Denton W. Crocker
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HANDBOOK
of the
CRAYFISHES
of
ONTARIO
THE CRAYFISHES OF ONTARIO
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CRAYFISHES
OF ONTARIO

DENTON W. CROCKER
and
DAVID W. BARR

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Foreword

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It is to three groups of readers that this book on the crayfishes of Ontario is directed. One group is biologists working in Ontario and concerned with crayfishes as a freshwater resource, as a component of the food of certain vertebrate animals under special study, as experimental animals, or in other ways. Because it can be taken as axiomatic in biology that evaluation of the ecological role of any group of organisms is penetrating only to the extent that it relates to the species level, there is provided a key for the identification of all species of crayfish now known to occur in Ontario. For each species there are distributional data illustrated by maps, and summaries of observations, both published and original, on the life history. Particular effort has been made to provide specific reference to other published studies on crayfishes, not only as documentation for data presented, but also to make it possible for those interested to move out into that extensive literature on their own.

Another group to whom this study is directed is workers studying crayfishes on a continental or world basis, and concerned with details of geographic distribution, comparative morphology, and the life history of species of crayfishes in all areas. For this group the study summarizes results from the most extensive survey of Ontario material that has yet been carried out, and shows what specimens are available in museum collections for whatever further analysis may be appropriate.

The remaining group is the growing number of naturalists and biology students for whom native crayfishes could become creatures of considerable interest if their diverse habits and distributional patterns could be associated with individual species in nature. For this audience the key to the species is supplemented with photographs to show that species of crayfish differ from each other in appearance.
as do different species within such groups as the minnows or the sparrows. Not only do they look different, but also their highly interesting burrowing and chimney-building habits, their habitats and geographic distributional patterns, combine to make each species a distinctive and recognizable entity.

This study fills yet another role by providing the first documentation of two species of crayfish which evidently have been introduced into Ontario waters—Orconectes r. rusticus and Orconectes obscurus. It is important that such new additions to the adventive fauna of the province be detected early in order that the interactions between native and introduced species can be followed and understood. Already there is some evidence that native populations of O. virilis are receding in localities where the introduced O. r. rusticus has been found.

It is clear that crayfishes comprise an important element in the food chains of many other creatures. Furthermore, because as individuals they are large, and as populations they are abundant, crayfishes have to be regarded as an important freshwater resource. Should management and conservation measures become necessary to offset depletion of this resource, it is to be hoped that this study may prove a useful basis for those measures.

It is also clear that crayfishes are an interesting part of the native fauna of Ontario, and that they pose a number of significant questions for biologists. For example, the distribution maps show very clearly the restricted ranges of several native species, and therefore crayfishes in Ontario ought to be excellent subjects in which to study factors limiting natural distribution. Crayfishes are also suitable for behavioural study because they are large and can be kept easily under observation in captivity.

Dr. Denton W. Crocker brings to this study his extensive experience with the crayfishes of northeastern North America, which includes authorship of The Crayfishes of New York State. He is Professor and Chairman in the Biology Department at Skidmore College, Saratoga Springs, New York, and a Research Associate in the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum. David W. Barr is a graduate in biology from the University of Toronto, where he was a Student Assistant in the Museum's Department of Entomology and Invertebrate Zoology during the summer months of the years between 1962 and 1965, when this study was carried out.
ONE OF THE EARLIEST RECORDS of crayfish investigation in Ontario is found in a paper by Charles Girard published in 1852, in which he names a new species, *Cambarus robustus*, and cites the collection locality as the Humber River, "near Toronto (Canada)." A few years later, in 1863, T. J. Cottle read a paper before the Canadian Institute in which he described *Astacus fodiens* (=*Cambarus fodiens*), a new burrowing crayfish from Ontario. Cottle not only gave an adequate morphological account of the species, but also gave details of its life history and behaviour. The only other Ontario crayfish recognized by him was *Astacus bartoni* (probably including both *C. b. bartoni* and *C. robustus*).

By 1903 J. A. Harris was able to include Ontario as part of the range for several of the species treated in his ecological catalogue of crayfishes, and in 1915 A. G. Huntsman published a pioneer study on the crayfishes of the province. This work contained information on eight of the nine species now known to occur in Ontario. He also suggested, in contrast to the opinions of his contemporaries, that *C. robustus* and *C. bartoni* were distinct species. Our data and those of Crocker (1957: 41) support his suggestion.

Materials collected and studied by Huntsman came to comprise the nuclei of the crayfish collections in the Royal Ontario Museum in Toronto and the National Museum of Canada in Ottawa. Since 1915 specimens have been contributed to the ROM collection by various well-known biologists and collectors, including J. R. Dymond, F. Johansen, G. H. Needler, J. G. Oughton, I. Radforth, and E. M. Walker. No further comprehensive studies were published during this period.

In 1956 the senior author prepared a card catalogue of the crayfish collection at the ROM, and the distributional data obtained became the point of departure for the present study.
An intensive survey was begun in 1963 as a project of the Department of Entomology and Invertebrate Zoology of the Royal Ontario Museum. During the course of the study, many specimens were received from across Ontario and the size of the holdings was tripled to 735 collections containing a total of nearly 5000 specimens. One extended field trip and a number of smaller expeditions have been made, and we have encountered all Ontario species in the field. The collection of the National Museum of Canada was examined by the junior author and the locality data are included here. Specimens contained in this collection are designated by NMC, all specimens without designation being in the collection of the Royal Ontario Museum.

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Dr. Glenn B. Wiggins, Curator of the Museum’s Department of Entomology and Invertebrate Zoology, has helped greatly in the organizing and planning of this study, for which we warmly thank him. Also he has made the full resources of his department available to us. Dr. Wiggins, furthermore, gave generously of his scientific and technical experience during the preparation of this publication.

Through the cooperation of Dr. C. H. D. Clarke, Chief of the Fish and Wildlife Branch, Ontario Department of Lands and Forests, the study has been substantially aided by over 300 collections of crayfishes, consisting of some 1600 specimens, made by regional officers of the Department.

All of the photographs of crayfishes were made by Mr. Leighton Warren of the Museum’s photographic department.

The line illustrations and retouching of the photographs were done by Miss C. N. Storwick, artist in the Museum’s Department of Entomology and Invertebrate Zoology.

Dr. E. L. Bousfield, Chief Zoologist, National Museum of Canada, kindly provided space and equipment for examination of the NMC crayfish collection by the junior author.
The Ontario Bird Banding Association made accommodation available during three visits to study the populations of *Cambarus d. diogenes* and *Orconectes immunis* at the southern tip of Long Point on Lake Erie.

The location of references to earlier crayfish investigations has been greatly facilitated by the assistance of the staff of the Royal Ontario Museum Library.

Professor J. H. Soper, Department of Botany, University of Toronto, supplied the base maps on which distribution data are plotted.

Two Skidmore College Faculty Research Grants assisted the senior author in making two of his four visits to Toronto.

Dr. Horton H. Hobbs Jr., Senior Scientist at the United States National Museum, generously gave of his time to read the manuscript. We remain fully responsible, however, for whatever errors of omission or commission may exist.

Finally, thanks are due to all the many collectors who contributed crayfish specimens to this study.

*July 1967*

D.W.C.

D.W.B.
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EXTERNAL STRUCTURE

A functional and descriptive knowledge of the external structure of crayfishes is necessary both in making identifications and in understanding the details of their life history and behaviour.

Figure 1 illustrates the external features of principal importance, using the common Ontario species *Orconectes virilis* as an example. Technical terms are also defined in the Glossary on pp. 143ff.

*General*

Crayfishes have a relatively unspecialized arthropod body composed of a linear series of jointed (articulated) segments, each true segment bearing one pair of appendages. The appendages of different body regions are modified for different functions, but all have a basically similar structure of articulated segments. This jointing of the appendages and of the body is necessary to allow movement, for the whole crayfish is encased in a hard, rigid, impermeable cuticle. The mature cuticle is a secretion product of the outer layer of living tissue, the hypodermis, strengthened by impregnation with calcium salts. This rigid multilayered "armour" acts as a support for the internal organs, and provides the mechanical framework for the attachment of muscles. Because of these functions, it is referred to as the exoskeleton.

In crayfishes, there are 18 true segments plus a presegmental portion at the anterior end and a postsegmental portion at the posterior end. The points at which the 18 body segments are grouped
into the conventional three regions (tagmata) of head, thorax, and abdomen are in some dispute. The embryonic cephalic lobe and the first four segments (bearing second antennae, mandibles, and the two pairs of maxillae) customarily have been taken to comprise the head, and we follow this convention. The comparative studies of Snodgrass (1951: 2, 30, 106), however, suggest that the head is a smaller component. He finds that, based on the exoskeletal-muscular anatomy, there is a logical point of separation of head from thorax between segment I, which bears the second antennae, and segment II, which bears the mandibles.

The cuticle of a typical segment as exemplified by the abdominal or tail segments is laid down in distinct plates which are constant in position. These are: a tergum or dorsal plate, two pleura or lateral plates (which are fused with the tergum), and a sternum or ventral plate. However, in many regions of the body, this fundamental arrangement is modified.

**Cephalothorax**

The presegmental area, the four head segments, and the eight thoracic segments are all fused to form a compact structure called the **CEPHALOTHORAX**. The primitively segmental nature of this region can be inferred from segmentally arranged exoskeletal plates and the
series of paired appendages, each of which must have been borne by one of the original segments. The nervous system also indicates a primitive segmentation of this region. The dorsal and lateral exoskeleton of the cephalothorax, however, shows little evidence of this segmentation and forms an entity called the carapace. Anteriorly the carapace projects over the bases of the eyes and antennae as the rostrum, terminated by the sharply pointed acumen. The only prominent subdividing feature of the carapace is a transverse fissure called the cervical groove. It curves forward on the sides of the carapace to meet the anterior margin. The portion of the carapace behind the cervical groove is a double-walled, hollow outpocketing from the anterior portion and the name carapace sometimes is restricted to it, although we are using the name in the more inclusive sense defined above. The lateral extensions of the carapace, posterior and ventral to the cervical groove, are referred to as branchiostegites, and form the outer walls of the gill chambers. The branchiostegites are not attached to the body along their ventral or posterior edges, with the result that the gill chambers are open to the water in front, below, and behind. In fact, the posterior half of the carapace is attached to the body only along a narrow, mid-dorsal region. This is visible in dorsal view as a concave-sided, median area termed the areola. The carapace may be ornamented with various tubercles and spines, the most conspicuous and constant of which are the lateral rostral spines at the base of the acumen, the lateral spine half-way along the cervical groove, and the branchiostegal spine at the end of the cervical groove, below the eye. The sternae of the cephalothorax have a complicated structure and largely are fused together in the anterior region. They bear the articulations for all appendages of the cephalothoracic region.

Abdomen

The fusion of tergum and pleura in each of the six abdominal segments gives rise to a series of strongly arched dorsolateral plates. These overlap each other and are connected by a thin layer of pliable cuticle. The sterna are reduced to transverse bars separated by large areas of thin, pliable cuticle. As a consequence, the abdomen is particularly flexible in the vertical plane and can be curled forward under the body. The postsegmental structure, which is called the telson, is divided into anterior and posterior sections and bears the anus on its ventral side. It has no appendages.
Head Appendages

The appendages of crayfishes are arranged in a serial, segmental order, each true body segment bearing one pair. The varied forms of the appendages are adaptations to a diversity of functions. The head appendages gather sensory information about the environment and handle food, while the thoracic appendages function in eating and in walking. The abdominal appendages are concerned with reproductive activities and swimming.

Beginning at the anterior end, the presegmental region bears the eyes, which are not considered to be appendages, and a pair of appendages, the antennules, which show little structural affinity with the appendages borne on the succeeding true segments. The eyes are of the compound type, common to many arthropods, and each is borne at the tip of a short stalk. Because these stalks are articulated at the base, they can be pointed in different directions, and this mobility partially compensates for the fact that the head is rigidly joined to the thorax. Eyes of this type do not form clear, sharp images, but are efficient in detecting quick movements and relative levels of light intensity. Some protection from mechanical damage is afforded to the eyes by the projecting, rooflike rostrum. Each of the antennules has two long, thin, whiplike branches. These bear sensory hairs, and are thought to function in the detection of chemicals dissolved in water. Each antennule also contains in its basal segment an equilibrium organ called a statocyst, which gives the animal information as to its orientation with respect to gravity.

The antennae are the appendages of the first true segment, and their function is also sensory, like that of the antennules. The antennae exhibit a basic structural pattern which also can be detected in variously modified forms in each of the remaining appendages. There is a basal portion, or protopodite, which bears two branches, a medial endopodite and a lateral exopodite. The antennal endopodite is a long, whiplike flagellum, while the exopodite is a flattened plate, referred to as the antennal scale. The basal segment of the antenna also bears the excretory pore through which the animal voids nitrogenous metabolic wastes and excess water.

The next three pairs of head appendages are grouped around and behind the mouth and are generally concerned with grasping and tearing food, and conveying the pieces into the mouth. The mandibles are short and massive with apposed, toothed surfaces. Their function
is not to grind the food, but to tear off pieces of manageable size. The grinding and shredding of the food is carried on in a complex, chitin-lined section of the digestive tract called the gastric mill. The first and second maxillae also aid in feeding, but part of the second maxilla, the gill bailer or scaphognathite, serves as an accessory respiratory structure. It is an elongate, flattened plate, which, by undulating movements, creates a current of water through the gill chamber and over the gills, thus providing a steady supply of dissolved oxygen.

*Thoracic Appendages*

The first three pairs of thoracic appendages are the first, second, and third maxillipeds, which aid the last three pairs of head appendages in ingesting food. The action of the third maxillipeds is especially noticeable when the large, segmented endopodites are used to seize a piece of food. These organs may also be used for cleaning debris from the antennae.

The next five pairs of appendages are termed pereiopods and are concerned mainly with walking and prehension. These are completely without exopodite, and the endopodite is composed of seven elongate, articulated segments. Proceeding distally from the base, the names of these segments are: coxa, basis, ischium, merus, carpus, propodus, and dactyl. The first three pairs of pereiopods have the dactyl articulated on the side of the propodus so that it apposes the projecting distal end of the latter. The result is a grasping claw, or chela, a pereiopod bearing it being referred to as a cheliped. The chelae of the first pereiopods are greatly enlarged and provided with strong muscles for closure. These modifications make these appendages (which are called the great chelipeds) unsuited for walking, and they are utilized, almost entirely, for more specialized activities such as the procuring of food, mating, burrowing, and defence. The remaining four pairs of pereiopods are used for walking, although they may be used also in other ways, such as the cleaning of the ventral surface of the female's own abdominal exoskeleton prior to egg laying.

Each pereiopod bears a double crease near the base of the ischium, marking a point where the leg may be broken voluntarily. If one of the pereiopods is grasped, and the animal is sufficiently alarmed, a reflex action of the muscles at this breaking point pinches off the distal part of the leg. Thus, if a predator seizes a leg, or if the crayfish
has difficulty in extricating a claw from the old exoskeleton during moulting, the whole leg will be sacrificed so that the animal can escape. Such a self-inflicted wound heals quickly, and the growth of underlying tissues produces a limb bud, which eventually gives rise to a new pereiopod. The new appendage is small and soft at first, but increases in size and degree of hardness at each subsequent moult. Such regenerated appendages often differ slightly in structure from the original (see Fig. 81), and this can be a problem if one is trying to identify a crayfish on the basis of the structure of a regenerated cheliped. In the laboratory any appendage may be regenerated, but in the field the pereiopods are the ones most often found in this condition.

In all Ontario species, the ischiun of the third pereiopods of the male bears a strong hook, which is directed proximally, much like the barb on a fish-hook. This is a secondary sexual organ, and functions in grasping the female during copulation. The male also bears the external openings of the vasa deferentia, or sperm ducts, on the medial surfaces of the basal segments of the fifth pereiopods. The external openings of the oviducts are borne on the medial surfaces of the basal segments of the third pereiopods of the female.

Abdominal Appendages

The abdomen of the female bears five pairs of short, weak, biramous (two-branched) appendages called pleopods or swimmerets, the first of these pairs being reduced in size and uniramous. These are usually fanned back and forth continuously, even while the animal is at rest, and probably aid in keeping the water circulating in the general vicinity of the body. The female also uses them to carry the eggs during the incubation period, the fanning then serving to keep the eggs well aerated. The male differs from the female in that the first two pairs of pleopods are modified to form accessory sexual organs (see Fig. 2) which serve to transfer sperm from the vasa deferentia to the seminal receptacle of the female during copulation. The highly modified first pleopods of the male (variously termed copulatory stylets or gonopods) are strongly sclerotized and bear no exopodite. They form the most important single character used to differentiate the crayfish species of eastern and central North America.

The copulatory stylets terminate (distally) in two elements, at least one of which is inserted into the seminal receptacle during copulation.
Figure 2. Underside of a male crayfish showing the copulatory stylets lying in the mid-line between the bases of the walking legs. The sperm duct openings are visible on the inner bases of the fifth walking legs.
The more anterior of these (considering the stylet to be directed ventrally) is called the **central projection**. In Figures 22-26 this is the terminal element on the left, and in Figures 27-30 it is the upper (more distal) element. The more posterior projection is called the **mesial process**. It is the terminal element on the right in Figures 22-26 and the lower element in Figures 27-30.

The two genera into which the nine species of crayfishes in Ontario are classified may be distinguished by features of the copulatory stylets. In *Orconectes*, the terminal elements may be long (Figs. 22-24), short (Figs. 25, 26), straight except at the tip (Figs. 24-26), or gently curved (Figs. 22, 23), but they are consistently slender and attenuate. In *Cambarus* both terminal elements are bent caudally at a right angle to the main axis of the shaft (Figs. 27-30), and are consistently shorter and more broadly pointed.

The second pair of pleopods of the male are also elongate and stout, but not so heavily selerotized as the first. They engage with the first pair during copulation and may act as braces for these organs or may form an integral part of the sperm channel. The homologies of the first two pairs of pleopods of the male with respect to the other crayfish appendages have been studied by Hart (1952, 1953, 1956). The homologies of the differing numbers and forms of terminal elements of the copulatory stylets among crayfish species have been studied by Hobbs (1942b, 1945) and Andrews (1910b).

The last true abdominal segment bears a pair of **uropods** in which endopodite and exopodite are greatly expanded, and which form with the telson a five-membered tail fan used in swimming. As mentioned previously, the postsegmental telson bears no appendages.

**Seminal Receptacle**

The seminal receptacle (annulus ventralis of many authors) is a reproductive structure of the female located on the ventral side of the thorax between the bases of the fourth and fifth pairs of pereiopods (see Fig. 3). Its form has been studied by Andrews (1905, 1906b, c). It is essentially a flat, thickened plate of cuticle, which contains a short, blind canal penetrating to its centre. On the outer surface there may be various fissures leading into this canal, as well as tubercles and ridges (Figs. 40-48). This organ receives sperm from the male and holds it until the time of fertilization. Within a limited fauna such as the Ontario crayfishes, the structure of the seminal receptacle can be a useful character for identifying mature females.
Figure 3 Underside of a female crayfish showing the seminal receptacle and the external openings of the oviducts.
Male Forms

In the subfamily Cambarinae, to which all Ontario crayfishes belong, the exoskeleton of the male occurs in two distinct forms, a feature first noted by Louis Agassiz and reported by Hagen (1870: 22). That these two forms alternate with each other in each individual male was first recorded by Faxon (1884a). The change from one form to another is the result of a normal moult, and affects many of the structures of the exoskeleton to a greater or lesser extent. It is now generally agreed that Form I is the sexually competent form. It is attained for the first time, after the last juvenile moult, when the male crayfish gains sexual maturity, and may be regained once or twice again during its life. Form I is characterized by increased length and sharpness of all spines and sclerotized structures, along with heavier chelipeds. In particular, the male's first pleopods are strong, with sharply pointed processes, the central projection having a horny, amber appearance (Figs. 22–30). In this form, these structures provide the most reliable method of separating species. The ischial spines are also larger and stronger. A Form II exoskeleton is found during the periods between seasons of sexual activity and closely resembles the juvenile form. The exoskeleton is less robust, the ischial hooks are shorter and weaker, and the first pleopods are more blunted and less heavily sclerotized (Figs. 31–39). The shape of the first pleopods is also more variable and less reliable as a specific character in this form.

HABITAT

Almost every type of freshwater situation in eastern North America may be utilized by one or more species of crayfish. The spectrum of habitats ranges from water-logged fields and stagnant ditches to deep, cold northern lakes gouged out of the Precambrian Shield (Fig. 4); from rapid, sparkling surface streams (Fig. 6) to subterranean cave waters.

In Ontario, three species of crayfishes may be characterized as consistent burrowers and are usually associated with small bodies of essentially stagnant water (Fig. 7). Colonies of Cambarus d. diogenes have been found in water-logged fields and dry marshes where there is surface water only in the spring. The burrows may or may not have a chimney of clay pellets at the surface. Cambarus fodiens usually constructs a mud chimney (Figs. 11 and 12) above the entrance to
Figure 4  The rocky shore of Whitefish Lake on the Precambrian Shield near Suomi, Ont. A habitat of *Orconectes virilis*.

Figure 5  Large, slow river, the Nottawasaga, near Alliston, Ont. A habitat of *Orconectes propinquus* and *O. virilis*. 
its burrows, which are built near the permanent or temporary waters of ditches, ponds, and marshes. A third species, _Orconectes immunis_, generally burrows only under adverse conditions. It may normally be taken in shallow, stagnant bodies of water such as farm ponds; but should the pond dry up in mid-summer, the crayfishes tunnel down to follow the retreating water table. All crayfishes living in still, shallow, surface waters face the problems of low oxygen tension, of high summer temperatures, and of a high content of suspended organic
material in the water. Burrowing below the surface provides lower temperatures and clearer water, although adequate dissolved oxygen is probably still a critical problem. In addition, a burrow provides greatly increased protection from predators, and the adoption of a largely vegetarian way of life makes up for the loss of the animal protein available in surface waters.

Of all our crayfishes, *Cambarus b. bartoni* appears to require the highest level of dissolved oxygen in its habitat. In southern Ontario
it is usually restricted to cold, fast streams, but on the Shield it can also utilize rocky lakes and some of the larger deep rivers flowing into the northern Great Lakes.

The rest of the Ontario crayfishes (C. robustus, O. virilis, O. p. propinquus, O. obscurus, and Ō. r. rusticus) would appear to share a common set of habitat requirements. However, the differences in distribution pattern for the endemic members of the group (C. robustus, O. p. propinquus, and O. virilis) indicate that subtle distinctions must exist. In the United States, and to some extent in southern Ontario, these forms inhabit sections of the larger rivers and streams having a stony bed (Fig. 5). The crayfishes usually hide under the stones for shelter by day and come out to hunt for food at night. Such crayfishes may have special adaptations which help to maintain their position if there is a strong current in the river or stream (Bovbjerg, 1952). When these species extend their ranges over the Precambrian Shield, the relatively slow, shallow rivers and streams to which they are accustomed largely disappear, and are replaced by deep, swift streams flowing over a bottom of granitic rubble. Some crayfishes enter these rivers, but far greater populations are developed in the Shield lakes. This is an entirely new habitat for these species, but the transition is made possible by the fact that slow rivers and stony lake shores share many physical characteristics in common (Corbet, 1963: 202-3). Some of the northernmost crayfishes in Ontario inhabit lakes of this sort.

Ontario has a number of caves which contain permanent pools, apparently suitable for occupation by crayfishes. To date, however, no specimens are known to have been taken from any of these subterranean waters.

LIFE HISTORY

The pioneer work on the reproduction and development of cambarine crayfishes was carried out by E. A. Andrews between 1895 and 1910. Indeed, the behaviour Andrews observed for Cambarus affinis ( = Orconectes limosus) still forms the basis of our present knowledge on the subject, and appears to have a widespread application to all cambarine species. The following account is drawn particularly from the reports of Andrews (1895–1910), but reference to more recent information is made.

Mating often takes place during a well-defined season of the year
and, when this occurs, the other periods of the life cycle tend also to be confined in time and to succeed each other regularly throughout the year. In these cases, the life history data accompanying museum specimens are often sufficiently correlated to give a dependable picture of the life cycle when considered along with field observations of mating, moulting, and so on. Even more objective and detailed results can be obtained by carrying out a quantitative study on large numbers of specimens, as has been done by Creaser (1933a), Van Deventer (1937), Penn (1943), Smith (1953), and Smart (1962). However, some crayfishes (an example from our fauna is _C. robustus_) seem to have no well-defined mating period and their activities are much more difficult to trace.

During the mating season the breeding males are in form I, and their sperm ducts are full of recently formed sperm (Fasten, 1914; Word and Hobbs, 1958; Smart, 1962). The males actively seek out a mating partner, but apparently have little or no power of sex recognition (Pearse, 1909). Thus, the first crayfish encountered is grasped, and its reactions to this seizure determine whether or not successful copulation will be carried out. If a male has been seized, it will fight back actively, and the aggressor soon gives up and moves off. However, if a receptive female has been seized, it enters a non-resistant, trance-like state with the antennae, chelipeds, and walking legs stretched forward, and the distal end of the abdomen curved ventrally and anteriorly. The male then manoeuvres the female over onto her back, grasping her outstretched chelipeds and walking legs with his own large chelae, and shifting his grip repeatedly to accomplish the process. When the female has finally been turned to lie on her dorsal side, the male is on top of her, holding her antennae, chelipeds, and walking legs with his large chelae. The female's abdomen is doubled over and the abdomen of the male fits closely around its curved dorsal surface. The mating position is shown in Fig. 87. Because the passivity of the grasped female is the only requirement for the beginning of copulation by the male, under experimental conditions a form I male will complete the whole mating process with a dead male crayfish (Andrews, 1910a: 241).

The male now begins a complex series of actions. It arches its body sufficiently to pass the left fifth pereiopod across, between the female and itself, and through to the right side. This action serves to depress the copulatory styli away from the ventral side of the male, and the fifth pereiopod remains anterior to them, keeping them erect. The
second pleopods are now engaged with the first, and the tips of the first pleopods are inserted into the fossa of the seminal receptacle. The male bears down, using its large chelae and tail as anchorage points, the first pleopods exerting considerable pressure on the seminal receptacle. When the male has pulled itself close enough to the female, the ischial hooks on its third pereiopods are inserted into the coxal membranes of the third pereiopods of the female. This effectively locks the male and female together with the male’s first pleopods inserted in the seminal receptacle. The process of sperm transfer can now begin.

The tips of the vasa deferentia are extruded from the male reproductive openings on the bases of the fifth pereiopods, to reach the base of a groove in each copulatory stylet. The eord of sperm then travels down the stylet and into the cavity of the seminal receptacle. The duration of such a copulation may range from a few minutes to several hours. After the male and female part, either may copulate with additional individuals. A female that has been fertilized recently may be recognized by the waxy sperm plug projecting from the seminal receptacle, which serves to protect the sperm from water. Protruding portions of the plug are, in time, eroded away.

The female carries the sperm in the seminal receptacle until the time of egg laying. Since oviposition is usually in the spring, this period may be only a few days or weeks in duration if copulation was also in the spring, or it may be as much as six months if copulation took place the previous autumn. Prior to egg laying, the female becomes nervous and excitable. She finds some secluded, dark place and begins to clean off the debris which has accumulated on her exoskeleton during the winter. This is largely accomplished by brushing movements of the fifth pereiopods over the under-side of the abdomen, but the chelate second and third pereiopods may be used to pick off any strongly fixed particles. When the cleaning process has been completed, the under-side of the abdomen is bone white. The sensitivity of the female is so great at this time that if disturbed two or three times in succession she may die (Taek, 1941: 426).

When the female is ready to extrude her eggs, she turns over on her back and curls the tip of the abdomen forward until the tail fan lies over the bases of the third pereiopods. Then a translucent, water-resistant, mucilaginous substance, called glair, is secreted from glands on the ventral side of the abdomen (Stephens, 1952). This fills the whole cavity enclosed by the folded abdomen, and rhythmic move-
ments of the abdomen carry it to the space between the telson and the ventral surface of the thorax. Now, all the area through which the eggs and sperm must travel is filled with this protective substance so that fertilization can take place in a water-free environment. First the spermatozoa are released from the seminal receptacle into the glair, and then the eggs are extruded from the external openings of the oviducts. The eggs pass through the glair and travel in the trough between the leg bases down the gradient of the ventral side of the thorax, and into the cavity enclosed by the abdomen. In the process, they pass over the seminal receptacle area and through the spermatozoa in the glair. It is probably here that fertilization takes place.

For several hours after extrusion, regular rhythmic movements of the pleopods and the abdomen roll the eggs back and forth around the cavity in which they lie. In this process, the eggs are kept well aerated and the glair becomes spread out and attenuated. Eventually the glair coats everything with a thin translucent film, which then hardens, cementing the eggs to the pleopods. As the pleopods are fanned, each egg pulls slightly away from its pleopod and develops a short stalk of hardened glair (Fig. 10). When this process is complete, the female can turn over. With a full load of eggs fixed to her pleopods, she is said to be “in berry” (Fig. 8).

The incubation period may last from 2 to 20 weeks depending on the season of laying and average water temperature. and during all this time the eggs are kept aerated by regular movements of the pleopods. Busch (1940) has studied the embryology of *Orconectes rusticus*. To hatch, the young crayfish must rupture both the embryonic skin which surrounds it in the egg, and the egg membrane. This embryonic skin remains attached inside the egg and also to the tip of the abdomen of the newly hatched crayfish, thus effectively anchoring it to the egg stalk and to its parent (Fig. 10). In this manner, for some time, the female carries around a load of living young, for which she provides protection and constant aeration (Fig. 9).

The newly hatched crayfish is the first of the three readily distinguishable juvenile instars during which the young are associated with the female parent. The first instar crayfish is characterized by disproportionately large eyes, a carapace swollen with yolk material, a large, pointed rostrum which is depressed between the eyes, a lack of first and sixth abdominal appendages (i.e. the telson is the only element in the tail fan), and the presence of hooked tips on the fingers of the
Figure 8 Female crayfish "in berry." *Cambarus diogenes*, carapace length 38 mm., from Long Point, Ont.
Figure 9  Female crayfish carrying a brood of hatchlings. *Oreonecetes immunis*, carapace length 24 mm., from Long Point, Ont.
Figure 10  Enlarged, slightly diagrammatic drawing of one pleopod of a female crayfish with eggs attached. One egg has hatched and the stage I juvenile is grasping the egg stalk with its hooked chelipeds. The pigmented eye regions of juveniles just ready to hatch show through the walls of other eggs. Partly from Andrews (1907: Plate VII, Fig. 45).
large chelae which are fastened into the egg stalk to add a second anchor point (Fig. 10). The first instar lasts two to seven days. The second instar young are no longer attached posteriorly to the remains of the egg but they regain the anterior hold with the large chelae. These have a more adult appearance, but are still without the five distinct members in the tail fan. They usually remain attached to the female throughout the 4 to 12 day duration of this stage. The third instar crayfish has nearly adult proportions although it may be only 10 mm. in length. Five distinct members are present in the tail fan, and the buds of the first abdominal appendages may have appeared. The third instar young usually cling to the pleopods of the female with their chelae and pereiopods, but can leave intermittently on short foraging expeditions. However, they return to the protection of the parent if alarmed.

Subsequent instars are entirely free-living and in most species may be captured throughout the summer in open water. Even the juveniles of burrowing species are often found in surface waters during the early part of the growing season.

The growth in size of young crayfishes is prevented between moults by the rigid, inexpansile exoskeleton. This limitation is overcome by a system of growth in rapid jumps followed by extended periods of no increase in size. As in other arthropods, which have the same problem, the animal eats for a period and builds tissue internally. Then it splits the exoskeleton at a point between the dorsal surfaces of the carapace and the abdomen, and crawls out, shedding all of its protective "armour." The body is now soft and can expand rapidly before the new exoskeleton hardens and prevents further growth. The moulting process (ecdysis) appears to be controlled by a moult-inhibiting hormone produced in the eyestalks (Passano, 1960). Six to ten such moults are required before the sexually mature state is reached. In species of *Orconectes* this is often accomplished by the autumn following hatching, at which time mating among mature individuals occurs in many species. If not, sexual maturity and reproduction are held off until the late summer and fall of the second year of life. The minimum size at maturity varies with the species (Crocker, 1957: 18, Table 2). In practice, sexual maturity is recognized by the attainment of form I in males or the presence of sperm plugs in females.

As previously discussed, the first moult after copulation brings the male into form II. This lasts until the next mating season approaches, when it moults to form I again. Males may participate in two annual
mating periods, but they seldom live longer than this. Females do not moult subsequent to copulation, possibly because of the presence of a high level of the moult-inhibiting hormone produced in the eye-stalks (Passano, 1960), until the third instar immatures have left them permanently. They also may copulate a second year and produce a second clutch of eggs, but few survive for a third season. The average life-span for Ontario crayfishes is about 20 months, although other species may be longer lived. Maximum size varies with the species, and is governed in part by the availability of food. In that crayfishes grow throughout life, length of life also determines their maximum size. The smallest Ontario species are *Orconectes p. propinquus* and *Cambarus b. bartoni*, in which maximum carapace lengths are under 40 mm. *O. virilis* achieves carapace lengths of 55 mm. or more.

ECOLOGY

*Introduction*

Neither crayfish nor man can live by himself alone, uninfluenced by or without himself influencing other organisms—plant, animal, or microbe. We are all bound together in an intricately tangled web of interdependencies involving the source of our energy and our very chemical substance and also involving the space in which we live out our lives.

We believe that the data we have brought together show that crayfishes play a part of great importance in aquatic communities in Ontario and elsewhere. First, there are the facts of their large numbers and ability to propagate rapidly, indicative of their ecological potential. Second, there is the large number of species of other animals known to eat crayfishes, indicative of a broad range of ecological dependence upon crayfishes. Third, the information on food habits of crayfishes suggests that larger individuals of stream species, and the individuals of pond species and burrowing species generally, although feeding on living animals and plants, also consume quantities of dead plants, dead animals, and detritus, indicative of the importance of crayfishes in maintaining an efficient energy flow within the community.

These three kinds of information lead us to the conclusion that crayfishes are important converters of materials not eaten by game
fishes, birds, or mammals into more of their own crayfish substance which is so extensively fed upon by all three of these vertebrate classes. Furthermore, crayfishes are one of the few large animals accomplishing the conversion of such materials, rivalled perhaps only by some species of snails and minnows.

It is significant that crayfishes, by their scavenging and plant-eating habits, are converting these materials into food for vertebrates in one step. These foods of crayfishes reach vertebrates via other pathways in the web of feeding relationships too, but these others are more likely to involve several steps with consequent loss of energy and substance at each step.

In addition to treating food relationships, this section deals with shelter. Information is given to show that in some environments crayfishes compete with other animals for shelter, while in others crayfishes construct shelter sites used by other animals.

Finally, we consider crayfish symbioses—those close, behavioural-metabolic relationships between crayfishes and other organisms which may harm crayfishes (parasitism) or which may do neither partner damage (commensalism).

**Abundance and Productivity**

That crayfishes are abundant organisms is apparent to all who have sampled even a few of the varied habitats in which they exist. The data given below summarize what is now known quantitatively about crayfish abundance. First, there are data on the number of eggs found attached to a female's pleopods, which is a measure of the maximum size of the next generation. Ovarian egg counts, a somewhat more accurate measure of this maximum, are referred to in the case of two studies where such counts have been made.

Abundance in a very practical sense may be measured by collecting the total population from a known area or by a marking-releasing-recapturing technique as used by Camougis and Hiehar (1959). These methods, within certain limits of error, tell us how many individuals actually are living at some specific locality.

Knowing the reproductive potential, one must then determine how fast crayfishes grow to reproductive maturity in order to have some sense of what quantity might be removed from an area without depleting it. We have brought together whatever data are known. Information on productivity can be determined also in a practical way
by obtaining records from areas where crayfishes have been taken year after year without (apparently) reducing the population. Only two sets of data seem clearly to fit this category.

*Reproductive potential.* Penn (1950) has summarized studies of the reproductive potential of crayfishes. His table is reproduced here as Table 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Size range (total length in mm.)</th>
<th>Attached eggs (on pleopods) per female</th>
<th>Authority</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Orconectes propinquus</em></td>
<td>32–72</td>
<td>40–250</td>
<td>Van Deventer (1937)</td>
</tr>
<tr>
<td><em>Orconectes rusticus</em></td>
<td>46–102</td>
<td>80–574</td>
<td>Langlois (1935)</td>
</tr>
<tr>
<td><em>Orconectes immunus</em></td>
<td>46–68</td>
<td>38–289</td>
<td>Tack (1941)</td>
</tr>
<tr>
<td><em>Cambarus bartoni</em></td>
<td>48–84</td>
<td>7–133</td>
<td>Ortmann (1906a)</td>
</tr>
<tr>
<td><em>Procambarus clarki</em></td>
<td>62–104</td>
<td>81–652</td>
<td>Penn (1943)</td>
</tr>
<tr>
<td><em>Cambarellus shufeldti</em></td>
<td>17–23</td>
<td>27–60</td>
<td>Penn (1942)</td>
</tr>
</tbody>
</table>

Ovarian egg counts are given by Penn (1943: 9, Table III) for *Procambarus clarki*. Smart (1962: Fig. 4) also includes ovarian egg counts in his study of *Cambarus l. longulus*, a species which on the basis of relationship and size approximates our Ontario species *C. b. bartoni*. His data ranged from 30 eggs in his smallest female to 129 eggs in the largest.

Although these counts of ovarian eggs and of eggs that have been laid are low in comparison with those of fishes, this is not surprising. It must be remembered that the eggs of crayfishes are fastened to the female’s pleopods, where they are kept clean and aerated by pleopod activity. Furthermore, the young, even after hatching, are kept by a special adhesive material (and later, for a while, by their own action) close to the mother. Such parental care results in far greater survival than in animals, such as fishes, where eggs are often simply broadcast untended into the water.

*Abundance.* The standing crop of crayfishes has been recorded by a few authors; their data are summarized in Table 2.

*Growth.* Crayfishes, like other arthropods such as insects and spiders, must shed their exoskeleton periodically in order to grow. The process
<table>
<thead>
<tr>
<th>Species</th>
<th>Standing crop</th>
<th>Date of sample</th>
<th>Locality</th>
<th>Authority</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unidentified</td>
<td>500 lb./acre</td>
<td>?</td>
<td>1-acre pond, Iowa</td>
<td>Davis and Wiebe (1930), from Penn (1950: 643)</td>
</tr>
<tr>
<td><em>C. h. bartoni</em> and <em>C. robustus</em></td>
<td>1687 individuals/acre (16 lb./acre)</td>
<td>?</td>
<td>1 cu. ft. of Pine Brook, Raquette River watershed, New York</td>
<td>Creaser (1934: 160) *</td>
</tr>
<tr>
<td>Unidentified</td>
<td>3.1 individuals/sq. ft. or 135,036/aacre</td>
<td>Aug. and Sept.</td>
<td>Stream in Virginia</td>
<td>Surber (1936), from Penn (1950: 643)</td>
</tr>
<tr>
<td><em>O. rusticus</em></td>
<td>Av. of 850 lb./acre or 59,224 individuals/acre</td>
<td>Early Aug.</td>
<td>3 fish-hatchery ponds, Ohio, from 0.34 to 0.60 acre in area</td>
<td>Langlois (1935: 5)</td>
</tr>
<tr>
<td>Unidentified</td>
<td>Max. of 89,056 individuals/acre or 272.8 lb./acre</td>
<td>Aug.</td>
<td>Rilles in stream near Columbus, Ohio</td>
<td>Wickliff (1940: 152)</td>
</tr>
<tr>
<td><em>O. immennis</em></td>
<td>Av. over 3 years of 731 lb./acre (694, 689, and 811)</td>
<td>?</td>
<td>4.35-acre pond in Michigan</td>
<td>Lydell (1938), from Tack (1941: 438)</td>
</tr>
<tr>
<td><em>O. immennis</em></td>
<td>From 46 to 256 lb./acre</td>
<td>Fall (probably)</td>
<td>4 hatchery ponds (3 of 1166 sq. ft. area, 1 of 5280 sq. ft. area), Ithaca, New York</td>
<td>Tack (1941: 438)</td>
</tr>
<tr>
<td><em>O. virilis</em></td>
<td>8300 individuals/aacre</td>
<td>Summer</td>
<td>Hobbs Brook Reservoir, Massachusetts</td>
<td>Camougis and Hiehar (1959: 230)</td>
</tr>
</tbody>
</table>

*Creaser, collecting by hand or net in an area of large boulders and overhanging banks, says that his counts are certainly low.

†Although Wickliff writes of productivity, he is actually measuring standing crop or immigration into depleted areas. Penn (1950: 643) gives incorrectly calculated data, taking data from Wickliff on individuals per square foot as representing crayfish when they in fact refer to combined fish-crayfish counts. Penn's figures are therefore too high.
is called moulting or ecdysis. They grow, therefore, in a series of abrupt steps rather than in an uninterrupted progression.

The rate of growth among crayfishes has been studied in a few instances. Smith (1953) has tabulated data on the growth of populations of *Orconectes clypeatus* (now *Faxonella clypeatus*). Penn (1943) presented data on the growth of *Procambarus clarki*. Van Deventer (1937) graphed the progressing modes of frequency distribution curves of size in *O. propinquus*. Smart (1962) has studied the growth of *Cambarus l. longulus*.

The increment of growth determined from measurements of carapace length before and after a moult averaged 2.42 mm. in *O. propinquus* in Illinois (Van Deventer, 1937: 26). 2.45 mm. in *O. limosus* (Andrews, 1904; see Van Deventer 1937: 25 for the calculation of this figure), 2.6 mm. for *P. clarki* (Penn, 1943: 11), and 0.41 mm. for the small species *F. clypeatus* (Black, 1958: 193).

Langlois (1935: 4) records the increasing size of *O. rusticus* in Ohio farm ponds by tabulating the decreasing numbers required to weigh a pound. These data range from 191 per pound on July 20 to 120 per pound on August 29.

The growth of individual crayfishes has been followed until recently only by holding individuals in aquaria or by the fortuitous discovery of individuals moulting under field conditions when a measurement could be made of the newly emerged animal and of its old exoskeleton. However, Slack (1955), in a small-scale pilot study, used injections of marking-machine ink to tag individuals of *O. propinquus* in the field. His method has been adapted successfully by Black (1963) to study, over a period of 14 months, the home ranges of two stream crayfishes in Louisiana. The hormonal control of moulting in crayfishes has been studied by, among others, Stephens (1955) and Scudamore (1948). Passano (1960) has reviewed moulting in crustaceans in general.

**Productivity.** The yield of crayfishes to man, over and above those dying from disease or parasitism or lost through predation or emigration, has been estimated by Penn (1950: 644) for *P. clarki* in Louisiana at 5000 individuals or 150 pounds per acre per year. Threinen (1958a: 6) estimates a yield of 82 pounds per acre per year of *O. virilis* from certain habitats in Wisconsin.

In so far as we are aware, no other studies clearly give this kind of information, although some of the standing crop data given above
largely may represent yield. Yet it would be of still greater ecological
value to go beyond the yield to man and determine the total mass of
crayfish substance which moves via predation, parasitism, and decomp-
position through those communities in which they are bound.

Range and Migration

The area occupied by crayfish populations has been investigated in
four studies. Camougis and Hichar (1959) report that for individuals
of introduced *O. virilis* in Massachusetts, "a home range, if it exists,
is in the order of hundreds of feet or more." They found no evidence
of territorialism. Henry (1951) records for *Pacifastacus klamathensis*
in Oregon that there is a downstream migration in late spring and
early summer, after which the young are reared and a moult occurs.
A return upstream takes place in the fall. Cummins (1921) has
noted some elements of a Michigan *C. fodiens* population migrating
pondward in spring. Black (1963) found that the home ranges of
two species of *Procambarus* in a Louisiana stream were considerably
less than 100 feet.

Roberts (1944) studied the factors regulating community activity
in crayfishes.

It is our general observation in Ontario and New York, supported
by Threinen (1958a: 4) in Wisconsin and by others, that in northern
latitudes crayfishes seek deeper water as winter approaches. They also
occur in deeper water during the daylight hours in summer, but tend
to migrate into shallower water to forage at night. Some may even
come out on shore, and burrowing species commonly may be found
crawling over the ground at night.

Much more work will be required before any real understanding of
home ranges and migrations in crayfishes is achieved.

Food Relationships

Crayfishes have been reported to be preyed upon by at least 46 species
of fishes, 10 amphibians, 20 reptiles, 38 birds, and 6 mammals
(including man).

*Fish, amphibian, and reptile predators.* A large sample (108 papers)
of the literature on predation by cold-blooded vertebrates in the
eastern United States has been reviewed by Penn (1950). Neill
(1951) comments upon and amplifies Penn's paper. Table 3 summarizes Penn's data for the five species of crayfishes most commonly reported.

Table 4 lists those predators in whose stomachs crayfishes occurred with a frequency of 10 per cent or more. Only samples containing 10 or more stomachs are included here, but Penn's study includes a number of other predator species which, on the basis of the papers he summarized, may be of lesser importance. These additional species, plus three snakes and one turtle from Neill (1951), consist of 14 game fishes, 14 non-game fishes, 5 amphibians, and 11 reptiles.

Table 3 SUSCEPTIBILITY OF FIVE CRAYFISH SPECIES TO PREDATION
(from data in Penn, 1950: 644–5)

<table>
<thead>
<tr>
<th>Crayfish prey</th>
<th>Fish species</th>
<th>Amphibian species (salamander)</th>
<th>Reptile species (turtles)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Orconectes propinquus</em></td>
<td>14</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td><em>Orconectes virilis</em></td>
<td>9</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td><em>Cambarus robustus</em></td>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Cambarus diogenes</em></td>
<td>7</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Orconectes immunis</em></td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>

Penn gives a few references to studies made in Ontario. These are Bensley (1915), Clemens *et al.* (1924), Rawson (1930), Ricker (1930, 1932, 1934), and Tester (1932).

Tack (1941: 440) lists the American toad (*Bufo americanus*) as a predator upon crayfishes.

E. J. Crossman of the Royal Ontario Museum informs us (*in litt.*) that crayfishes are one of the major food items for *Esox vermiculatus* and *Esox americanus*. Thomas (1967: Table 4 and Fig. 3) records extensive fall feeding upon *Pacifastacus leniusculus* by striped bass. *Roccus saxatilis*, in the lower Sacramento River of California.

**Bird predators.** The most inclusive list of bird predators upon crayfishes is given by Lagler and Lagler (1944). Their Michigan data should largely be applicable to Ontario. They enumerate 36 species as follows: pied-billed grebe, 7 herons (Ardeidae), 4 surface-feeding ducks (Anatinae), 4 diving ducks (Nyrociinae), ruddy duck, 3 mergansers (Merginae), 6 hawks (4 buteos, marsh hawk, and pigeon hawk), sandhill crane, 2 rails, killdeer, ring-billed gull, 4 owls, and the eastern belted kingfisher.
Table 4  PREDATION UPON CRAYFISHES BY FISHES, AMPHIBIANS, AND REPTILES  
(condensed from Penn. 1950: Tables 2, 3, and 4)

<table>
<thead>
<tr>
<th>Predator species</th>
<th>Total number of stomachs examined</th>
<th>Per cent of stomachs containing crayfishes</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Game fishes</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Salmo gairdneri</em>, rainbow trout</td>
<td>227</td>
<td>28</td>
</tr>
<tr>
<td><em>Salvelinus fontinalis</em>, brook trout</td>
<td>567</td>
<td>10</td>
</tr>
<tr>
<td><em>Esox niger</em>, chain pickerel</td>
<td>284</td>
<td>24</td>
</tr>
<tr>
<td><em>Micropterus dolomieu</em>, smallmouth bass</td>
<td>1670</td>
<td>34</td>
</tr>
<tr>
<td><em>Lepomis cyanellus</em>, green sunfish</td>
<td>19</td>
<td>47</td>
</tr>
<tr>
<td><em>Chaenobryttus gulosus</em>, warmouth</td>
<td>81</td>
<td>42</td>
</tr>
<tr>
<td><em>Ambloplites rupestris</em>, rock bass</td>
<td>124</td>
<td>45</td>
</tr>
<tr>
<td><em>Roccus chrysops</em>, white bass</td>
<td>14</td>
<td>29</td>
</tr>
<tr>
<td>(b) Non-game fishes</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Amia calva</em>, bowfin</td>
<td>232</td>
<td>60</td>
</tr>
<tr>
<td><em>Cyprinus carpio</em>, carp</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td><em>Semoilus atromaculatus</em>, creek chub</td>
<td>105</td>
<td>22</td>
</tr>
<tr>
<td><em>Semoilus corporalis</em>, fallfish</td>
<td>22</td>
<td>23</td>
</tr>
<tr>
<td><em>Hybopsis biguttatus</em>, hornyhead chub</td>
<td>13</td>
<td>15</td>
</tr>
<tr>
<td><em>Ichthysus natalis</em>, yellow bullhead</td>
<td>63</td>
<td>10</td>
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<tr>
<td><em>Ichthysus nebulosus</em>, brown bullhead</td>
<td>107</td>
<td>19</td>
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<tr>
<td>(c) Amphibians</td>
<td></td>
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<tr>
<td><em>Necturus maculosus</em>, mudpuppy</td>
<td>124</td>
<td>15</td>
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<tr>
<td><em>Amphiuma means tidactylum</em>, three-toad</td>
<td>180</td>
<td>47</td>
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<tr>
<td><em>Cryptobranchus alleganiensis</em>, hellbender</td>
<td>67</td>
<td>90</td>
</tr>
<tr>
<td><em>Rana catesbeiana</em>, bullfrog</td>
<td>95</td>
<td>26</td>
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<tr>
<td>(d) Reptiles</td>
<td></td>
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<tr>
<td><em>Alligator mississippiensis</em>, American alligator</td>
<td>305</td>
<td>87</td>
</tr>
<tr>
<td><em>Natrix septemvittata</em>, queen snake</td>
<td>57</td>
<td>94</td>
</tr>
<tr>
<td><em>Liodytes aleni</em>, striped swamp snake</td>
<td>164</td>
<td>65</td>
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<tr>
<td><em>Cheлюдra serpentina</em>, snapping turtle</td>
<td>569</td>
<td>31</td>
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<tr>
<td><em>Emys blandingi</em>, Blanding's turtle</td>
<td>92</td>
<td>78</td>
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<tr>
<td><em>Graptemys geographica</em>, map turtle</td>
<td>40</td>
<td>25</td>
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<tr>
<td><em>Chrysemys picta marginata</em>, Midland painted turtle</td>
<td>556</td>
<td>13</td>
</tr>
<tr>
<td><em>Pseudemys scripta troostii</em>, Cumberland turtle</td>
<td>104</td>
<td>26</td>
</tr>
<tr>
<td><em>Trionyx ferox spinifera</em>, eastern spiny softshell turtle</td>
<td>19</td>
<td>58</td>
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</tbody>
</table>

Eipper (1956), from a study of remains in nests of kingfishers in New York, reports that those birds that had eaten crayfishes had fed almost exclusively upon *Cambarus* spp. Surprisingly, however, *Orcobuectes* sp. was more abundant in the feeding area as evidenced by dip netting and shocking.

Taek (1941: 440) reports the crow and bronzed grackle as feeding upon crayfishes in addition to some of the species in the Laglers' list noted above.
Mammal predators. Lagler and Ostenson (1942) record otters feeding upon crayfishes. Dearborne (1932) gives data which show mink, raccoons, and opossums to be important predators. Errington (1941) adds the muskrat to the list.

The food of crayfishes. Crayfishes appear to be as nearly omnivorous as any animal can be. Although it is often thought that they are mainly scavengers, most Ontario species appear to eat living or recently killed animals and fresh vegetation in preference to decaying material. Most of our species probably rely heavily for their diet on aquatic vascular plants and algae, but also may consume any terrestrial vegetation that falls into the water. A certain amount of morbund or dead and decaying plant and animal bodies probably is consumed, but it is doubtful that these constitute the main source of nourishment in southern Ontario. It seems, however, that crayfishes living in oligotrophic lakes of the Precambrian Shield with low populations of macroscopic aquatic invertebrates and plants must subsist on something else; perhaps they ingest bottom sediment and digest the minute plant and animal life occurring in this material. Forney (1956: 7) considers this to be true for O. immunis under culture conditions in small fish ponds in New York, and Tack (1941: 435) has watched O. immunis at night scraping the algal growth from stones.

Burrowing forms must feed largely on the roots of terrestrial plants and on tender, terrestrial seedlings.

There is little exact information on the animals predatory species of crayfishes feed upon in nature, but very probably all sorts of aquatic invertebrates are seized and eaten. Tack (1941: 435) reports animal food preferences of aquarium-kept O. immunis as being, in decreasing order, isopod crustaceans, fish fry, ground dried shrimp, dead goldfish, and goldfish eggs. A hindrance to an understanding of crayfish diets is the great degree to which food is minced in crayfish stomachs. Tack (1941: 437) did manage, however, to determine the contents of stomachs of O. immunis from three small rearing ponds, sampled in lots of 10 to 50 crayfish through the active season (April to September). Vascular plant fragments averaged 80 per cent by volume (range of 49%–97%). Detritus was the next most abundant material and animal remains least so. In one of 20 stomachs, however, Daphnia sp. accounted for 25 per cent (May 30).

Creaser (1934), studying the Raquette River, New York, examined
stomachs of *Cambarus robustus*. In general, he found that the larger specimens had fed more upon aquatic plants and the smaller ones upon insects (mayfly nymphs, chironomid and caddis fly larvae). The young of these stream crayfish are, therefore, competitors with trout for food. This characteristic of this particular crayfish species, so unforgivable from a game-fisherman's point of view, may well be outweighed greatly by the fact that crayfishes themselves are trout food (see Table 4).

Crayfishes do not attack such larger animals as fish (Langlois, 1935), but they will kill and eat other crayfishes which have recently moulted and are still soft.

Deschiens and Lamy (1954) fed snails (*Planorbis glabratus, P. adowensis, Bulinus contortus*, and *Physopsis africana*) to aquarium-kept *O. affinis*, and suspected that such feeding occurred in nature.

**Shelter Relationships**

Even those crayfish species that inhabit open water very seldom live on clear, sandy bottom areas where there is no natural cover. A possible exception to this generalization may occur in the deeper (30–60 ft.) waters of large lakes. W. B. Scott (ROM) and D. W. Webb (Department of Zoology, University of Toronto) have told us that while scuba diving they have seen many crayfishes resting unprotected on the bottom, even during the day. However, in shallower waters crayfishes typically conceal themselves in muddy water, among aquatic vegetation, under rocks, or in underwater burrows.

Crayfishes inhabiting shallow, mud-bottomed ponds are usually protected from the view of predators by abundant aquatic vegetation and by a constant roiling of the water with a suspension of silt or clay particles. The crayfishes, by their activities, are themselves responsible for the roil, and when large populations inhabit small ponds, the suspension may be so dense as to block out sunlight and cause the death of aquatic plants (Langlois, 1935). In Ontario, the species that have been found under these circumstances are *O. immunis* (commonly), *O. virilis* (rarely), *O. obscurus* (in one instance), and *C. fodiens* (mature individuals in early spring, juveniles in early summer). Langlois (1935) states that *O. r. rusticus* also lives in such habitats in Ohio fish ponds.

If there is debris in the water, such as logs, boards, pieces of cardboard, or tin cans, crayfishes will almost certainly hide under it
during the daylight hours. Rocky bottoms provide an abundance of such hiding places and constitute the most common type of crayfish habitat in Ontario. If the substrate beneath the rocks is gravel or stone, crayfishes are largely restricted to crawling under rocks where there is some sort of natural space. This appears to be true for *O. virilis, O. p. propinquus, O. r. rusticus, C. robustus,* and *C. b. bartoni* when they occur in this situation. *O. p. propinquus,* however, has also been observed in ponds and lakes where there are many flat stones lying on a clay-mud substrate. Here, this species dredges out a shallow cavity under the rock and rests during the day with its antennae, eyes, rostrum, and tips of the chelipeds protruding from the entrance (Fig. 16). In some instances, the crayfish pulls in a small stone after itself, to seal the passage. The cavity is usually no more than two or three centimetres in depth, but has been observed, in one instance, to form a short, slanting burrow about six inches long (Fig. 17). Field observations of *O. p. propinquus* during burrow construction indicate that it flexes its chelipeds in front of itself and shoves mud out from under the rock in the manner of a snow-plough. Newly constructed burrows are marked by a low pile of excavated mud in front of the entrance.

Not only do crayfishes seek shelter under stones and various objects of debris, but so also do a variety of amphibians and particularly fishes. Salamanders (*Eurycea bislineata, Necturus maculosus,* etc.), many species of darters and minnows, and such fish as *Cottus* and *Lota,* as well as the young of others—all these seek shelter. It has been our experience that usually, if a crayfish is found under a stone, then a fish or salamander will not be there and vice versa. It is our impression, therefore, that crayfishes and these other organisms are competing for shelter sites.

Even though there may be such competition, Threinen's (1958a) data show that large numbers of fishes and crayfishes are able to live together in riffles.

Those species that live where there is no surface water, or where the water table fluctuates throughout the year, construct more elaborate burrows; these have excited the interest of zoologists for over one hundred years. On Long Point, part of Ontario's Lake Erie shore, *Cambarus d. diogenes* constructs shallow burrows in wet, open fields or damp marsh areas. There is usually an oval cavity 8 to 15 cm. below the ground surface, with two or three narrow entrance tunnels leading upward (Fig. 13). Where the colony is dense, these burrows
Figure 11 Shapeless chimney of *Cambarus fodiens* burrowing in highly sandy clay soil (Toronto, Ont.).

are sometimes connected by short tunnels, which probably arise from the chance meeting of two burrowing individuals. In the open field, mud chimneys have not been seen, whereas chimneys seem to be
Cambarus fodiens regularly constructs a burrow with an oval cavity near the surface and one to three short entrance tunnels capped by clay chimneys which may or may not be structured, according to soil type (Figs. 11 and 12). In these respects the burrowing is roughly similar to that of *C. d. diogenes*, but, in addition, there is usually a straight, narrow tunnel leading directly downward from some point in the cavity of the burrow (Fig. 14). It is not known how deep these may go, as we have followed them only 30 to 60 cm. below the cavity.
Such a tunnel would seem to be valuable as an escape route when predators threaten, but individuals of *C. fodiens* are invariably taken just at the top of it, seemingly making no attempt to retreat farther down. Possibly this is a safety feature, utilized only at times when the water table falls below the level of the resting chamber.

We have found *O. immunis* burrowing only in very hard clay soils in this province. The resultant difficulty of excavation has prevented a study of the structure of the burrow, beyond the observation that the upper 30 to 60 cm. seems to consist of a narrow tunnel, directed downward at an angle somewhat less than perpendicular to the ground surface. The entrance is usually capped by a clay chimney of varying design (Fig. 15). Huntsman (1917: 131) found *O. immunis* burrowing in stiff blue clay near Tintern (Niagara Peninsula) and observed that the chimneys “had apparently been destroyed by passing animals or by the weather.” He also reports (p. 132) seeing *C. robustus* in underwater burrows in the Credit River near Port Credit. He accounts for this behaviour, which he considers to be unusual, by a scarcity of stones and the small size of the stream, which may have undergone intermittent drying.

All of the chimneys mentioned above are conical to cylindrical piles of grey mud and clay, and are the best indicator of the presence of a colony of burrowing crayfish. Newly constructed chimneys often show a pelleted appearance (Fig. 12), suggesting that they have been constructed of small balls of clay, brought up from the burrow. The top of the chimney is usually open. Older chimneys, or chimneys built in relatively sandy areas, look more like loose heaps of gritty clay pushed out of the hole at random (Fig. 11). In fact, this may be the manner in which some species work. Also, older chimneys are often plugged at the top by a ball of clay, which is pushed up from below and seals the entrance. Although much controversy as to the methods of burrow construction has been raised in the past (Harris, 1903; Williams and Leonard, 1952), no experimental, or even direct, observational work has been done on the burrowing behaviour of Ontario crayfishes.

The burrows of *C. d. diogenes* in Michigan (and probably also in Ontario) not only fulfil the needs of these crayfishes, but also serve as retreats for a variety of other animals. We have no data for *C. fodiens*, but suspect that, because it has burrowing habits somewhat similar to those of *C. d. diogenes*, its burrows too will be found to harbour other organisms.

Carpenter (1953) studied the hibernation retreats (hibernacula) of snakes and amphibians in Michigan. In one crayfish burrow, in February, he was able to dig out five common garter snakes, one of them located 27 inches underground (4 inches below the crayfish itself), and in April, another crayfish burrow also yielded a common
garter snake. A third burrow in February produced a striped chorus frog. On three occasions, Carpenter found dead snakes (common garter snake, Dekay’s snake) in or adjacent to crayfish burrows. They appeared to have been fed upon, but the evidence was only circumstantial that crayfishes had done the feeding. It was even less clear that the killing was done by crayfishes.

Neill (1951) reports taking a number of vertebrates from crayfish burrows in Georgia during that part of the summer season in which these vertebrates are inactive (estivate) or at least do not roam. They were the fish genera *Lucania*, *Aphredoderus*, *Elassoma*, and *Schilbeodes*, and the amphibian genera *Pseudotriton*, *Amphiuma*, and *Siren*. He suspects that other fishes and larval amphibians also use these holes. He further suggests the possibility of vertebrates using crayfish burrows to move from former homes into newly made pools.

Finally, Neill calls attention to work on a salamander (*Ambystoma c. cingulatum*) and a frog (*Rana areolata circulosa*) whose association with crayfish burrows is so constant that they are termed inquilines.

Creaser (1931b: 244) lists three species of small crustaceans (a copepod, an ostracod, and an amphipod) taken from a burrow of *C. diogenes* located in a dried slough in the Ozark Mountains of Missouri. A quart of water from the burrow contained over 6000 of these organisms. He notes the possibility that such burrows are of great importance generally in the re-establishment of populations in temporary ponds.

Thorp (1949) has studied the effects of burrowing crayfishes and other organisms on soils. On the basis of chimney abundance and weight in a Texas locality, and the fact that they are quickly rebuilt after mowing operations, he calculates that these crayfishes may move as much as 10 tons of earth per acre. Whether this much is moved each year, however, depends in part upon chimney survival through the winter.

**Symbiosis**

The sorts of relationships included under this term range from that of simple plant cells growing on the crayfish shell to that of a parasite burrowing into the crayfish body and deriving nourishment from it. Biologists have had trouble forming a precise definition of symbiosis, and the history of the use of the term includes a variety of meanings. We use it in its original broad sense, meaning what the structure of
the word intends, “living together.” This sense seems to be gaining favour and approval today. Rather than take the next step and arbitrarily define how close two organisms must be before they are to be considered together, we shall let the examples give body to the word.

Commensalism. Under this term, meaning “eating at the same table,” most properly used when food relationships are known, we also include a number of loose symbiotic associations which may or may not be commensalism in the strict sense.

The surface of the crayfish shell is used by a wide variety of organisms simply as a place of attachment. Probably most of these do not hunt crayfishes (do not respond preferentially to chemical or visual signals which belong specifically to crayfish). They merely by chance come upon the solid crayfish surface and fix themselves there either temporarily or permanently. Such shell-dwellers that we have seen include algae (especially diatoms), threads of fungus, protozoa (species of *Epistyli*; see photograph in Osburn, 1912: 927), and rotifers. Abbott (1912) and Forbes (1878) report eggs of water bugs (corixids) attached to crayfishes.

Two kinds of organisms, branchiobdellids and ostracods, seem to have a much closer kind of association with crayfishes, a relationship which is more clearly commensalism in the strict sense. Branchiobdellids, an order (Holt, 1965) of clitellate annelid worms, superficially look somewhat like minute leeches about an eighth of an inch long (Fig. 18). They loop over the surface of the shell, especially the underparts or in the gill chamber, living out their lives on the crayfish, and with few exceptions nowhere else. Goodnight (1940: 66) holds the view that few if any branchiobdellids are harmful to their host and that they feed largely on diatoms gleaned from the surface of the crayfish body. However, Holt (1963: 99) reports that one species, *Cambarincola branchiophila*, “almost surely feeds by clipping gill filaments off its host and sucking the blood thereby made available.” The literature records branchiobdellids on all of our nine Ontario species of crayfishes except *C. fodiens*. We ourselves have seen branchiobdellids on *C. robustus, O. virilis*, and *O. p. propinquus* in Ontario even though we have not searched for them methodically.

The ecology of branchiobdellids has been investigated in two instances. Berry and Holt (1959) reported that between two species of *Xironodrilis*, there are differences in resistance to high temperature,
but not to low amounts of oxygen. McManus (1960a) made field studies in New York streams of three branchiobdellid species and four species of crayfish hosts: *C. b. bartoni, C. robustus, O. p. propinquus,* and *O. immuris.* One conclusion drawn is that branchiobdellid species, at least in these particular streams, occupy only certain portions of the total stream length. It was not determined whether this was due to changing physicochemical features of the streams or to changing abundances of the crayfish hosts. McManus' data clearly show a branchiobdellid preference for, though not a restriction to, particular species of crayfishes.

A problematic feature of branchiobdellid biology is the means by which they colonize young and freshly moulted crayfishes. McManus (1960a: 427) says: "Worms lacking a host probably do not seek one actively, but remain sessile [attached] and transfer to a new host when it brushes past." He also states that young *C. robustus,* reared in streams but isolated from other crayfishes, never become hosts and that even when unconfined they are without worms during the first
month of crayfish life. He concludes that young *C. robustus* become hosts simply by moving about and contacting sources of worms.

The other major group of commensals is the ostracod family Entocytheridae. They are small (1–3 mm.), primarily gill-chamber-inhabiting crustaceans. Hart (1962) has revised the systematics of the group, recognizing 2 subfamilies, 10 genera, and 68 species. Almost nothing is known of the life history, food habits, or physiological ecology of any of these. We do not know how many of these species are in Canada although one has been described from here.

Prins (1964) records large numbers of the harpacticoid copepod, *Attheyella carolinensis*, as occurring on *Cambarus tenebrosus* and *Orconectes r. rusticus* in Kentucky.

**Parasitism.** It is typical of parasites to live in or on more than one host in the course of what are sometimes highly complex life cycles. Crayfishes are involved as hosts in a variety of protozoan, fluke, tape-worm, and nematode cycles. The most recent study of these has been undertaken by Sogandares-Bernal (1965) in Louisiana. He examined specimens of nine species of crayfishes and found a total of two species of protozoans and eight species of flukes.

It is an open field for investigation to discover the parasite relationships of Canadian crayfishes. Two species of particular importance to man are discussed in the chapter The Interactions between Crayfishes and Man.

**Population Interactions**

**Hybridization.** Hybridization of crayfish species apparently has occurred several times in Ontario, always when one or both of the introduced species *O. obscurus* and *O. r. rusticus* comes into contact with the closely related native species *O. p. propinquus*. This is diagnosed as hybridization on circumstantial evidence, namely the observation that populations of *O. obscurus* and *O. rusticus* show atypical characters at several localities where they may easily have come into contact with resident populations of *O. p. propinquus*. Such characters include the presence of a rostral carina, reduction of the median ventral carpal spine, reduction of the right-angled shoulder on the anterior margin of the copulatory stylets of form I males, and the lowering and separation of the anterior tubercles of the seminal receptacle. Thus, in Cutler Lake, near Massey, Ontario, and in Lucky
Lake near Plevna, we have taken *O. obscurus* with some *O. p. propinquus* characters. In North (Lea) Lake near Coe Hill, Ontario, crayfish specimens exhibit characters referable to *O. obscurus*, *O. r. rusticus*, and *O. p. propinquus*. However, in none of the examples cited was a typical individual of *O. p. propinquus* collected. This leaves open the possibility that the character changes noted are caused by some ecological effect of the new habitat upon these populations.

**Competition.** Two or more crayfish species are often found in the same habitat, but generally they have existed together for long periods and presumably inhabit separate niches. That is, each species population utilizes the habitat in a slightly different way and does not compete directly with other species populations for the essentials of life (food, living space, shelter, etc.). However, when a crayfish species is introduced into an area outside its normal range, it may come into direct competition with a long-established resident population of a different species. In such a situation, especially if the two species do not interbreed, one or other of the populations will be eliminated and the remaining one comes to occupy the niche alone. This appears to have been the case in Long Bay, Lake of the Woods, where *O. r. rusticus* has been introduced (probably by fishermen). As is shown by the map in Figure 19, collections were made in Long Bay on either side of Reed Narrows in an attempt to determine the extent of the *O. r. rusticus* population. The two species were never collected together, and it appears that the resident *O. virilis* population has been completely eliminated in the area occupied by *O. r. rusticus*. All other collections from the Lake of the Woods and surrounding areas contain *O. virilis* only. There appears to be no hybridization between the two populations.

The present distribution of these two species populations may be static, with a sort of equilibrium established along the boundaries, or it may be that *O. r. rusticus* is expanding its area and will eventually occupy a much larger portion of the lake.

Schwarz *et al.* (1963) record that in Maryland the introduced *O. virilis* is rapidly expanding its area of occupation against the native *O. limosus* and *C. b. bartoni*.

Turner (1926: 175) suggests, on the basis of the pattern of distributions, that *O. r. rusticus* is replacing *O. propinquus sanborni* in Ohio, and Rhoades (1962a) has studied this interaction. The behavioural aspects of competition have been investigated by Penn
and Fitzpatrick (1963) for two species of *Cambarellus*. Eberly (1960) has examined the competition between two cave-inhabiting crayfish species, and Huheey (1961) has extended Eberly's conclusions.

Almost nothing is known of the mechanisms of reproductive isolation operating among populations of different crayfish species occupying the same habitat. However, as such situations are very common and easily accessible in Ontario, there is abundant opportunity here for the investigation of this question.
The Interactions between Crayfishes and Man

In the preceding chapter we have tried to demonstrate, in accord with the basic ecological premise that every species is affected in some degree by every other species, that crayfishes and other animals, including man, have innumerable indirect and often devious avenues by which their lives impinge on each other. There are also a number of ways in which crayfishes and man affect one another in direct, immediate, and sometimes forceful ways, and it is these more direct interactions that are the subject of this chapter.

POSITIVE ASPECTS

The Human Uses of Crayfishes

The three major uses of crayfishes in North America are as food, fish bait, and specimens for biological investigation.

In the United States in 1960, according to data in Power (1962), the bulk of crayfishes came from the Pacific coast, Gulf coast, and Mississippi River drainages. His data (pp. 17 and 21) show that, in 1960, 717,000 pounds came from the Gulf coast drainages, 609,000 pounds from the Mississippi River drainage area, 29,000 pounds from the Pacific coast, and only 2000 pounds from the Great Lakes drainages. Many of these crayfishes no doubt ultimately reached a state of dismemberment in a student dissecting pan (Threinen, 1958a: 4). Others were used for bait and some, particularly in Louisiana, were eaten by man. Unfortunately, the proportions serving these three uses are not known.

At present in Ontario, the most extensive human use of our local
crayfishes is as bait. No doubt some are eaten, particularly by people who have brought a taste for crayfishes with them from Europe or elsewhere, but we know of this only as a local and restricted use.

**Bait.** The use of crayfishes for bait is largely, though not wholly, confined to fishing for small-mouthed black bass (*Micropterus salmoides*), although an examination of Table 4 shows that other game fishes take crayfishes also. In consequence of this restricted use of crayfishes as bait, the bait dealers handling any large quantity of them are located in those areas where bass fishing is popular. Apparently in most areas the natural supply is at present equal to the demand. However, a private crayfish-culturing venture has been successfully in operation for seven years at Port Rowan, Ontario. Some information on the commercial methods of culturing and harvesting is given in the chapter Techniques for Studying and Culturing Crayfishes.

**Food.** Crayfishes are eaten by many fishes, amphibians, reptiles, birds, and mammals, including man, who regards them as a rewarding repast. They are eaten less by man today, however, than in times past. According to Faxon (1885a) and Andrews (1906d), crayfishes were once sold in city markets of the eastern United States. Faxon (1885a: 89) reports: "*C. affinis* [= *Orconectes limosus*] is the common crayfish exposed to sale in the markets of New York and other eastern cities." Turner (1926: 158) states that in 1908 the marketed catch of *O. virilis* from the lakes of Wisconsin was 348,000 pounds. Engle (1926: 100), quoting a Wisconsin conservation commissioner, accords the crayfishes of that state the somewhat dubious distinction of being used "almost entirely for free lunches in saloons."

Today, most of the eating of American crayfishes by man occurs in Louisiana. Viosca (1961: 19) provides a Louisiana recipe for "crawfish stew," and Washburn (1953: 2) offers another for "crawfish bisque." The very reading of these is a mouth-watering experience. Perhaps we should better heed Ortmann (1906a: 493–4), who says, "a dish of crawfishes is not to be despised. It is true our species never attain the size of the highly esteemed European forms but I know from my own experience that, as regards quality, the former are not inferior to the latter. Young specimens (and chiefly soft shells) may be fried in butter and eaten shell and all, while the abdominal muscles of older ones, when boiled in water are very good." We see no obstacle, other than the conservative food habits of people generally, to Ontario
crayfishes becoming a delicacy if properly marketed. Our common species, *O. virilis*, is the same one so abundantly consumed in former times in Wisconsin. It remains only for enterprise combined with knowledge to bring to Ontarians a rare treat. The chemical composition of crayfish meat has been investigated by Dabrowski *et al.* (1966).

At least two writers have suggested the use of crayfishes as feed in raising other animals. Turner (1926: 158), studying the crayfishes of Ohio, says: "It seems very reasonable that a canning industry might be established which could preserve the abdominal muscles and livers and grind up the dried remaining parts into meal." He envisions the use of this product as a feed in the artificial propagation of fishes.

Fisher (1912: 323) records a use for crayfishes collected from cotton fields in the southern United States. He says that when they are boiled, mixed with meal, and allowed to dry, they make an extremely valuable egg-producing food for poultry.

**Biological investigations.** Crayfishes are well suited as objects of dissection because of their low cost, convenient size, and the ease with which their organs can be exposed and identified. Also, they serve well as subjects for physiological experimentation and behavioural studies because they keep alive well in the laboratory and are of suitable structure and size.

The larger size of the southern United States species (*Procambarus clarki* principally) and of the western species of *Pacifastacus* makes it likely that these will hold a large portion of the market for purposes of dissection unless shortages should develop. However, in the northwestern Wisconsin operations, running about 249,300 crayfishes or 25,000 pounds in 1957, Threinen (1958a: 4) reports that a large percentage of the crop of *O. virilis* (our commonest species in Ontario) was sold to biological supply houses at $3.00 per hundred.

R. L. Peterson, owner of Boreal Biological Laboratories, Toronto, tells us that his company distributes 30,000 to 40,000 preserved crayfishes of all sizes and 2000–3000 live crayfishes per year to educational institutions in Ontario. The majority of the live specimens are collected in Ontario, but during the winter, "lakers" are imported from Wisconsin. The preserved material is almost entirely imported, about half from the southern United States and about half from Wisconsin. Dr. Peterson estimates that his firm supplies about 60 per cent of the Ontario market for crayfishes, which enables us to calculate
a yearly use in Ontario of over 60,000 specimens for educational purposes.

Commercial Harvesting and Culturing

We know of no studies that have investigated the effects upon crayfish populations of commercial harvesting or culturing ventures. Culturing of crayfishes should have no harmful effects if the species used are native to the area. The escape of non-native species from pond cultures, however, could disturb the local ecological equilibrium.

Given the present harvesting techniques, we would speculate that diminishing profits would deter the commercial operator from harvesting before populations diminished to a dangerously low level. Stream species are safe because stream-harvesting techniques are very inefficient, but the effects of commercial ventures operating in the larger lakes will ultimately have to be studied to ensure the continued survival of the stocks of lake crayfishes.

Techniques for culturing and harvesting are given in the last chapter.

NEGATIVE ASPECTS

Crayfishes as Pests

The chimney-building crayfishes, by their burrowing, chimney-building, and food habits, may at times be pests.

We quote from a U.S. Fish and Wildlife Service fishery leaflet (Anonymous, 1952) a list of some of the problems that may be caused by burrowing: "Burrowing species of crawfish may cause serious damage to dams of farm ponds, fish-hatchery dikes and pond bottoms, irrigation ditches, lily pools, ornamental pools, and similar installations. Serious losses of water may occur when burrowing weakens dams or embankments, or this burrowing may cause dams or embankments to be washed out. Lawns, gardens, and agricultural crops are also frequently damaged by crawfish."

Sun-baked mud chimneys are reported by Ortmann (1906a: 496) to interfere with the operation of mowing machinery in Pennsylvania, Maryland, and West Virginia.

Fisher (1912) records considerable damage done to cotton crops in Mississippi, the crayfishes destroying the seedlings by tearing away the seed-leaves (cotyledons).
No reports of damage of any sort by crayfishes in Ontario have come to our attention, but control measures have been developed which would be effective should a problem arise (Anonymous, 1952).

Crayfishes as Hosts to Parasites

The parasites found in crayfishes are mentioned in the section Symbiosis in the preceding chapter, but two species require mention here.

The kidney worm, *Dioctophyma renale*, is a parasitic nematode whose life cycle is known to move progressively through branchiobdellid worms, species of the fish genus *Ameiurus* (bullheads, catfish, or hornpout), and mammals (Woodhead, 1950). The following Ontario records are given by Riley (1916: 804, 806): Toronto (from dog), Go Home Bay? (from mink), Kingston (from dog).

The kidney worm requires mention in our report because its branchiobdellid hosts occur almost exclusively on the surface of crayfishes. For a review of branchiobdellid biology see the section Symbiosis.

A curious feature of the kidney worm's existence in mammals is its almost exclusive location in the right kidney: in only a few cases has it been found in the left. Mammal hosts include wolverine, mink, and members of the dog family (Meyer and Witter, 1950: 367). Outbreaks of these worms on mink farms present an economic problem, but infestation is easily avoided by preventing mink from having access to bullheads or by cooking the fish before using them as feed.

A second parasite, a lung fluke (*Paragonimus kellicotti*), occurs both in crayfishes and in man or other mammals. It is important, therefore, that crayfishes be cooked properly before they are eaten.

A suggestion made by Deschiens and Lamy (1954) indicates, however, that crayfishes can be of positive value in regard to parasites and should be mentioned here. Noting that crayfishes eat snails, they propose that they be used as a natural control on snails that harbour stages in the life cycle of flukes causing schistosomiasis.
Crayfishes as a Global Group

Crayfishes are members of the phylum Arthropoda (invertebrate animals with segmented legs) and thus are related distantly to such groups as insects and spiders. More specifically, they belong to the class Crustacea and show many similarities to such forms as fairy shrimps, water fleas (copepods, cladocerans), crabs, lobsters, and shrimps. The general nature of these relationships is illustrated in Figure 20.

All of the crayfishes of the world are grouped along with lobsters in the superfamily Nephropsidea, crayfishes comprising three of its four families. The Astacidae occur in the Northern Hemisphere only, while the Parastacidae and Austroastacidae are restricted to the Southern Hemisphere. In addition to this hemispherical separation, climatic zones must also play a part in crayfish distribution as crayfishes are largely absent from the region bounded by 20 degrees north and 20 degrees south latitude. Their ecological niche in these areas is occupied by freshwater crabs (Smith and Weldon, 1923; Huxley, 1880).

To explain this strongly discontinuous distribution, it has been suggested (Huxley, 1880; Smith and Weldon, 1923) that a cosmopolitan marine ancestor common to all the modern families of crayfishes probably took up a freshwater existence in two or more different instances and that radiation and speciation proceeded along different lines from that time forward.

The Astacidae are further differentiated into four subfamilies of distinctly different morphology, behaviour, and geographic distribution. These subfamilies and their contained genera are listed in Figure 21. The subfamilies Cambarinae and Cambarellinae inhabit Mexico and Cuba and those parts of North America lying east of the Rocky Mountains with the exceptions of Procambarus clarki, which has
CRAYFISHES
AND LOBSTERS

HERMIT CRABS
CRABS
SOW "BUGS" (ISOPODS) AND SCUDS (AMPHIPODS)
SHRIMPS AND PRAWNS
INSECTS
CENTIPEDES
MILLIPEDES
SPIDERS, SCORPIONS, MITES, ETC.

FAIRY SHRIMPS, WATER FLEAS, COPEPODS, BARNACLES, ETC.

CLASS CRUSTACEA
ORDER DECAPODA

PHYLUM ARTHROPODY

EARTHWORMS, LEECHES, AND OTHER ANNEILD.

ECHINODERMS CHORDATES, ETC.

LESSER ANIMALS WITHOUT BACKBONES

SNAILS, CLAMS, AND OTHER MOLLUSCS

Figure 20 Simplified view of animal classification emphasizing categories containing crayfishes.
been introduced into California, and *Orconectes transjuga* introduced into Oregon (Fitzpatrick, 1966). The subfamily Cambaroidinae is in east Asia (*Cambaroides*) and western North America (*Pacifastacus*). The Astacinae is composed of two genera, *Astacus*, found in middle and east Europe, and *Austropotamobius*, found in middle and west Europe. In certain respects, species of the Cambaroidinae resemble the cambarine crayfishes (Ortmann, 1902: 287), but they differ in gill count. *Pacifastacus* is easily distinguished from eastern North American crayfishes by the lack in the former of three structures—ischial hooks in the males, seminal receptacles in females, and a transverse suture of the telson. *Pacifastacus* also has a simpler structure of the copulatory stylets of the male.

The subfamily Cambarinae is considered to be the most specialized group of crayfishes, but the characters which suggest this (seminal receptacle, ischial hooks, and complex copulatory stylets) are largely associated with reproduction, and also apparently have been evolved independently by *Cambaroides* (Ortmann, 1902: 287). These features facilitate "internal" insemination, a contrast to *Astacus*, *Austropotamobius*, and *Pacifastacus*, where the sperm are deposited by the copulatory stylets as spermatophores cemented on the underside of the female exoskeleton.

Ortmann's (1902) investigations (see also Rhoades, 1962b) led him to propose that the Astacidae arose in eastern Asia. From this area, one group migrated west to give rise to *Astacus* and *Austropotamobius* in Europe, while another group apparently migrated around the north shores of the Pacific Ocean to enter North America.

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**Figure 21** The subfamilies and genera of the crayfish family Astacidae. Basic taxonomic pattern from Laguarda (1961: 70). H. H. Hobbs assisted in the species count.
and give rise to *Pacifastacus. Cambaroides* would represent the direct descendants of the early Asian group still living near the ancestral home, while the subfamilies Cambarinae and Cambarellinae would be derived from a section of the ancestral stock of *Pacifastacus* which crossed the continental divide into Mexico.

Since its entry into eastern North America, the Cambarinae has undergone explosive radiation. It has been the object of considerable systematic work over the past one hundred years and during much of that time has been considered to consist of one large genus, *Cambarus*. Most workers since Faxon (1885a), however, have seen a high degree of diversity within this group, and several systems for generic and subgeneric groupings have been proposed (Faxon, 1885a; Ortmann, 1905a and b, 1931; Fowler, 1912; Faxon, 1914).

Of the six genera now used in the Cambarinae, *Procambarus, Paracambarus,* and *Faxonella* were formed by the elevation of subgenera—*Procambarus* and *Paracambarus* by Hobbs (1942a) in his revision of the Cambarinae, and *Faxonella* by Fitzpatrick (1963). *Orconectes* was salvaged from taxonomic obscurity and *Cambarus* was given its current restricted sense by Hobbs (1942a). The name *Troglocambarus* has represented a genus since its inception. Laguarda (1961: 69) separated the genus *Cambarellus* from the Cambarinae into a new subfamily of its own on the basis of gill count.

The three most extensive cambarine genera—*Procambarus, Cambarus,* and *Orconectes*—may be characterized as follows, based largely on diagnoses in Hobbs (1942a, 1965).

*Cambarus* is probably the most advanced (in morphological and behavioural traits) of the genera of the Cambarinae, and its distribution covers most of eastern and central North America. The two terminal processes of the first pleopods of the form I male are short, heavy, acute, and are bent caudad at an angle of approximately 90 degrees to the main shaft in all but two species (neither occurring in Ontario). The central projection is corneous and bladelike while the mesial process is softer and sometimes bulbiform. Only the ischia of the male’s third pereiopods bear hooks.

*Procambarus* is a primitive genus which is most prevalent in the southern United States and Mexico. There are two to five truncate, platelike or spiniform, terminal processes on the first pleopods of the male. This organ is usually not tapered, the terminal processes being situated on the blunt distal end. Hooks are present on the ischia of the third, or of the third and fourth, pereiopods in the male.
Orconectes is a morphologically advanced but behaviourally generalized genus of widespread distribution in eastern and central North America. The first pleopods of the form I male always terminate in two distinct parts which are tapered extensions of the shaft of the organ. These processes are straight or gently curved, short or long, pointed spines. In the form I male, the central projection is corneous while the mesial process is usually much softer. In general, only the ischia of the third pereiopods of the male bear hooks, but occasionally they are present on the fourth pereiopods also.

A consideration of the progression of relatively primitive to relatively advanced genera, at the same time as their geographical ranges are noted, can provide us with some idea as to the probable zoogeographical and evolutionary history of the group. Ortmann (1902: 285) suggests that the Cambarinae originated in Mexico and migrated into the United States in a northeasterly direction. The original ancestral line differentiated as it moved north, giving rise to Procambarus and Cambarellus in the south and to Orconectes and Cambarus farther north. The latter genera thence extended their ranges westward to the foothills of the Rockies, and northward into Canada.

The distribution of endemic crayfishes in Ontario is governed solely by geological and ecological factors, the same two forces that are responsible for the distribution patterns of all organisms. The influence of geological events on the fauna of this province has been well stated by Radforth (1944: 9):

The present distribution of the flora and fauna of Ontario has developed within the last 20,000 to 35,000 years, (Coleman, 1922—p. 68), the time estimated to have elapsed since the beginning of the last ice retreat in eastern North America. Before that time all of Ontario lay beneath a vast glacier and any living organisms which had inhabited the area before the onset of the glaciation were forced to withdraw into areas not affected by it, or were exterminated. When the ice sheet began its last retreat in a general northerly direction, new land areas and new waterways were made available. These were populated in the course of time by plants and animals, due to the natural tendency of species to spread into every available habitat.

It is evident, then, that all of our Ontario crayfishes are recent immigrants from glacial refugia in the central and eastern areas of the United States. There has not been speciation within the province, of the type one finds so abundantly in the southern United States where there is a long history of continuous habitation.
Thus, the problems inherent in Ontario crayfish distributions are: (1) determining the point(s) of entry in the northward migration, (2) determining the route(s) of migration within the province, and (3) determining the limiting factors imposing the northern boundaries of the species ranges. The first two questions can be attacked deductively from geographical and geological data. The answer to the third probably will depend almost entirely on ecological considerations. However, a careful study of the detailed ecology and physiology of all our species will be necessary before it is possible to evaluate the factors responsible for range limits.
Identification of Ontario Crayfishes

SYSTEMATIC LIST OF ONTARIO CRAYFISHES

Family Astacidae
   Subfamily Cambarinae
      Orconectes Cope (1872: 419)
         Type species: Orconectes inermis Cope, 1872, by monotypy
         Propinquus Section (Ortmann 1905a: 108)
            Propinquus Group (Ortmann 1905a: 109)
               Orconectes propinquus propinquus (Girard), 1852
               Orconectes obscurus (Hagen), 1870
            Rusticus Group (Ortmann 1905a: 109)
               Orconectes rusticus rusticus (Girard), 1852
         Virilis Section (Ortmann, 1905a: 109-10)
            Virilis Group (Ortmann, 1905a: 110)
               Orconectes virilis (Hagen), 1870
               Orconectes immunis (Hagen), 1870

Cambarus Erichson (1846: 88)
   Type species: Astacus bartoni Fabricius, 1798, subsequent designation
                 by Faxon (1898: 644)
   Bartoni Section (Ortmann, 1905a: 119)
      Cambarus bartoni bartoni (Fabricius), 1798
      Cambarus robustus Girard, 1852
   Diogenes Section (Ortmann, 1905a: 119)
      Cambarus diogenes diogenes Girard, 1852
      Cambarus fodiens (Cottle), 1863

USE OF THE KEY

Determination of the species to which a given crayfish specimen belongs involves an examination of the exoskeleton for details of shape, size, and ornamentation with spines and tubercles. All of this examination can be carried out with a $5\times$ hand lens and a dissecting
needle, which can be used to lift organs and to feel for low tubercles. A low-power, stereoscopic, dissecting microscope makes much of this work easier, but it is not essential. A millimetre scale will usually give sufficiently accurate areola measurements for computing the ratio used in the first couplet of the key. However, more precise results are possible using a dissecting microscope fitted with an ocular micrometer. A specimen should first be identified with the help of the key and then should be compared with the appropriate summary diagnosis, species description, and illustrations provided for each of the species found in Ontario, particularly if there is any doubt about the determination.

The key is a rapid and convenient way of comparing a specimen at hand with descriptions of all Ontario crayfish species. The first couplet is read and a decision made as to which of the two alternatives is applicable to the specimen. Then one proceeds to the couplet indicated (by number) at the end of the correct alternative, and repeats this process for each pair of alternatives in succession until the species name is reached. Full use of the illustrations provided should be made in forming each decision during the identification.

We have attempted to use a wide range of body structures as key characters here so that first and second form males, as well as females and in many cases immature crayfishes, can be identified. However, the most reliable species identification character is the shape of the copulatory stylets of a form I male crayfish, and this should be used whenever possible.

### KEY TO THE SPECIES OF CRAYFISHES RECORDED FROM ONTARIO*

1. The ratio "length of areola/width of areola" greater than 9.6; a relatively narrow areola, usually permitting no more than two punctations to occur side by side in its narrowest portion
   2. The ratio "length of areola/width of areola" less than 9.6; a relatively broad areola, usually permitting at least three punctations to occur in a horizontal row in its narrowest portion
   5
2. Areola linear or obliterated in its narrowest portion (Figs. 56, 57)
   3. Areola not linear or obliterated in its narrowest portion
   4
3. Carapace with triangular suborbital projection; cervical groove continuous laterally (Figs. 56, 68) **Cambarus diogenes**, Fig. 83

*See Glossary and Figure 1 for the meaning of unfamiliar terms.
Carapace without suborbital projection; cervical groove interrupted laterally (Fig. 57)  

**Cambarus fodiens**, Fig. 85

4. Movable finger (daetyl) of large chela with a notch at its base on the inner side (Fig. 61); ventral margin of joint between daetyl and propodus with only one tuberele; male I copulatory styles with terminal processes strongly curved caudally and subequal in length (Fig. 22); female seminal receptacle with fossa off to one side (Fig. 40)  

**Orconectes immunis**, Fig. 77

Inner side of movable finger straight; often with two small tubereles on ventral margin of joint between daetyl and propodus (Fig. 60); terminal processes of male I copulatory styles weakly curved caudally, the lateral longer than the mesial (Fig. 23); fossa of seminal receptacle large and central (Fig. 41)

**Orconectes virilis**, Fig. 75

5. With lateral rostral spines or tubereles (Figs. 51, 52, 53)  
Without lateral rostral spines or tubereles (Figs. 54, 55)  

6. Sides of rostrum slightly concave (Fig. 51); fingers of large chelae with distinct subterminal black bands (Fig. 73); central projection of form I and II male copulatory styles longer than mesial process (Figs. 24, 33); seminal receptacle oval (Fig. 42)  

**Orconectes rusticus**, Fig. 73

Sides of rostrum straight (Fig. 53); fingers of chelae without distinct black bands; terminal processes of both form I and II male copulatory styles subequal in length (Figs. 25, 26, 34, 35); seminal receptacle diamond shaped (Figs. 43, 44)

7. Usually with rostral carina (Fig. 52); usually without median spine or tuberele on ventral anterior margin of carpus (Fig. 59); form I male copulatory styles without a distinct, right-angled shoulder on anterior margin, although there may be a shallow indentation here (Fig. 25); tip of mesial process in both male I and male II styles acutely pointed in lateral view (Figs. 25, 34); seminal receptacle with two low tubereles (which are never fused along the mid-line) on anterior margin (Fig. 43)  

**Orconectes propinquus**, Fig. 69

Usually without rostral carina (Fig. 53); with a median tuberele or low spine on ventral anterior margin of carpus (Fig. 58); form I male copulatory styles with a distinct, right-angled shoulder on anterior margin (Fig. 26); tip of mesial process in both male I and male II styles blunt in lateral view (Figs. 26, 35); seminal receptacle with two high tubereles, which are fused along the mid-line, on anterior margin (Fig. 44)  

**Orconectes obscurus**, Fig. 71

8. Inner margin of palm with a single row of low tubereles (Fig. 64); palm inflated, without conspicuous depression near outer margin; rostrum square, tapering acutely to its tip (Fig. 54); carapace without lateral spines (Fig. 54); inner border of antennal scale usually directed rather abruptly caudad; tip of mesial process of
form I male copulatory stylets generally pointing ventrally (Fig. 29) **Cambarus bartoni**, Fig. 79

Inner margin of palm with two rows of low tubercles (Fig. 65); palm with depression, visible from both dorsal and ventral sides, near its outer margin; rostrum rectangular, not tapering abruptly to its tip (Fig. 55); carapace often with lateral spines (Figs. 55, 67); inner border of antennal scale usually directed mesial before turning caudal; tip of mesial process of form I male copulatory stylets generally pointed dorsally (Fig. 30) **Cambarus robustus**, Fig. 81

CAPTIONS FOR FIGURES 22-68


25 *O. propinquus*, carapace length 19 mm.; Ont., Mansfield, Dufferin Co., permanent stream-fed pond; 20 May 1962; D.W.B.

26 *O. obscurus*, carapace length 35 mm.; Ont., Massey, Maple L., Sudbury Dist.; 11 Aug. 1964; D.W.C. and D.W.B.

27 *Cambarus diogenes*, carapace length 33 mm.; Ont., southern tip of Long Point, Norfolk Co., burrow in damp marsh among reeds; 25 May 1963; D.W.B.

28 *C. fodiens*, carapace length 28 mm.; Ont., Toronto (Leaside), York Co., marsh S.E. of corner of Leslie and Eglinton Sts.; 29 June 1963; D.W.B.

29 *C. bartoni*, carapace length 35 mm.; Ont., Corley Twp., Algoma Dist., Lake no. 21; 22 July 1960; N. Patrick.

30 *C. robustus*, carapace length 51 mm.; Ont., Go Home Bay (Georgian Bay), Muskoka Dist.; July 1907; A. G. Huntsman.

31 *Orconectes immunis*, carapace length 26 mm.; Ont., southern tip of Long Point, Norfolk Co., shallow pond near lighthouse; 25 May 1963; D.W.B.


34 *O. propinquus*, carapace length 23 mm.; Ont., Mansfield, Dufferin Co., permanent stream-fed pond; 20 May 1962; D.W.B.

35 *O. obscurus*, carapace length 27 mm.; Ont., Massey, Maple L., Sudbury Dist.; 11 Aug. 1964; D.W.C. and D.W.B.

36 *Cambarus diogenes*, carapace length 46 mm.; Ont., southern tip of Long Point, Norfolk Co., burrow in damp marsh; 17 July 1965; D.W.B. and C. G. Barr.


39 *C. robustus*, carapace length 33 mm.; Ont., Go Home Bay (Georgian Bay), Muskoka Dist.; July 1907; A. G. Huntsman.


Cambarus diogenes, with eggs, carapace length 34 mm.; Ont., southern tip of Long Point. Norfolk Co., burrow in damp marsh; 25 May 1963; D.W.B.


C. robustus, carapace length 33 mm.; Ont., Teeterville, Big Ck. (below dam), Norfolk Co.; 12 Aug. 1963; R. W. Finch.

Orconectes immuns, carapace length 25 mm.; Ont., southern tip of Long Point, Norfolk Co., shallow pond by lighthouse; 25 May 1963; D.W.B.

O. virilis, carapace length 31 mm.; Ont., Mattagami R. (3 mi. below Long Rapids), Cochrane Dist.; 10 Sept. 1963; Paul Millette.

O. rusticus, carapace length 45 mm.; Ont., Plevna, Plevna L., Frontenac Co.; 2 June 1964; P. B. Littkeman.


C. diogenes, carapace length 37 mm.; Ont., Turkey Point, Norfolk Co.; 8 and 9 April 1941; Sprague Troyer.

C. fodiens, carapace length 30 mm.; Ont., Toronto (Leaside), York Co., S.E. of corner of Leslie and Eglinton Sts.; 29 June 1963; D.W.B.

Orconectes obscurus, carapace length 32 mm.; Ont., Droppedge L. (near Palmer Rapids), Raglan Twp., Renfrew Co.; 24 July 1963; P. B. Littkeman; ventral view.


O. virilis, carapace length 31 mm.; Ont., Mattagami R. (3 mi. below Long Rapids), Cochrane Dist.; 10 Sept. 1963; Paul Millette; ventral view.

O. immuns, carapace length 25 mm.; Ont., southern tip of Long Point, Norfolk Co., shallow pond by lighthouse; 25 May 1963; D.W.B.; dorsal view.

Cambarus fodiens, carapace length 30 mm.; Ont., Schomberg, Holland Marsh, York Co.; 20 June 1965; D.W.B. and C. G. Barr; dorsal view.

C. diogenes, carapace length 32 mm.; Ont., southern tip of Long Point, Norfolk Co., burrow in damp marsh; 25 May 1963; D.W.B.; dorsal view.


C. robustus, carapace length 38 mm.; Ont., Mansfield, Dufferin Co., rapid, cold stream; 20 May 1962; D.W.B.; dorsal view.

Orconectes virilis, carapace length 31 mm.; Ont., Mattagami R. (3 mi. below Long Rapids), Cochrane Dist.; 10 Sept. 1963; Paul Millette.


C. diogenes, carapace length 37 mm.; Ont., Turkey Point, Norfolk Co.; 8 and 9 April 1941; Sprague Troyer.
Figures 22-30 Form I right copulatory stylets of the nine Ontario crayfish species. Lateral view.
Figures 31-39  Form II right copulatory stylets of the nine Ontario crayfish species. Lateral view.
Figures 40–48 Seminal receptacles of mature females of the nine Ontario crayfish species. Anterior edge toward top of page.
Figures 49-57  Carapaces of form I males of the nine Ontario crayfish species. Dorsal view.
Figures 58–65 Distal three great cheliped segments of eight of the nine Ontario crayfish species. All specimens are right appendages of form I males.
Figures 66–68 Right lateral views of (66) a cylindrical carapace, (67) a dorsoventrally compressed carapace, and (68) a laterally compressed carapace. All are form I males.
Systematic Account of
Ontario Crayfishes

THE GENUS "ORCONECTES"

This genus is represented in Ontario by five species, three native (propinquus, virilis, and immunis) and two introduced (obscurus, rusticus). These species all have a roughly cylindrical carapace, styliform terminal processes on the copulatory stylets (Figs. 22–26), and (in most cases) lateral rostral spines (Figs. 49–53). The reduction of these spines in immunis appears to be a modification associated with a burrowing existence. All of our species have well-defined mating periods and a synchronized life cycle. With the exception of O. immunis these species are all stream and lake dwellers. All are omnivorous feeders.

Orconectes propinquus propinquus (Girard)
(Figures 25, 34, 43, 52, 59, and 69)

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

TYPES: Lost (Crocker, 1957: 35).

TYPE LOCALITY: See discussion in Crocker (1957: 35–36). 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.].”
**Taxonomic Remarks:** In addition to Girard’s taxon, three subspecies have been described, *O. p. sanborni* (Faxon), 1884b, *O. p. jeffersoni* Rhoades, 1944a, and *O. p. erismophorous* Hobbs and Fitzpatrick, 1962.

**Diagnosis**

*O. p. propinquus* is the smallest Ontario crayfish and is readily identified by the presence of a rostral carina and the lack of a median spine or tubercle on the anteroventral margin of the carpus of the first pair of pereiopods. The description given at the end of this section applies only to populations where *O. p. propinquus* does not occur in common with *O. obscurus*. When the two species occur together, hybridization and resultant intermediacy of characters may occur.

**Habitat**

*O. p. propinquus* is rare where the bottom consists solely of mud or silt. In southern Ontario it is found mainly in rocky streams and rivers, although it can also be found along the shores of clear, stony ponds and lakes. On the Shield, this species is found extensively in lakes with a bottom of granitic rubble. The habitat preference is much the same as that of *O. virilis* with which it is often associated in collections. In general, populations are larger in ponds than in rivers but a polluted stream in southwestern Ontario has yielded a high-density population.

**Life History**

The life history of this species has been worked out for a population at Urbana, Illinois by Van Deventer (1937). As Ontario populations appear to behave in much the same manner, a summary of Van Deventer’s work (slightly modified for Ontario) is presented below.

Mature females and form I males mate from approximately mid-July through September, starting immediately upon the mid-July moult of males from form II to form I. Eggs are laid the following spring, from late April to early June, and are carried for four to six

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*Note added in proof. A systematic evaluation of the Propinquus group of *Orconectes* (Fitzpatrick, J. F. 1967. The Ohio Journal of Science, 67 (3): 129–72) has come to our attention too late for evaluation and inclusion in the body of this study. In reference to the two species of this group which occur in Ontario, Fitzpatrick considers *O. propinquus* to be without subspecies. The former subspecies, *O. p. sanborni* and *O. p. jeffersoni*, are elevated to full species. The former *O. p. erismophorous* is made a subspecies of *O. sanborni*. The second Ontario species *O. obscurus* is not changed in taxonomic status.*
Figure 69  *Orconectes propinquus*, male form I, carapace length 32.5 mm.; Ont., Cardiff, Paudash Lake, Haliburton Co.; May 1965; S. Wilcox.
weeks. Hatching takes place from mid-May to mid-July. The young are carried for about two weeks, and become free-swimming (carapace length 5 mm.) following their second juvenile moult. Adult females that have borne young undergo a moult immediately after the brood leaves. Adult males moult earlier (May?), going from the winter form I condition to form II. During the summer the juveniles moult 6 to 10 times so that by late September or early October they have attained a carapace length of 16 to 20 mm. At this size, most of the individuals of both sexes will be sexually mature, and mating often occurs during the first fall.

Thus, the individuals that mate the first year produce a brood the following spring. Although some may live on to repeat the reproductive process in their second fall and spring, most die as yearlings. Those individuals that are not mature the first fall continue growing throughout the second summer, mate the second fall, and produce eggs the next spring. Very few individuals of this group live to reproduce during the third fall and spring, most dying as two-year-olds.

Dates for the capture in Ontario of females with eggs are 30 April (1 specimen), 12 June (2 specimens), 18 June (2 specimens), 2 July (1 specimen), and 12 July (1 specimen).

The frequency of occurrence of the two forms of the male in July and August is shown in Table 5. Only six mature males with full data are available for each of the months of May and June, indicating the need for collecting in these months. We cannot, therefore, pin-point the spring moult of adult males from form I to form II.

Seasonal data for this species in New York given by Crocker (1957: 49, Table 3) are not presented by weeks. Furthermore, a re-examination of his raw data reveals that little collecting was done in the first half of July (Table 6). However, a comparison of Tables 5 and 6 does suggest that the moult from form II to form I is later in Ontario than in New York, a result to be expected on the basis of climate. Comparing the data for the third week of July, we see that

Table 5  SEASONAL DATA FOR Orconectes p. propinquus MALES IN ONTARIO

<table>
<thead>
<tr>
<th>Week:</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 2 3 4</td>
<td>1 2 3 4</td>
</tr>
<tr>
<td>Form I</td>
<td>2 3 134</td>
<td>195 10 71 44 42</td>
</tr>
<tr>
<td>Form II</td>
<td>16 9 46</td>
<td>41 1 5 12 2</td>
</tr>
</tbody>
</table>
Table 6  JULY SEASONAL DATA FOR  
*Orconectes* p. *propinquus* MALES IN  
NEW YORK

<table>
<thead>
<tr>
<th>Week</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Form I</td>
<td>3</td>
<td>1</td>
<td>42</td>
<td>37</td>
</tr>
<tr>
<td>Form II</td>
<td>—</td>
<td>2</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>

whereas in New York about 90 per cent of males have returned to form I, in Ontario only about 75 per cent have done so. In the fourth week 95 per cent of New York males are in form I, but in Ontario only 83 per cent have accomplished this moult.

Ecology

*O. p. propinquus* appears to be a generalized feeder, as is probably true of all of the open-water species. It spends much of its time under flat stones, sometimes constructing a shallow burrow in which to rest (Figs. 16, 17).

Distributional Summary (Figure 70)

*Orconectes* p. *propinquus* is the second most widely distributed crayfish in the province, and the most commonly encountered form in southern Ontario, where it appears to be ubiquitous in suitable habitats. The range extends north and westward, entering the arctic and Lake Superior drainages, but current records do not go beyond a straight-line boundary joining Moosonee (James Bay) and Michipicoten Harbour (Lake Superior). This present boundary may recede to the northwest when further collecting has been done in the area. The single record from Burditt Lake, Rainy River District, is discordant with both the Ontario and continental distributions, and cannot be explained at present except as an introduction by sport fishermen.

The North American distribution of *O. propinquus* is taken up largely by the subspecies occurring in Ontario, *O. p. propinquus*. Three other subspecies have been described as mentioned under Taxonomic Remarks. They occupy regions on the southern and southeastern borders of the area occupied by *O. p. propinquus*, lying in the states of West Virginia, Ohio, Kentucky, and Indiana.

*O. p. propinquus* is (1) absent from New Hampshire (Aiken,
Figure 70 Distribution of Orconectes propinquus in Ontario. Inset shows total range of the species; stippled area is occupied by subspecies other than O. p. propinquus.
1965). (2) present in at least portions of the western border of Vermont (Crocker, personal collections), (3) present in the Lake Ontario drainages of New York (Crocker, 1957: 78, Fig. 5), (4) on the northern border of Ohio (Turner, 1926: 179, Map 4), (5) the common species throughout Indiana (Hay, 1896: 498), (6) in both northern and southern parts of Michigan (Creaser, 1931a: 266, Map 5), (7) in the southern half of Wisconsin (Creaser, 1932: 329, Fig. 10), and (8) in eastern Iowa (Faxon, 1885a: 162).

Locality Records in Ontario

ALGOMA DIST.: Edith L., Meredith Twp., no date, 1 ♀ I, 2 ♀♀ mat.; Elizabeth L., Duncan Twp., no date, 1 ♀ mat.; Goulais R., L. Superior, 23 Aug. 1954, 1 ♀ imm., 1 ♀♀ mat., 1 ♀ imm.; Goulais R., Algoma (Whitman Dam), no date, 4 ♀♀ mat., 1 ♀ imm., 1 ♀ mat.; Kindiogami L., Twp. 3B, 1 Sept. 1963, 1 ♀ I, 1 hermaphrodite; Lake no. 9, Twp. 6H, 2 ♀♀ mat.; MacLennan, St. Joseph Channel, 1 July 1931, 1 ♀ mat., 3 ♀♀ mat.; McClung L., Twp. 3E, July 1963, 1 ♀ I; Mijinemungshing L., Twp. 29 RXX, 1 ♀ II; Northland L., Deroche Twp., 2 ♀II; St. Joseph Island, 8 Aug. 1958, 17 ♀♀ mat., 6 ♀♀ mat.; Seymour L., Twp. 2E, 3 ♀♀ II; L. Superior. Sunset Inn, 27 June 1960, 1 ♀ II (NMC); L. Superior, Sunset Inn, 27 June 1960, 1 ♀ mat. (NMC); L. Superior, Batchawana Bay, 2 June 1960, 1 ♀ I (NMC).


CARLETON CO.: Burritts Rapids, 15 June 1958, 1 ♀ mat.; Galetta, 15 June 1895, 1 ♀ mat. (NMC); Hudson, Ottawa R., 16 Oct. 1953, 1 ♀ I; Ottawa, 1918, 1 ♀ II, 1 ♀ mat., 1 ♀ with eggs (NMC); Ottawa R., 13 Oct. 1918, 1 ♀ mat.; Ottawa R., Bate Is., 23 Oct. 1953, 5 ♀♀ I, 6 ♀♀ imm., 6 ♀♀ mat. (NMC); Rideau R., 12 May 1918, 2 ♀♀ I, 1 ♀ II, 3 ♀♀ mat. (NMC); Stittsville, 10 June 1903, 1 ♀ I, 1 ♀ imm., 1 ♀ imm. (NMC).

COCHRANE DIST.: Abitibi R. (bet. New Post and Moose R.), Oct. 1920,


ELGIN CO.: Big Otter Ck., Bayham Twp., 1 ♂ II.


GREY CO.: Durham, Saugeen R., 30 May 1957, 1 ♀ imm. (NMC); Eugenia Falls, 7 July 1919, 3 ♂♂ mat., 2 ♀♀ mat.; Eugenia L., Artemesia Twp., no date, 1 ♂ 1; Kimberly, Eugenia R., 2 ♂♂ 1, 2 ♂♂ imm., 3 ♀♀ mat., 5 ♀♀ imm.; McCullough L., Saugeen R., 6 Aug. 1964, 1 ♂ 1, 1 ♂ II, 1 ♀ imm.; McEachran, Bighead R., 2 ♂♂ imm., 6 ♀♀ imm.; Owen Sound, Bothwell's Ck. (Telfer Ck.), 27 July 1964, 1 ♂ 1, 10 ♂♂ imm., 8 ♀♀ imm.; Owen Sound, Pottawatami R., 27 July 1964, 2 ♂♂ I, 5 ♂♂ imm., 3 ♀♀ mat., 6 ♀♀ imm.; Owen Sound, Sydenham R., 25 July 1964, 3 ♂♂ I,
1 ♂ II, 6 ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ ♀ &n
Wroxeter, Maitland R., 17 July 1963, 2 ♂ 1, 7 ♂ 11, 1 ♀ mat.; Wroxeter, trib. of Maitland R., 29 July 1963, 2 ♂ 1; Wroxeter, Maitland R., 4 July 1963, 3 ♂ 11, 2 ♀ mat.; Wroxeter, Maitland R., 29 July 1963, 1 ♂ 1.


LANARK CO.: Almonte, stream at Mill of Kintail, 18 May 1959, 1 ♂ II (NMC).


MANITOULIN DIST.: Killarney, Georgian Bay, 14 June 1912, 8 ♂ mat., 3 ♀ mat.; Manitou R., Manitoulin Is., 22 Aug. 1964, 5 ♂ 1, 2 ♂ imm., 7 ♀ mat.; South Baymouth, South Bay, Manitoulin Is., 22 Aug. 1964, 2 ♂ I.


OXFORD CO.: Plattsville, 2 July 1927, 1 ♀ mat.; stony ck., W. of Tillsonburg, 1 ♂ imm., 1 ♀ mat., 1 ♀ imm. (NMC); stony ck., 4 mi. N.W. of Tillsonburg. 29 May 1957, 1 ♂ II (NMC).


PEEL CO.: Erindale, Credit R., 7 Aug. 1919, 3 ♂♂ mat., 1 ♀ mat.; Port Credit, L. Ontario, 6 June 1927, 1 ♂ mat., 1 ♀ mat.


PETERBOROUGH CO.: Deer Bay Ck., Harvey Twp., 28 July 1964, 2 ♂♂ I; Havelock, Oak L., 8 Aug. 1964, 2 ♂♂ I, 2 ♂♂ II, 1 ♀ mat.


RENFREW CO.: Dore L., Sept. 1918, 1 ♂ I, 3 ♀♀ mat. (NMC).


Waterloo co.: Baden, Baden Ck., 16 July 1964, 2 ♂♂ II, 2 ♀ ♀; Bamberg, Bamberg Stream, 16 July 1964, 1 ♂ I, 1 ♂ II, 2 ♀ ♀; Blair, Blair Ck., 16 July 1964, 1 ♂ I, 1 ♂ II, 1 ♀ ♀; Fishermills, Fishermill Ck., 16 July 1964, 1 ♂ I, 2 ♂ II, 1 ♀ ♀; Hawkesville, Conestogo R., 22 Oct. 1922, 3 ♂♂ mat., 5 ♂♂ imm., 4 ♀ ♀, 2 ♀ ♀ imm.; Hespeler, outlet of Puslinch L., 18 July 1964, 2 ♂♂ I, 2 ♀ ♀; Hespeler, Speed R., 18 July 1964, 1 ♂ I, 1 ♂ II, 1 ♀ ♀; Maryhill, Hopewell Ck., 16 July 1964, 4 ♂♂ I; New Dundie, Mannheim Stream, 16 July 1964, 3 ♂♂ I, 1 ♀ ♀; Wellesley, Wellesley Ck., 16 July 1964, 2 ♂♂ I, 3 ♀ ♀; Wellesley, Nith R., 18 July 1964, 1 ♂ I, 1 ♂ imm., 1 ♀ ♀, 2 ♀ ♀ imm.; West Montrose, Elora Ck., 16 July 1964, 3 ♂♂ I, 1 ♀ ♀; Winterborne, Cox Ck., 16 July 1964, 2 ♂♂ I, 2 ♀ ♀; Zuber’s Corners, Grand R., 16 July 1964, 3 ♂♂ I, 2 ♀ ♀ mat.

Welland co.: Chippawa, Boyer’s Ck., at Niagara Parkway, Apr. 1958, 1 ♂ imm., 1 ♀ imm.; Chippawa, Tee Ck., at Queen Elizabeth Hwy., Apr. 1958, 1 ♂ I, 1 ♀ ♀; Chippawa, Usher’s Ck., Apr. 1958, 2 ♂♂ I, 2 ♀ ♀ mat.; Fergus, Grand R., 6 ♂♂ mat., 1 ♂ imm., 9 ♀ ♀ mat., 1 ♀ imm.; Fort Erie, Black Ck., Apr. 1958, 3 ♂♂ I, 1 ♂ II, 4 ♀ ♀ mat.; Humberstone Twp., 10 Sept. 1963, 1 ♂ I, 1 ♂ II.

Wellington co.: Carroll Ck., Peel Twp., 8 July 1964, 1 ♂ I, 1 ♂ II, 1 ♀ ♀ mat.; Conestogo R., Peel Twp., 18 July 1964, 3 ♂♂ I, 1 ♀ ♀; Harriston, trib. of Maitland R., 25 July 1963, 5 ♂♂ I, 1 ♀ ♀; Harriston, Maitland R., 25 July 1963, 1 ♀ ♀; Harriston, Maitland R., 27 July 1963, 1 ♂ I; Harriston, Maitland Ck., 18 July 1964, 3 ♂♂ I, 1 ♀ ♀; Rothsay, Moorefield, Moorefield Ck., 18 July 1964, 3 ♂♂ I, 2 ♂♂ II; Stinton, Conestogo Dam,


Description

Male form I. Carapace cylindrical, lateral surface anterior to cervical groove bearing tubercles only, dorsal surface smooth and punctate. Only one small, but distinct, lateral spine on each side, minute branchiostegal spine also present. Postorbital ridges short and grooved on outer face, postorbital spines short and acute. Cervical groove broken on sides. Areola relatively broad, permitting at least three punctations to occur in horizontal row in narrowest portion.

Rostrum long, narrow, and well excavated, the margins raised and nearly parallel. Acumen long, slender, concave sided, terminal spine acute. Lateral spines small, often only tubercles in large specimens. Distinct median carina usually present.

Antennal scale slightly longer than rostrum, with an acute terminal spine, broadest near the middle.

Flagellum of antenna stout and much shorter than body.

Epistome kidney-shaped (reniform) and about as long as broad, sides convex and raised.

Chela fairly short, sides nearly parallel. Slightly tuberculate on inner surface, nearly smooth above. Dactyl weakly sinuate, tips of fingers incurved, brown, and horny. Immovable finger sometimes with sparse patch of setae at base, medial border of palm straight.

Carpus of cheliped with short, shallow furrow dorsally, one strong medial spine and another at distal end ventrally. Distal margin of ventral surface usually without either spine or tubercle.

Merus of cheliped with one or two spines on upper surface at distal end, two spines on lower surface, and usually a distinct row of small spines on inner lower margin.

Telson tapering, proximal section bispinose (sometimes trispinose) on each side, about as long as distal section, distal section rounded behind.

Copulatory stylets styiform and nearly straight; short, reaching nearly to bases of second pair of pereiopods when abdomen flexed; often
with slight notch and slope (but never an acute, right-angled shoulder) on anterior margin. Tip of mesial process (both forms I and II) ends in relatively sharp point (never blunt or dilated).

**ISCHIAL HOOKS** located on third pereiopods.

**COLOUR** in life basically olive-grey-brown dappled with darker brown. Bases of antennae bluish-grey; flagella light orange. Large chelae bluish-grey tipped with light orange. Carapace with blue strip following cervical groove and a semicircular chestnut-coloured spot on anterior margin above branchiostegal spine. Segments of the pereiopods are grey while articulations and claws are pink to salmon. Abdominal segments bluish-grey, posterior edge of each marked by thin orange-brown line, each bearing a pair of submedial dark grey spots and a sublateral pair of light grey spots.

**Male form II.** Similar to male form I, but chelae weaker and rostrum less strongly carinated. Copulatory stylets shorter, the distal processes more swollen, the free tips shorter and more nearly blunt, although each still ends in a relatively sharp point.

**Female.** Similar to male form I, but chelipeds shorter and rostrum less strongly carinated. Seminal receptacle diamond shaped, flat, and slightly depressed in middle; often with two low tubercles near anterior border (never fused in the mid-line); a single, central, caudal tubercle crossed by sinuate fissure running anteriorly into left side of small crescentic fossa in centre of receptacle.

**Orconectes obscurus** (Hagen)
(Figures 26, 35, 44, 53, 58, and 71)

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

**TYPES:** “Cotypes, M.C.Z. No. 181, 3353, 3354; U.S.N.M. No. 4971; Mus. Nat. Hist. Paris; Wurzburg Mus.: Australian Mus., Sydney.” Subsequent designation by Faxon (1914: 418). The cotypes in M.C.Z. and U.S.N.M. have been examined by the senior author.

**TYPE LOCALITY:** Genessee River, Rochester, Monroe County, N.Y. (Hagen, 1870: 70)
Diagnosis

This is a rare crayfish in Ontario, occurring in only a few localities. It is very similar to O. p. propinquus but usually can be distinguished by the lack of a rostral carina and the presence of a tubercle or low spine on the ventral anterior margin of the carpus. However, the copulatory styles of the male and seminal receptacle of the female provide the best means of separating these two species (see Description). O. obscurus does not have the concave-sided rostrum and jet-black-banded finger-tips characteristic of O. r. rusticus.

Habitat

In Ontario, this species has been found in only a few lakes and one river of the Precambrian Shield where the bottom may be silt, gravel, or granitic rubble. In its natural range in the Ohio River drainage system, its habitat is much like that of O. p. propinquus.

Life History

Ortmann (1906a: 407-76) gives life history data for this species, which correspond in all but small details to those of Van Deventer (1937) for O. p. propinquus. Doubtless, small changes in the timing of life history events will occur in this province but because of the rarity of the species here, no significant data are available.

Ecology

The few Ontario observations suggest that this species lives in much the same way as O. p. propinquus.

Distributional Summary (Figure 72)

As can be seen in the inset map of Figure 72, the natural range of O. obscurus does not actually come into contact with the Ontario border at any point, although it is closest in northwestern New York State (Crocker, 1957). This fact, when combined with the isolated nature of the collecting sites in Ontario, constitutes good evidence that O. obscurus is an introduced species, probably transported from New
Figure 71 Orconectes obscurus, male form II, carapace length 31 mm.; Ont., Palmer Rapids, Madawaska River, Renfrew Co.; 1 August 1965; D.W.B. and C. G. Barr.
Figure 72  Five collection sites for *Orconectes obscurus* in Ontario. Inset shows total range of the species.
York, Ohio, Pennsylvania, or West Virginia by sport fishermen as bait, and subsequently released. This hypothesis is supported by the fact that all the Ontario localities for this species are vacation, cottage, or sport-fishing areas.

The total natural range of *O. obscurus* is small. It is confined to eastern Ohio (Turner, 1926: 176, Map 4; Rhoades, 1944b: 95), western Pennsylvania (Ortmann, 1906a: Plate 42), West Virginia (Schwartz and Meredith, 1960: 42), and the Allegheny, Genesee, and Mohawk rivers in New York (Crocker, 1957: 78, Fig. 5).

**Locality Records in Ontario**

**Frontenac Co.**: Plevna, Lucky L., 13 Aug. 1964, 5 ♂♂ I, 3 ♂♂ II, 2 ♀ ♀ mat., 1 ♀ imm.


**Nipissing Dist.**: Algonquin Prov.Pk., Cedar L., 17 Aug. 1964, 1 ♂ II, 1 ♀ mat.


**Description**

*Male form I*. Carapace very similar to that of *O. p. propinquus* but more robust on the average; sides of areola more concave.

Rostrum much like that of *O. p. propinquus*, but in vast majority of cases with no trace of median carina; lateral spines may be reduced to mere angles in large, old individuals.

Antennal scale, flagellum of antenna, and epistome all similar to corresponding structures described for *O. p. propinquus*.

Chela more robust than in *O. p. propinquus*, wider and more distinctly depressed. Fingers widely gaping at base, dactyl strongly sinuate.

Carpus of cheliped differs from that of *O. p. propinquus* in consistently having well-developed tubercle or spine on distal margin of ventral side (may be absent in regenerated claws).

Merus of cheliped similar to that of *O. p. propinquus*.

Telson narrow, tapering; proximal section bispinose on each side, posterior margin of distal section straight to slightly convex. The two sections of equal length.
COPULATORY STYLETS of same general structure as those of *O. p. propinquus* but differ in following details: slightly longer, reaching past posterior margin of coxae of second pereiopods; mesial process of nearly uniform thickness with tip rounded bluntly and slightly compressed anteroposteriorly; anterior margin with abrupt (almost 90°), well-marked shoulder at point slightly dorsal to point of separation of distal processes. ISCHIAL HOOKS borne on third pereiopods. COLOUR IN LIFE much like that of *O. p. propinquus.*

**Male form II.** Similar to male form I. Copulatory stylets similar to those of *O. p. propinquus* except tip of mesial process always rounded and blunt.

**Female.** Similar to male form I but outline of chela more ovate, fingers shorter, dactyl less strongly sinuate. Seminal receptacle differs consistently from that of *O. p. propinquus*: median fossa with more strongly marked surface depression; anterior border with two distinct, subconical tubercles fused along the median line; posterior margin elevated into flat, low tubercle and crossed by narrow sinuous fissure.

**Orconectes rusticus rusticus** (Girard)
(Figures 24, 33, 42, 51, and 73)

*Cambarus rusticus* Girard, 1852: 88
*Cambarus juvenilis* Hagen (in part), 1870: 66 (authority of Faxon, 1914: 418)
*Cambarus wisconsinensis* Bundy, 1876: 4 (authority of Faxon, 1914: 418)
*Cambarus (Faxonius) rusticus* Girard. Ortman, 1905a: 107–9, 112
*Orconectus rusticus* (Girard). Hobbs, 1942a: 352
(not) *Cambarus rusticus* Girard. Williamson, 1901 (authority of Ortman, 1906a: 349)

**Types:** “... probably destroyed in the Chicago fire in 1871; paratype (?), Acad. Nat. Sci. Philad.,” Faxon (1914: 418).

**Type Locality:** “The Ohio, at Cincinnati” (Girard, 1852: 88). This is the only locality given by Girard.

**Taxonomic Remarks:** Part of Hagen's *C. juvenilis* is *Faxonius luteus* Creaser (=*Orconectes luteus*) according to Creaser (1933b: 7). Williamson's record for *C. rusticus* in Allegheny Co., Pa. is *C. obscurus* Hagen according to Ortman (1906a: 349). Williams and Leonid (1952: 987) consider that the Kansas records of *C. rusticus* given by Faxon and Steele in the above references are *O. luteus.*

Ortman (1931: 71–84) considers that there are, in addition to Girard's
taxon, three subspecies of *O. rusticus*. Hobbs (1948a:140) agrees. These are *O. r. forceps* (Faxon), *O. r. placidus* (Hagen), and *O. r. mirus* (Ortmann). They are found in one or more of the states of Tennessee, Alabama, Kentucky, and Virginia. Rhoades (1944a:125-6) has described *O. r. barrenensis* from Kentucky and "probably Tennessee."

**Diagnosis**

This is a rare crayfish in Ontario, occurring in only six localities. It is unique among Ontario crayfishes in the possession of distinct jet-black bands near the tips of the fingers of the large chelae, and in having a rostrum with slightly concave sides.

**Habitat**

In Ontario, *O. rusticus* has been introduced into and seems to be maintaining itself in stony lakes of the Precambrian Shield.

**Life History**

This account of the life history and ecology is based upon Langlois' (1935) discussion of *O. rusticus* in fish ponds in Ohio. In Ontario, it is certain that some of the habits mentioned by him (e.g. burrowing) will be altered because this crayfish is found in a different habitat in this province. Probably there are changes also in the details of life history.

The principal mating season occurs during the periods of descending temperature characteristic of September and October. At this time, pairs may be seen copulating on their sides or on top of one another on the pond bottoms. All females are found to contain large, well-developed ova which are black in colour, the number varying directly with the size of the female.

Immediately after copulation, the females burrow into the banks of the pond at the water line. The tunnels constructed are horizontal and never longer than two and one-half feet, and each may contain several females when the population is dense. A few old males may be found in tunnels at this time also, but the young-of-the-year males remain in open water. A few females oviposit in late October, but the majority wait until the following April and May when they are just one year old. Eggs hatch in approximately twenty days and in another three to five days the juveniles become free living. Young-of-the-year
Figure 73 *Orconectes rusticus*, male form I, carapace length 35 mm.; Ont., Plevna, Plevna Lake, Frontenac Co.; 1 August 1965; D.W.B. and C. G. Barr.
are sexually mature after one summer's growth and participate in the fall mating period.

Ecology

In Ohio fish ponds, *O. r. rusticus* fed upon waste from food cast to the fish. They migrated to the shoals of the ponds regularly each evening to feed, and could be baited there with meat scraps.

In Ontario, crayfish of this species probably exist in much the same manner as those of *O. virilis*, feeding upon aquatic invertebrates, vegetation, and detritus, and secreting themselves under the stones of Shield lakes.

Distributional Summary (Figures 19 and 74)

*O. r. rusticus* is predominantly a crayfish of the midwestern United States and by much the same sort of evidence cited for *O. obscurus*, it is clearly an introduced species in Ontario. Indeed, at Plevna Lake, where it occurs in large numbers, the junior author found that most of the summer vacationers were residents of Ohio.

The subspecies in Ontario has the most extensive North American distribution of the five that have been described. The other four are listed under Taxonomic Remarks, and occupy a region at the southern border of *O. r. rusticus*, including most of Tennessee and small areas in western Virginia, northern Mississippi and Alabama, and Kentucky.

*O. r. rusticus* has not been found in Pennsylvania (Ortmann, 1906a), West Virginia (Newcombe, 1929), Wisconsin (Creaser, 1932), or Kansas (Williams and Leonard, 1952). Neither it nor any other subspecies of *O. rusticus* has been taken in Reelfoot Lake in western Tennessee (Hobbs and Marchand, 1943). *O. r. rusticus* occupies only the extreme southern edge of Michigan (Creaser, 1931a: 267). Ohio records given by Turner (1926) have been extended by Rhoades (1944b: 96). We have determined the western limits from data in Harris (1903, Plate V, Fig. 12), modified by Creaser (1931a: 267).

Locality Records in Ontario


**Haliburton Co.:** Head L., Dysart Twp., 10 Aug. 1964, 1 ♂ I.
Figure 74. The six collection sites for *Orconectes rusticus* in Ontario. Inset shows total range of the species; stippled area is occupied by subspecies other than *O. r. rusticus*.

Description

Male form I. CARAPACE cylindrical but flattened above, smooth and punctate dorsally, granulate laterally. Lateral spine small, branchiostegal spine very small or lacking. Postorbital ridges short, grooved on outer face, terminating anteriorly in short but acute spine. Cervical groove deep, sinuate, and broken on sides. Areola relatively wide, usually with three or more punctations side by side in narrowest portion.

ROSTRUM long and narrow, sides slightly concave, deeply excavated dorsally. Margins raised and divergent at base. Lateral spines acute; may be reduced in larger specimens. Acumen slender, triangular; terminal spine acute, upturned, brown, and horny.

ANTENNAL SCALE as long as rostrum, widest proximal to middle.

FLAGELLUM OF ANTENNA stout, about as long as body.

EPISTOME triangular, about as long as broad, sides convex, apex blunt with median tooth.

CHELÆ large and strong, medial border of propodus tuberculate, fingers and hand ornamented with numerous punctations, fingers gaping at base. Immovable finger sometimes slightly bearded, movable finger sinuate, the tip incurved.

CARAPUS of cheliped strong, furrow on dorsal surface shallow; short, strong spine on medial surface, low spine or strong tubercle in centre of distal margin of ventral side.

MERUS bearing two small spines at distal end dorsally. Two stronger spines beneath with (sometimes) several smaller ones in addition.

TELSON wide. Proximal section bispinose on each side, distal section with straight to slightly concave posterior margin. Distal section shorter than proximal.

COUPULATORY STYLETs long, reaching to bases of second pereiopods when abdomen flexed, with two long, slender, tapering, straight distal processes. These processes deeply divided and slightly twisted, mesial process shorter than central projection and not as slender.

ISCHIAL HOOKS borne on third pereiopods.

COLOUR IN LIFE basically olive-green on dorsal surface. Flagella of
antennae chestnut-brown. Large chelae reddish-brown to olive-green, tubercles and spines yellow in larger specimens; a distinct subterminal black band surrounds each finger just basal to the light orange-brown tip. Articulation membranes of all pereiopods with red, orange, or rust-coloured traces, more intense distally and paler proximally; chelae and claws of all walking legs with some orange.

Dorsal surface of carapace marked with light-coloured punctations, marked by a large squarish black area in posterior median area of dorsal surface of cephalic portion (stomach area), origins of mandibular muscles visible as dark spots on either side of this. Leading edge of carapace with triangular rufous spot, edged anterodorsally with cream just above branchiostegite spine. A broad, rufous, crescent-shaped spot borne at posteroventral corner of each branchiostegite and, anterior to this, a green-tinged, creamy streak proceeds forward from the inner face of the crescent. Dorsal areas of branchiostegites may form a grey-blue to olive-black saddle in some individuals. Each of first five abdominal segments with a dorsal transverse chestnut band. Green spots form symmetrical pattern, like lion’s face, on light orange background of dorsal surfaces of abdominal segment VI and telson. Expanded edges of abdominal terga greenish and lighter than median dorsal arca, each bearing rufous spot.

Ventral surface basically greenish-white; tubercles of the seminal receptacle may be green.

Male form II. Similar to male form I, but most structures less sharp and heavy. Copulatory stylets less heavily sclerotized, distal processes not as deeply divided but still slender and acute.

Female. Very similar to male form I. Seminal receptacle oval, bituberculate on anterior margin, with deep median depression, posterior wall raised into median tubercle divided by very narrow sinuous fissure.

Orconectes virilis (Hagen)
(Figures 23, 32, 41, 50, 60, 66, and 75)

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

Types: “Types, M.C.Z., No. 1151; paratypes M.C.Z. Nos. 194 and 203 (Lake Superior), No. 196 (Quincy, Ill.), No. 3342 (Lake Winnipeg), No. 3343 (Red River of the North). No. 3344 (Saskatchewan River); Mus. Hist. Nat. Paris (Lake Superior); Wurzburg Mus. (Lake Superior); Australian Mus., Sydney,” Faxon (1914: 420). The types and the M.C.Z. paratypes have been examined by the senior author.

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

This is our most widespread crayfish species and can be identified by the combination of lateral rostral spines, a narrow areola, and a straight medial margin on the movable finger. The last-mentioned feature, and the presence of two small distal tubercles on the ventral margin of the articulation between dactyl and propodus, serve to separate it from *O. immunis*, the species most similar to it in our fauna.

Habitat

Throughout most of its range, *O. virilis* is characteristic of streams and rivers with rocky bottoms. Individuals usually choose large, flat rocks to hide under. However, in much of Ontario and in some of the northern United States (Threinen, 1958a; Aiken, 1965), this species occurs in stony lakes, often in quite deep water. In many of these situations, it is the sole crayfish inhabitant of the lake. In Ontario, as mentioned by Harris (1903: 134–5) for Kansas and Crocker (1957: 60) for New York, it may occasionally be taken in slow-moving, mud-bottomed streams, in company with *O. immunis*.

Life History

No extensive study of the life history of *O. virilis* has been made in southern Ontario, but what is known here seems to agree fairly well with the account given by Threinen (1958a, b) for the species in Wisconsin.

Mature males are in form I from August through May, and study of the testes indicates that mating occurs in two distinct periods: August to October, and April to May (Fasten 1914: 603). Eggs are laid from mid-May to mid-June and are carried for several weeks. Threinen (1958b) states that the young grow for two summers before reaching maturity, and then in late summer of their second year, mating activity begins. These same individuals may participate in mating again the following spring. After this, most males will die (Threinen, 1958a) while the females will produce a brood. Most of the females die after the young leave (Threinen, 1958a), but a few may live to mate again the third fall. If any males survive, they will become form II during their third summer and then form I again the
Figure 75 *Orconectes virilis*, male form I, carapace length 31.5 mm.; Ont., Alliston, Nottawasaga River, 1 mile below Nicolston Dam, Simcoe Co.; 20 June 1965; D.W.B. and C. G. Barr.
next fall. It is unlikely that any members of either sex survive the fourth spring. This account must be considered provisional until further data are obtained.

We have no specimens with full data collected in April and only one each for March and May (both form I males). The June data for males (Table 7) suggest that the bulk of mature individuals are in form II, but collecting or field observations are badly needed. No doubt males are generally in form I in April and most of May, but we hesitate to accept the idea of a spring mating period until field observations substantiate it. Although data are lacking on the timing of the spring moult from form I to form II, our July data show that by the end of that month most males are back to form I, about 50 per cent in the third week and 80 per cent in the fourth week.

Table 7 SEASONAL DATA FOR Orconectes virilis MALES IN ONTARIO

<table>
<thead>
<tr>
<th>June</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td>Week</td>
<td>1</td>
<td>2 3 4</td>
</tr>
<tr>
<td>Form I</td>
<td>0</td>
<td>1 0 1</td>
</tr>
<tr>
<td>Form II</td>
<td>0</td>
<td>1 4 1</td>
</tr>
</tbody>
</table>

Females with eggs have been taken in Ontario on 12 May (1 specimen), 8 June (2 specimens), 18 June (1 specimen), 20 June (1 specimen), 26 June (1 specimen), 8 July (1 specimen), and 11 July (1 specimen). The two July specimens are from the northern half of Ontario (Kenora district) and suggest a somewhat later egg-laying season. However, we have 10 egg-bearing females from the Cochrane district, taken on an unspecified day in June.

Ecology

*O. virilis* is probably a generalized feeder, living under stones in both lakes and rivers. In Ontario lakes, it has been reported as deep as 30 feet (gill net, Shirley Lake, Algonquin Provincial Park, 3 July 1964, D. W. Webb; 1 mature female).

Distributional Summary (Figure 76)

*Orconectes virilis* is our most widely distributed and abundant crayfish and is the only native species found north and west of a line drawn between Moosonee (James Bay) and Michipicoten Harbour (Lake
Superior). It occurs throughout southern Ontario (although somewhat sparsely in the southwest), and has been recorded as far west as Rainy River and as far north as Sandy Lake in Kenora District (approximately 53° N. latitude). However, it seems doubtful that *O. virilis* ranges to Ontario’s northern boundary, for no crayfish are present at Winisk (D. Baldwin, personal communication).

"*O. virilis* is the dominant crayfish in New Hampshire in terms of size, distribution and number" (Aiken 1965: 242). Reports have not been published for Maine, Massachusetts, Connecticut, or Rhode Island, but Camougsis and Hichar (1959) report *O. virilis* at Lincoln, Massachusetts. It is not found in New Jersey (Francois, 1959), Pennsylvania (Ortmann, 1906a), West Virginia (Newcombe, 1929), or Kentucky (Rhoades, 1944a). Williams and Leonard (1952) did not find this species in Kansas and report (p. 991) that earlier records of it for Kansas, Missouri, and Colorado are actually misidentifications of *O. nais*. *O. nais* is structurally similar to, but serologically distinct from *O. virilis* according to Pryor and Leone (1952).

The western and northwestern boundaries, shown on the inset map of Figure 76, are speculative, but based on localities reported by Faxon (1885a) for Canada and on several Montana localities reported by Holthuis (1962).

**Locality Records in Ontario**


3  ♂ II; Wiarton. Isaac L., 22 Aug. 1964, 4 ♂ I, 4 ♀ mat.; Wiarton, Georgian Bay, 22 Aug. 1964, 1 ♂ I (soft), 1 cast skin (♂ II).

CARLETON CO.: Billings Bridge. Rideau R., 31 Aug. 1937, 1 ♂ mat., 1 ♂ imm., 2 ♀ ♀ mat., 1 ♀ imm.; Browns Inlet, Rideau Canal, 24 Nov. 1959, 3 ♂ ♂ I, 2 ♂ ♂ II, 1 ♂ imm., 15 ♀ ♀ mat., 2 ♀ ♀ imm., 8 ♂ ♂ I, 2 ♂ ♂ II, 4 ♀ ♀ mat., 2 ♀ ♀ imm. (NMC); Browns Inlet, Rideau Canal, Nov. 1953, 1 ♂ II, 1 ♀ mat. (NMC); Burritts Rapids, 15 June 1958, 4 ♂ ♂ II, 4 ♀ ♀ mat. (NMC); Fallowfield, Jock R., 28 Aug. 1937, 1 ♂ imm.; Greens Ck., 2 Sept. 1937, 2 ♀ ♀ mat.; Hogs Back, Rideau R., 7 Nov. 1954, 1 ♀ mat. (NMC); Hogs Back, Rideau R., Nov. 1953, 1 ♀ mat. (NMC); Hogs Back, Rideau R., 31 Oct. 1953, 4 ♂ ♂ I (NMC); Metcalfe, Caston R., 2 ♀ ♀ mat., 1 ♀ imm.; Ottawa, Browns Inlet, Rideau Canal, 18 Nov. 1957, 2 ♂ ♂ I, 2 ♂ ♂ II, 2 ♂ ♂ imm., 13 ♀ ♀ mat. (NMC); Ottawa, Browns Inlet, Rideau Canal, 16 Nov. 1957, 1 ♂ II, 2 ♀ ♀ mat. (NMC); Ottawa, Laurier St. Bridge, 26 Mar. 1964, 1 ♂ I; Ottawa, Leamy Ck., 28 July 1918, 1 ♂ imm. (NMC); Ottawa, Feb. 1954, 1 ♀ mat. (NMC); Ottawa, 1900, 1 ♂ II, 1 ♀ imm. (NMC); Ottawa, Mar. 1954, 2 ♀ ♀ mat. (NMC); Ottawa, Rideau Canal, 11 Apr. 1917, 1 ♂ mat. (NMC); Ottawa, Rideau Canal, 16 June 1918, 1 ♀ imm. (NMC); Ottawa, Rideau R., 12 Oct. 1919, 1 ♂ mat., 1 ♀ imm.; Ottawa, Rideau R., 3 Sept. 1917, 2 ♂ ♂ imm., 1 ♀ imm. (NMC); Ottawa, Rideau R., 6 May 1917, specimens damaged (NMC); Ottawa, Rideau R., 28 June 1917, 1 ♂ II (NMC); Ottawa, Rideau R., Hogs Back, 4 May 1962, 1 ♂ I (NMC); Overbrook, Ottawa, 11 June 1956, 1 ♂ imm. (NMC); Rideau Ferry P.O., Sept. 1953, 1 ♂ mat., 1 ♀ mat.; Rideau R., 9 Aug. 1917, 2 ♂ ♂ II, 1 ♂ I (?) (NMC); from fishery, no data, 1 ♀ imm. (NMC); Rideau R., Hogs Back, 1 ♂ I (NMC); Rideau R., 1 ♂ I, 2 ♀ ♀ mat. (NMC); Rideau R., 4 Aug. 1956, 1 ♂ I (NMC); Rideau R., 12 May 1918, 1 ♀ with eggs; Watts Ck., nr. Connaught Ranges, 3 Sept. 1937, 1 ♂ mat.


ESSEX CO.: Camp Laird, Muddy Ck., 15 June 1931, 2 ♦ ♦ mat.; Lamington, 2 ♦ ♦ mat. (NMC).

FRONTENAC CO.: Moscow L. Lodge, Moscow L., 4 ♦ ♦ 1 (NMC); Mississagagon L., Barrie Twp., 8 and 9 Oct. 1963, 1 ♦ 1; Plevna, Govan L., 23 July 1964, 1 ♦ ♦ mat.

GLENARRY CO.: Bainsville, Sutherland Ck., 16 June 1938, 2 ♦ ♦ mat., 1 ♦ ♦ mat.


HALTON CO.: Glen Williams, Credit R., 27–28 July 1964, 2 ♦ ♦ mat.

HASTINGS CO.: Marmora, Lily Ck., 29 July 1964, 2 ♦ ♦ 1.


LAMBTON CO.: Sarnia, L. Huron, 1 ♂ imm.

LANARK CO.: Andrewsville, Rideau Ck., 26 Aug. 1937, 1 ♂ mat., 1 ♀ mat.

LEEDS CO.: Chaffey’s Locks, L. Opinicon, 20 June 1964, 1 ♂ II (?); Rideau Ferry, Birch L., 31 Aug. 1959, 1 ♂ 1; Rows Corner, 8 June 1938, 4 ♂♀ mat.


MUSKOKA DIST.: Echo L., L. of Bays, 30 Aug. 1916, 1 ♀ mat.; Go Home Bay, 3 ♂♀ mat., 2 ♀♀ mat.; Go Home, 8 June 1903, 2 ♀♀ with eggs; Huntsville, Roe L., 10 Aug. 1937, 1 ♀ mat.


OXFORD CO.: stony creek, Tillsonburg, 29 May 1957, 1 ♀ mat. (NMC); stony creek W. of Tillsonburg, 30 Aug. 1956, 1 ♂ (NMC).


RUSSELL CO.: Carlsbad Springs. 2 Sept. 1937, 1 ♀ mat.; Casselman, Butternut Ck., 9 Sept. 1939, 1 ♂ mat.


WELLAND CO.: Chippawa. Tee Ck., Apr. 1958, 1 ♂ I.

WELLINGTON CO.: Harriston, Maitland R., 27 July 1963, 1 ♂ II.

YORK CO.: De Grassi Point, L. Simcoe, 1 ♂ mat., 1 ♀ mat.; Holt, Conc. 5, E. Gwillimbury Twp., Black R., 17 Aug. 1964, 1 ♂ I, 1 ♂ imm., 1 ♀

**Description**

In Ontario, *O. virilis* has an extensive range and there is some morphological variation. The following account describes a geographically intermediate population from the Mattagami River, Kapuskasing District. The original description of this species by Hagen (1870: 63–64) is a full one.

**Male form 1. Carapace** cylindrical, smooth, and thickly punctate dorsally; the lateral surfaces lightly granulate and bearing a well-developed lateral spine and small branchiostegal spine. Postorbital spine acute, postorbital ridges grooved on outer face and swollen behind. Areola relatively narrow, permitting no more than two punctations to occur side by side in narrowest portion, narrowest near anterior end; cervical groove deep, sinuate, and broken on sides.

**Rostrum** broad, long, well excavated, with straight sides and raised converging margins; lateral teeth prominent and acute (may become tuberculate in large specimens); acumen long and slender, with concave sides, terminal spine acute.

**Antennal scale** slightly longer than rostrum, medial border rounded, widest about the middle; distal spine small and acute.

**Flagellum of antenna** shorter than body but longer than carapace; stout at base but finely tapered distally.

**Epistome** nearly square, fairly flat, posteromedial area depressed slightly; sides rounded and raised, anterior edge with shallow median notch.

**Chela** broad and rather flattened; medial border of palm and dactyl biseriately tuberculate; both fingers strongly punctate above, each with a well-defined smooth ridge dorsally; inner margin of immovable finger straight, that of dactyl weakly sinuate, both provided with strong tubercules. Base of immovable finger bearing a moderately thick tuft of setae (beard). Often two teeth on ventral margin of joint between dactyl and propodus.

**Carpus** of cheliped longer than wide, with moderately deep furrow dorsally; bearing a strong (medial) spine on inner margin and a slightly smaller one both anterior and posterior to it. Ventral anterior border with median spine, occasionally with small accessory one between this and medial spine. Small spine at ventral point of articulation with propodus.

**Merus** of right cheliped with one or two spines above near distal end and double row of acute spines on ventral border.

**Telson** tapering, proximal section bispinose on each side and longer than distal section (length ratio of 3:2); posterior margin variable, rounded, straight, or sinuate.

**Copulatory stylets** long, reaching to caudal border of bases of cheli-
Orconectes immunis (Hagen)
(Figures 22, 31, 40, 49, 61, and 77)

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


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

Taxonomic Remarks: The subspecies which have been assigned to this species in the past are now considered to be invalid. C. i. spinirostris Faxon was characterized by the presence of rostral spines, a character which varies both with age' (Creaser, 1931a: 262 and 1933b: 13–14; Ortmann,
1931: 93, 94) and across an east to west cline (Williams and Leonard, 1952: 1005). Creaser's O. i. pedianus was based on the ratio of areola length to head length, which has also been shown to vary continuously from east to west (Williams and Leonard, 1952: 1003-5).

Diagnosis

This is the most slender and fragile-looking of our crayfishes, and it is usually found in stagnant water or in terrestrial burrows. It is most similar to O. virilis, but it can usually be distinguished by the basal incision on the medial margin of the movable finger and the presence of only one tubercle on the ventral margin of the articulation between dactyl and propodus.

Habitat

O. immunis is typically found in stagnant ponds and ditches or slow-moving streams where the water is seldom more than a foot or two deep. The bottom is usually mud and there is characteristically a heavy growth of rooted aquatic vascular plants. Small farm ponds seem to support particularly large populations.

Because this species can burrow into the ground when necessary, it can utilize the temporary pond habitat. O. immunis has also been collected in two lakes in Algonquin Provincial Park, well outside its normal range and zone of habitat preference. These colonies may have been started by fishermen bringing in live bait from more southern areas of the province.

Life History

Tack (1941) has published an extensive study on the habits and life history of this species as it occurs in mud-bottomed fish ponds at Ithaca, New York. We give here a summary of his work (with dates given slightly later to correspond to Ontario conditions).

Copulation takes place from mid-July to early October, mostly yearling individuals participating. Eggs are laid later in October and are carried through the winter, to hatch during the last half of May. We have but one collection containing females with young taken on Long Point, Norfolk Co., on 25 May. The juveniles spend the summer growing and may reach a carapace length of 13 to 29 mm. by September. A few become sexually mature at this time and participate in
Figure 77 *Orconectes immunis*, male form I, carapace length 28 mm.; Ont., southern tip of Long Point, Norfolk Co., shallow pond by lighthouse; 17 July 1965; D.W.B. and C. G. Barr.
mating activities, but the majority do not mature until late in the following summer. Mature males are in form I from July through the following April. Then they moult to become form II for about two months and later revert to the sexually competent form in late June. The normal life span is two years.

**Ecology**

Tack (1941) found that this species is largely herbivorous, feeding on the abundant vegetation of the Ithaca fish ponds or, at night, on terrestrial plants close to the shore.

In ponds and streams the juveniles hide in aquatic vegetation while the matures stay out of sight in the deeper (usually muddy) water. They are active both by day and by night, but the adults are more strictly nocturnal. In temporary ponds, *O. immunis* can construct burrows when the pond dries up and may remain in these during the winter. In permanent waters the adults and young enter deeper water in the fall and spend the winter under stones or in submarine burrows.

This species can travel across dry ground at night, especially if there is rain or a heavy dew, and in this way can move from pond to pond.

**Distributional Summary (Figure 78)**

Records for *O. immunis* are restricted to southern Ontario and are most strongly concentrated in the region lying to the south and west of Lake Simcoe (Lake Huron and Lake Erie drainages). The species is rare to the east of Lake Simcoe, but its distribution here is concordant with its continental range and so we are not completely safe in classifying these records as introductions. It does, however, seem that northward expansion of *O. immunis* is severely limited by the southern boundary of the Precambrian Shield.

*O. immunis* is present in New Hampshire (Aiken, 1965) and the northern half of New York (Crocker, 1957). Scattered records are available for Massachusetts (Faxon, 1914: 378). Faxon (1914: 380–1) regards those crayfishes east of Berkshire Co., Massachusetts, as being introductions by man. This species is absent from Pennsylvania (Ortmann, 1906a), New Jersey (Francois, 1959), and West Virginia (Newcombe, 1929). It is not found in the Big South Fork of the Cumberland River in Tennessee (Hobbs and Shoup, 1942),
but is present in the northwestern corner of the state at Reelfoot Lake (Hobbs and Marchand, 1943). Creaser and Ortenburger (1933) found *O. immunis* in east-central Oklahoma. The range in Kansas is restricted to the northeastern corner of the state (Williams and Leonard, 1952: 1002, Fig. 7). The range limits in Colorado and Nebraska are given by Engle (1926: 94, Fig. 1), in Wisconsin by Creaser (1932: 328, Fig. 9), and in Michigan by Creaser (1931a: 265, Map 4).

**Locality Records in Ontario**

**BRANT CO.:** Middleport. July and Aug. 1918, 1 ♀ mat. (?); near
Middleport, July–Aug. 1918, 3 ♂♂ 1, 1 ♀ imm., 1 ♀ mat. (NMC).

**BRUCE CO.:** Southampton. Saugeen R., 23 July 1963, 1 ♀ mat.

ELGIN CO.: Aylmer, May 1921, 1 ♂, 1 ♀; Aylmer. Holiday Beach Prov. Pk., 1 ♂ 1, 4 ♂♂ imm., 4 ♀♀ mat., 4 ♀♀ imm.; Big Otter R., Bayham Twp., 4 ♂♂ 1, 1 ♂ 11, 1 ♂ imm., 4 ♀♀ mat., 1 ♀ mat. (?), 1 ♀ imm.; Salford, Aug. 1964. 3 ♂♂ 1, 3 ♀♀ imm.


HALDIMAND CO.: Dunnville, Maple Ck., 8 Aug. 1963, 1 ♂ 1, 1 ♀ imm.; Dunnville, 7 Aug. 1963, 1 ♂ 1, 4 ♂♂ imm., 5 ♀♀ mat., 5 ♀♀ imm.; Nelles Corners, 15 Aug. 1964, 1 ♂ 1, 3 ♂♂ imm., 2 ♀♀ mat., 1 ♀ imm.


LEEDS CO.: Chaffey’s Locks, L. Opinicon, 28 June 1964, 1 ♂ 11; Chaffey’s Locks, L. Opinicon, 1 ♂ 11.


OXFORD CO.: Plattsville, 2 July 1927, 1 $\delta$ mat. (?); stony creek W. of Tillsonburg, 24 Aug. 1956, 2 $\delta\delta$ imm., 2 $\varpi\varpi$ imm. (NMC).

PERTH CO.: Listowel, Middle Maitland R., 25 July 1963, 1 $\varpi$ mat.; Listowel, Little Maitland R., 22 July 1963, 2 $\delta\delta$ imm., 1 $\varpi$ imm.; Trowbridge, Middle Maitland R., 31 July 1963, 1 $\varpi$ imm.

WATERLOO CO.: Wellesley, Jantzi Ck., 16 July 1964, 3 $\varpi\varpi$ mat.

WELLCAND CO.: Chippawa, Apr. 1958, 1 $\delta$ 1; Chippawa. Boyer’s Ck., Apr. 1958, 1 $\varpi$ mat.; Chippawa, Usher’s Ck., Apr. 1958, 1 $\varpi$ mat.; Fenwick, Pelham Twp., 8 Nov. 1963, 7 $\delta\delta$ imm., 1 $\varpi$ mat., 1 $\varpi$ imm.

Description

**Male form I.** Carapace cylindrical, smooth but densely punctate above, with low tubercles on lateral surfaces of anterior portion. Postorbital ridges grooved on outer face and terminated anteriorly by blunt tubercle. Cervical groove slightly sinuate, interrupted laterally; short, sharp lateral spine present; branchiostegal spine very small or absent. Areola relatively narrow, usually permitting no more than two punctations to occur side by side, narrowest anteriorly.

Rostrum longer than broad, deeply excavated dorsally, with raised converging sides. Lateral rostral spines small, indistinct, or absent. Acumen triangular with concave sides.

Antennal scale considerably longer than rostrum, unevenly rounded medially, widest slightly proximal to middle, apex truncate; terminal spine small.

Flagellum of antenna slender, shorter than body but longer than carapace.

Epistome roughly triangular, anterior margin with shallow notch and minute median tooth; sides convex and slightly raised, finely and irregularly toothed.

Chela of medium size, more slender than for any other Ontario species, punctate, tuberculate along medial border of dactyl and propodus. Opposed edges of fingers each with row of tubercles, small and rounded distally, larger proximally. Dactyl excised at base inside and provided with prominent tooth just above notch. Upper surface of both fingers with smooth rib bordered on each side by line of deep punctations. Immovable finger bearded ventrally near base.

Carpus of cheliped longer than broad, deeply furrowed above with one large spine on medial border and several smaller spines medially and ventrally. One prominent median spine on distal margin of ventral surface.

Merus of cheliped with two weak spines above and double row of stronger ones beneath.

Telson tapering, relatively narrow, proximal and distal sections of approximately equal length. Proximal section bispinose on each side, posterior border of distal section slightly concave.

Copulatory stylets reach to bases of second pereiopods when abdomen flexed; terminating in two styliform, curved processes which are
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subparallel, subequal in length, and divided for about one-third of length of entire organ. Tips of processes bent gradually at approximately a 90° angle to axis of shaft. Central projection corneous, mesial process non-corneous, excavated on cephalic border.

**ISCHIAL HOOKS** situated on third pereiopods, strongly pointed and slightly hooked.

**COLOUR IN LIFE** basically olive green or brown, although first abdominal segment may show touch of red dorsally. Dorsal side decorated with light, symmetrical pattern. Appendages have pinkish hue.

*Male form II*. Same as male form I except that chelae less heavily developed and ischial hooks have more rounded apex. Copulatory stylets with thicker, non-corneous terminal processes, still subparallel and subequal in length, but blunt, less strongly curved, and less widely divergent distally.

*Female*. Same as male form I, but chelae smaller. Seminal receptacle ovoid to triangular, wider than long; fossa sigmoid in form, lying far to one side. Walls raised and inflated, posterior wall crossed by narrow fissure.

**THE GENUS CAMBARUS**

This genus is represented in Ontario by four endemic species which are uniformly robust and basically brown in colour. There are no lateral rostral spines and the carapace is dorsoventrally (Fig. 67) or laterally (Fig. 68) compressed. The terminal processes of the copulatory stylets are short, heavy, and bent abruptly caudad at approximately 90° to the axis of the organ. At least two of the species (*robustus, bartoni*) appear to lack a single, well-defined, annual mating period, while a third (*diogenes*) apparently has some irregularities in the life cycle.

**Cambarus bartoni bartoni** (Fab.)
(Figures 29, 38, 47, 54, 64, and 79)

*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, 1905a: 117
*Cambarus (Cambarus) bartoni* (Fabricius). Fowler, 1912: 340, 341
holotype: "(fragment only), Kiel Museum," Faxon (1914: 423).


Diagnosis

This is a medium-sized, stream- and lake-inhabiting crayfish species with a wide areola and no lateral rostral spines. It can be distinguished from the similar species C. robustus by the short, square rostrum and the presence of only a single row of tubercles on the medial border of the palm.

Habitat

In the United States, most authors (Harris, 1903; Crocker, 1957) agree that this species is usually confined to relatively swift, cold, mountain streams, preferably with a stony bottom. In areas of Ontario south of the Precambrian Shield, it can be found in swift, cool, stony streams in hilly but not necessarily mountainous country. In fact, one limited population of rather small individuals has been located in a mere trickle of drainage water (1–3 cm. deep, 1–10 cm. wide) where it passes through a cool, shaded stony area (Mansfield, Ontario). This species is never found in large rivers in the southern part of the province.

On the Shield, C. b. bartoni thrives in swift, rocky rivers having a steep gradient, and large populations may also be built up along the shores of Shield lakes.

Life History

C. b. bartoni does not appear to have a restricted time of mating, egg laying, and hatching as do the species of Orconectes. Crocker's data (1957: 66, Table 14) indicate a reduction in the proportion of form I males in June and July in New York. We have sufficient data for two months only, July (11 form I and 31 form II) and August (10 of each form). We have no field observations of copulation in this species, although Ortmann (1906a: 486), based on studies in Pennsylvania, gives May and October. Ortmann reports females with eggs in July and August, and with young in February (New Jersey), March, August, September, and November. McManus (1960b)
Figure 79 *Cambarus bartoni*, female, carapace length 25 mm.; Ont., Mansfield, Dufferin Co., small, slow stream; 20 June 1965; D.W.B. and C. G. Barr.
refutes the suggestion (Ortmann, 1906a) that *C. b. bartoni* spawns in winter in northern states. Crocker (1957: 66) records females with young in April and August in New York. We have one record of a female with young for 2 August 1958 from the Algoma District shore of Lake Superior.

Chidester (1908, 1912) reported on the life history of a species he identified as *C. bartoni*. However, on the basis of its reported pond habitat (1908: 712, 713; 1912: 280) and 90 mm. maximum total length (1912: 286) we believe that his observations were made on some other species.

**Ecology**

There are few data on the food of *C. b. bartoni*, but its habitat preference would suggest that it must be largely carnivorous for there is relatively little aquatic vascular vegetation or dead organic material available in a swiftly flowing stream.

Individuals of this species are usually found hiding under large, flat rocks in streams or among the granite boulders in Shield lakes and rivers. There are records of burrows constructed by *C. b. bartoni* in the eastern United States (Ortmann, 1906a: Plate 41, Fig. 1; Francois, 1959: 120-1), but it is never considered to be primarily a burrower. It has never been observed to burrow in Ontario.

**Distributional Summary (Figure 80)**

*Cambarus b. bartoni* displays an ecological preference for rapid streams, which is probably largely responsible for its distinctive Ontario distribution. It has entered the province from the southeast and spread northwestward onto the Precambrian Shield, entering the Ottawa River, Georgian Bay, and Lake Superior drainage areas. In general, it appears to go no farther north or west than Michipicoten Harbour (Lake Superior) although there is one apparently valid record from the Kapuskasing (Moose) River. Neither has *C. b. bartoni* been able to penetrate far into southern Ontario (Lake Erie and Lake Huron drainages), possibly because of the moderate gradient and relatively sluggish flow of most of the streams and rivers of this region.

Locality records for *C. b. bartoni* in Quebec, New Brunswick, Maine, and the other New England States are given by Faxon (1885a:
Figure 80  Distribution of *Cambarus bartoni* in Ontario. Inset shows the total range of the Ontario subspecies, *C. b. bartoni*; the uncertain status of the many so-called subspecies at the southwestern border of the range makes this limit problematic.
60–61). Francois (1959: 121, Fig. 6) depicts the absence of this species from the southern half of New Jersey. The western boundary in Ohio has been determined by Turner (1926: 184, Map 5) and Rhoades (1944b: 97). and in Kentucky by Rhoades (1944a: 134). The remainder of the periphery of distribution is uncertain owing to the uncertain status of the many *C. bartoni* subspecies occurring in these areas.

**Locality Records in Ontario**

**Algoma Dist.:** Gamitagama L., Twp. 30 RXIX, 2 ♂ II, 1 ♀ mat.; Helenbar L., Twp. 151. 1 ♂ II, 4 ♀♀ mat.; Kenny L., Twp. 28RXV, 4 ♀♀ mat.; Long L., Twp. 169, 1 ♀ mat.; Maquon L., Twp. 29 RXX, 22 Aug. 1963, 1 ♂ II, 1 ♀ mat.; Mijinenungshing L., Twp. 29RXX, 1 ♂ II; Old Vienna L., Twp. 30RXIX, 1 ♂ I, 1 ♀ mat.; Rouissain L., Whitman Twp., 13 Aug. 1961, 1 ♂ I; L. Superior, Hwy. 17, 2 Aug. 1958, 1 ♂ II, 1 ♀ mat., 1 ♀ with eggs; L. Superior, Harmony Bay, at mouth of Chippewa R., 9 June 1959, 1 ♂ II (NMC); Tee L., Twp. 1A, 1 ♂ I; Twin L., 1 ♂ I.


**Cochrane Dist.:** Moose R., 8 July 1919, 4 ♂♀ mat., 7 ♀♀ imm.

**Dufferin Co.:** Mansfield, 20 June 1965, 1 ♀ mat. (?).

**Dundas Co.:** Iroquois, St. Lawrence R., 8 Feb. 1957, 1 ♂ I, 2 ♂ ♀ imm.


**Frontenac Co.:** Cataraca R., 1 ♀ imm.


NORTHERN LOMBARD CO.: Cobourg, 2 ♂♂ II.

PARRY SOUND DIST.: Magnetawan, Ahmie L., 21 Aug. 1964, 1 ♀ mat.


WATERLOO CO.: Hespeler, outlet of Puslinch L., 18 July 1964, 1 ♂ I.

Description

Male form I. Carapace dorsoventrally compressed; lateral surfaces tuberculate, tubercles posterior to cervical groove very low; smooth and sparsely punctate above. Postorbital ridges short, low, grooved laterally, ending anteriorly in blunt tubercle. Cervical groove continuous laterally, lateral spines absent; very small, blunt branchiostegal spines present. Areola relatively wide, usually with three or more punctations occurring side by side.
side in its narrowest portion, punctations large, relatively few, tending to fall into three cephalocaudal rows.

**Rostrum** nearly square, tapering acutely to its tip. Acumen short, with concave sides, not strongly depressed; terminal spine acute, directed dorsad. Margins not interrupted by spines, thickened, but rostrum not deeply excavated above.

**Antennal Scale** slightly longer than rostrum; inner border usually directed rather abruptly caudad; widest about the middle; terminal spine short, acute.

**Flagellum of Antenna** shorter than body but longer than carapace.

**Epistome** almost square, with pair of obtuse anterolateral angles and acuminate projection in centre of anterior margin. Central area depressed, margins raised slightly.

**Chela** shorter than that of *C. robustus*, medial margin of propodus with single row of low tubercles; both fingers with incurved, brown horny tips, each with a single row of low tubercles along opposed margins. Propodus inflated, without conspicuous depression near outer margin (shallow depression may occur on dorsal surface, caused by fusion of punctations, but ventral surface always fully rounded).

**Carpus** of chelipod longer than wide with long, deep, wide dorsal depression, bearing one strong spine on medial border and a pair of much smaller spines posterior to it; median low spine or strong tubercle on distal margin of ventral side.

**Merus** of cheliped with one or two weak spines or small tubercles on dorsal surface at distal end, and two rows of small spines on lower margin.

**Telson** tapering posteriorly, proximal section bispinose (sometimes trispinose) on each side, distal section equal to proximal in length, rounded behind.

**Copulatory Stylets** much like those of *C. robustus* except that tip of mesial process always points slightly ventral to horizontal.

**Ischial Hooks** borne on third pereiopods.

**Colour in Life** like *C. robustus* except that basic brown colour tends to be richer, less greenish. We have seen a population in which a number of the individuals are a chalky grey-blue, in the Oxtongue River, below the Tec Lake dam, just outside the western border of Algonquin Provincial Park.

**Male form II.** Generally similar to male form I. Copulatory stylets resemble those of form II male of *C. robustus* except that tip of mesial process still points slightly ventrad.

**Female.** General morphology much like that of male form I. Seminal receptacle resembles that of *C. robustus* but more oval in outline, caudal border smoothly rounded, ridge on caudal border does not project laterally as an abrupt shoulder; tubercles, ridges, and fissures less pronounced, reducing over-all relief. Deepest part of fossa displaced either to left or right of centre.
Cambarus robustus (Girard)
(Figures 30, 39, 48, 55, 65, 67, and 81)

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

Diagnosis

This is a large crayfish with a wide areola and no lateral rostral spines. It can be distinguished from the similar species C. bartoni by the elongate, rectangular rostrum and the presence of two rows of tubercles on the medial border of the palm.

Habitat

In Ontario, this species is found in large rivers or swift streams, invariably on a stony bottom. It is rare in the lakes of the Precambrian Shield but may be found in stony-bottomed ponds, especially if these are along the course of a stony stream.

Life History

Cambarus robustus, like C. b. bartoni, apparently does not have a restricted breeding, egg laying, and hatching season. In New York (Crocker, 1957: 61, Table 12), in months with more than 10 specimens available (April through October), first form individuals constitute at least 32 per cent of the adult males. In fact, they are the less abundant form only in July and August. Crocker (1957: 62) records field observations of copulation in October. He reports May copulations also, but these were under crowded conditions in a
Figure 81  *Cambarus robustus*, male form I, carapace length 42 mm., right claw regenerated; Ont., Mansfield, Dufferin Co., rapid stream; 20 June 1965; D.W.B. and C. G. Barr.
lamprey trap. Females with eggs are found in July in New York (Crocker, 1957: 63) and Pennsylvania (Ortmann, 1906a: 488), and females with young have been taken in New York in April and August (Crocker, 1957: 63). We have too few specimens with full data to offer a life history time-table for Ontario.

Ecology

Creaser (1934: 160) states that small individuals prey on insect larvae and nymphs, while larger individuals feed mainly on aquatic plants. In the laboratory most specimens can be induced to feed on bits of fresh, minced meat or live meal-worm larvae.

In the summer, individuals of all sizes are found under large, flat rocks in the stream habitat. One winter collection by the junior author indicates that the creatures remain there in a semi-active state, even when the ice is six to eight inches thick and the flowing water is supercooled.

Distributional Summary (Figure 82)

*Cambarus robustus* is limited in Ontario to the Georgian Bay, Lake Huron, Lake Erie, and Lake Ontario drainage basins. It appears to be common in a broad band joining Georgian Bay to the Niagara Peninsula but is relatively scarce both east and west of this region. The reasons for the form of this distribution are not readily apparent from the data at hand.

The distributional limits of *C. robustus* contributing to a picture of its total range have been determined in New York by Crocker (1957: 82, Fig. 6), in Pennsylvania by Ortmann (1906a: 449), in Ohio by Turner (1926: 184, Map 5) as modified by Rhoades (1944b: 96), and in West Virginia by Newcombe (1929: 277). This species was not found in the Cheat River watershed in West Virginia and Pennsylvania (Schwartz and Meredith, 1960). Eberly (1954: 252) reports the only known locality in Indiana.

Locality Records in Ontario

BRUCE CO.: L. Huron off MacPherson Pt., 15 Aug. 1964, 2 ♂ I, 1 ♀ mat.; L. Huron off Scott Pt., 19 Aug. 1964, 1 ♂ II, 1 ♀ mat.; Scott Pt., L. Huron, 1 ♂ I, 1 ♂ II, 2 ♀♀ mat.
Figure 82 Distribution of *Cambarus robustus* in Ontario. Inset shows the total range of the species.


GREY CO.: Durham, Saugeen R., 30 May 1957, 1 ♀ imm. (NMC); Flesheron, Saugeen R., 30 May 1957, 1 ♂ very small (NMC); Meaford, Bighead R., 1 ♂ imm., 3 ♀♀ imm.; Meaford, 2 ♂♂ I; Scone. N. branch of Saugeen R., 6 Aug. 1964, 1 ♂ imm.


LAMBTON CO.: Mooretown, St. Clair R., 1 July 1965, 1 ♂ I, 1 ♀ mat.


MANITOULIN DIST.: L. Huron, Macrae Pt., 8 June 1964, 1 ♂ I; L. Huron, Macrae Pt., 9 June 1964, 5 ♂♂ I, 3 ♂♂ II, 3 ♀♀ mat.


MUSKOKA DIST.: Go Home Bay, July 1908, 4 ♂♂ I; Go Home Bay, 2 ♂♂ I, 1 ♀ mat.; Honey Harbour, 1919, 1 ♂ II, 1 ♀ mat.

NIPISSING DIST.: Algonquin Prov. Pk., L. Opeongo, 10 July 1963, 3 ♂♂ II; L. Nipissing, Sand Ck., 27 July 1932, 1 ♂ I; North Bay, stream, 15 July 1965, 1 ♀ imm.; L. Timagami, N. of Bear Is., 8 July 1937, 1 ♂ I; River Valley Village, McWilliams Twp., July 1964, 1 ♂ I.


OXFORD CO.: Otter Ck., S.E. of Tillsonburg, 27 Apr. 1956, 1 ♂ imm., 1 ♀ imm.

Georgian Bay, 1 ♀ II, 6 ♀♀ mat.; McCoy Is., Shawanigan, Georgian Bay, 1 ♀ I, 2 ♀♀ mat., 1 ♀ imm.; Rock Island L., Shawanaga Twp., 11 Sept. 1964, 1 ♀ I.

PEEL CO.: Credit R., bridge below forks, 28 Apr. 1935, 1 ♀ II, 6 ♀♀ imm.; Erindale, Credit R.. 7 Aug. 1919, 1 ♀ mat.; Port Credit, 1927, 1 ♀ II, 1 ♀ imm.


WATERLOO CO.: Blair, Blair Ck., 16 July 1964, 1 ♀ II; Wellesley, Wellesley Ck., 16 July 1964, 2 ♀♀ II.


YORK CO.: Humber R., King Twp., 15 July 1937, 1 ♀ mat.; Toronto, Don R., 1912. 1 ♀ II; Toronto, Don R., 8 May 1921, 1 ♀ mat.; Toronto, 1930, 1 ♀ II.

Description

Male form I. CARAPACE dorsoventrally compressed and flattened above, small branchiostegal spine present and strong lateral spine usually present. Lateral surfaces profusely tuberculate, tubercles small posterior to cervical groove and larger anterior to it. Postorbital ridges short, deeply grooved on lateral face, and tapering posteriorly; postorbital spines short and acute. Cervical groove with only slight break laterally, nearly continuous. Areola relatively broad, with at least three punctations occurring in horizontal row in narrowest portion; bearing small, numerous punctations which do not tend toward an arrangement in three rows.

ROSTRUM oblong, not tapering abruptly to its tip, tip not well bent down; terminal spine directed dorsally, may be blunt in larger individuals. Margins thickened and slightly raised, not interrupted by lateral spines. Rostrum shallowly excavated above.

ANTENNAL SCALE a little longer than rostrum, inner border usually directed mesiad before turning caudad, broadest anterior to middle, about as wide as areola; terminal spine long and acute.

FLAGELLUM OF ANTENNA very broad at base but tapering finely, about as long as body.

EPISTOME triangular and acuminate anteriorly. Margins with one or two obtuse angles giving a scalloped effect, strongly raised.
CHELA large and strong. Daetyl and propodus both ribbed and densely punctate, each provided with a row of strong tubereles on inner margins of fingers; tips of fingers incurved, brown, and horny. Inner margin of palm with two rows of low tubereles, although these may be lacking in regenerated claws. Propodus with depression, visible in both dorsal and ventral views, near its lateral margin.

CARPUS of cheliped longer than broad, with a long and deep, but fairly broad furrow above; one strong spine on medial surface, a small one caudally on this surface, and a small spine mid-ventrally. Distal margin of ventral surface with strong median spine.

MERUS of cheliped with two or three fairly large spines on dorsal surface at distal end, with two rows of strong spines on ventral surface.

TELSON broad, tapering slightly posteriorly; proximal section bispinose on each side; distal section a little shorter than proximal (length ratio 6:5) and rounded posteriorly.

COPULATORY STYLETS short, reaching to bases of third pereiopods when abdomen flexed, and heavy. The two terminal elements curved abruptly caudally at an angle of 90° to the main axis of the organ; central projection heavily sclerotized and flattened into a sickle-like blade; mesial process less heavily sclerotized, short, thick, and terminating in a point which is usually directed dorsally.

ISCHIAL HOOKS long, situated on third pereiopods.

COLOUR IN LIFE basically deep greenish-brown on dorsal surfaces of carapace, chelae, and abdomen. Carapace may be slightly dappled above with lighter and darker areas. Larger tubereles and spines yellowish-brown. Claws and distal tips of walking legs greenish, edges of articulation areas on chelipeds rosy-red. Undersurface uniformly light yellowish-brown.

Male form II. Similar to male form I but chelipeds not as heavy, ischial spines less prominent. Copulatory stylets blunter, less heavily sclerotized, thicker, form more variable. Mesial process has tip directed dorsally as in form I.

Female. Similar to male form I but chelipeds not as heavy. Seminal receptacle with raised posterior margin which projects as shoulder on each side, caudal border not smoothly rounded. Fossa off centre and ridge originating in the posterior margin runs into it. Small sinuate fissure runs from fossa across posterior margin. Deeper, straight fissure runs from fossa forward, dividing anterior portion into two large, low, flat tubereles. Deepest part of fossa displaced either to left or right of centre.

**Cambarus diogenes diogenes** Girard
(Figures 27, 36, 45, 56, 63, 68, and 83)

*Cambarus diogenes* Girard, 1852: 88–90
*Cambarus nebrascensis* Girard, 1852: 91
*Cambarus obesus* Hagen, 1870: 81
*Cambarus* (**Bartonius**) *diogenes* Girard. Ortmann, 1905a: 97, 120
Cambarus (Cambarus) diogenes Girard. Fowler, 1912: 341
Cambarus diogenes diogenes Girard. Hobbs, 1942a: 354


TYPE LOCALITY: "... in the neighborhoods of the city of Washington...", Girard (1852: 89).

TAXONOMIC REMARKS: The current restricted sense of Cambarus originates in Hobbs (1942a: 354) and eliminates the need for subgenera in this genus.

See Hobbs (1942a: 337, footnote 2) for the correction of a misstatement in Fowler (1912: 341).

Marlow (1960) has validated the subspecific status of C. d. ludovicianus.

Diagnosis

This is a large semiterrestrial, burrowing crayfish with no lateral rostral spines and a linear areola. It is similar to C. fodiens but can always be distinguished by the presence of a triangular suborbital projection of the carapace and the fact that the cervical groove is continuous laterally.

Habitat

In Ontario individuals of this species typically are found constructing colonies of burrows in wet meadows and marshes. These areas probably have standing water at least temporarily in the spring. In the United States burrows also have been found near such permanent surface waters as a spring-fed pool, an artesian well, marsh and farm ponds, but they may also burrow far from surface water of any kind (Williams and Leonard, 1952: 1009). Adults are often taken in streams, rivers, and lakes during the breeding season (early spring).

Life History

The full details of the life history for C. d. diogenes are not known. However, the summary of Williams and Leonard (1952: 1009) gives a partial understanding of some of the main events.

Copulation may take place both in the fall (October) and again in the spring (March, April, May). Eggs are presumably laid in April and June. However, ovigerous females have been collected from April through August and in January. The only record of a female with young is in June. There is a general moult during late spring.
Figure 83 *Cambarus diogenes*, female, carapace length 40 mm.: Ont., southern tip of Long Point, Norfolk Co., burrow in damp marsh; 17 July 1965; D. W. B. and C. G. Barr.
These scanty data make clear the need for much more work on the habits of C. d. diogenes before it can be related properly to the other members of its genus.

Ecology

The main food of this species is not known but its habitat would suggest that terrestrial vascular plants are important in the diet. Individuals may leave their burrows at night to forage on the ground.

The burrows of C. d. diogenes in Ontario are described in some detail on p. 34. They differ from those of O. immunis in having a resting chamber close to the surface and from those of C. fodiens in generally lacking a deep escape tunnel. Recent summaries of recorded observations of C. d. diogenes burrows are given by Williams and Leonard (1952: 1007–9) and Marlow (1960: 246–8).

Distributional Summary (Figure 84)

Cambarus d. diogenes is the rarest Ontario crayfish, occurring only in scattered colonies along the north shore of Lake Erie. It would appear to have entered the province in the extreme southwest but has never spread north into the large and seemingly favourable area of southwestern Ontario. This is strange indeed when one remembers that this species is common and widespread across the United States east of the Mississippi River, is apparently well adapted for dispersal across land, and is found as far north as the northern peninsula of Michigan. However, if southwestern Ontario is a climatically marginal habitat for this species, its range may be limited by competition with the ecologically similar species C. fodiens. At present, we cannot explain the single record for C. d. diogenes in northwestern Ontario at Atikokan.

The total range of C. diogenes as shown in the inset of Figure 84 is taken from Marlow (1960).

Locality Records in Ontario

Essex Co.: Pt. Pelee, May–July 1913, 1 ♂ I or II, 1 ♀ mat. (NMC); Pt. Pelee, May–July 1913, 1 ♂ I.

Norfolk Co.: Long Pt., southern tip, 25 May 1963, 1 ♂ I, 1 ♂ imm., 1 ♀ with eggs; Long Pt., southern tip, 25 May 1963, 2 ♂♂ I, 1 ♀ mat., 1 ♀ with eggs; Long Pt., southern tip, 17 July 1965, 1 ♂ II, 1 ♀ mat.; Turkey Pt., 8 and 9 Apr. 1941, 1 ♂ I.
Figure 84 Distribution of *Cambarus diogenes* in Ontario. Inset shows the total range of the species (including *C. d. ludoviciana* in a small area in Louisiana). See text for one additional western Ontario locality.


**Description**

*Male form* *I.* *Carapace* laterally compressed, much contracted behind, smooth above, very lightly granulate on sides, without lateral or branchiostegal spines. Acute suborbital projection present. Postorbital ridges short, low, grooved laterally, swollen posteriorly, occasionally terminated by small, blunt tuberele anteriorly. Cervical groove deep and sinuate, continuous laterally. Arcola linear for much of its length, with small anterior triangular area, and larger, poorly defined one posteriorly.

*Rostrum* short, broad, well excavated, and strongly depressed between the eyes. Margins thickened and raised, not interrupted by lateral spines. Acumen short and triangular, its margins concave, the terminal spine turned abruptly dorsad.
ANTENNAL SCALE small, slightly shorter than rostrum, almost rectangular in outline, broadest at about middle. Terminal spine small and acute.

FLAGELLUM OF ANTENNA slender, shorter than body but longer than carapace.

EPISTOME triangular, rounded anteriorly, a little longer than broad, margins convex and raised.

CHÆLA large and strong, swollen, and heavily punctate. Inner margin of propodus tuberculate, finger flattened on lateral margin. Dactyl tuberculate at base on medial margin. Cutting edge of both fingers with row of large tubercles, tips of fingers corneous and incurved. Cutting edge of dactyl irregular (or straight with small tubercles in regenerated claws) but not deeply incised at base.

CARPUS of chelipeds short and thick, deeply furrowed above, small spine on medial margin, two smaller spines or tubercles posterior to it. One strong median spine on distal margin of ventral side.

MERUS of cheliped thick and strong, two small spines at distal end of dorsal side, double row of very small spines below.

telson narrow, tapering distally. Proximal section bispinose on each side. Distal section longer than proximal (length ratio 5:4), narrow, rounded behind.

COPILATORY STYLETS stout and short, reaching bases of third pereiopods when abdomen flexed, ending in two short distal processes which are bent abruptly caudad at an angle of about 90° to axis of appendage. Central projection thin, corneous, and falciform; mesial process large, strong, with medially directed, awllike tip.

ISCIAL HOOKS acutely pointed, borne on third pereiopods.

COLOUR IN LIFE basically rich reddish-brown above with darker brown dappling on carapace and claws and lighter symmetrical pattern on dorsal side of abdomen. Lighter and slightly flesh-tinted on lateral areas of body; margins of rostrum, chela, and abdomen orange-red.

Male form II. Similar to male form I but chela less robust and ischial hooks with rounded tips. Terminal processes of copulatory stylets thicker, non-corneous, with tips more closely apposed. Mesial process with awllike tip as in male form I.

Female. Similar to male form I except antennae shorter, chela less robust, and abdomen longer and broader. Seminal receptacle roughly square, about as long as broad, consisting of two interlocked, irregularly crescentic portions which are raised along margins to form prominent, rounded ridge. Deepest part of fossa displaced either to left or right of centre.

Cambarus fodiens (Cottle)
(Figures 28, 37, 46, 57, 62, and 85)

Astacus fodiens Cottle, 1863: 217
Cambarus argillicola Faxon, 1885b: 115
Cambarus fodiens (Cottle). Huntsman, 1915: 158
Cambarus (Bartonius) argillicola Faxon. Ortmann, 1905a: 97, 120
Cambarus (Cambarus) argillicola Faxon. Fowler, 1912: 341 (by implication)

Types: None has been designated. None of Cottle’s specimens is known now to exist.

Type locality: “. . . indigenous to this Province . . . ,” Cottle (1863: 216).

Taxonomic remarks: The current restricted sense of Cambarus originates in Hobbs (1942a: 354), and eliminates the need for subgenera in this genus.

See Hobbs (1942a: 337, footnote 2) for the correction of a misstatement in Fowler (1912: 341).

The quotation under Type Locality is the only indication given by Cottle as to the source of his specimens. By “Province,” he presumably means Upper Canada, roughly equivalent to what is now Ontario. Huntsman (1915) takes this to be so, and says (p. 158), “Cottle records it from Ontario, but does not give the locality. A few years previous to the time of publication of his article, he was residing at Woodstock [Oxford County].”

The types of Faxon’s C. argillicola are at M.C.Z. (cat. no. 3459), collected from Detroit, Mich. (Faxon, 1914: 426).

Diagnosis

This is a medium-sized, semiterrestrial, burrowing crayfish with no lateral rostral spines and a linear areola. It can be distinguished from the similar species C. diogenes by the lateral interruption of the cervical groove and the lack of a triangular suborbital projection of the carapace.

Habitat

C. fodiens is usually associated with marshy fields, drainage ditches, marshes, and ponds. Burrows are usually constructed in clay soil, which may be mixed in varying degrees with sand or coarse gravel. Colonies may be a few square yards in area (10–20 chimneys) or as large as an acre in extent.

Life History

This account is drawn partly from that of Creaser (1931a), but some observations on Ontario populations have been added.

Copulation probably occurs in the fall and in early spring when
Figure 85 *Cambarus fodiens*, male form I, carapace length 30 mm.; Ont., Schomberg, York Co., roadside ditch at Holland Marsh; 23 May 1965; D.W.B. and C. G. Barr.
adults enter open water as soon as the snow melts. Eggs are laid early, and ovigerous females are found from March through April. Hatching occurs in April, and free-living young are found by the latter half of May. As soon as mating and rearing are completed the adults return to burrows.

The young can burrow before they become very large and probably begin this activity by mid-summer. Burrowing must begin earlier in temporary ponds where the water disappears by the end of June. It is not certain whether the majority of juveniles require one growing season or two to achieve sexual maturity.

Ecology

The burrowing habit is probably associated with a largely herbivorous diet. However, in the laboratory, *C. fodiens* will feed on terrestrial or aquatic vegetation, bits of raw meat, and meal-worm larvae.

The burrows of this species are described on p. 36. They differ from those of *O. immuniis* in having a resting chamber close to the surface of the ground and from those of *C. diogenes* in having a deep escape tunnel leading down from the chamber.

Distributional Summary (Figure 86)

*Cambarus fodiens* is the common burrowing crayfish of southern Ontario. It too appears to have entered the province in the southwest and spread northeastward to approximately the level of Lake Simcoe. Our records probably do not constitute a fair sampling of this species because the general collector tends to overlook crayfishes that are not in a conspicuously aquatic habitat. The animals leave their burrows only in the spring, and unless the special significance of their clay chimneys has been recognized, their presence in an area will go largely unnoticed. Thus we would expect careful collecting to reveal many more colonies in the southwest and, perhaps, a few eastward to the edge of the Precambrian Shield. Beyond this, further range extension will likely be prohibited by the scarcity of suitable habitats.

Hobbs (1948b: 229–30) discusses the distribution of *C. fodiens*, and we have used his data as the basis for the inset map in Figure 86. The range extension into southwest Georgia provided by Hobbs and Hart (1959: 187–8) has been included. Our diagram admittedly has been drawn with broad strokes and is to be considered a first approximation.
Figure 86  Distribution of *Cambarus fodiens* in Ontario. Inset shows the total range of the species.

**Locality Records in Ontario**

**BRANT CO.:** New Durham, 24 July 1930, 1 ♀ mat.
**ELGIN CO.:** Aylmer, Holiday Beach Prov. Pk., 1 ♀ imm.
**Essex CO.:** Pelee Is., 16 Apr. 1963, 2 ♀♀ with young (NMC); Pelee Is., 16 Apr. 1963, 1 ♂ 1 ♀ with young (NMC).
**HALTON CO.:** Oakville, 14 May 1922, 6 ♂♂ imm., 2 ♀♀ imm., 3 ?? imm.
**KENT CO.:** Wheatley, nr. Wheatley Harbour, May 1962, 1 ♀ with young.
**LAMBTON CO.:** Perch Ck., Sarnia Twp., 16 July 1964, 1 ♀ imm.; Mud Ck., Bosanquet Twp., 16 July 1963, 1 ♂ imm.; Walpole Is., 7 May 1959, 1 ♂ II.
**WELLINGtON CO.:** Fergus, Downing’s Swamp, 25 June 1919, 1 ♂ 1 ♀, 1 ♂ II, 1 ♀ mat.
YORK CO.: Kettleby, 24 May 1937, 1 $\delta$ imm., 2 $\varphi$ imm.; Schomberg, Holland Marsh, 6 June 1964, 2 $\delta\delta$ imm., 2 $\varphi\varphi$ imm.; Schomberg, Holland Marsh, 6 June 1964, 2 $\varphi\varphi$ mat.; Schomberg, 20 June 1964, 1 $\varphi$ mat.; Schomberg, 20 June 1965, 1 $\delta \ I$, 3 $\varphi\varphi$ mat., 80 imm.; Toronto, Don Valley (nr. Leaside), 1 $\varphi$ with young; Toronto, Don Valley (nr. Leaside), 29 June 1963, 2 $\delta\delta$ I, 2 $\varphi\varphi$ mat.; Toronto, Don Mills, ditch beside CPR line, June 1958, 1 $\varphi$; Toronto (Scarborough), 31 May 1965, 1 $\varphi$ mat.; Toronto (Avenue Rd. and Wilson Ave.), 15 Apr. 1941, jar no. 1, 4 $\delta\delta$ I, 2 $\delta\delta \ II$, 4 $\varphi\varphi$ mat.; jar no. 2, approx. 10 $\varphi\varphi$ mat.; York Twp., May 1951, 2 $\varphi\varphi$ mat. (NMC).

Description

Male form I. Carapace laterally compressed, nearly smooth above, slightly granulate on sides, without lateral or branchiostegal spines. No prominent suborbital projection. Postorbital ridges grooved externally, without anterior spine. Cervical groove deep, sinuate, and broken on sides. Areola linear or obliterated in middle, anterior triangular space very small, posterior one larger.

Rostrum short, broad, depressed, excavated above. Margins thickened and raised, converging gradually toward tip, then converging rapidly to form triangular acumen, not interrupted by lateral spines. Terminal spine small, acute, turned abruptly dorsad.

Antennal scale small, shorter than rostrum, broadest distal to middle, truncate anteriorly, terminal spine very small.

Flagellum of antenna shorter than body.

Epistome wider than long, kidney-shaped (reniform), margins strongly convex, and raised slightly.

Chela strong, inflated, nearly smooth. Fingers flattened and thickly punctate, upper surface of each with ridge bordered by row of punctations. Dactyl with deep incision at base of cutting edge. Immovable finger shorter than dactyl, almost straight, often bearded at base.

Carpus of cheliped strong, deeply furrowed above, with one large spine on medial surface, and one or two small ones posteriorly. Distal margin of ventral side bears large median spine.

Merus of cheliped with a few very small spines dorsally near distal end, two rows of small toothlike spines beneath.

Telson narrow, tapering posteriorly. The two sections about equal in length, proximal section bispinose on each side, distal section rounded behind.

Copulatory stylets short, reaching to bases of third periopods when abdomen flexed, strong, terminating in two short processes which are curved abruptly caudad at angle of approximately 90° to axis of appendage. Central projection thin, falciform, and heavily sclerotized. Mesial process strong and thick, with pronounced angle in ventral margin, peglike tip pointing dorsally.
ISCHIAL HOOKS short but acutely pointed, borne on third pereiopods.

COLOUR IN LIFE basically dark, olive-brown on dorsal surface, carapace dappled with lighter and darker brown markings, lateral margins and tips of chelae orange. Underside light grey tinted with orange, chelae light orange.

Male form II. Much like male form I but chelae weaker and almost always bearded. Copulatory styles thicker and less heavily sclerotized, distal processes short and blunt.

Female. Similar to male form I but abdomen broader. Seminal receptacle with anterior border depressed to a level with the thoracic sterna, irregularly oval, with deep central depression surrounded posteriorly and laterally by U-shaped, swollen ridge, broken in median position by narrow fissure. Deepest part of fossa displaced either to left or right of centre.

OTHER CRAYFISH SPECIES THAT MAY BE FOUND IN ONTARIO

*Orconectes limosus* (Rafinesque) was reported from Iroquois, Dundas Co., Ontario by Huntsman (1915). However, it has not been possible to re-collect this species in the province, and the validity of the early record seems dubious (Crocker, 1957: 79–80).

Several large crayfishes of the genus *Procambarus* are distributed extensively by biological supply houses for use as live classroom material. Thus, these crayfishes could easily be introduced into Ontario if classroom specimens were released. Also *Procambarus blandingii acutus* is reported to occur naturally around the southern end of Lake Michigan in Wisconsin and Michigan. There is a remote possibility that specimens might be taken in Ontario.

A subspecies of *Orconectes propinquus*, *O. p. sanborni*, occurs in Ohio on the south shore of Lake Erie, directly across from south-western Ontario. It looks much like *O. p. propinquus* but lacks a rostral carina.
Techniques for Studying and Culturing Crayfishes

COLLECTION

Small-Scale Operations

The basic equipment for field collecting consists of a pair of chest-high waders, a kitchen sieve, a sturdy knapsack with shoulder-strap, and a number of polyethylene bottles. These items are sufficient to enable the collector to capture the crayfishes of most shallow ponds, streams, and lake shores. By turning over stones carefully, one can often startle the crayfish underneath into swimming; a quick scoop with the sieve and some luck then effect the capture. The specimen should be transferred forthwith to a jar of preservative carried in the knapsack. One quickly learns to keep in mind, when collecting those animals that do not swim away when exposed, that crayfish move backwards when alarmed and trying to escape. Thus, the net should be placed behind the crayfish and a hand slowly moved up in front to ease it into the net. If it swims, then quickness and luck are again called for. Where there is a great deal of aquatic vegetation and few stones, sweeping a D-frame aquatic net through the vegetation will yield many crayfish, particularly immature individuals. For habitats with a relatively smooth bottom that is free of large obstructions, greater quantities of crayfish can be taken by seining. A 10-foot seine operated by two men can be used to collect hundreds of crayfish per hour in a favourable situation.

Crayfish living in deeper waters (over one metre deep) must be collected by trapping or netting. Ordinary minnow traps baited with fish entrails or bread scraps will yield many crayfish from deep waters.
In northwestern Ontario, bait dealers who use these traps to obtain minnows usually get a quantity of *O. virilis* with each catch. Crayfish also seem prone to become entangled in gill nets set out for fish. If no trap is available, good results can be obtained by wrapping the bait (fish entrails) in a few square feet of old gill net and sinking this package to the bottom overnight. In trying to get at the bait, the crayfish become tangled in the net and can be pulled up and cut out the next morning. SCUBA diving not only makes deep-water collecting possible but also permits the observation of underwater behaviour.

**Commercial Harvesting**

In areas where crayfishes are abundant, they may be harvested directly from their natural habitats. From small, shallow ponds and embayments of larger bodies of water, seining is effective. Commercial quantities may be taken in this way, but trapping is a common procedure and, as reported by Threinen (1958a), appears to be highly effective in Wisconsin. Live-bait (minnow) dealers in the Lake of the Woods area are also able to procure sufficient crayfishes to meet the demand in the course of minnow trapping.

In the Wisconsin operation, traps are constructed of 0.5 in. by 1 in. welded wire, shaped into a cylinder 8 in. in diameter by 18 in. long. One end is closed by the same wire, and the other is fitted with a hinged, inward-directed cone containing a 1.5 in. opening. The entire trap is tarred to give it a dark colour. Labour and materials are said to cost about $5.00 per trap. Bait is a 0.25 lb. piece of fresh carp, and 12 feet of tarred twine and an 8 in. cedar buoy serve to locate and haul the trap.

Threinen records that in the actual operation, one man was tending a total of about 600 traps distributed among three lakes, a task requiring an efficient operative procedure. A day’s catch from one of the lakes (116 traps) averaged 11.3 crayfish per trap.

**PRESERVATION**

The best killing and preserving agent for crayfishes is 80 per cent ethyl or isopropyl alcohol, which leaves the appendages flexible and the exoskeleton hard. A few days after collecting, the original fluid in jars more than one-third full of specimens should be gently poured off (leaving one inch of the fluid in the bottom in order to retain any
commensal ostracods or branchiobdellid worms) and replaced by fresh 80 per cent alcohol. If necessary, 5 per cent formalin, as used for preserving fish specimens, can be employed in the field, but if crayfishes are left in it too long the limbs become brittle and hard to manipulate, and after several years in formalin, the exoskeleton also tends to become soft. Specimens that have been put in formalin following capture should be washed as soon as possible for a day or more in gently running water, and then transferred to 80 per cent alcohol.

Collections from different localities or from the same locality taken on different dates should be placed in separate containers and the appropriate data recorded with a soft pencil on a good-quality paper label placed inside the jar. The following data are essential: name of nearest town or other identifying feature that can be located on a map, name of the body of water, collection date, collector's name. Additional remarks regarding the nature of the habitat (water depth, type of bottom, whether in a burrow, and so on) are also useful.

PHOTOGRAPHY

Habit photographs for this study were recorded on fine-grain, black-and-white film in the studio. Specimens were prepared for photography by killing them in a relaxed and naturally coloured state by means of an oil-based rotenone solution added to the water until it became cloudy white.

After four or five hours in this solution the specimens were removed, rinsed in water to remove any oil film, and photographed in about two inches of water. The final prints were touched up slightly with black, white, and grey tempera colours, to clarify some structural details.

Live specimens can be photographed in aquaria provided the water and the glass are clean (see Fig. 87). The glass area through which the picture is taken should be bubble-free and should have a plane surface.

AQUARIUM CULTURE

Crayfish can be observed at close range in aquaria over lengthy periods of time. So far we have not been able to carry through the
whole reproductive cycle in small indoor aquaria, but individuals of certain species can be kept in captivity for a year or more during the late immature and adult periods of their life history. Here it is possible to observe such activities as feeding, moulting, excavating, swimming, mating (Fig. 87), and egg laying (observed with difficulty).

Perhaps the most convenient way to keep most species is in a glass container (1 gallon capacity or larger), preferably a standard rectangular aquarium, as the flat glass sides permit undistorted observation of the animals. For the stream and lake species (O. virilis, O. p. propinquus, and C. robustus), the aquarium should be filled nearly full of water and gravel and large, flat stones should be provided on the bottom. Aeration of the water by an aquarium pump and one or two air-stones will allow more individuals to exist in the same aquarium. The air hose must be passed through some sort of partial aquarium cover (e.g. a triangular piece of one-quarter inch plywood fitting over one corner) to prevent the crayfish from climbing it and escaping. These same species also thrive well in a running-water system. At the Museum we have used an adaptation of the rearing equipment described by Wiggins (1959). The wooden frame and its cages were removed, and the sides of the metal tanks were extended upwards with plexiglass walls to prevent the crayfish from climbing out. The drain spouts were also covered with screen to prevent smaller specimens from escaping. C. b. bartoni also does well in this running-water apparatus.

Pond and slow-water crayfish species (such as O. immunnis, C. fodiens, and C. d. diogenes) seem to thrive better in about two inches of standing water which is allowed to become turbid. The turbidity provides cover and renders the crayfish less sensitive to persons walking near the aquarium. Once again, more crayfish can be maintained if the water is aerated. The habitually burrowing species, C. fodiens and C. d. diogenes, can easily be induced to burrow indoors if provided with a container (surface area 250 sq. cm. or larger) containing about a 10-inch depth of moist clay. There should also be about five inches of water in the bottom of the container. C. fodiens will build elegantly structured clay chimneys under these conditions.

In feeding crayfish in captivity, we have had most success using small chunks of fresh meat (ground beef) or live meal-worm larvae (either whole or broken in two). Other foods that have also proved satisfactory are various other kinds of cooked and fresh meats, and vegetation such as aquatic plants and dandelions (especially for the
Figure 87 Copulation in *Orconectes propinquus*. Crowded aquarium conditions in August. The male’s right accessory copulatory stylet (second abdominal appendage) is dimly visible (a). Ahead of it note the distal end of the male’s left fifth walking leg (b) which has been passed across the body ventrally in front of the stylets, thus depressing them into copulating position.
burrowing species). If fresh meat is used, a pea-sized chunk per crayfish per day seems to be sufficient.

POND CULTURE

Several studies of crayfish culture methods have been made. Tack (1941) worked with *O. immunis*, and Langlois (1935) with *O. rusticus*. Viosca (1961) gives a number of details relative to 16 "crawfish farms" in Louisiana. He writes (p. 5): "During the 1959-60 crawfish season, these pioneer projects already comprised over 2,000 acres, with a production potential of as much as two million pounds of these tasty crustaceans annually."

Forney (1956) has written the article that applies most closely to conditions in Ontario. His report concerns the experimental culture of *O. immunis* in artificial ponds in New York. A summary outline of his recommendations follows:

Species recommended: *Orconectes immunis*

Pond areas tried: 1/30 to 5 acres

Pond area recommended: Under 1 1/2 acre (easiest to seine and manage)

Stocking instructions:

Fall: 600-1000 mature (2½ in.) crayfish per acre

Spring: 300-500 females with eggs per acre

Fertilization of pond: Commercial fertilizer (6-12-6 or 10-10-5) broadcast from shore over pond surface; 200 lb. per acre at 3-week intervals during spring and summer. Manure may be used instead, 30 bushels per acre at same intervals

Feeding: Supplementing natural food with soybean meal, fish meal, cracked corn, and potatoes was tried (quantities not given). Hay, fresh or dried, may have considerable value; about 5 tons per acre portioned out through the summer

Forney states that fertilization of the pond greatly increases the abundance of microscopic plants and animals. *O. immunis* appears to survive and grow as well on these as on larger submerged vegetation, which, therefore, is not a necessary pond component. He also points out that minnows are frequently stocked along with crayfish for a double bait dividend. There is a disadvantage here, however, in that the two must be separated by hand after seining, and many minnows are injured or killed in the process.
The commercial raising of crayfishes has been accomplished successfully in Ontario. According to conservation officer John W. Allen, *O. immunis* has been raised for seven or eight years in quarter-acre ponds as a private operation at Port Rowan. Forney's directions were followed closely, and yields have run as high as 4000 crayfish per quarter-acre per year.
Glossary of Terms Used in the Study of Crayfishes

ACUMEN: pointed anterior tip of rostrum (q.v.) (Fig. 1).
ACUMINATE: possessing a narrow, pointed tip.
ANNULUS VENTRALIS: see SEMINAL RECEPTACLE.
ANTENNA: long, whiplike sensory organ situated at anterior end of body (Fig. 1).
ANTENNAL SCALE: lateral bladelike structure at base of antenna (Fig. 1); the antennal exopodite.
ANTENNULE (first antenna): one of a pair of sensory appendages of the head, each with two filaments (flagella) (Fig. 1).
ANTERIOR: front, nearest the head end.
APICAL: at the apex or unattached tip.
AREOLA: an area (usually hour-glass shaped) on the mid-dorsal surface of the thorax (Fig. 1); bounded by grooves or lines which mark the dorsomedial limits of the gill chambers.
ARTHROPOD: segmented animal lacking a backbone and possessing an exoskeleton and paired, jointed appendages on some or all of the segments.
ARTICULATION: joint.
ARTICULATION MEMBRANE: thin, flexible section of exoskeleton separating two thicker areas, allowing these areas to move in relation to one another.
BIRAMOUS: two-branched; with an inner (mesial) branch, the endopodite, and an outer (lateral) branch, the exopodite, set on a common stalk, the protopodite.
BISPINOSE: two-spined.
BRANCHIOSTEpite: lateral extension of carapace covering gill chamber (Fig. 1).
CARAPACE: the exoskeletal covering of the cephalothorax.
CARINA: median dorsal ridge near tip of rostrum (Fig. 52).
CARPUS: the third segment from the free tip of pereiopods (counting movable finger as segment one) (Fig. 1).
CAUDAD (CAUDALLY): toward the rear or tail end.
CENTRAL PROJECTION: the more lateral and longer of the two parts of the male's mating organ (first abdominal appendage); contains the sperm canal; see also MESIAL PROCESS.

CEPHALAD: toward the head.

CEPHALIC: of the head.

CEPHALOTHORAX: the fused head and thorax (Fig. 1).

CERVICAL GROOVE: deep groove dividing carapace into an anterior cephalic and a posterior thoracic portion (Fig. 1).

CHESA: grasping pincer or claw; large chelae sometimes called hands; composed of the segments called dactyl and propodus.

CHELATE: bearing a chela.

CHELIPED: a leg that bears a chela.

COPULATION: the joining of male and female for sperm transfer.

COPULATORY STYLET: modified first pleopod of male crayfish (Figs. 2 and 22-30), used in sperm transfer; also called gonopod.

CORNEOUS (CORNIFIED): of a horny texture.

CRUSTACEAN: an arthropod (q.v.) which absorbs oxygen by means of gills and has two pairs of antennae (q.v.).

CUTICLE: general term for a non-cellular membrane covering all or part of the surface of an animal and secreted by the underlying cells.

DACTYL: the first segment at the free tip of pereiopods; the smaller movable part of the pincer or chela; sometimes called movable finger (Fig. 1).

DISTAD: in the distal direction.

DISTAL: toward the free tip (away from the body).

DORSAL: in the dorsal direction.

DORSAL: of the back or upper side.

ENDOPODITE: see BIRAMOUS.

EPISTOME: plate on ventral side of head which bears a roughly triangular extension on its forward edge.

EXOPODITE: see BIRAMOUS.

EXOSKELETON: shell.

FISSURE: a narrow, deep cleft in the surface of the seminal receptacle.

FLAGELLUM OF ANTEINA: the thin, elongate, whiplike extension of the antenna (the antennal endopodite).

FOSSA: a wide, deep cavity or sinus in the surface of the seminal receptacle.

GLAIR: a thick, gummy, semitransparent secretion product of glands on the underside of the abdomen of female crayfishes.

GONOPOD: see COPULATORY STYLET.

HAND: the great chela, composed of the segments called dactyl and propodus.

HEAD: portion of cephalothorax anterior to cervical groove.

HYPODERMIS: the thin monolayer of cells lying just under the arthropod exoskeleton and responsible for producing it.

INSTAR: that portion of the life history of an immature arthropod between one moult and the next.

ISCHIUM: the fifth segment from the free tip of pereiopods (Fig. 1).
LATERAL: of the side.
LATERAL ROSTRAL SPINES: lateral spines at base of acumen on rostrum (Fig. 1).
MEDIAD (MESIAD): toward the middle.
MEDIAL (MESIAL): of the middle.
MEDIAN: in the middle; on the mid-line.
MERUS: the fourth segment from the free tip of pereiopods (Fig. 1).
MESIAD (MEDIAD): toward the middle.
MESIAL (MEDIAL): of the middle.
MESIAL PROCESS: terminal process located mesially on male’s mating organ; see also CENTRAL PROJECTION.
MID-SAGITTAL PLANE: a dorsoventral plane in the mid-line running antero-posteriorly separating the organism into mirror-image halves.
MORPHOLOGY: the study of form or structure.
MOVABLE FINGER: see DACTYL.
PFREIOPOD: any of the ten walking legs (including the large chelate legs).
PLEIPOD: simple, fanlike, two-branched appendage of the abdominal segments.
PLEURON (pl. pleura): overhanging plate on side of abdominal segments; hidden by carapace and gills in the thorax.
POSTERIAD: in a posterior direction.
POSTERIOR: of the hind or tail end.
POSTORBITAL RIDGE: ridge on upper lateral aspect of head, just behind and nearly continuous with side of rostrum (Fig. 1).
PROCESS: any projecting structure; particularly a terminal part of the male copulatory stylet.
PROPODIS: the second segment from the free tip of pereiopods; includes the immovable finger and palm (Fig. 1).
PROTOPODITE: see BIRAMOUS.
PROXIMAL: basal; especially of an appendage, that portion closest to the body.
PUNCTATE: bearing punctations.
PUNCTATION: small pit in the exoskeleton.
RENIFORM: kidney- or bean-shaped.
ROSTRUM: dorsomedial cephalic extension of carapace partially covering eyestalks and bases of antennae and antennules (Fig. 1).
SCLEROTIZED: made hard and rigid (referring to exoskeleton).
SEMINAL RECEPTACLE: sperm receptacle on sternum of female between posterior two pairs of walking legs; also called annulus ventralis (Figs. 3 and 40-48).
SINUS: a cavity.
SPECIES: (working definition) a group of organisms which interbreed freely in nature.
SPINE: any sharp-pointed eminence of the exoskeleton which is not located on a copulatory stylet.
SQUAMOUS: flat, scalelike.
STATOCYST: organ of balance located at the base of each antennule.
STERNUM: the ventral sclerotized plate or bar of a segment.

SUBORBITAL PROJECTION: angulate process on anterior border of carapace below eye.

SUTURE: a narrow fissure or cleft between two heavily sclerotized areas of the exoskeleton.

TAGMA: a group of segments forming a body region.

TELSON: median postsegmental body division at posterior terminus of body (Fig. 1).

TERGUM: a dorsal exoskeletal plate.

THORAX: portion of body between cervical groove and abdomen; consists of eight segments which are partially fused.

TRUNCATE: appearing as though cut off square on the end.

TRUNK: the thorax (q.v.).

TUBERCLE: a low, rounded eminence of the exoskeleton.

VENTRAL: of the underside.
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