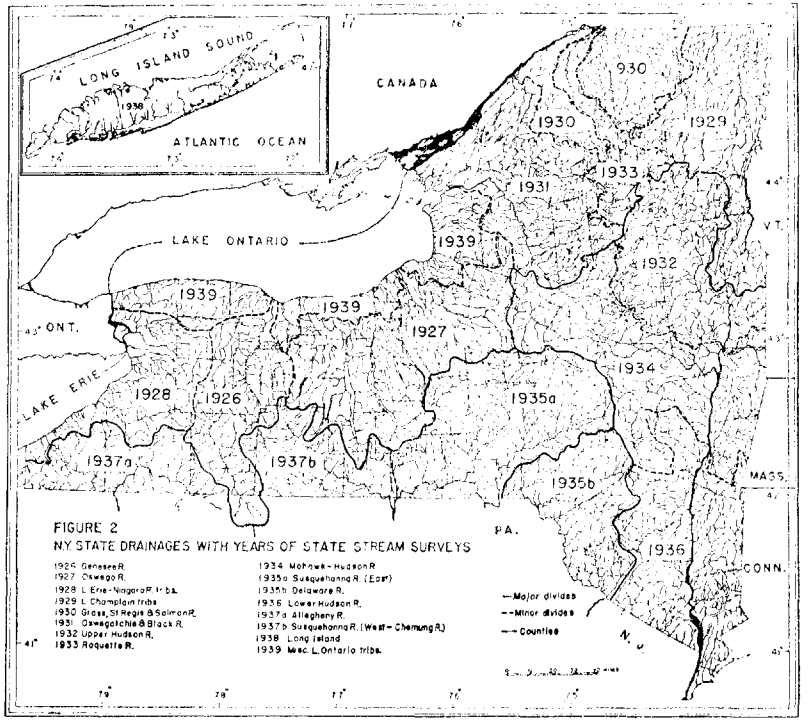
The only New York State locality for this species, Bronx River, has been studied by F. R. Nevin (1937: 228-230) with reference to the quantities of food organisms of fish. He reports that in the vicinity of White Plains, crayfish (unidentified) and mollusks occur in greatest quantity (weight per square foot) and that it is also here that sewage pollution is greatest. He also states that, except for the northern part, the stream has few stony areas and that when stones are present they are set in sand. Finally, he mentions that pollution other than sewage is prevalent within the limits of New York City and that the stream margins here are mud, mingled with a mass of decaying vegetation.

My August 1952 collection from Bronx River at White Plains North Station (NYSM 6999) was made in knee-deep muck.

Crayfish associates. Three NYSM collections from the lower Hudson River contain *O. limosus* in addition to *P. b. blandingi*.

DISTRIBUTION

Figure 2, following, should provide a ready reference to the names of the drainage systems in New York State and to the years during which stream surveys were made.



Procambarus b. blandingi

(FIGURE 3)

Procambarus blandingi consists of three subspecies: *P. b. blandingi* (Harlan), *P. b. acutus* (Girard) and *P. b. cuevachicae* (Hobbs). *P. b. blandingi* is restricted, in so far as is known, to the Atlantic coastal plain from the Bronx River, New York to at least as far south as South Carolina. *P. b. acutus* is distributed in the Mississippi River system. *P. b. cuevachicae* is described from La Cueva Chica, a limestone cave in the State of San Luis Potosi, Mexico.

The questionable status of the members of the *blandingi* complex has already been mentioned and it is inadvisable to attempt dis-

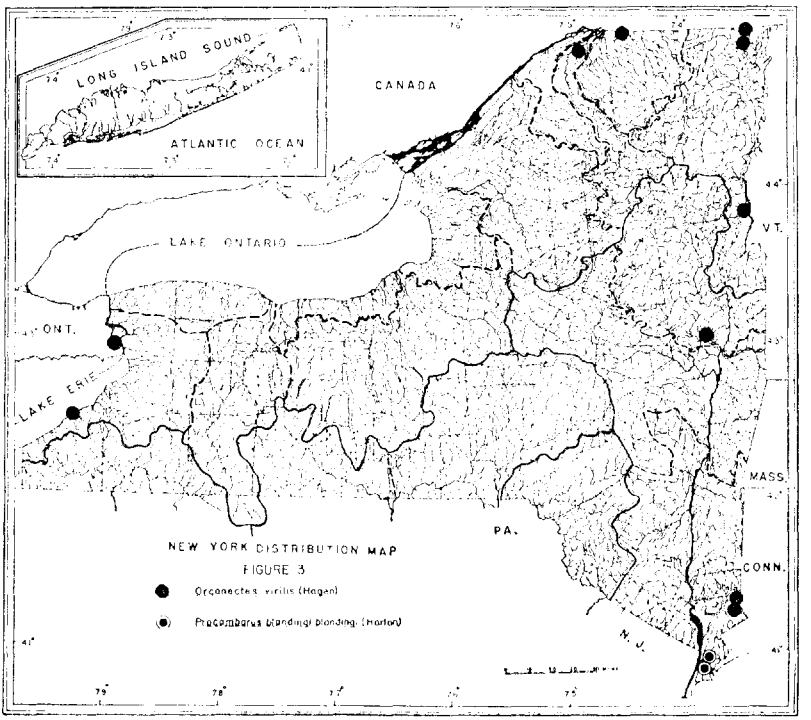
tributional theorizing until larger series become available and are studied.

The pattern of distribution in a very general sense has been investigated by Ortmann (1905*a*: 103-106). He places the origin of what is now the genus *Procambarus* in Mexico, and of the Blandingi section in the southern States, chiefly Alabama and Georgia. Ortmann (p. 105) states of the Blandingi group that it ". . . invaded (*C. fallax*) northern Florida and spread out northeastwardly along the Atlantic coastal plain (*C. blandingi-typicus*), and also it migrated westward and northward, up the Mississippi Valley (*C. hayi* and *blandingi acutus*)."

P. b. blandingi has reached New York by following the retreating ice northward along the coastal plain, but has not left its lowland habitat.

The only acceptable published report of this subspecies in New York (Faxon 1885*b*: 19) gives no specific locality.

Mayer (1911: 88) says, "In the neighborhood of New York we find three common species." He lists *P. b. blandingi* as one of these, but no specific localities are given, and the description of habits appears to have been taken from Abbott (1873: 80).



Orconectes virilis

(FIGURE 3)

Orconectes virilis ranges through a number of states in streams tributary to the Mississippi River. Northward it extends into Saskatchewan and Ontario. In Ontario, Huntsman (1915: 161) reports it as "... quite abundant in Georgian Bay but not [as abundant] in Lake Ontario." It is pointed out under the discussion of distribution of *C. robustus* that its limits in Canada are unknown. *O. virilis* is absent from Pennsylvania (Ortmann 1906). Turner (1926: 176-178, map 1 on p. 171) gives records for southwestern Ohio, but Rhoades (1944*a*: 96) has not been able to substantiate these records in the field. He states that *O. virilis* will undoubtedly be found in the extreme northeastern counties of the State, which Turner also suggested. Pearse (1910: 18) describes it as the most abundant species in the northern part of Michigan.

In New York, its distribution as now known suggests two entrances from the west, for there are no known populations on the coastal plain of Lake Ontario between the five northeastern localities and the Lake Erie-Niagara River records. The separating area has been well sampled (see figures 4, 5 and 6) and the habitat is relatively uniform and apparently not unlike that in the localities where *O. virilis* has been taken in New York.

The Lake Erie-Niagara River localities may represent an entrance as early as the time of Lake Maumee. The northeastern records are accounted for by an entrance from the west into what are now western St. Lawrence waters, through the Kirkfield or Ottawa outlets (Leverett and Taylor 1915: 410 and plate 21). These outlets existed in Lake Algonquin time before the invasion of the Champlain Sea. Furthermore, during this time the Hudson and Champlain waters were united and the localities in the Hudson River drainage in Saratoga Springs and in Westchester County may perhaps be explained as relict populations. However, one cannot ignore Faxon's (1885*b*: 98) report that *O. virilis* and *O. immunis* are two of the western species of crayfish most esteemed as food and that they are sometimes sent to the New York market from Milwaukee and other western cities.

Hagen (1870: 65) gives the oldest record for this species in New York. Faxon (1885*b*: 98) has cast doubt on Hagen's record, a dry specimen from Lake George, pointing out that the labels of dry specimens are easily transferred. However, I have substantiated Hagen's record by taking *O. virilis* at Ticonderoga on August 20,

1952 (NYSM 6985). The only other previous New York record is for the Raquette River watershed (Creaser 1934).

Orconectes immunis

(Figure 4)

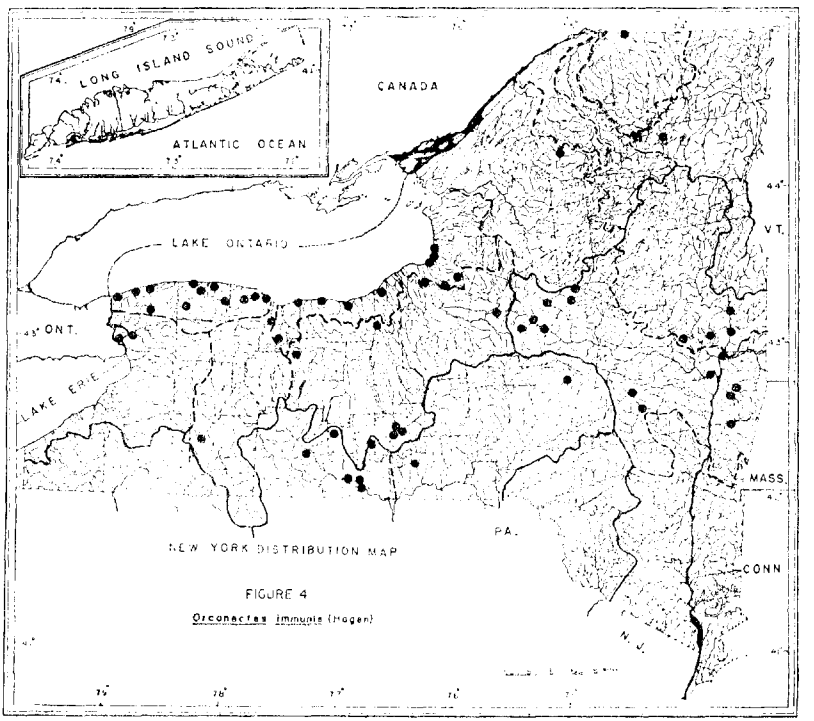
The distribution of *O. immunis* is generally widespread and like that of its close relative *O. virilis*. That the two close forms can occupy such a similar territory is probably due to their different habitat requirements. In the west at least, *O. virilis* appears to be typically a stream form and *O. immunis* an inhabitant of ponds and ditches.

The literature contains nine New York locality records for this species:

Faxon (1898: 654). MCZ 4330; Small stream tributary to Oneida Lake.

Ortmann (1906: 467). Rensselaer Lake, Rensselaer County.

Faxon (1914: 378-379). USNM 22,417; pond near mouth of Cattaraugus Creek, Chautauqua County.
USNM 22,408; Silver Creek, Chautauqua County.
USNM 22,418; Fish Creek, Buffalo, Erie County



USNM 22,409; Stony Island at the eastern end of Lake Ontario, Jefferson County.

Creaser (1934). Raquette River.

Nevin and Townes (1935). Mohawk-Hudson drainage.

Tack (1941). Ithaca, Tompkins County.

Thus three records are known (USNM 22, 417; 22,408; 22,418) in the Erie-Niagara drainage in addition to the two shown in figure 4. Its apparent scarcity in this drainage may be due to poor coverage.

The distribution of *O. immunis* in New York can be accounted for by an entrance from the west in Lake Lundy time or perhaps not until Lake Iroquois (Fairchild 1912: plate 17).

In view of the absence of *O. immunis* from the Allegheny River, I attribute the single locality shown in figure 4 in the upper Genesee River above the falls at Portageville, to introduction by man.

An isolated locality for this species in the eastern Susquehanna (Oakes Creek, NYSM 1935: 702) shown in figure 4, might be accounted for by a connection between glacial Lake Herkimer in the Mohawk Valley and the Susquehanna through the Otsego Valley (Fairchild 1912: 39, plate 1). If one assumes that *O. immunis* reached the isolated locality through this Lake Herkimer outlet, then one is still faced with a problem: Why did it not achieve wider distribution? Perhaps competition with the already established *O. limosus* prevented the spread of *O. immunis*, but there is no information bearing on this from other areas because the two species do not normally come in contact. In fact, present knowledge of the distributions of these two species indicates that only in New York and the northern New England States (from which latter there is almost no information) could one expect to find them together. Collecting in the eastern Susquehanna has not been intensive, but coverage is fair (figures 5 and 7) and I do not think the apparent general absence of this species from the region can be attributed to poor sampling.

Ortmann (1906: 466-467) was unable to find *O. immunis* in Pennsylvania, and it is my opinion that the Susquehanna River drainage records in New York near the confluence of the Chemung and Susquehanna proper are also best explained by recent entry. Dr. Robert Ross, now of Virginia Polytechnic Institute, has told me that in the Cayuta Lake area in times of flood, one can stand on the Susquehanna-Oswego River divide knee deep in water. This offers a satisfactory explanation for the entrance both of *O. immunis* and *O. p. propinquus* (figure 5) into the Susquehanna River system.

O. p. propinquus and *O. obscurus*

(Figure 5)

Ortmann (1906: 434-447) has discussed the distribution of these two species and a third form, *O. p. sanborni*, in detail. The distributions of *O. p. propinquus* and *O. obscurus* in New York present no contradictions.

Ortmann places the origin of these three crayfishes, each in one of three tributaries of the preglacial Old Erigan River which ran in a northeasterly direction. With the advance of the ice, three populations of the original stock were isolated and underwent differentiation – *O. p. propinquus*, most westerly in the Old Miami or Cincinnati River; *O. p. sanborni* in the center in the Old Kanawha; *O. obscurus* in the east in the Old Monongahela. The ice, melting and receding, formed lakes of the eastern and central areas which eventually drained southwest and united all three localities. The western area became the lower Ohio River, the central became the middle Ohio and the eastern became the upper Ohio, which also united with the Allegheny River.

However, the western region opened up first and *O. p. propinquus* was enabled to make its way to Lake Maumee, thus accounting for the distribution in Indiana, Illinois, Iowa and Wisconsin. Data now made available for New York indicate that *O. p. propinquus* followed eastward the shores of Lake Maumee and its subsequent stages, Lake Lundy and Lake Iroquois, and was also able to enter the St. Lawrence when it was formed.

One is tempted to account for the presence of *O. obscurus* in the Genesee River by entry through the Olean outlet, a connection between the Genesee and Allegheny (stage 2 of Fairchild 1912: plate 10). However, it is a question whether or not *O. obscurus* entered the Susquehanna River system during a later connection between it and the Genesee (Fairchild, 1912: plate 11). It is possible, of course, that *O. obscurus* entered the Genesee before the Genesee-Susquehanna connection appeared and that it did not utilize this subsequent connection.

My two records of *O. obscurus* in the Susquehanna system are from isolated ponds (NYSM 1937: 2049 and 4517). The coverage of the area is poor and further collecting is needed before it can be said whether they more probably represent natural populations or introductions by man.

However, should the Susquehanna records be best explained as introductions by man, there is another means by which *O. obscurus* may have made the passage across the Allegheny-Genesee divide

after the closure of the Genesee-Susquehanna connection. This would therefore make it unnecessary to assume that, although the connection was available to *O. obscurus*, it was not utilized. Ortmann (1906: 443), unable to find *O. obscurus* in the Susquehanna drainage in Pennsylvania, accounts for its presence in the Genesee by known instances of the capture of morainic lakes, originally draining into the Allegheny system, by Genesee River tributaries (Fairchild, 1896: 447). These captures may have occurred after the closure of the Genesee-Susquehanna connection.

The populations of *O. obscurus* which occur in a restricted area of the Lake Erie drainage in Ohio and Pennsylvania are accounted for by cases of stream capture which are known in this area or by migration through canals (Ortmann, 1906; 441-442). This species has apparently been restricted from migration down the Ohio River by the presence there of its close relative *O. p. sanborni.*

O. obscurus may have moved eastward as early as Lake Whittlesey time, utilizing lakes at the edge of the ice, and may have entered the Mohawk River drainage as late as very early Lake Iroquois time, when a connection at what is now Rome would have permitted this (Fairchild, 1912: plate 16). Collection USNM 74,708 is an additional record for this species in the Mohawk River. At this same time there was also a union of the Mohawk and Black River drainages which would account for the records of *O. obscurus* in the Black River. However, its present distribution in the Mohawk and Black Rivers may also be accounted for by a following of the Erie barge canal eastward and an entrance into the Black River through the Trenton feeder. A single specimen is the basis for the record of *O. obscurus* at Long Lake in the town of Long Lake in the headwaters of the Raquette River drainage. Verbal testimony from bait dealers in this area indicates that large numbers of crayfishes are brought into the Adirondacks from numerous regions, particularly from the barge canal in the vicinity of Utica.

The species-locality of an old (1893) collection of *O. obscurus* in the United States National Museum (USNM 44,751), labeled as coming from Cattaraugus Creek in the Lake Erie drainage of New York (reported by Faxon, 1914: 374), has been substantiated by my collecting in 1952 (NYSM 7015). A connection between the Allegheny River and a glacial lake in the Cattaraugus Valley (Fairchild, 1912: plate 11) could account for the entrance of *O. obscurus* into this area.

Collection USNM 74,712 consists of five male *O. obscurus*, collected by H. K. Townes, August 31, 1934, in Kinderhook Creek at Kinder-

hook (Columbia County). I am unable to account for this species-locality. It is 100 miles from the upper Mohawk where the main body of the Hudson drainage members of this species is located. Subsequent collecting in the Kinderhook-Valatie area (DWC 132) has produced only *O. limosus*.

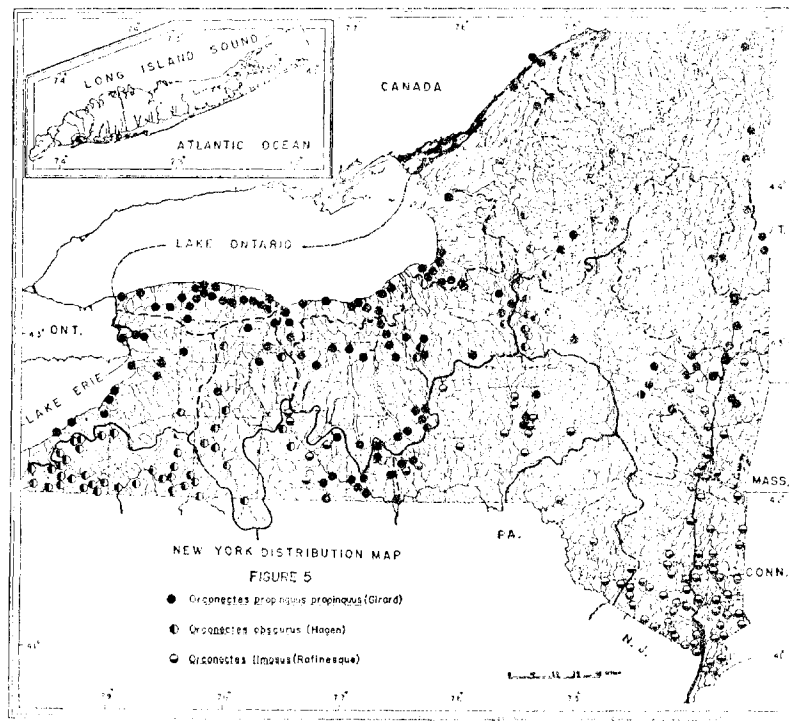
O. p. propinquus must not have entered the northern drainages of New York State before Lake Hall time, for previous to this time there were connections between the Genesee and Susquehanna and also direct drainages through what are now the Finger Lakes. I can not believe that the records for *O. p. propinquus* in the Susquehanna at the present time are due to an early entrance. In this system there are now, at least, no crayfishes which in present times are competitors with *O. p. propinquus*. *O. limosus* and *C. b. bartoni* have distinctly different habitat preferences. One wonders why it should not have achieved wider distribution had it entered early. It seems preferable to account for the localities near the confluence of the Chemung and Susquehanna proper by an entrance at Cayuta Lake, draining into Cayuta Creek (also known as Shephard's Creek). Under *O. immunis* it is pointed out that stream capture is taking place in the Cayuta Lake area at the present time. Figure 5 seems to indicate that in the restricted region involved, *O. p. propinquus*, the invader, is replacing *O. limosus* from the latter's home territory.

Three isolated localities for this species in the eastern Susquehanna (Unadilla River; NYSM 7006, 7009, 7011) shown in figure 5, might be accounted for by a southern outlet of glacial Lake Herkimer (in the Mohawk Valley) passing into the Susquehanna through the Unadilla Valley (Fairchild 1912: 39, plates 1 and 13). However, if this species is gaining territory in competition with *O. limosus* slightly further west, then one would expect it to have gained far greater territory here in the eastern Susquehanna if it arrived here at a much earlier time. I consider the three records to be a result of recent introductions.

The distributions of *O. p. propinquus* and *O. immunis* are similar, not only in the Susquehanna River system in New York, but throughout the State.

Five previously recorded New York localities are available for *O. obscurus:* Genesee River at Rochester (Hagen 1870: 70); Allegheny River drainage at Salamanca (Ortmann 1905c: 402–404); Cattaraugus Creek, Lake Erie drainage (Faxon 1914: 374); Mohawk-Hudson drainage (Nevin and Townes 1935); Lake Chautauqua, Allegheny drainage (Townes 1938).

New York localities for *O. p. propinquus* are given by Girard (1852: 88), Hagen (1870: 68-69), Faxon (1885*a*: 360; 1885*b*: 91; 1914: 373-374), Ortmann (1906: 363), Goodnight (1940*a*: 171; 1940*b*: 34), Creaser (1934) and Nevin and Townes (1935). Creaser discusses distribution in the Raquette River system and Nevin and Townes do the same for the Mohawk-Hudson. The other references cited list a total of 41 localities. None of these forms an exception to the distributional pattern in New York as determined in the present study.



Orconectes limosus

(FIGURE 5)

Outside of New York, the only locality records for this species which, up to the present time, have not been doubted by any students of crayfishes, lie in the States of Pennsylvania, Virginia, District of Columbia, Maryland and New Jersey.

Four locality records lie in drainage systems entirely outside the major distributional area of this species at a distance from the area of at least 130 miles. These records are: Niagara (Hagen 1870: 62), Lake Erie (Hagen 1870: 61), Lake Superior (Faxon 1885*b*: 87),

and Ontario (Huntsman 1915: 160). Faxon (1885*b*: 87) retains the localities Lake Erie and Niagara, but (1890: 629) drops the Lake Erie record because the specimens "... are too small to determine with certainty." Ortmann (1905*a*: 131-2) doubts the three older records and a year later (1906: 430) says, "No positive record from New York State is at hand (see DeKay, 1844, p. 23, and Paulmier, 1905, p. 117)."

I have seen the Niagara specimens (MCZ Crust. 179). As small as they are (the largest carapace length is 17.0 mm.) they are definitely *O. limosus*. Ortmann (1905*a*: 132) explains this record by suggesting that these specimens were put by mistake into a bottle containing *O. p. propinquus*. Hagen (1870: 62, 69) does give the same locality and collector (L. Agassiz) for these two species.

The Lake Superior specimens are apparently lost. Faxon (1885*b*: 87) reports them as being in the collections of the Boston Society of Natural History. In the summer of 1955, I was not able to locate them at the Boston Museum of Science or at MCZ.

The Lake Erie specimens were reported by Faxon (1885*b*: 87) as being in the collections of the Peabody Academy of Science. I am informed through conversation and correspondence with Dorothy E. Snyder of the Peabody Museum (Salem, Mass.) that this collection is not now at the museum. Some materials were moved from the Peabody Museum to the MCZ in 1942, but this collection apparently was not one of them. However, there is a specimen at MCZ (Crust. 306; new catalog 3800) which the Crustacea catalog reports as being received from the Peabody Academy of Science in November, 1885. The old label in the jar reads, "*Cambarus affinis*?, Lake Erie, F. W. Putnam." It may be that this is one of the Peabody Academy specimens in question. It is a female, carapace length 17.2 mm., and is not *Cambarus affinis* (= *O. limosus*). It is most like *O. p. sanborni*, for it has a seminal receptacle like *O. p. propinquus*, yet it lacks a rostral carina. This subspecies occurs in the Lake Erie watersheds of Ohio and Pennsylvania (Ortmann 1906: 439 and plate 42, figure 3).

The Ontario specimens were taken at Iroquois, a town on the St. Lawrence River about five miles west of Waddington, N. Y. The collector of these specimens, Dr. A. R. Cooper, wrote me on July 19, 1955, that he could not now remember the circumstances of collecting, in particular whether or not the crayfishes were local. On the basis of Huntsman's figures (1915: figures 8*c*, 9*c*, 10*c* and 12*d*) which are unquestionably *O. limosus*, the specimens were correctly identified, but Huntsman did not specifically state from which specimens

the figures were drawn. In August 1952, I collected at Iroquois and also directly across the river, but obtained only *O. p. propinquus* and *C. b. bartoni* (NYSM 6987, 6989).

In summary, the present status of these four records is: (1) the Niagara specimens are accurately identified, but a mixup of specimens might have occurred; (2) the Lake Superior specimens are apparently lost; (3) the Lake Erie specimens have been either lost, or, if a specimen now at MCZ is one of them, it is not, and probably therefore the rest were not, *O. limosus;* (4) there is no reason to doubt the Ontario record except because of the isolated locality. None of these records has been substantiated in the last 50 years of collecting on the U. S. boarders of Lake Superior (Wisconsin: Graenicher 1913, Creaser 1932; Michigan: Pearse 1910, Creaser 1931) and Lake Erie (Ohio: Turner 1926, Rhoades 1943 and 1944*b*; Pennsylvania: Ortmann 1906) or in the St. Lawrence River drainages in New York (present study).

An old record for New York without specific locality, given by Hagen (1870: 62) is omitted by Faxon (1885*b*: 87). No reason is given for the omission, but it is presumably because of the lack of specific locality data. I have examined the collection (MCZ Crustacea catalog 270), a single female, and I consider it definitely to be *O. limosus.*

Mayer (1911) says, "In the neighborhood of New York we find three common species." However, no specific localities are given. Furthermore, of the three species, the locality for the figured specimen of *Cambarus bartoni* is given as Orange Mountains, N. J. The discussion of *Cambarus blandingi* appears to be taken from Abbott (1873: 80), and *Cambarus affinis* is mentioned in connection with its being "... commonly sold in the New York markets." I would hesitate to assign any one of these three species to the State on the basis of these statements.

Two specific localities for *Orconectes limosus* in New York are given by Osborne (1912: 924): Central Park Lake, New York City, and Prospect Park Lake, Brooklyn. His description and photograph of this species (Osborne 1912: 925) leave no doubt as to its identity. Townes (1937: 226) reports *O. limosus* at Coxsackie, Greene County, Hudson River drainage. Until the present study, these have been the only unquestioned specific New York localities.

Human agencies may have had something to do with the dispersal of *O. limosus.* Faxon (1885*b*: 89) says, "*C. affinis* is the common crayfish exposed to sale in the markets of New York and other eastern cities."

The entrance of *O. limosus* into New York State has probably been effected by separate entrances in the Delaware, Hudson and Susquehanna systems, perhaps following closely the recession of the ice.

Until the validity of northern records is ascertained it is hardly possible to discuss further the routes of dispersal of this species.

The nearest relatives of *O. limosus* are found in Kentucky, Southern Indiana and Missouri, and, as Ortmann points out (1905*a*: 114), this geographical isolation of *O. limosus* accompanied by morphological isolation indicates the antiquity of the *Limosus* section.

Cambarus robustus

(Figure 6)

Ortmann (1906: 449) was unable to find *C. robustus* in the Susquehanna or Delaware drainages in Pennsylvania and it is apparently restricted in that State to the watersheds of the Allegheny River and Lake Erie. The one exception is Ortmann's record from Chartiers Creek, Allegheny County, and this stream enters the Ohio River opposite the entrance of the Allegheny.

In Ohio, which has been extensively surveyed for crayfishes, Turner (1926: 185, and map 5, p. 184) gives nine localities for *C. robustus* in the northeastern portion of the State in Lake Erie drainages. In addition he gives nine other localities in the Ohio River drainage. Seven are in the Scioto River system and have been referred by Rhoades (1944*b*: 96) to his *C. b. sciotensis*. Of the remaining two localities, one is Big Jelloway Creek, given by Turner (p. 185) as Knox County, but the record on his map 5 is in Licking County. The drainage here is apparently the Muskingum River. The other record is the Ohio River, Lawrence County, at the southern tip of the State. These last two localities may also be *C. b. sciotensis*.

Creaser (1931: 267-269, map 6) has plotted the range of this species in Michigan. It is apparently absent from Wisconsin (Creaser 1932: 336, table 1). The materials on which the records for this species at the periphery of its range are based should be reexamined wherever possible. This is particularly true to the south where there are records for the State of West Virginia (Faxon 1914: 388 and Newcombe 1929: 285). Records for Virginia, Maryland and Illinois, given by Faxon (1885*b*: 61 and 1890: 622) are subsequently dropped by him (Faxon 1914: 388).

Ortmann (1906: 392-3, 450) points out that the records he gives for *C. robustus* in Maryland, Virginia and Kentucky may be a different form.

Fowler (1912) does not report *C. robustus* from New Jersey, but he gives no specific account of how extensive his collecting was.

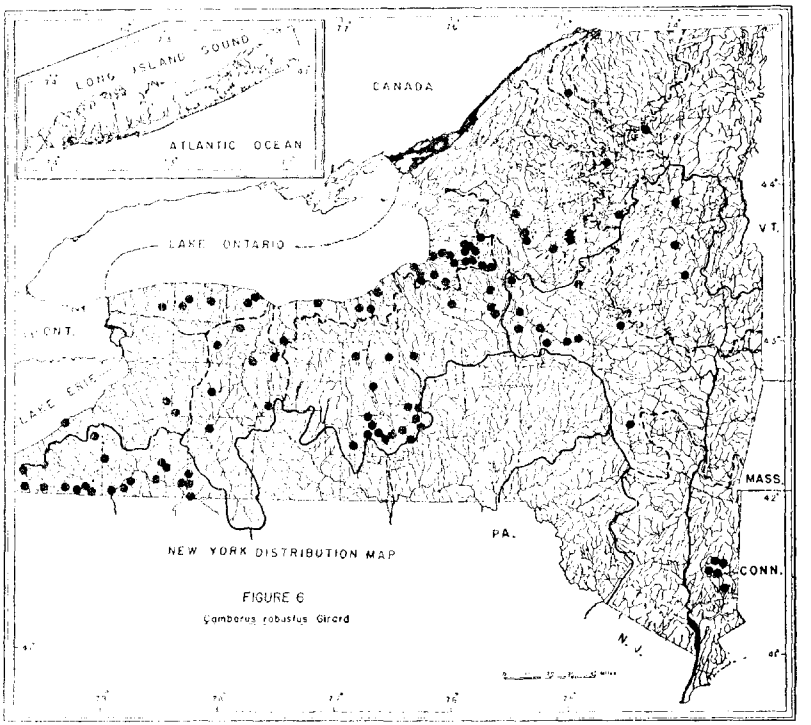


FIGURE 6
Cambarus robustus Girard

Fowler's description of *C. b. bartoni* seems to exclude *C. robustus* except possibly for the statement concerning the areola: "... with about three to five rows of punctures irregularly." His figures (plates 100, 101) are distinctly *C. b. bartoni* in shape of hand and rostrum.

In addition to the type locality, the other reports of *C. robustus* in Canada are mostly from near Toronto, Province of Ontario (Faxon 1885*b*: 61). However, Huntsman (1915) reports it from western Ontario also. Information from both Ontario and Quebec is much needed in order to define the limits of this species as well as of *C. b. bartoni* and *O. virilis* in Canada.

Thus, there is left, of records from the literature which have not been doubted and including the New York distribution here presented, the following picture of the distribution of this species. *C. robustus*, as known at the present time, inhabits an area extending eastward to the Hudson River drainage system, and in the west to Michigan. To the north it is reported from Canada and to the south its boundaries are poorly defined, probably not entering the Ohio River drainage in the State of Ohio, and restricted to the Allegheny River and Lake Erie drainages in Pennsylvania. It is

absent from the Susquehanna and Delaware drainages in New York State.

A total of 15 specific locality records for *C. robustus* in New York is given by Hagen (1870: 80), Faxon (1885*c*: 358; 1885*b*: 61; 1898: 649; 1914: plate 3) and Ellis (1920: 250). Creaser (1934) reports the distribution of this species in the Raquette River system. None of these records is in disagreement with the general pattern of distribution in New York as established by the present study.

C. robustus has apparently originated from a present member of, or a stock ancestral to, *C. montanus*, and its region of origin appears to be southeastern Ohio or western West Virginia. From here it has migrated to the north and then to the east and west.

One might easily postulate that *C. robustus* and *O. obscurus* originated together in the same area, of course from different stocks. If, in the distributional summary based on Ortmann, which I have given under the distribution of *O. obscurus* and *O. p. propinquus*, the name *C. robustus* be substituted for *O. obscurus*, there is no apparent contradiction to the line of reasoning.

It is here suggested then that *C. robustus* differentiated in one of the tributaries (the Old Monongahela) of the preglacial Erigan River along with *O. obscurus*. Its dispersal, subsequent to the recession of the ice, has been basically the same as for *O. obscurus*, but with the difference that it has extended itself further to the north, west and east. This has been possible because, on reaching the Great Lakes drainages, *O. obscurus* found a close relative, *O. p. propinquus*, already occupying these areas. *C. robustus*, on the other hand, although having habitat preferences similar to those of *O. p. propinquus*, is much more distantly related to it and has a distinctly different life history. It is apparently much less in competition with *O. p. propinquus* than is *O. obscurus*. To the north and east, *C. robustus* occupies nearly the same range as *O. p. propinquus*, but has not extended as far west, and this is explained by *O. p. propinquus* having a more direct and earlier start in that direction. *C. robustus* arriving later, at a time when the glacial lakes were smaller, would have access to fewer stream systems.

Although *C. robustus* has progressed further to the north, east and west than has *O. obscurus*, it does not apparently extend as far south in the Allegheny River system. Ortmann (1906: 449) admits, however, that it may be in Forest, Venango and Armstrong Counties.

It should be noted further that the relationship between the present distributions of *C. robustus* and *C. b. sciotensis* is similar to the relationship between the present distributions of *O. obscurus*

and *O. p. sanborni* (see Ortmann 1906: pl. 42, fig. 3). The line of reasoning applied by Ortmann (1906: 434-438) to the origins of *O. obscurus* and *O. p. sanborni* may equally well be applied to *C. robustus* and *C. b. sciotensis*. *C. robustus* is analogous to *O. obscurus* and *C. b. sciotensis* is analogous to *O. p. sanborni*. Here is evidence, in addition to morphological similarities, of the close relationship between *C. robustus* and *C. b. sciotensis*.

Ortmann (1905*a*: 121) places the origin of what is now the genus *Cambarus* at the southern extremity of the Appalachian system of mountains.

Cambarus bartoni bartoni

(FIGURE 7)

Records of *C. b. bartoni* in New York are given by Rafinesque (1817: 42, as *Astacus pusillus* and *A. ciliaris*), DeKay (1843: 22-23), Hagen (1870: 79), Smith, S. I. (1874: 639), Faxon (1885*b*: 60; 1885*c*: 358; 1914: 383-4), Ortmann (1905*a*: 134; 1906: 384), Paulmier (1906: 134), Creaser (1934), Nevin and Townes (1935) and Goodnight (1940*b*: 34, 38). Creaser and Nevin and Townes discuss distributions in the Raquette and Mohawk-Hudson Rivers respec-

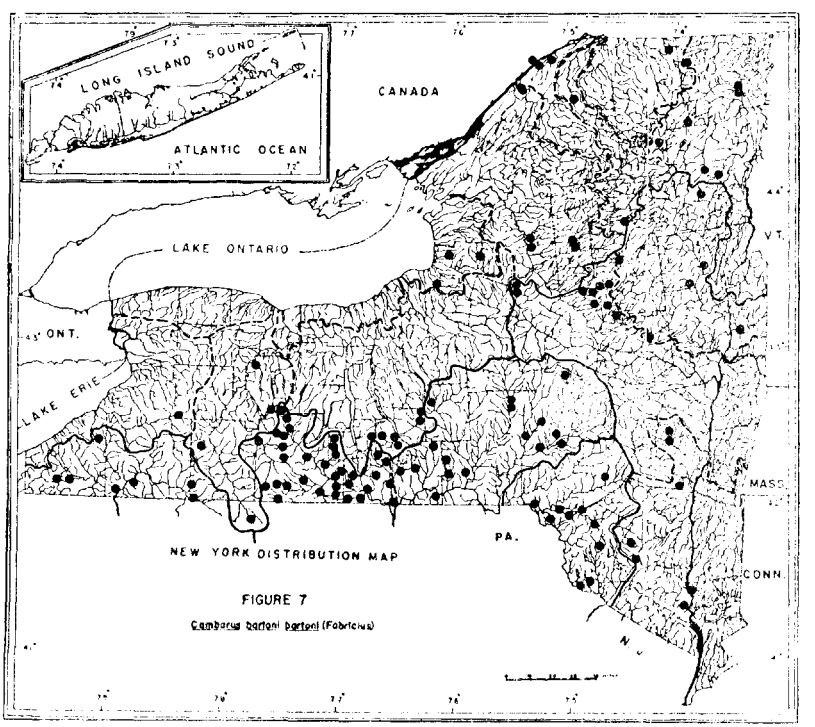


FIGURE 7

Cambarus bartoni bartoni (Fabricius)

tively. DeKay's report gives no specific localities, but is interesting because of its age. The remaining authors give a total of 38 specific, at least somewhat restricted, localities. None of these is in disagreement with the general pattern of distribution in New York as established by the present study.

C. b. bartoni probably occurs throughout New York. The regions in which it is absent on the distribution map are the Erie-Niagara drainages and the miscellaneous tributaries along the southern shore of Lake Ontario.

Tables 16, 17 and 18 show that material is poor for the Erie-Niagara system and furthermore, Faxon (1885*b*: 60) gives Niagara (Niagara Co.) and Forestville (Chautauqua Co.) as localities for this species. More collecting here will undoubtedly turn up at least a few more records.

There are no records in the literature for the occurrence of this species in the miscellaneous Lake Ontario tributaries where figure 7 shows it to be apparently lacking. The New York State Museum crayfish collection is particularly rich for this region, yet not one specimen of the present species has been collected. I think the reason for its absence here is the lack of suitable habitats. This is a lowland area with numerous slow, meandering streams, entirely different from habitat preferences of *C. b. bartoni* elsewhere. There is a record (Faxon 1885*b*: 60) for *C. b. bartoni* at Rochester in the Genesee River which is in the east-west center of the area in question. Certainly there are no physical barriers to its dispersal along the shore of Lake Ontario east and west from Rochester. One can most reasonably conclude that it is absent because there are very few suitable places for it to live.

The entrance of *C. b. bartoni* into New York was probably made at several points. It may have entered the Hudson directly, or through the Susquehanna into the Mohawk-Hudson by way of the Unadilla outlet (Fairchild 1912, plate 5). Its entrance into the Genesee could have been accomplished through a connection which persisted through stages three and four of Fairchild (1912, plates 11 and 12), or later (stage five) by way of what are now the Finger Lakes. The entrance of *C. b. bartoni* into the Allegheny River drainage probably took place outside of New York. From the Allegheny it may also have entered the Genesee through the Olean outlet.

Any consideration of dispersal of this species must take into account its habitat. As a mountain stream form it is particularly susceptible to dispersal by stream capture and its dispersal along

TABLE 16

Summary of crayfish collections in the New York State Museum taken during stream survey operations, 1926-1939

Species \ Drainage	Oswego R.		L. Erie Niagara R.		L. Champlain		Grass, St. Regis & Salmon R.		Oswegatchie & Black R.		Hudson River						Raquette R.		Delaware R.		Susquehanna River				Allegheny R.		Misc. L. Ontario tribs.		Total	
											Upper —1932		Mohawk —1934		Lower —1936						East —1935		West —1937							
Year[a]	1927		1928		1929		1930		1931								1933		1935						1937		1939			
	Coll.[b]	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.
Cambarus b. bartoni					4	4	1	1			5	31	14	19	8	9	1	76	9	14	4	5	36	64	5	7	3	5	90	235
C. robustus	1	1	3	3	1	1					1	1	5	14	5	8	2	6							17	43	54	183	89	260
Cambarus sp.															2	2									2	2	1	1	5	5
Orconectes immunis			1	3	2	2			1	1	3	8	10	33							1	3	7	15			37	90	62	155
O. limosus													13	25	99	212			5	14	2	3	7	20					126	274
O. obscurus	1	2											10	18									2	6	46	192			59	218
O. p. propinquus	7	11	19	40	2	2	1	1			4	6	13	65									11	33			83	199	140	357
O. virilis			2	10	1	1									2	2													5	13
Orconectes sp.																							4	4	1	2	3	6	8	12
Procambarus b. blandingi															3	5													3	5
Total	8[c]	14	22	56	10	10	2	2	1	1	13	46	59	174	115	238	2	82	14	28	7	11	57	142	53	246	150	484	513	1,534

[a] No crayfish were saved from the Genesee R. (1926) or Long Island (1938) surveys.
[b] Number of collections containing a given species.
[c] Number of crayfish—containing collections taken during a given year, not the sum of the column of figures above.

TABLE 17

NYSM crayfishes collected by D. W. Crocker in August 1952

Species \ Drainage	Oswego R.		L. Erie-Niagara R.		L. Champlain		Grass, St. Regis & Salmon R.		Oswegatchie & Black R.		Hudson R.		Delaware R.		Susquehanna R.		Total	
	Coll.[a]	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.
Cambarus b. bartoni			1	4	1	2	3	19			2	9	2	10	7	83	16	127
C. robustus	5	35	1	6							5	18					11	59
Orconectes immunis			1	13							4	6			1	3	6	22
O. limosus											2	52	1	14	7	44	10	110
O. obscurus	2	30[b]	1	31							3	183[b]					6	244
O. p. propinquus	7	117[b]	2	47	4	57	3	12	2	10	4	84[b]			4	84	26	411
O. virilis			1	13	1	8					1	44					3	65
Procambarus b. blandingi											1	6					1	6
Total	8[c]	182	3	114	5	67	3	31	2	10	11	402	3	24	11	214	46	1,044

[a] Number of collections containing a given species.
[b] In these collections it was difficult to distinguish between *O. obscurus* and *O. p. propinquus* and therefore the number of specimens assigned to these species may not be correct.
[c] Number of collections made in a given drainage, not the sum of the column of figures above.

TABLE 18

Summary of New York State crayfishes in the personal collection of the author through July 12, 1951

Species \ Drainage	Genesee R.		Oswego R.		L. Champlain		Grass & Salmon R.		Oswegatchie & Black R.		Hudson R.		Raquette R.		Susquehanna R.		Allegheny R.		Misc. L. Ontario tribs.		Total	
	Coll.[a]	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.	Coll.	Spec.
Cambarus b. bartoni	5	25	13	86	4	12	1	6	4	7			1	2	10	55	3	14			41	207
C. robustus	8	37	42	550	1	8			7	87	1	1	1	6			8	69	3	31	71	789
Cambarus sp.																	1	1			1	1
Orconectes immunis	3	7	14	491			1	1													18	499
O. limosus											4	23			4	104					8	127
O. obscurus	9	117							3	9	1	19	1	1			8	122			22	268
O. p. propinquus	7	119	34	893	2	2	1	8	3	19			2	18	4	99			4	75	57	1,233
O. virilis					1	1	1	5													2	6
Orconectes sp.															2	4					2	4
Total	20[b]	305	69	2,020	8	23	3	20	10	122	6	43	4	27	17	262	9	206	5	106	151	3,134

[a] Number of collections containing a given species.
[b] Number of collections made in a given drainage, not the sum of the column of figures above.

the Appalachian system, independent of drainages, is evidence that this has actually occurred.

Of the general distribution of *C. b. bartoni*, Ortmann (1905*a*: 122) states, "This species has followed, in its dispersal, chiefly in the direction of the strike of this mountain chain [Appalachian] and reaches now from Tennessee to Maine and New Brunswick [it is also in Ontario (Huntsman 1915)]. Eastward it hardly descends to the Atlantic plain, at any rate it does not spread over it, and westward it goes as far as Indiana, always preferring smaller streams in mountainous or hilly regions."

The origin of the genus *Cambarus*, as already noted under *C. robustus*, has been placed by Ortmann at the southern extremity of the Appalachian system of mountains.

OTHER NEW YORK SPECIES

Three crayfish species, *Cambarus fodiens* (Cottle), *C. d. diogenes* Girard and *C. uhleri* Faxon, may occur in New York in addition to the eight forms already discussed. All three are members of the Diogenes section of the genus and are burrowing species.

C. fodiens (= *C. argillicola* Faxon) is known from Ontario through Ohio, Michigan, Indiana, and Illinois (Hobbs, 1948: 229). It should be searched for in western and northern New York in marshes and temporary ponds.

C. uhleri is known from Maryland where it inhabits salt marshes and brackish or fresh-water ditches. Similar habitats in New York may possibly support populations of this species.

C. d. diogenes has been reported 75 miles from the New York border in Ohio (Turner, 1926: 187, map 6), 60 miles from the New York border in Pennsylvania (Ortmann, 1906: 405) and 30 miles from the New York border in New Jersey (Fowler, 1912: 352).

Synonymies for these three species and descriptions and figures of *C. fodiens* (as *C. argillicola*) and *C. uhleri* are given in Faxon (1885*b*). Ortmann (1906) describes *C. d. diogenes* in Pennsylvania.

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