Systematics of the Freshwater Amphipod Genus *Crangonyx* (Crangonyctidae) in North America

Jun Zhang

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SYSTEMATICS OF THE FRESHWATER AMPHIPOD GENUS CRANGONYX
(CRANGONYCTIDAE) IN NORTH AMERICA

by

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A Dissertation submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
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August 1997

Approved by

John R. Holminger (Director)

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ABSTRACT
SYSTEMATICS OF THE FRESHWATER AMPHIPOD GENUS CRANGONYX (CRANGONYCTIDAE) IN NORTH AMERICA.

Jun Zhang
Old Dominion University, 1997
Director: Dr. John R. Holsinger

The systematics of the amphipod genus Crangonyx of North America (north of Mexico) is revised, based on available collections (ca. 2240) and literature dealing with the genus. A grand total of 42 North America species of Crangonyx are recognized in the present study, 24 of them new to science. All species are described or redescribed and figured, utilizing external morphological features. Keys to both species groups and individual species are given. Phylogenetic trees are built using computer programs (PAUP, Hennig86, MacClade) based on 26 characters. Wagner parsimony produced 18 parsimonious trees and Fitch parsimony produced 45 trees. The consensus tree of both methods and a hypothesis phylogenetic tree of the North America species of Crangonyx are developed along with a discussion of Crangonyx phylogeny and character evolution. Six monophyletic species groups are recognized.

With respect to the origin of Crangonyx, putative ancestors of the genus probably originated as very old freshwater lineage dating back at least to the Mesozoic and possibly earlier. The ancestor of modern Crangonyx species possibly resembled C. forbesi and separated from the common ancestor of Synurella and Crangonyx somewhere on Laurasia. Species of Crangonyx have exploited a wide variety of surface and groundwater habitats in North America. Many of the spring/seep dwellers are apparently predated to life in subterranean waters. A detailed distribution map is given for each species with an interpretation of its biogeography. Almost all species of the genus occur in eastern North America, east of the Rock Mountains. The species of Crangonyx with distribution in glaciated areas also occur south of the southern extent of Pleistocene glaciation. Distribution patterns are analyzed and compared with phylogeny in an attempt to evaluate extrinsic barriers, dispersal limits and other geographic and geological considerations that might have a bearing on species ranges.

Eleven species of Crangonyx in North America are troglobites, many of which are found in karst areas in the Appalachians and Interior Low Plateaus regions. The origin of troglobitic members of the genus is attributed to active or passive invasion and colonization of subterranean waters by preadapted epigean ancestors, sometimes under climatic constraint and sometimes by adaptive shifts into new niches. Perhaps a few troglobitics species originated through peripheral isolation in subterranean waters from previously established troglobites.

Human introduction of C. pseudogracilis in Europe and C. floridanus in Japan is explained by the ballast water theory, which suggests that small aquatic organisms, such as certain species of amphipods, are transported in the ballast water of ocean-going ships.

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CHAPTER I

INTRODUCTION

Amphipod crustaceans are one of the largest groups of the freshwater invertebrates with respect to number of species and overall biodiversity. Eleven families and 19 genera are represented in the freshwaters of North America. This study revises the systematics of the freshwater amphipod genus *Crangonyx* according to modern standards.

*Crangonyx* belongs to the family Crangonyctidae, the largest family of freshwater amphipods in North America. Of the two largest genera of Crangonyctidae, *Stygobromus* and *Crangonyx*, *Crangonyx* is the least studied. Holsinger (1972) first reviewed the taxonomy of this genus, with a key to the North America species and detailed geographic distributions for each species. He established several species groups based on morphological similarity and also identified important taxonomic problems. He found there were about 20-25 undescribed species and that the taxonomic status of some of the described species was not clear. Many species were poorly described and difficult to identify. Knowledge of individual and population variability was incomplete. Several years later, Holsinger (1977) gave a much more detailed diagnosis of this genus, listed all known species of *Crangonyx* and discussed its distribution and ecology. Many problems and questions about *Crangonyx* still had not been solved. For example: How many species of *Crangonyx* occur in North America? What is the phylogenetic relationship among *Crangonyx* species?

A complete taxonomic revision of *Crangonyx* addresses the remaining questions regarding their taxonomy, phylogeny and biogeography. There are other cogent reasons for this study. *Crangonyx* has more epigean species than any other freshwater amphipod genus in North America, and occurs in a wide variety of freshwater habitats. This genus may be important for environmental monitoring, and gaining a better understanding of the ecology of freshwater communities. The study of biodiversity in *Crangonyx* is also important for biospeleology, because seven described species occur in caves and several newly recognized species also inhabit subterranean groundwater. This study will also try to answer the following biospeleological questions: What are the relationships among surface and subterranean species? Did the subterranean species evolve, under climatic stress, by exploiting newly available environments, or by some other mechanism? The rapid deterioration of freshwater habitats and concomitant loss of biodiversity requires us to describe the invertebrate fauna of North America as quickly as possible. This study, combined with the works by Holsinger on *Stygobromus*, will give us a much more complete understanding of the systematics, zoogeography and phylogenetics of crangonytid amphipods.

Forty-two North American (north of Mexico) species of *Crangonyx* are recognized and covered in this study: 24 of them are new to science. All species are described or redescribed, utilizing external morphological features. Phylogenetic trees are built using computer programs (PAUP, Hennig86, MacClade) with a discussion of *Crangonyx* phylogeny and character evolution. A detailed distribution
map is given for each species with an interpretation of biogeography. The evolution of subterranean species is discussed in some detail.

REVIEW AND HISTORICAL PERSPECTIVE

The genus *Crangonyx* was established by Bate in 1859 for the subterranean species *Crangonyx subterraneus*, which was found in a well at Ringweed, Hampshire, England. Bate (1859) gave the following generic diagnosis: "Like *Gammarus*, but, not having fasciculi of spines upon the posterior segments of the pleon, and having the posterior pair of pleopoda unibranched. Telson single." Forty years later, Stebbing (1899) thought *Crangonyx* did not have a small inner ramus on the third uropod according to Bate's description of the type species, so he erected *Eucrangonyx* for species with a small inner ramus on the third uropod and assigned to it those species of *Crangonyx* with this structure. Schellenberg (1934) solved the problem of *Crangonyx* vs. *Eucrangonyx*, when he found that the specimens of English *Crangonyx subterraneus*, contrary to the claim of Bate, possess a rudimentary inner branch of the third uropod. Thus, Stebbing's genus *Eucrangonyx* is a junior objective synonym of *Crangonyx*. Because Bate gave just two diagnostic morphological characters of *Crangonyx* (one of them actually wrong), many non-*Crangonyx* subterranean freshwater species were assigned to *Crangonyx* but later removed to other genera.

In his comprehensive review of the family Crangonyctidae, Holsinger (1977) summarized *Crangonyx* and gave a thorough generic diagnosis. Although he listed 25 species of *Crangonyx*, he pointed out that the four Asiatic species are very questionable members of the genus. Three of them (*C. schizurus*, *C. satiferus*, and *C. shimizui*) are now assigned to other genera, while the status of *C. arsenjevi*, although probably a species of *Crangonyx*, cannot be definitively determined (see Holsinger, 1977 for more detailed explanation). The following paragraphs give a brief history of the description of *Crangonyx* species and their discovery (although some species were first assigned to *Eucrangonyx*).

The first described species of *Crangonyx* was *C. subterraneus*, described by Bate for specimens from a well in England. Smith (1871) described the second species *C. gracilis* from Lake Superior. Packard (1881) described *C. antennatus* from Nickajack Cave, Marion County, Tennessee. Smith (1888) described *C. packardi* from a well in Orleans, Indiana. Embody (1911) described *Eucrangonyx serratus* from a site near Ashland, Virginia. Derzhavin (1927) described *E. arsenjevi* from springs in the Ussury River basin of extreme southeastern Russia, but as noted above its taxonomic status is unclear. Borutzky (1928) described *C. chlebnikovi* from a cave in the Ural Mountains of Russia. Schellenberg (1935) described *C. paxi* from an artificial gallery (mine shaft) in the Klesnica Vally near Kletno in the Sudeten Mountains of southwestern Poland (then in Germany). Hubricht and Mackin (1940) described three new species of *Eucrangonyx*, and Hubricht (1943) later moved them to *Crangonyx*. These species include *C. forbesi* from Missouri, *C. obliquus* from Arkansas, and *C. shoemakeri* from Washington, DC. Ellis (1940) described *C. richmondensis* from a swamp in South Carolina. Shoemaker (1941) described *C. hobbsi* from caves in
Florida and later (1942) described *C. dearolfi* from caves in Pennsylvania. Hubricht and Harrison (1941) described *C. occidentalis* from the state of Washington, but Bousfield subsequently (1958) suggested that it was a subspecies of *C. richmondensis*. Hubricht (1943) described *C. anomalus* from springs in southern Ohio and northern Kentucky. Bousfield (1958) described *C. minor*, *C. pseudogracilis*, *C. rivularis*, and *C. setodactylus* from eastern North America. He described *C. alpinus* from Oregon (1963a) and *C. floridanus* and *C. grandimanus* from Florida (1963b). The most recent description of a species was of *Crangonyx aberrans* by Smith (1983) from Massachusetts.

Of the 23 species presently assigned to the genus *Crangonyx*, 19 are found in North America, three species (all subterranean) are found in Europe, and only one species, *C. arsenjevi*, is found in Asiatic Russia (poorly described, although the drawing of uropod 3 is diagnostic for *Crangonyx* [see Derzhavin, 1927]). I recognized 18 of the 19 described species from North America in the present study. *Crangonyx alpinus* proved to be a synonym of *C. richmondensis*. Moreover no subspecies of *C. richmondensis* are recognized by me (see remarks section of *C. richmondensis* description). A total 42 species are treated in this study, 24 of which are newly described and 18 are completely redescribed and figured except *C. aberrans*.

**OBJECTIVES**

There are three objectives in this study:

1. Alpha-level taxonomy: description of new species and redescription of the old species to revise the taxonomy of *Crangonyx* in North America based on all available collections and all pertinent literature.

2. Phylogenetic analysis: utilization of the taxonomic data in cladistic analyses to construct a phylogeny of *Crangonyx*.

3. Biogeographic analysis: clearly define the patterns of species distribution, correlate these patterns with phylogeny, and evaluate extrinsic barriers, dispersal limits and other geographic and geological considerations.

**MATERIAL AND METHODS**

**Material**

Specimens came primarily from the research collections of J. R. Holsinger and by loan from the National Museum of National History (Smithsonian Institution). Several other institutions with smaller collections also made their specimens available. Almost all *Crangonyx* collections reported in the literature from North America were examined. There included about 2240 collections, each containing 1-100 (or more) specimens. Types of all known species from North America are deposited in one of three places:
nine in the Nation Museum of Natural History under the catalog numbers of the former United States National Museum (USNM); eight in the Canadian Museum of Nature (except the holotype of \textit{C. pseudogracilis}, which cannot be found in their collections and is possibly lost); two in the Museum of Comparative Zoology at Harvard University, although only one could be found and examined (the holotype of \textit{C. alpinus} cannot be found and is possibly lost).

The following is a list of the institutions or research collections where specimens of \textit{Crangonyx} are deposited. The abbreviations that follow each listing are used throughout the text.

- American Museum of Natural History (AMNH)
- Canadian Museum of Nature (CMN)
- Florida State Museum (FSM)
- Holsinger, J. R., Department of Biological Sciences, Old Dominion University (JRH)
- Milwaukee Public Museum (MPM)
- Museum of Comparative Zoology, Harvard University (MCZ)
- National Museum of Natural History of the Smithsonian Institution (USNM);
- North Carolina State Museum of Natural History (NCMNH).

All holotypes and many paratypes of new species designated in this paper will be deposited in the National Museum of Natural History. Selected paratypes for new species described from Virginia will be deposited in the Virginia Museum of Natural History in Martinsville, VA. Remaining paratypes are deposited in Dr. Holsinger's research collection. The entire Holsinger research collection will eventually be deposited in the National Museum of Natural History. Under the material examined section for each species, if the deposition of a collection is not indicated for a museum by an abbreviation in parentheses, it is in the Holsinger research collection.

Five species are recorded from municipalities in southeastern Virginia that have undergone name changes because of the merger of cities and counties into larger units with city names. In the "material examined" section for these species, the original county place names are used for all collections made prior to the mergers. These localities are: Norfolk County (now the city of Chesapeake); Elizabeth City County (now the city of Hampton); Warwick County (now the city of Newport News); Nansemond County (now the city of Suffolk); and Princess Anne County (now the city of Virginia Beach). For collections made after the mergers, the current city name is given, with the original county name in parentheses.

Methods

Morphological analysis and species identification

All specimens in available collections were examined and where necessary compared with the type
specimens. Specimens were first examined under a dissecting microscope, and then under a compound microscope after slide mounted appendages were prepared if needed. Routine determination can be made with the aid of a dissecting microscope for some species. However, slides must be prepared for accurate identification of most species, as well as for morphological analysis for all species. Prepared slides were examined with the aid of a compound microscope for smaller sized species and for purposes of illustration. Illustrations of important detailed external morphological structures of species of the Crangonytidae are found in Holsinger’s (1972) handbook. Dissecting and slide making techniques were adopted from Holsinger (1967) and Barnard (1969). I follow Holsinger’s (1972) terminology and definitions of external morphological structures.

The results of the morphological analyses will also be used to determine geographic variation, as well as to distinguish individual species, and to establish morphological difference among species. Based on morphological analysis, each species is given a unique morphological diagnosis to establish its specific status. Some species proved to be synonyms of others, whereas some collections proved to contain more than one species. Also new species were found in both new and old collections. Every collection was determined to species level and either assigned to species already described or, if found to be undescribed, to a new species. Keys to all species were constructed.

In comparison with many arthropod groups, amphipods are taxonomically difficult because the genitalia are soft finger-like processes that cannot be used for identification. However, every external body part has some diagnostic value and I used a combination of characters to identify species. Although this procedure generally works well, it may also cause some problems as pointed out below.

As stated by Holsinger (1967), there are two major problems inherent in amphipod taxonomy: (1) continuous growth and development through successive instars, and (2) variation in size and proportion of a number of taxonomically important characters in older animals. Another problem is the seasonal changes of selected diagnostic characters. Geographic variation is also a problem. I used sexually mature males and females whenever possible as a basis for morphological analysis, description and illustration.

It is easy to distinguish between mature females and males of species of Crangonyx. Mature males have a pair of soft finger-like penes on the ventrum of the 7th pereonite, calceoli on antenna 2, and a curled or laterally deflected outer ramus of uropod 2, which is often reduced in size. Mature females have brood plates (with long marginal setae when fully developed). In some species, however, immature females may have penes and/or calceoli and it is sometimes difficult to distinguish immature individuals. I used the following criteria: if a specimen has penes but also brood plates (in most cases the brood plates have not completely developed), it is assigned as a female. All specimens lacking the secondary sex characters described above are considered juveniles.
Description and illustration

Every species is given a detailed description and drawn. The format is based on Holsinger's (1978) monograph on *Stygobromus*. The drawings were made with the aid of a drawing tube (camera lucida) mounted on a Leitz compound microscope. For each species, a specimen of each sex was dissected and the appendages mounted on slides according to the methods described by Holsinger (1967).

The following appendages of the female were drawn: antenna 1 and 2, the gnathopods (1 and 2), part of pereopod 3, pereopod 4, part of pereopods 5-6, pereopod 7, all pleonal plates, all uropods, telson, and the mouthparts. The antenna 2, gnathopods (1 and 2), pereopod 7, uropods, and telson were drawn for males.

Phylogenetic analysis

The purpose of this aspect of the research was to explore the phylogenetic relationships of species of *Crangonyx* using cladistic methods in accordance with the principle of maximum parsimony. Maximum parsimony methods search for minimum-length trees—trees that minimize the amount of evolutionary change needed to explain the available data under a prespecified set of constraints upon permissible character change (Swofford, 1991). Another important phylogenetic criterion is that monophyletic groups can only be defined on the basis of synapomorphies (Hennig, 1966).

Many crustacean studies including this one have shown that at the species level, cladistic studies cannot achieve well corroborated phylogenies. Three main problems may prevent reliable results: (1) the abundance of homoplasies, (2) difficulty in finding useful outgroups, and (3) the uncertainties of polarities.

Holsinger (1986) first gave a hypothesized phylogenetic relationship for the extant genera of Crangonyctidae and later refined it (Holsinger, 1994) using cladistic methodology. The resulting cladogram of Holsinger (1994) was used as a reference in this study. The method of outgroup comparison for polarizing characters given by Maddison et al. (1984) was followed. Based on Holsinger's (1994) result, *Synurella* was used as the sister group of *Crangonyx*. Further removed outgroups consisted of *Stygonyx*, *Stygobromus* and *Bactrurus*.

Cladistic analysis results in assumptions about synapomorphs, which in turn define nested subsets of species within the genus. Characters used in the analysis were chosen on the basis of morphological analysis of species. Autapomorphies were used to establish (anagenetic) lineages but deleted from the cladogram. A character data matrix of *Crangonyx* was then established and used in the computer programs to construct cladograms. Phylogeny was generated using PAUP 3.0 (Swofford, 1991) and also tested using Hennig86 (Farris, 1988). The branch-and-bound algorithm in PAUP 3.0 is too slow to be useful with my data set. Instead, I used the heuristic search option with TBR branch swapping and random (50 replicates in the final analysis) addition of taxa. Two variations of parsimony methods were tried: Wagner parsimony.
which permits characters to revert freely to the plesiomorphic state, and Fitch parsimony, which permits multistate characters unordered and any character state can transform directly into any other state. MacClade 3.0 (Maddison and Maddison, 1992) was used for data and tree handling, and for computation of various tree statistics.

The most parsimonious cladogram was selected on the basis of parsimony principles. After the cladistic analysis, several monophyletic subgroups of *Crangonyx* were established and a clear picture of species relationship within *Crangonyx* emerged. Hypotheses about speciation and biogeographic patterns were developed by combining phylogenetic data and geographic distributions of species.

**Biogeography**

All locality records for each species were plotted on distribution maps. Interpretation of these results was utilized to explain the origin and distribution patterns of species of *Crangonyx*. A attempt was made to determine the relationship between species and the limits of their geographic distribution. As a result, I was able to determine that some species are endemic to a given area, whereas others have much broad distributions which do not correspond to a specific area. Based on these analysis, I attempted to determine if present distributions are the result of vacariance, or dispersal, or a combination of both (Humphries and Parenti, 1986. Myers and Giller, 1988). In some instances, attempts were made to relate splits on the cladogram to certain climatic and/or geological changes that might have influenced geographic isolation.
CHAPTER II

MORPHOLOGICAL ANALYSIS OF **Crangonyx** CHARACTERS

The following is a list of characters that resulted from morphological analysis. They are used in species identification, description, and cladistic analysis.

Female:

**Body length.**—This is a measurement from the front of the head to the end of uronite 3 (excluding antennae, telson and uropod 3). Since intraspecific variation in size occurs between generations and geographically widespread populations, differences in this character, especially minor ones, are of limited diagnostic value. However, it is important for comparative purposes.

**Head region.**—For most species, the lateral lobe of head is broadly rounded anteriorly without an inferior sinus. For a few species, especially *C. hobbsi* and *C. grandimanus*, the lateral lobe is slightly concave with a distinct inferior sinus as seen in typical *Stygobromus* species.

Eyes can be very large and ovate or irregular in shape to very small and rounded for surface species, or reduced to a few specks or totally absent for stygobiont species. The presence or absence of eyes and their shape and size are very good diagnostic characters for some species, but they are also variable in others, especially for species with both surface and subterranean populations. The eyes of subterranean populations are reduced in different degrees. This can be easily observed in *C. setodactylus* and *C. floridanus*.

**Antenna 1.**—Peduncular segment 1 is always stout and slightly longer or subequal to peduncular segment 2, which is about 1.5 times longer than peduncular segment 3. However in *C. grandimanus* peduncular segment 2 seems elongated and about 2 times longer than peduncle 2. The number of segments of the flagellum varies between large and small specimens and different populations and hence has little diagnostic value. But it is interesting to note that for most species the range of the number of flagellar segments is from 20-27. For a few species, such as *C. dearofi*, *C. grandimanus*, *C. forbesi* the number of segments may reach 36. For them the longer flagellum is a diagnostic character.

**Antenna 2.**—The length and distribution of marginal clusters of setae on peduncle segments 4 and 5 has no diagnostic value for most species. However, they are can be very densely distributed and have little variation for a few species such as *C. dearofi* and *C. forbesi*. Peduncular segment 4 is slightly longer than peduncle 5 except in *C. grandimanus*, in which it becomes much longer and is a diagnostic character for that species.

**Mandibles.**—The terminology used to describe the setae configuration of segment 3 of palp is according to Stock (1974). The presence (or absence) and number of A-setae and B-setae is diagnostic of species groups. Three states can be recognized: with several A and several B setae, with several A and 1-2
B setae and with only 1-2 A setae.

Maxilla 1.—The number of apical plumose setae of inner plate is a diagnostic character of species group and species. Although the number can vary between specimens, the range of the variation was found to be very small: 1-2 less or more setae. The number is from 3 in some species to more than 10 in others.

Maxilla 2.—The number of plumose setae on the inner margin of inner plate is a very good diagnostic character of species groups and species. Like the apical plumose setae of the inner plate of maxilla 1, the intraspecific variation is very small. The number is from 1 in some species to more than 10 in others. In many species the plumose setae are in an oblique row.

Maxilliped.—The outer lobe of maxilliped has a row of small slender spines on the inner margin but the number is variable. For most species these spines are pectinate but for a few species (C. dearolfi, C. hubrichti and C. serratus) they are not. Inner lobe apical setae and spine shape and number are also variable. The outer lobe is distinctly higher than the inner lobe, except in C. hubbsi, in which it is just slightly higher than the inner lobe.

The ratio of the nail length versus the dactyl length of the palp is diagnostic for species groups. The range of the ratio is from 0.17 to 0.50, but for most species it is about 0.33. The number of setae on the inner margin is highly variable in some species, although it is about 2-3 for most species, or 4-5 for others. In C. forbesi it is always 6-9. Besides setae, 3-4 spine teeth are also on the inner margin of the dactyl in C. insolitus. The number of setae on the outer margin of the dactyl is always 1, except for C. dearolfi which has about 4.

Gnathopods I and 2.—The shape and size of the propod and carpus, shape of the spine teeth, and the arrangement of superior medial setae are very good diagnostic characters of species groups and species. Three states are easily recognized: (1) The propod is broader and longer and 2 or more times larger than carpus, the palmar margin is strongly oblique and longer than the posterior margin and armed with "normal" notched spine teeth, the anterior margin is always more than 2 times longer than posterior margin, and most superior medial setae are inserted in groups of setae 2-5. The posterior margin of the carpus is short and always less than half as long as the anterior margin. (2) The propod is slightly broader than the carpus, which is 1/2 to 3/4 the length of the propod, the palmar margin is always slightly oblique and shorter than the posterior margin and armed with "normal" notched spine teeth or simple spine teeth, the anterior margin is not significantly longer than the posterior margin, and the superior medial setae are singly inserted. The posterior margin of the carpus is always longer than half the length of the anterior margin. (3) The propod and carpus are both long and slender, the same width as the other segments of gnathopods, the carpus may even be longer than the propod. The palmar margin is much shorter than the posterior margin and armed with simple spine teeth or symmetrically notched, slender spine teeth. The posterior margin of both propod and carpus are armed with many groups of very long setae.

The kind of spine teeth and their arrangement on the defining angle are strongly diagnostic for species groups and species but also very difficult to observe. The notched-serrate spine tooth is found there for
many species but absent for others. For some species at the end of the outside of the defining angle there is a large strongly notched or simple spine tooth.

The palmar margin of the propod is straight, convex or concave. The posterior margin of the propod always bears several groups (3-7) of setae, but in *C. forbesi* the number of groups is about 10.

The dactyl has one tooth at the base of the nail but it may have more teeth along the inner margin, a diagnostic character of the *shoemakeri* groups. The number of setae on the outer margin of the dactyl is diagnostic for species.

Pereopods 3-7.—The number of setae along the coxal margins are described and are good characters for some species. The posterior margin of the bases of pereopod 5-7 have serrations that range from very shallow (e.g. *C. anomalus*) to deep (e.g. *C. richmondensis*) to very deep (e.g. *C. serratus*) and is characteristic for many species. The number of serrations is diagnostic for some species.

The number of setae on the anteroproximal margin of the bases of pereopod 5-7 is highly variable but in a few species there are no setae here, which is a characteristic for them. The posterior margins of the bases of pereopods 5-7 in *C. anomalus* are greatly expanded, which easily distinguishes it from other species.

The coxal gills of pereopods 3-6 are attached to the inside of the coxae. However, that of pereopod 7 actually originates from the thin membrane between the coxa and the basis, thus it is not a true coxal gill as the older literature suggests.

Pleonal plates I-3.—The presence or absence of subventral spines on pleonal plate 1 and the total number of these spines on pleonal plate 2 and 3 are important characters of species groups and species. The distoposterior corner can be produced and acute or not produced and round (although in some cases the precise condition is very difficult to determine). In some species the corner varies from slightly produced to very produced. The number and arrangement of the setae on the posterior margins are very important characteristics for species. Ventral spines and setae are found in *C. insolitus*.

Pleopod 1.—The presence or absence of setae along the posterior margin of peduncle is characteristics of species groups. The number of retinaculae for most species is 2 but it can up to 6 and is a good characteristic of species groups.

Uropods 1-2.—The total number of spines on the peduncle and inner and outer rami are described. The number of spines on the peduncle of uropod 1 is diagnostic for some species. Tiny basofacial-like spines are found on the peduncle of uropod 1 in *C. insolitus*. Although this is the first recorded occurrence of this structure in the Crangonyctidae, these spines are much smaller and situated lower on the peduncle than in other groups of amphipods (such as the hadziids). However, because they are unique in *Crangonyx*, they are a useful diagnostic character for this species.

Uropod 3.—The ratio of outer ramus length versus peduncle length is diagnostic for species groups. The number of spine groups on the inner ano outer margin of the outer ramus is characteristic of some species.
Telson.—The shape of the telson and the number of apical spines are diagnostic for species groups and individual species. The depth of the apical notch or cleft is highly variable in some species but also more constant in others. The presence of dorsal and lateral spines is a characteristic of C. aberrans. In C. serratus, dorsal spines are found in the middle of the long, deeply cleft telson.

Male:

Body length.—When mature, males are almost always smaller and slimmer than females. This may be due to the fact that the male does not need to carry eggs for development. However in C. anomalus some males are longer than the longest females and have the same body shape.

Antenna 2.—Calceoli are present on peduncle segments 4 and 5 and the first several flagellar segments, excepting males of C. hobbsi and C. caecus. The absence of calceoli is characteristic of these two species.

Gnathopods 1 and 2.—The propod is always much broader and more than 2 times longer and larger than the carpus, but in C. hobbsi and C. longicarpus the propod is not broader and just slightly longer and larger than carpus, which becomes longer. The palmar margin of the propod is armed with notched spines, except in C. huculispina in which the spines are rod-like. The sexual dimorphism of gnathopods is an important diagnostic character for species groups.

Uropod 2.—Along with comparatively small body size, calceoli on antenna 2 and proportionately larger gnathopods, a sexually dimorphic uropod 2 has proven to be the most important diagnostic character for species. The outer ramus is typically curved laterally to backward in mature males and also often reduced in size. Significant interspecific variation is found in the arrangement of spine shape and number of spines on the outer ramus. For many species it proved to be the only good character for accurate identification.
CHAPTER III

PHYLOGENETIC ANALYSIS

CHARACTERS AND CHOICE OF OUTGROUP

The cladistic analysis of *Crangonyx* is based on 26 characters (Tables I. 2). The characters chosen are based on morphological analysis and comparison with outgroup species, which has shown them to have phylogenetic significance.

The phylogeny of Crangonyctidae was first investigated by Holsinger (1986) and amended by him in 1994 using cladistic analysis. According to Holsinger’s (1994) phylogenetic hypothesis, among the 6 extant genera, *Crangonyx*, *Synurella* and *Lyurella* have a common ancestor by virtue of a single synapomorphy: lateral lobe of head broadly rounded with inferior sinus indistinct. *Crangonyx* is in turn separated from the common ancestor of *Lyurella* and *Synurella* by having an autapomorphy: uropod 3 has a very small inner ramus and the outer ramus is longer than the peduncle. On the other branch are three subterranean genera: *Bactrurus*, *Stygobromus* and *Stygonyx*. They are united by five synapomorphies. Pseudocrangonyctidae, which consists of *Procrangonyx* and *Pseudocrangonyx* and is apparently closely related to Crangonyctidae, is the outgroup in the Holsinger (1994) study. I accept Holsinger’s (1994) phylogenetic hypothesis about Crangonyctidae and chose the outgroup of *Crangonyx* based on it. The first outgroup of *Crangonyx* is *Synurella* and the second outgroup consists of *Stygobromus* and *Stygonyx*.

*Synurella* includes 18 species (Holsinger, 1977), and like *Crangonyx* it occurs in both Eurasia and North America. Three epigean species occur in the eastern United States and specimens of these species were examined. The morphology of *Synurella* is very similar to *Crangonyx*. *Lyurella* contains only one species, *L. hyrcana*, which is known only from two freshwater springs near the southwestern end of the Caspian Sea in the Talish region of Russia.

Since the phylogeny of *Synurella* and *Lyurella* was not known at the present time, character states must be extracted from literature for these two genera. Many species of *Synurella* and *Lyurella* are poorly described, and considerable variation of character states exists. The polarity of character states cannot be completely determined by the rules set by Maddison and Maddison (1984). This is not a rare case. The polarity of only a few characters can be positively determined. For other characters, they can be polarized by a program according to the most parsimonious solution.

In my analysis, all 26 characters were initially left unordered. The most reliable criterion for the transformation series is the cladogram itself and the congruence with other characters. The character state transformations are the outcome of the analysis, and not a prior assumption (Swofford, 1991).

Qualitative, discontinuous quantitative and continuous quantitative characters are used in this analysis. Qualitative characters are based on presence or absence, or on differences in shape. Discontinuous
Table 1. Characters and character states used in the phylogenetic analysis of *Crangonyx* species from North America. Based on mature males and females.

<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
<th>0</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Mandible: segment 3 of palp</td>
<td>with more than 2 A and 2 B setae</td>
<td>with 1-2 A and/or 1-2 B setae only</td>
<td>0</td>
</tr>
<tr>
<td>2. Maxilla 1: number of apical plumose setae on inner plate</td>
<td>&gt; 3</td>
<td>2-3</td>
<td>0</td>
</tr>
<tr>
<td>3. Maxilla 2: number of plumose setae on inner face of inner plate</td>
<td>&gt; 3</td>
<td>1-3</td>
<td>0</td>
</tr>
<tr>
<td>4. Maxillipede: ratio of nail length: dactyl length of palp</td>
<td>0.33-0.50</td>
<td>0.20-0.25</td>
<td>0</td>
</tr>
<tr>
<td>5. Gnathopod 1 of female: spine teeth on palmar margin of propod</td>
<td>notched</td>
<td>symmetrically notched</td>
<td>0</td>
</tr>
<tr>
<td>6. Gnathopod 1 of female: defining angle of propod with strongly notched-serrate and/or serrate spine teeth</td>
<td>present</td>
<td>absent</td>
<td>0</td>
</tr>
<tr>
<td>7. Gnathopod 1 of female: teeth on inner margin of dactyl of propod and 1 tooth near the nail</td>
<td>with no other teeth</td>
<td>with a row of teeth or 1 to several teeth</td>
<td>0</td>
</tr>
<tr>
<td>8. Gnathopod 1 of female: propod 2 times or more larger than carpus</td>
<td>no</td>
<td>yes</td>
<td>0</td>
</tr>
<tr>
<td>9. Gnathopod 1 of female: number of superior medial setae per set</td>
<td>more than 2 setae</td>
<td>typically 1 seta only</td>
<td>0</td>
</tr>
<tr>
<td>10. Male and female with sexually dimorphic gnathopod 1</td>
<td>present</td>
<td>absent</td>
<td>0</td>
</tr>
<tr>
<td>11. Gnathopod 2 of female: spine teeth on palmar margin of propod</td>
<td>notched</td>
<td>symmetrically notched</td>
<td>0</td>
</tr>
<tr>
<td>12. Gnathopod 2 of female: propod 2 times or more larger than carpus</td>
<td>no</td>
<td>yes</td>
<td>0</td>
</tr>
</tbody>
</table>

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Table 1. continued

13. Gnathopod 2 of female: defining angle of propod with very distinctive notched-serrate and/or serrate spine teeth
   0: absent
   1: present

14. Gnathopod 2 of female: teeth on inner margin of dactyl of propod and 1 tooth near the nail
   0: with no other teeth
   1: with a row of teeth or 1 to several teeth

15. Male and female with sexually dimorphic gnathopod 2
   0: present
   1: absent

16. Gnathopod 2 of female: number of superior medial setae per set
   0: consists more than 2 setae
   1: mostly consists 1 seta only

17. Gnathopod 2 of female: palmar margin with 2 or more rows of spine teeth per side or with more than 20 notched spine teeth per side
   0: absent
   1: present

18. Gnathopods of female: carpus slender, subequal or longer than propod
   0: no
   1: yes

19. Pleopod 1 of female: many setae along posterior margin of peduncle
   0: present
   1: absent

20. Pleopod 1 of female: number of retinaculae
   0: = 2
   1: > 2

21. Telson of female: number of spines on each lobe
   0: > 4
   1: = 4

22. Gnathopod 1 of male: defining angle of propod with notched-serrate and/or serrate spine teeth
   0: present
   1: absent

23. Gnathopod 2 of male: defining angle and palmar margin of propod with the similar spine teeth
   0: yes
   1: no

24. Gnathopods of male: spine teeth on palmar margin of propod
   0: notched
   1: mostly simple
   2: rod-like and unnotched

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Table 1. continued

25. Outer ramus of male uropod 2 with comb spines
   0: absent
   1: present

26. Gnathopod 1 of male and female: defining angle with 1 row of spines on inside and 2 rows of non-serrate spine teeth on outside
   0: absent
   1: present
Table 2. Character matrix for the species of Crangonyx from North America.

<table>
<thead>
<tr>
<th>Character</th>
<th>Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>00000 00001 11111 11112 22222 2</td>
</tr>
<tr>
<td></td>
<td>12345 67890 12345 67890 12345 6</td>
</tr>
</tbody>
</table>

Synurella aberrans 00000 00000 00000 00000 00000 0
aberrans          10000 01010 00110 10000 11001 0
acicularis        10002 00010 20100 10000 11100 0
aka               10002 00010 20100 10000 11000 0
anomalus          00010 10101 01101 01011 00000 1
antennatus        10000 01111 01001 10000 10000 0
baculispina       10002 00010 20000 10100 10120 0
barbi             10002 00010 20100 10000 11100 0
housfieldi        10000 00010 00100 10000 10000 0
castellanum       10002 00010 20100 10000 11000 0
caeus             10002 00010 20100 10000 11100 0
consimilis        10002 00010 20100 10000 11101 0
cooperi           10000 00010 00100 10000 11100 0
cornutus          00010 10101 01001 00111 00001 1
dearolfi          01110 10101 01001 01011 00000 1
disjunctus        00110 10101 01001 01011 01000 0
floridanus        10002 00010 20100 10000 11101 0
fontinalis        10000 00010 00100 10000 10000 0
forbesi           00000 00101 01001 01011 01000 0
gracilis          10002 00010 20100 10000 11100 0
grandimanus       01110 10101 01001 01011 01000 0
hobbsi            10002 00010 20100 10100 11110 0
hubrichti         01110 10101 01001 01011 01111 0
indianensis       00110 10101 01001 01011 11110 1
insolitus         00000 00111 00001 00111 01000 0
lewisi            10000 00010 00100 10000 11000 0
longicarpus       10001 10010 10000 11110 10000 0
longidactylus     10002 00010 20100 10000 11101 0
minor             10000 01010 00110 10000 11000 0
montanus          10002 00010 20100 10000 11100 0
obliquus          11110 10100 01001 01011 00000 1
ohioensis         10002 00010 20100 10000 11100 0
orientalis        10000 00010 00100 10000 11001 0
packardi          10002 10010 20000 10000 10000 0
polustris         10002 00010 20100 10000 11000 0
pseudogracilis    10002 00010 20100 10000 11101 0
richmondensis     11110 10101 01001 01011 10000 1
rivularis         10002 00010 20100 10000 11100 0
serratus          00000 00101 01001 10000 10000 0
setodactylus      10000 01010 00110 10000 11000 0
shoemakeri        10000 01010 00110 10000 11001 0
specus            10000 00101 01101 10000 11100 0
stagnicolous      10002 00010 20100 10000 11100 0

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quantitative characters are based on counts of spines or setae. Continuous quantitative characters are based on relative length of appendages. As in the Notenboom (1988) and Stewart and Griffiths (1995) cladistic studies of freshwater amphipods, ratios and counts are included in this study. As Stewart and Griffiths (1995) stated: "These characters avoided the use of subjective character state definitions, and were needed because of the shortage of usable characters." Like the above two studies, when coding these data, care was taken to identify a clear gap.

RESULTS OF PHYLOGENETIC ANALYSIS AND DISCUSSION

The Wagner parsimony produced 18 most parsimonious trees and the Fitch parsimony produced 45 trees. The consensus tree of both methods are given (Figs. 1-2). Using MacClade to analyze the character transformation of these two consensus trees reveals only three differences. In Wagner parsimony, for characters 5, 11 and 24, state 0 can only transform to either state 1 or 2, and states 1 and 2 can transform to each other. In Fitch parsimony, for characters 5 and 11, state 0 can only transform to 2, and 2 can only transform to 1. For character 24, state 0 can either transform to 1 or 2 and no other changes are allowed.

For character 5 and 11, my hypothesis is that the state 0 can transform to 1 and 2, and no other transformations are allowed. It is similar to that of Wagner parsimony but excludes the possibility that state 1 can transform to 2 or vice versa. State 2 of character 5 and 11 is palmar margin of female gnathopod propod with slender symmetrical spine teeth. Since only one species, *C. longicarpus*, which is found only on the Coastal Plain of Virginia and North Carolina, has this character, it is probable that this character is not in the evolutionary intermediate stage between notched spine teeth and simple spine teeth. If this is the case, as Fitch parsimony suggests, many species with this character should be found further inland.

For character 24, the transformation of Fitch parsimony seems reasonable, since both states 1 and 2 are believed to have evolved directly from state 0, and the species with this state may very well be separated from each other.

Because of these three character transformation differences, we get two different consensus trees (Figs 1-2). Despite the difference, both trees bear many similarities, with several of the same species groups well defined in both trees. Both trees define the *shoemakeri* group by characters 7 and 14, the *richmondensis* group by characters 4, 6, 8 and 10, and the *gracilis* group by characters 5 and 11. Although we do get some well defined species groups, we can see from both consensus trees that phylogenetic relationship between some of the groups and species in these groups still cannot be solved by this analysis. This is the case because of the many difficulties mentioned earlier as being inherent in species level phylogenetics of *Crangonyx*idae.

Based on the two consensus trees and a prior assumption based on observation of species of *Crangonyx* species, I selected the hypothesis phylogenetic tree of *Crangonyx* species of North America shown in figure 3. The hypothesis tree is one step more than the consensus tree of Wagner parsimony and
Figure 1.—Consensus tree from cladistic analysis of North America Crangonyx using Wagner parsimony. Tree length (TL) = 57; CI = 0.51. Underlined characters indicate a reversal of that character.
Figure 2.—Consensus tree from cladistic analysis of North America _Crangonyx_ using Fitch parsimony. TL = 55; CI = 0.53. Underlined characters indicate a reversal of that character.

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Figure 3.—The phylogenetic hypothesis of North America *Crangonyx* based on the two consensus trees (Figs. 1-2) and the observations of *Crangonyx* species. TL = 58; CI = 0.53. Underlined characters indicate a reversal of that character.
3 steps more than that of Fitch parsimony. As in the above two consensus trees, only species groups or subgroups can be recognized and the phylogenetic relationships of some groups are not clear.

The first branch, which is defined by characters 8, 10, 12 and 15, includes 3 species groups (insolitus, forbesi and richmondensis) and 3 ungrouped species (Crangonyx antennatus, C. serratus, and C. specus). These three species group composes a clade. Characters 8 and 12 in C. insolitus, which are in the plesiomorphic state, may indicate this species is nearer to the ancestor species of the branch than the hypothesis suggests. However characters 16, 19 and 20 place it near the forbesi and richmondensis groups.

The richmondensis group, which is defined by characters 4, and 26, is the most advanced and has the second greatest species diversity of all species groups. It contains 9 species and is represented in a wide variety of freshwater environments: it is the most widely distributed group in North America.

The second branch is defined by character 9 and seems to take an opposite evolutionary path. It includes 3 species groups (shoemakeri, longicarpus and gracilis), and 5 ungrouped species (Crangonyx houstieldi, C. cooperi, C. fontinalis, C. lewisi and C. orientalis). The shoemakeri group and the 5 ungrouped species are at the bottom of this branch. They all have notched spine teeth on palmar margins of gnathopods of the female. This is an ancestral character. Morphologically they are closely similar and the phylogenetic analysis will not separate them into different higher branches. Instead they all come from the same node.

The shoemakeri group is defined by characters 7 and 14 in both Wagner and Fitch parsimony trees but there is a probability that these two characters may also be independently derived. The distribution of four species of shoemakeri group are not continuous and the species differences are greater than with the five ungrouped species. If future studies indicate that this species group is paraphyletic, we may conclude that parsimony methods may not be the best criterion to reveal the phylogenetic relationship among Crangonyx.

The longicarpus species group contains only one known species, C. longicarpus, and is defined by characters 5, 6, 9, 11 and 19. It is an unusual species with very slender, symmetrically notched spine teeth on the gnathopods of the female. It is known only from the Coastal Plain of Virginia and North Carolina. It seems to be an evolutionary end point, derived earlier from the ancestor of the gracilis group prior to the wide distribution of the gracilis group species. As more species of gracilis group evolved, it is possible that C. longicarpus became extinct in many places and is now found only on the Coastal Plain.

The gracilis group is defined by characters 5, 9 and 11 and is the largest species group of Crangonyx: it contains 18 species. The species of the gracilis group are all small in size and the palmar margins of the female gnathopod propods have unnotched spine teeth. These species inhabit a wide variety of freshwater habitats and are widely distributed in North America. The morphological difference between many of the species is very small and species identification depends primarily on the structure of male uropod 2.

Females of many of these species are almost always alike. The cladistic analysis did not reveal any phylogenetic relationship among the gracilis group species, except for a floridanus subgroup that is defined by character 25. Small morphological differences and the lack of a clear phylogenetic relationship...
may suggest that all species evolved from a widely distributed, common ancestor following geographic isolation. However, an alternative hypothesis is that some of the species may not, by strict definition, be truly biological species.
CHAPTER IV

TAXONOMY

FAMILY CRANGONYCTIDAE BOUSFIELD, 1973

Schellenberg (1936) recognized the *Crangonyx* group of the family Gammaridae, which included 15 genera of freshwater amphipods. Following the work of Schellenberg (1936), several workers discussed this group concept and accumulated more knowledge about it (see Holsinger, 1967 and Holsinger, 1977 for more details). Bousfield (1973) erected the family Crangonyctidae to encompass many of the genera which had been assigned previously to the *Crangonyx* group. Holsinger (1977) summarized this family and all genera, including a list of species, distribution and ecology of genera and a key to the genera. Holsinger (1977) recognized 6 genera in the family Crangonyctidae: *Bacturus, Crangonyx, Lyurella, Palaeogammarus, Stygobromus*, and *Synurella*. Subsequently, Bousfield and Holsinger (1989) described the new genus *Stygonyx* and included a new key to the genera of Crangonyctidae.

**Genus Crangonyx** Bate, 1859

*Crangonyx* Bate, 1859

*Eucrangonyx* Stebbing, 1899

Diagnosis.—Uronites free: lateral lobe of head broadly rounded anteriorly without inferior sinus or rarely narrowly rounded with weak inferior antennal sinus; eye relatively large, small or absent. First peduncular segment of antenna 1 subequal in length to second. Antenna 2 of mature male with calceoli except in 2 subterranean species. Outer plate of maxillipeds with stiff setae and small pectinate spines along the inner margin. Lower lip with well developed outer lobes and small, typically indistinct inner lobes. Gnathopods: propod of second larger than first; thin and long rastellate setae present on posterior margin of propod, segment 5 and segment 4 (except 1 species with short thick rastellate setae on posterior margin of segment 5). Coxal plates 1-4 deep, deeper than corresponding body segments, longer than broad. Pereopod 6 longer than 7. Coxal gills rather large, subovate, present on pereopods 3-7, although modified on 7. Single, median sternal gills present on pereonites 2 and 3. Simple paired sternal gills on pereonites 6 and 7 and usually on pleonite 1. Brood plates of sexually mature female typically rather large in size and expanded distally. Pleonal plates: distoanterior corners usually distinct, often produced and acute; posterior margins typically with 1 short seta each, but sometimes up to 3 setae. Uropod 2 sexually dimorphic in mature males with outer ramus reduced and deflected laterally and sometimes curled backward. Uropod 3 biramous: outer ramus 1-segmented, up to 2.5 times length of peduncle, armed...
Figure 4.—Geographic distribution of the genus *Cryptonyctereutes*. Shaded areas in black indicate contiguous distribution; black dots indicate isolated occurrences.
laterally and apically with spines: inner ramus small and scale-like. Telson typically rather short, usually broader than long; apical margin incised from 1/4 to 2/3 distance to base (but seldom more than 1/2); apical lobes with few spines; lateral and dorsal margins typically without spines.

Type-species: *Crangonyx subterraneus* Bate. 1859 by monotypy.

Distribution and ecology. -- The global distribution of *Crangonyx* is shown in figure 4.

Remarks. -- Based on the hypothesized phylogenetic relationship given by Holsinger (1994). *Crangonyx* has a close relationship with *Lyurella* and *Synurella*: united by a single synapomorphy: lateral lobe of head usually broadly round and with inferior antennal sinus usually indistinct. However, the lateral lobe is more narrowly rounded and there is an inferior antennal sinus in at least a few *Crangonyx* species. This is thought to be an apomorphic character that was derived from the ancestral species with broadly rounded lateral lobe. *Crangonyx* can be easily distinguished from *Lyurella* and *Synurella* and other genera of the family Crangonyctidae by the outer ramus of 3rd uropod, which is longer than the peduncle and by the presence of a scale-like inner ramus.

Key to the Species Groups and Ungrouped Species of *Crangonyx* in North America

(based on mature males and females)

1. Palmar margin of gnathopodal propods of female lined with small, weak simple spine teeth: superior medial setae of gnathopodal propod 2 singly inserted ........................................... *gracilis* group

Palmar margin of gnathopodal propods of female lined with distally notched spine teeth: superior medial setae of gnathopodal propod 2 in transverse rows of 1, 2, 3 or more ................................................................. 2

2. Inner margin of gnathopodal dactyls of female armed with blade-like teeth ........................................... *shoemakeri* group

Inner margin of gnathopodal dactyls of female without blade-like teeth except one near the nail ............... 3

3. Carpus and propod of gnathopods of female very long: carpus equal to or longer than propod palmar margin of gnathopodal propods of female lined with slender, symmetrically notched spine teeth ...................................................................................................................................... *longicarpus* group

Carpus and propod not elongate: carpus shorter than propod: palmar margin lined with thick, non-symmetrically notched spine teeth ................................................................................................................. 4

4. Bases of pereopods 5-7. posterior margins deeply serrate; telson of female much longer than broad, notched up to 2/3 distance to base, with dorsal spines ................................................................. *C. serratus* Bases of pereopods 5-7. posterior margins not deeply serrate: telson longer than broad or border than long, notched up to 1/2 distance to base, without dorsal spines ........................................................................................................... 5

5. Superior medial setae of gnathopod 2 usually singly inserted ................................................................. 8

Superior medial setae usually inserted in groups of 2 or more setae ................................................................................................................. 6

6. Gnathopods 1 and 2: propod more than 2 times larger than carpus, lacking notched-serrate and/or serrate

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spine teeth on defining angle..................................................richmondensis group
Gnathopod 1 and 2: propod up to 2 times larger than carpus; with notched-serrate and/or serrate spine
teeth on defining angle..........................................................7

7. Ventral margin of female pleonal plates with spines and setae: peduncles of female uropods 1 and 2 of
with small spines on ventral side..........................................insolitus group
Ventral margin of female pleonal plates lacking spines and setae; spines absent from the ventral side of
peduncles of female uropods 1 and 2......................................forbesi group

8. Outer ramus of male uropod 2 with comb spines........................................C. orientalis
Outer ramus of male uropod 2 without comb spines..........................................................9

9. Posterior margins of pleonal plates with 2-3 setae, and 1 seta barely above distoposterior corner
.............................................................................................................C. housfieldi
Posterior margins of pleonal plates with 1 seta located well above distoposterior corner...............10

10. Propod of female gnathopod 2 with 1 very large spine on outer margin at end of defining angle
.............................................................................................................11
Propod of female gnathopod 2 with 1 large and 1 or more small spines on outer margin at end of
defining angle........................................................................13

11. Outer ramus of male uropod 2 with 3-5 spines clumped near distomedially, forming a comb spine row:
palmar margin of propods of female gnathopods strongly oblique........................................C. antennatus
Outer ramus of male uropod 2 with spines not distomedial; palmar margin of propods of female
gnathopods not very oblique......................................................12

12. Outer ramus of male uropod 2 with 5 evenly distributed spines medially, lateral margin with more than
5 spines......................................................................................C. fontinalis
Outer ramus of uropod 2 of male with 1-2 spines..................................................C. specus

13. Outer ramus of male uropod 2 with 1-2 spines distomedial, lateral margin with more than 5
spines evenly distributed.........................................................C. lewesi
Outer ramus of male uropod 2 of male with very thin spines (setal-like)...............................C. coopen

The shoemakeri Group

Diagnosis.--Adult size range ca. 10.0-17.0 mm. Palm of female gnathopod propods armed with large
notched spine teeth, superior medial setae singly inserted. Gnathopods 1 and 2 sexually dimorphic: propod
of gnathopods 1 and 2 of female not 2 times larger or longer than carpus, inside of defining angle with
notched-serrate spine teeth, outside with serrate spine teeth, inside margin of dactyl armed with blade-like
teeth forming a row, length of palm shorter than posterior margin. Male gnathopod propods larger and
wider, carpus smaller and narrower, propod more than 2 times larger than carpus and much broader,
defining angle of gnathopod 1 of male with notched-serrate spine teeth, defining angle of propod of

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Figure 5.--Geographic distribution of the *shoemakeri* group in North America. Shaded areas denote areas of contiguous or near contiguous distribution.
gnathopod 2 with same type spine teeth as on palm, palm length longer than posterior margin, inner margin of dactyl lacking teeth. Uropod 3 of female shorter.

Remarks.—The *shoemakeri* group is composed of four species, with disjunct distributions in New England, Maryland-Virginia, and the east-central US (fig. 5).

Key to the Species of the *shoemakeri* group

1. Inner margin of dactyls of pereopods 3-7 with 2-3 setae; palm of female gnathopod propods not concave

   ............................................................................................................................................................... *C. setodactylus*

   Inner margin of dactyl of pereopods 3-7 with 1 seta; palm of female gnathopod propods slightly
to distinctly concave............................................................................................................................................... 2

2. Inner margin of dactyl of female gnathopods with a row of blade-like teeth; telson with apical spines

   only.............................................................................................................................................................................. *C. aberrans*

   Inner margin of dactyl of female gnathopods with few teeth, not forming a row; telson with dorsal
   and/or lateral spines.................................................................................................................................................

3. Outer ramus of male uropod 2 with comb spines............................................................................. *C. shoemakeri*

   Outer ramus of male uropod 2 without comb spines, bearing several short spines only......................... *C. minor*

*Crangonyx shoemakeri* (Hubricht and Mackin)

Figures 6-10

*Eucrangonyx shoemakeri* Hubricht & Mackin, 1940:198, fig. 6 [in part] [type-locality: pools along the

*Crangonyx shoemakeri* (Hubricht & Mackin).—Bousfield, 1958:95-96.—Holsinger, 1972:47, figs. 12a, 12c,
Hubricht, 1943:690-691.—Kenk, 1949:48.—Cole, 1957:36, fig. 2f]

Material examined.—WASHINGTON D.C.: Burleith Woods in Georgetown, numerous specimens in
approximately 23 collections (USNM) from small streams, springs and bogs. W. H. Ball, N. Blandford, D.
Padgett, and A. Pizzini (the majority), 1934-1939; Chain Bridge area near Potomac River, numerous
specimens in approximately 20 collections (USNM) from mostly pools and ponds. W. D. Appel, W. H.
Wood. 1894-1941; Wetzel's Spring and immediate vicinity (Georgetown), numerous specimens in
approximately 34 collections (USNM), L. Hubricht, A. Pizzini (the majority), and A. Shansey; other D. C.
localities, including Georgetown, Kenilworth, Montrose Park, National Zoological Park, and Oxon Run.
Figure 6. *Euryonyx showakeri* (Hubricht and Mackin). Male cotype (8.5 mm), entire animal from left side, temporary pools along Potomac River, 3.2 km NW of Georgetown, Washington, D.C.
Figure 7.—*Crangonyx shoemakeri* (Hubricht and Mackin). Female cotype (12.5 mm), temporary pools along Potomac River, 3.2 km NW of Georgetown, Washington, D. C.: a. antenna 1; b, c. maxillae 1, 2; d, lower lip; e. left mandible; f. inner and outer plates of maxilliped (greatly enlarged); g, h. gnathopods 1, 2 (palmar margins enlarged).
Figure 8.—Crangonyx shoemakeri (Hubricht and Mackin). Female cotype (12.5 mm), temporary pools along Potomac River, 3.2 km NW of Georgetown, Washington, D. C.: a, b, c, d, pereopods 3, 4, 5, 6 (in part); e, pereopod 7; f, pleonal plates; g, h, i, uropods 1, 2, 3; j, telson.
Figure 9.—*Crangonyx shoemakeri* (Hubricht and Mackin). Male cotype (6.4 mm), temporary pools along Potomac River, 3.2 km NW of Georgetown, Washington, D. C.: a, antenna 2; b, c, gnathopods 1, 2 (palmar margins enlarged); d, e, f, uropods 1, 2, 3; g, telson.
Figure 10.—Distribution of *Crangonyx shoemakeri* in North America. Solid circles represent 1-6 closely proximate localities.


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collections (JRH) from seeps and small springs. P. H. Stevenson. April-May 1993: Culpepper Co.: flood pool, Rappahannock River. 5 ⋆, 1 ♀. A. Weaver. 26 Mar 1967: small swamp 8.0 km E of Amisville. 28 specs (5 ⋆, 2 ♀), collector not given. 10 May 1940 (USNM): Dinwiddie Co.: old well, 20 km WSW of Darvils. 1 ⋆, P. H. Stevenson. 29 Mar 1993: Fairfax Co.: Dyke (habitat not given). 2 ⋆, W. D. Appel. 18 Feb 1911 (USNM); swamp near Mount Vernon. 4 ⋆, 1 ♂. W. S. Webb. 22 Apr 1917 (USNM): tiny spring and run 3.2 km ESE of Fairfax. 2 ⋆, 10 ♂, 6 juvs. J. R. Holsinger et al., 13 Jul 1967: spring on Dogue Creek. 29 specs (10 ⋆, ♀). P. Opler. 23 Nov 1978: spring in Fairfax Co. (specific location not given). 12 ⋆, A. Pizzini. 12 Nov 1949 (USNM); pool below spring, Annandale. 1 ⋆, W. H. Ball. 19 Nov 1940 (USNM); stagnant pond between Aqueduct Bridge and Chain Bridge. 25 specs (5 ⋆, ♀), G. W. Gill. 3 Apr 1913 (USNM); small pools between Belle Haven and Dyke. 2 ⋆, 3 ♀. W. H. Ball. 14 Apr 1935 (USNM): Black Pond area, 3 collections (USNM) from ponds. H. S. Barber and C. R. Shoemaker. 1915 and 1929: Capt. Hickory Creek-Forestville area, 4 collections (USNM) from spring and streams. A. Pizzini. Feb.-Mar. 1947: muck hole 1.6 km W of Centreville, 2 ♀, collector not given. 10 May 1940 (USNM); small pool 1.6 km below Chain Bridge. 10 ⋆, 2 ♀. A. Pizzini. 4 Nov 1934 (USNM); Choppawamsic Park near Quantico, 3 collections (USNM) from spring and bog. A. Pizzini. Mar and May 1947; small spring in Colchesler. 4 ⋆, 1 ♀. W. H. Ball. 24 Dec 1934 (USNM); Difficult Run between Leesburg Rd and Potomac River. 5 ⋆, 3 ♀, 2 juvs. W. H. Ball. 4 Feb 1940 (USNM); small stream on hillside in open woods near Difficult Run. 6 ⋆, 3 ♀, 1 juv. W. H. Ball. 30 Dec 1934 (USNM); small pond near Difficult Run. 1 ⋆, C. R. Shoemaker and W. D. Appel. 10 Dec 1911 (USNM); pool in woods at Dyke. 1 juv. W. H. Ball. 7 Apr 1934 (USNM): stream source 1.6 km S of Forestville, 8 ⋆, A. Pizzini. 8 Mar 1947 (USNM); spring seepage tributary off W side of swamp trail, 0.5 km NNE of Fairview. 20 specs (8 ⋆, ♀, 7 juvs). C. S. Hobson. 8 Apr 1994: Great Falls area, 4 collections (USNM) from seeps, ponds and pools. H. S. Barber and C. R. Shoemaker. 1924-1934, and 3 collections (JRH). C. S. Hobson. 1994; pond ca. 1.6 km W of McLean. 8 ⋆, 1 ♀. A. Pizzini. 6 Feb 1938 (USNM); Packard Creek on R. S. Bray property. Fairfax City. 6 ⋆, 1 ♀, 7 juvs. R. S. Bray. 12 Jul 1941 (USNM); Scott Run and immediate vicinity, numerous specimens in approximately 15 collections (USNM) from springs and small streams, mostly by A. Pizzini. 1935-1939, and 2 collections (JRH) from springs. J. R. Holsinger. A. Pizzini and M. Straskraba. 1965-1967; stream near Trammel's Landing above Great Falls. 25 specs (8 ⋆, ♀). A. Pizzini. 28 Mar 1938 (USNM); Hanover Co.: railroad pond, 2 mi N of Ashland. 1 ⋆, L. Hubricht. 1 Apr 1950 (USNM); Henrico Co.: small stream 1.6 km N of Bryan Park. Richmond. 10 ⋆, 3 ♀. L. Hubricht. 8 May 1944 (USNM); Loudon Co.: spring 1.6 km N of Leesburg. 1 ⋆, 2 ♀. J. C. Bridewell. 20 Apr 1939 (USNM); Middleburg: 2 collections (USNM) from stream and spring bog. A. Pizzini. 1938-1939, and 1 collection (JRH) from bog. J. R. Holsinger. May 1965; Madison Co.: spring on Double Top Mountain, Syria. 15 ⋆, 3 ♀, T. Ulke. 25 Aug 1935 (USNM); spring at Syria. 11 ⋆, 2 ♀, 2 juvs. A. Pizzini. 4 Sep 1938 (USNM); New Kent Co.: seep and small stream in Crump Swamp. 24 km E of Richmond. 12 ⋆, 4 ♀. 1 juv. J. R. Holsinger. 23 Apr 1970 and 21 ⋆, 8 ♀, 2 juvs. 19 Mar 1972: Nottoway Co.: small pond 1.8 km NE of Birch Lake and 3 ⋆. P. H. Stevenson. 29 Mar 1993: Prince William Co.: stream along
Occoquan Creek near Hoadly P.O., just below mouth of Bull Run. 10♀, 2♂, 1 juvs. W. H. Ball. 30 Nov 1940 (USNM); Rappahannock Co.: small swamp, 4.8 km W of Washington. 6♀, 1♂. T. K. Ellis. 11 May 1940 (USNM).

Diagnosis.—Distinguished from *C. setodactylus* and *C. minor* by having comb spines on the outer ramus of uropod 2 of male and from *C. aberrans* by lacking dorsal and lateral spines on telson, having more plumose setae on inner surface of inner plate of maxilla 2, more setae on inner margin of dactyl of maxilliped palp and on ventral margin of coxa of pereopod 7. Largest male, 9.5 mm; largest female, 13.5 mm.

Female.—Eye small and round. Antenna 1, 55-57 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with up to 27 segments. Antenna 2, flagellum with up to 9 segments. Mandibles subequal, spine row with about 5 spines; segment 2 of palp with about 7 long setae, segment 3 with 1 A seta, 3 C setae. 4 E setae and a row of D setae, lacking B-seta. Maxilla 1: inner plate with 4-5 apical plumose setae; palp with 5-6 slender spines on apex. Maxilla 2, inner plate with oblique row of 5-7 plumose setae on inner margin. Maxilliped: inner plate apically with 2 bladelike spines, 5 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 3-4 slender pectinate spines on inner margin and 1 apical plumose seta; dactyl with 4-5 setae along inner margin; dactyl nail very long, about 1/3 length of dactyl.

Propod of gnathopod 1 slightly less 2 times longer than carpus; palm concave in middle, subequal in length to posterior margin, with 11 spine teeth on inside, 11 on outside; defining angle with 5 notched-serrate spine teeth on inside, 1 large notched and 3 serrate spine teeth on outside; posterior margin with about 4 sets of setae inserted in groups of 2-5. Dactyl of gnathopod 1 with row of about 9 short setae and 14 blade-like teeth along inferior margin; nail short. Ventral margin of coxa 1 with 16 setae.

Propod of gnathopod 2 about 2 times longer than carpus; palm concave, shorter than posterior margin, with 13 spine teeth on inside, 4 on outside; defining angle with 1 large notched spine tooth and 2 serrate spine teeth on outside. 5 notched-serrate spine teeth on inside: superior medial setae singly inserted; posterior margin with 5 sets of setae in groups of 2-6. Dactyl of gnathopod 2 with row of 9 short setae and 12 blade-like teeth along inferior margin; dactyl nail short. Ventral margin of coxa 2 with 15 setae.

Coxa of pereopod 3 with 12 marginal setae. Coxa of pereopod 4 with 19 marginal setae; dactyl of pereopod 4 about 35 percent length of propod. Pereopod 5: basis with 15 shallow serrations along posterior margin, 9 sets of short spines in groups of 1-3 on anterior margin. 3 long setae on anteroproximal margin. Pereopod 6: basis with 16 shallow serrations along posterior margin, 8 sets of short spines on anterior margin, 4 setae on anteroproximal margin. Pereopod 7: coxa with 5 setae along the posterior margin; basis with 20 shallow serrations along posterior margin, 10 sets of short spines on anterior margin; dactyl about 30 percent length of propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner acute but not produced; posterior margin of plate 2 nearly straight, with 1 seta, distoposterior corner produced and
acute, ventral margin with 4 (subventral) spines; posterior margin of plate 3 nearly straight, with 1 seta. distoposterior corner neither produced nor acute, ventral margin with 5 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outer margin.

Uropod 1: inner ramus about 65 percent length of peduncle, armed with about 13 spines; outer ramus with about 12 spines; peduncle with row of 12 outer and 1 inner spines. Uropod 2: inner ramus subequal in length to peduncle, armed with about 15 spines; outer ramus with about 13 spines; peduncle with 6 outer and 3 inner spines. Uropod 3: inner ramus with 1 spine; outer ramus about 1.5 times longer than peduncle, inner and outer margins each with 3-4 sets of spines in groups of 1-3. Telson slightly broader than long, notched about 1/5 distance to base; each lobe with 3-4 apical spines, which are less than 1/2 length of telson.

Male.—Differing from female as follows: smaller size, but with approximately same body shape. Antenna 2: calceoli present on peduncular segments 4 and 5 and first 2-5 segments of flagellum.

Propod of gnathopod 1 proportionately much broader than and 2 times longer than carpus; palm slightly concave, shorter than posterior margin, armed with 12 spine teeth on inside and 12 on outside; defining angle with 2 notched and 4 notched-serrate spine teeth on inside, 3 notched and 2 serrate spine teeth on outside.

Propod of gnathopod 2 more than 2 times longer than carpus; palm strongly oblique, with 9-12 spine teeth on inside, 17 on outside; defining angle with 4 spine teeth on inside and 7 on outside.

Uropod 2: inner ramus with about 14 spines; outer ramus with inner row of comb spines on distal half, about 7 short spines on outer margin, apex with 3 spines; peduncle with 4 thin outer spines, and 2 inner spines. Uropod 3: outer ramus about 2 times longer than peduncle. Telson little longer than broad, notched 1-3-1 2 distance to base; each lobe with 3 apical spines, which are about 2/3 length of telson.

Distribution and ecology.—The range of *C. shoemakeri* extends from south-central Maryland south and southwest to south-central Virginia (fig 10). This species is an inhabitant of temporary pools and ponds (often with grassy bottoms), springs, small streams, and bogs. Ovigerous females occur from February to May, followed by immatures during the summer.

Remarks.—Hubricht and Mackin (1940) described *C. shoemakeri* from coty material collected in Washington, D.C., but they also assigned specimens from Illinois and Oklahoma to this species (which proved to be *C. minor*), in which males lacked comb spines on uropod 2. Hubricht (1943) also later reported this species from numerous localities in Kentucky, Illinois, Indiana, Michigan, Missouri and Ohio. However, Bousfield (1958) was correct in doubting that these collections were *C. shoemakeri*, and Holsinger (1972) and the present study have shown these collections to contain three different species, including *C. setodactylus, C. minor* and *C. forbesi*.
Crangonyx setodactylus Bousfield


Crangonyx shoemakeri (Hubricht and Mackin).—Hubricht. 1943:690 [in part].

Material examined. —ONTARIO. Oxford Co.: Spitier Creek. 4 miles W of Norwich. holotype ♂.

eallotype ♂. 4 ♀ paratypes. L. Bousfield. 29 May 1957 (CMN): Stony Creek. 6.4 km W of Tillsonburg. 5 ♀.

E. L. Bousfield. 29 May 1957 (USNM). INDIANA. DeKalb Co.: outlet of drain. 9.1 km E of Corunna. 10

spec. L. Hubricht. 19 Apr 1942 (USNM): Hendricks Co.: spring. 4.5 km ENE of Plainfield. 6 ♂. L.

Hubricht. 17 Apr 1942 (USNM): Henry Co.: small stream. 2.1 km NW of Blountsville. 100 spec. (♀. ♀. juvs). L. Hubricht. 27 Apr 1941 (USNM). Huntington Co.: slough. 5.3 km NE of Huntington. 100 spec.

L. Hubricht. 19 Apr 1942 (USNM): Noble Co.: outlet of drain. 0.9 km SE of Kendallville. 38 spec. L.

Hubricht. 19 Apr 1942 (USNM): Putnam Co.: temporary stream. 8.5 km ENE of Harmony. 49 ♂. L.

Hubricht. 16 Apr 1942 (USNM); county not given: small tributary of Richland Creek on Indiana Rt 44. 1 ♀. N. Hynes. 5 Jan 1963 (USNM). KENTUCKY. Bourbon Co.: small spring. 5.1 km ENE of Millersburg. 8 ♀.

L. Hubricht. 25 Apr 1941 (USNM): spring. 9.1 km SW of Paris. 20 spec. L. Hubricht. 25 Apr 1941

(USNM); Boyle Co.: Salt River Drainage near Atoka. 2 ♀. S. Lrider. 6 Mar 1971: Bullitt Co.: stream W of Mt. Carmel Church. 3 ♀. 1 ♂. N. Hynes. 9 Jan 1985 (USNM): creek at T-junction W of Crutchmere Hollow. 5 ♀. 5 ♀. N. Hynes. 9 Jan 1985 (USNM); small stream just E of Mt Carmel Church. 19 ♀. 1 ♂. N.

Hynes. 9 Jan 1985 (USNM); Carroll Co.: tributary to Ky. River. 6.2 km SSW of Carrollton. 6 ♂. L. E.

and M. R. Cooper. 26 Mar 1967: Clark Co.: Big Stoner Creek at SR Rt 15. 24 spec. R. Fox. 6 Feb 1971:

spring. 9.6 km NE of Winchester. L. Hubricht. 22 Apr 1949 (USNM): stream ca. 11.2 km W of Clark County courthouse on Colby Pike. 8 ♂. 5 ♀. R. Fox. 1 Jan 1971: Fayette Co.: Bryan Station Spring. 3 ♀. 2

♂. J. R. Holsinger. 1 Feb 1964 and 9 ♂. 6 ♀. R. Fox et al.. 3 Jan 1971: lake on US 421-25 ca. 100 m NW of State Road 4. SE of Lexington. 1 ♂. R. Fox. 1 Jan 1971: Maedico Creek. ca. 8.0 km W of Clark-Fayette Co. line on Todds Road. 3 ♂. 18 ♀. R. Fox. 1 Jan 1971: Pompoon Creek. ca. 11.2 km W of Clark-Fayette co. line on Todds Road. 5 ♂. 7 ♀. R. Fox. 1 Jan 1971: spring stream entering N of Elkhorn Creek. 8 ♂. 9 ♀.

R. Fox et al.. 3 Jan 1971: unmarked stream beside Bryan Station Rd. ca. 1.6 km NE of St Rt 4. NE of Lexington. 20 spec. R. Fox et al.. 3 Jan 1971: Bryan Station Rd (habitat not given). 0.5 km NE of Eastin Rd. 0.5 km NE of Lexington. 300 spec. L. Hubricht. 25 Apr 1941 (USNM): Coldstream Farm Stream. 3

Figure 11.—*Crangonyx setodactylus* Bousfield. Female (10.8 mm), Bryn Station Springs, NE of Lexington, Fayette Co., Kentucky: a. b. maxillae 1. 2: c. lower lip: d. left mandible: e. dentate part of right mandible: f. inner and outer plates of maxilliped (greatly enlarged): g. h. gnathopods 1. 2 (palmar margins enlarged).
Figure 12.—*Crangonyx setodactylus* Bousfield. Female (10.8 mm). Bryan Station Springs, NE of Lexington, Fayette Co., Kentucky: a, antenna 1; b, e, pereopods 4, 7; c, d, pereopods 5, 6 (in part); f, pleonal plates; g, h, i, uropods 1, 2, 3; j, telson.
Figure 13.—*Crangonyx setodactylus* Bousfield. Male (9.7 mm). Bryan Station Springs, NE of Lexington, Fayette Co., Kentucky: a. antenna 2; b, c. gnathopods 1, 2 (palmar margins enlarged); d, e. uropods 2, 3; f. telson.
Figure 14.—Distribution of *Crangonyx setodactylus* in North America. Solid circles represent 1-20 closely proximate localities. The dotted line indicates the approximate southern extent of glaciation during the Pleistocene.
Diagnosis.—Distinguished from other members of the *shoemakeri* group by having 2-3 setae on inner margins of dactyl of pereopods 3-7; straight palms of gnathopod propods in female; pleonal plate 1 with subventral spines; and with many subventral spines on pleonal plates 2-3. Largest male. 12.0 mm; largest female. 17.0 mm.

Female.—Eye small and round. Antenna 1. about 50 percent length of body. about 1.7 times longer than antenna 2; primary flagellum with up to 28 segments. Antenna 2. flagellum with 10-11 segments.

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Mandibles subequal, spine row with 5-7 spines: segment 2 of palp with about 8 long setae, segment 3 with 2 A setae, 1 B setae, 2 C setae, 4-5 E setae and row of D-setae. Maxilla 1: inner plate with 7-8 apical plumose setae; palp with 7-8 slender spines on apex. Maxilla 2, inner plate with oblique row of 7-9 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 2 naked spines, and 3-5 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 3-4 slender pectinate spines on inner margin and 1 apical plumose seta; dactyl with 4 setae along inner side; dactyl nail very long, about 1/3 length of dactyl.

Propod of gnathopod 1 less than 2 times longer than carpus; palm almost straight, shorter in length than posterior margin, with 10 spine teeth on inside, 9 on outside; defining angle with 4 notched-serrate spine teeth on inside, 1 large notched and 2 serrate spine teeth on outside; posterior margin with about 5-6 sets of setae inserted in groups of 2-4. Dactyl of gnathopod 1 with row of 7 short setae and 5-7 blade-like teeth along the inner margin, nail long. Ventral margin of coxa 1 with 13 setae.

Propod of gnathopod 2 less than 2 times longer than carpus; palm almost straight, shorter than posterior margin, with 13 spine teeth on inside, 12 on outside; defining angle with 3 notched (one very large) and 2 serrate spine teeth on outside, 2 notched and 2 notched-serrate spine teeth on inside; inferior medial setae singly or doubly inserted; superior medial setae singly inserted; posterior marginal with 5-6 sets of setae in groups of 3-7. Dactyl of gnathopod 2 with row of 6 short setae and about 5 blade-like teeth along inner margin; dactyl nail long. Ventral margin of coxa 2 with 16 setae.

Coxa of pereopod 3 with 12 marginal setae. Coxa of pereopod 4 with 20-22 marginal setae; dactyl of pereopod 4 about 33 percent of propod. Pereopod 5: basis with 10 shallow serrations along posterior margin; 7 sets of short spines in groups of 1-3 on anterior margin; 3-4 long setae on the anteroproximal margin. Pereopod 6: basis with 14 shallow serrations along posterior margin; 15 sets of short spines on anterior margin; 3 long setae on anteroproximal margin. Pereopod 7: coxa with about 3 setae along posterior margin; basis with 14 shallow serrations along posterior margin; about 19 sets of short spines on anterior margin; dactyl about 30 percent length of propod. Dactyl of pereopods 3-7 with 2-3 setae on inner margin.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner acute but not produced, ventral margin with 1-2 (subventral) setae; posterior margin of plate 2 nearly straight with 1-2 setae, distoposterior corner slightly produced and acute, ventral margin with 7 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner neither produced nor acute, ventral margin with 7 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outer margin.

Uropod 1: inner ramus 70 percent length of peduncle, armed with about 10 spines; outer ramus with about 10 spines; peduncle with row of 7 outer and 1 inner spines. Uropod 2: inner ramus armed with about 12 spines; outer ramus with 9 spines; peduncle with 5 outer and 3 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.5 times longer than peduncle, inner and outer margins each with 3-4 set of
spines in groups of 1-3. Telson broader than long, notched about 1/4 distance to base; each lobe with 3 apical spines and 1-2 subapical plumose setae, spines a little shorter than 1/2 length of telson.

Male. -- Differing from female as follows: smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5 and first 4 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger than carpus, palm longer than posterior margin, armed with about 10 spine teeth on inside, 17 spine teeth on outside; defining angle with 3 notched and 1 notched-serrate spine teeth on inside and 3 notched and 2 serrate on outside. Propod of gnathopod 2 more than 2 times larger than carpus, palm margin strongly oblique, longer than posterior margin, with 17 spine teeth on inside, 20 spine teeth on outside; defining angle with 6 spine teeth on inside and 9 on outside.

Uropod 2: inner ramus with about 12 spines: outer ramus strongly curved laterally, with about 11 spines: peduncle with 4 outer spines and 2 inner spines. Uropod 3: outer ramus about 2 times longer than peduncle.

Distribution and ecology. -- The range *C. setodactylus* extends from southeastern Ontario south and west across southern Michigan through much of Ohio, eastern and central Indiana and into northcentral Kentucky (fig. 14); it is also found in the most eastern part of Kentucky. In Ontario and Ohio, its range overlaps with that of *C. minor*, with which it is closely related.

This species is commonly found in a variety of cold-water habitats, including small streams, outlets of drains, springs, sloughs and temporary pools and very rarely in cave streams. The cave populations may have greatly reduced eyes but the eyes are never completely lost.

Remarks. -- Almost all collections reported by Hubricht (1943) as *C. shoemakeri* from Ohio, Michigan and Kentucky were examined by me and found to belong to *C. setodactylus*.

*Crangonyx minor* Bousfield

**Figures 15-18**

*Crangonyx minor* Bousfield, 1958:98-100, fig. 15 [type-locality: Stony Creek, 4 mi W of Tillsonburg.


*Eucrangomyx shoemakeri* Hubricht and Mackin, 1940:198 [in part].

*Crangonyx shoemakeri* (Hubricht and Mackin).-- Hubricht, 1943:690- 691 [in part].

Material examined. -- ONTARIO. Oxford Co.: Stony Creek, 6.4 km W of Tillsonburg, holotype ♂, allotype ♀ (NMC), paratypes 4 ♂ and 2 ♀. E. L. Bousfield, 29 May 1957 (USNM); ARKANSAS. Greene Co.: seep 8.0 km N of Brookland, 2 ♂, 1 juv. D. Barnett, 16 Feb 1970. ILLINOIS. Bond Co.:
Figure 15.—*Crangonyx minor* Bousfield. Female (11.8 mm). Outlet of drain, 2.4 km SW of Galesburg, Knox Co., Illinois: a. antenna 1; b. c. maxillae 1, 2; d. lower lip; e. dentate part of left mandible; f. right mandible; g. h. gnathopods 1, 2 (palmar margins enlarged).
Figure 16.—Crangonyx minor Bousfield. Female (11.8 mm). Outlet of drain, 2.4 km SW of Galesburg, Knox Co., Illinois: a, b, c, d, pereopods 3, 4, 5, 6 (in part): e, pereopod 7; f, pleonal plates: g, h, i, uropods 1, 2, 3; j, telson.
Figure 17.—*Crangonyx minor* Bousfield. Male (6.3 mm), Outlet of drain, 2.4 km SW of Galesburg, Knox Co., Illinois: a. antenna 2; b, c. gnathopods 1, 2 (palmar margins enlarged); d, e, f. uropod 1, 2; g. telson.
Figure 18.—Distribution of *Crangonyx minor* in North America. Solid circles represent 1–1 closely proximate localities. The dotted line indicates the approximate southern extent of glaciation during the Pleistocene.
temporary stream 0.8 km W of Beavercreek, 5 ♀, 10♂, L. Hubricht, 16 Apr 1942 (USNM); Clark Co.: spring 3.0 km ENE of Marshall, 7 ♂, L. Hubricht, 16 Apr 1942 (USNM); Champaign Co.: Oxbow, Urbana, 2 ♀, 1 ♂, J. G. Mackin, Spring 1931 (USNM); pond at St. Joseph, 1 ♀, 1 ♂, J. and W. Rapp, 31 Mar 1946 (USNM); Douglas Co.: pitfall trap in wetland, 3.2 km N of Arcola Prairie, 25 ♀, E. A. Lisowski, 8 Nov - 6 Dec 1993; Effingham Co.: temporary stream 1.6 km SW of Funkhouser, 100 specs (♀, ♂), L. Hubricht, 16 Apr 1942 (USNM); ditch 3.0 km WSW of Altamont, 35 ♀, 18 ♂, L. Hubricht, 16 Apr 1942 (USNM); Henderson Co.: outlet of drain 2.7 km W of Biggsville, 1 ♀, L. Hubricht, 25 Apr 1942 (USNM); Jackson Co.: seep in sandstone in Giant City State Park, 1 ♂, J. J. Lewis, 5 May 1974; Knox Co.: Arbingdon, 15 ♂, W. P. Hay, collection date not given (USNM); outlet of drain, 3.2 km N of Arbingdon, 55 specs (♀, ♂), L. Hubricht, 4 May 1941 (USNM); outlet of drain 2.6 km SW of Galesburg, 100 specs (♀, ♂), L. Hubricht, 4 May 1941 (USNM); Madison Co.: spring 0.6 km SW of Troy, 29 ♀, 15 ♂, L. Hubricht, 16 Apr 1942 (USNM); temporary pool near Silver Creek, 3.6 mi W of St. Jacab, 2 ♀, 2 ♂, L. Hubricht, 16 Apr 1942 (USNM); Mcdonough Co.: outlet of drain, 3.2 km E of Good Hope, 18 ♀, 4 ♂, L. Hubricht, 4 May 1941 (USNM); outlet of drain, 4.8 km S of Colmar, 5 ♀, 44 ♂, L. Hubricht, 4 May 1941 (USNM); Peoria Co.: spring 5.0 km W of Princeville, 17 ♀, 40 ♂, L. Hubricht, 4 May 1941 (USNM); St. Clair Co.: temporary pool, ditch 1.6 km S of Falling Spring, 4 ♀, 1 ♂, L. Hubricht, 24 Apr 1938 (USNM); temporary pond, roadside ditch, N of Duplo, 1 ♀, L. Hubricht, 24 Apr 1938 (USNM); Union Co.: temporary pool near McCann School, 2.5 mi NE of Aldridge, 10 ♀, 10 ♀, L. Hubricht, 14 Apr 1940 (USNM); small spring-fed marsh, 4.0 km E of Ware, 50 specs (♀, ♂), L. Hubricht, 27 Apr 1940 (USNM), IOWA. Des Moines Co.: outlet of drain 0.3 km NW of Danville, 46 specs (♀, ♂), L. Hubricht, 24 Apr 1942 (USNM); outlet of drain 5.8 km E of Middletown, 15 ♀, 20 ♂, L. Hubricht, 25 Apr 1942 (USNM); Washington Co.: slough of English River 4.0 km E of Riverside, 15 ♀, 17 ♂, L. Hubricht, 24 Apr 1942 (USNM); outlet of drain, 1.6 km S of Haskins, 51 ♀, 10 ♂, L. Hubricht, 24 Apr 1942 (USNM), KENTUKEY. Edmonson Co.: seep 1.6 km NW of Mammoth Cave, 20 ♀, 8 ♂, L. Hubricht, 13 Apr 1957 (USNM); Grayson Co.: rill 7.2 km SW of Leitchfield, 2 ♀, 1 ♂, L. Hubricht, 4 May 1958 (USNM), MISSOURI. Carroll Co.: tile drain in Bosworth, 1 ♀, J. Craig, 29 Apr 1974; Jackson Co: 1 mi W of Lake Tapawingo (habitat not given), 13 ♀, 3 ♂, P. J. Spangler, 30 Mar 1952 (USNM); Lincoln Co.: marsh 3.2 km S of Apex, 14 ♀, 2 ♂, L. Hubricht, 22 Mar 1941 (USNM); St. Charles Co.: temporary pool 0.5 km S of St. Peters, 26 ♀, 40 ♂, L. Hubricht, 22 Mar 1941 (USNM); St. Louis Co.: Marsh, N end of Creve Coeur Lake, 3 ♀, 1 ♂, 1 juv. L. Hubricht, 8 Mar 1936 (USNM); slough of Mississippi River 1.6 km S of Grimsby, 15 ♀, 1 ♂, L. Hubricht, 29 Feb 1936 (USNM) and 15 ♀, 4 ♂, 25 Apr 1938 (USNM); Wayne Co.: temporary pond, just E of Greenville, 1 ♀, 1 juv. L. Hubricht, 5 Apr 1941 (USNM); OHIO. Butler Co.: dug well on Francis Farm at Sandow, 2 ♀, 1 ♂, S. R. Williams, collection date not given (USNM); Cuyahoga Co.: small shallow pool in woods near Gates Mills, 2 ♀, 2 ♂, N. C. Furtos, 8 Apr 1933 (USNM); Erie Co.: stream near hatchery. Blue Hole, Castalia, 2 ♀, N. C. Furtos, 22 Jul 1931 (USNM); Tuscarawas Co.: New Philadelphia (habitat not given), 13 ♀, 5 ♂, V. Sterki, collection date not given (USNM), OKLAHOMA. Pontotoc Co.: temporary stream E of Ada.

Diagnosis.--A member of shoemakeri group easily distinguished from C. shoemakeri and C. aberrans by absence of comb spines on uropod 2 of male; from C. setodactylus by having only 1 seta on inner margin of dactyl of pereopods 3-7, more setae on coxa ventral margin of pereopod 7, unproduced distoposterior corners of pleonal plates, and outer ramus of uropod 2 of male without inner spines (with about 4 short outer spines). Largest male, 8.5 mm; largest female, 12.5 mm.

Female.—Eye large and ovate. Antenna 1, about 52 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with up to 24 segments. Antenna 2, flagellum with 8-10 segments. Mandibles subequal, spine row with 5-7 spines; segment 2 of palp with 7 long setae, segment 3 with 2 A setae, 1 B seta, 1 C seta. 5 E setae and row of 14 D setae. Maxilla 1: inner plate with 7-8 apical plumose setae; palp with 5-6 slender spines on apex. Maxilla 2, inner plate with oblique row of 8 plumose setae on inner margin. Maxilliped: inner plate apically with 3-4 bladelike spines, 3 naked setae, and about 9 plumose setae extending from inner margin to apex; outer plate with 4-5 slender pectinate spines on inner margin and 1 plumose seta on apex; dactyl with 5 setae along inner margin; dactyl nail long, about 1.3 length of dactyl.

Propod of gnathopod 1 less than 2 times longer than carpus; palm shorter than posterior margin, concave, with 10 spine teeth on inside, 11 on outside; defining angle with 5 notched-serrate spine teeth on inside, 1 large notched and 2-3 serrate spine teeth on outside; superior medial setae in 3 sets, singly or doubly inserted; posterior margin with 5 sets of setae in groups of 1-4. Dactyl of gnathopod 1 with row of short setae and blade-like teeth along inner margin; dactyl nail long. Ventral margin of coxa 1 with 15 setae.

Propod of gnathopod 2 less than 2 times longer than carpus; palm shorter than posterior margin, concave, with about 9 spine teeth on inside, 11 on outside; defining angle with 2-3 notched and 4 notched-serrate spine teeth on outside, 3 notched and 1-3 serrate spine teeth on outside; about 6 superior medial setae, singly inserted; posterior margin with 5 sets of setae in groups of 2-5. Dactyl of gnathopod 2 with row of short setae and blade-like teeth along inner margin. Ventral margin of coxa 2 with 13 setae.

Coxa of pereopod 3 with 12 marginal setae. Cox of pereopod 4 with 23 marginal setae. Dactyl of pereopod 4 about 33 percent length of corresponding propod. Pereopod 5: basis with 15 shallow serrations along posterior margin; 5 short spines on anterior margin; 3-4 long setae on the anteroproximal margin.

Pereopod 6: basis with 18 shallow serrations along posterior margin. 9 sets short spines in groups of 1-2 on anterior margin; 3-4 long setae on anteroproximal margin. Pereopod 7: coxa with 4-6 setae along posterior margin; basis with 17-19 serrations along posterior margin. 15 short spines on anterior margin; 2 long setae.
on anteroproximal margin.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner not produced; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner acute but not produced, ventral margin with 5 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner not produced, ventral margin 5 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outer margin.

Uropod 1: inner ramus 70 percent length of peduncle, armed with about 12 spines: outer ramus with 14 spines: peduncle with 9 outer and 1 inner spines. Uropod 2: inner ramus armed with 10 spines: outer ramus with 16 spines; peduncle with 2 outer spines, 3 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.5 times longer than peduncle, inner and outer margin each with 3-4 sets of spines in groups of 1-3. Telson broader than long, notched about 1/3 distance to base, each lobe with 2-3 apical spines, spines about 1/2 length of telson.

Male.—Differing from female as follows: smaller size with slender, elongate body. Antenna 2: flagellum with 8 segments, calceoli present on peduncular segments 3-5 and first 3 segments of flagellum.

Propod of gnathopod 1 more than 2 times longer than carpus: palm slightly longer than posterior margin, oblique and convex, with 11 spine teeth on inside, 12 on outside: defining angle with 1 notched and 4 notched-serrate spine teeth on inside, 4 notched and 2 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times longer than carpus: palm longer than posterior margin, oblique and convex, with 13 spine teeth on inside, 13 on outside: defining angle with 6 spine teeth on inside and 8 on outside.

Uropod 2: inner ramus with 12 spines: outer ramus strongly deflected and curved, with 4 short outer spines and 4 spines on apex, lacking inner spines; peduncle with 5 outer spines, and 2 inner spines.

Variation.—Significant variation was found in the number of blade-like teeth along the inner margin of dactyl of gnathopods in female. Normally the teeth are arranged one by one on the margin, but in some specimens blade-like teeth may occur as just several or one in the middle of the margin.

Distribution and ecology.—This species is recorded from southeastern Iowa, central and southern Illinois, northwestern Missouri, central Kentucky, northeastern Arkansas, western Tennessee, southern Oklahoma and southern Ontario (fig. 18). In Ontario and Ohio, its range overlaps with that of C. setodactylus.

Crangonyx minor inhabits a variety of aquatic habitats, including small streams, sloughs, ditches, drains, springs, and ponds.

Remarks.—Almost all collections reported by Hubricht (1943) as Crangonyx shoemakeri from Illinois, Iowa and Missouri and examined by me in this study belong to C. minor. The type localities for C. minor and C. setodactylus are only a few kilometers apart.

This species has not been found in Indiana to date. The previous records for Indiana (see Holsinger, 1972, map 19; Barnard & Barnard, 1983, map 11; and Pennak, 1989, page 483) are incorrect: they are actually records for C. setodactylus.
Crangonyx aberrans Smith

Figures 19-20

Crangonyx pseudogracilis Bousfield.—Smith, 1981:11, fig. 6. [in part].


Diagnosis.—A small species of shoemakeri group distinguished from all other species of Crangonyx by presence of dorsal, lateral, and ventrolateral spines on the telson; and from other members of the shoemakeri group by having just a few teeth on inner margin of dactyls of gnathopods of female; and specifically from C. setodactylus. and C. minor by having comb spines on uropod 2 of male. Largest male, 6.5 mm; largest female, 10.0 mm.

Description.—Smith (1983) gave a very accurate description and good illustrations of this rather unusual species. The following is a brief supplement to Smith's description.

Female: Antenna 1. primary flagellum with up to 20 segments; inner margin of outer lobe of maxilliped with 4-6 slender pectinate spines; posterior margin of propod and carpus of gnathopods armed with weakly rastellate setae; pleonal plates 1-3, each with 1 seta on posterior margin; distoposterior corner of pleonal plate 3 weakly acuminate with 2 submarginal spines; for most specimens outer margins of dactyl of pereopods 6-7 have only 1 setae.

Distribution and ecology.—This species was originally found in northeastern Massachusetts, but new locality records have extended its range south to Connecticut and Rhode Island (fig. 20). It is an inhabitant of small rivers, brooks, and swamps.

Remarks.—The presence of notched spine teeth on the palms of gnathopodal propods of C. aberrans distinguishes it from all species of the gracilis group. It is assigned to the shoemakeri group because of the following two characters: (1) spine teeth of defining angle of gnathopods like those of other three species of the shoemakeri group; (2) inner margin of gnathopodal dactyl with blade-like teeth in female as in other species of shoemakeri group (although just a few in number).

Crangonyx aberrans is unique among Crangonyx by having lateral spines on telson. However dorsal spines are found on the telson of C. serratus. and in some specimens of C. dearolfi.
Figure 19. *Crangonyx aberrans* Smith. Female holotype (7.0 mm). Spot Pond Brook, Stoneham, Massachusetts: outer plate of maxilliped (greatly enlarged).
Figure 20. Distribution of \textit{C. varius} in the North America. Solid circles represent single localities.
The longicarpus group

Diagnosis.—Adult size range, 5.5-9.4 mm. Segment 3 of palp of mandibles with 2 A setae and 1 B seta. Maxilla 1: inner plate with 8 apical plumose setae. Maxilla 2, inner plate with oblique row of 8 plumose setae on inner margin. Gnathopods of female: carpus slightly longer or subequal to propod. posterior margin armed with many sets of long setae; propod palm armed with symmetrically-notched spine teeth: superior medial setae singly inserted: defining angle of propod of gnathopod 1 with several notched spine teeth on inside (direction of notch is opposite the dactyl), defining angle of propod of gnathopod 2 with "normal" notched spine teeth. Gnathopods of male: carpus subequal in length to propod in gnathopod 1 and shorter and slightly narrower in gnathopod 2; palm armed with (normal) spine teeth: the defining angle like that of female. Peduncular segment of pleopod 1 with only 2 retinaculae, but with a few setae on outer margin.

Remarks.—This group is composed of a single species that inhabits the Coastal Plain of southeastern Virginia and northeastern North Carolina. The symmetrically-notched spine teeth on the propod palms of gnathopods of the female may represent an evolutionary intermediate stage between larger notched spine teeth and small simple spine teeth. It is likely that additional species with this distinct character will be found in the future.

Crangonyx longicarpus, new species

Figures 21-25

Material examined (paratypes unless designated otherwise).—NORTH CAROLINA. Hertford Co.: Winton, 1 ♂ (not paratype), collector unknown, 23 Mar 1940 (USNM). VIRGINIA. Henrico Co.: Brook Hill, N of Richmond, 3 ♂, A. Pizzini, 30 Apr 1939 (USNM); Isle of Wight Co.: small stream, 1.6 km S of Rescue, 2 ♂, 1 ♀, L. Hubricht, 12 Mar 1944 (USNM); outlet of drain on Taylor Farm, 5.6 km N of Chuckatuck, 1 ♂, J. R. Holsinger, 27 Mar 1983; James City Co.: Taskinas Creek tributary headwaters, about 2.5 km NE of Christensons Corners, 1 ♂ (not paratype), C. S. Hobson and D. J. Stevenson 29 Dec 1994; Nansemond Co.: Whaleyville, 2 ♂, 1 ♀, R. Bray, 22 Mar 1940 (USNM); springs, 3.2 km W of Driver, 6 ♂, L. Hubricht, 26 Mar 1944 (USNM); Norfolk Co.: small stream, 0.8 km W of Churchland, 2 ♂, L. Hubricht. 30 Jan 1944 (USNM); Northampton Co.: Crayfish burrows along Rt. 600 at Seaview, holotype ♂, 18 ♂, 25 ♀, F. W. Grimm and J. M. Odell, 6 Dec 1964 (USNM); Holly Grove Creek, Rt. 606 crossing, 1 ♂, P. H. Stevenson, 27 Oct 1992; Suffolk (Nansemond County), shallow well opening to drain tiles, Barlow Farm, 3.2 km NNE of Chuckatuck, 3 ♂, 1 ♀, J. R. Holsinger, 27 Mar 1983; Warwick Co.: pools in woods, 4.0 km NW of Newport News, 11 ♂, 9 ♀, L. Hubricht, 23 Jan 1944 (USNM); York Co.: hillside seepage N of Colonial Parkway Bridge, 6 ♂, 2 ♀, S. M. Roble, 22 Aug 1994.
Figure 21. *Cymogammarus argus*, new species. Female paratype (7.5 mm), entire animal from left side, crab fish burrows along R 600 at Seaview, Northampton Co., Virginia.
Figure 22.—*Crangonyx longicarpus*, new species. Female paratype (8.5 mm), crayfish burrows along Rt. 600 at Seaview, Northampton Co., Virginia: a. antenna 1; b. c. gnathopods 1, 2 (palmar margins and dactyls enlarged); d. uropod 2.
Figure 23.—*Crangonyx longicarpus*, new species. Female paratype (8.5 mm), crayfish burrows along Rt. 600 at Seaview, Northampton Co., Virginia: a. b. maxillae 1, 2; c. lower lip; d. left mandible; e. dentate part of right mandible; f. inner and outer plates and dactyl of palp of maxilliped (greatly enlarged): g. pereopod 4; h. pereopod 6 (in part); i. pereopod 7; j. pleonal plates; k. uropod 3; l. telson.
Figure 24.—*Crangonyx longicarpus*, new species. Male paratype (6.2 mm), crayfish burrows along Rt. 600 at Seaview, Northampton Co., Virginia: a, antenna 2; b, c, gnathopods 1, 2 (palmar margins enlarged); d, pereopod 7; e, f, g, uropods 1, 2, 3; h, telson.
Figure 25.— Distribution of *Conocephalus longicornis* in North America. Solid circles represent 1-2 closely proximate localities. The dotted line denotes the "fall line" or "fall zone" between the Coastal Plain and Piedmont.
Diagnosis.—A small species distinguished from all other species of *Crangonyx* by having unique slender symmetrically-notched spine teeth on gnathopods of female. Superficially resembling *C. hobbsi* by the with very long carpus and propod of gnathopods in both sexes. In female gnathopods, the carpus is longer than propod. Largest male, 6.2 mm; largest female, 9.4 mm.

Female.—Eye large and round. Antenna 1, about 50 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with about 24 segments. Antenna 2: flagellum with 10 segments, peduncular segments 4 and 5 each with 3-4 sets of marginal long setae. Mandibles subequal. spine row with 6-8 spines; segment 2 of palp with about 10 setae, segment 3 with 2 A setae, 1 B seta, 2 C setae, 4 E setae and a row of D setae. Maxilla 1: inner plate with 8 apical plumose setae; plap with 13 slender spines on apex. Maxilla 2, inner plate with oblique row of 8 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 2 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and about 6 pectinate spines on inner margin and 3 apical plumose setae; dactyl with 4-5 setae on inner margin, dactyl nail very long, about 1.3 length of dactyl.

Gnathopod 1: carpus longer than propod, posterior margin very long, with many very long setae; propod palm much shorter than posterior margin, little convex, not oblique, with about 5 symmetrically notched slender spine teeth on inside, 7-9 on the outside: defining angle with five (normal) spine teeth on inside, 3 on outside; superior medial setae few in number and mostly singly inserted; posterior margin with 4-5 sets of setae in groups of 1-3. Dactyl with about 3 short setae on inner margin, nail very long, about 1.3 length of dactyl. Ventral margin of coxa 1 with 9-11 setae, some very long.

Gnathopod 2: carpus equal or slightly longer than propod, posterior margin very long, with 9-10 sets of very long setae; propod palm much shorter than posterior margin, little convex and oblique, with about 5 symmetrically notched, slender spine teeth on inside, up to 13 on outside; defining angle with 5 (normal) spine teeth on inside, 3 on outside. 1 very large; superior medial setae about 13 in number, singly inserted; posterior marginal with 7 sets of long setae in groups of 2-1. Dactyl with 6 short setae on inner margin, nail very long, about 1.4 length of dactyl. Ventral margin of coxa 1 with 6 setae.

Coxae of pereopod 3 with 6 marginal setae. Coxa of pereopod 4 with 22 marginal setae, dactyl of pereopod 4 about 20 percent length of propod. Pereopod 5: basis with 14 shallow serrations on posterior margin; 8 short spines on anterior margin; 3 long setae on the anteroproximal margin; Pereopod 6: basis with 15 shallow serrations along posterior margin; 8 short spines on anterior margin; 3 long setae on anteroproximal margin; Pereopod 7: coxa with 2 setae along the posterior margin; basis with 12 shallow serrations along posterior margin; 6 short spines on anterior margin; 3 long setae on anteroproximal margin; dactyl more than 1/3 length of propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta. distoposterior corner not produced; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner produced, ventral margin with 4 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner round and not produced, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2
retinaculæ and less than 10 setae on distal half of outer margin.

Uropod 1: inner ramus about 80 percent length of peduncle, armed with 12 spines; outer ramus with about 11 spines; peduncle with 5 outer and 4 inner spines. Uropod 2: inner ramus armed with 10 spines; outer ramus with 10 spines; peduncle with 2 outer and 4 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 2 times longer than peduncle, inner and outer margin each with 3-4 sets of spines in groups 1-3. Telson little broader than long, notched about 1/3 distance to base, each lobe with 2 apical spines.

Male.—Differing from female as follows: smaller with more slender, elongate body. Antenna 2: calceoli percent on peduncular segments 4 and 5, and first 3 segments of flagellum.

Gnathopod 1: carpus shape like that of female, but slightly shorter than propod. Propod palm with 5 (normal) spine teeth on inside, 7 (normal) spine teeth on outside; defining angle with 4 spine teeth on inside and 3 on outside; upper half of posterior margin with 4-5 sets of long setae in groups of 1-2.

Gnathopod 2: carpus shape like that of female, smaller and shorter than propod. Propod palmar margin little convex and oblique, with 6 (normal) spine teeth on inside, 6 on outside; defining angle with 6 spine teeth on inside and 3 on outside.

Uropod 2: inner ramus with about 9 spines; outer ramus not curved, with about 3 inner and 2 outer spines, apex with 4-5 spines; peduncle with 2 outer and 3 inner spines.

Type-locality.—A ditch along VA Rt. 600 in Northampton Co., VA. The 44 type-specimens were collected from burrows of the crayfish *Cambarus diogenes*. The precise location of the ditch cannot be determined.

Distribution and ecology.—This species occurs on the Coastal Plain of southeastern Virginia and northeastern North Carolina (fig. 25). Populations in Northampton County on the eastern shore of Virginia are separated from other localities by the Chesapeake Bay. *Crangonyx longicarpus* inhabits small streams, brooks, outlets of drain, springs, ditches, creeks, and small woodland pools. Ovigerous females were found in collections from January to March.

Etymology.—The epithet *longicarpus* combines "long" and "carpus", referring to the long carpus of gnathopods 1 and 2 in both male and female.

The *richmondensis* group

Diagnosis.—Adult size range. 14.0-20.0 mm. Sexually mature females larger than male, except in *C. anomalus* in which mature males may be larger than mature females. Segment 3 of palp with 2 or more A setae and 1 or more B setae. Maxilla 1: inner plate with 4-5 or sometimes fewer apical plumose setae. Maxilla 2, inner plate with oblique row of up to 7 plumose setae on inner margin in some species but only 3 or fewer in other species. Lacking distinct sexual dimorphism in gnathopods. Gnathopods 1 and 2: propod more than 2 times larger than carpus and much broader; palm of propod much longer than posterior
Figure 26.—Geographic distribution of the *richmondensis* group in North America. Shaded areas denote areas of contiguous or near contiguous distribution. Note: Sable Island distribution not shown (see fig. 30).
margin, armed with many notched spine teeth, always 2 rows per side; superior medial setae inserted in
groups of 2-6; defining angle of propod of gnathopod 1 with 1 row of notched spine teeth on inside, the
direction of notch being opposite the dactyl; outside with 1 row of small notched or simple spine teeth and
1 row of larger notched spine teeth, lacking serrate spine teeth or with only a few; defining angle of propod
of gnathopod 2 with (normal) notched spine teeth (like those on the palm margin). Bases of pereopods 5-7
with many spines on posterior margin and many serrations on anterior margin. Peduncle of pleopod 1 with
more than 2 retinaculae (normally 4-6) and many long setae on outer margin.

Remarks.—This group is composed of nine large species, with the widest geographic distribution of
any group in North America (fig. 26). The richmondensis group is rather closed allied morphologically
with the forbesi group but differs in a number of significant ways as indicated in their respective diagnoses.

Key to the Species of the richmondensis group

1. Basis of pereopods 5-7 greatly expanded posteriorly, posterior margin with numerous (more than 30)
   very weak serrations..............................................................................................................................C. anomalus

   Basis of pereopods 5-7 not greatly expanded posteriorly, posterior margin without numerous weak
   serrations..................................................................................................................................................2

2. Spine teeth tri- or quadri-fid near proximal end of female gnathopodal propods: eyes absent

   ......................................................................................................................................................................C. dearolphi

   Spine teeth typically bifid (normal); eyes present or absent..................................................................3

3. Posterior margin of pleonal plates 2 and 3 strongly oblique and distinctly produced; eyes absent

   .............................................................................................................................................................C. grandimanus

   Posterior margin of pleonal plates 2 and 3 normal; eyes well developed.............................................4

4. Posterior margins of bases of pereopods 5-7 with deep serrations, especially near distal end........C. obliquus

   Posterior margins of bases of pereopods 5-7 with shallow serrations..................................................6

5. Dactyl of female gnathopod 2 with 2 or more setae on outer margin ............................................C. richmondensis

   Dactyl of female gnathopod 2 with 1 seta on outer margin................................................................C. disjunctus

6. Telson much broader than long; corners of pleonal plates 1-3 neither produced nor acute; inner margin
   of maxilla 2 with oblique row of more than 6 plumose setae..........................................................C. indianensis

   Telson longer than broad or length and width subequal; corner of pleonal plate 2 produced and acute,
   those of pleonals plate 1 and 3 produced or not; inner margin of maxilla 2 with 1-4 plumose setae........7

7. Distoposterior corners of pleonal plates 1 and 3 produced...............................................................C. hubrichti

   Distoposterior corners of pleonal plates 1 and 3 not produced..........................................................C. commitus

8. Outer ramus of male uropod 2 with 2-4 thick spines on inside.........................................................C. disjunctus

   Outer ramus of male uropod 2 with 1-2 large thick spines on inside and 2-3 very small spines on outside

   ............................................................................................................................................................C. cornutus
Crangonyx richmondensis Ellis

Figures 27-30


Crangonyx occidentalis Hubricht and Harrison. 1941:331, figs. A-L [type-locality: Echo Lake, near the Seattle-Everett Highway, just south of the King County line, Washington].--Barnard & Barnard. 1983:435, map 11.


Figure 27.—Crangonyx richmondensis Ellis. Female paratype (14.0 mm), pond on Richmond Plantation, Cordesville, Berkeley Co., South Carolina: a. b. antennae 1, 2; c. d. maxillae 1, 2; e. lower lip; f. left mandible; g. inner and outer plates and palp dactyl of maxilliped (greatly enlarged); h. i. gnathopods 1, 2 (palmar margins enlarged).
Figure 28.—*Crangonyx richmondensis* Ellis. Female paratype (14.0 mm), pond on Richmond Plantation, Cordesville, Berkeley Co., South Carolina: a, pereopod 3 (in part); b, c, pereopods 4, 7; d, peduncle of pleopod 1 (retinacula enlarged); e, pleonal plates; f, g, h, uropods 1, 2, 3; i, telson.

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Figure 29.—*Crangonyx richmondensis* Ellis. Male paratype (7.4 mm), pond on Richmond Plantation, Cordesville, Berkeley Co., South Carolina: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7; e. f. g. uropods 1, 2, 3; h. telson.
Figure 30.—Distribution of Crangonyx richmondensis in North America. Solid circles represent 1-12 closely proximate localities. The dotted lines indicate the approximate southern extent of glaciation during the Pleistocene and enclose pockets of alpine glaciation in western North America. The Sable Island locality (approximately 175 km E of Nova Scotia) reported by Bousfield (1970b) not shown.

MASSACHUSETTS. Norfolk Co.: Blue Hills. Milton. 4♀, F. N. Young. 24 Aug 1940 (USNM); Worcester Co.: Sanctuary Pond. N of Grafton. 2♀, 3♂. C. E. Addy. 16 Aug 1943 (USNM). MICHIGAN. Calhoun Co.: Beadle Lake. 6.2 km S of Battle Creek. 4♀, L. Hubricht. 20 Oct 1946 (USNM); Washenaw Co.: permanent pond. E side of Platt Road. ca. 12 km SSE of Ann Arbor. numerous specimens in 14 collections (USNM). R. Kenk. 1940-1941: pond just S of Ypsilanti Airport. 8.0 km SE of Ann Arbor. 100 spec. L. Hubricht. 29 Apr 1941 (USNM); marsh. 12.0 km N of Milan. 50 juvs. L. Hubricht. 28 Jul 1946 (USNM); pond off Platt Road. 0.8 km N of Benis Road. 100 spec. L. Hubricht. 30 Apr 1941 (USNM).

MINNESOTA. Fillmore Co.: Etna Creek. 1♀, 2♂, 1 juv. D. A. Webster. 16 May 1946 (USNM). NORTH CAROLINA. Beaufort Co.: open grounds. Beaufort. 2♀, 1♂. A. S. Pearse. 29 Mar 1934 (USNM); Lenoir Co.: Beaverdam swamp. at US 258. ca. 0.4 km SSE of Jonestown. 2♂. J. H. Reynolds. 23 Jan 1979 (NCMNH); Trent River at St Rd 1130. 0.8 km NE Nobles Crossroads. 2♀, J. H. Reynolds. 24 Jan 1979 (NCMNH); Wilson Co.: Little Contentnea Creek at CR 1531. ca. 6.2 km E of Saratoga. 1♀, P. S. Freed. 4 Feb 1979 (NCMNH); Whiteoak swamp at CR 1507. ca. 3.2 km NW Saratoga. 4♀, P. S. Freed. 4 Feb 1979 (NCMNH). OHIO. Wayne Co.: habitat not given. Funk. 1♀, A. Weaver. 26 Mar 1958. OREGON. Benton Co.: McFoddene's Swamp. 19.2 km S of Corvallis. 3♀, collector not given. Mar 1950 (USNM); Douglas Co.: Diamond Lake. 2♀, 1♂. G. S. Schuytema. 18 Jun 1973; Fish Lake. 3♀, A. Rath. 12 Jul 1937 (USNM); Lane Co.: Gold Lake. 5♀, F. Z. 16 Sep 1936 (USNM); Lower Marlyn Lake, 2♀, F. Z.. 15 Sep 1936 (USNM); Upper Marlyn Lake. 19♀, F. Z.. 15 Sep 1936 (USNM); Linn Co.: Clear Lake. 13♀, 10♂, 8 juvs. F. Z.. 17 Jun 1936 (USNM); Chiquits Lake. 2♀, F. Z.. 10 Jul 1936 (USNM); Daly Lake. 2♀, F. Z.. 2 Sep 1936 (USNM); Don Lake, 12♀, F. Z.. 10 Sep 1936 (USNM); Duffy Lake. 1♀, 1♂, F. Z.. 15 Jul 1936 (USNM); Fish Lake. 3♀, F. Z.. 15 Jun 1936 (USNM); Hunts Lake. 3♀, 9♂. F. Z.. 31 Jul 1936 (USNM); Jorn Lake. 5♀, 1♂. F. Z.. 7 Jul 1936 (USNM); Marion Lake. 3♀, 4♂. F. Z.. 1 Jul 1936 (USNM); Mowich Lake. 6♀, F. Z.. 16 Jul 1936 (USNM); Red Butte lake. 12♀, 6♂, 2 juvs. F. Z.. 14 Jul 1936 (USNM); Marion Co.: Elk Lake. 30 spec. S. T. Brooks. 25 Sep 1932 (USNM), 1♀, 1♂, F. Z.. 12 Jun 1936 (USNM) and 6♀, 4♂, 17 Jun 1936 (USNM) and 9♀, (collector not given); Upper Twin Lake. 1♀, F. Z.. 13 Aug 1936 (USNM); Russell Lake. 8♀, 4♂. F. Z.. 6 Aug 1936 (USNM). SOUTH CAROLINA. Berkeley Co.: slough. 4.8 km NW of Cordesville. 1♀, L. Hubricht. 21 Apr 1941 (USNM); pond. Gough. near Cordesville. 10♀, T. K. Ellis. 11 Dec 1939 (USNM) and near Gough. 4♀, 8♂, 1 Jan 1940 (USNM).
Richmond Plantation. Gough, numerous specimens (USNM) from Alligator Pond, dammed-up area. Upper and Lower reserves. T. K. Ellis. 1939-1941: swamp. 9.6 km N of Pineopolis. 1 ♂, 1 ♀. collector not given. 4 Apr 1940 (USNM); Charleston Co.: Caw Caw Swamp. 1 ♂, T. K. Ellis. 3 Apr 1941 (USNM); middle of Caw Caw Swamp. New Road. 10 ♂, 4 ♀. T. K. Ellis. 3 Apr 1941 (USNM); Clarendon Co.: Santee National Wildlife Refuge. 2 ♀. C. K. Biembaum. 15 Jan 1983 (USNM); Colleton Co.: beside Hwy 63 at Ricepatch Creek. 1 ♂. P. H. Carlson. 29 Nov 1982 (USNM); Hampton Co.: Cope Creek at Dirt Road. 2 ♂, P. H. Carlson. 2 Oct 1983 (USNM); Jasper Co.: slough. 3.2 km SSW of Ridgeland. 3 ♂, L. Hubricht. 21 Apr 1941 (USNM); Orangeburg Co.: swamp. 4.0 km SE of Bowman. 1 ♂, 15 ♀. L. Hubricht. 22 Apr 1941 (USNM); Richland Co.: pond in Congaree River swamp on road to Wateree. 2 ♂. collector not given. 4 Apr 1940 (USNM); WASHINGTON. Clallam Co.: Lake on Beaver Creek. 3.2 km N of Sappho. 5 ♂, C. H. Harrison. 13 Jun 1939 (USNM); Gray Harbor Co.: Lake Quinault. 1 ♂, C. H. Harrison. 13 Jun 1939 (USNM); Island Co.: Cranberry Lake, Camano Island. 60 specs. C. H. Harrison. 23 Aug 1939 (USNM); Deer Lake. Whidbey Island. 25 specs. C. H. Harrison. 8 Jul 1939; Goss Lake. Whidbey Island. 9 ♂, 12 juvs. C. H. Harrison. 8 Jul 1939 (USNM); Lone Lake. Whidbey Island. 2 ♂, C. H. Harrison. 8 Jul 1939 (USNM); Lake Oliver. Whidbey Island. 30 specs. C. H. Harrison. 10 Jul 1939 (USNM); Lake Pondilla. Whidbey Island. 2 ♀. C. H. Harrison. 20 Mar 1939 (USNM); Kristoferson's Lake. Camano Island. 40 specs. C. H. Harrison. 30 Aug 1939 (USNM); pond in gravel pit. 1.6 km S of mud lake. Whidbey Island. 50 specs. C. H. Harrison. 10 Jul 1939 (USNM); Silver Lake. Whidbey Island. 8 ♂, C. H. Harrison. 5 Jul 1939 (USNM); King Co.: Echo Lake, near Seattle-Everett Hwy. (US 99), just S of King Co. Line. 25 ♂, 15 ♀. C. H. Harrison. 1 Jan 1940 (USNM); Echo Lake, Richmond Highlands. 100 specs. C. H. Harrison. 9 Sep 1939 (USNM); Plantation Pond. 30 specs. C. H. Harrison. 13 May 1939 (USNM); Snohomish Co.: Chase Lake. 30 specs. C. H. Harrison. 8 Oct 1939 (USNM). WEST VIRGINIA. Greenbrier Co.: Meadow River wetlands. 2 ♀, D. C. Tarter. 19 Apr 1996; Tucker Co.: Tributary to Red Creek. Dolly Sods. 8 ♂. 1 ♀. C. Parrish. 4 May 1974. WISCONSIN. Green Co.: Allen Creek. Green and Rock counties line. 1 ♂, collector not given. 29 Sep 1989 (MPM); Juneau Co.: 2 ♀, collector not given. 23 Jun 1980 (MPM); Manitowoc Co.: pond at Marken Rd. 0.3 km S of Hwy C. 30 specs (2 ♀). B. Klausmeier. 9 Sep 1994 (MPM); Marquette Co.: large pond at County Trunk Highway E & Y south. 15 ♂, J. P. Jass. 23 Aug 1994 (MPM); Waukesha Co.: just W of Eagle. 3 ♂, collector not given. 8 Jun 1972 (MPM). 2 ♀, collector not given. 23 Jun 1989 (MPM), 12 ♂, 2 ♀, collector not given. 3 Jun 1979 (MPM); pond near Eagle. S of Hwy 59, 4.8 km W of Hwy N. 3 ♂, 28 juvs. J. P. Jass & B. Klausmeier. 3 Jun 1994 (MPM).

Diagnosis.--Nominate species of the richmondensis group distinguished from other members of the group by: having deep serrations along posterior margins of bases of pereopods 5-7; well developed distoposterior corners and few subventral spines of pleonal plates; uropod 2 of male with only 2 small inner and 2 small outer spines. Distinguished from the closely similar C. obliquus by having only 1 seta on outer margin of dactyl of gnathopods. Largest male. 11.00 mm; largest female. 20.00 mm.

Female.--Eye small and ovate. Antenna 1. about 60 percent length of body. about 1.8 times longer than
antenna 2: primary flagellum with up to 29 segments. Antenna 2, flagellum with 8-9 segments. Mandibles
subequal. spine row with 5-6 spines; segment 2 of palp with 7-11 long setae, segment 3 with 3 A setae. 1 B
seta, 2-3 C setae. 4-5 E setae and a row of D setae. Maxilla 1: inner plate with 3 apical plumose setae; palp
with 7-8 slender spines on apex. Maxilla 2, inner plate with 1 plumose seta on inner margin. Maxilliped:
inner plate apically with 4-5 blade-like spines. 1 naked spine. and up to 7 plumose setae extending from
inner margin to apex; outer plate with naked setae and 5-6 weak pectinate spines on inner margin and 1
plumose seta on apex; dactyl with up to 4 setae on inner margin; dactyl nail long. 1/4 length of dactyl.

Propod of gnathopod 1 more than 2 times larger and longer than carpus and much more broader; palm
corner. longer than posterior margin. armed with 2 rows of about 25 spine teeth on inside, 2 rows of about
24 on outside; defining angle with 7 spine teeth on inside. outside with 1 row of small spine teeth and 1
row of 5 large spine teeth; superior medial setae in 2-3 sets, inserted singly or doubly: 2-3 sets setae on
proximal half of posterior margin in groups of 2-5. Dactyl with row of up to 7 short setae on inner margin.
nail very short. Ventral margin of coxa 1 with 14 setae.

Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm strongly oblique.
corner, about 2 times longer than posterior margin. armed with 2-3 rows of about 34 spine teeth on inside.
2-3 rows of about 35 on outside; defining angle with 2 spine teeth on inside and 2 on outside; superior
medial setae in 7-8 sets inserted in groups of 1-3. posterior margin with 6 sets of setae in groups of 3-8.
Dactyl with row of short setae on inner margin. nail very short. Ventral margin of coxa 2 with 14 setae.

Coxa of pereopod 3 with 13 marginal setae. Coxa of pereopod 4 with 22 short marginal setae. dactyl of
pereopod 4 about 35 percent length of corresponding propod. Pereopod 5: basis with 15 shallow serrations
along posterior margin: 8-9 short spines on anterior margin: 10 long setae on anteroproximal margin.
Pereopod 6: basis with 13 serrations along posterior margin; 8 short spines on anterior margin: 8 long setae
on anteroproximal margin. Pereopod 7: coxa with 2 setae on the posterior margin; basis with 20 serrations
along posterior margin. becoming deeper distally: 7-8 short spines on anterior margin: 8-9 long setae on
anteroproximal margin; dactyl of pereopod 4. 30 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta. distoangular corner produced
and acute; posterior margin of plate 2 nearly straight with 1 seta. distoposterior corner produced and
distinctly acute. ventral margin with 4-5 (subventral) spines; posterior margin of plate 3 nearly straight with
1 seta. distoposterior corner strongly produced and acute, ventral margin with 1-3 (subventral) spines.
Peduncle of pleopod 1 with about 6 retinaculae, posterior margin with many setae, proximal half of
anterior margin with about 7-8 long setae.

Uropod 1: inner ramus 80 percent length of peduncle. armed with 14 spines; outer ramus with 14
spines; peduncle with row of 9 outer and 6 inner spines. Uropod 2: inner ramus armed with 14 spines.
outer ramus with 13 spines; peduncle with 5 outer and 5 inner spines. Uropod 3: inner ramus with 1 spine.
outer ramus about 2.1 times longer than peduncle, inner and outer margin each with 5-6 sets of spines in
groups of 1-3. Telson about as broad as long, notched about 1/3 distance to base, each lobe with 2-3 apical
spines: spine length about 1/3 of telson.

Male.—Differing from female as follows: much smaller with more slender, elongate body. Antenna 2: calceoli percent on peduncular segments 4 and 5, and first 4 segments of flagellum.

Uropod 2: inner ramus with 11 spines; outer ramus curved nearly to right angle with peduncle, with 2 inner and 2 outer spines, apex with 5 short spines; peduncle with 4 inner and 4 outer spines.

Variation.—The shape of pereopod 5-7 can be slightly more slender in some populations. The number of apical spines on the telson varies but is usually 2-3 per lobe.

Distribution and ecology.—This is the most widely distributed species of Crangonyx. In western North America it occurs as far north as southeastern Alaska and in eastern North America as far north as Newfoundland; in the south it occurs in southern Florida (fig. 30). Although widely distributed across much of North America, a majority of the collections have been made from the northern Pacific coastal region, the Great Lakes area, and on the southern Atlantic Coastal Plain.

The habitat of this species includes lakes, streams, ponds, swamps, bogs, ditches, drains and rarely caves. Sexually mature males, 7.5-11.0 mm; sexually mature females, 12.0 to 20.0 mm. Newly hatched young 2.0-3.0 mm. Ovigerous females occur from about January to June, after that only immature animals are found throughout the summer and fall. The life span is probably of about 1 year (Holsinger, 1972).

Remarks.—After examination of all the collections of C. richmondensis, I cannot find any good characters to separate the three previously named subspecies of C. richmondensis. The characters given by Bousfield (1958) to separate the subspecies were found to be variable and overlapping. Therefore, I cannot recognize them as different subspecies. Moreover, after examination of pertinent material, I could not find any morphological differences between C. alpinus and C. richmondensis thus I consider the former a synonym of C. richmondensis.

Crangonyx anomalus Hubricht

Figures 31-34


KENTUCKY. Bourbon Co.: spring 12.8 km SW of Millersburg, 1 ♂, L. Hubricht, 25 Apr 1941 (USNM); spring, 9.1 km SW of Paris, 1 ♀, L. Hubricht, 25 Apr 1941 (USNM); Clark Co.: stream about 11.2 km W
Figure 31.—*Crangonyx anomalus* Hubricht. Female cotype (15.5 mm), spring, 1.6 km E of Warrentown, Fayette Co., Kentucky: a, b. antennae 1, 2; c, d. maxillae 1, 2; e. lower lip; f. left mandible; g. inner and outer and palp dactyl of maxilliped. Female cotype (16.6 mm), same location: h, i. gnathopods 1, 2 (palmar margins enlarged).
Figure 32.—Crangonyx anomalus Hubricht. Female cotype (15.5 mm), spring, 1.6 km E of Warrentown, Fayette Co., Kentucky: a. head (in part); b. pereopod 3 (in part); c. pereopod 4; d. pleonal plates; e. peduncle of pleopod 1 (retinaculae enlarged); f, g, h. uropods, 1, 2, 3. Female cotype (16.6 mm), same location: i. pereopod 7.
Figure 33.—*Crangonyx anomalus* Hubricht. Male cotype (15.4 mm), spring. 1.6 km E of Warrentown, Fayette Co., Kentucky: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7; e. g. uropods 1, 3; f. uropod 2 (some spines enlarged); h. telson.
Figure 34.—Distribution of *Crangonyx anomalus* in North America. Solid circles represent 1-5 closely proximate localities.
of Clark County Court House on Colby Pike. 3 ♀, R. Fox, 1 Jan 1971; Fayette Co.: Coldstream Farm, pond No. 2, 1 ♂, 1 ♀, 3 juvs, collector not known. 30 Jan 1964; Idle Hour spring No. 2, 1 ♂, 1 ♀. J. R. Holsinger and R. M. Norton, 11 Apr 1965; seep-fed swamp off Tates Creek Rd., Lexington. 15 ♂, 13 ♀. J. R. Holsinger and R. McAdams. 5 Apr 1965; Maedico Creek. ca. 9.0 km W of Clark. 1 ♀. R. Fox, 1 Jan 1971; Pompoon creek ca. 11.2 km W of Clark. 1 ♂, 2 juvs. R. Fox, 1 Jan 1971; Waveland Farm spring-fed stream. 1 ♂, 1 ♀. J. R. Holsinger. 7 Mar 1964 and 1 ♀. 11 Apr 1965: Bryan Station Rd., 0.5 km NE of Eastin Rd., 4.8 km NE of Lexington. 100 specimens (♀, ♀). L. Hubricht, 25 Apr 1941 (USNM); spring, 1.6 km E of Warrentown, cotypes. 33 ♂, 39 ♀. L. Hubricht, 22 Nov 1940 (USNM); Garrard Co.: spring, 3.2 km NW of Lancaster, 3 ♂, 10 ♀. L. Hubricht, 24 Apr 1941 (USNM); Jefferson Co.: intermittent brook at Poplar Level Rd. and Audubon Rd., Louisville, 1 ♂, G. A. Cole, 13 Mar 1954 (USNM); Mason Co.: spring, 2.6 km N of Washington, 1 ♂, L. Hubricht, 25 Apr 1941 (USNM). OHIO. Brown Co.: spring, 8.0 km S of Georgetown. 4 ♂, 1 ♀. L. Hubricht, 25 Apr 1941 (USNM); spring rill, 2.9 km S of Georgetown, 5 ♂, L. Hubricht, 25 Apr 1941 (USNM); Clermont Co.: Shayler Run (sta., 4E), 1 ♂, 1 ♀. E. L. Robinson, 9 Mar 1970; Clinton Co.: small spring, 0.7 mi SE of Westboro, 1 ♂, 1 juv. L. Hubricht, 25 Apr 1941 (USNM); Greene Co.: springs. John Bryan State Park, 2 mi W of Clifton. 1 ♂, 2 ♀. 1 juv. L. Hubricht, 26 Apr 1941 (USNM); Shelby Co.: "5 mile cave" (=Miami River Cave ?). 3 ♀. A. Pizzini, 27 Nov. 1936 (USNM).

Diagnosis.--A large species easily distinguished from other members in the genus by strongly expanded posterior margins of pereopod bases. more than 30 minute serrations on the posterior margins of bases; and outer ramus of uropod 2 in male, which has 3- or 4-notched spines on inside. Largest male. 20.0 mm; largest female. 19.0 mm.

Female.--Eye round, reduced in size. Antenna 1. 50-55 percent length of body, about 1.7 times longer than antenna 2; primary flagellum with 27-32 segments. Antenna 2: flagellum with up to 11 segments: peduncular segments 4 and 5 with 4-6 sets of marginal setae radially arranged. Mandibles subequal. spine row with 6-8 spines; segment 2 of palpal with about 16-17 long setae: segment 3 with 3-4 A setae, 4 B setae (2 sets), 5 C setae, 5-6 E setae and a row of about 15 D setae. Maxilla 1: inner plate with 4-5 apical plumose setae; palp with 5-7 slender spines and 5 naked setae on apex. Maxilla 2, inner plate with oblique row of 7 plumose setae on inner margin. Maxillipede: inner plate apically with 4-5 bladelike spines. 2 naked setae, and 7-9 plumose long setae extending from inner margin to apex: outer plate with row of naked setae and 4-5 slender pectinate spines on inner margin and 1 apical plumose seta; inner margin of dactyl with 4-5 setae. nail long, about 1/4 length of dactyl.

Propod of gnathopod 1 more than 2 times longer than carpus; palm oblique, slightly convex, longer than posterior margin, inside and outside margins each with 2 rows of spine teeth, including 1 row of about 20 small spine teeth and 1 row of about 24 large spine teeth; defining angle with about 5 2-notched or 3-notched spine teeth on inner side. 1 row of 1 large and 4 small 2-notched or 3-notched spine teeth and 1 row of small 4-5 spine teeth on outside: 4 sets of superior medial setae in groups of 2-5: posterior margin.
with about 4 sets of setae in groups of 2-6. Dactyl of gnathopod 1 with row of 10 short setae on inner margin. Nail very short. Ventral margin of coxa 1 with 17-18 setae.

Propod of gnathopod 2 more than 2 times longer than carpus: palm strongly convex, oblique, longer than posterior margin, inside and outside margin each with 2 rows notched spine teeth, including 1 row of 23-25 small spine teeth and 1 row of 23-25 large spine teeth; defining angle with 3 large and 3 small spine teeth on inside. 1 very large, long spine teeth and 9 small spine teeth on outside: 7 sets of superior medial setae, mostly in groups of 5; posterior margin with 10 sets of setae in groups of 3-7. Dactyl of gnathopod 2 with row of very short setae on inner margin; dactyl nail very short. Ventral margin of coxa 2 with 13 setae.

Coxa of pereopod 3 with 16 marginal setae. Coxa of pereopod 4 with 32 marginal setae: dactyl of pereopod 4 about 35 percent length of propod. Pereopod 5: basis greatly expanded posteriorly, with more than 30 very shallow serrations on posterior margin; 11 sets of spines in groups of 1-3 on anterior margin: 6 setae on the anteroproximal margin. Pereopod 6: basis greatly expanded posteriorly. Distoposterior lobe well developed, more than 30 very shallow serrations along posterior margin: 10 sets of spines in groups of 1-3 on anterior margin: 5 long setae on anteroproximal margin. Pereopod 7: coxa with 3 setae along posterior margin and 4-5 small spines on the posterior margin of basis; basis greatly expanded posteriorly, with more than 30 very shallow serrations along posterior margin; 8 sets of short spines on anterior margin: 4 long setae on anteroproximal margin: dactyl about 33 percent length of propod.

Pleonal plates: posterior margin of plate 1 convex, with 1 short seta. Distoposterior corner not produced but weakly acute: posterior margin of plate 2 nearly straight with 1 seta. Distoposterior corner not produced but subacute. Ventral margin with up to 12 (subventral) spines: posterior margin of plate 3 nearly straight with 1 seta. Distoposterior corner not produced but subacute. Ventral margin with 9-11 subventral spines. Peduncle of pleopod 1 with 5-6 retinaculae and many long setae on outer margin.

Uropod 1: inner ramus 60 percent length of peduncle, armed with about 14 spines; outer ramus with about 13 spines: peduncle with 10-11 outer and 4-5 inner spines. Uropod 2: inner ramus armed with about 15 spines: outer ramus armed with about 9 spines: peduncle with 4 outer and 3-4 inner spines. Uropod 3: inner ramus with 1-2 spines. Outer ramus about 2 times longer than peduncle, inner and outer margin each with 3-4 sets of spines in groups of 3-5. Telson broader than long, notched about 1/4 distance to base, each lobe with 5-7 apical spines: spines longer than 1/2 length of telson.

Male.—Differing from female as follows: longer with same body shape or smaller with slender body shape. Antenna 2: calceoli small, present on peduncular segments 4 and 5 and first 4 segments of flagellum.

Uropod 2: outer ramus with 2 short, 3- or 4-notched spines on inside, 4-5 curved short spines on apex; inner ramus with about 17 spines; peduncle arcuate, reduced in size, with 4 outer and 4 inner spines. Telson slightly broader than long, notched about 3-7 distance to base.

Distribution and ecology.—This species is an inhabitant of springs and spring-fed streams in
northcentral Kentucky, southern Illinois, southeastern Indiana, and southwestern Ohio (fig. 34). It was also collected from single cave streams in Indiana and Ohio. Ovigerous females were found in collections made in winter and early spring. The southern Illinois population is highly disjunct, inasmuch as it occurs approximately 250 km from the heart of the range in northern Kentucky.

Remarks.—*C. anomalus* is unique in the genus *Crangonyx* by having some males larger than the largest known females. However, this observation is possibly biased by too few samples. In all collections of *C. anomalus* examined to date, a majority of females are larger and longer than the males, and only a few males are larger than the largest females. These may also be morphological variation between different populations, resulting in some populations with males that are more robust and larger than females. Since sexually mature females (with larger, well developed brood plates) sometimes have penes in other *Crangonyx* species (e.g. *C. indiamensis*), it is also remotely possible that the large males in *C. anomalus* transform from females when brood plates are lost after brooding. Future investigation is needed to answer these questions.

*Crangonyx indiamensis*, new species

Figures 35-38

*Crangonyx gracilis* Smith.—Banta, 1907:78.

Figure 35.—Crangonyx indiannensis, new species. Female paratype (18.5 mm). Rays Cave, Green Co., Indiana: a, b, antenna 1, 2; c, d, maxillae 1, 2; e, lower lip; f, dentate part of left mandible; g, right mandible; h, inner, outer plates and palp dactyl of maxilliped (greatly enlarged); i, j, gnathopods 1, 2 (palmar margins enlarged).
Figure 36.—*Crangonyx ianensis*, new species. Female paratype (18.5 mm), Rays Cave, Green Co., Indiana: a. b. c. pereopods 4, 5, 6 (in part); d. pereopod 7; e. pleonal plates; f, g, h. uropods 1, 2, 3; i. telson.
Figure 37.—*Crangonyx indianensis*, new species. Male paratype (11.5 mm). Rays Cave, Green Co., Indiana: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. e. f. uropods 1, 2, 3. Male paratype (12.5 mm). Rays Cave, Green Co., Indiana: g. telson.
Figure 38.--Distribution of *Crangonyx indianaensis* in North America. Solid circles represent 1-2 closely proximate localities. Karst regions of southern Indiana are enclosed by dotted lines.

Diagnosis.—A large species of the richmondensis group, distinguished from other members of this group by unproduced and subacute distoposterior corners of female pleonal plates; posterior margins of pereopods 5-7 with very shallow serrations; maxilla 2 inner plate with oblique row of up to 7-9 plumose setae; and much broader telson of the female. Largest male, 10.0 mm; largest female, 20.0 mm.

Female.—Eye small and ovate. Antenna 1, about 55 percent length of body, about 2 times longer than antenna 2: primary flagellum with 20 segments. Antenna 2, flagellum with 6 segments. Mandibles subequal, spine row with 7-8 spines; segment 2 of palp with 13-14 short and 7-8 long setae; segment 3 with 4 A setae, 2 B setae, 2-3 C setae, 5-6 E setae and a row of D setae. Maxilla 1: inner plate with 5-7 apical plumose setae; palp with 8-9 slender spines on apex. Maxilla 2, inner plate with oblique row of 7-9 plumose setae on inner margin. Maxilliped: inner plate apically with 4 bladelike spines, 2 naked spines, and 5-7 plumose setae on the inner margin and on apex: outer plate with row of naked setae and 5-7 slender pectinate spines on inner margin and 1 apical plumose seta; dactyl with 6-7 setae on inner margin; dactyl nail short.

Propod of gnathopod 1 about 2 times larger and longer than carpus and much broader; palm about 2 times longer than posterior margin, convex and very oblique, inside and outside each with 2-3 rows of spine teeth, including 33 spine teeth on inside, 37 on the outside; defining angle with 4 notched but weakly serrate spine teeth on inside. 1 large and 4 small notched spine teeth and 1 row of 4 notched spine teeth on outside: superior medial setae in 3-4 sets, inserted in groups of 3-4; setae on posterior margin densely inserted, 4-5 sets on proximal half. Dactyl with row of short setae on inner margin, nail short. Ventral margin of coxa 1 with 23 setae.

Propod of gnathopod 2 more than 2 times larger and longer than carpus and much broader; inside and outside palmar margin each with 2-3 rows of notched spine teeth, including 45 spine teeth on inside, 49 on outside; defining angle with 3 spine teeth on inside, 1 very large one on outside: superior medial setae in 7 sets in groups of 3-8; posterior margin with 6-7 sets of setae in groups of 4-10. Dactyl with row of short setae on inner margin; dactyl nail very short. Ventral margin of coxa 2 with 18 setae.

Coxa of pereopod 3 with 18 marginal setae. Cox of pereopod 4 with 33 marginal setae: dactyl of pereopod 4. 45 percent length of propod. Pereopod 5: basis with 20 shallow serrations along posterior margin; 9 sets of short spines on anterior margin; 4-5 long setae on anteroproximal margin. Pereopod 6: basis with 24 very shallow serrations along posterior margin; 11 short spines on anterior margin; 4 setae on anteroproximal margin. Pereopod 7: coxa with 6-8 setae on posterior margin; basis with 23 very shallow

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serrations along posterior margin: 11 short spines on anterior margin; 3 setae on anteroproximal margin; dactyl about 30 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 convex, with 1 seta, distoposterior corner subacute but not produced; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner subacute but not produced, ventral margin with 8 (subventral) spines; posterior margin of plate 3 slightly convex with 1 seta, distoposterior corner subacute but not produced, ventral margin with 5 (subventral) spines. Peduncle of pleopod 1 with about 7 retinaculae, many setae on outside margin, a few setae on inside margin.

Uropod 1: inner ramus about 75 percent length of peduncle, armed with 16 spines; outer ramus with 14 spines; peduncle with 11 outer and 7 inner spines. Uropod 2: inner ramus much longer than outer ramus, armed with 14 spines; outer ramus with 10 spines; peduncle with 5 outer and 4 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 2 times longer than peduncle, inner and outer margin each with 4-5 sets of spines in groups of 1-3. Telson much broader than long (about 1.5 times), notched about 1/5-1/4 distance to base, each lobe with 3 apical spines; spines about 1/2 length of telson.

Male.--Differing from female as follows: smaller with more slender, elongate body. Antenna 2: calceoli percent on peduncular segments 4 and 5, and first 3 segments of flagellum.

Propod of gnathopod 1 with 21 spine teeth on inside, 23 on outside, defining angle with 1 notched and 4 notched but weakly serrate spine teeth on inside, 10 notched spines on outside (1 very large); 3 sets of superior medial setae in groups of 2-3; posterior margin setae densely inserted on proximal half.

Palmar margin of propod of gnathopod 2 strongly oblique, with 28 spine teeth on inside, 28 on outside; defining angle with 6 spine teeth on inside, 10 on outside (1 very large); 7 sets of superior medial setae in groups of 2-5.

Uropod 2: inner ramus with 12 spines; outer ramus reduced in size, curved slightly, with 2 short spines on inner and outer margins, apex with 4 spines; peduncle with 4 outer and 4 inner spines.

Variation.--All females examined had penes and some had calceoli. Therefore it was often difficult to distinguish males from immature females.

Type-locality.--Rays Cave, located in Greene County, Indiana, consists primarily of a single stream passage that is developed in the Beech Creek limestone of Mississippian age (Powell, 1961). According to J. R. Holsinger (pers. comm.), the type series was collected from under rocks in a shallow stream 100-300 meters or more inside the cave. Specimens were light grayish to pale yellowish in color when alive. Darkly pigmented specimens of _Gammarus minus_ were abundant near the entrance and in the stream issuing from the mouth of the cave. There was little or no overlap between these two species in the cave stream.

Distribution and ecology.--Although this species occurs in many caves of southern Indiana, it is not trogloborphic. Its range, which is restricted to the karsts region of southern Indiana, covers a linear distance of 120 km (fig. 38).

_Crangonyx indianensis_ was collected from cave streams and surface springs. Ovigerous females were found in June and November collections. In caves it was found living with other amphipods, viz., _C._
Packardi, Gammarus minus, and the isopods Caecidotea stygia, and Lirceus sp.

Etymology.—The specific name refers to the occurrence of this species in the state of Indiana.

Remarks.—The species that Banta (1907) found in Mayfield Cave and called C. gracilis actually belongs to the new species described above. Although C. packardi has also been collected from this cave (see material examined section under C. pacakardi), Banta (1907) stated that the specimens he examined from Mayfield Cave had well-developed and distinctly pigmented eyes and the largest specimens were up to 18 mm long. These match the characteristics of C. indianaensis and not C. packardi (or C. gracilis). Specimens of C. indianaensis were also collected from Mayfield Cave by T. C. Barr, Jr. on 20 Aug 1957 and their identity was verified by me in the present study.

**Crangonyx cornutus**, new species

*Figures 39-42*

Material examined (paratypes unless designated otherwise).—ALABAMA. Jackson Co.: ditch at Stevenson, 4 ♂, J. E. Cooper and M. R. Cooper, 9 Apr 1966; Madison Co.: crayfish burrows in Ka Lea Park, 4 ♂, M. R. Cooper, 12 Jun 1967; slough, 4.3 km NW of Gurley, holotype ♀, 65 specs (♂, ♀). L. Hubricht, 12 Apr 1941 (USNM). TENNESSEE. Davidson Co.: spring, "Fortland" near Shelby Park, Nashville, 6 ♂, 6 ♀, L. Hubricht, 31 May 1941 (USNM).

Diagnosis.—A medium-sized species morphologically similar to other species of the richmondensis group but distinguished from them by unique features of uropod 2 of male, which has 1-2 large (thick) spines on the middle of outer ramus (c.f., C. disjunctus); and more setae on maxillae. Largest male, 8.5 mm; largest female, 14.0 mm.

Female.—Eye small, round. Antenna 1, about 60 percent length of body, about 1.9 times longer than antenna 2; primary flagellum with about 28 segments. Antenna 2, flagellum with 9 segments. Mandibles subequal, spine row with 5-7 spines; segment 2 of palp with 12 setae. segment 3 with 3 A setae. 2 B setae, 3 C setae. 5 E setae and a row of D setae. Maxilla 1: inner plate with 5 apical plumose setae; palp with 8 slender spines on apex. Maxilla 2, inner plate with oblique row of 4-5 plumose setae on inner margin. Maxilliped: inner plate apically with 4 bladelike spines, 2 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 2-3 slender pectinate spines on inner margin and 1 apical plumose seta; dactyl with 3 setae on inner margin; dactyl nail short, about 1.4 length of dactyl.

Propod of gnathopod 1 more than 2 times longer than carpus; palm very oblique, convex, longer than posterior margin, with 13 spine teeth on inside, 16 on the outside; defining angle with 4 notched spine teeth on inside. 2 rows of spine teeth on outside (1 row of 5-6 small spines and 1 row of 1 slightly large and 3 small notched spine teeth); superior medial setae few in number and mostly doubly inserted; setae on...
Figure 39. *Crangonyx cornutus*, new species. Female paratype (11.5 mm), slough, 4.3 km NW of Gurley, Madison Co., Alabama: a. antenna 1; b. c. maxillae 1, 2; d. lower lip; e. left mandible; f. dentate part of right mandible; g. inner and outer plates and palp dactyl of maxilliped (greatly enlarged); h. i. gnathopods, 1, 2 (palmar margins greatly enlarged).
Figure 40.—Crangonyx cornutus, new species. Female paratype (11.5 mm), slough, 4.3 km NW of Gurley, Madison Co., Alabama: a, b, c, d, pereopods 3, 4, 5, 6 (in part); e, pereopod 7; f, pleonal plates; g, h, i, uropods 1, 2, 3; j, telson.
Figure 41.—Crangonyx cornutus, new species. Male paratype (7.2 mm), slough, 4.3 km NW of Gurley, Madison Co., Alabama: a. antenna 2 (in part); b, c. gnathopods 1, 2 (palmar margins greatly enlarged); d. uropod 2 (outer ramus enlarged); e. uropod 3; f. telson. Male paratype (7.2 mm), same location: g. uropod 2 (outer ramus enlarged).
Figure 42. Distribution of *C. ornatus* in North America. Solid circles represent single localities.
posterior margin in 3 sets, inserted in groups of 1-3. Dactyl with 3 setae on outer margin, nail short. Ventral margin of coxa 1 with 9 setae.

Propod of gnathopod 2 more than 2 times longer than carpus: palm very oblique, convex, much longer than posterior margin, with 19 spine teeth on inside, 16 on outside; defining angle with 8 spine teeth on inside, 8 on outside (1 very large); superior medial setae in 7 sets inserted in groups of 1-3; posterior margin with 5 sets setae in groups of 3-6. Dactyl with 3-4 setae on outer margin. Ventral margin of coxa 2 with 11 setae.

Coxa of pereopod 3 with 10 marginal setae. Coxa of pereopod 4 slightly longer than broad, with 18 marginal setae, dactyl of pereopod 4 about 35 percent length of propod. Pereopod 5: basis with 14 shallow serrations along posterior margin; 7 short spines on anterior margin; 6 setae on anteroproximal margin.
Pereopod 6: basis with 13 shallow serrations along posterior margin; 8 short spines on anterior margin; 5 setae on proximal margin. Pereopod 7: coxa with 3 setae on posterior margin; basis with 17 shallow serrations along posterior margin; 7 short spines on anterior margin; 4 setae on another proximal margin; dactyl about 33 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner acute but not produced; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner strongly produced and acute. Ventral margin with 4 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner also strongly produced and acute, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with up to 5 retinaculae, many setae on outside margin, few on proximal end of inner margin.

Uropod 1: inner ramus 75 percent length of peduncle, armed with 15 spines: outer ramus with 13 spines: peduncle with 10 outer and 5 inner spines. Uropod 2: inner ramus armed with 15 spines: outer ramus with 10 spines: peduncle with 4 outer and 4 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 2 times longer than peduncle, inner and outer margin each with 4 sets of spines in groups of 1-5. Telson broad, about as broad as long, notched about 1/6 distance to base, each lobe with 2 apical spines: spines less than 1/2 length of telson.

Male.—Differing from female as follows: smaller with more slender, elongate body. Antenna 2: calceolus percent on peduncular segments 4 and 5, and first 3 segments of flagellum.

Uropod 2: outer ramus strongly curved, with 1-2 very large spines on inner margin in the middle. 2-3 very small outer spines, apex with 3-5 short spines: peduncle with 3-4 outer and 4 inner spines. Uropod 3: inner ramus with 1 spine: outer ramus about 2.5 times length of peduncle, inner and outer margins each with 3 sets of spines in groups of 1-2.

Type-locality.—slough. 4.3 km NW of Gurley, Madison County, Alabama.

Distribution and ecology.—The range of this species, which to date is based on 3 collections in northern Alabama and 1 collection in central Tennessee, covers a linear distance about 150 km (fig. 42). Its habitats include a ditch, a slough, springs, and crayfish burrows. It was found together with C. consimilis in

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a spring in Tennessee and with *C. floridanus* in a ditch in Jackson Co., Alabama. Ovigerous females were collected in April and May.

**Etymology.**—The epithet *cornutus* is from Latin meaning "homed," which is in reference to the large, horn-like spine on the outer ramus of male uropod 2 of male.

*Crangonyx obliquus* (Hubricht and Mackin)

Figures 43–46

*Eucrangonyx obliquus* Hubricht and Mackin. 1940:195. fig. 4 [type-locality: a small creek W of the college chapel, Clarksville, Johnson Co., Arkansas].


Material examined.—ALABAMA. Green Co.: roadside ditch. 1.3 km N of Boligee. 5 ♂, 1 ♀. L. Hubricht. 11 Feb 1962 (USNM). ARKANSAS. Faulkner Co.: temporary stream. 1.0 km S of Wooster. 6 ♂, 5 ♀. L. Hubricht. 3 May 1940 (USNM); Jefferson Co.: slough. 6.9 km NE of Altheimer. 1 ♂, 1 ♀. L. Hubricht. 7 Apr 1941 (USNM): Johnson Co.: oxbows of small stream behind the college chapel, Clarksville. 4 ♂, 4 ♀. L. Hubricht. 3 May 1940 (USNM); small creek W of the college chapel. Clarksville. holotype ♂. L. Hubricht. 28 Apr 1936 (USNM); Monroe Co.: stream 7.2 km SW of Clarendon. 1 ♂, 7 ♀. L. Hubricht. 7 Apr 1941 (USNM): slough. 1.7 km N of Holly Grove. 3 ♂, 6 ♀. L. Hubricht. 7 Apr 1941 (USNM); Perry Co.: cypress swamp 3.2 km N of Perry. 26 specs (♂, ♀). L. Hubricht. 5 May 1940 (USNM); Phillips Co.: temporary pool 8.8 km N of Barton. 1 ♂, 1 ♀. L. Hubricht. 6 Apr 1940 (USNM); Yell Co.: temporary pool 0.6 km W of Danville. 1 ♂, 3 juvs. L. Hubricht. 4 May 1940 (USNM). ILLINOIS. Johnson Co.: Heron Pond 1.6 km NW of Foreman. 6 ♂, L. M. Page and B. M. Burr. 30 Mar 1973. LOUISIANA. Beauregard Par.: 4.8 km N of Newlin (habitat not given). 2 ♂, G. H. Penn. 7 Feb 1941 (USNM); Lafourche Par.: Bayou Beouf. Kraemer. 7 ♂, 18 Apr 1936 (USNM): Pointe Coupee Par.: roadside pool 3.2 km E of Lottie. 8 ♂, 1 ♀. L. Hubricht. 12 Apr 1964 (USNM); Lincoln Par.: slough 1.4 km S of Dubach. 2 ♂. L. Hubricht. 8 Apr 1941 (USNM); Morehouse Par.: ditch on E side of US 165. ca. 7.2 km S of Bastrop. 1 ♂ (USNM) and 6 ♂, J. E. and M. R. Cooper. 15 Mar 1967; Ouachita Par.: small ditch. 3.2–4.8 km NW of Monroe. 1 ♂. J. E. and M. R. Cooper. 25 Dec 1965. MISSISSIPPI. Forrest Co.: small stream in swamp near Black Creek. 3.2 km SW of Brooklyn. 1 ♂. L. Hubricht. 2 Mar 1963 (USNM); Harrison Co.: Pass Christian (habitat not given). 1 ♂. J. and W. Rapp. 17 Feb 1946 (USNM); Lauderdale Co.: pool 4.8 km E of Lost Gap. 1 ♂. L. Hubricht. 3 Feb 1962 (USNM); roadside pool, US Rt. 80 at 31 St.

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Figure 43.—*Crangonyx obliquus* (Hubricht and Mackin). Female topotype (12.4 mm). Oxbows of small stream behind the college chapel, Clarksville, Johnson Co., Arkansas: a. b. antennae 1, 2; c. d. maxillae 1, 2; e. lower lip; f. right mandible; g. h. gnathopods 1, 2 (palmar margins enlarged).
Figure 44.--*Crangonyx obliquus* (Hubricht and Mackin). Female topotype (12.4 mm), oxbows of small stream behind the college chapel, Clarksville, Johnson Co., Arkansas: a, d, c, pereopods 4, 6, 7 (in part); b, pereopod 5; e, pleonal plates; f, g, h, uropods 1, 2, 3; i, telson.
Figure 45.—*Crangonyx obliquus* (Hubricht and Mackin). Male topotype (10.1 mm), oxbows of small stream behind the college chapel, Clarksville, Johnson Co., Arkansas: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7 (in part); e. f. g. uropods 1, 2, 3; h. telson.
Figure 46.—Distribution of *Crangonyx obliquus* in North America. Solid circles represent 1-3 closely proximate localities. The dotted line denotes the outer boundary of the Coastal Plain.

Diagnosis.—Morphologically closely similar to C. richmondensis but distinguished by having 2-3 setae on outer margins of dactyl of gnathopods in both males and females. Largest male. 10.0 mm; largest female. 20.0 mm.

Female.—Eye large and ovate. Antenna 1, about 50 percent length of body, about 1.5 times longer than antenna 2; primary flagellum with 28 segments. Antenna 2, flagellum with 7-8 segments. Mandibles subequal, spine row with 5-6 spines; segment 2 of palp with 8-9 long setae, segment 3 with about 2 A setae. 1 B seta. 2 C setae. 3 E setae and a row of D setae. Maxilla 1: inner plate with 3 apical plumose setae; palp with 5-6 slender spines on apex. Maxilla 2, inner plate with 1 plumose seta on inner margin. Maxilliped: inner plate apically with 3-5 bladelike spines, 1 plumose spines, 2 naked spines, and 4-5 plumose setae extending from inner margin to apex: outer plate with row of naked setae and 3-4 weak pectinate spines on inner margin; dactyl inner margin with 3-4 setae. nail long, about 1.4 length of dactyl.

Propod of gnathopod 1 about 2 times larger and longer than carpus: palm convex, oblique, much longer than posterior margin. inside and outside each with 2 rows of notched spine teeth, about 19 on inside. 23 on the outside: defining angle with 5 notched spine teeth on inside, two rows of spine teeth on outside: inner row with 5 small spines, outer row with 1 very large and 5 small spines; superior medial setae in 3 sets, singly or doubly inserted; posterior margin with 3-4 sets of setae singly inserted or in groups of 2-4 on proximal half. Dactyl with row of short setae on inner margin. outer margin with 2-3 setae, nail very short. Ventral margin of coxa 1 with 7-8 setae.

Propod of gnathopod 2 more than 2 times larger and longer than carpus and much broader: palm convex, very oblique, much longer than posterior margin, inside and outside each with 2 rows of notched spine teeth, about 22 on inside, about 21 on outside; defining angle with 5 spine teeth on inside. 10 on outside: about 4 sets of superior medial setae in groups of 1-3; posterior margin with 5 sets of setae in groups of 2-4. Dactyl with row of short setae on inner margin. outer margin with 2-3 setae. nail very small and short. Ventral margin of coxa 2 with 10 setae.

Coxa of pereopod 3 with 12 marginal setae. Coxa of pereopod 4 with 17 marginal setae. Pereopod 5: basis with 13 shallow serrations along posterior margin; 9 spines on anterior margin; 3 long setae on the anteroproximal margin. Pereopod 6: basis with 14 serrations along posterior margin; 8 short spines on
anterior margin: 5 long setae on anteroproximal margin. Pereopod 7: coxa with 3 setae on the posterior margin; basis with 13 serrations along posterior margin; 10 short spines on anterior margin; 4 long setae on anteroproximal margin; dactyl about 25 percent the length of propod.

Pleon plates: posterior margin of plate 1 convex, with 1 seta, distoposterior corner produced and acute; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner distinctly produced and strongly acute, ventral margin with 2-3 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner produced and acute, ventral margin with 1 (subventral) spines. Peduncle of pleopod 1 with about 4 retinaculae; many setae on outside margin.

Uropod 1: inner ramus 75 percent length of peduncle, armed with 16 spines; outer ramus with 14 spines; peduncle with row of 5 outer and 8 inner spines. Uropod 2: inner ramus armed with 16 spines; outer ramus with 13 spines; peduncle with 4 outer and 5 inner spines. Uropod 3: inner ramus with 1 seta, outer ramus about 2.2 times longer than peduncle, inner and outer margin each with 4-6 sets of spines in groups of 1-3; peduncle with several spines on lateral border and apex. Telson about as broad as long, notched about 1/2 distance to base, each lobe with 2 apical spines up to 1/3 length of telson.

Male.—Differing from female as follows: smaller with more slender, elongate body. Antenna 2: calceoli percent on peduncular segments 4 and 5, and first 3 segments of flagellum.

Uropod 1: inner ramus about 60 percent of peduncle, lacking inner spines but with 3 long outer spines, apex with 5 spines; outer ramus with 13 spines; peduncle with 8 outer and 4 inner spines. Uropod 2: inner ramus with 13 spines; outer ramus strongly curved laterally, with 2 short inner and 2 short outer spines, apex with 5 spines; peduncle with 4 outer and 3-4 inner spines.

Distribution and ecology.—The range (about 850 km across) of this species, which is largely restricted to the Coastal Plain of south-central United States, is situated primarily within the lower Mississippi River drainage basin (fig. 46). Only a few locality records exist outside the Coastal Plain and occur just to the north of it.

This species is found in a variety of habitats, including roadside ditches, small streams, small creeks, sloughs, cypress swamps, ponds, and pools. Sexually mature female, 13.5-20.0 mm, sexually mature male, 8.0-10.0 mm. It has been found in association with the amphipods *C. pseudogracilis* and *Synurellci bifurca.*

Remarks.—Nicholas (1960) mistakenly called this species a troglobite and Krekeler and Williams (1966) repeated Nicholas' error by listing it as a true cave animal from Indiana. They did not give any collection records for it, however. McDaniel and Smith (1976) also mistakenly listed this species as a troglophile in the cave fauna of Arkansas, another mistake undoubtedly influenced by the original error of Nicholas (1960).
**Crangonyx disjunctus**, new species

Figures 47-50

Material examined (paratypes unless designated otherwise).—NORTH CAROLINA. Gates Co.: Hamburg ditch and marsh. Dismal Swamp. 9 ♀, 6 ♂. S. Hetrick. 2 Mar 1974; Hartford Co.: Winton. 2 ♀. (collector and habitat not given). 23 Mar 1940 (USNM). VIRGINIA. Chesapeake (Norfolk County): roadside ditch. 1.6 km S of Wallacetown. 2 ♀. J. R. Holsinger and C. H. Holsinger. 18 Apr 1971; sphagnum bog. VA Chain ferry. North Ditch. Dismal Swamp. 4 ♀. R. Rose. 15 Nov 1985; Elizabeth City Co.: small stream. 6.4 km NW of Hampton. 7 ♀, 8 ♂. L. Hubricht. 23 Jan 1944 (USNM); Hampton (Elizabeth City County): shallow pool near forested wetland on NASA Langley Research Center. 1 ♀. R. T. Tuner et al. 14 Mar 1994; small pool. forested wetland on western side of NASA Langley Research Center. Hampton. 1 ♀. R. L. Bedenbaugh. 17 Mar 1994; Henrico Co.: Brook Hill N of Richmond. 5 ♀, 20 ♂. A. Pizzini. 30 Apr 1939 (USNM); Highland Co.: spring on Sapling Ridge. 2 ♀. C. Pague. May 1990 (not paratype); Isle of Wight Co.: outlet of drain tile on Taylor Farm. 5.6 km N of Chuckatuck. 2 ♀. J. R. Holsinger. 24 Apr 1983; small stream. 1.6 km N of Bartlett. 5 ♀. L. Hubricht. 2 Apr 1944 (USNM): roadside ditch. 0.5 km N of Carrollton. 12 ♀, 4 ♂. L. Hubricht. 30 Jan 1944 (USNM); small stream. 1.6 km S of Rescue. holotype ♀. 74 specs (♀, ♂). L. Hubricht. 12 Mar 1944 (USNM); vernal pond in wetland. ca. 6.4 km NW of Windsor. 1 ♀. H. Jones. 12 Apr 1994; Nansemond Co.: small spring and stream. 3.2 km ESE of Chuckatuck. 1 ♀. J. R. Holsinger and D. Culver. 5 Feb 1969; Washington ditch. Dismal Swamp. 3.2 km ENE of Saunders. 46 specs (♀, ♂). L. Hubricht. 21 Nov 1943 (USNM); pool in Dismal Swamp near Washington Ditch. 2 ♀. K. Garrett and B. H. Powell. 28 Apr 1971; Dismal Swamp, just N of Washington Ditch. 5 ♀. J. R. Holsinger. 8 May 1971; pool 70 meters from Lynn Ditch. Dismal Swamp. 1 ♀. 5 ♀. K. Garrett. 30 Jan 1972; temporary pool in woods. 1.6 km E of Driver. 3 ♀, 4 ♂. 1 juv. L. Hubricht. 26 Mar 1944 (USNM); stream in swamp. 2.4 km NE of Saunders. 80 specs (♀, ♂). L. Hubricht. 21 Nov 1943 (USNM); Whaleyville (habitat not given). 5 ♀, 1 ♂. R. Bray. 22 Mar 1940 (USNM); small stream in swamp. 2.4 km W of Baker Store. 20 ♀, 1 ♂. L. Hubricht. 12 Nov 1944 (USNM); New Kent Co.: roadside pond. 3 mi E of Providence Ford. 5 ♀, 1 juv. J. R. Holsinger. 13 Apr 1972; Norfolk Co.: roadside ditch. Bowers Hill. 9 ♀, 2 ♂. L. Hubricht. 25 Feb 1945 (USNM); small stream. 0.8 km W of Churchland. 8 ♀, 13 ♂. L. Hubricht. 30 Jan 1944 (USNM); stream in swamp. 3.2 km S of North Landing. 7 ♀, 4 ♂. 9 juvs. L. Hubricht. 9 Apr 1944 (USNM); stream in swamp. 4.8 km S of North Landing. 11 ♀, 3 ♂. L. Hubricht. 9 Apr 1944 (USNM); temporary pond. 3.2 km WSW of Bowers Hill. 8 ♀, L. Hubricht. 21 Nov 1943 (USNM); temporary pond. Dismal Swamp. 3.2 km SSE of Bowers Hill. 80 specs (♀, ♂). L. Hubricht. 14 Nov 1943 (USNM); Northampton Co.: small stream. 1.6 km S of Capeville. 15 ♀. L. Hubricht. 16 Apr 1944 (USNM); Princess Anne Co.: temporary pool in swamp. 1.6 km SE of Thalia. L. Hubricht. 45 specimens. 25 Nov 1943 (USNM); Southampton Co.: Charles Plantation (habitat not given). Franklin. 7 ♀, 1 ♂. R. Bray. 22 Mar
Figure 47.—*Crangonyx disjunctus*, new species. Female paratype (13.3 mm), small stream, 1.6 km S of Rescue, Isle of Wight Co., Virginia: a, head (in part); b, antenna 1; c, d, maxillae 1, 2; e, lower lip; f, dentate part of left mandible; g, right mandible; h, inner and outer plates and palp dactyl of maxilliped (greatly enlarged); i, j, gnathopods 1, 2 (palmar margins enlarged).
Figure 48.—*Crangonyx disjunctus*, new species. Female paralyze (13.3 mm), small stream, 1.6 km S of Rescue, Isle of Wight Co., Virginia: a, b, c, pereopods 3, 5, 6 (in part); d, pereopod 7; e, pleonal plates; f, retinacula of pleopod (enlarged); g, h, i, uropods 1, 2, 3; j, telson.
Figure 49.—*Crangonyx disjunctus*, new species. Male paratype (9.5 mm), small stream, 1.6 km S of Rescue, Isle of Wight Co., Virginia: a, antenna 2; b, c, gnathopods 1, 2 (palmar margins enlarged); d, e, uropods 2, 3; f, telson.
Figure 50.—Distribution of *Crangonyx disjunctus* in North America. Solid circles represent 1-3 closely proximate localities. The dotted line denotes the "fall line" or "fall zone" between the Coastal Plain and Piedmont.
1940 (USNM): Virginia Beach (Princess Anne County): Stumpy Lake near golf course. 8.0 km S of Kempsville. 1 ♀, 10 juvs. J. R. Holsinger and C. H. Holsinger. 2 May 1971; Warwick Co.: swamp. 0.8 km NE of Harpersville. 7 ♀, 16 ♂. L. Hubricht. 23 Jan 1944 (USNM); ditch. 2.4 km NE of Morrison. 37 ♀, 22 ♂. L. Hubricht. 23 Jan 1944 (USNM); pool in woods. 4.0 km NW of Newport News. 1 ♀, 7 ♂. L. Hubricht. 23 Jan 1944 (USNM); small stream 0.5 km SW of Tabb. 4 ♀, 12 ♂. L. Hubricht. 23 Jan 1944 (USNM); pond 0.6 mi S of Grafton Church. 3 ♀. P. H. Stevenson and S. H. Holbrook. 13 Feb 1993; pond on Rt. 17, 1.1 km S of Harris Grove. 14 ♀, 11 ♂. J. R. Holsinger et al. 9 Mar 1994.

Diagnosis.—A large species of the *richmondensis* group distinguished from other members of the group by inner plate of maxilla 1 with up to 5 apical plumose setae; inner plate of maxilla 2 with 3-4 plumose setae on inner margin near apex; uropod 2 of male with only 2-4 thick bladelike spines on outside. Largest male, 11.5 mm; largest female, 19.5 mm.

Female.—Eye small and round. Antenna 1. 55 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with 27 segments. Antenna 2, flagellum with 8 segments. Mandibles subequal. spine row with 6 spines; segment 2 of palp with 10-11 long setae. segment 3 with 3-4 A setae. 1 B seta. 3 C setae. 3-4 E setae and a row of D setae. Maxilla 1: inner plate with 5 apical plumose setae; palp with 5-6 slender spines on apex. Maxilla 2, inner plate with 3-4 plumose setae on inner margin near apex. Maxilliped: inner plate apically with 4 bladelike spines, 1 naked spine, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked spines and 4-5 slender pectinate spines on inner margin; dactyl with 2-3 setae on inner margin near nail; dactyl nail short, less than 1/4 length of dactyl.

Propod of gnathopod 1 more than 2 times larger and longer than carpus and much broader; palm very oblique, convex. longer than posterior margin, inside and outside each with 2-3 rows of notched spine teeth. 21 on inside. 23 on the outside: defining angle with 7 spine teeth on inside, 1 row of 1 large and 5 small spine teeth and 1 row of 7 small spine teeth on outside; posterior margin with 4-5 sets of setae inserted in groups of 1-5 on proximal half. Dactyl with row of short setae on inner margin. nail very short. Ventral margin of coxa 1 with 12 setae.

Propod of gnathopod 2 more than 2 times larger and longer than carpus; palm more oblique, convex. much longer than posterior margin, inside and outside each with 2 rows of spine teeth. about 20 on inside. 18 on outside: defining angle with 8 spine teeth on inside, 15 on outside (1 very large); superior medial setae doubly or singly inserted: posterior margin with 6 sets of setae in groups of 2-6. Dactyl with row of short setae on inner margin. nail very short. Ventral margin of coxa 2 with 11 setae.


Pereopod 6: basis with 15 shallow serrations along posterior margin: 10 short spines on anterior margin: 12 short and long setae on anteroproximal margin. Pereopod 7: coxa with 3 setae on the posterior margin: basis with 18 shallow serrations along posterior margin: 14 short spines on anterior margin: 9 short and
long setae on anteroproximal margin: dactyl about 30 percent the length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner acute but not produced; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner strongly produced and acute, ventral margin with 6 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner produced and acute, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 3 retinaculae, about 5 setae on distal end of outside margin, about 10 setae on proximal half of inside and outside margins.

Uropod 1: inner ramus 80 percent length of peduncle, armed with 14 spines; outer ramus with 12 spines; peduncle with row of 8 outer and 6 inner spines. Uropod 2: inner ramus armed with 16 spines; outer ramus with 11 spines; peduncle with 4 outer and 5 inner spines. Uropod 3: inner ramus with 1-2 spines. outer ramus about 2 times longer than peduncle. inner and outer margin each with 4-5 set of spines in groups 1-5. Telson broader than long, notched about 1/4 distance to base, each lobe with 3-4 apical spines; spines less than 1/2 length of telson.

Male.--Differing from female as follows. Smaller with more slender, elongate body. Antenna 1: primary flagellum with 15 segments. Antenna 2: flagellum with 8 segments, calceoli percent on peduncular segments 4 and 5 and first 5 segments of flagellum.

Propod of gnathopod 1 palm with 12 notched and 4 simple spine teeth on inside. 13 notched spine teeth on outside: defining angle with 3 spine teeth on inside and 1 large and 6 small spine teeth on outside. Propod of gnathopod 2 palm margin strongly oblique, with 19 spine teeth on inside. 16 on outside: defining angle with 7 spine teeth on inside and 10 on outside.

Pereopod 7: basis with 16 serrations along posterior margin: 5-6 short spines on anterior margin: 2 long setae on anteroproximal margin: dactyl about 33 percent length of corresponding propod.

Uropod 1: inner ramus with 12 spines; outer ramus with 11 spines; peduncle with 7 outer and 4 inner spines. Uropod 2: inner ramus with 15 spines; outer ramus strongly curved laterally, with 2-4 outer bladelike spines, no inner spines, apex with 5 spines; peduncle with 4 outer and 3 inner spines. Uropod 3: inner ramus with 1 spine; outer ramus about 1.8 times length of peduncle, inner and outer margins each with 3-4 sets of spines in groups of 1-4. Telson broader than long, notched about 1/5 distance to base: each lobe with 3 apical spines; spines about 1/2 length of telson.

Type-locality.--Small stream, about 1.6 km S of Rescue, Isle of Wight County, VA.

Distribution and ecology.--The range of this species is restricted to the Coastal Plain of southeastern Virginia and northeastern North Carolina, with exception of a single highly disjunct locality in extreme western Virginia, approximately 200 km west of the eastern localities (fig. 50). To date this species has not been found in the intervening Blue Ridge Mountains or Piedmont.

On the Coastal Plain, C. disjunctus was found in ditches, marshes, streams, swamps, pools, and ponds. Sexually mature females are 10-19.5 mm, and sexually mature male are 9.0-11.0 mm. Ovigerous females
were collected during January, March, April and May. This species has been found together with other amphipods, including *C. serratus*, *C. polustris* and *C. orientalis*. It co-occurs with *C. polustris* and *C. orientalis* in Grafton Ponds (in York Co., Virginia).

**Etymology.**—The epithet *disjunctus* is from Latin meaning "disunited," so named because of the distinctly disjunct population in extreme western Virginia.

*Crangonyx dearolfi* Shoemaker

**Figures 51-54**


**Material examined.**—MARYLAND. Washington Co.: Cave in field at Charles Mill. 3 juvs. R. Franz. 7 Sep 1968; Natural Well near Downsville. 1 ♂. 1 ♀. R. Franz. 11 Jun 1969; Hogmaw Cave (Rohrersville caves). 1 ♂. R. Franz. 21 Jan 1967 and 2 ♀. 9 Dec 1967. PENNSYLVANIA. Berks Co.: Hobo Cave, holotype ♀ (USNM 78266), 4 ♀, 1 ♂. K. Dearolf. 28 Jul 1938 (USNM); Cumberland Co.: Carnegie Cave, 1 ♂. B. P. Smeltzer. collection date unknown (USNM); Dauphin Co.: Brownstone Cave, 1 ♀. K. Dearolf. 3 Sep 1937 (USNM); Franklin Co.: Python Pit Cave. 1 ♀. B. Barton. 25 Jun 1993; York Co.: York Cave (or North York Cave), 1 ♀. P. J. Spangler. 1948 (USNM); "cave in Pennsylvania" (county not given). 1 ♀. R. E. Hoffmaster. 1949 (USNM).

**Diagnosis.**—A large troglobitic species of the *richmondensis* group easily distinguished from all other species of *Crangonyx* by having tri-fid or quadri-fid spine teeth on palms of gnathopod propods: longer antenna 1, and more spinose appendages. Largest male. 15.4 mm; largest female. 22.0 mm.

**Female.**—Eye consisting of only few degenerate elements or completely absent. Antenna 1. about 50 percent length of body, about 1.4 times longer than antenna 2; primary flagellum up to 37 segments. Antenna 2. flagellum with 15 segments, calceoli may be present on first several segments of flagellum; peduncular segments 3, 4 and 5 with many sets of marginal setae (3-10 setae per set). Mandibles subequal, spine row with 8-9 spines: segment 2 of palp with 12-13 long setae, segment 3 with 4 A setae, 6 B setae, 2 C setae, 5-6 E setae and a row of D setae. Maxilla 1: inner plate with 3-4 apical plumose setae: palp with 5-7 slender spines and 5-6 setae on apex. Maxilla 2. inner plate with oblique row of 2-3 plumose setae on inner margin. Maxilliped: inner plate apically with 5-6 bladelike spines, 4 naked setae, and 5-6 plumose setae on inner margin: outer plate with row of naked setae and naked slender bladelike spines on inner margin: dactyl inner margin with 5-6 setae. outer margin with 4-5 setae: dactyl nail short, about 1/5 length of dactyl.

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Figure 51.—*Crangonyx dearolfi* Shoemaker. Female (19.0 mm), natural well near Downsville, Washington Co., Maryland: a. b. maxillae 1, 2; c. lower lip; d. right mandible; e. inner and outer plates and palp dactyl of maxilliped (greatly enlarged); f. g. gnathopods 1, 2 (palmar margins enlarged).
Figure 52.—*Crangonyx dearolfi* Shoemaker. Female (19.0 mm), natural well near Downsville, Washington Co., Maryland: a, b, antennae 1, 2; c, d, e, pereopods 3, 4, 7 (in part); f, peduncle of pleopod 1 (retinacula enlarged); g, pleonal plates; h, i, uropods 2, 3; j, telson.
Figure 53.—*Crangonyx dearolfi* Shoemaker. Male (14.0 mm), natural well near Downsville, Washington Co., Maryland: a. antenna 2; b, c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7; e, f, g. uropods 1, 2, 3.

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Figure 54.—Distribution of *Crangonyx dearelli* in North America. A solid circle represents 1-3 closely proximate localities.
Propod of gnathopod 1 much broader than, and more than 2 times larger and longer than carpus: palm almost 2 times longer than the length of posterior margin, strongly oblique and convex: inside and outside each with 2 or 3 rows of spine teeth, largest spine teeth in outer row, more than 30 spine teeth on each side, large spine teeth especially near hinge of dactyl tri-fid or quadri-fid: defining angle with 7-9 spine teeth on inside, outside with two rows spine teeth, inner row with 7-10 small, weakly notched-serrate teeth and outer row with 1 large notched and about 7 serrate spine teeth; superior medial setae in 3-4 sets in groups of 3-5; inferior lateral setae more than 10 and mostly singly inserted; posterior margin with 5-6 sets of setae in groups of 2-10. Dactyl with a row of very short setae on inner margin; outer margin with up to 8 setae; dactyl nail very short; Ventral margin of coxa 1 with 16-19 setae.

Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm strongly oblique, convex in the middle and slightly concave at the defining angle, about 2 times longer than posterior margin, inside and outside each with 2 rows of notched spine teeth, more than 30 spine teeth on each side, small spine teeth in inner row, large spine teeth especially near hinge of dactyl tri-fid, quadri-fid, or quinti-fid: defining angle with 1 large spine tooth on outside, 4 on inside: about 6 sets of superior medial setae in groups of 2-6; posterior margin with 5-6 sets of setae in groups of 5-10. Dactyl with row of very short setae on inner margin, outer margin with up to 9 setae. Ventral margin of coxa 2 with 11-20 setae.

Coxa of pereopod 3 with 12-13 marginal setae; dactyl with 5 setae on inner margin. Coxa of pereopod 4 with 19-22 marginal setae, dactyl with 5 setae on inner margin. Pereopod 5: basis with 17-21 shallow serrations along posterior margin; 11 sets of spines in groups of 1-3 on anterior margin; dactyl with 5 setae on inner margin. Pereopod 6: basis with 25 serrations along posterior margin; 11 sets of spines in groups of 1-3 on anterior margin. Pereopod 7: coxa with 6 setae on the posterior margin; basis with 24 very shallow serrations along posterior margin; 12 sets of spines in groups of 1-2 on anterior margin; dactyl of pereopod 7 about 25 percent the length of corresponding propod. 4 setae on inner margin.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner very small, subacute but not produced. Ventral margin with 1-2 (subventral) spines; posterior margin of plate 2 nearly straight with 1 or 2 setae, distoposterior corner slightly produced, acute: ventral margin with 8-9 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner rounded, not produced, ventral margin with 7-9 (subventral) spines. Peduncle of pleopod 1 with 2-3 retinaculae, one of which may be 2-segmented and notched at end of second segment; up to 6 long setae on outside margin distally.

Uropod 1: inner ramus slightly shorter than peduncle, armed with 14 spines: outer ramus with 14 spines: peduncle with 11 outer and 7 inner spines. Uropod 2: inner and outer ramus each with 14 spines: peduncle with 6-7 outer and 6 inner spines. 3. Uropod 3: inner ramus lacking spines, outer ramus about 1.7 times longer than peduncle, inner and outer margin each with 4-5 sets of spines in groups 2-4. Telson slightly broader than long, notched about 2/5 distance to base, each lobe with 5-8 apical spines: spine length less than 1.2 length of telson: may with 1-2 dorsal spines.
Male.—Differing from female as follows. Smaller size at sexual maturity. Antenna 2: flagellum with up to 12 segments, calceoli percent on peduncular segments 4 and 5, and first 5 segments of flagellum. Uropod 2: inner ramus with 10 spines; outer ramus weakly deflected, narrowing at apex, with 2 spines on inside. 4 short spines on outside. 4 spines on apex; peduncle with 5 outer and 6 inner spines.

Distribution and ecology.—This rare troglobitic species is recorded from five caves in southeastern Pennsylvania and three in central Maryland (fig. 54). It occurs in pools and small streams. Sexually mature males are 14 to 15.4 mm, sexually mature females are 19.0 to 22.0 mm and newly hatched young are 3.5 mm. Only a single ovigerous female is recorded from a January collection. It was made from Natural Well near Downsville in Maryland.

Remarks.—Shoemaker (1942) first described this species from Hobo Cave, Wernersville, Berks County, Pennsylvania. Although he described only a male, the description and figures are quite definitive for the species. Two important points should be mentioned. In Shoemaker's drawing of the head (fig. 7a), the lateral lobe is not broadly rounded and has a weak inferior antennal sinus. The presence of an inferior antennal sinus in the lateral lobe of the head is atypically for *Crangonyx*. inasmuch as most species in the genus have a broadly rounded lobe without a sinus. Shoemaker also pointed out that the coxal gill of pereopod 7 did not originate from the inner surface of the coxa but from the upper margin of the inside of the basis. Steele and Steele (1991) also reported this condition in other amphipods and believed it to be the normal situation for gammaridean amphipods with the so called "7th pereopod coxal gill". All species of *Crangonyx* observed in this study have the “7th pereopod coxal gill” attached to the upper margin of the basis and not to the coxa.

*Crangonyx grandimanus* Bousfield

Figures 55-59


Material examined—FLORIDA. Alachua Co.: Dudley Cave, 1 ♂. J. Martin, 16 Oct 1937 (USNM); Goat Sink, 1 ♂. 1 juv. H. H. Hobbs, Jr., 14 Mar 1938 (USNM); High Springs Cave, 1 ♂. H. H. Hobbs, Jr., 28 Feb 1935 (USNM); Huggins Cave, 3 ♂. 1 ♂. L. Hubricht, 17 Apr 1941 (USNM), holotype ♂, R. D. Warren, 17 Dec 1961 (CMN); Citrus Co.: Gum Tree Cave (=Gum Cave or Sweetgum Cave), 1 ♂, collector unknown, 30 Apr 1937 (USNM); Dade Co.: Little Bird Nursery well, collections in USNM made by G. Miller as follows: 1 ♂, 13 Oct 1967, 1 ♂, 1 ♂, 14 Feb 1968, 1 ♂, 24 Feb 1968, 4 ♂, 1 ♂, 28 Feb 1968, 3 ♂, 5 ♂, 12 Mar 1968, 15 specs, 27 Mar 1968, 8 specs, 15 Apr 1968, 1 ♂, 2 May 1968, 1 ♂, 22 May 1968, 1 ♂.
Figure 55.—*Crangonyx grandimanus* Bousfield. Female (11.7 mm), River Sink, Wakulla Co., Florida: a. b. antennae 1, 2; c. d. gnathopods 1, 2 (palmar margins enlarged); e. pleonal plates.
Figure 56.—Crangonyx grandimanus Bousfield. Female (11.7 mm), River Sink, Wakulla Co., Florida: a. b. maxillae 1, 2; c. lower lip; d. left mandible; e. dentate part of right mandible; f. inner and outer plates and palp dactyl of maxilliped.
Figure 57.—*Crangonyx grandimanus* Bousfield. Female (11.7 mm), River Sink, Wakulla Co., Florida:
a. c. d. pereopods 3, 5, 6; b. e. pereopods 4, 7; f. g. h. uropods 1, 2, 3; i. telson.

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Figure 58.—*Crangonyx grandimanus* Bousfield. Male (10.3 mm), River Sink, Wakulla Co., Florida: a. antenna 2; b, c. gnathopods 1, 2 (palmar margins enlarged); d, e, f. uropods 1, 2, 3; g. telson.
Figure 59.—Distribution of *Crangonyx grandimanus* in North America. A solid circle represents 1-5 closely proximate localities.
Diagnosis.—A large troglobitic species of the richmondensis group distinguished from other members of the group by having strongly produced distoposterior corners of pleonal plates 2 and 3: posterior margins of basis of pereopods 3-7 with shallow serrations: peduncle 5 longer than peduncle 4 of antenna 2; and peduncle 2 much longer than peduncle 3 of antenna 1. Largest male 13.0 mm; largest female 17.0 mm.

Female.—Eyes absent. Antenna 1, about 65-70 percent length of body, about 1.8-2.0 times longer than antenna 2: primary flagellum about 30 (25-37) segments. Antenna 2: peduncle 5 longer than peduncle 4: flagellum with up to 9 segments; with calceoli in some specimens. Mandibles subequal, spine row with 7 spines: segment 2 of palp with 14 long setae, segment 3 with 3 A setae, 2 B setae, 3 C setae, 6 E setae and a row of 20 D setae. Maxilla 1: inner plate with 2-3 apical plumose setae; palp with 2 slender spines and 2 rows of setae on apex. Maxilla 2, inner plate with 1 plumose setae on inner margin. Maxilliped: inner plate apically with 4 bladelike spine teeth. 2 naked setae, and 4 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 2 small slender pectinate spines on inner margin: inner margin of dactyl with 5 setae; dactyl nail short, about 1/5 length of dactyl.

Propod of gnathopod 1 more than 2 times larger and longer than carpus and much broader; palm strongly oblique, convex, almost 2 times longer than posterior margin, with about 20 spine teeth on inside. 24 on the outside: defining angle with 6 spine teeth on inside, outside with two rows spine teeth, inner row with 4 small and outer row with 1 large and 8 small spine teeth; superior medial setae few in number and singly or doubly inserted; posterior margin with about 13 setae in a cluster in the defining angle area: dactyl of gnathopod 1 lacking short setae on inner margin, nail very short, ventral margin of coxa 1 with 7-8 setae.

Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm oblique, convex, about 2
times longer than posterior margin, with 21 spine teeth on inside, 26 on outside; defining angle with 2 spine teeth on inside, 2 simple spine teeth on inner surface; 1 very large unnotched and 3 small notched spine teeth on outside; 6 sets of medial setae in groups of 3-4; posterior margin with 5 sets of setae in groups of 5-6. Dactyl lacking short setae on inner margin, nail very short. Ventral margin of coxa 2 with 5 setae.

Coxa of pereopod 3 with 8 marginal setae. Coxa of pereopod 4 with 19 marginal setae. Pereopod 5: basis with 13 shallow serrations along posterior margin; 7 short spines on anterior margin; 4 long setae on the anteroproximal margin. Pereopod 6: basis with 11 serrations along posterior margin; 6 short spines on anterior margin; 5 long setae on anteroproximal margin. Pereopod 7: coxa with 2 setae on the posterior margin; basis with 12 shallow serrations along posterior margin, deeper at apex; 6 short spines on anterior margin; 3 setae on anteroproximal margin; dactyl about 35 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 strongly convex, with 1-2 setae. distoposterior corner very small, not produced; posterior margin of plate 2 with up to 4 setae, strongly oblique. ventral margin with 2 (subventral) spines; posterior margin of plate 3 also oblique, with 1-4 setae, distoposterior corner subquadrate. ventral margin with 2-4 (subventral) spines. Peduncle of pleopod 1 with 4 retinaculae; 3 setae on inside margin proximally, 9 setae on outside margin.

Uropod 1: inner ramus 60 percent length of peduncle, armed with 12 spines: outer ramus with 11 spines; peduncle with row of 7 outer and 6 inner spines. Uropod 2: inner ramus armed with 12 spines; outer ramus with 12 spines; peduncle with 3 outer and 4 inner spines. Uropod 3: inner ramus with 1 spines, outer ramus about 2.1 times longer than peduncle, inner and outer margin each with 4 sets of spines in groups of 1-3. Telson as broad as long, notched from 1/4 to 1/2 distance to base, each lobe with 3-4 apical spines: spines about 1/2 length of telson.

Male.--Differing from female as follows. Smaller in size. Antenna 2: calceoli percent on peduncular segments 4 and 5 and first 3 segments of flagellum.

Uropod 2: inner ramus with 11 spines: outer ramus smaller and narrower than inner ramus, with 2 inner and 3 outer spines, apex with 4 spines; peduncle with 4 outer and 5 inner spines.

Distribution and ecology.---This range of this large, distinct troglobitic species, which is restricted to Florida, extends from Madison County in the north to Dade County in the south, covering a linear distance of about 625 km. However, a large disjunction of about 350 km separates the southern most record in Dade County from those in central Florida west of Orlando (fig. 59).

*C. grandimanus* is recorded from caves, wells, and karst springs. It is almost always associated with *C. hobbsi* and sometimes with *C. floridanus* in nature. Sexually mature males are 8.0-13.0 mm and sexually mature females are 10.0-17.0 mm. Ovigerous females have been collected during February, March, and December and sexually mature females also occur in October samples.
Crangonyx hubrichti, new species

Figures 60-62

Material examined (paratypes unless designated otherwise).--ILLINOIS. Champaign Co.: drainage ditch. Savoy. 5 ♂, H. J. Van Cleave. 9 May 1942 (USNM); Effingham Co.: ditch. 3.0 km WSW of Altamont. holotype ♂. 14 ♂, L. Hubricht. 16 Apr 1942 (USNM): temporary stream. 1.6 km SW of Funkhouser. 1 ♂, L. Hubricht. 16 Apr 1942 (USNM); Madison Co.: spring. 0.64 km SW of Troy. 5 ♂, L. Hubricht. 16 Apr 1942 (USNM).

Diagnosis.—A medium-sized species of the richmondensis groups distinguished from other members of the group by inner plate of maxilla 1 which bears 3 apical plumose setae and inner plate of maxilla 2, which has 2 plumose setae on inner margin; weak serrations along posterior margin of basis of pereopods 5-7; unproduced disto-posterior corners of pleonal plates. Largest female. 15.5 mm; males unknown.

Female.—Eye large and ovate. Antenna 1. about 50 percent length of body, about 2 times longer than antenna 2; primary flagellum with about 22 segments. Antenna 2. flagellum with 6-8 segments. Mandibles subequal, spine row with 4-5 spines; segment 2 of palp with 12 setae, segment 3 with 3 A setae. 3 B setae. 3-5 C setae. 5-6 E setae and a row of D setae. Maxilla 1: inner plate with 3 apical plumose setae; palp with 5-6 slender spines on apex. Maxilla 2. inner plate with 2 plumose setae on inner margin. Maxilliped: inner plate apically with 4 bladelike spines. 1 naked spine, and 5-6 plumose setae extending from inner margin to apex: outer plate with row of naked setae and 5-6 slender spines (not pectinate) on inner margin and 1 apical plumose seta; inner margin of dactyl with 4 setae; dactyl nail long. about 1.4 length of dactyl.

Propod of gnathopod 1 about 2 times larger and longer than carpus: palm convex, longer than posterior margin. inside and outside margins each with 2 rows of notched spine teeth. 13 on inside, 14 on outside: defining angle with 8 spine teeth on inside, 6 small and 1 large notched spine teeth and 1 row of 8 simple spine teeth on outside: superior medial setae in 3-4 sets inserted in groups of 3: 4 sets of setae on posterior margin singly inserted in groups of 2-3. Dactyl with row of 4 short setae on inner margin, nail long. Ventral margin of coxa 1 with 14 setae.

Propod of gnathopod 2 about 2 times larger and longer than carpus: palm convex, oblique, slightly longer than posterior margin, inside and outside each with 2 rows of notched spine teeth. 15 on inside, 17 on outside: defining angle with 4 spine teeth on inside, 7 on outside: superior medial setae in 6-7 sets inserted in groups of 2-4: posterior margin with 5-6 sets of setae in groups of 3-6. Dactyl with row of 7 short setae on inner margin. Ventral margin of coxa 2 with 14 setae.

Coxa of pereopod 3 with 12-14 marginal setae. Coxa of pereopod 4 with 27 marginal setae; dactyl of pereopod 4, 33 percent length of corresponding propod. Pereopod 5: basis with 18 shallow serrations along posterior margin; 10 short spines on anterior margin; 6 long setae on the anteroproximal margin. Pereopod 6: basis with 18 shallow serrations along posterior margin; 8 short spines on anterior margin; 6
Figure 60.—Crangonyx hubrichti, new species. Female paratype (13.2 mm), ditch, 3.0 km WSW of Altamont, Effingham Co., Illinois: a. head (in part); b. c. antennae 1, 2; d. e. maxillae 1, 2; f. lower lip; g. dente part of left mandible; h. right mandible; i. inner and outer plates and palp dactyl of maxilliped (greatly enlarged); j, k. gnathopods 1, 2 (palmar margins enlarged).
Figure 61.—*Crangonyx hubrichti*, new species. Female paratype (13.2 mm), ditch, 3.0 km WSW of Altamont, Effingham Co., Illinois: a, b, c, d. pereopods 3, 4, 5, 6; e. pleonal plates; f, g, h. uropods 1, 2, 3; i. telson.
Figure 62.--Distribution of *Congomys latricola* in North America. Solid circles represent single localities.
short setae on anteroproximal margin. Pereopod 7: coxa with 5 setae on the posterior margin; basis with 20 very shallow serrations along posterior margin; 7 short spines on anterior margin; 4 long setae on anteroproximal margin; dactyl about 30 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta. distoposterior corner acute but not produced; posterior margin of plate 2 nearly straight with 1 seta. distoposterior corner produced and acute. ventral margin with 5 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta; distoposterior corner subacute but not produced. ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 5 retinaculae. about 20 long setae on outside margin. 7-8 short setae on proximal half of inside margin.

Uropod 1: inner ramus 70 percent length of peduncle. armed with 13 spines; outer ramus with 12 spines; peduncle with row of 9 outer and 1 inner spines. Uropod 2: inner ramus with 14 spines; outer ramus with 13 spines; peduncle with 3 outer and 2 inner spines. Uropod 3: inner ramus with 1 spine. outer ramus about 2 times longer than peduncle. inner and outer margin each with 4-5 set of spines in groups of 1-4. Telson a little broader than long. notched about 1/2 distance to base. each lobe with 2-3 apical spines: spines slightly less than 1/2 length of telson.

Type-locality.—Ditch. 3.0 km WSW of Altamont. Effingham Co., Illinois.

Distribution and ecology.—The range of this species covers approximately 200 km in south-central Illinois (fig. 62). It is recorded from ditches. a temporary stream, and a spring. Ovigerous females (13.0-15.5 mm) were collected in April. Crangonyx hubrichti was always found together with C. minor.

Etymology.—It is a pleasure to name this species in honor of its discoverer. Leslie Hubricht. who has made numerous positive contributions to our knowledge of the freshwater invertebrates of North America.

The forbesi group

Diagnosis.—Closed related to the richmondensis group but distinguished from that group as follows. Adult size range. 14.0-22.0 mm. Maxilla 1: inner plate with about 11 apical plumose. Maxilla 2: inner plate with oblique row of 9-12 plumose setae on inner margin. Propod of gnathopod 1: defining angle inside with notched-serrate spine teeth. outside with 1 row of 6-7 small notched spine teeth and 1 row of 1 large notched and 7 serrate spine teeth. Propod of gnathopod 2: 7-9 sets of superior medial setae mostly inserted in groups of 4-6: posterior margin with 10 sets of setae in groups of 4-9. Peduncle of pleopod 1 with 8-9 retinaculae. about 12 setae on outer margin and about 7 setae on inner margin proximally.

Remarks.—This group is composed of a single species. C. forbesi. which is widely distributed in east-central United States.
Crangonyx forbesi (Hubricht and Mackin)

Figures 63-67

Eucrangonyx forbesi Hubricht and Mackin, 1940:196-197, fig. 5 [type-locality: outlet of drain (spring), Osage Hills Golf Course, Kirkwood, St. Louis Co., Missouri].


Crangonyx shoemakeri (Hubricht & Mackin).—Hubricht, 1943:690 [in part].

Material examined.—ARKANSAS. Fulton Co.: Mammoth Spring, 1 ♀, L. Hubricht, 9 Apr 1939 (USNM); small spring near Mammoth Spring, 5 specs, L. Hubricht, 18 Jul 1942 (USNM); Lawrence Co.: spring, 5.9 km S of Imboden, 40 specs, L. Hubricht, 6 Apr 1941 (USNM). ILLINOIS. Gallatin Co.: seep near salt well, 5 ♀, 8 juvs, J. J. Lewis, 27 Apr 1974; Jackson Co.: small intermittent stream, Little Grand Canyon, 8.0 km W of Etherton, 40 specs (♀, ♂), L. Hubricht, 20 Oct 1940 (USNM); spring in Happy Hollow, Fountain Bluff, 3.7 mi S of Gorham, 5 ♀, L. Hubricht, 14 Jul 1940 (USNM); Carbondale, 1 ♀, J. G. Weise, 26 Oct 1951; Cave No.1. 1 ♀, S. B. Peck, 24 Mar 1966; walled spring, Fountain Bluff, 1 ♀, 3 ♂, 3 juvs, J. J. Lewis, 10 Feb 1974; Jersey Co.: spring near Grafton, 4 ♀, S. B. Peck, 26 Nov 1965; Johnson Co.: Firestone Creek Cave, 1 ♀, J. J. Lewis, 15 Dec 1973; Monroe Co.: Camp Vandeventer Cave, 1 ♀, S. B. Peck, 27 Nov 1965; Dry Run Cave, 6 ♀, 4 juvs, S. B. Peck, 26 Jun 1965; Fogelpole Cave, 1 ♀, 2 ♂, S. B. Peck, 25 Jun 1965; spring, 3.2 km N of Fountain Gap, 3 ♀, L. Hubricht, 26 May 1937 (USNM); Fruths Spider Cave, 1 ♀, S. B. Peck, 25 Jun 1965; Horsethief Cave, 1 ♀, 1 ♂, S. Peck, 29 Nov 1965; Pautler Cave, 1 ♀, S. B. Peck, 27 Nov 1965; Terry Spring (Long Slash) Cave, 3 ♀, 1 ♂, S. B. Peck, 27 Nov 1965; Wildes Cave, 4 ♀, 1 ♂, L. Hubricht, 31 Jul 1938 (USNM); spring, 3.2 km E of Waterloo, 5 ♀, L. Hubricht, 24 Oct 1937 (USNM); ditch leading into Moredock Lake, 6.2 km NE of Valmeyer, 1 ♀, L. Hubricht, 26 May 1937 (USNM); spring, 4.8 km N of Fountain Gap, 20 specs, L. Hubricht, 26 May 1937 (USNM); Illinois Caverns (Morrison Cave), 40 specs, L. Hubricht, 28 Aug 1938 (USNM) and 2 ♀, T. C. Barr, Jr. and T. Wallwork, 20 Oct 1961; Pike Co.: Lost Creek Cave, 10 ♀, 3 ♂, S. B. Peck, 25 Nov 1965; St. Clair Co.: Stemmlers Cave, 5 ♀, 3 ♂, 1 juv, L. Hubricht, 16 Jan 1938 (USNM) and 1 ♀, 2 juvs, J. R. Holsinger and R. M. Norton, 13 Jun 1965; Union Co.: spring, Alto Pass, 5 ♀, 1 juv, J. G. Weise, 2 Nov 1951; small spring, just N of Ecological area, Pine Hills, La Rue, Shawnee National Forest, 1 ♀, D. Bechler, 12 Mar 1977; spring, 3.2 km E of Reynoldsville, 9 ♀, 2 ♂, L. Hubricht, 5 Nov 1939 (USNM); spring, 15 m E of...
Figure 63.—*Crangonyx forbesi* (Hubricht and Mackin). Female (17.0 mm), entire animal from left side, inlet of Cave, 0.2 mile N of Frankford, Pike Co., Missouri.
Figure 64.—Crangonyx forbesi (Hubricht and Mackin). Female (17.0 mm), small spring near entrance to Normundy Osteopathic Center, Kirkwood, St. Louis Co., Missouri: a. antenna 1; b, c. maxillae 1, 2; d. lower lip; e. dentate part of left mandible; f. right mandible; g. inner and outer plates and palp dactyl of maxilliped; h, i. gnathopods 1, 2 (palmar margins enlarged).
Figure 65.—*Crangonyx forbesi* (Hubricht and Mackin). Female (17.0 mm), small spring near entrance to Normundy Osteopathic Center, Kirkwood, St. Louis Co., Missouri: a, b, c. pereopods 4, 5, 6 (in part): d. pereopod 7: e, f, g. uropods 1, 2, 3: h. pleonal plates: i. telson. Female (12.0), McDowell Cave, Miller Co., Missouri: j. telson. Female (12.5), spring on tributary of Crooked Creek, Guyandotte, Putnam Co., West Virginia: k. telson.

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Figure 66. *Crangonyx forbesi* (Hubricht and Mackin). Male (12.2 mm), small spring near entrance to Normundy Osteopathic Center, Kirkwood, St. Louis Co., Missouri: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. e. f. uropods 1, 2, 3; g. telson.
Figure 67.—Distribution of Crangonyx forbesi in North America. Solid circles represent 1-20 closely proximate localities. The dotted line marks the approximate southern extent of glaciation during the Pleistocene.
Tellor's Farm. 3 ♂ J. G. Weise, 21 Dec 1951; county not given. 4.8 km N of Hwy 146 on Beach Grove Road. 5 specs. J. G. Weise, 7 Feb 1952. INDIANA. Dubois Co.: Vowell Cave. 1 ♂, 2 ♂. R. M. Norton, 19 Jul 1967; Floyd Co.: spring and spring-fed stream just E of Edwardsville. 60 specs. J. R. Holsinger and R. M. Norton. 12 Jun 1965; Grant Co.: temporary pools. 8.0 km W of Jonesboro. 35 specs. L. Hubricht, 27 Apr 1941 (USNM); Hancock Co.: ditch. 5.3 km E of Greenfield. 25 specs. L. Hubricht. 17 Apr 1942 (USNM); Harrison Co.: Wallier Cave. 1 ♂ S. B. Peck. 24 Jan 1964; Hendricks Co.: temporary spring. 6.2 km SW of Belleville. 30 specs. L. Hubricht. 16 Apr 1942 (USNM); Henry Co.: outlet of drain. 5.6 km W of Knightstown. 7 ♂, 2 ♀. L. Hubricht. 17 Apr 1942 (USNM); small stream. 2.1 km NW of Blountsville. 15 specs. L. Hubricht. 27 Apr 1941 (USNM); Jefferson Co.: Wilson's Cave. 6 ♂, S. B. Peck. 9 Aug 1964; Jennings Co.: Hooker Cave. 1 ♂. R. M. Norton. 14 Aug 1967; Lawrence Co.: Gyger Bend Cave. 2 ♂, H. H. Hobbs. III. collection date not given; Bronson Cave. 2 ♂, 6 ♂, 2 juveniles. J. R. Holsinger. 19 Jun 1965; Donnehues Cave. 1 ♂ J. R. Holsinger and E. Lavangino. 8 Aug 1964; Martin Co.: Ellis Spring. 5.6 km E of Loogootee. 50 specs. L. Hubricht. 21 Nov 1941 (USNM); Monroe Co.: Barters Bog. 6 ♂, 2 ♀. Bleyman. Nov. 1962 (USNM): Jordan River. Bloomington. 3 ♂, 2 ♀. D. L. Weaver. Mar 23 1957 (USNM); Carmichael Cave. 2 ♂, H. H. Hobbs. III. collection date not given; Mays Cave. 1 ♂. H. H. Hobbs. III. collection date not given; Pattons Cave. 3 ♀, 1 ♂, 8 juveniles. W. Tozer. 7 May 1965; Reeves Cave. 5 ♀, 1 juvenile. H. H. Hobbs. III. collection date not given; Orange Co.: Elrod Cave. 1 ♂, 1 juvenile. L. Hubricht. 29 Aug 1942 (USNM); spring. 13.8 km S of Paoli. 13 ♂, 3 ♀. L. Hubricht. 2 Sep 1939 (USNM); Owen Co.: Porter Cave. 1 ♂. R. M. Norton. 1 Aug 1967; Heights Pit Cave. 1 ♂, 3 ♀. 1 juvenile. W. Tozer. 9 May 1965; Putnam Co.: Triple Springs near Pleasant Gardens. 50 specs. L. Hubricht. 16 Apr 1942 (USNM); Spencer Co.: small tributary of Richland Creek on Rt. 48. 5 ♂, 1 ♀. N. Hynes. 5 Jun 1963 (USNM); Washington Co.: Flowstone Cave. 10 ♂. J. J. Lewis. 15 Sep 1973; Joe Hall Cave. 2 ♀. R. M. Norton. 18 Jul 1967; Wayne Co.: small spring. ca. 12.8 mi W of Economy. 30 specs. L. Hubricht. 27 Apr 1941 (USNM); County and habitat not given: Irvington. 8 ♂. W. P. Hay. collection date unknown. (USNM). KANSAS. Cherokee Co.: Schermerhorn Park Cave spring. 2.4 km S of Galena. 1 ♂, 4 ♀. J. Danoff-Burg. 18 Jan 1991; spring-run from cave at Schermerhorn Park. 3.7 km S of Galena. 4 ♂, 2 ♀. P. Leichti et al. 18 Mar 1981. KENTUCKY. Barren Co.: swale. 1.6 km E of Bonayr. 5 ♂, 7 ♀. L. Hubricht. 20 Mar 1956 (USNM); Breckinridge Co.: spring. 5.6 km E of Cloverport. 6 ♂, 1 ♀. L. Hubricht. 12 May 1957 (USNM); Penitentiary Cave. 1 ♂. R. M. Norton. 19 Oct 1963; Butler Co.: Jeff Taylor Spring. 1.6 km SSW of Martin Ferry. 28 specs (♀, ♂, juveniles). L. Hubricht. 2 Jun 1941 (USNM); Christian Co.: Chandler Cave. 1 ♂, T. C. Barr. Jr. and W. Andrews. 16 Jul 1965; spring on Pollard Farm. 26.4 km NW of Hopkinsville. 27 specs. 30 May 1941 (USNM); Crittenden Co.: Blowing Spring close to Ellen Clark Cave. 11 ♂, T. C. Barr. Jr. and W. Andrews. 7 Jul 1965; Ellen Clark Cave. 10 ♂, 1 juvenile. W. Andrews and T. C. Barr. Jr. 7 Jul 1965; Edmonson Co.: spring. 2.4 km E of Brownsville. Mammoth Cave National Park. 1 ♂, 1 ♀. L. Hubricht. 19 May 1956 (USNM); stream in small cave. 1.6 km NW of Arthur. 1 ♂, L.

Missouri: Outlet of drain, 0.5 mi N of Ottawa lake, 2 ♀, L. Hubricht. 18 Apr 1942 (USNM).

Hubricht. 21 Apr 1937 (USNM); Quarry Cave No.1. 1♀, 4♂. J. E. Gardner. 17 Mar 1981; temporary pond. 3.2 km S of Gray Summit. 1♀. L. Hubricht. 28 Mar 1937 (USNM); spring. 3.2 km S of Gray summit. 500 specs (♀, ♂ juvs). L. Hubricht. 29 May 1937 (USNM); Mushroom Cave. 1♀. J. L. Craig. 1 Jun 1974; Onyx Cave. 1♂, M. L. Grumbine. 8 Jan 1966; Hickory Co.; Vanderman Cave. 6♀, 6♂. J. E. Gardner. 15 Dec 1982; small stream 6.2 km NE of Weaubleau. 23 specs. L. Hubricht. 17 May 1942 (USNM); Iron Co.; small spring. 3.2 km N of Bellevue. 75 specs. L. Hubricht. 29 Sep 1940 (USNM); Jasper Co.; Dowlers (Days) Cave Spring. Sarcoxie. 3♀, 1♂, 6 juvs. L. Hubricht. 22 Mar 1942 (USNM); Jefferson Co.; Sims Cave. 2♀. T. March. 27 Mar 1966; spring. 0.2 km S of Ware. 30 specs. L. Hubricht. 30 Mar 1941 (USNM); small spring. 1.6 km W of Horine. 200 specs. L. Hubricht. 21 May 1936 (USNM); small spring. 2.4 km N of Antonia. 10♀. L. Hubricht. 6 Jun 1937 (USNM): Rice’s Spring. 4.8 km NE of Goldman. 7♀. L. Hubricht. 20 Nov 1938 (USNM); spring on hillside on Selma Creek. 0.8 km NNW of Selma. 1♀. L. Hubricht. 2 Jun 1937 (USNM); unnamed stream on Jefferson College campus at Hillsboro. 1♀, 14♂. F. Hill. 1 Jan 1971; Pleasant Valley Cave. 1♀. 2♂. T. Smither. 18 Mar 1966 and 1♀, 1♂. D. and M. Bechler. 20 Mar 1977; spring at Selma. 1♀. R. Kenk. 4 Oct 1967; Laclede Co.; spring at mouth of Davis Cave. 18♀, 9♂. L. Hubricht. 4 Jul 1940 (USNM); spring. 3.8 km W of Hazelgreen. 17♀, 7♂. L. Hubricht. 23 May 1942 (USNM); small stream near Bennett Spring. 24 specs. L. Hubricht. 16 May 1942 (USNM); Mary Lawson Cave. 2♀. L. Hubricht. 26 Mar 1958 (USNM); Lincoln Co.: Cave Spring. 4.0 km S of Winfield. 3♀, 1♂. L. Hubricht. 22 Mar 1941 (USNM); Sherwood Forest Cave. 7.6 km NE of Froy. 1♀, 1♂. J. E. Gardner. 15 Apr 1982; Madison Co.: spring. 0.8 km S of Mill Creek. 25 specs. L. Hubricht. 5 Apr 1941 (USNM); Maries Co.: Boulware Cave. 30 specs. L. Hubricht. 17 Apr 1941 (USNM); Marion Co.: spring. 6.2 km N of Palmyra. 1♀. L. Hubricht. 22 Mar 1941 (USNM); Miller Co.: Barnett Cave. 20 specs. L. Hubricht. 24 Aug 1940 (USNM); De Graffenreid Spring Cave. 3♀, 9♂. J. E. Gardner. 15 Mar 1982; Ferguson Crawl Cave. 1♀. J. E. Gardner. 23 Feb 1984; McDowell Cave. 12♀, 1♂. J. E. Gardner. 19 May 1981; small stream in small cave. 0.5 km SE of Miller City Home. 4.8 km E of Tuscumbia. 4 juvs. L. Hubricht. 24 Aug 1940 (USNM); Oregon Co.: Blowing Spring Cave. 2♀, 1♂. M. Sutton. 5 Apr 1992; Brawley Hollow Cave No.1. 1♀. M. Sutton. 17 Dec 1994; Greer Springs. 2.1 km N of Greer. 100 specs. L. Hubricht. 23 Oct 1939 (USNM); Greer Spring Cave. 3♀, 1♂. J. E. Gardner. 29 Sep 1981; Lower Cane Bluff Cave. 2♀. M. Sutton. 10 Sep 1994; McDowell Cave. 9♀, 1♂. J. E. Gardner. 21 Jul 1981; spring in Cook Hollow. 9♀, 3♂. T. Aley. 1972; Posy Spring Cave. 2♀. M. Sutton. 11 Jan 1992; Onyx Cave. 1♀, 1♂, 1 juv. M. Sutton. 3 May 1992; Bat Cave. 3♀, 1♂. J. E. Gardner. 21 Jul 1979 and 2♀. M. Sutton. 30 Oct 1993; Adams Cave No.2. 1♀. M. Sutton. 24 Aug 1991; Adams Cave No.1. 3♀, 2♂. M. Sutton. 24 Aug 1991; Barrett Spring Cave. 1♀. M. Sutton. 10 Mar 1991; Bliss Spring Cave. 1♀. M. Sutton. 17 May 1993; Dead Man Cave. 6♀, 2♂. J. E. Gardner. 31 Oct 1979; Turner Spring Cave. 3♀, 5♂. J. E. Gardner. 8 May 1980; Willow Tree Cave. 11♀, 1♂. J. E. Gardner. 6 Nov 1979; Ozark Co.: Bat Spring Cave. 10♀, 1♂. J. E. Gardner. 27 Jun 1979 and 34♀. J. E. Gardner. 12 Jul 1979; Perry Co.: Garbage Hole Cave. 3♀, 2 juvs. J. J. Lewis. 3 Feb 1973; Mystery Cave. 3♀, 21 juvs. J. J. Lewis. 31 Mar 1974; Schindler Cave (= Mertz Cave

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Diagnosis.—A large species distinguished by having comparatively more spinose body than most other
species of *Crangonyx*. Also having up to 10 sets of setae on posterior margin of propod of gnathopods, more flagellar segments (up to 36) and setae on antennae 1, 8-9 retinaculae on pleopod peduncular segment, and 6-9 setae on inner margin of dactyl of maxilliped; telson much broader than long, notched less than 1/3 distance to base; outer ramus of male uropod 2 curved backward, with inner marginal spines only. Largest male. 18.0 mm; largest female. 22.0 mm.

Female. -- Eye small and ovaic. Antenna 1, about 50 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with 36 segments. Antenna 2, flagellum with 8-9 segments, peduncular segments 4 and 5 with 6-7 sets of marginal setae. Mandibles subequal. spine row with 8 spines: segment 2 of palp with 18 long setae. segment 3 with 4 A setae, 2 B setae, 4 C setae, 6 E setae and a row of 19 D setae. Maxilla 1: inner plate with 11 apical plumose setae; palp with 5 slender spines on apex. Maxilla 2: inner plate with oblique row of 9-12 plumose setae on inner margin. Maxilliped: inner plate apically with 8 bladelike spine teeth. 2 naked setae, and up to 17 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 11 slender pectinate spines on inner margin; dactyl with 6-9 setae on inner margin; dactyl nail long, about 1/3 length of dactyl.

Propod of gnathopod 1 about two times larger and longer than carpus and much broader: palm slightly longer than posterior margin, almost straight, inside and outside each with 2 rows of spine teeth, inner row with small spines and outer row with larger spines, 25 on inside. 28 on outside; defining angle with 3 notched spine teeth and 4 notched-serrate spine teeth on inside. 1 inner row of 6-7 small notched spines and 1 large notched and 7 serrate spine teeth on outside; 2-4 sets of superior medial setae in groups of 2-4; posterior margin with 4-6 sets of setae in groups of 2-4. Dactyl with a row of many short setae on inner margin. nail short. Ventral margin of coxa 1 with 24 setae.

Propod of gnathopod 2 about 2 times larger and longer than carpus; palm oblique, convex, subequal in length to posterior margin, inside and outside margin each with 2 rows of spine teeth (larger teeth in outer row, smaller teeth in inner row), about 22-28 spine teeth on inside, 20-30 on outside; defining angle with 4 spine teeth on inside, 7-9 on outside; 7-9 sets of superior medial setae, mostly inserted in groups of 4-6; posterior margin with 10 sets of setae in groups of 4-9. Dactyl with row of many short setae on inner margin, nail short. Ventral margin of coxa 2 with 20 setae.

Coxa of pereopod 3 with 14 marginal setae. Coxae of pereopod 4 with 30 marginal setae, dactyl of pereopod 4. 30 percent length of corresponding propod. Pereopod 5: basis with 16 shallow serrations along posterior margin; 9 sets of 1-2 short spines on anterior margin: 4 long setae on anteroproximal margin. Pereopod 6: basis with 21 serrations along posterior margin: 9 short spines on anterior margin: 3 long setae on anteroproximal margin. Pereopod 7: coxa with 3 setae on the posterior margin; basis with 25 serrations along posterior margin: 13 short spines on anterior margin: dactyl about 31 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, disto-posterior corner not produced; posterior margin of plate 2 nearly straight with 1 seta, disto-posterior corner produced. ventral
margin with up to 11 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner slightly produced, ventral margin with 6 (subventral) spines. Peduncle of pleopod 1 with 8-9 retinacula; with 12 setae on outer margin, 7 setae on proximal half of inside margin.

Uropod 1: inner ramus about 60 percent length of peduncle, armed with 15 spines; outer ramus with 13 spines; peduncle with row of 11-12 outer and about 2-4 inner spines. Uropod 2: inner ramus much longer and thicker than outer ramus, armed with 13 spines; outer ramus with 10 spines; peduncle with 5 outer and 3-4 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.8 times longer than peduncle, inner and outer margin each with 3-4 set of spines in groups 2-3. Telson much broader than long, notched 1/5 to little less than 1/2 distance to base, each lobe with 3-7 apical spines: spines up to 1.2 length of telson.

Male.--Differing from female as follows. Smaller size at maturity. Antenna 2: calceoli present on peduncular segments 4 and 5 and first 5 segments of flagellum. Uropod 2: inner ramus with 11 spines; outer ramus much smaller than inner ramus, strongly curved backward, with 2 spines on inside, lacking outer spines, apex with 5 spines; peduncle with 4 outer and 3 inner spines.

Variation.--Females were always found to have penes. The facial setae on inner lobe of maxilla 2 and plumose setae on inner lobe of maxilla 1 may be reduced to 4-6. Eyes are reduced in some cave populations.

Distribution and ecology.--This large, somewhat variable species, is a common inhabitant of cave streams and springs in central and southern Missouri, southern Illinois, northern Arkansas, northeastern Oklahoma, southeastern Kansas, central and southern Indiana, west-central Kentucky and southwestern Ohio. It is also recorded from southeastern Michigan, northern Ohio, western West Virginia and southwestern Pennsylvania (fig. 67). It also occurs in surface streams and ponds.

*Crangonyx forbesi* is equally common in springs and caves and does not show a significant loss of pigment or eye structure when it occurs in caves. The size is quite variable; sexually mature males range from 10.0 to 18.0 mm and sexually mature females from 14.0 to 22.0 mm. Newly hatched young are 2.0 to 3.0 mm in length. Ovigerous females are known from all four seasons, implying that breeding is continuous throughout the year.

*Crangonyx forbesi* is often associated with other amphipods—commonly with *Gammarns troglophilus* and occasionally with *Gammarns acherondytes* and *Bactornis brachycaudus*.

**The insolitus group**

Diagnosis.--Closely related to the *C. forbesi* (group) but distinguished from that species as follows. Adult size range, 5.6-9.9 mm; spine teeth on inner margin of dactyl of maxilliped; propod of gnathopods less than 2 times larger and longer than carpus, palms with fewer spine teeth; defining angle of propod of gnathopod 1 of male on outside with only one row of 1 large non-serrate and 2-3 serrate spine teeth:
pleonal plates with ventral spines and setae; short lateral spines on peduncle of uropods 1 and 2.

Remarks.—The *insolitus* group is based on a single species from a cave in southern Missouri. It is the only species in the family Crangonyctidae with ventro-lateral spines on the peduncles of uropods 1 and 2.

*Crangonyx insolitus*, new species

Figures 68-71

Material examined.—MISSOURI. Shannon Co.: Blue Spring Cave, 17.6 km E of Eminence, holotype ♂, 2 ♀ (paratype), I ♀ (paratype), J. E. Gardner, 2 May 1984.

Diagnosis.—A relatively small species easily distinguished from all other species of *Crangonyx* by having 2 tiny ventrolateral spines on peduncles of uropods 1 and 2: spine teeth on inner margin of dactyl of maxilliped: and pleonal plates with ventral spines and setae. Largest male, 5.6 mm: largest female, 9.9 mm.

Female.—Eye large and ovate. Antenna 1, about 60 percent length of body, about 2 times longer than antenna 2: primary flagellum with about 32 segments. Antenna 2, flagellum with 10 segments. Mandibles subequal, spine row with 7-9 spines: segment 2 of palp with 16 setae, segment 3 with 3 A setae, 3 B setae, 3 C setae, 5 E setae and a row of D setae. Maxilla 1: inner plate with 8 apical plumose setae: palp with 9 slender spines on apex. Maxilla 2, inner plate with oblique row of 10 plumose setae on inner margin. Maxilliped: inner plate apically with 5 bladelike spines, 2 naked spines, and 5-6 plumose setae extending from inner margin to apex: outer plate with row of naked setae and 8 slender pectinate spines on inner margin: 3-4 spine teeth and 4-5 setae on inner margin of dactyl; dactyl nail very long. 15 of dactyl.

Propod of gnathopod 1 less than 2 times larger and longer than carpus: palm almost straight, subequal in length to posterior margin, with 9 spine teeth on inside, 11 on the outside; defining angle with 5 notched-serrate spine teeth on inside, 1 large notched and 4 serrate spine teeth on outside; 3 sets of superior medial setae inserted in groups of 1-3: 6 sets of posterior marginal setae inserted in groups of 1-3. Dactyl with 2 setae on outer margin, nail long. Ventral margin of coxa 1 with 27 short setae.

Propod of gnathopod 2 less than 2 times larger and longer than carpus: palm slightly convex, subequal in length to posterior margin, with 11 spine teeth on inside, 13 on the outside; defining angle with 3 spine teeth on inside, 1 large and 1 small tooth on outside; 6 sets superior medial setae inserted in groups of 2-5, typically with 4 setae per set; posterior margin with 5 sets of setae in groups of 3-6. Dactyl with row of short setae on inner margin and 2 setae on outer margin. Ventral margin of coxa 2 with 20 short setae.

Coxa of pereopod 3 with 22 marginal setae. Coxa of pereopod 4 with 40 marginal setae; dactyl of pereopod 4, 45 percent length of corresponding propod. Pereopod 5: coxa with 3 setae on distoposterior corner; basis with 25 shallow serrations along posterior margin; 12 short spines on anterior margin: 2 short setae on anteroproximal margin. Pereopod 6: coxa with 6 setae on distoposterior corner and 3 setae on
Figure 68.—*Crangomyx insolitus*, new species. Female paratype (9.4 mm). Blue Spring Cave, 17.6 km E of Eminence, Shannon Co., Missouri: a, antenna I; b, c, maxillae I, 2; d. lower lip; e. left mandible; f. dentate part of left mandible; g. inner and outer plates and palp dactyl of maxilliped (greatly enlarged); h, i. gnathopods I, 2 (palmar margin enlarged).
Figure 69.—*Crangonyx insolitus*, new species. Female paratype (9.4 mm), Blue Spring Cave, 17.6 km E of Eminence, Shannon Co., Missouri: a, c, d, pereopods 3, 5, 6 (in part); b, e, pereopods 4, 7; f, pleonal plates; g, h, i, uropods 1, 2, 3; j, telson.
Figure 70.—*Crangonyx insolitus*, new species. Male paratype (5.6 mm). Blue Spring Cave. 17.6 km E of Eminence, Shannon Co., Missouri: a. antenna; b. c. gnathopods 1, 2; d. pereopod 7 (in part); e. f. g. uropods 1, 2, 3; h. telson.
Figure 71.—Distribution of *Trunggora aequalis* in North America. Solid circle represents a single locality.
anteroventral margin; basis with 23 shallow serrations along posterior margin; 8 sets of short spines in
groups of 1-2 on anterior margin; 4 long setae on anteroproximal of anterior margin. Pereopod 7: coxa with
7 setae on the posterior margin; basis with 28 shallow serrations along posterior margin; 12 short spines on
anterior margin; dactyl 33 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta. distoposterior corner acute but
not produced. with 1 seta on ventral margin near corner; posterior margin of plate 2 nearly straight with 1
setae. distoposterior corner produced and acute. ventral margin with 6-7 (subventral) spines. 3 ventral
spines and 2 ventral setae; posterior margin of plate 3 nearly straight with 1 seta. distoposterior corner
acute, ventral margin with 8 (subventral) spines. 4 ventral spines and 5 ventral setae. Peduncle of pleopod 1
with up to 5 retinaculae. about 10 setae on outside distally.

Uropod 1: inner ramus 70 percent length of peduncle, armed with 17 spines; outer ramus with 14
spines; peduncle with row of 17 outer and 8 inner spines and 2 tiny lateral spines near ventral margin.
Uropod 2: inner ramus armed with 13 spines; outer ramus with 11 spines; peduncle with 7 outer and 5
inner spines and 2 tiny lateral spines near ventral margin. Uropod 3: inner ramus with 1 spine. outer ramus
about 2 times longer than peduncle, inner and outer margin each with 4 sets of spines in groups 2-3. Telson
distinctly broader than long, notched about 1/3 distance to base. each lobe with 5 apical spines; spines less
than 1/2 length of telson.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2:
calceoli present on peduncular segments 4 and 5. and first 3 segments of flagellum. Propod of gnathopod 1
more than 2 times larger and longer than carpus; palm with 4 spine teeth on inside. 7 on outside: defining
angle with 3 notched-serrate spine teeth on inside. 1 large notched and 2 serrate spine teeth on outside.

Propod of gnathopod 2 more than 2 times larger and longer than carpus: palmar margin strongly
oblique. with 8 spine teeth on inside. 6 on outside: defining angle with 3 spine teeth on inside and 4
notched spine teeth on outside.

Uropod 1: inner and outer ramus each with 9 spines; peduncle with 9 outer and 4 inner spines. lacking
tiny ventralateral spines. Uropod 2: inner ramus with 9 spines; outer ramus curved to complete right angle
with peduncle. with 1 inner spine, outer spines absent. apex with 5 small spines: peduncle with 3 outer
spines. 2 inner spines and 2 tiny lateral spines near ventral margin.

Type-locality.—Blue Spring Cave, 17.6 km E of Eminence, Shannon County. Missouri.

Distribution and ecology.—This rare species is known only from its type-locality (fig. 71). where it was
collected from a pool in the entrance. in company with 5 specimens of the common epigean amphipod
*Hyalella azteca*.

Etymology.—The epithet *insolitus* is from Latin. meaning "unusual." "uncommon" and "strange".
Figure 72: Geographic distribution of the gracilis group in North America. Shaded area indicates contiguous or near contiguous distribution of the R group in North America. Note also the five isolated pockets (also shaded) of distribution in the western U.S.
The *gracilis* group

Diagnosis.—Adult size, 5.0-11.0 mm. Segment 3 of palp with only 1-2 A setae, lacking B setae. Maxilla 1: inner plate with 5-6 apical plumose setae. Maxilla 2, inner plate with oblique row of 5-6 plumose setae on inner margin. Gnathopods with distinct sexually dimorphism. Gnathopods of female: propod less than 2 times larger and longer than carpus; palm of propod shorter than posterior margin, armed with simple spine teeth; defining angle with notched-serrate and serrate spine teeth; superior medial setae singly inserted. Gnathopods of male: carpus proportionately smaller and shorter, propod proportionately larger and broader, propod more than 2 times larger and longer than carpus; palm of propod shorter, equal or longer than posterior margin, armed with notched spine teeth; defining angle of gnathopod 1 with notched-serrate and serrate spine teeth, that of gnathopod 2 may or may not have serrate spine teeth. Posterior margins of pereopods 5-7 with fewer serrations, and anterior margin with fewer spines in both female and male in comparison with other species in the genus.

Remarks.—This group is composed of 24 species, and like the *richmondensis* group, it is widespread (fig. 72). However, species of the *richmondensis* group are larger, have stouter gnathopods with many notched spine teeth, in contrast to species of the *gracilis* group, which are distinctly smaller and have weak gnathopods with simple spine teeth. Many species of these two groups share the same habitat, suggesting that they have different ecological niches. For example, the large, well armed gnathopods of the *richmondensis* group species suggest the possibility of a carnivorous life style, whereas the weak, poorly armed gnathopods of *gracilis* group species suggest a significantly different feeding habit.

Key to the species of the *gracilis* group

1. Carpus and propod of female gnathopods very long; carpus of gnathopod 2 longer than propod
   ........................................................................................................................................................................2

2. Eyes absent; carpus and propod of male gnathopods very long with simple and few notched spines
   ........................................................................................................................................................................C. hubbsi

3. Outer ramus of male uropod 2 with comb spines.................................................4

4. Posterior margins of pleonal plates 1-3 with 2-3 setae, but lacking a seta barely above the distoposterior corner.................................................................................................................................5

5. Posterior margins of pleonal plates 1-3 with 1 seta only.....................................6

6. Posterio
5. Pleonal plates with few subventral spines (less than 8): outer ramus of uropod 3 about 1.5 times longer than peduncle...........................................................................................................................................C. consimilis

Pleon al plates with more than 14 subventral spines: outer ramus of uropod 3 about 1.9 times longer than peduncle...........................................................................................................................................C. longiduCyllus

6. Outer ramus of male uropod 2 with ventral spines........................................................................C. pseudograncilis

Outer ramus of male uropod 2 without ventral spines.........................................................................C. floridanus

7. Posterior margins of pleonal plates 1-3 with 2 setae, one just above distoposterior corner
..............................................................................................................................................................C. stagnicolus

Posterior margins of pleonal plates 1-3 with 1 seta each................................................................................C. pseudograncilis

8. Propod of female gnathopod 2 with 1 very large spine on distal end of outer margin of defining angle
........................................................................................................................................................................9

Propod of female gnathopod 2 with 1 or more small spines on distal end of outer margin of defining
angle....................................................................................................................................................................10

9. Eyes greatly reduced to specks: inner and outer margin of outer ramus of male uropod 2 with evenly
distributed spines........................................................................................................................................C. harri

Eyes large: outer ramus of male uropod 2 with 1 spine on inside and 3 spines on outside
........................................................................................................................................................................11

C. montanus

10. Inside of outer ramus of male uropod 2 with several thick spines near distal end, outside with setal-like
spines................................................................................................................................................................11

Lacking spine cluster near the distal end of male uropod 2, and outside lacking setal-like spines
........................................................................................................................................................................12

11. Eyes reduced to specks or lacking: telson of female broader than long: distoposterior corners of pleonal
plates 1 and 3 neither produced nor acute..................................................................................C. castellamum

Eyes normal: telson of female about as broad as long: distoposterior corners of pleonal plates
1-3 strongly acute...........................................................................................................................................C. acticulairs

12. Inside of outer ramus of male uropod 2 with 1-2 spines near end.................................................................13

Inside of outer ramus of male uropod 2 with 0-1 spine in the middle or with more than 3 evenly
distributed spines...................................................................................................................................................14

13. Eyes present (not reduced): inside of outer ramus of male uropod 2 with 1 spine in the notch near end
....................................................................................................................................................................C. pallustris

Eyes greatly reduced or absent: inside of outer ramus of male uropod 2 with 1-2 spines near end but
without notch ....................................................................................................................................................C. ohiensis

14. Inside of outer ramus of male uropod 2 with more than 3 evenly distributed spines.........................15

Inside of outer ramus of male uropod 2 with 0-1 spines................................................................................17

15. Eyes greatly reduced or absent: defining angle of gnathopod propods of both sexes with only notched
spine teeth......................................................................................................................................................C. puckardi

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Eyes large; defining angle of gnathopod propods of both sexes with notched and serrated spine teeth.................................................................................................................................................................. 16

16. Telson longer than broad, notched 1/2 distance to base.......................................................C. aka
Telson broader than long, notched less than 1/2 distance to base..............................................C. rivularis

17. Eyes large; distoposterior corners of pleonal plates 1-3 produced and acute......................C. gracilis
Eyes absent or represented by specks; distoposterior corners of pleonal plates 1-3 not produced .................................................................................................................................................. C. caecus

Species of the gracilis group unassigned to subgroups

The following 12 species of the gracilis group remain unassigned to subgroups pending further study.

Crangonyx gracilis Smith

Figures 73-77


Crangonyx gracilis gracilis Smith.--Hubricht. 1943:691 [in part].


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Figure 73.—*Crangonyx gracilis* Smith. Female (9.2 mm), pond just S of Ypsilanti Airport. 8.0 km SE of Ann Arbor. Washtenaw Co., Michigan: a, b. antennae 1, 2; c, d. maxillae 1, 2; e. lower lip; f. inner and outer plates of maxilliped (greatly enlarged); g. dentate part of left mandible; h. right mandible; i, j, k. uropods 1, 2, 3; l. telson.
Figure 74.—*Crangonyx gracilis* Smith. Female (9.2 mm), pond just S of Ypsilanti Airport, 8.0 km SE of Ann Arbor, Washtenaw Co., Michigan: a, e, d. pereopods 3, 5, 6; b, e. pereopods 4, 7; f. pleonal plates.
Figure 75. *Crangonyx gracilis* Smith. Female (9.2 mm), pond just S of Ypsilanti Airport, 8.0 km SE of Ann Arbor, Washtenaw Co., Michigan: a, b. gnathopods 1, 2 (palmar margins enlarged). Male (7.0 mm), same location: c. antenna 2 (in part).
Figure 76.—*Crangonyx gracilis* Smith. Male (7.0 mm), pond just S of Ypsilanti Airport, 8.0 km SE of Ann Arbor, Washtenaw Co., Michigan: a. b. gnathopods 1, 2 (palmar margins enlarged); c. pereopod 7; d. e. uropod 2, 3. Male (5.7 mm), same location: f. uropod 2 (in part); g. telson.
Figure 77.—Distribution of Crangonyx gracilis in North America. Solid circles represent 1-13 closely proximate localities.

The dotted line indicates the approximate southern extent of glaciation during the Pleistocene.
(USNM); soil water in ant nest. Palatine. 1 spec. A. M. Holmquist. 15 Feb 1925 (USNM):

km S of Oak Grove. 6 ♂, 5 ♀, L. Hubricht, 21 Apr 1942 (USNM); Reeseville pool of stream into Trib.
Beaver Dam River, 1 ♀, 6 juvs, J. P. Jass and B. Klausmeier, 22 Jul 1994 (MPM); Fond Du Lac Co.: creek.
4.3 km SW of Lamartine, 30 spec (♀, ♂), L. Hubricht, 21 Apr 1942 (USNM); swampy water, Auburn
township. 2 ♀, collector unknown, 12 May 1971 (MPM); Jefferson Co.: Near Palmyra, ponds on Emma
Carlin Trail, many juvs, collector unknown, 31 Mar 1980 (MPM); Kenosha Co.: Near New Munster, 2 ♂,
collector unknown, 29 Sep 1989 (MPM); unnamed stream at County Trunk Highway AH. 3.5 km E jet
Hwy 83. 8 ♂, 4 ♀, J. P. Jass and B. Klausmeier, 6 May 1994 (MPM); marsh N of Junction Co. Highways F
& JI. 2 ♂, J. P. Jass and B. Klausmeier, 6 May 1994 (MPM); pool S of Wheatland on Co. Hwy W just N.
junct Hwy 50. 5 ♀, 9 ♂, J. P. Jass and B. Klausmeier, 6 May 1994 (MPM); Manitowoc Co.: Mud Creek at
County Trunk Highway J. 2.9 km S of Valders, 1 juv. B. Klausmeier, 9 Sep 1994 (MPM); Milwaukee Co.: 
City of Oak Creek, Bender Park, 1 ♀, collector unknown, 21 Apr 1990 (MPM); Menomonee River, just W
of 70th St bridge, 2 ♀, B. Klausmeier, 16 Sep 1994 (MPM); Ozaukee Co.: 2.4 km S of Newburg, 25 spec.
collector unknown, 5 May 1980 (MPM); Near Saukville, 1 ♂, 1 ♀, collector unknown, 12 May 1989
(MPM); Sapa Spruce Bog, W of Saukville, 1 ♂, 12 ♀, J. P. Jass and B. Klausmeier, 15 Jul 1994 (MPM);
Portage Co.: temporary pool, 16 km N of Stevens Point. 50 spec., L. Hubricht, 22 Apr 1942 (USNM);
Racine Co.: Goosel Branch on Olson Rd., 0.8 km E of Hwy S south, 34 spec. J. P. Jass and B. Klausmeier,
13 May 1994 (MPM); pond at County Trunk Highway G & Waukesha Co. line, 7 ♂, 1 ♀, J. P. Jass and B.
Klausmeier, 13 May 1994 (MPM); Root River at 7 Mile Road just W of Hwy 194, 2 ♂, J. P. Jass and B.
Klausmeier, 13 May 1994 (MPM); grassy pool, N side, and 7 Mile Rd., just W of Root River Canal bridge.
12 ♂, 8 ♀, J. P. Jass and B. Klausmeier, 13 May 1994 (MPM); Wind Lake outlet channel, 20 ♂, 6 ♀, J. P.
Jass and B. Klausmeier, 13 May 1994 (MPM); Sheboygan Co.: Sheboygan River at County Trunk
Highway M, less 1.6 km S junct J. 4 ♂, 1 ♀, 6 juv. J. P. Jass and B. Klausmeier, 5 Aug 1994 (MPM);
Waukesha Co.: Skettle Moraine State Forest, 1 ♂, many juvs, collector unknown, 3 Jun 1979 (MPM); Just
N of Eagle. 4 ♀, collector not given, 9 May 1980 (MPM); Scuppernong Creek, 1 ♂, collector not given, 20
Sep 1979 (MPM); Bark River, near Dousman at Hwy 18 Bridge, 1 ♂, J. P. Jass and B. Klausmeier, 3 Jun
1994 (MPM); roadside ditch cattails, County Trunk Highway (Watertown) just W of J. 64 spec. J. P. Jass
and B. Klausmeier, 1 Apr 1994 (MPM); unnamed stream, 2 spec. J. P. Jass and B. Klausmeier, 13 Oct
1994 (MPM); Cattail Pond, 9 ♂, J. P. Jass and B. Klausmeier, 13 Oct 1994 (MPM); marsh N of Co. Hwy
NN, less 0.8 km E of Co. Hwy Z north, 32 spec. J. P. Jass and B. Klausmeier, 3 Jun 1994 (USNM);
Waushara Co.: cattail pond N side County Trunk Highway XX, 9 spec., J. P. Jass and B. Klausmeier, 13
Oct 1994 (MPM); unnamed stream at County Trunk Highway XX, 2 spec. J. P. Jass and B. Klausmeier,
13 Oct 1994 (MPM); ditch, 4.8 km S of Aurorahville, 30 spec., L. Hubricht, 22 Apr 1942 (USNM);

Diagnosis.—A relatively small species closely allied morphologically with C. pseudogracilis and C.
floridanus but distinguished from them by lacking comb spines on outer ramus of uropod 2 of male, and
having either 1 spine or lacking spines on the outside margin of the outer ramus. Largest male, 5.5 mm;
largest female, 9.0 mm.
Female.--Eye large, ovate. Antenna 1. about 50 percent length of body, about 1.8 times longer than
antenna 2; primary flagellum with about 20-23 segments. Antenna 2, flagellum with 8-9 segments.
Mandibles subequal, spine row with 5 spines: segment 2 of palp with 7 long setae: segment 3 with 1 A
seta, 1-2 C setae, 3-4 E setae and a row of 10 D setae, lacking B seta. Maxilla 1: inner plate with 4-7 apical
plumose setae: palp with 5-6 slender spines on apex. Maxilla 2, inner plate with oblique row of 4-8
plumose setae on inner margin. Maxilliped: apically with 4 bladelike spine teeth, 2 naked spines, and 8
plumose setae extending from inner margin to apex; outer plate with row of naked setae and 3-4 slender
pectinate spines on inner margin, 1 apical plumose seta: dactyl with 1-2 setae on inner margin near nail:
dactyl nail very long, about 1/3 length of dactyl.
Propod of gnathopod 1 less than 2 times larger and longer than carpus: palm length shorter than
posterior margin, slightly convex, with about 5 unnotched spine teeth on inside. about 8 on the outside:
defining angle with 6 notched-serrate spine teeth on inside. 1 large notched and 3 serrate on outside;
superior medial setae few in number and singly inserted; 5 posterior margin setae singly inserted. Dactyl
with a row of 3-4 short setae on inner margin, nail long. Ventral margin of coxa 1 with 7-8 setae.
Propod of gnathopod 2 less than 1.5 times larger than carpus which up to 3/4 length of corresponding
propod: palm slightly convex and oblique, much shorter than posterior margin, with about 4 unnotched
spine teeth on inside, 10 on outside: defining angle with 1 notched spine tooth and 3-4 notched-serrate
spine teeth on inside, 1 large notched and 1 small notched-serrate spine teeth on outside: superior medial
setae up to 7, singly inserted: posterior margin with 4-5 sets of setae in groups of 1-5. Dactyl with row of
short setae on inner margin. Ventral margin of coxa 2 with 7 setae.
Coxa of pereopod 3 with 6-8 marginal setae. Coxa of pereopod 4 with 13-15 marginal setae. dactyl of
pereopod 4, 35 percent length of corresponding propod. Pereopod 5: basis with 9 shallow serrations along
posterior margin; 7 sets of 1-2 short spines on anterior margin; 2 long setae on the anteroproximal of
anterior margin. Pereopod 6: basis with 12 serrations along posterior margin: 6 short spines on anterior
margin: 4 long setae on anteroproximal of anterior margin. Pereopod 7: coxa with 3 setae on the posterior
margin: basis with 15 serrations along posterior margin: deeper near apex: 5-6 short spines on anterior
margin: 3 setae on anteroproximal: dactyl about 35 percent length of corresponding propod.
Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner produced
and acute: posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner strongly produced
and acute, ventral margin with 3-4 (subventral) spines: posterior margin of plate 3 nearly straight with 1
seta, distoposterior corner slightly produced and acute, ventral margin with 4 (subventral) spines. Peduncle
of pleopod 1 with 2 setae: lacking setae on outside margin. 1 spine on proximal inner margin.
Uropod 1: inner ramus about 70 percent length of peduncle, armed with about 12 spines; outer ramus
with 11 spines: peduncle with row of 7-8 outer and 3 inner spines. Uropod 2: inner ramus slightly shorter
than peduncle. inner ramus armed with 12 spines; outer ramus with 9 spines: peduncle with 4 outer spines.
2 inner spines. Uropod 3: inner ramus lacking spines. outer ramus about 1.8 times longer than peduncle.
inner and outer margin each with 3 set of spines in groups 1-4. Telson broader than long, notched about 1/3:1/2 distance to base, each lobe with about 3 apical spines.

Male.--Differing from female as follows. Smaller, with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5 and first 4 segments of flagellum. Propod of gnathopod 1 more than 2 times larger and longer than carpus and broader; palm slightly oblique and convex, subequal in length to posterior margin; with 7 spine teeth on inside, 8 on outside. defining angle with 4-5 notched-serrate spine teeth on inside; 2 notched and 1-3 serrate spine teeth on outside, and with have another row of 4 small serrate spine teeth in larger specimens.

Propod of gnathopod 2 more than 2 times larger and longer than carpus; palmar margin oblique, slightly convex, subequal in length to posterior margin, with 9-10 spine teeth on inside, 10 on outside; defining angle with 2 notched spine teeth and 3 serrate spine teeth on inside and 4-5 notched spine teeth on outside. Uropod 2: outer ramus deflected laterally about 45 degrees from midline; with either 1 spine or lacking spines on inside, bearing 2-4 short spines on outside, apex with 5 short spines; peduncle with 3 spines on outside, about 4 spines on inside.

Distribution and ecology.--C. gracilis is found primarily in the Great Lakes region, where it has been collected from Wisconsin, Michigan, Illinois, Ohio, and Ontario (fig. 77). The eastern-most record is in central Massachusetts and the southern-most records are in southeastern West Virginia and southeastern Virginia.

C. gracilis inhabits lakes, creeks, ponds, rivers, streams, marshes, ditches, swales, and spring-fed ponds throughout most of its range, but it is found in caves in southeastern West Virginia. Ovigerous females were found in collections made in April to June, and September.

Crangonyx barrs, new species

Figures 78-82

Figure 7g—"C. ranyo nyx burni," new species. Male paratype (6.0 mm), entire animal from left side, seep, ravine 0.7 mile NW of Indian Hill, Mammoth Cave National Park, Edmonson Co., Kentucky.
Figure 79.—Crangonyx barri, new species. Female paratype (7.8 mm). Mammoth Cave system (Cathedral Domes), Edmonson Co., Kentucky: a. antenna I; b. c. gnathopods 1, 2 (palmar margins enlarged); d. pleonal plates.
Figure 80. -- *Crangonyx barri*, new species. Female paratype (7.8 mm). Mammoth Cave system (Cathedral Domes), Edmonson Co., Kentucky: a. b. maxillae 1. 2; c. lower lip; d. left mandible; e. dentate part of right mandible; f. inner and outer plates and palp dactyl of maxilliped; g. i. pereopod 3. 6 (in part); h. j. pereopods 4. 7.
Figure 81.—*Crangonyx barri* new species. Female paratype (7.8 mm), Mammoth Cave system (Cathedral Domes), Edmonson Co., Kentucky: a, b. uropods 2, 3: c. telson. Male paratype (5.8 mm), same location: d. antenna 2: e. f. gnathopods 1, 2 (palmar margins enlarged): g, h, i. uropods 1, 2, 3: j. telson.

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Figure 82.—Distribution of *Crangonyx barri* in North America. Solid circles represent 1-6 closely proximate localities.

Diagnosis.—A relatively small stygobiont species, distinguished from other species of the gracilis group by propod of gnathopod 2 of female, which bears a very large spine tooth on outer margin at end of defining angle; unproduced pleonal plates; and spines on outer ramus of uropod 2 of male distributed.

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evenly on both inside and outside margins. Largest male. 7.0 mm; largest female. 8.5 mm.

Female.—Eye greatly reduced, with several facets only. Antenna 1, 55-60 percent length of body, about
2.0 times longer than antenna 2; primary flagellum with 20 segments. Antenna 2, flagellum with 7-9
segments. Mandibles subequal, spine row with 7-8 spines; segment 2 of palp with 12 long setae. segment 3
with 1 A seta, 4 C setae, 4-5 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 6-8
apical plumose setae; palp with several slender spines on apex. Maxilla 2. inner plate with oblique row of
6-8 plumose setae on inner margin. Maxilliped: inner plate apically with 2 bladelike spines. 1 naked spine.
and 5-6 plumose setae on the inner margin to on apex; outer plate with row of naked setae and 3-4 slender
pectinate spines on inner margin; dactyl with 2 setae near nail on inner margin; dactyl nail long, 1.3 length
of dactyl.

Propod of gnathopod 1 less than 2 times larger and longer than carpus; palm almost straight, shorter
than posterior margin, with 9 unnotched spine teeth on inside. 7 on the outside; defining angle with 5
notched-serrate spine teeth on inside, 1 large unnotched and 1 serrate spine teeth on outside; inferior and
superior medial setae singly or doubly inserted; posterior marginal setae singly or doubly inserted. Dactyl
with a row of short setae on inferior margin, nail long. Ventral margin of coxa 1 with 7-8 setae.

Propod of gnathopod 2 less than 2 times larger and longer than carpus; palm convex, shorter than
posterior margin, with 8 unnotched spine teeth on inside. 11 on outside; defining angle inside with 1 large
and 3 notched-serrate spine teeth, outside with 2 unnotched teeth and 1 very large unnotched spine teeth at
end; superior medial setae singly or doubly inserted; posterior margin with 6-7 sets of setae in groups of 2-
4. Dactyl with row of short setae on inferior margin. Ventral margin of coxa 2 with 9 setae.

Coxa of pereopod 3 with 10 marginal setae. Coxa of pereopod 4 with 12 marginal setae, dactyl of
pereopod 4. 33 percent length of corresponding propod. Pereopod 5: basis with 14 shallow serrations
along posterior margin; 9 short spines on anterior margin; 3 long setae on anteroproximal margin. Pereopod
6: basis with 12 serrations along posterior margin; 6 short spines on anterior margin; 2 setae on
anteroproximal margin. Pereopod 7: coxa with 3 setae on the posterior margin; basis with 12-15 serrations
along posterior margin; 6 short spines on anterior margin; 1 long seta on anteroproximal margin; dactyl of
pereopod 7. 35 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 convex, with 1 (rarely 2) setae, distoposterior corner neither
produced nor acute; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner not
produced, subacute, ventral margin with 4-5 (subventral) spines; posterior margin of plate 3 nearly straight
with 1 seta, distoposterior corner indistinct rounded, ventral margin with 4 (subventral) spines. Peduncle of
pleopod 1 with 2 retinaculae, lacking setae on outer margin.

Uropod 1: inner ramus 80 percent length of peduncle, armed with 12 spines; outer ramus with 14
spines; peduncle with 10 outer and 3 inner spines. Uropod 2: inner ramus armed with 14 spines; outer
ramus with 15 spines; peduncle with 4 outer and 4 inner spines. Uropod 3: inner ramus with 1 spine, outer
ramus about 2 times longer than peduncle, inner and outer margin each with 2-3 set of spines in groups 1-3.
Telson broader than long, notched about 1/4 distance to base, each lobe with 2 apical spines: spines about 1.2 length of telson.

Male.—Differing from female as follows. Smaller than with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5 and first 3 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus: palm with 6 spine teeth on inside, 8 on outside; defining angle with 4 notched-serrate spine teeth on inside, 1 large notched and 1 small serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm strongly oblique, with 9-10 spine teeth on inside, 12 on outside; defining angle with 1 notched and 3 notched-serrate spine teeth on inside, 3 notched and 1 very large notched spine teeth on outside.

Uropod 2: inner ramus with 12 spines; outer ramus curved, with 6 or more short spines on both outer margins. apex with 4 spines; peduncle with 4 outer and 4 inner spines.

Type-locality.—Mammoth Cave system (Cathedral Domes). Edmonson County, Kentucky.

Distribution and ecology.—This subterranean species is widely distributed in karst regions of southern Indiana and central Kentucky (fig. 82). Although it is primarily an inhabitant of small cave streams, it also occurs in cave drip pools. In addition, there is one record from a surface stream (presumably a wash-out) and several springs and seeps. Ovigerous females were collected from May to December and brood 10-20 yellow eggs. Sexually mature males, 4.0 to 7.0 mm; sexually mature females, 5.0 to 8.5 mm.

*Crangonyx barri* has occasionally been found in association with the amphipods *C. forbesi*, *C. lewisi*, *Stygohromus exilis*, and *Synurella dentata*, and the isopods *Lirceus* sp. and *Caecidotea* sp.

Etymology.—It is pleasure to name this species in honor of Dr. Thomas C. Barr, Jr., Emeritus Professor of Zoology, University of Kentucky, for his assistance with the collection of many of the samples examined in this study and to honor his many important contributions to our knowledge of biospeleology in North America.

*Crangonyx montanus*, new species

Figures 83-86

Material examined (paratypes unless designated otherwise).—VIRGINIA. Alleghany Co: small swamp. Fairview-Clifton Forge. 33 specs, no collector given, 17 May 1940 (USNM) and 3 ♂, 2 ♀. 20 May 1940 (USNM); Bath Co.: small spring-fed swamp. Nimrod Hall. 18 ♂, 10 ♀. T. K. Ellis, 20 May 1940 (USNM); large spring, 8.0 km S of Nimrod Hall, 16 ♂, 3 ♀, 1 Juv. T. K. Ellis, 20 May 1940 (USNM); spring at edge of road upper end of Panthers Gap, holotype ♂, 40 specs (♀, ♂), no collector given, 18 May 1940 (USNM); Lyle Chapel, 13 ♂, 2 ♀, no collector and habitat given, 21 May 1940 (USNM); Rockbridge Co.: spring on Rt. 42 in Patthers Gap, 6.4 km W of Goshen. 2 ♂ (not paratypes), R. L. Hoffman, Mar 1948 (USNM); spring-fed pond on Rt. 759 SE of Natural Bridge Station. (not paratypes). C. K. Biernbaum, 10
Figure S3.—Crangonyx montanus. new species. Female paratype (7.0 mm), small spring-fed swamp. Nimrod Hall, Bath Co., Virginia: a, head (in part); b, antenna 1; c, d, maxillae 1, 2; e. lower lip; f, left mandible; g, dentate part of right mandible; h, inner and outer plates and palp dactyl of maxilliped (greatly enlarged); i, j. gnathopods 1, 2 (palmar margins enlarged).
Figure 84.--Crangonyx montanus. new species. Female paratype (7.0 mm), small spring-fed swamp.
Nimrod Hall. Bath Co., Virginia: a. b. c. d. pereopods 3. 4. 5. 6 (in part): e. pleonal plates: f. g. h.
uropods 1. 2. 3: i. telson.

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Figure 85.—*Crangonyx montanus*, new species. Male paratype (4.0 mm), small spring-fed swamp. Nimrod Hall, Bath Co., Virginia: a. b. gnathopods 1, 2 (palmar margins enlarged); c. pereopod 7 (in part); d. e. f. uropods 1, 2, 3; g. telson; h. uropod 2.
Figure 86.--Distribution of *Crangonyx montanus* in North America. Solid circles represent single localities.
July 1989. WEST VIRGINIA. Greenbrier Co.: Bell karst window near Bell entrance to Ludington Cave. 5 ♀ (not paratypes), D. Fong, 5 Mar 1995.

Diagnosis.—A small species of the gracilis group morphologically very similar to C. harri but distinguished from it by having well developed eyes: more distinct corners of produced pleonal plates: and fewer spines on outer ramus of uropod 2 of male. Largest male, 5.0 mm: largest female, 8.0 mm.

Female.—Eye large, ovate. Antenna 1, about 50 percent length of body, about 1.8 times longer than antenna 2: primary flagellum with about 20 segments. Antenna 2, flagellum with 8-9 segments. peduncle 4 with 2-3 sets and peduncle 5 with 3-4 set marginal setae. Mandibles subequal, spine row with 6 spines; segment 2 of palp with 6-7 long setae, segment 3 with 1 A seta, 2 C setae, 3 E setae and a row of D setae. lacking B seta. Maxilla 1: inner plate with 4 apical plumose setae; palp with 5-6 slender spines and 3 setae on apex. Maxilla 2. inner plate with oblique row of 5 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 2 naked spines, and 5-6 plumose setae extending from inner margin to apex. outer plate with row of naked setae and 3-4 pectinate slender spines on inner margin. 1 apical plumose seta; dactyl with 2-3 setae near nail on inner margin; dactyl nail very long, 1.3 length of dactyl.

Propod of gnathopod 1 less than 2 times larger and longer than carpus; palm almost straight, subequal in length to posterior margin. with about 4 unnotched spine teeth on inside, 6 on outside; defining angle with 1 large notched and 2 small serrate spine teeth on outside. 3 small notched-serrate spine teeth on inside; superior medial setae few in number and singly inserted; posterior margin with 4 sets of setae singly inserted or in groups of 2. Dactyl with a row of 5-6 short setae on inferior margin. nail long. Ventral margin of coxa 1 with 6 setae.

Propod of gnathopod 2 less than 2 times larger and longer than carpus; palm almost straight, oblique, slightly shorter than posterior margin. with about 6 unnotched spine teeth on inside, 8 on outside; defining angle with 1 large notched and two small notched-serrate spine teeth on outside. 1 large notched spine tooth on outside end; superior medial setae singly inserted, posterior margin with 5 sets of long setae in groups of 1-6. Dactyl with row of 3-4 short setae on inner margin. Ventral margin of coxa 2 with 6 setae.

Coxa of pereopod 3 with 6 marginal setae. Coxa of pereopod 4 with 12 marginal setae, dactyl about 40 percent length of corresponding propod. Pereopod 5: basis with 7 shallow serrations along posterior margin; 7 short spines on anterior margin: 2-3 long setae on anteroproximal margin. Pereopod 6: basis with 10 shallow serrations along posterior margin; 5 short spines on anterior margin: 2-3 long setae on anteroproximal margin. Pereopod 7: coxa with 2 setae on the posterior margin; basis with 10 shallow serrations along posterior margin; 5 short spines on anterior margin; 1 seta on anteroproximal margin: dactyl about 35 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner small, acute; posterior margin of plate 2 nearly straight with 1 or 2 setae, distoposterior corner weakly produced and acute, ventral margin with 3 (subventral) spines; posterior margin of plate 3 slightly convex with 1 seta, distoposterior corner not produced, subacute, ventral margin with 3 (subventral) spines. Peduncle of
pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus about 70 percent length of peduncle, armed with 9 spines; outer ramus with 9 spines; peduncle with 8 outer and 2 inner spines. Uropod 2: inner ramus, inner ramus armed with 11 spines; outer ramus with 9 spines; peduncle with 3 outer spines, 2 inner spines. Uropod 3: inner ramus with lacking spines; outer ramus about 2 times longer than peduncle, inner and outer margin each with 3-4 set of spines in groups 1-3. Telson slightly broader than long, notched about 1/3 distance to base, each lobe with 3 apical spines; spines about 1/2 length of telson.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 2 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus: palm with 5 spine teeth on inside, 7 on outside; defining angle with 4 notched-serrate spine teeth on inside and 1 notched and 2 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm longer than posterior margin, palm strongly oblique, slightly convex, with 9 spine teeth on inside, 8 on outside: defining angle with 1 notched and 4 notched-serrate spine teeth on inside, 3 notched spine teeth on outside.

Uropod 2: inner ramus with 10 spines: outer ramus slightly deflected laterally, with 0-1 inner spines, 3 outer spines, apex with 4-5 spines; peduncle with 4 outer and 1 inner spines.

Type-locality.—Spring at edge of road, upper end of Panthers Gap, Bath County, Virginia.

Distribution and ecology.—This species is recorded from several localities in west-central Virginia and 1 locality in eastern West Virginia, all in the Appalachian Valley and Ridge province (fig. 86). The range covers a linear distance (east to west) of about 80 km. This species inhabits springs, spring-fed swamps, and spring-fed ponds. Ovigerous females were collected in May.

Etymology.—The epithet montanus is from Latin, "pertaining to mountains," which refers to the occurrence of this species in the mountains of western Virginia and eastern West Virginia.

_Crangonyx rivularis_ Bousfield

_Figures 87-90_


Material Examined.—ONTARIO. Halton Co.: Speyside stream, 1 ♂, N. Hynes, 3 Jun 1975 (USNM); Grey Co.: Rocky Saugeen River, small tributary 6.4 km N of Durham, holotype ♂, allotype ♂, 18 ♂, 7 ♀, 6 ♂, 4 ♀, 5 ♀, 4 ♀, E. L. Bousfield, 30 May 1957 (CMN); Dufferin Co.: water cress roots, Orangeville, 5 ♂, 4 ♀, 5 ♀, 4 ♀, E. L. Bousfield, 30 May 1957 (USNM); Spring W of Toronto. 2 ♂, A. Pizzini, 17 May 1935 (USNM) and 6
Figure 87.—*Crangonyx rivularis* Bousfield. Female (6.0 mm), Orangeville, Ontario, Canada: a. antenna 1; b, c. maxillae 1, 2; d. lower lip; e. left mandible; f. dentate part of right mandible; g. inner and outer plates and palp dactyl of maxilliped (greatly enlarged); h, i. gnathopods 1, 2 (palmar margins enlarged).
Figure 88. — *Crangonyx rivularis* Bousfield. Female (6.0 mm), Orangeville, Ontario, Canada: a, b, c. pereopods 3, 5, 6 (in part): d. pereopod 7: e. pleonal plates: f. telson: g, h, i. uropods 1, 2, 3. Female (6.5 mm), same location: j. pleonal plates.
Figure 89.—*Crangonyx rivularis* Bousfield. Male (4.1 mm), Orangeville, Ontario, Canada: a, antenna 2; b. c. gnathopods 1. 2. (palmar margins enlarged); d. pereopod 7; e. f. uropods 2; g. uropod 3; h. telson

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Figure 90.—Distribution of *Crangonyx rivularis* in North America. Solid circles represent 1-8 closely proximate localities. The dotted line indicates the approximate southern extent of glaciation during the Pleistocene.
ILLINOIS. Adams Co.: spring near house. Siloam Spring State Park. 5  5 Jul 1935 (USNM).
B. Peck. 22 Apr 1966; Bond Co.: temporary pond. 1.0 km E of Baden. 7  19 Apr 1942 (USNM);
Cumberland Co.: ditch. 5.8 km ENE of Greenup. 31  16 Apr 1942 (USNM); Jackson Co.: seeps in bluff
on nature trail at cave. Makanda entrance of Giant City State Park. 1  5 May 1974; LaSalle Co.: temporary
pond. 0.8 km NE of Seneca. 50 specs. L. Hubricht. 3 May 1941 (USNM); Madison Co.: temporary pool,
near Silver Creek. 5.8 km W of St. Jacob. 2  16 Apr 1942 (USNM); Monroe Co.: Moredock Lake.
3. km N of Valmeyer. 7  12 May 1937 (USNM); temporary pond. roadside ditch. North Dupo. 38  24 Apr
1938 (USNM); St. Clair Co.: temporary pool. ditch. 1.6 km S of Falling Spring. 300 specs. L. Hubricht.
24 Apr 1941 (USNM); marsh at 5300 State Street. East St. Louis. 20 specs. L. Hubricht. 12 May 1937
(USNM). INDIANA. Elkhart Co.: seep. 22.4 km E of Nappanee. 19  19 Apr 1942 (USNM);
Huntington Co.: slough. 5.3 km NE of Huntington. 100 specs. L. Hubricht. 27 Apr 1941 (USNM);
LAKE Co.: temporary pond. 1.0 km W of New Chicago. 30 specs. L. Hubricht. 2 May 1941 (USNM);
LaPorte Co.: temporary pond. 7.7 km NE of La Porte. 10  2 May 1941 (USNM); Monroe Co.:
spring near Jacks Deafet Creek. Bloomington. 1 juv. N. Hynes. 20 Oct 1962 (USNM) and 17
Dec 1962 (USNM); Porter Co.: outlet of drain. 0.8 km E of River. 50 specs. L. Hubricht. 20 Apr 1942
(USNM). KENTUCKY. Bourbon Co.: small spring. 4.5 km SW of Millersburg. 25 specs. L. Hubricht.
25 Apr 1941 (USNM); spring. 9.1 km SW of Paris. 8  21 Apr 1941 (USNM); Boyle Co.:
Salt River system. Atoka. 2 specs. collector not given. 6 Mar 1971; Bullitt Co.: Creek at T-junction. W of
Crutchmere Hollow. 7  9 Jan 1985 (USNM); Estill Co.: Clifford Pearson Cave. 2  1  20 Jan 1968;
Hardin Co.: slough just W of West Point. 8  1  21 Apr 1956 (USNM); Fayette Co.: temporary pond,
118 specs (s, jsvs), 19 Apr 1965 and 100 specs. 5 May 1965; pond on Coldstream Farm. 25 specs
2  11 Apr 1965; Crasmere Farm No.1 spring. Higbee Mill Road. 1  7 Mar 1964; Idle Hour spring No.1.
on Rd 25. 1  11 Apr 1965; Idle Hour Spring No.2. near Rd 25. 1  11 Apr 1965; Russell Cave Spring.
11.2 km NE of Lexington. 4  22 Nov 1940 (USNM) and 1
16 Nov 1963; sheps fed swamp off Tates Creek Road. Lexington. 1  1 Mar 1965; spring-fed stream on
Waveland Farm near Lexington. 2  11 Apr 1965; Jefferson Co.: Cave Hill Cave. Louiseville. 1  9 Jun
1975; intermittent ditch in George Rogers Clark Park. 5  1955; small tributary of Pope Lick.
1  9 Jan 1985 (USNM); pond in Shawnee Park. Louiseville. 5  1  29 Mar 1954; sheks branch
crosses Old Heady Rd. 2  29 Mar 1954; G. A. Cole, collection date not given: Jessamine Co.: spring.
4.3 km N of Nicholasville. 6  4  24 Apr 1941 (USNM); spring 9.8 km N of Nicholasville. 1  24 Apr
1941 (USNM);
Hubricht, 24 Apr 1941 (USNM): Lincoln Co.: small spring, 1.6 km of Preacherville. 7 ♂, 6 ♀. L. Hubricht.
19 Apr 1942 (USNM): Calhoun Co.: pools in swamp. 5.6 km ESE of Battle Creek. 40 specs. L. Hubricht.
13 Apr 1947 (USNM): Eaton Co.: outlet of drain. 1.6 km NE of Olivet. 20 specs. L. Hubricht.
19 Apr 1942 (USNM): Genesee Co.: small stream. 7.2 km N of Fenton. 2 ♂, 3 ♀. L. Hubricht.
19 Apr 1942 (USNM): Lenawee Co.: slough. 0.8 km W of Hudson. 9 ♂, 13 ♀. L. Hubricht.
17 Apr 1942 (USNM): Williams Co.: outlet of drain. 0.3 km NE of Williams Center. 40 specs (2 ♂, 2 ♀). L. Hubricht.
28 Apr 1941 (USNM). MISSOURI. St. Louis Co.: temporary pool. 4.8 km NW of Pattonville. 150 specs. L. Hubricht.
17 Apr 1938 (USNM): temporary pond, Benbush. 47 specs. L. Hubricht. 8 Mar 1936 (USNM); pond, E of Morschels. 4 ♂, 19 ♀. L. Hubricht (USNM); slough. 8.0 km W of Florissant. 20 specs. L. Hubricht.
24 May 1941 (USNM); temporary pool. 0.8 km W of Vugus. 100 specs. L. Hubricht. 17 Apr 1938 (USNM);
slough near Mississippi River. 1.6 km S of Grimsby. 36 specs. L. Hubricht. 25 Apr 1938 (USNM).
NEW YORK. Herkimer Co.: marsh near Mohawk River. Ilion. 8 ♂, 6 ♀. L. Hubricht. 28 Mar 1943 (USNM);
temporary pool. Frankfort. 21 ♂, 20 ♀. L. Hubricht. 4 Apr 1943 (USNM); spring near Mohawk River. 15.2
km SE of Little Falls. 50 specs. 18 Apr 1943 (USNM). OHIO. Preble Co.: small stream, 3.2 km W of
Alexandria. 23 ♂, 4 ♀. L. Hubricht. 17 Apr 1942 (USNM); Williams Co.: outlet of drain. 0.3 km NE of
Wiliams Center. 40 specs (♂, ♀). L. Hubricht. 28 Apr 1941 (USNM). WEST VIRGINIA. Cabell Co.:
Green Bottom Swamp. 4 ♂, 6 ♀. D. C. Tarter, collection date not given, and 4 ♂, 6 ♀. 20 Mar 1995; Greenbrier
Co.: Meadow River Wetlands. 6 ♂, D. C. Tarter. 19 Apr 1996.

Diagnosis.—Distinguished from other members of the gracilis group by having notched-serrate spine
teeth on defining angle of propod of gnathopods of both sexes, shallow serrations on posterior margins of
pereopod 5-7, inner and outer margins of outer ramus of male uropod 2 with up to 7 short, well spaced
spines. Largest male, 4.5 mm; largest female 8.5 mm.

Female.—Eye large, ovate. Antenna 1, about 50 percent length of body, about 1.8 times longer than
antenna 2; primary flagellum with up to 20 segments. Antenna 2, flagellum with 7-9 segments. Mandibles
subequal, spine row with 4-5 spines: segment 2 of palp with 4-5 long setae, segment 3 with 1 A seta, 1 C
seta, 3-4 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 4-5 apical plumose setae:
palp with 5-6 slender spines on apex. Maxilla 2, inner plate with oblique row of 4-5 plumose setae on inner
margin. Maxilliped: inner plate apically with 3 bladelike spines, 1 naked spine, and 3-4 plumose setae
extending from inner margin to apex: outer plate with row of naked setae and 2-4 slender pectinate spines
on inner margin; dactyl with 2 setae on inner margin near nail; dactyl nail long about 1/3 length of dactyl.

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Propod of gnathopod 1 less than two times larger and longer than carpus: palm almost straight, shorter than posterior margin, with 5 unnotched spine teeth on inside. 4 on the outside; defining angle with 4-5 notched-serrate and 1 serrate spine teeth on inside. 1 large notched and 3 serrate spine teeth on outside: superior medial setae few in number and singly inserted: 4 sets of setae on posterior margin, singly inserted or in groups of 2. Dactyl with a row of short setae on inner margin, nail very long. Ventral margin of coxa 1 with 7-8 setae.

Propod of gnathopod 2 less than 2 times larger and longer than carpus: palm almost straight, much shorter than posterior margin, with 4 unnotched spine teeth on inside. 7 on outside; defining angle with 1 large notched spine tooth and 2-3 serrate spine teeth on outside. 1 notched and 4-5 notched-serrate spine teeth on inside: superior medial setae singly inserted; posterior margin with 4 sets of setae in groups of 1-5. Dactyl with row of short setae on inferior margin, nail very long. Ventral margin of coxa 2 with 6 setae.

Coxa of pereopod 3 with 6-8 marginal setae. Coxa of pereopod 4 with 13 marginal setae. Dactyl of pereopod 4. 40 percent length of corresponding propod. Pereopod 5: basis with 7 very shallow serrations along posterior margin: 5-8 short spines on anterior margin: 2 long setae on the anteroproximal margin. Pereopod 6: basis with 9 shallow serrations along posterior margin: 6 short spines on anterior margin: 2 long setae on anteroproximal margin. Pereopod 7: coxa with 3 setae on the posterior margin: basis with 10 shallow serrations along posterior margin, deeper at apex: 6 short spines on anterior margin: 1-2 long setae on anteroproximal margin; dactyl about 35 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta. distoposterior corner variable, weakly produced and acute or not; posterior margin of plate 2 nearly straight with 1 (rarely two) setae. Distoposterior corner produced and acute (or somewhat subacute), ventral margin with 4 (subventral) spines: posterior margin of plate 3 nearly straight with 1 seta. Distoposterior corner produced and acute. Ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus 80 percent length of peduncle, armed with 8 spines: outer ramus with 7 spines: peduncle with 5 outer and 1 inner spines. Uropod 2: inner ramus with 8 spines: peduncle with 2 outer and 1 inner spines. Uropod 3: inner ramus lacking spines. outer ramus about 1.7 or more times longer than peduncle, inner and outer margins each with 2-3 set of spines in groups of 1-3. Telson broader than long, notched about 1/8-1/4 distance to base, each lobe with 2-3 apical spines: spines more than 1 2 length of telson.

Male.—Differing from female as follows. Smaller, body more slender and elongate. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 4 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus and much broader: palm almost straight, longer than posterior margin, with 7 spine teeth on inside. 8 on outside: defining angle with 5 notched-serrate spine teeth on inside and 2 notched and 2 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus; palmar margin strongly oblique, convex.
longer than posterior margin, with 9-12 spine teeth on inside, 9 on outside: defining angle with 2 notched and 3 serrate spine teeth on inside and 4 notched-serrate spine teeth on outside.

Uropod 2: inner ramus with 11 spines; outer ramus curved, with 4-6 short well spaced inner spines, 5-7 short outer spines, apex with 2-3 spines; peduncle with 4 outer and 3 inner spines.

Distribution and ecology.—This species is widespread in east-central North America, being recorded from southeastern Ontario, northern and southern Indiana, northern and southeastern Illinois, central Kentucky, northern and southeastern Ohio, central and southern Michigan, eastern Missouri, and southern West Virginia (fig. 90).

*Crangonyx rivularis* inhabits rivers, streams, springs, ditches, ponds, small lakes and rarely caves. Sexually mature males, 3.5 to 4.5 mm; sexually mature females, 5.5 to 8.5 mm. Ovigerous females were collected in March, April, May, July and November.

*Crangonyx packardi* Smith

Figures 91-94

*Crangonyx packardi* Smith, 1888:35-36. figs. 5-11 [type-locality: wells in Orleans, Indiana].--Hay.


Krekeler & Williams. 1966:394.

*Eucrangonyx packardi* (Smith).--Stebbing, 1899:423; 1906:389.--Weckel. 1907:35.

Figure 91. *Crangonyx packardi* Smith. Female (5.7 mm), Donaldson Cave, Lawrence Co., Indiana:
a. b. antennae 1, 2; c. d. gnathopods 1, 2 (spine teeth on defining angle enlarged); e. f. maxillae 1, 2;
g. lower lip; h. inner plate and palp dactyl of maxilliped; i. right mandible.

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Figure 92.—Crangonyx puckardi Smith. Female (5.7 mm). Donaldson Cave, Lawrence Co., Indiana:
a, c, d. pereopods 3, 5, 6 (in part); b, e. pereopods 4, 7; f. pleonal plates; g, h, i. uropods 1, 2, 3; j.
telson.
Figure 93.—Crangonyx packardi Smith. Male (3.4 mm). Donaldson Cave, Lawrence Co., Indiana: a. antenna 2; b, c. gnathopods 1, 2; d, e. uropods 1, 2. Male (3.2 mm), same location: f. pereopod 6; g. pereopod 7 (in part); h. uropod 2; i. telson.
Figure 94.—Distribution of *Crangonyx packardi* in North America. Solid circles represent 1-6 closely proximate localities.
Diagnosis.—A relatively small stygobiont species of the *gracilis* group, which is distinguished from other members of the group by lacking notched-serrate spine teeth on defining angle of propod of gnathopods of both sexes; having shallow serrations on posterior margins of pereopods 5-7; and outer ramus of uropod 2 of male, which bears 5-6 short inner and 4-5 short outer spines. Largest male, 5.5 mm; largest female, 8.0 mm.

Female.—Eye greatly reduced to few specks or completely absent. Antenna 1, about 50 percent length of body, about 2 times longer than antenna 2; primary flagellum with 16 segments. Antenna 2, flagellum with 6 segments. Mandibles subequal, spine row with 5 spines; segment 2 of palp with 8-9 long setae, segment 3 with 1-2 A setae, 2-3 C setae, 3-4 E setae and a row of D setae, lacking B setae. Maxilla 1, inner plate with 4-8 apical plumose setae; palp with 5-6 slender setae on apex. Maxilla 2, inner plate with oblique row of 5-6 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spine teeth, 2 naked setae, and 4-7 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 2-3 slender pectinate spines, dactyl with 2 setae on inner margin near nail; dactyl nail very long, about 1.2 length of dactyl.

Propod of gnathopod 1 less than 1.5 times larger than carpus, palm straight, shorter than posterior margin, with 4 unnotched spine teeth on inside, 6 on outside; defining angle with 3-4 spine teeth on inside. 1 large unnotched and 1 laterally notched spine teeth on outside; superior medial setae few in number and singly inserted; posterior margin with 5 sets of setae singly or doubly inserted. Dactyl with 2-3 short setae on inner margin, nail very long. Ventral margin of coxa 1 with 4 long setae.

Propod of gnathopod 2 slightly longer than carpus; palm almost straight, shorter than posterior margin, with 4 unnotched spine teeth on inside, 6 on outside; defining angle with 2-3 spine teeth on inside, 1 large and 1 small unnotched spine teeth on outside; 5 superior medial setae singly inserted; posterior margin with 5 sets of setae in groups of 1-5. Dactyl with row of short setae on inner margin. Ventral margin of coxa 2 with 6 setae.

Coxa of pereopod 3 with 6 marginal setae. Coxa of pereopod 4 with 9-12 marginal setae. Dactyl of pereopod 4, 40 percent length of corresponding propod. Pereopod 5, basis with 8 very shallow serrations along posterior margin; 5 short spines on anterior margin. Pereopod 6, basis with 8 very shallow serrations along posterior margin; 5 short spines on anterior margin. Pereopod 7, coxa with 2 setae on the posterior margin; basis with 10 shallow serrations along posterior margin; 6 short spines on anterior margin; dactyl about 35 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta. Distoposterior corner not produced, subacute; posterior margin of plate 2 nearly straight with 1 seta. Distoposterior corner acute but not produced, ventral margin with 4 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner slightly subacute but not produced, ventral margin with 3 (subventral) spines.
Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus 65 percent length of peduncle, armed with 11 spines; outer ramus with about 10 spines; peduncle with 9 outer and 4 inner spines. Uropod 2: inner ramus armed with 12 spines; outer ramus with 8 spines; peduncle with 2-3 outer spines, 3 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.7-2 times longer than peduncle, inner and outer margin each with 2-3 set of spines in groups of 1-3. Telson about as broad as long, notched about 1/6-1/3 distance to base, each lobe with 1-2 apical spines.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 2 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus; palm shorter than or equal in length to posterior margin, with 5 spine teeth on inside, 7 on outside: defining angle with 4 spine teeth on inside and 1 notched and 1 serrate or unnotched spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus; palmar margin strongly oblique, convex, equal or slightly longer than posterior margin, with 10 spine teeth on inside, 12 on outside: defining angle with 2 spine teeth on inside, 2 on outside. Uropod 2: inner ramus with 11 spines; outer ramus slightly deflected, with 5-6 inner and 4-5 outer spines, apex with about 4 spines; peduncle with 2 outer and 2-3 inner spines.

Distribution and ecology.—This species is recorded from southern Indiana, southern Illinois, south-central and western Kentucky, west-central Missouri, and eastern Kansas (fig. 94). Its range, which is extensive for a stygobiont amphipod, covers a linear distance about 1000 km and crosses three physiographic provinces, extending from the Interior Low Plateaus in the east to the Osage Plains in the west.

In caves, *C. packardi* is found in drip pools, streams, and stream pools. It is also recorded from surface seeps and springs. In Indiana caves, it is sometimes associated with *C. indus* or *C. lewsi*. In Kansas caves, it is sometimes associated with the large troglobitic amphipod *Stygobromus clanti*on. Ovigerous females were collected from March to August and in November. Sexually mature females are 4.5 to 8.0 mm and sexually mature males are 3.0-5.5 mm.

Remarks.—Earlier references to literally all *Crangonyx* from caves in the Interior Low Plateaus region were this species. However, it is obvious from the present study that several species were once called "packardi."

*Crangonyx stagnicolous*, new species

Figures 95-98

Material examined (paratypes unless designated otherwise).—MARYLAND. Calvert Co.: Grays Cypress Swamp, 1 ♂, C. R. Shoemaker, 17 Apr 1938 (USNM); Dorchester Co.: swamp, 5.3 km W of
Figure 95.—*Crangonyx stagnicolous*, new species. Female paratype (6.4 mm), swamp near Mount Vernon, Fairfax Co., Virginia: a, b, antennae 1, 2; c, d, maxillae 1, 2; e, left mandible; f, inner and outer plates and palp dactyl of maxilliped (greatly enlarged); g, h, gnathopods 1, 2 (palmar margins enlarged).
Figure 96.—*Crangonyx stagnicolous*, new species. Female paratype (6.4 mm), swamp near Mount Vernon, Fairfax Co., Virginia: a, b, c, pereopods 3, 4, 5 (in part); d, pereopod 7; e, pleonal plates; f, g, h, uropods 1, 2, 3; i, telson.
Figure 97.—*Crangonyx stagnicolor*, new species. Male paratype (3.8 mm), swamp near Mount Vernon, Fairfax Co., Virginia: a, antenna 2; b, c, gnathopods 1, 2 (palmar margins enlarged); d, pereopod 7; e, uropod 2; f, telson. Male paratype (4.1 mm), Swamp near Mount Vernon, Fairfax Co., Virginia: g, uropod 2 (spines on inner and outer margins of ramus shown separated). Male (5.5 mm), Ridge, St. Marys Co., Maryland: h, outer ramus of uropod 2 (enlarged).
Figure 98.--Distribution of *Crangonyx stagnicolous* in North America. Solid circles represent 1-5 closely proximate localities. The dotted line denotes the "fall line" or "fall zone" between the Coastal Plain and Piedmont.
Cambridge, 1 ♂, R. W. Jackson, 20 Apr 1943 (USNM); St. Marys Co.: ditch on Ridge, 7 ♂, 1 ♀, W. H. Ball, 26 Apr 1930 (USNM). VIRGINIA. Fairfax Co.: marshy ponds, Springfield, holotype 2 ♀, 4 ♂, 3 ♀, J. R. Holsinger, 7 Apr 1973; Mount Vernon, 1 ♂, M. K. Brady, 10 May, 1924 (USNM); pools near Black Pond, 65 specs (♂, ♀, juvs), W. D. Webb, 25 Nov 1915 (USNM); small pool between Dyke and Belle Haven, 8 ♂, 2 ♀, W. H. Ball, 14 Apr 1935 (USNM); seep near Mount Vernon, 22 ♂, 10 ♂, W. D. Webb, 22 Apr 1917 (USNM); pool in Sweet Gum stand, New Alexandria, 3 ♀, W. H. Ball, 24 Apr 1935 (USNM); small pools near New Alexandria, 2 ♀, W. H. Ball, 22 Apr 1935 (USNM); seep ca. 1.2 km NE of Cheney School, Dogue Creek drainage, Ft. Belvoir, 15 specs. C. S. Hobson and D. J. Stevenson, 13 Apr 1995; seep on E bank of Accotink Creek, ca. 0.6-0.7 km WNW of jct. 613 and 617, 5 specs. C. S. Hobson and D. J. Stevenson, 13 Apr 1995.

Diagnosis.—A small species of the gracilis group distinguished from other members of the group by having 2 setae on posterior margins of pleonal plates, 1 of which is inserted just above distoposterior corner; shorter uropod 3 with ratio of length of outer ramus to peduncle less than 1.5; male with large well spaced comb-like spines on outer ramus of male uropod 2. Largest male, 5.2 mm; largest female, 9.0 mm.

Female.—Eye large and ovate. Antenna 1, about 50 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with about 20 segments. Antenna 2, flagellum with 7-9 segments. Mandibles subequal. spine row with 5 spines; segment 2 of palp with 7 long setae. segment 3 with 1-2 A setae, 2 C setae, 4-5 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 6 apical plumose setae: palp with 9 slender spines on apex. Maxilla 2, inner plate with oblique row of 5-6 plumose setae on inner margin. Maxilliped: inner plate apically with 2 bladelike spines. 1 naked spine, and 5-6 plumose setae extending from inner margin to apex: outer plate with row of naked setae and 3-4 slender pectinate spines on inner margin: 2-3 setae on inner margin of dactyl near nail: dactyl nail very long, about 1.3 length of dactyl.

Propod of gnathopod 1 less than 2 times larger and longer than carpus: palm almost straight, shorter than posterior margin, with 5 unnotched spine teeth on inside, 6 on the outside: defining angle with 5 notched-serrate spine teeth on inside, 1 large notched and 3 serrate spine teeth on outside; superior medial setae few in number and singly inserted; posterior margin with 6 singly inserted setae. Dactyl with row of short setae on inner margin, nail very long. Ventral margin of coxa 1 with 7-8 setae.

Propod of gnathopod 2 less than 2 times larger and longer than carpus: palm almost straight, shorter than posterior margin, with 6 unnotched spine teeth on inside, 8 on outside: defining angle with 1 large notched spine tooth and 4 notched-serrate spine teeth on outside: superior medial setae singly inserted: posterior margin with 2-4 setae. Dactyl with row of short setae on inner margin. Ventral margin of coxa 2 with 8 setae.

Coxa of pereopod 3 with 8 marginal setae. Coxa of pereopod 4 with 12 marginal setae, dactyl of pereopod 4, 40 percent length of corresponding propod. Pereopod 5: basis with 8 very shallow serrations along posterior margin: 6-8 short spines on anterior margin: 4 long setae on the anteroproximal margin.

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Pereopod 6: basis with 8-9 shallow serrations along posterior margin; 9 short spines on anterior margin; 1 seta on anteroproximal margin. Pereopod 7: coxa with 3 setae on the posterior margin; basis with 11 shallow serrations along posterior margin; 7 short spines on anterior margin; 3 long setae on anteroproximal margin; dactyl about 40 percent length of corresponding propod.

Pleon plates: posterior margin of plate 1 slightly convex, with 2 setae. 1 at distoposterior corner. distoposterior corner slightly acute but not produced; posterior margin of plate 2 slightly convex with 2 setae. 1 at the distoposterior corner. distoposterior corner acute but not produced, ventral margin with 2 (subventral) spines; posterior margin of plate 3 slightly convex with 2 setae. 1 at distoposterior corner. distoposterior corner acute but not produced, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus 75 percent length of peduncle, armed with 9 spines; out ramus with 10 spines: peduncle with 10 outer and 1 inner spines. Uropod 2: inner ramus armed with 10 spines; outer ramus with 8 spines; peduncle with 4 outer and 3 inner spines. Uropod 3: inner ramus lacking spines. outer ramus about 1.5 times longer than peduncle. inner and outer margin each with 2-3 set of spines in groups of 1-3. Telson broader than long, notched about 1/4 distance to base. each lobe with 3 apical spines: spines about 1/2 length of telson.

Male.—Differing from female as follows. Smaller than female, with more slender, elongate body.
Antenna 2: calceoli percent on peduncular segments 4 and 5, and first 4 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus and much broader. Propod of gnathopod 1 with 8 spine teeth on inside. 9 on outside, defining angle with 5 notched-serrate spine teeth on inside. 1 notched and 3 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm margin strongly oblique, with 10 spine teeth on inside, 10 on outside; defining angle with 1 notched and 1 serrate spine tooth on inside and 2 similar spine teeth on outside.

Uropod 2: inner ramus lacking spines or with 3 short inner spines. 3-4 long outer spines. 3-5 spines on apex; outer ramus curved, with 4-7 outer spines and comb-like row of spines on outside on distal half, apex with 3-5 spines; peduncle with 4 outer and 2 inner spines. Uropod 3: inner ramus lacking spines: outer ramus about 2 times length of peduncle.

Type-locality.—Marshy ponds on Accotink Creek, just below Lake Accotink, Springfield, Fairfax County, Virginia.

Distribution and ecology.—The range of this species, which is restricted at present to the western margin of the Coastal Plain in northern Virginia and a small part of the Coastal Plain in southern Maryland, covers a linear distance of about 100 km (fig. 98).

C. stagnicolous inhibits cypress swamps, marshy ponds, and small pools and is sometimes associated with C. poliusiris. Ovigerous females were collected in April and August. Sexually mature males, 4.0-5.5 mm: sexually mature females, 6.5-9.0 mm.

Etymology.—The epithet stagnicolous is from Latin, meaning "living in a swamp."
Remarks.—*C. stagnicolous* shares with *C. bousfieldi* the presence of a seta just above the distoposterior corner of the pleonal plate. Although this character is unique to these two species of *Crangonyx*, it is probable a homoplasy.

*Crangonyx aka*, new species

Figures 99-102

Material examined (paratypes unless designated otherwise).—ARKANSAS. Pope Co.: unmarked stream ca. 0.8 km S of Hector on state rd. 27, holotype ♂, 25 ♀, 15 ♂. R. Fox, 28 Dec 1970; Saline Co.: seep, 8.0 km N of Paron, 30 specs (♀, ♂). L. Hubricht, 5 May 1940 (USNM); Van Buren Co.: unmarked stream, 8.0 km W of Rupert, on state rd. 16, 8 ♂, 3 ♀. R. Fox, 28 Dec 1970; unmarked stream, 5.0 km W of Rupert, 4 ♂, 4 ♀. R. Fox, 28 Dec 1970.

Diagnosis.—A small species of the *gracilis* group closely allied morphologically with *C. rivularis* but distinguished from that species by the telson, which is notched 1/2 distance to base; spines on inner margin of outer ramus of male uropod 2 distributed evenly; gnathopod 2 of male lacking notched-serrate spine teeth on propod defining angle; setae absent from anteroproximal margin of pereopod 5-7. Largest male: 5.5 mm; largest female, 7.4 mm.

Female.—Eye large and ovate. Antenna 1, about 50 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with about 24 segments. Antenna 2, flagellum with 8 segments. Mandibles subequal, spine row with 4-5 spines; segment 2 of palp with 7-8 long setae, segment 3 with 1-2 A setae, 1 B seta, 1-2 C setae, 4 E setae and a row of D setae. Maxilla 1: inner plate with 6 apical plumose setae; palp with 5-7 slender spines on apex. Maxilla 2, inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 1 naked spine, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 7-8 slender pectinate spines on inner margin; dactyl with 1-2 setae on inner margin near nail; dactyl nail very long, 1/3 length of dactyl.

Propod of gnathopod 1 less than 2 times larger and longer than carpus; palm almost straight, subequal to posterior margin, with 7 unnotched spine teeth on inside, 6 on the outside: defining angle with 4 notched-serrate spine teeth on inside, 1 large notched and 2 serrate spine teeth on outside; superior medial setae singly inserted; 4 sets of posterior marginal setae inserted in groups of 2-5. Dactyl with row of short setae on inner margin, nail long. Ventral margin of coxa 1 with 5 short setae.

Propod of gnathopod 2 less than 2 time larger and longer than carpus; palm almost straight, shorter than posterior margin, with 8 unnotched spine teeth on inside, 9 on outside: defining angle with 1 notched and 2 notched-serrate spine teeth on inside, 1 large notched and 2 unnotched spine teeth on outside: superior medial setae singly inserted, posterior margin with 5 sets of setae in groups of 1-5. Dactyl with row of short setae on inner margin. Ventral margin of coxa 2 with 6 setae.
Figure 99.—*Crangonyx aki*, new species. Female paratype (6.9 mm), unmarked stream ca. 0.8 km S of Hector on state rd. 27, Pope Co., Arkansas: a, b. antennae 1, 2; c, d. maxillae 1, 2; e. lower lip; f, g. left and right mandible; h, i. gnathopods 1, 2 (palmar margins enlarged); j. pereopod 3 (in part).
Figure 100.—Crangonyx aka, new species. Female paratype (6.9 mm). unmarked stream ca. 0.8 km S of Hector on state rd. 27. Pope Co., Arkansas: a, d. pereopods 4, 7; b. c. pereopods 5, 6 (in part); d. pereopod 7; e. pleonal plates; f. g. h. uropods 1, 2, 3; i. telson.
Figure 101.—*Crangonyx aka.* new species. Male paratype (4.8 mm), unmarked stream ca. 0.8 km S of Hector on state rd. 27, Pope Co., Arkansas: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7; e. f. g. uropods 1, 2, 3; h. telson.
Figure 102.—Distribution of Orangonyx aka in North America. Solid circles represent 1-2 closely proximate localities.
Coxa of pereopod 3 with 6 marginal setae. Coxa of pereopod 4 with 11 marginal setae. Dactyl of pereopod 4: 35 percent length of corresponding propod. Pereopod 5: basis with 12 very shallow serrations along posterior margin; 7 short spines on anterior margin. Pereopod 6: basis with 13 serrations along posterior margin; 7 short spines on anterior margin. Pereopod 7: coxa with 3 setae on posterior margin; basis with 15 slight serrations along posterior margin; 5 short spines on anterior margin; dactyl about 33 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 convex, with 1 seta, distoposterior corner produced and acute; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner strongly produced and acute, ventral margin with 3 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner small and acute but not produced, ventral margin with 4 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculæ, lacking setae on outside margin.

Uropod 1: inner ramus 80 percent length of peduncle, armed with 11 spines; outer ramus with 12 spines: peduncle with 7 outer and 1 inner spines. Uropod 2: inner ramus armed with 10 spines; outer ramus with 8 spines; peduncle with 4 outer spines, and 4 inner spines. Uropod 3: inner ramus lacking spines, outer ramus about 2 times longer than peduncle, inner and outer margins each with 2-3 set of spines in groups of 2-4. Telson slightly longer than broad, notched 1/2 distance or slightly more to base, each lobe with 4 apical spines.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli percent on peduncular segments 4 and 5, and first segment of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus: palm with 10 spine teeth on inside, 10 on outside; defining angle with 3 notched-serrate spine teeth on inside, 1 large notched and 2 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm strongly oblique, convex, with 11 spine teeth on inside, 11 on outside; defining angle with 3 spine teeth on inside and 2 on outside.

Uropod 2: inner ramus with 12 spines; outer ramus only slightly modified, with 6 short spines on inner margin along the whole length and 5-6 longer spines on outer margin, apex with 4 spines; peduncle with 3 outer and 3-4 inner spines. Telson longer than broad, notched about 1/2 distance to base: each lobe with 2 apical spines; spines about 1/3 length of telson.

Type-locality.—Stream, about 0.8 km S of Hector on state route 27, Pope County, Arkansas.

Distribution and ecology.—The range of this species, which at present is only known from 4 collections from central Arkansas, covers a linear distances of about 80 km from north to south and covers parts of three different physiographic regions (fig. 102).

It was collected from streams and a seep. Ovigerous females are recorded from May and December. Sexually mature females are 6.2 to 7.4 mm and sexually mature males are 4.2 to 5.5 mm.

Etymology.—The epithet *aka* is derived from a contraction of Arkansas, referring to the occurrence of this species in the state of Arkansas.
Crangonyx caecus, new species

Figures 103-106


Diagnosis.—A relatively small cavernicolous species closely allied morphologically with C. castellanum but distinguished from that species by lacking calceoli on antenna 2 in mature males, and having fewer spines on inside margin of outer ramus of uropod 2 of male. Largest male, 5.7 mm; largest female, 7.3 mm.

Female.—Eyes absent. Antenna 1, about 50 percent length of body, about 1.8 times longer than antenna 2: primary flagellum with about 15 segments. Antenna 2, flagellum with 8-9 segments. Mandibles subequal. spine row with 4-5 spines: segment 2 of palp with 10 long setae. segment 3 with 1 A seta. 2-3 C setae. 4 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 5-6 apical plumose setae: palp with 5-6 slender spines on apex. Maxilla 2, inner plate with oblique row of 5-6 plumose setae on inner margin. Maxilliped: inner plate apically with 4 bladelike spines, 1 naked spine, and 5-6 plumose setae extending from inner margin to apex: outer plate with row of naked setae and 5 weak pectinate spines on inner margin; dactyl with 1-2 setae on inner margin near nail; dactyl nail very long, about 1.2 length of dactyl.

Propod of gnathopod 1 less than 2 times larger and longer than carpus; palm shorter than posterior margin, almost straight, with 4-6 unnotched spine teeth on inside, 5-7 on the outside; defining angle with 3-5 notched-serrate spine teeth on inside and 1 large notched or unnotched spine tooth and 1-2 small serrate spine teeth on outside; superior medial setae few in number and singly inserted: 6 sets of setae on posterior margin singly inserted or in groups of 2-4. Dactyl with row of short setae on inner margin, nail very long. Ventral margin of coxa 1 with 9 setae.

Propod of gnathopod 2 less than 2 times larger and longer than carpus; palm almost straight, oblique, shorter than posterior margin, with 6 unnotched spine teeth on inside, 7-9 on outside; defining angle with 1 large notched spine tooth and 1-2 serrate spine tooth on inside. 1 large unnotched and 1 serrate or unnotched spine teeth on outside; superior medial setae singly inserted, posterior margin with 6 sets of

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Figure 103.—*Crangonyx caecus*, new species. Female paratype (6.5 mm), Cascade Cave, Carter Co., Kentucky: a. b. antennae 1, 2; c, d. maxillae 1, 2; e. lower lip; f. dentate part of left mandible; g. right mandible; h. inner and outer plates and palp dactyl of maxilliped; i, j. gnathopods 1, 2 (palmar margins enlarged); k. pereopod 3 (in part); l. pleonal plates.
Figure 104.—Crangonyx caecus, new species. Female paratype (6.5 mm), Cascade Cave, Carter Co., Kentucky: a, d, pereopods 4, 7; b, c, pereopods 5, 6 (in part); e, f, g, uropods 1, 2, 3; h, telson.
Figure 105.—*Crangonyx caecus*. new species. Male paratype (4.7 mm), Cascade Cave, Carter Co., Kentucky: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7; e. f. g. uropods 1, 2, 3; h. telson
Figure 106. Distribution of _Crangonyx corporatus_ in North America. Solid circle represents 1-6 closely proximate localities.
setae in groups of 2-4. Dactyl with row of short setae on inner margin, nail long. Ventral margin of coxa 2 with 9 setae.

Coxa of pereopod 3 with 8 marginal setae. Coxal of pereopod 4 with 15 marginal setae. Dactyl of pereopod 4: 45 percent length of corresponding propod. Pereopod 5: basis with 15 very shallow serrations along posterior margin; 7 short spines on anterior margin; 3 long setae on the anteroproximal margin. Pereopod 6: basis with 12 very shallow serrations along posterior margin; 9 short spines on anterior margin; 3 long setae on anteroproximal margin. Pereopod 7: coxa with 2 setae on posterior margin; basis with 12 shallow serrations along posterior margin; 7 short spines on anterior margin; 3 setae on anteroproximal margin; dactyl about 40 percent the length of corresponding propod.

Pleonal plates: posterior margin of plate 1 neatly straight, with 1 seta, distoposterior corner not produced; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner not produced, subacute, ventral margin with 5 (subventral) spines; posterior margin of plate 3 convex, with 1 seta, distoposterior corner rounded, indistinct, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus about 70 percent length of peduncle, armed with 14 spines; outer ramus with 16 spines; peduncle with 13 outer and 4 inner spines. Uropod 2: inner ramus armed with 14 spines; outer ramus with 9 spines; peduncle with 5 outer and 4 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.5 times longer than peduncle, inner and outer margins each 2-3 sets of spines in groups of 1-2. Telson much broader than long (about 1.5 times), notched about 1.4 distance to base, each lobe with 2 apical spines; spines more than 1/2 length of telson.

Male.—Differing from female as follows; smaller with more slender, elongate body. Antenna 2: flagellum with 5-6 segment; calceoli absent (at least in specimens examined).

Propod of gnathopod 1 more than 2 times larger and longer than carpus and broader; palm with 10 spine teeth on inside, 10 on outside; defining angle with 3 notched and 2 serrate spine teeth on inside and 1 large unnotched and 1 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus; palmar margin strongly oblique, convex, with 12 spine teeth on inside, 14 on outside; defining angle with 2 notched-serrate spine teeth on inside and 1 large unnotched and 1 small unnotched or serrate spine teeth on outside.

Uropod 2: inner ramus with 10 spines; outer ramus unmodified, with 1 spine on inner margin and 6 spines on outer margin; peduncle with 2-3 outer and 3-4 inner spines. Uropod 3: outer ramus about 1.2 times length of peduncle.

Type-locality.—Cascade Cavern ("North Cave"), Carter Caves State Park, Carter County, Kentucky. The type-locality is one of several caves situated within the boundaries of Carter Caves State Park. In Cascade Cave, *C. caecus* is common in shallow (rimstone) pools with silty bottoms.

Distribution and ecology.—This species is known only from six caves in Carter County in northeastern Kentucky (fig. 106). It inhabits mainly pools, although it is recorded once from a stream and once from a
drip pool. Ovigerous females were collected in June and September. Sexually females are 5.5 to 7.3 mm and sexually males are 3.0 to 5.0 mm.

Etymology.--The epithet caecus is from Latin, meaning "blind."

Crangonyx ohioensis, new species


Diagnosis.--A relatively small stygobiont species closely allied morphologically with C. castellanum and C. caecus but distinguished from them by the telson, which is just slightly broader than long in female; outer ramus of male uropod 2 having only 1-2 small spines on inner margin near end; and also from the latter by presence of calceoli on antennae 2 of male. Largest male, 5.5 mm; largest female, 7.5 mm.

Female.--Eye greatly reduced to few black specks. Antenna 1, about 50 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with about 20 segments. Antenna 2, flagellum with 8 segments. Mandibles subequal, spine row with 4-6 spines; segment 2 of palp with 5-8 long setae, segment 3 with 1-2 A setae, 2 C setae, 4-5 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 5 apical plumose setae; palp with 7 slender spines on apex. Maxilla 2, inner plate with oblique row of 5 plumose setae on inner margin. Maxilliped: inner plate apically with 2 bladelike spines, 2 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 4 slender pectinate spines on inner margin; dactyl with 2 setae near nail on inner margin; dactyl nail very long, 1/2 length of dactyl.

Propod of gnathopod 1 less than 2 times larger and longer than carpus; palm slightly convex, shorter than posterior margin, with 6 unnotched spine teeth on inside, 7 on the outside; defining angle with 5 notched-serrate spine teeth on inside, 1 large unnotched and 3 serrate spine teeth on outside; superior medial setae few in number and singly inserted; 4 sets of setae on posterior margin, singly inserted or in groups of 2-5. Dactyl with row of short setae on inferior margin, nail very long. Ventral margin of coxa 1 with 8 long setae.

Propod of gnathopod 2 less than 2 times larger and longer than carpus; palm convex, shorter than posterior margin, with 7 unnotched spine teeth on inside, 11 on outside; defining angle with 1 large notched and 4 serrate spine teeth on inside, 1 large unnotched and 2 serrated spine teeth on outside:
Figure 107.—Crangonyx ohioensis, new species. Female paratype (6.8 mm), seep, 8.0 km E of Olive Hill, Carter Co., Kentucky: a, b. antennae 1, 2; c, d. maxillae 1, 2; e, lower lip; f, g. left and right mandible; h. inner and outer plates and palp dactyl of maxilliped (greatly enlarged); i, j. gnathopods 1, 2 (palmar margins enlarged); k. pereopod 6 (in part).
Figure 108.--*Crangonyx ohioensis*, new species. Female paratype (6.8 mm), seep, 8.0 km E of Olive Hill, Carter Co., Kentucky: a, c. pereopods 3, 4 (in part); b, d. pereopods 4, 7; e. pleonal plates; f, g, h. uropods 1, 2, 3; i. telson.
Figure 109.—*Crangonyx ohioensis*, new species. Male paratype (5.2 mm), seep. 8.0 km E of Olive Hill, Carter Co., Kentucky: a. antenna 2; b. pereopod 7; c. d. gnathopods 1, 2 (palmar margins enlarged); e. uropod 1; f. g. right and left uropod 2; h. uropod 3; i. telson.
Figure 110.—Distribution of Ctenomyx dinoecetus in North America. Solid circles represent single localities.
superior medial setae singly inserted; posterior margin with 4 sets of setae in groups of 1-6. Dactyl with row of short setae on inner margin. Ventral margin of coxa 2 with 8 long setae.

Coxa of pereopod 3 with 10 marginal setae. Coxa of pereopod 4 with 9 marginal setae, dactyl of pereopod 4. 45 percent length of corresponding propod. Pereopod 5: basis with 10 shallow serrations along posterior margin; 4 short spines on anterior margin; 3 long setae on the anteroproximal margin. Pereopod 6: basis with 12 shallow serrations along posterior margin; 6 short spines on anterior margin; 4 setae on anteroproximal margin. Pereopod 7: coxa with 2 setae on the posterior margin; basis with 11 shallow serrations along posterior margin; 4 short spines on anterior margin; 3 long setae on anteroproximal margin; dactyl about 35 percent the length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner small, acute but slightly produced; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner acute but not produced, ventral margin with 3 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner weakly acute, not produced, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus 80 percent length of peduncle, armed with 11 spines; outer ramus with 13 spines; peduncle with 12 outer and 2 inner spines. Uropod 2: inner ramus armed with 12 spines; outer ramus with 10 spines; peduncle with 4 outer spines, and 4 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.2 times longer than peduncle, inner and outer margin each with 2-3 set of spines in groups of 1-3. Telson slightly broader than long, notched about 1/6 distance to base, each lobe with 3 apical spines; spines up to 3/4 length of telson.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 4 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus and much broader; palm straight, with 9 spine teeth on inside, 9 on outside; defining angle with 4 notched-serrate spine teeth on inside, 1 notched-serrate and 1 notched and 3 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus; palmar margin oblique, slightly concave, with 13 spine teeth on inside, 13 on outside; defining angle with 2 notched and 3 serrate spine teeth on inside and 3 notched spine teeth on outside.

Uropod 2: inner ramus with 10 spines; outer ramus deflected laterally, with 2 inner spines, 5-6 short outer spines, apex with 2-3 spines; peduncle with 3 outer spines, and 2-3 inner spines. Uropod 3: inner ramus with 1 spine; outer ramus about 1.6 times length of peduncle. Telson broader than long, notched about 1/3 distance to base.

Type-locality.—Seep, 8.0 km E of Olive, Carter Co. Kentucky.

Distribution and ecology.—This stygobiont species is recorded from a seep in southern Indiana, two seeps in northeastern Kentucky, and one well and one cave in southern Ohio (fig. 110). Although a specific location for the well in Ohio was not given by the collector, it is believed to be in the southern part...
of the state. All specified localities are limited to the Ohio River drainage. From east to west, the range covers a linear distance of about 200 km.

This species is apparently an inhabitant of shallow groundwaters. Ovigerous females were collected in April and July and brood pouches contained up to 30 "yellow" eggs. Sexually mature females, 6.0 to 7.5 mm; sexually mature males, 4.8 to 5.5 mm.

Etymology.—The specific name refers to the occurrence of this species in the Ohio River drainage.

_Crangonyx acicularis_, new species

Figures 111-114

Material examined (paratypes unless designated otherwise).--TENNESSEE. Sullivan Co.: spring-fed stream, 8.0 km E of Bluff City. 20 specs (♀, ♂), M. Richmond et al., 20 Jan 1968: stream, 6.9 km E of Kingsport, holotype ♀, 4 ♀, 2 ♂, R. Larue, 5 Feb 1968: stream just SW of Kingsport, 1 ♂, R. Larue, 4 Feb 1968: stream just E of Kingsport, 1 ♂, R. Larue, 5 Feb 1968. VIRGINIA. Montgomery Co.: small spring near Ingles Ferry, 3.2 km S of Radford, 5 ♀, 5 ♂, L. Hubricht, 17 Dec 1948 (USNM).

Diagnosis.—A small species of the _gracilis_ group very similar to _C. castellianum_ as evidenced by very thin setal-like spines on outside of outer ramus of male uropod 2 and several thick setal-like comb spines near apex on inside. Distinguished from _C. castellianum_ by the produced and acute distoposterior corner of pleonal plate 2 and longer uropod 3. Largest male, 5.8 mm; largest female, 7.2 mm.

Female.—Eye large and ovate in shape. Antenna 1, about 55 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with 17 segments. Antenna 2, flagellum with 8-9 segments. Mandibles subequal, spine row with 5 spines; segment 2 of palp with 5-6 long setae, segment 3 with 1 A seta, 1 C seta, 3-4 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 6 apical plumose setae; palp with 6-8 slender spines on apex. Maxilla 2, inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 2 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and about 5 slender pectinate spines on inner margin. 1 apical plumose seta; dactyl with 2 setae on inner margin near nail; dactyl nail very long, more than 1/3 length of dactyl.

Propod of gnathopod 1 less than 2 times larger and longer than carpus; palm slightly convex, not oblique, shorter than posterior margin, with 6 unnotched spine teeth on inside, 6 on the outside; defining angle with 5-6 notched-serrate spine teeth on inside, 1 large notched and 2-3 notched or notched-serrate spine teeth on outside; superior medial setae few in number and singly inserted; 4 sets of setae on posterior margin setae singly inserted or in groups of 2-4. Dactyl with a row of 4-5 short setae on inner margin, nail long. Ventral margin of coxa 1 with 8 setae.

Propod of gnathopod 2 less than 2 times larger and longer than carpus; palm almost straight, much

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Figure 111. *Crangonyx acicularis*, new species. Female paratype (6.5 mm), stream, 6.9 km E of Kingsport, Sullivan Co., Tennessee: a, b. antennae 1, 2; c, d. maxillae 1, 2; e. lower lip; f. dentate part of left mandible; g. right mandible; h. inner and outer plates and palp dactyl of maxillipeds (greatly enlarged); i, j. gnathopods 1, 2 (palmar margins enlarged).
Figure 112.—Crangonyx acicularis, new species. Female paratype (6.5 mm), stream, 6.9 km E of Kingsport, Sullivan Co., Tennessee: a, b, c, pereopods 3, 4, 5 (in part); d, pereopod 7; e, pleonal plates; f, g, h, uropods 1, 2, 3; i, telson.
Figure 113.—Crangonyx acicularis, new species. Male paratype (4.7 mm), stream, 6.9 km E of Kingsport, Sullivan Co., Tennessee: a. antenna 2; b, c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7; e, f, g. uropods 1, 2, 3; h. telson.
Figure 114.—Distribution of *Crangonyx acicularis* in North America. Solid circles represent 1-2 closely proximate localities.
shorter than posterior margin, with 6 unnotched spine teeth on inside, 7 on outside; defining angle with 1 notched and 4 notched-serrate spine teeth on inside. 3 unnotched and 1 large notched. 2 serrate spine teeth on outside: superior medial setae singly inserted; posterior margin with 5 sets of setae in groups of 3-7. Dactyl with row of 6 short setae on inner margin, nail long. Ventral margin of coxa 2 with 7 setae.

Coxa of pereopod 3 with 9 marginal setae. Coxa of pereopod 4 with 15 marginal setae, dactyl of pereopod 4. 50 percent length of corresponding propod. Pereopod 5: basis with 12 very shallow serrations along posterior margin: 5 short spines on anterior margin: 3 long setae on the anteroproximal margin. Pereopod 6: basis with 13 shallow serrations along posterior margin: 5 short spines on anterior margin: 3 long setae on anteroproximal margin. Pereopod 7: coxa with 3 setae on the posterior margin: basis with 16 shallow serrations along posterior margin: 5 short spines on anterior margin: 2 long setae on anteroproximal margin: dactyl about 35 percent the length of corresponding propod.

Pleonal plates: posterior margin of plate 1 convex, with 1 seta, distoposterior corner slightly produced and acute. ventral margin may with 1 (subventral) spine; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner strongly produced and acute. ventral margin with 6 (subventral) spines; posterior margin of plate 3 straightly convex with 1 seta, distoposterior corner subacute. ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus 75 percent length of peduncle, armed with 12 spines: outer ramus with 11 spines: peduncle with row of 7 outer and 1 inner spines. Uropod 2: inner ramus armed with 5 inner and 4 outer spines, apex with 5 spines; peduncle with 3 outer and 2 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.8 times longer than peduncle. inner and outer margin each with 3-4 set of spines in groups of 1-3. Telson slightly broader than long, notched about 2/5 distance to base. each lobe with 3 apical spines: spines about 1/2 length of telson.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 3-4 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus and much broader: palm slightly convex and slightly longer than posterior margin, with 7 spine teeth on inside. 8 on outside. defining angle with 1 notched and 4 weakly notched-serrate spine teeth on inside and 1 notched and 2 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus: palmar margin oblique, convex, subequal in length to posterior margin, with 9 spine teeth on inside. 11 on outside: defining angle with 4 notched and 1-2 notched-serrate spine teeth on inside. 3 notched spine teeth on outside.

Uropod 2: inner ramus with 11 spines: outer ramus deflected slightly posteriorly. with 3 inner spines. 3 thin outer spines. apex with 5 spines: peduncle with 2-4 thin outer spines. and 2 large inner spines.

Type-locality.—Surface stream. 6.9 km E of Kingsport. Sullivan County. Tennessee.

Distribution and ecology.—The range of this species, which is known only from five collections from Sullivan County. Tennessee and 1 collection from Montgomery County. Virginia, is limited to a relatively
small part of the Appalachian Valley and Ridge (fig. 114). It covers a linear distance of about 200 km.

The species inhabits small springs and spring-fed streams. Ovigerous females were collected in January. Sexually mature males are 3.5 to 5.8 mm and sexually mature females are 6.3 to 7.2 mm.

Etymology.--The epithet *acicularis* is from Latin, meaning "needle" or "pin." in reference to the needle-like spines on uropod 2 of male.

*Cragonyx polustris*. new species

Figures 115-118

Material Examined (paratypes unless designated otherwise).--MARYLAND. Anne Arundel Co.: tributary to Patuxent R., Patuxent Refuge, 1 ♂, collector not given, 8 Feb 1941 (USNM); Charles Co.: rill, 4.3 km S of La Plata, 5 ♂, 1 ♀, L. Hubricht, 28 Feb 1959 (USNM); Calvert Co.: pond near beach of North Beach and Chesapeake Beach, 4 ♂, 1 ♀, R. Greenfield, 22 Mar 1932 (USNM); Dorchester Co.: swamp, 5.3 km W of Cambridge, 4 ♂, R. W. Jackson, 20 Apr 1943 (USNM); Prince Georges Co.: seeps in woods just off Suitland Rd., 0.7 mi. SE of Suitland, 23 ♂, 3 ♀, 1 juv. J. R. Holsinger, 4 Feb 1973; St. Marys Co.: woodland stream. Mechanicsville, 1 ♀, W. H. Ball, 11 May 1937 (USNM); spaghnum bog in woods. Ridge, 11 ♂, 31 ♀, W. H. Ball, 26 Apr 1930 (USNM). NEW JERSEY. Burlington Co.: temporary pools, 0.8 km SW of Riverside, 100 specs (♂, ♀), L. Hubricht, 12 Mar 1938 (USNM); temporary pools, N of Riverton, 2 ♂, 1 ♀, L. Hubricht, 12 Mar 1938 (USNM). NORTH CAROLINA. Gates Co.: Hamburg ditch and marsh. Dismal Swamp, 3 ♂, S. Hetrick, 2 Mar 1974; marsh near Hamburg ditch. Dismal Swamp, 2 ♂, J. Matta, 22 Jan 1974. VIRGINIA. Caroline Co.: seeps, 100 m NW of Martins Corner. Ft. A. P. Hill, S. M. Roble, 18 Apr 1994; seeps, 200 m W of Martins Corner, S. M. Roble, 25 Apr 1994; Elizabeth City Co.: pools, 6.4 km N of Newport News, 3 ♂, L. Hubricht, 23 Jan 1944 (USNM); Fairfax Co.: pool under pines. Dyke, 3 ♂, W. H. Ball, 31 Dec 1934 (USNM); small pool between Dyke and Belle Haven, 8 ♂, 8 ♂, W. H. Ball, 14 Aug 1935 (USNM); small pool near Dyke, 1 ♀, W. H. Ball, 27 Apr 1935 (USNM); pond near Mount Vernon, 2 ♂, C. R. Shoemaker, 1 Mar 1927 (USNM); small pools near New Alexandria, 2 ♂, 1 ♀, W. H. Ball, 22 Apr 1935 (USNM); pools in sweet gum stand, New Alexandria, 2 ♂, 1 ♀, 24 Apr 1935 (USNM); marshy ponds on Accotink Creek just below Lake Accotink. Springfield, 11 ♂, 11 ♀, J. R. Holsinger 7 Apr 1973; Hampton (Elizabeth City County): small pool, palustrine forested wetland on western side of NASA Langley Research center, 17 ♂, 14 ♀, R. L. Bedenbaugh et al., 17 Mar 1994; Henrico Co.: Brook Hill N of Richmond, 3 ♂, A. Pizzini, 30 Apr 1939 (USNM); Isle of Wight Co.: rill in woods, 2.4 km NE of Bartlett, holotype ♂, 100 specs (♂, ♀, juvs), L. Hubricht, 2 Apr 1944 (USNM); small stream, 1.6 km N of Bartlett, 5 ♂, 2 ♀, L. Hubricht, 2 Apr 1944 (USNM); roadside ditch, 0.5 km N of Carrollton, 1 ♂, L. Hubricht, 30 Jan 1944 (USNM); seeps, 3.2 km SE of Bartlett, 30 ♂, 4 ♀, L. Hubricht, 30 Jan 1944 (USNM); small stream, 1.6 km S of Rescue, 9 ♂, 2 ♀, L. Hubricht, 12 Mar 1944.
Figure 115.—Crangonyx polustris, new species. Female paratype (5.5 mm), rill in woods. 2.4 km NE of Bartlett. Isle of Wight Co., Virginia: a, head (in part); b, antenna 1; c, d, maxillae 1, 2; e, lower lip; f, left mandible; g, inner and outer plates and palp dactyl of maxilliped (greatly enlarged); h, i, gnathopods 1, 2 (palmar margins enlarged).
Figure 116. *Crangonyx polustris*, new species. Female paratype (5.5 mm), rill in woods, 2.4 km NE of Bartlett, Isle of Wight Co., Virginia: a, c, d. pereopods 3, 5, 6 (in part); b, e, pereopods 4, 7; f. pleonal plates; g, h, i, uropods 1, 2, 3; j, telson.
Figure 117.—Crangonyx polustris, new species. Male paratype (3.2 mm), rill in woods, 2.4 km NE of Bartlett, Isle of Wight Co., Virginia: a. antenna 2; b, c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7 (in part); e, f, g. uropods 1, 2, 3; h. telson.
Figure 118.--Distribution of *Crangonyx palustris* in North America. Solid circles represent 1-6 closely proximate localities. The dotted line denotes the "fall line" or "fall zone" between the Coastal Plain and Piedmont.
(USNM): Lancaster Co.: shallow well and roadside ditch near old trash dump in woods. 4.8 km E of White Stone. 17 9. 2 $. S. Hetrick. 10 Mar 1982; seep pool in woods. 4.8 km E of White Stone, 7 $. 5 $. J. R. Holsinger and R. Godfrey. 17 Apr 1983; shallow well, seep and swamp. 4.8 km E of White Stone, 26 $. 2 $. 6 juvs. J. R. Holsinger et al., 9 March 1994; Nansemond Co.: pool in Dismal Swamp near Washington Ditch, 4 $. 1 $. L. Hubricht, 30 Apr 1944 (USNM); seep-fed pool in woods. ca. 4.8 km NW of center of Suffolk, 3 $. 1 $. J. R. Holsinger, 25 Mar 1984; pools in Dismal Swamp. K. Garrett and B. H. Powell, 20 specs ($$. $. juvs), 28 Apr 1971; small stream in swamp. 6.4 km W of Suffolk center, 1 $. 1 $. L. Hubricht, 25 Feb 1945 (USNM); temporary pool in woods. 1.6 km E of Driver, 3 $. 1 $. L. Hubricht, 26 Mar 1944 (USNM); small stream, 4.8 km S of Bay View, 25 $. 2 $. L. Hubricht, 16 Apr 1944 (USNM); Norfolk Co.: small spring, 0.8 km SE of Churchland, 9 $. 1 $. L. Hubricht, 11 Mar 1945 (USNM); stream in swamp, 4.8 km S of North Landing, 4 $. 1 $. L. Hubricht, 9 Apr 1944 (USNM); Warwick Co.: ditch 2.4 km NE of Morrison, 1 $. L. Hubricht, 23 Jan 1944 (USNM); pools in woods, 4.0 km NW of Newport News, 2 $. L. Hubricht, 23 Jan 1944 (USNM); York Co.: small seeping spring pond in woods, 4.5 km SW of Yorktown, 7 $. 2 $. J. G. Mackin, 17 Feb 1946 (USNM); ditch, 1.6 km SE of Tabb, 3 $. L. Hubricht, 23 Jan 1944 (USNM); small marsh-pond in woods, 4.0 km W of Yorktown, 7 $. 1 $. L. Hubricht, 9 Apr 1944 (USNM); pond, 1.0 km S of Grafton Church, 1 $. P. H. Stevenson and S. H. Holbrook, 13 Feb 1993; Lakeside forest subdivision, ca. 0.8 km NE of junction of rds 620 and 17, 2 $. 7 $. C. S. Hobson, 27 Apr 1994; pond on Rt. 17, 1.1 km S of Harris Grove, 23 $. 17 $. J. R. Holsinger et al., 9 March 1994;­

Diagnosis.—A relatively small species of the gracilis group distinguished from other members of the group by having a single spine in a small notch on the inner side (near the end) of outer ramus of male uropod 2: small, rounded distoposterior corners of pleonal plates: and very short uropod 3 with few spines on peduncle. Largest male, 5.5 mm: largest female, 9.0 mm.

Female.—Eye small and round. Antenna 1, about 46 percent length of body, about 1.7 times longer than antenna 2: primary flagellum with about 15 segments. Antenna 2, flagellum with 6-7 segments.

Mandibles subequal, spine row with 4-6 spines; segment 2 of palp with 5 long setae, segment 3 with 1 A seta, 2 C setae, 4 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 4 apical plumose setae: palp with 5-6 slender spines on apex. Maxilla 2, inner plate with oblique row of 5 plumose setae on inner margin. Maxilliped: inner plate apically with 2 bladelike spines. 1 naked spine, and 4 plumose setae extending from inner margin to apex: outer plate with row of naked setae and 3-4 pectinate slender spines on inner margin: dactyl with 2 setae near nail on inner margin: dactyl nail very long. about 1/2 length of dactyl.

Propod of gnathopod 1 slightly larger and longer than carpus: palm slightly convex, subequal to length of posterior margin, with 4 unnotched spine teeth on inside. 5 on the outside: defining angle with 3 notched-serrate spine teeth on inside, 1 large unnotched and 1 serrate spine tooth on outside; superior medial setae few in number and singly inserted; 4 sets of setae on posterior margin singly inserted or in groups of 2. Dactyl with 2-3 short setae on inferior margin, nail long about 1/3 length of dactyl. Ventral
margin of coxa 1 with 8 setae.

Propod of gnathopod 2 less 2 times larger and longer than carpus; palm slightly shorter than posterior margin, with 3 unnotched spine teeth on inside, 4 on outside; defining angle with 1 large unnotched spine teeth and three notched-serrate spine teeth on inside, 2 unnotched and 2 serrate spine teeth on outside; superior medial setae singly inserted, posterior margin with 4 sets of setae in groups of 3-4. Dactyl with 2-3 short setae on inferior margin. Ventral margin of coxa 2 with 6 setae.

Coxa of pereopod 3 with 8 marginal setae. Coxa of pereopod 4 with 12 marginal setae. Dactyl of pereopod 4. 40 percent length of corresponding propod length. Pereopod 5: basis with 8 shallow serrations along posterior margin: 5 short spines on anterior margin: 3 long setae on the anteroproximal margin.

Pereopod 6: basis with shallow 8 serrations along posterior margin: 5 short spines on anterior margin: 3 long setae on anteroproximal margin. Pereopod 7: coxa with 2-3 setae on the posterior margin: basis with 9 shallow serrations along posterior margin: 7 short spines on anterior margin: 3 long setae on anteroproximal margin: dactyl about 35 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner small, rounded, not produced; posterior margin of plate 2 slightly convex, with 1 seta, distoposterior corner rounded, not produced. Ventral margin with 5 (subventral) spines; posterior margin of plate 3 slightly convex, with 1 seta, distoposterior corner small, rounded, not produced, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus about 65 percent length of peduncle, armed with 9 spines: outer ramus with 10 spines: peduncle with row of 7 outer and 1 inner spines. Uropod 2: inner ramus armed with 2 inner and 3 outer spines, apex with 5 spines: outer ramus lacking inner spines, 3 outer spines, apex with 5 spines: peduncle with 3 outer spines, and 2 inner spines. Uropod 3: inner ramus lacking spines, outer ramus about 1.5 times longer than peduncle, inner and outer margin each with 1-2 set of spines in groups 1-2. Telson broader than long, notched about 1:3 distance to base, each lobe bearing 2 apical spines: spines about 1:2 length of telson.

Male.--Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 2 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus: palm with 7 spine teeth on inside, 5 on outside; defining angle with 3 notched-serrate spine teeth on inside and 2 notched and 1 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm margin oblique, with 7 spine teeth on inside, 8 on outside; defining angle with 1 notched and 2 weak serrate spine teeth on inside, 3 notched spine teeth on outside.

Uropod 2: inner ramus with 7 spines: outer ramus weakly deflected laterally, with 1 bladelike inner spine on notch near apex, 4 small, bladelike spines on outer margin: peduncle with 2 slender outer spines and 2 large inner spines.

Type-locality:--A rill (small brook or rivulet) in woods. 2.4 km NE of Bartlett, Isle of Wight County.
Distribution and ecology.—The range of this species extends from west-central New Jersey southwestward through southern Maryland and eastern Virginia as far south as extreme northeastern North Carolina (fig. 118). With the exception of a few localities just west of the "fall line" immediately south of Washington, DC, *C. polustris* is restricted to the Coastal Plain.

This species inhabits swamps, springs, ponds, woodland pools, streams, roadside ditches, and seeps. Ovigerous females were collected in February, March, April and August. Sexually mature males are 3.5 to 5.5 mm and sexually mature females are 4.0 to 9.0 mm.

Etymology.—The epithet *polustris* is from Latin, meaning "marshy" or "boggy," in reference to one of the primary habitats of this species.

*Cragonyx castellanum*, new species

Figures 119-122

Material examined (paratypes unless designated otherwise).—KENTUCKY. Rockcastle Co.: Crooked Creek Cave, 3 ♀, T. C. Barr, Jr., 27 May 1964; Crooked Creek Cave No.2, 1 ♂, T. Seibert, Dec 1972; Goochland Cave, 1 ♀, T. Seibert, Sept 1972; Greenhill School Cave, 6 ♀, 2 ♂, R. M. Norton, 5 Sep 1964; Millers Cave No.1, 3 ♀, T. Seibert, Sep 1972; Mullins Spring Cave, 3 ♀, 1 ♂, T. Seibert, Nov 1972; Pine Hill Cave, 2 ♀, J. Reddell, 4 Mar 1967 and 1 ♀, G. A. Coover, 1 Feb 1975; Sinks of Roundstone Cave, holotype ♀, 3 ♀, 6 ♂, 1 juv, J. R. Holsinger, 19 Jul 1964; Teamers Cave, 1 ♀, 2 ♂, J. R. Holsinger, 8 May 1965; Pulaski Co.: Piney Grove Cave, 2 ♀, L. Hubricht, 16 Dec 1956 (USNM) and 2 ♀, T. C. Barr, Jr., 16 Dec 1956.

Diagnosis.—A relatively small cavemicolous species of the *gracilis* group, closely similar to *C. caecus* but differing from that species by lacking spines on inner margin of outer ramus of male uropod 2 and presence of 2 thin (setal-like) spines on outer margin. Largest male, 5.5 mm; largest female, 8.2 mm.

Female.—Eyes either absent or greatly reduced, when present limited to several black specks. Antenna 1, about 60 percent length of body, about 2 times longer than antenna 2; primary flagellum with up to 20 segments. Antenna 2, flagellum with up to 8 segments. Mandibles subequal, spine row with 5-6 spines; segment 2 of palp with 7 long setae, segment 3 with 1 A seta, 2 C setae, 4-5 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 7 apical plumose setae; palp with 5-7 slender spines on apex. Maxilla 2, inner plate with oblique row of 6-7 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines. 2 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with naked long setae and 3-4 small weak more or less pectinate spines on inner margin, 1 apical plumose seta; dactyl with 2 setae in inner margin near the nail; dactyl nail very long, 1/3 length of dactyl.
Figure 119.—*Crangonyx castellanum*, new species. Female paratype (7.0 mm), Sinks of Roundstone Cave, Rockcastle Co., Kentucky: a, antenna 1. Female paratype (8.2 mm), same location: b, c, maxillae 1, 2; d, lower lip; e, left mandible; f, dentate part of right mandible; g, inner and outer plates and palp dactyl of maxilliped; h, i, gnathopods 1, 2 (palmar margins enlarged).

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Figure 120.—Crangonyx castellanum, new species. Female paratype (7.0 mm). Sinks of Roundstone Cave, Rockcastle Co., Kentucky: b. pereopod 3 (in part); c, d. pereopods 4, 7. Female paratype (8.2 mm), same location: a. head (in part); e. peduncle of pleopod 1 (retinacula and other spine enlarged); f. pleonal plates; g, h, i. uropods 1, 2, 3; j. telson.
Figure 121.—Crangonyx castellanum, new species. Male paratype (5.0 mm), sinks of Roundstone Cave, Rockcastle Co., Kentucky: a, antenna 2; b, c, gnathopods 1, 2 (palmar margins enlarged); d, uropod 2 (end of outer ramus enlarged); e, uropod 3; f, telson.
Figure 122.—Distribution of *Cragonyx castellanum* in North America. Solid circles represent 1-3 closely proximate localities.
Propod of gnathopod 1 less 2 times larger and longer than carpus: palm slightly convex, subequal in length posterior margin, with 6-7 unnotched spine teeth on inside, up to 13 on the outside: defining angle with 4 notched-serrate spine teeth on inside. 1 large unnotched and 2 serrate spine teeth on outside: inferior and superior medial setae few in number and singly inserted; 4-5 sets of setae on posterior margin inserted in groups of 3-5. Dactyl with a row of 5 short setae inferior margin, nail long. Ventral margin of coxa 1 with 10 setae.

Propod of gnathopod 2 less 2 times larger and longer than carpus: palm slightly convex and oblique, slightly shorter than posterior margin, with up to 11 unnotched spine teeth on inside, 15 on outside: defining angle with 1 or 2 large notched spine teeth and 2 small notched-serrate spine teeth on inside. 1 or 2 very large and strong unnotched spine teeth and 1 small serrate spine tooth on outside: up to 8 superior medial setae singly inserted; posterior margin with 5 sets of setae inserted in groups of 2-6. Dactyl with row of 6 short setae on inferior margin. Ventral margin of coxa 2 with 8-9 long setae.

Coxa of pereopod 3 with 8 marginal long setae. Coxa of pereopod 4 with 12 marginal setae, dactyl of pereopod 4. 45 percent length of corresponding propod. Pereopod 5: basis with 12 very shallow serrations along posterior margin; 7 short spines on anterior margin; 3-4 long setae on the anteroproximal margin. Pereopod 6: basis with 12 shallow serrations along posterior margin; 6 short spines on anterior margin; 3 setae on anteroproximal margin. Pereopod 7: coxa with 2 setae on the posterior margin; basis with 12-13 shallow serrations along posterior margin; 7 short spines on anterior margin; 1 seta on anteroproximal margin; dactyl about 35 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 convex, with 1 seta, distoposterior corner not produced, subacute; posterior margin of plate 2 weakly convex, with 1 setae, distoposterior corner weakly produced, subacute, ventral margin with 4-5 (subventral) spines; posterior margin of plate 3 convex with 1 seta, distoposterior corner neither produced nor acute, ventral margin with 3 (subventral) spines. Pleopod 1: peduncular segment with 2 retinaculae. 1 small spine sometimes at middle of inner margin, setae lacking on outer margin.

Uropod 1: inner ramus 60 percent length of peduncle, armed with 13 spines: outer ramus with 13 spines; peduncle with row of 12 outer and 3-4 inner spines. Uropod 2: inner ramus with 11 spines: outer ramus with 9 spines; peduncle with 5 outer and 4 inner spines. Uropod 3: inner ramus with 1 long spines, outer ramus about 1.5 times longer than peduncle, inner and outer margin each with 2-3 set of spines in groups of 1-3. Telson much broader than long, notched about 1/4 distance to base, each lobe with 2-3 apical spines; spines about 1/2 length of telson.

Male.--Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli percent on peduncular segments 4 and 5 and first 3 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus: palm with 9 spine teeth on inside, 11 on outside: defining angle with 3 notched and 1 notched-serrate spine teeth on inside, 4 notched and 1 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than
carpus: palm margin convex and strongly oblique, with 10-12 spine teeth on inside, 12 on outside; defining angle with 5-6 spine teeth on inside and 6 on outside.

Uropod 2: outer ramus deflected laterally, without inner spines but with 2 thin, setal-like outer spines, apex with row of 4 inner and row of 3 outer spines; peduncle with 3 outer spines and 3 inner spines. Telson broader than long, notched about 1/3-1/2 distance to base.

Distribution and ecology.—This species is known only from caves on the western margin of the Cumberland Plateau in Rockcastle and Pulaski counties, Kentucky (fig. 122), where it inhabits drip pools and small streams. Of the 37 females collected to date, only one specimen (6.0 mm) was ovigerous.

Etymology.—The epithet *castellanum* is from Latin meaning “keepers of a castle,” so named in reference to the occurrence of this species in Rockcastle County.

The *hobbsi* subgroup

Diagnosis.—Adult size range, 7.0-11.0 mm. Eyes absent. Calceoli absent from antenna 2 of male. Maxilla 1 inner plate with up to 16 apical plumose setae. Maxilla 2 inner plate with oblique row of up to 11 plumose setae on inner margin. Outer plate of maxilliped just slightly higher than inner plate. Carpus and propod of gnathopods in both sexes very thin and long. Carpus longer than propod of female gnathopod 2: palmar margin of propod of male with simple spine teeth, very few notched spine teeth; defining angle with notched-serrate spine teeth on inside and serrate spine teeth on outside. Outer ramus of female uropod 3 longer and thicker than in other species of the genus.

Comments.—The *hobbsi* subgroup is composed of a single species.

*Crangonyx hobbsi* Shoemaker

Figures 123-128


Figure 123.—*Crangonyx hobbsi* Shoemaker. Female (9.0 mm), entire animal from left side, Homosassa Spring, Homossassa Spring Park, Citrus Co., Florida.
Figure 124.—*Crangonyx hobbsi* Shoemaker. Female (9.3 mm). Huggins Cave, Alachua Co., Florida:
a. b. antennae 1, 2; c, d. gnathopods 1, 2 (palmar margins enlarged).
Figure 125.—*Crungonyx hobbsi* Shoemaker. Female (7.3 mm), Huggins Cave, Alachua Co., Florida: a, c, d, pereopods 3, 5, 6 (in part); b, e, pereopods 4, 7. Female (9.3 mm), Huggins Cave, Alachua Co., Florida: f, pleonal plates; g, h, i, uropods 1, 2, 3; j, telson.
Figure 126.—*Crungonyx hobbsi* Shoemaker. Female (9.3 mm), Huggins Cave, Alachua Co., Florida: a, b, maxillae 1, 2; c, lower lip; d, dentate part of left mandible; e, right mandible; f, inner and outer plates of maxilliped (greatly enlarged).
Figure 127.—Crangonyx hobbsi Shoemaker. Male (6.2 mm). Huggins Cave. Alachua Co., Florida: a. antenna 2; b, c, gnathopods 1, 2 (palmar margins enlarged); d, e, f, uropods 1, 2, 3; g, telson.
Figure 128.–Distribution of *Crangonyx hobbsi* in North America. A solid circle represents 1-5 closely proximate localities.
Diagnosis.—A medium sized subterranean species distinguished from all other species of the genus by thin, elongate carpus and propod of gnathopods in both sexes (carpus longer than propod of gnathopod 2 in female); setose mouthparts, especially inner plate of maxilla 1 with up to 16 apical plumose setae, and
inner plate of maxilla 2 with oblique row of up to 11 plumose setae on inner margin: much longer and thicker outer ramus of uropod 3 of female: and absence of calceoli on antenna 2 of male. Largest male. 9.0 mm; largest female, 11.0 mm

Female--Eyes absent. Antenna 1, about 80 percent length of body, about 2.2-3.0 times longer than antenna 2: primary flagellum with up to 27 segments. Antenna 2, flagellum with 8-9 segments. Mandibles subequal, spine row with 9-11 spines: segment 2 of palp with 4 long setae, segment 3 with 1-2 A setae, 1 B seta (very low location near A setae), 2 C setae, 5 E setae and a row of D setae. Lower lip: lacking inner lobes, lateral process of outer lobe subacute. Maxilla 1: inner plate with 16 apical plumose setae; palp with 5-6 slender spines on apex. Maxilla 2, inner plate with oblique row of 11 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 3 naked spines, and 9 plumose setae extending from inner margin to apex: outer plate with row of naked setae on the inner margin; inner plate slightly higher than outer plate; dactyl with 2 setae on inner margin near nail; dactyl nail long, 1/3 length of dactyl.

Gnathopod 1: propod and carpus very long; carpus slightly longer than propod, posterior margin with very long setae; propod palm with 2 unnotched spine teeth on inside, 4 on the outside; defining angle with 3-7 spine teeth on inside, 1 large unnotched and 2 serrate spine teeth on outside: inferior and superior medial setae few in number and singly inserted; posterior margin with 4 sets of setae singly or doubly inserted; dactyl nail very long about 1/3 length of dactyl. Ventral margin of coxa 1 with 5 setae.

Gnathopod 2: carpus of gnathopod 2 much longer than propod, posterior margin with very long setae; propod palm with 3 unnotched spine teeth on inside, 4 on outside; defining angle with 3 unnotched and 2 notched-serrate spine teeth on outside, 7 notched-serrate spine teeth on inside; inferior and superior medial setae singly inserted, posterior margin with 6-7 sets of setae in groups of 2-5. Dactyl with several short setae on inner margin. Ventral margin of coxa 2 with 5 setae.

Coxa of pereopod 3 with 3 marginal setae. Coxa of pereopod 4 with 9 marginal setae. dactyl 50 percent length of corresponding propod. Pereopod 5: basis with 10 shallow serrations along posterior margin: 5 short spines on anterior margin; 1 long seta on anteroproximal margin. Pereopod 6: basis with 12 shallow serrations along posterior margin: 4 short spines on anterior margin; 1 long seta on anteroproximal margin. Pereopod 7: coxa with 1 seta on the posterior margin: basis with 10 shallow serrations along posterior margin: 5 short spines on anterior margin; dactyl about 25 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 almost straight, with 1 seta, distoposterior corner not produced and weakly acute. ventral margin with 2 (subventral) spines: posterior margin of plate 2 weakly oblique with 2 or 3 setae, distoposterior corner produced and subquadrangular acute. ventral margin with 5 (subventral) spines: posterior margin of plate 3 nearly straight or slightly oblique with 1 or 2 setae, distoposterior corner produced and subquadrangular, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae: lacking setae on outside margin.

Uropod 1: inner ramus subequal to peduncle length, armed with 16 spines; outer ramus with 15 spines;
peduncle with 3 outer and 1 inner spines. Uropod 2: inner ramus armed with 14 spines; outer ramus with
17 spines; peduncle with 1 outer and 1 inner spines. Uropod 3: inner ramus with 1-2 spines, outer ramus
about 2.5 times longer than peduncle, inner and outer margin each with 4-6 set of spines in groups of 1-3.
Telson broad equal to long, notched about 1/3 distance to base, each lobe with 3 apical spines; spines less
than 1/2 length of telson.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2:
flagellum with about 6 segments, peduncle and flagellum lacking calceoli.

Propod palm of gnathopod 1 with 5 notched or unnotched spine teeth on inside. 8 notched or
unnotched spine teeth on outside; defining angle with 7 serrate spine teeth on inside and 3 notched or
unnotched and 2 serrate spine teeth on outside. Carpus of gnathopod 1 very long but shorter than propod.
Propod of gnathopod 2 palm margin strongly oblique, with 9 notched or unnotched spine teeth on inside.
11 unnotched spine teeth on outside: defining angle with 6 serrate and 1 spine teeth on inside, 3 unnotched
or notched on outside. Carpus of gnathopod 2 very long but shorter and narrower than propod.

Uropod 2: outer ramus, neither deflected nor curved, outer ramus with 6 inner and 4 outer spines, apex
with 4 spines; peduncle with 1 outer and 1 inner spines.

Distribution and ecology.—This species is widely distributed in the northern and central limestone karst
regions of Florida and is also recorded from a well in Dade County in the extreme southern part of the state
(fig. 128). It is frequently associated with the stygobiont amphipod *Crangonyx grundimanus*. Breeding
apparently takes place the year round but ovigerous females are never abundant at any given time
(Holsinger, 1972).

The *baculispina* subgroup

Diagnosis.—Adult size range, 6.0-7.5 mm. Gnathopods of female: carpus and propod very thin and
long; carpus equal or longer than propod, posterior margin armed with long setae; palm of propod with
simple spine teeth; defining angle of propod of gnathopod 1 with serrate spine teeth, that of gnathopod 2
with "normally" notched spine teeth. Gnathopods of male: propod more than 2 time larger and much
broader; palm of propod armed with unnotched rodlike spine teeth; defining angle of propod with
"normally" notched spine teeth inside.

Comments.—The *baculispina* subgroup is composed of a single species.

*Crangonyx baculispina*, new species

Figures 129-132

Material examined (paratypes unless designated otherwise).—VIRGINIA. Lancaster Co.: shallow well
Figure 129.—*Crangonyx baculispina*, new species. Female paratype (6.0 mm), seep pool in woods near old dump just off Rt. 645, 4.8 km E of White Stone. Lancaster Co., Virginia: a, antenna 1; b, c, maxillae 1, 2; d, lower lip; e, right mandible; f, dentate part of left mandible; g, inner and outer ramus and palp dactyl of maxilliped (greatly enlarged); h, i, gnathopods 1, 2 (palmar margins enlarged); j, pereopod 5 (in part).
Figure 130.—*Crangonyx baculispina*, new species. Female paratype (6.0 mm), seep pool in woods near old dump just off Rt. 645, 4.8 km E of White Stone, Lancaster Co., Virginia: a. c. pereopods 3, 6 (in part); b, d. pereopods 4, 7; e. pleonal plates; f, g, h. uropods 1, 2, 3; i. telson.
Figure 131. *Crangonyx baculispina*, new species. Male paratype (4.0 mm), seep pool in woods near old dump just off Rt. 645, 4.8 km E of White Stone, Lancaster Co., Virginia: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d, e, f. uropods 1, 2, 3; g. telson.
Figure 132.--Distribution of *Cramptonyx baculispina* in North America. Solid circle represents 3 closely proximate localities.
and/or roadside ditch near old dump just off Rt. 645. 4.8 km E of White Stone. 4 ♂, 2 ♀; S. Hetrick, 10 Mar 1982; seep pool in woods near old dump just off Rt. 645. 4.8 km E of White Stone. holotype ♀; 3 ♂, 1 ♂; J. R. Holsinger and R. Godfrey, 17 Apr 1983; swamp in woods near old dump just off Rt. 645. 4.8 km E of White Stone. 1 ♂; J. H. Holsinger et al., 9 Mar 1994. Largest male. 4.0 mm; largest female. 7.5 mm.

Diagnosis.—A small species morphologically similar to other members of gracilis group but distinguished from them by carpus of gnathopods which is longer than propod in females (cf. C. hobbsi); and with unnotched rodlike spines on propods of male gnathopods (unique among all Crangonyx species). Largest female. 7.5 mm; largest male. 4.0 mm.

Female.—Eye large and ovate. Antenna 1, about 50 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with about 16 segments. Antenna 2, flagellum with 8-9 segments. Mandibles subequal. spine row with 5 spines; segment 2 of palp with 7 long setae, segment 3 with 1-2 A setae, 1 C seta, 5 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 6 apical plumose setae: palp with 7 slender spines on apex. Maxilla 2, inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 3 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and about 2 slender pectinate spines on inner margin; dactyl with 2 setae on inner margin near nail; dactyl nail very long. 13 length of dactyl.

Propod of gnathopod 1 equal in length to carpus; posterior margin relatively long, with long setae: palm almost straight, shorter than posterior margin, with 4 unnotched spine teeth on inside. 4 on outside: defining angle with four serrate spine teeth on inside. 1 notched. 1 large and 1 serrate spine teeth on outside: inferior singly inserted; superior medial setae few in number and singly inserted; 4 sets of posterior margin setae singly inserted or in groups of 1-4. Dactyl with row of short setae on inner margin. nail very long. Ventral margin of coxa 1 with 8 long setae.

Propod of gnathopod 2 equal in length to carpus; posterior margin elongate, with long setae: palm almost straight, much shorter than posterior margin, with 2-3 unnotched spine teeth on inside. 5-6 on outside: defining angle with 3 spine teeth on inside. 1 large unnotched and 1 serrate spine teeth on outside: inferior medial setae and superior medial setae singly inserted, posterior margin with 5 sets of setae in groups of 1-3. Dactyl with row of short setae on inner margin. Ventral margin of coxa 2 with 8 setae.

Coxa of pereopod 3 with 9 marginal setae. Coxa of pereopod 4 with 16 marginal setae, dactyl of pereopod 4. 35 percent length of corresponding propod. Pereopod 5: basis with 8 shallow serrations along posterior margin: 8 short spines on anterior margin: 1 long seta on anteroproximal margin. Pereopod 6: basis with 11 shallow serrations along posterior margin. 7 short spines on anterior margin: 3 setae on anteroproximal margin. Pereopod 7: coxa with 1 seta on the posterior margin; basis with 10 shallow serrations along posterior margin, 8 short spines on anterior margin: 3 setae on anteroproximal margin: dactyl about 33 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, disto-posterior corner acute but not produced; posterior margin of plate 2 nearly straight with 1 or 2 setae, disto-posterior corner slightly

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produced and acute, ventral margin with 4 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner small and subacute but not produced, ventral margin with 5 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus 80 percent length of peduncle, armed with 12 spines; outer ramus with 13 spines; peduncle with 5 outer and 2 inner spines. Uropod 2: inner ramus armed with 11 spines; outer ramus with 11 spines; peduncle with 3 outer and 3 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.5 times longer than peduncle, inner and outer margins each with 3-4 set of spines in groups of 1-3. Telson broader than long, notched about 2/5 distance to base. each lobe with 3 apical spines; spines less than 1.2 length of telson.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 3 flagellar segments. Propod of gnathopod 1 more than 2 times larger and longer than carpus and much broader; palmar margin with 10 unnotched, curved rodlike spine teeth on inside, 8 on outside; defining angle with 4 normal spine teeth on inside and 1 unnotched, curved rodlike and 2 small laterally notched spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus; palm margin strongly oblique, with 12 unnotched curved rodlike spine teeth on inside, 12 on outside; defining angle with 1 unnotched curved rodlike and 2 notched teeth on inside and 2 unnotched curved rodlike and 1 laterally notched spine teeth on outside.

Uropod 2: outer ramus curved laterally but not strongly so, shorter and narrower than inner ramus. inside with 3 spines, outside with 2 spines; outer ramus with about 9 spines; peduncle with 2 outer spines and 1 inner spine. Uropod 3: outer ramus about 2 times length of peduncle. Telson longer than broad, notched about 1/2 distance to base; each lobe with 3 apical spines; spines about 1.2 length of telson.

Type-locality.—Seep pool in woodland near or old trash dump just off Rt. 645, 4.8 km E of White Stone, Lancaster County, Virginia.

Distribution and ecology.—This rare species is known only from its type-locality and immediate vicinity, where it was collected from a seep pool, shallow hard-dug well and swamp (fig. 132). Ovigerous female were collected during March and April. *Crangonyx baculispina* was found living in association with the epigean amphipod *C. polustris* and the stygobiont amphipod *Stygobromus indentatus*, and an isopod *Caecidotea* sp.

Etymology.—The epithet *baculispina* refers to the rodlike spines on the margins of the propods of the male gnathopods.

The *floridanus* subgroup

Diagnosis.—Adult size range. 5.0-10.0 mm. Distoposterior corner of pleonal plates 1-3 strongly produced, acute. Outer ramus of uropod 2 of male with comb spines.

Comments.—Four species are assigned to this subgroup: *C. floridanus*, *C. pseudogracilis*, *C.
Crangonyx floridanus Bousfield

Figures 133-136


Eucrangonyx gracilis (Smith).—Shoemaker, 1933:15.

Crangonyx pseudogracilis Bousfield—Bousfield. 1961:5.

Figure 133.—*Crangonyx floridanus* Bousfield. Female (8.2 mm). Stream between Elloree and St. Matthews, Orangeburg Co., South Carolina: a. b. antennae 1. 2; c. d. maxillae 1. 2; e. lower lip; f. left mandible; g. dentate part of right mandible; h. inner, outer plates and palp dactyl of maxilliped (greatly enlarged); i, j. gnathopods 1. 2 (palmar margins enlarged).
Figure 134.—*Crangon* sp. *floridanus* Bousfield. Female (8.2 mm). Stream between Elloree and St. Matthews, Orangeburg Co., South Carolina: a. b. c. d. pereopods 3, 4, 5, 6 (in part): e. pereopod 7: f. pleonal plates: g. h. i. uropods 1, 2, 3: j. telson.
Figure 135.—Crangonyx floridanus Bousfield. Male (6.0 mm). Stream between Ellorcee and St. Matthews, Orangeburg Co., South Carolina: a, antenna 2; b, c. gnathopods 1, 2 (palmar margins enlarged); d, pereopod 7; e, f, h, uropods 1, 2, 3; g, uropod 2 from other side (in part); i, telson.
Figure 136—Distribution of Cryptomyx johorhum in North America. Solid circles represent 1-15 closely proximate localities. Dotted lines indicate the approximate southern extent of glaciation during the Pleistocene and also enclose areas of alpine glaciation in the west. Note that the two disjunct localities for this species in the western US are somewhat questionable.
outlet N side Milton Reservoir, 9 ♂, 7 ♀. R. W. Pennak, 9 May 1953 (USNM). FLORIDA. Alachua Co.: cypress Swamp at Gainesville, 5 ♂, R. E. Woodruff, 6 Apr 1959 (USNM); Hatchet Creek, 6 ♂, 1 ♀. G. and L. Van Hyming, 8 Feb 1938; Gainesville (habitat not given), 1 ♂. A. G. Mutchber, 29 Sep 1914 (USNM) and 2 ♂, 1 ♀. J. Martin, 1 May 1937 (USNM); Newman's Lake near Gainesville, 11 ♂, 1 ♀. F. N. Young, 8 Jan 1930 (USNM); N of Highland Springs, 6 ♂, 6 ♀. H. H. Hobbs, Jr., 12 May 1937 (USNM); pond C. 3 ♂, 1 ♀. J. Martin, 5 Mar 1934 and 4 ♂, 4 Apr 1933 (USNM); Santa Fe Lake, 1 ♂. J. Martin, 2 Apr 1935 (USNM) and 5 ♂, 8 Apr 1937 (USNM); sink, 28 ♂, 2 ♀. J. Martin, 14 Mar 1937 (USNM); swamp 7.2 km E of Gainesville, 100 specs (♀, ♂). L. Hubricht, 18 Apr 1941 (USNM); swamp 8.8 km SW of Orange Heights, 70 specs (♀, ♂). L. Hubricht, 18 Apr 1941 (USNM); Wauberg Lake Station, 7 ♂, 7 ♀. R. P. Trogdon (collection date not given) (USNM) and 2 ♂, J. Martin, 23 Feb 1933 (USNM); 1 ♂, J. Martin, 24 Mar 1927 (USNM); Baker Co.: Bayhead Pond, 1 ♂, J. Martin, 12 May 1937 (USNM); swamp stream, 5 ♂, J. Martin, 12 May 1937 (USNM); Brevard Co.: St. Johns R. at Lake Winder, 2 ♂, 1 ♀. R. Fox, 9 Feb 1970; St. Johns R., SW of Lake Helen 'blazes, 4 ♂, R. Fox, 9 Feb 1970; St. Johns R. at canal on E shore of Lake Poinsett, 1 ♂, R. Fox, 9 Feb 1970; St. Johns R. 1.2 km away between Lake Winder and Poinsett, 3 ♂, 1 ♀. R. Fox, 9 Feb 1970; Clay Co.: Kingsley Lake, 2 ♂, H. H. Hobbs, Jr., 30 Apr 1935 (USNM); Columbia Co.: cypress swamp, 5 ♂, 1 ♀. H. H. Hobbs, Jr., 12 May 1937 (USNM); Mill Pond Spring, Ichatucknee Springs State Park, 1 ♂, A. Woodruff (collection date not given), (Woodruff Collection); Mission Spring, Ichatucknee Springs State Park, 5 ♂, A. Woodruff (collection date not given), (Woodruff collection); NW of Lake City, 2 ♂, H. H. Hobbs, Jr., 4 Feb 1938 (USNM); Dade Co.: Little Bird Nursery well, Miami, 1 ♂. G. Miller, 29 Oct 1968 (USNM) and 2 specs, 29 Nov 1968; Franklin Co.: Crayfish burrow on St. Rt. 65, 4.8 km E of East Bay, 2 ♂, R. E. Ashton, Jr., 10 Jul 1978 (NMCNH); Hamilton Co.: 6.7 km N of White Springs, 1 ♂, 3 ♀. H. H. Hobbs, Jr., 4 Feb 1938 (USNM); 8.0 km N of White Springs, 2 ♂, 2 ♀. H. H. Hobbs, Jr., 4 Feb 1938 (USNM); Highlands Co.: shallows at edge of cypress swamp, under organic debris, Highlands Hammock State Park, holotype 9 ♂, allotype ♀, paratypes ♂ and ♀, E. L. Bousfield, 22 Jan 1962 (CMN); Jackson Co.: China Cave, 2 ♂, P. Moler and B. W. Mansell, 4 Feb 1986; Cottondale (habitat not given), 5 ♂, 2 ♀. J. Martin, 17 Apr 1937 (USNM); Gerards Cave, paratypes ♂ and ♀, A. E. Smalley, 20 Oct 1960 (NMC), 1 ♂, J. E. and M. L. Cooper, 16 Apr 1965, 3 ♀, 1 ♂. H. S. Harris, Jr., 20 Apr 1967, 3 ♂, 2 ♀. D. S. Lee, 28 Jul 1968 and 2 fragments, S. B. Peck, 5-9 Sep 1968; Haideotriton Cave, 2 ♀, 3 ♂, 1 juv. D. Franz, 24 Jun 1970; Gerones Cave, 5 ♂, 1 juv. (collector not given), 15 Oct 1969 and 3 ♂, 1 ♀, D. B. Means et al., 31 Jul 1969 (USNM); Judge Cave, 7 ♂, 1 juv. S. B. Peck, 9 Apr 1969; Millers Cave, 4 ♂, S. B. Peck, 6 Apr 1969; Tupelo Swamp, 11.1 km SE of Marianna, 100 specs (♀, ♂) juv. L. Hubricht, 15 Apr 1941 (USNM); Lake Co.: small stream near Umatilla, 3 ♂, 2 ♀. J. Martin, 19 Mar 1938 (USNM); Leon Co.: small stream in Silver Lake Recreational Area, Apalacheicola National Forest, 1 ♂, R. E. Woodruff, 1 Feb 1960 (USNM); swamp, 11.7 km E of Tallahassee, 30 specs (♀, ♂). L. Hubricht, 16 Apr 1941 (USNM); Levy Co.: Waccasassa R. at St. Rt. 24, 2 ♂, 2 ♀. R. Fox, 9 Feb 1970; Manatee Springs State Park, 3 ♂, A. Woodruff (collection date not given), (Woodruff Collection); Madison Co.: 12.8 km E
of Lamont. 3 2, H. H. Hobbs, Jr., 5 Feb 1938 (USNM); Okaloosa Co.: Crestview (habitat not given). 4 2, 1 2, H. H. Hobbs, Jr., 11 Dec 1937 (USNM); Seminole Co.: In crayfish burrows. 3.5 km NE of Sanford. 20 juvs. L. Hubricht, 19 Apr 1941 (USNM); Suwannee Co.: Azure Cave. 1 juv. J. Yager, 2 Jan 1987; Wakulla Co.: stream. 32 km S of Tallahassee. 2 2, 5 juvs. J. G. Mackin, 6 Jul 1937 (USNM). 36 collections, mostly by J. Martin, 1937-38 from north-central Florida (probably from Alachua County).

GEORGIA. Barrow Co.: small feeder stream. 0.4 km N of Mulberry R. at St. Rt. 11. 6 2, 4 2. J. Patten, 26 Feb 1978; Catoosa Co.: Catoosa Springs. 8.0 km E of Ringgold. 2 2, 3 2, 3 juvs. J. R. Holsinger, 10 Jun 1967; Chatham Co.: swamp. 4.8 km NE of Port Wentworth. 36 specs (2 2, 2). L. Hubricht, 21 Apr 1941 (USNM); Clarke Co.: Sandy Creek. 3.2 km N of Athens. 7 2, 6 2. G. W. Dickson, 19 Feb 1977; Sandy Creek. 6.3 km N of Athens. 6 2, G. W. Dickson, 16 Feb, 1978; Cobb Co.: Owens Spring near Austell. 11 2, 5 2. L. Hubricht, 3 Aug 1939 (USNM); Decatur Co.: locality not given. J. Martin. collection date not given (USNM); DeKalb Co.: spring on Walter Candler Estate, Emory University. 1 2. W. D. BwmbacK. 19 Apr 1960 (USNM); Lincoln Co.: small spring. base of Graves Mtn. 8.0 km SW of Lincolnton. 7 2, 1 2. L. Hubricht, 15 May 1960; Meriwether Co.: small spring of Warm Springs. 15 2, 7 2. J. H. Chandler, Jr., 28 Jan 1980 (USNM); Polk Co.: spring. 3.2 km E of Aragon. 4 2, 1 2. L. Hubricht, 8 May 1951 (USNM); spring below mouth of Deatons Cave. 4.0 km SW of Taylorsville. L. Hubricht, 8 May 1951 (USNM); Wayne Co.: swamp. 1.8 km N of Jesup. 12 2, 5 2. L. Hubricht, 20 Apr 1941 (USNM).

KANSAS. Pottanatomie Co.: Pressure Springs. base of Tuttle Creek. Reservoir dam. 11 2, 16 2, 1 juv. J. Danoff-Burg et al., 23 Jun 1991; seepage below Tuttle Creek Reservoir Dam. 11 2, 1 2. M. Moffett, 27 May 1981.

KENTUCKY. Christian Co.: Reeves Cave (=Thomas Cave). 1 2. R. La Val, 4 Jul 1964 and 2 2, 4 2. J. R. Holsinger and T. C. Barr, Jr., 12 Aug 1965. MARYLAND. Anne Arundel Co.: Patapsco River at Hammond's Ferry Road. 3 2, 1 2. L. Hubricht, 28 Mar 1959 (USNM); Frederick Co.: Hunting Creek Lake at Cunningham Falls Park on Rt 77 W of Thurmont. 2 2, 5 2. C. K. Biembaum, 17 Jul 1992; Montgomery Co.: Chilton Woods Spring, 1.7 km NW of intersection of Whites Ferry Rd and Martinsburg Rd. 1 2, 1 2. D. Feller, 6 Mar 1995; Maryland Line Spring, S side of Beach Dr. at Maryland/DC line. 8 specs. D. Feller, 10 Mar 1995. MASSACHUSETTS. Hampton Co.: Holyoke Power Canals. Connecticut River. 32 2, 3 2. D. G. Smith, 5 Jul 1984. MISSISSIPPI. Clarke Co.: pool near Long Creek. W of Middleton. 21 2, 11 2. L. Hubricht, 3 Feb 1962 (USNM); Forrest Co.: small stream in swamp. nr. Black Creek. 3.2 km SW of Brooklyn. 3 2, 1 2, 1 2. L. Hubricht, 2 Mar 1963; Lafayette Co.: spring near Oxford. G. Gaston. 25 specs (2 2, 2). 11 May 1991. Lauderdale Co.: pools in swamp. 1.6 km NW of Kewanee. 30 specs. L. Hubricht, 4 Feb 1962 (USNM); roadside pool. US 80 at 31st Ave. 100 specs. L. Hubricht, 8 Mar 1964 (USNM); swamp pool. Bonita. 100 specimens. L. Hubricht, 9 Mar 1963 (USNM); Rankin Co.: slough. 1.2 km W of pelatchee. 1 2, 1 juv. L. Hubricht, 9 Apr 1941; Smith Co.: seep near realleaf 4.8 km W of Sylvanara. Winston Co.: pools 4.0 km S of Noxipater. 2 2. 17 Mar 1963 (USNM); Wayne Co.: roadside ditch 2.4 km SW of Waynesboro. 48 specs (2 2, 2). L. Hubricht, 16 Feb 1963 (USNM).

MISSOURI. Butler Co.: slough. 9.8 km N of Neelyville. 100 specs (2 2, 2). L. Hubricht, 5 Apr 1941.
(USNM): Camden Co.: Camp Resing Sun Cave. 8.8 km NE of Lenn: Madison Co.: spring. 0.8 km S of Mill Creek. 1 juv. L. Hubricht. 5 Apr 1941 (USNM); Scott Co.: small pool on road. 0.8 km N of Forulfelt. 2 ♂, 1 ♀. W. L. Pfleger and G. McDonald. 27 Feb 1976; St. Louis Co.: slough near Mississippi River. 1.6 km S of Grimsby. 170 specs (♀, ♂) (USNM) and 1 ♂ (NMC). L. Hubricht. 25 Apr 1938; temporary pond. 3.2 km N of Fenton. ca. 130 specs. L. Hubricht, 12 Jan 1936; temporary pond, near River Kirkwood. 1 ♂, 3 ♀. L. Hubricht. 10 Apr 1938; Taney Co.: Lake Taneycomo at Rockaway Beach. 25 specs (♀, ♂ juvs). W. Pfleger, 22 Oct 1970.

NORTH CAROLINA. Carteret Co.: pond ca. 16 km W of Moorhead City. 5 ♂, 1 ♀. N. Hynes. 26 Apr 1980 (USNM); cypress pond. 11 km from Moorhead City. 6 ♂, 1 ♀. N. Hynes. 21 Apr 1982 (USNM); Chatham Co.: small stream at US 15. 0.8 km N of Bynum. 50 specs. 6 Mar 1972; rill and pool near Rocky River. 11.7 km S of Pittsboro. 33 ♂, 25 ♀. L. Hubricht. 8 Apr 1950 (USNM); Granville Co.: shallow well at end of ST Rt 1947. 1 ♀, 7 juvs. W. F. Adams. 5 Sep 1991; shallow well on farm at end of Rt 1778. 1 ♀, 2 juvs. W. F. Adams. 18 Jun 1991; Macon Co.: Club Lake, on Rt 106. just outside Highlands. 20 ♂, 6 ♀. C. K. Biembaun. 14 Jul 1991; Moore Co.: old lake bottom between Southern Pines and Carthage. 20 ♀ (collector not given). 4 Feb 1940 (USNM); swamp. NE of Southern Pines. 3 ♂, 2 ♀ (collector not given). 19 Mar 1940 (USNM); small spring in pine woods.

Southern Pines. 6 ♂, 1 ♀. T. K. Ellis. 7 Mar 1940 (USNM); swamp on Little River. 4.8 km N of Southern Pines Airport. 5 ♂, 5 ♀. T. K. Ellis. 8 May 1940 (USNM); pasture spring and stream. Southern Pines. 5 ♂, 2 juvs (collector not given), 8 Mar 1940 (USNM); Little Crane Creek. Cameron. Rt 1. 2 ♂. J. F. Hanson. 13 Dec 1956 (USNM); Orange Co.: marsh. Chapel Hill. 2 ♂. J. Allwein. 19 Jan 1964; Pamlico Co.: creek. 2.1 km W of Grantsboro. 16 ♂, 1 ♀. L. Hubricht. 23 May 1959 (USNM). Wake Co.: ditch beside St Rt 55. between St Rt 54 and Us 64. 30 ♀. J. Green. 28 Nov 1972; Little River (Neuse) at Rd 2224. 7.7 km E of Rolesville. 4 ♀. A. L. Braswell. 1 Dec 1977; intermittent stream near Shearon Harris Lake. 25 specs. J.E. Cooper and A. L. Braswell. 19 Apr 1995; small pond, Reedy Creek Rd. 10 ♂, 10 ♀. W. M. Brooks. 8 Feb 1994; roadside ditch on Pulleytown Rd. 6 ♀, 20 ♂. W. M. Brooks. 8 Feb 1994.

OHIO. Wayne Co.: Shreve Creek. 2 ♂, 4 ♀. A. Weaver. 10 Feb 1964. OREGON. Clackamas Co.: small pond on Oswego Lake Co. Club. 3 ♂, 4 ♀. J. Bond. 2 Mar 1958 (CMN) and 6 ♂, 4 juvs. 8 Jan 1961 (CMN); boggy inlet of Lake Oswego. 3 ♂, J. Bond. 18 Feb 1958 (CMN); Lane Co.: Corner Lake. 3 ♂, 12 juvs. F. Ziesenheim. summer. 1937 (CMN); Emma Lake. 6 ♀, 4 ♂. F. Ziesenheim. 25 Sep 1937 (CMN); Eastern Brook Lake. 1 ♂, 3 juvs. F. Ziesenheim. 27 Sep 1937 (CMN). PENNSYLVANIA. Chester Co.: spring. 1.6 km E of West Grove. 50 specs (♀, ♂). L. Hubricht. 17 Aug 1939 (USNM); Dauphin Co.: intake structure at Three Mile Island.


Diagnosis.—A species of the *gracilis* group closely similar morphologically to *C. pseudogracilis* but

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distinguished from it and other members of the group by having comb spines on outer ramus of male uropod 2 but lacking ventral spines there; distoposterior corners of pleonal plates 1-3 well developed; distoposterior margins of pereopods 5-7 with deep serrations. Largest male, 8.0 mm; largest female, 12.0 mm.

Female.—Eye large and ovate. Antenna 1, about 55 percent length of body, about 1.5-1.8 times longer than antenna 2: primary flagellum with up to 19 segments. Antenna 2, flagellum with 7-8 segments. Mandibles subequal, spine row with 5 spines: segment 2 of palp with 6-9 long setae, segment 3 with 1 A seta, 2-5 C setae, 4-5 E setae, and a row of 9 D setae, lacking B seta. Maxilla 1: inner plate with 5-6 apical plumose setae: palp with 5-6 slender spines on apex. Maxilla 2, inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 1-2 naked setae, and 6 plumose setae extending from inner margin to apex: outer plate with about 5 slender pectinate spines and row of naked setae on inner margin. 1 apical plumose setae: dactyl with 2 setae (rarely 4 setae) on inner margin: dactyl nail very long, about 1/3 length of dactyl.

Propod of gnathopod 1 slightly longer than carpus: palm shorter than posterior margin, slightly convex, with about 6 unnotched spine teeth on inside, about 10 on the outside: defining angle with 4 notched-serrate spine teeth on inside, 1 large notched and 2 serrate spine teeth on outside: about 4 superior medial setae, singly inserted: posterior margin with 5 sets of setae in groups of 1-4. Dactyl with 3-4 short setae on inner margin: nail very long. Ventral margin of coxa 1 with 8-9 setae.

Carpus of gnathopod 2 very long, 2/3 the length or subequal in length to propod, with up to 5 sets of setae on posterior margin. Propod of gnathopod 2 palm much shorter than posterior margin, slightly convex, oblique, with about 6 unnotched spine teeth on inside, about 10 on outside: defining angle with 1 large notched spine tooth and 3 notched-serrate spine teeth on inside, 1 large notched and 1 small serrate spine teeth on outside: 5-7 superior medial setae, singly inserted: posterior margin with 4 sets of setae in groups of 1-4. Dactyl with 4-5 short setae on inner margin. Ventral margin of coxa 2 with 8 setae.

Coxa of pereopod 3 with 7 marginal setae. Coxa of pereopod 4 with 16 marginal setae, dactyl of pereopod 4, 45 percent length of corresponding propod. Pereopod 5: basis with 9 serrations along posterior margin; 7-8 short spines on anterior margin: 2 setae on the anteroproximal margin. Pereopod 6: basis with 13 serrations along posterior margin; 6 short spines on anterior margin: 2 setae on anteroproximal margin. Pereopod 7: coxa with 2-3 setae on the posterior margin; basis with 13 slightly deep serrations along posterior margin; 4 short spines and 2 short setae on anterior margin: dactyl about 33 percent the length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner strongly produced and acute; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corners strongly produced and acute, ventral margin with 2-3 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner strongly produced and acute, ventral margin with 2-3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

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Uropod 1: inner ramus 70 percent length of peduncle, armed with 12 spines; outer ramus with 12 spines; peduncle with 5-8 outer and 4 inner spines. Uropod 2: inner and outer ramus each armed with 12 spines; peduncle with 4 outer and 5 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.8-2.0 times longer than peduncle, inner and outer margin each with 3-4 set of spines in groups 1-2. Telson about as broad as long, notched about 1/4-1/2 distance to base, each lobe with 2-3 apical spines; spines less than 1/2 length of telson.

Male.—Differing from female as follows, smaller with more slender, elongate body. Antenna 2: calceoli percent on peduncular segments 4 and 5, and first 2 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus: palm slightly shorter than posterior margin, slightly oblique, almost straight, 10 spine teeth on inside, 10 on outside: defining angle with 4-5 notched-serrate and 1-2 serrate spine teeth on inside, 1 small and 1 large notched spines and 2 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm margin strongly oblique, convex, slightly shorter than posterior margin, with 13 spine teeth on inside, 15 on outside: defining angle with 4 notched and 2 serrate spine teeth on inside: 2-3 large notched and 1 small serrate spine teeth on outside.

Uropod 2: inner ramus with 11 spines; outer ramus deflected laterally with inner row of comb spines on distal half to two-thirds, outer margin with 5 spines, apex with 3 spines; peduncle with 3 outer and 3-4 inner spines.

Variation.—The row of comb spines on the outer ramus of uropod 2 of mature males extends from the apex and covers 1/3 to 2/3 of the length of the ramus. The distoposterior corners of pleonal plates 1-2 vary from just slightly produced and acute in inland populations to strongly produced and acute in coastal plain populations.

Distribution and ecology.—This species is widely distributed in the eastern and east-central United States, occurring as far west as central Kansas (fig. 136).

*C. floridanus* inhabits swamps, ponds, streams, and occasionally cave pools. Specimens from caves in Florida have comparatively smaller (degenerate) eyes. Sexually mature males, 3.0 to 8.0 mm; sexually mature females 5.0-10.0 mm. Ovigerous females have been collected during the months of February through October, thus indicating that breeding possibly occurs the year around (Holsinger, 1972).

Remarks.—The specimens examined from Colorado and Oregon are morphologically similar to the eastern populations, but their natural occurrence there is questionable and it is likely that they are introduced populations. Specimens of this species were also found in Japan (2 ♂, 2 ♀, pond, Furotone, Chiba Prefecture, Japan, 30 Jan 1992, H. Kusano) and sent to Dr. Holsinger by Dr. Hiroshi Morino, Ibaraki University, Japan. They were examined by me in this study. The Japanese population is undoubtedly an introduction (See discussions in Chapter V).
Crangonyx pseudogracilis Bousfield

Figures 137-141


Eucrangonyx gracilis (Smith).—Hynes, 1951:152.

Material examined.—ONTARIO. French River, 1 ?., 3 juvs, N. Hynes, 29 Jul 1975 (USNM); Napanee River at Napanee, Lennox & Addington Co., 3 ? paratypes (NMC 2107), 9 Jun 1950; Rideau River, below Hog's Back, Ottawa, 1 ?., E. L. Bousfield, 12 May 1956 (NMC); QUEBEC. Ottawa River (Hull Park), 2 ?., F. Johansen, 6 Jul 1919, Lake St. Louis Perrot, 2 ?., 1 ?, J. S. Bleakeny, 28 Aug 1955 (USNM) and Ile Perrot, quarry pond, 1 ?., 1 ?.; 28 Aug 1955 (NMC). ALABAMA. Greene Co.: roadside ditch, 1.3 km N of Boligee, 100 specs (?., ?), 11 Feb 1962 (USNM). ARKANSAS. Arkansas Co.: slough, 4.3 km ENE of Humphreys, 7 ?., 6 ?., L. Hubricht, 7 Apr 1941 (USNM); Ashley Co.: Chemin-a-Haut creek just N of Hamburg, 5 ?., J. E. and M. R. Cooper, 16 Mar 1967; roadside ditch, 8.0 km SW of Hamburg on US 82, 1 ?., 1 ?, J. E. and M. R. Cooper, 16 Mar 1967; ditch on Ark Hwy 133, 1.3 km S of Crossett Experimental Forest, 2 ?., J. E. and M. R. Cooper, 16 Mar 1967; Calhoun Co.: small stream, 5.9 km S of Thornton, 14 ?., 6 ?, L. Hubricht, 8 Apr 1941 (USNM); Conway Co.: temporary pool, 3.7 km SE of Menifee, 3 May 1940 (USNM); Cross Co.: temporary pool, 3.7 km N of Cherry Valley, 2 ?., 15 ?., L. Hubricht, 6 Apr 1941 (USNM); Dallas Co.: slough, 3.2 km NE of Fordyce, 1 ?., L. Hubricht, 7 Apr 1941 (USNM); Faulkner Co.: temporary stream, 1.0 km S of Wooster, 30 specs (?., ?), L. Hubricht, 3 May 1940 (USNM); Garland Co.: Bear Spring at Bear, 15 ?., H. W. Robison, 15 Sep 1979; Grant Co.: unnamed stream on dirt Road, 20 ?., 3 ?., R. Fox, 27 Dec 1970; Jefferson Co.: slough, 6.9 km NE of Altheimer, 20 ?., 5 ?, L. Hubricht, 7 Apr 1941 (USNM); Arkansas River, backwater at Tarr Camp, ca. 11.2 km E of Redfield, 2 ?, R. Fox, 21 Dec 1970; stream, 1.6 km W of Jefferson on Jefferson-Sheridan Rd, 10 ?., 5 ?., R. Fox, 21 Dec 1970; small creek, 0.8 km S of Locust Cottage, 40 specs (?., ?), L. Hubricht, 11 Apr 1936 (USNM); Johnson Co.:
Figure 137.—*Crangonyx pseudogracilis* Bousfield. Female (7.9 mm). Lake St. Louis. Perrot. Quebec. Canada: a, b. antennae 1, 2; c, d. gnathopods 1, 2 (palmar margins enlarged).
Figure 138.—*Crangonyx pseudogracilis* Bousfield. Female (7.9 mm), Lake St. Louis, Perrot, Quebec, Canada: a. b. maxillae 1, 2: c. lower lip: d. dentate part of left mandible: e. right mandible: f. left half of maxilliped (greatly enlarged).
Figure 139.—*Crangonyx pseudogracilis* Bousfield. Female (7.9 mm). Lake St. Louis. Perrot. Quebec, Canada: a. c. d. pereopods 3, 5, 6 (in part); b. e. pereopods 4, 7; f. pleonal plates; g. h. i. uropods 1, 2, 3; j. telson.

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Figure 140.—Crangonyx pseudogracilis Bousfield. Male (5.0 mm), Lake St. Louis, Perrot, Quebec, Canada: a. b. gnathopods 1, 2 (palmar margins enlarged); c. pereopod 7; d. e. f. uropods 1, 2, 3; g. telson.
Figure 141.—Distribution of *Crangonyx pseudogracilis* in North America. Solid circles represent 1-5 closely proximate localities. The dotted lines indicate approximate southern extent of glaciation during the Pleistocene and also enclose pockets of alpine glaciation in the west. Question marks indicate tentative identifications. Note three isolated (questionable) locality records in western US.
small creek. W of the College Chapel, Clarksville. 50 specs (♀, ♂), L. Hubricht, 28 Apr 1936 (USNM):
Lawrence Co.: roadside ditch. 1.0 km W of Hoxie, 100 specs (♀, ♂), L. Hubricht, 6 Apr 1941 (USNM):
Monroe Co.: slough. 1.8 km N of Holly Grove, 70 specs (♀, ♂), L. Hubricht, 7 Apr 1941 (USNM):
Newton Co.: large spring near Willcockson, 1♀. L. Hubricht, 8 Apr 1939 (USNM):
intermittent stream ca. 100 m N of intersection of St Rds 24 and 36B, 2♀, 4♂. R. Fox and Bartlett, 26 Dec 1970:
Ouachita Co.: White Oak Creek at St Rd 24 bridge ca. 6.4 km W of Chidester. 6♀, 10♂. R. Fox and Bartlett, 26 Dec 1970:
Bragg Lake on St Rd 24 between Bragg City and Chidester. 17♀, 4♂. R. Fox et al., 26 Dec 1970:
Perry Co.: temporary pool. 8.8 km N of Barton, 50 specs (♀, ♂), L. Hubricht, 6 Apr 1941 (USNM):
slough. 0.8 km SE of Turner. 30 specs (♀, ♂), L. Hubricht, 7 Apr 1941 (USNM): Pulaski Co.: Clear Creek
at St Rd 365 bridge. 2.4 km N of intersection with US-65. 20 specs. R. Fox, 27 Dec 1970:
stream crossing St Rd 365 ca. 4.8 km N of intersection with US-65. 50 specs (♀, ♂), R. Fox, 27 Dec 1970:
Union Co.: temporary pool. 2.9 km N of Eldorado, 30 specs. L. Hubricht, 8 Apr 1941 (USNM):
Yell Co.: temporary pool. 0.6 km W of Danville. 1♀, 5♂. L. Hubricht, 5 Apr 1940 (USNM):
KENTUCKY. Laurel Co.: slough. 1.8 km N of Lily, 100 specs.. L. Hubricht, 24 Apr 1941:
Little Laurel River, 11♀, 12♂. R. Fox, 11 Dec 1970:
3♀, 2♂. J. N. Carpenter, 20 Jan 1968:
LOUISIANA. Avoyelles Par.: (habitat not given), 6 juvs. J. P. Newman, 29 Jul 1975:
2 juvs. 5 Aug 1975, 3 juvs. 11 Sep 1975 and 1♀, 1♂, 13 Oct 1975:
Pointe Coupee Par.: roadside pool. 3.2 km E of Lottie, 50 specs (♀, ♂), L. Hubricht, 12 Apr 1964 (USNM):
Lincoln Par.: temporary pool. 1.6 km E of Choudrant. 16♀, 6♂. L. Hubricht, 8 Apr 1941 (USNM):
slough. 1.4 S of Dubach. 27♀.
L. Hubricht, 8 Apr 1941 (USNM):
Morehouse Par.: Chemin-a-Haut St.Pk., 12♀. 1♂. J. E. and M. R. Cooper, 15 Mar 1967:
ditch on US Hwy 165, ca. 6.2 km SW Bastrap. 3♀. J. E. and M. R. Cooper, 15 Mar 1967:
Natchitoches Par.: small stream, 3.2 km S of Saline. 20♀, 1♂. L. Hubricht, 12 Apr 1936 (USNM):
Orleans Par.: roadside ditch on side of Haynes Blvd. 4.5 km S of juct US 90, 1♀. L. Fleming, 29 Nov 1970:
Ouachita Par.: slough. 4.8 km S of Swartz, 150 specs (♀, ♂). L. Hubricht, 8 Apr 1941 (USNM):
ditch on St Rd 553 near Lamkin, 6♀, 2♂. J. E. and M. R. Cooper, 13 Mar 1967:
small ditch. 3.7 km NW of Monroe. 4♀, 3♂. J. E. and M. R. Cooper, 25 Dec 1965:
borrow pit behind levee of Ouachita R., 3♀, 4♂. L. Hubricht, 8 Apr 1941 (USNM):
St. Tammany Par.: temporary pond. 35♀, 4♂. W. Moore, 18 Feb 1967 (USNM):
Union Par.: Lake D'Arbonne, 3♀. J. E. and M. R. Cooper, 14 Mar 1968:
New Orleans, 6♀, 1♂. N. E. Hubert, (collection date not given) (USNM).
MICHIGAN. Calhoun Co.: swamp near Kalamazoo River. Urbandale, Battle Creek, 19♀, 11♂. L. Hubricht, 7 Jun 1947 (USNM):
Wayne Co.: ditch. 0.8 km E of Melvindale. 1♀, 1♂. L. Hubricht, 24 Mar 1946 (USNM). MINNESOTA.


Oklahoma. Cherokee Co.: unnamed spring, ca. 13.6 km S of Talequah, 1♀, 1♂. J. J. Hoover and W. B. Milstead, 22 May 1981 and 2 specs. 4 Jun 1982; Johnston Co.: Cummings Spring, ca. 0.8 km N of Connerville, 1♀, 2♂. J. J. Hoover and W. B. Milstead, 14 Jun 1982; Mayes Co.: unnamed spring, ca. 0.3 km N of Locust Grove, 6♀, 1♂. J. J. Hoover and W. B. Milstead, 20 May 1981 and 11♀, 6♂, 2 juvs. J. J. Hoover and W. B. Milstead, 3 Jun 1982; McIntosh Co.: slough of Canadian River S of Eufaula, 3♂. L. Hubricht, 10 May 1940 (USNM); Pushmataha Co.: Lily Lake, 3.2 km N of Antlers. 9♀, J. G. Mackin, 2 May 1935 (USNM); Osage Co.: Doddy Miller Spring, ca. 12.0 km NE of Barnsdall, 3♀, J. J. Hoover and W. B. Milstead, 1 Jun 1981 and 2♀, 1 Jun 1982. TENNESSEE. Lake or Obion Co.: Edge sawgrass. Reelfoot Lake, 1♀. V. C. Sheffoed, 9 Apr 1943 (USNM) and 1♀, J. and W. Rapp, 12 Apr 1946 (USNM).

O 1.6 km W of Wolfram Rd., 5 ♂, 6 ♀. 2 Juvs. J. P. Jass. 20 Sep 1994 (MPM): Fond Du Lac Co.: Long
at County Trunk Highway F. near Silverl. 7 ♂, 1 ♂. J. P. Jass and B. Klausmeier. 6 May 1994 (MPM):
Rock Co.: near Fulton Rock River trib. at Gibbes Lake Road. 1 ♂. J. P. Jass & B. Klausmeier. 10 Jan 1994
(MPM): Walworth Co.: trib. of Mukwonago River at county trunk highway. 3 ♂. 1 ♂. J. P. Jass and B.
P. Jass and B. Klausmeier. 7 Oct 1994 (MPM): Green Lake boatlanding, W shore. 3 ♂. 1 ♀. 5 Juvs. J. P.

Diagnosis.—A member of the gracilis group morphologically closely similar to C. floridanus.
Distinguished from other members of the group by large eyes; strongly produced distoposterior corners of
pleonal plates 1-2: comb spines on outer ramus of uropod 2 of male. Further distinguished by having
special ventral spines on inner margin of outer ramus of male uropod 2 (unique among species of
Crangonyx). Largest male. 6.5 mm; largest female. 10.5 mm.

Female.—Eye large and ovate. Antenna 1. 55-57 percent length of body. about 1.8 times longer than
antenna 2: primary flagellum with about 20 segments. Antenna 2, flagellum with 6-8 segments. Mandibles
subequal. spine row with 5-6 spines; segment 2 of palp with 6 long setae. segment 3 with 1 A seta. 2-3 C
setae. 4 E setae and a row of D setae. lacking B seta. Maxilla 1: inner plate with 6 apical plumose setae:
palp with 5-6 slender spines on apex. Maxilla 2. inner plate with oblique row of 6-7 plumose setae on inner
margin. Maxilliped: inner plate apically with 4 bladelike spines. 1 plumose spine. 2 naked spines. and 5-6
plumose setae extending from inner margin to apex; outer plate with row of naked setae and 4-6 slender
pectinate spines on inner margin; dactyl with 2 setae on inner margin near nail; dactyl nail very long. about
1-3 length of dactyl.

Propod of gnathopod 1 slightly larger and longer than carpus; palm almost straight with 5 unnotched
spine teeth on inside, 8 on the outside; defining angle with 5 notched-serrate spine teeth on inside. 1 large
notched and 2 small serrate spine teeth on outside: inferior and superior medial setae singly inserted; setae
on posterior margin singly or doubly inserted. Dactyl with a row of short setae on inner margin. nail long.
Ventral margin of coxa 1 with 7 setae.

Propod of gnathopod 2: slightly larger than carpus; palm almost straight, much shorter than posterior
margin, with about 3 unnotched spine teeth on inside, 5 on outside; defining angle with 1 very large
notched spine tooth and 2 serrate spine teeth on outside. 1 large and 3 small notched-serrate spine teeth on
inside: superior medial setae singly inserted; posterior margin with 5-6 sets of setae in groups of 1-6.
Dactyl with row of short setae on inner margin. Ventral margin of coxa 2 with about 8 setae.

Coxa of pereopod 3 with about 11 marginal setae. Coxa of pereopod 4 with about 17 marginal setae.
dactyl of pereopod 4. 45 percent length of corresponding propod. Pereopod 5: basis with about 11 shallow

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta: distoposterior corner produced and acute: posterior margin of plate 2 nearly straight with 1 seta: distoposterior corner strongly produced and acute: ventral margin with 5 (subventral) spines: posterior margin of plate 3 nearly straight with 1 seta: distoposterior corner produced: ventral margin with 4 (subventral) spines: Peduncle of pleopod 1 with 2 retinaculae: lacking setae on outside margin.

Uropod 1: inner ramus 65 percent length of peduncle: armed with 11 spines: outer ramus with 9 spines: peduncle with 6 outer and 3 inner spines: Uropod 2: inner ramus armed with 11 spines: peduncle with 4 outer spines: 2 inner spines: Uropod 3: inner ramus with 1 spines: outer ramus about 2 times longer than peduncle: inner and outer margin each with 3-4 set of spines in groups 1-3: Telson slightly broader than long or as broad as long: notched about 2/5-1/2 distance to base: each lobe with about 3 apical spines: spines up to 1/2 length of telson.

Male.--Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: flagellum with 6 segments: calceoli percent on peduncular segments 4 and 5: and first 4 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus: palm with 9 spine teeth on inside: 11 on outside: defining angle with 6 notched-serrate spine teeth on inside and 3 notched and 2 serrate on outside.

Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm margin strongly oblique: with 11 spine teeth on inside: 11-12 on outside: defining angle with 2-4 notched and 2 weak: notched-serrate teeth on inside and 3-6 notched and/or 1 unnotted spine teeth on outside.

Uropod 2: inner ramus with 12 spines: outer ramus with row of comb spines on distal 2/5 of inner margin: outer margin with 7 spines (not in comb row): inner side also with 1-5 ventral spines on distal half: apex with 2-3 spines: peduncle with 3 outer spines: and 2 inner spines.

Distribution and ecology.--This species is widely distributed in east-central United States and southern Canada (fig. 141): It occurs largely west of the Appalachians: extending approximately from the Great Lakes region south and southwest to Louisiana and Texas: The specimens in populations from eastern Kentucky possess the diagnostic ventral spines on the inner margin of the outer male uropod 2: but occur farther east than most other populations: Although the specimens from Arizona and Nevada are morphologically very similar to the eastern populations: their exact taxonomic species status was not determined in the present study: and their identity remains somewhat questionable.

of surface freshwater habitats as well as two caves in Kentucky. Ovigerous females are collected throughout the year. Sexually mature males are 4.5 to 6.5 mm and sexually mature female are 7.5 to 10.5 mm.

Remarks.—Crangonyx pseudogracilis was introduced into Great Britain, where it identified as C. gracilis (Hynes 1951, 1955a, b). Subsequently, it was found to have invaded and then spread widely in the Netherlands (Pinkster et al., 1980, 1983; Platvoet et al., 1985, 1989). I confirmed the identity of this species in the Netherlands by examination of specimens on loan from the Zoological Museum of the University of Amsterdam from the following localities: stream in Friesland (42°1', 1°'s) and canal in Groningen Province (42°3', 4°'s).

Crangonyx consimilis, new species

Figures 142-145

Material examined (paratypes unless designated otherwise).—ALABAMA. Limesone Co.: Gaston Cave, 33°3', 3°'s, W. B. Jones et al., 5 May 1958; Madison Co.: slough, 4.3 km NW of Gurley, 3°3', L. Hubricht, 12 Apr 1941 (USNM). MISSISSIPPI. Oktibbeha Co.: pond, 5.3 km from Harved Biology Bldg., near Starkville, 1°2', M. J. Harris, 17 Feb 1968. TENNESSEE. Bedford Co.: spring, 4.0 km W of Shelbyville, 200 specs (9°, 9°'s, juvs), L. Hubricht, 1 Jun 1941 (USNM); Cheatham Co.: spring near Good Spring Church, 4.2 km SE of Pleasant, 6°3', L. Hubricht, 31 May 1941 (USNM); Cannon Co.: Davenport Cave spring, 4.0 km S of Woodburg, 1°9', J. R. Holsinger and R. B. Godfrey, 9 Jul 1983; Davidson Co.: Nashville, 4°2', 6°, E. B. Williamson, 3 Mar 1901 (USNM); small stream near Nashville, 9°2', 1°', R. Fleming, 2 Apr 1936 (USNM); Stream, "Fortland", near Shelby Park, Nashville, holotype (3°, ca. 400 spec. (9°, 9°'s, juvs), L. Hubricht, 31 May 1941 (USNM); Spring on Dr. Fort's Farm near Shelby Park, 1°', L. Hubricht, 31 May 1941 (USNM); Shelby Park, Nashville, 10°2', 7°', R. Fleming, 7 Mar 1936 (USNM); Otters Creek, Nashville, 18°3', R. Fleming, 26 Oct 1935 (USNM); Radnor Lake, 1°3', 1°', M. Wright, 5 May 1945 (USNM); Richland Creek, Nashville, 5°2', 2°, R. Fleming, 29 Feb 1936; water cress in spring, Nashville, 8°2', 9°', R. Fleming, 7 Mar 1936; Dickson Co.: Piney River, 8.6 km SW of Dickson, 3°2', 1°', L. Hubricht, 11 Sep 1955 (USNM); spring, 2.1 km E of Charlotte, 30 specs (9°, 9°'), L. Hubricht, 11 Sep 1955 (USNM); Maury Co.: springs, 3.7 km SW of Spring Hill, 200 specs (9°, 9°'), L. Hubricht, 31 Mar 1941 (USNM); Rutherford Co.: Broyles Cave, 4.0 km N of Beach Grove, 2°2', 21 Aug 1967: Oaklands Spring, Murfreesboro, 80 specs (9°, 9°'s, juvs), C. R. McGhee and L. E. Fleming, 19 Dec 1969; stream in Rainbow Cave, 1°2', L. Hubricht, 1 Jun 1941 (USNM); Stewart Co.: Lost creek spring, Rd. 235, 10 specs (9°, 9°', juvs), D. L. Gillis, 14 Jul 1989; Williamson Co.: small spring, 1.9 km NE of Franklin, 400 specs (9°, 9°', juvs), L. Hubricht, 31 May 1941 (USNM); Wilson Co.: spring, 3.5 km N of Bairds Mill, 100 specs (9°, 9°', juvs), L. Hubricht, 1 Jun 1941 (USNM).
Figure 142.—Crangonyx consimilis, new species. Female paratype (8.5 mm), spring, near Shelby Park, Nashville, Davidson Co., Tennessee: a, b, antennae 1, 2; c, d, maxillae 1, 2; e, lower lip; f, left mandible; g, inner and outer plates and palp dactyl of maxilliped; h, i, gnathopods 1, 2 (palmar margins enlarged).
Figure 143.—*Crangonyx consimilis*, new species. Female paratype (8.5 mm), spring, near Shelby Park, Nashville, Davidson Co., Tennessee: a, head (in part); b, c, d, pereopods 3, 5, 6 (in part); e, pereopod 7; f, pleonal plates; g, h, i, uropods 1, 2, 3; j, telson.

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Figure 144.—*Crangonyx consimilis*. new species. Male paratype (6.4 mm), spring, near Shelby Park, Nashville, Davidson Co., Tennessee: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7; e. g. uropod 1, 3; f. uropod 2 (distal end of outer ramus enlarged); h. telson.
Figure 145.- Distribution of Cryptomyx cosinoides in North America. Solid circles represent 1-9 closely proximate localities.
Diagnosis.—A small species of the gracilis group very similar to *C. longidactylus* but distinguished from it by having fewer subventral spines on pleonal plates and shorter uropod 3. Largest male, 6.7 mm; largest female, 10.0 mm.

Female.—Eye large and ovate. Antenna 1, about 50 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with up to 20 segments. Antenna 2, flagellum with up to 8 segments. Mandibles subequal. Spine row with 5-6 spines: segment 2 of palp with 6 long setae, segment 3 with 1 A seta, 2 C setae, 3 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 8 apical plumose setae; palp with 7 slender spines on apex. Maxilla 2, inner plate with oblique row of 8 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 3 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and slender pectinate spines on inner margin and 2 apical plumose setae; dactyl with 2 setae on inner margin; dactyl nail very long, 1.3 length of dactyl.

Propod of gnathopod 1 less than 2 times larger and longer than carpus; palm almost straight, slightly shorter than posterior margin, with 7 unnotched spine teeth on inside, 8 on the outside; defining angle with 3 notched-serrate spine teeth on inside, 2 large notched and 1 small serrate spine teeth on outside; superior medial setae few in number, singly inserted: 4 sets of setae on posterior margin, singly inserted or in groups of 2: dactyl with long nail. Ventral margin of coxa 1 with 18 setae.

Propod of gnathopod 2 less than 2 times larger and longer than carpus; palm slightly convex, shorter than posterior margin, with 6 unnotched spine teeth on inside, 7 on outside; defining angle with 2 notched and 1 notched-serrate spine teeth on inside, 2 large notched spine teeth on outside; superior medial setae singly inserted, posterior margin with 6 sets of setae in groups of 2-6. Ventral margin of coxa 2 with 14 setae.

Coxa of pereopod 3 with 12-14 marginal setae. Cox of pereopod 4 with 18 marginal setae, dactyl about 35 percent length of corresponding propod. Pereopod 5: basis with 11 shallow serrations along posterior margin; 7 sets of short spines on anterior margin; 1 long seta on anteroproximal margin. Pereopod 6: basis with 12 serrations along posterior margin; 6 short spines on anterior margin; 1 seta on anteroproximal margin. Pereopod 7: coxa with 3-4 setae on the posterior margin; basis with 17 slight serrations along posterior margin; 8 short spines on anterior margin; dactyl about 33 percent length of corresponding propod. Pleonal plates: posterior margin of plate 1 slightly convex, with 3 setae, distoposterior corner produced and acute, ventral margin with 1-2 (subventral) spines; posterior margin of plate 2 slightly convex with 2 or 3 setae, distoposterior corner strongly produced and acute, ventral margin with 4 (subventral) spines; posterior margin of plate 3 nearly straight with 1-3 setae, distoposterior corner not produced but weakly acute, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae; 1 'eking setae on outside margin.

Uropod 1: inner ramus 70 percent length of peduncle, armed with 10 spines; outer ramus with 10 spines; peduncle with 10 outer spines, and 1 inner spines. Uropod 2: inner ramus armed with 11 spines;
peduncle with 5 outer spine, 2 inner spines. Uropod 3: inner ramus lacking spines, outer ramus about 1.5 times longer than peduncle. inner and outer margin each with 2-3 set of spines in groups of 2-3. Telson slightly broader than long, notched about 1/3 distance to base. each lobe with 3 apical spines: spines about 1/2 length of telson.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli percent on peduncular segments 4 and 5 and first 3 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus: palm with 8 spine teeth on inside. 9 on outside: defining angle with 1 notched spine tooth and 4 notched-serrate spine teeth on inside. 2 notched and 1-2 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus: palmar margin strongly oblique, with 8 spine teeth on inside. 9 on outside: defining angle with 3 notched and 1 serrate spine teeth on inside. 5 notched spine teeth on outside.

Uropod 2: inner ramus with 14 spines of unequal length: outer ramus with row of comb spines on distal 1 2-2'3 of inner margin, face of outer margin with 5 short spines: apex with 3-4 spines: peduncle with 3 outer spines, and 2 inner spines.

Type-locality.—Spring near Shelby Park in eastern Nashville. Davidson County. Tennessee.

Distribution and ecology.—This species is widely distributed in central Tennessee and also occurs in northern Alabama and east-central Mississippi (fig. 145). Ovigerous females were collected from March to September and in December, suggesting that breeding is continuous throughout the year. Sexually mature males are 3.5 to 6.7 mm and sexually mature females are 5.0 to 10.0 mm.

Etymology.—The epithet *consimilis* is from Latin, meaning "like in all respects." in reference to the similarity of this species to other members of the *floridanus* subgroup.

*Crangonyx longidactylus*, new species

Figures 146-149


Diagnosis.—Closely similar to *C. consimilis* but distinguished from it by defining angle of propod of gnathopod 2 with very large spine tooth at end: more subventral species on pleonal plates: longer uropod 3: and small comb spines on outer ramus of uropod 2 of male. Largest male 5.5 mm: largest female 9.0 mm.

Female.—Eye large and ovate. Antenna 1, 53-55 percent length of body, about 1.8-2.0 times longer than antenna 2; primary flagellum with 20 segments. Antenna 2, flagellum with 8 segments. Mandibles
Figure 146.—Crangonyx longidactylus, new species. Female paratype (9.0 mm), swale, 1.6 km E of Bonayr, Barren Co., Kentucky: a. head (in part); b. antenna I; c, d. maxillae I, 2; e. lower lip; f. dentate part of left mandible; g. right mandible; h. inner, outer plates and palp dactyl of maxilliped (greatly enlarged); i, j. gnathopods 1, 2 (palmar margins enlarged).
Figure 147.—*Crangonyx longidactylus*, new species. Female paratype (9.0 mm), swale, 1.6 km E of Bonayr, Barren Co., Kentucky: a, c, d, pereopods 3, 5, 6 (in part); b, e, pereopods 4, 7; f, pleonal plates; g, h, i, uropods 1, 2, 3; j, telson.
Figure 148.—Crangonyx longidactylus, new species. Male paratype (5.0 mm), swale, 1.6 km E of Bonayr, Barren Co., Kentucky: a. antenna 2; b, c, gnathopods 1, 2 (palmar margins enlarged); d, pereopod 7; e: dactyl of pereopod 5; f, g, h, uropods 1, 2, 3 (comb spine on outer ramus of uropod 2 enlarged); i, telson.
Figure 149.--Distribution of *Tragopogon longidactylus* in North America. Solid circles represent single localities.
subequal, spine row with 4-5 spines: segment 2 of palp with 11 setae, segment 3 with 1 A seta, 2 C setae. 3-4 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 8 apical plumose setae: palp with 6-7 slender spines on apex. Maxilla 2, inner plate with oblique row of 7 plumose setae on inner margin. Maxilliped: inner plate apically with 4 bladelike spines. 1 naked spine, and 5-6 plumose setae extending from inner margin to apex: outer plate with row of naked setae and 5-6 pectinate spines on inner margin: dactyl with 2 setae on inner margin near nail; dactyl nail long, 1/3 length of dactyl.

Propod of gnathopod 1: propod less than 1.5 times larger and less than 2 times longer than carpus: palm almost straight, slightly shorter than posterior length, with 6 unnotched spine teeth on inside, 8 on the outside; defining angle with 5 small notched-serrate spine teeth on inside, 1 large notched and 3 small serrate small spine teeth on outside; superior medial setae few in number, singly or doubly inserted; about 7 sets of setae on posterior margin, singly inserted or in groups of 2-3. Dactyl with row of 4-5 short setae on inner margin, nail about 1/3 length of dactyl. Ventral margin of coxa 1 with 9 setae.

Propod of gnathopod 2 less than 1.5 time larger and less than 2 times longer than carpus: palm almost straight or slightly oblique, shorter than posterior margin length, with 5 unnotched spine teeth on inside, 6 on outside; defining angle with 1 notched and 3 notched-serrate spine teeth on inside; 3 unnotched and 1 large notched spine teeth on outside; superior medial setae singly inserted; posterior margin with 6 sets of setae in groups of 2-8. Ventral margin of coxa 2 with 9 setae.

Coxa of pereopod 3 with 9 marginal setae. Coxa of pereopod 4 with 20 marginal setae. Dactyl of pereopod 4, 45 percent length of corresponding propod length. Pereopod 5: basis with 14 shallow serrations along posterior margin; 8 short spines on anterior margin; 2 long setae on anteroproximal margin. Pereopod 6: basis with 11 serrations along posterior margin: 9 short spines on anterior margin: 3 long setae on anteroproximal margin. Pereopod 7: coxa with 3 setae on the posterior margin: basis with 19 shallow serrations along posterior margin: 6 short spines on anterior margin: 1-2 long setae proximally on anterior margin: dactyl long and thin, about 35 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner produced and acute, ventral margin with 1 (subventral) spine; posterior margin of plate 2 nearly straight with 2 or 3 setae; distoposterior corner strongly produced and acute, ventral margin with up to 9 (subventral) spines in 2 rows; posterior margin of plate 3 nearly straight with 2 setae, distoposterior corner weakly produced and subacute, ventral margin with 6 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus 70 percent length of peduncle, armed with 10 spines: outer ramus with 11 spines: peduncle with 8 outer and 2 inner spines. Uropod 2: inner ramus armed with 12 spines; outer ramus with 10 spines; peduncle with 4 outer and 4 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.9 times longer than peduncle, inner and outer margin each with 3-4 sets of spines in groups 1-3. Telson as broad as long, notched about 1/4 distance to base, each lobe with 3-4 apical spines.

Male.--Differing from female as follows. Smaller with more slender, elongate body. Antenna 2:
calceoli present on peduncular segments 4 and 5, and first 4 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus: palm slightly convex and oblique, with 11 spine teeth on inside, 11 on outside: defining angle with 4 serrate teeth on inside, 1 notched and 2 serrate on outside. Propod of gnathopod 2 more than 2 times larger and longer than carpus: palm margin strongly oblique, slightly convex, with 12 spine teeth on inside, 14 on outside; defining angle with 4 notched and 1 notched-serrate spine teeth on inside and 4 spine teeth on outside.

Uropod 2: inner ramus with 12 spines: outer ramus with inner row of comb spines on distal 1-2-2-3, outer margin with 7 spines, apex with 3 spines; peduncle with 3 outer and 3 inner spines.

Type-locality.—A swale. 1.6 mm E of Bonayr, Barren County, Kentucky.

Distribution and ecology.—The range of this species, which is highly disjunct, is based on 3 localities in south-central Kentucky and 1 in southwestern North Carolina (fig. 149). It covers a linear distance of about 320 km.

*C. longidactylus* inhabits a swale, a cave spring and two reservoirs. One ovigerous female was found in a March collection. In its type-locality, this species was associated with *C. richmondensis*. The specimens from the cave spring were lightly pigmented when alive.

Etymology.—The epithet *longidactylus* combines the "long" and "dactyl," in reference to the elongate dactyls of pereopods 5-7.

Species Unassigned to Groups

The eight species treated below have not been assigned to species groups pending further study. Three of them — *Crangonyx serratus*, *C. specus* and *C. antennatus* — have probable affinities with each other. The other five species — *C. orientalis*, *C. cooperi*, *C. lewisi*, *C. fontinalis* and *C. housfieldi* — have affinities with each other and may collectively constitute a species group.

*Crangonyx serratus* (Embody)


Figure 150.—*Crangonyx serratus* (Embody). Female (14.5 mm), small stream 0.5 km SW of Tabb, York Co., Virginia: a. antenna 1; b, c, maxillae 1, 2; d, left mandible; e, dentate part of right mandible; f, inner and outer plates and palp dactyl of maxilliped (greatly enlarged); g, h, gnathopods 1, 2 (palmar margins enlarged).
Figure 151.—*Crangonyx serratus* (Embody). Female (14.5 mm), small stream 0.5 km SW of Tabb. York Co., Virginia: a, b, c, pereopods 4, 5, 6 (in part); d, pereopod 7; e, pleonal plates; f, g, h, uropods 1, 2, 3; i, telson.
Figure 152.—*Crangonyx serratus* (Embody). Male (9.9 mm), small stream 0.5 km SW of Tabb, York Co., Virginia: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. e. f. uropods 1, 2, 3; g. telson.
Figure 153.—Distribution of *Crangonyx serratus* in North America. Solid circles represent 1-5 closely proximate localities. The dotted line denotes the "fall line" or "fall zone" between the Coastal Plain and Piedmont.

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Stevenson. 10 Sep 1992; Turkey Track Creek. 7 km NW of Bowling Green. Ft. A. P. Hill. 1 ♂, P. H.
Stevenson. 10 Sep 1992; tributary to Permansend Creek. 1 ♂, 1 ♀. P. H. Stevenson. 19 Apr 1993; seepage
0.8 km ESE of Broadus. 3 ♂, 2 ♀. P. H. Stevenson. 12 Apr 1993; Chesapeake (Norfolk County): Jericho
Ditch near Lake Drummond. 4 ♂, 5 ♀. D. H. Hawland, 28 Mar 1972; Washington Ditch at merger with
Lake Drummond in Dismal Swamp. 36 specs (♂, ♀, juveniles). J. R. Holsinger. 5 Oct 1986; Greensville Co.:
steep, narrow, swamp stream. 3.7 km S of Sussex Co. line on Rt. 301. 1 ♂. L. Hubricht. 1 Apr 1950 (USNM):
spring-fed pond near Ashland. 2 cotype ♀, Ashland. G. E. Embody. 11 Mar 1908 (USNM 40828) and 2 ♂.
16 Mar 1909, (collector not given) (USNM); Isle of Wight Co.: cypress swamp. 3.2 km NE Zuni. 4 ♂. R.
L. Hoffman. 6 Apr 1947 (USNM); Courthouse pond. 2 juveniles. R. Bray. 7 Jun 1938 (USNM); seeps 3.2 km
SE of Bartlett. 1 ♂. L. Hubricht. 2 Apr 1944; Nansemond Co.: Jericho Ditch. 2.1 km SW of Magnolia. 7 ♂,
1 juvenile. L. Hubricht. 30 Apr 1944 (USNM); Lake Drummond in Dismal Swamp. 1 ♂. C. R. Shoemaker. 29
May 1922 (USNM); Parkers Pond. Suffolk. 2 ♂. R. Bray. 24 Mar 1940 (USNM): stream in swamp. 2.4
km NE of Saunders. 14 ♂, 7 ♂. L. Hubricht. 21 Nov 1943 (USNM); small stream in swamp. 6.4 km W of
Suffolk. 33 ♂, 18 ♂. L. Hubricht. 12 Nov 1944 (USNM); Waleyville. 1 ♂. R. Bray. 22 Mar 1940 (USNM):
Norfolt Co.: roadside ditch. Bowers Hill. 9 ♂, 15 ♂. L. Hubricht. 25 Feb 1945 (USNM); roadside ditch.
4.0 km WSW of Bowers Hill. 13 ♂, 9 ♂. L. Hubricht. 21 Nov 1943 (USNM); ditch in Dismal Swamp. 3.2
km S of Bowers Hill. 22 ♂, 5 ♂. L. Hubricht. 14 Nov 1943 (USNM); stream in swamp. 3.2 km S of North
Landing. 5 ♂, 2 ♂. L. Hubricht. 9 Apr 1944 (USNM); stream in swamp. 4.8 km S of North Landing. 1 ♂.
L. Hubricht. 9 Apr 1944 (USNM); Northwest River. 1 ♂. L. Hubricht. 25 Mar 1945 (USNM);
R. Bray. 22 Mar 1940 (USNM): Suffolk (Nansemond County). seep in marsh area in ravine leading to
Murphys Pond ca. 4.8 km NW of Suffolk. 1 ♂. J. R. Holsinger. 1 Apr 1984: pond at Virginia Tech
agriculture center. Holland. 1 juvenile. C. Frew. Jun 1992; Sussex Co.: Blackwater River 6.4 km N of
Wakefield. 3 ♂. L. Hubricht. 14 Oct 1945 (USNM): Southwest swamp on Rt. 301 just S of Stony Creek. 3
♂, J. E. and M. E. Cooper. 3 Jan 1965; Warwick Co.: swamp. 0.8 km NE of Harpersville. 2 ♂, 17 ♂. L.
Hubricht. 23 Jan 1944 (USNM); York Co.: small stream 0.5 km SW of Tabb. 5 ♂, 9 ♂. L. Hubricht. 23 Jan
(USNM), 2 juveniles. A. Pizzini. 25 Jun 1938 (USNM) and 1 ♂. 12 Mar 1941 (USNM). 3 ♂, 2 ♂. W. H. Ball.
20 Jan 1934 (USNM) and 1 ♂. 1 ♂. H. S. Barber and C. R. Shoemaker. 10 Apr 1926 (USNM).

Diagnosis.—A relatively large species easily distinguished from all other species of the genus by
having very deep serrations along posterior margins of bases of pereopod 5-7; very long and deeply
notched telson with mid-dorsal spines; peduncle of uropod 2 of male with unique apical process (not seen
in any other species of Crangonyx); and posterior margins of carpus of gnathopods 1 and 2 with strongly
developed rastellate setae (not seen in any other Crangonyx but similar to those of Stygobromus). Largest
male, 11.0 mm; largest female, 16.0 mm.
Female.—Eye small and round. Antenna 1. about 50 percent length of body, about 2 times longer than antenna 2; primary flagellum with up to 28 segments. Antenna 2. flagellum with up to 11 segments. Mandibles subeual, spine row with 4-6 spines; segment 2 of palp with 11-12 long setae. segment 3 with 3 A setae. 2-3 B setae. 3 C setae. 5-6 E setae and a row of D setae. Maxilla 1: inner plate with 5 apical plumose setae; palp with 7 slender spines on apex. Maxilla 2. inner plate with oblique row of 5 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines. 1 naked spine. and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and about 6 slender bladelike spines on inner margin: dactyl inner margin with 1-2 setae near nail; dactyl nail very short.

Propod of gnathopod 1 about 2 times longer than carpus: propod palm little convex. much longer than posterior margin. with 16 spine teeth on inside. 18 on the outside; defining angle with 6 serrate spine teeth on inner side. 2 small and 1 large notched and 4 serrate spine teeth on outside: superior medial setae few in number and inserted in groups of 2-3; posterior margin with about 4 sets of setae inserted in groups of 1-5. Dactyl with a row of 11 short setae on inner margin. outer margin with up to 8 setae; dactyl nail very short. Posterior margin of carpus of gnathopod 1 short, with rastellate setae. Ventral margin of coxa 1 with 9 setae.

Propod of gnathopod 2 about 2 times longer than carpus: palm convex. oblique. much longer than posterior margin. with 17 spine teeth on inside. 18 on outside; defining angle with 6 spine teeth on outside (the last one very large), 3 small spine teeth on inside; inferior medial setae singly or doubly inserted: superior medial setae singly inserted: posterior margin with 5-6 sets of setae inserted in groups of 3-5. Dactyl with row of up to 16 short setae along inferior margin. outer margin with up to 8 setae; dactyl nail very short. Posterior margin of carpus of gnathopod 2 very short. with rastellate setae. Ventral margin of coxa 2 with 7 setae.

Coxa of pereopod 3 with 12 marginal setae. Coxa of pereopod 4 with 18 marginal setae. dactyl of pereopod 4 about 40 percent length of corresponding propod. Pereopod 5: basis with 13 very deep serrations on posterior margin: 9 sets of short spines in groups of 1-2 on anterior margin. Pereopod 6: basis with 15 very deep serrations along posterior margin; 8 sets of short spines on anterior margin. Pereopod 7: coxa with about 6 setae along the posterior margin in deep serrations: basis with 16 very deep serrations along posterior margin; 10 sets of short spines on anterior margin; dactyl about 33 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 convex, with 1 seta. distoposterior corner strongly produced and acute. ventral margin with 2 (subventral) spines; posterior margin of plate 2 nearly straight with 1-2 setae. distoposterior corner strongly produced and acute. ventral margin with 8 (subventral) spines; posterior margin of plate 3 uneven, with 1 seta. distoposterior corner strongly produced. and acute. ventral margin 5 (subventral) spines. Peduncle of pleopod 1 with 2-3 retinaculae. lacking setae on outer margin.

Uropod 1: inner ramus 65 percent length of peduncle. armed with about 13 spines; outer ramus with
about 13 spines: peduncle with 9 outer and 6 inner spines. Uropod 2: inner ramus armed with about 13 spines; outer ramus with about 12 spines; peduncle with row of 5 outer and 6 inner spines. Uropod 3: inner ramus lacking spines, outer ramus about 2 times longer than peduncle, inner and outer margin each with 3-4 set of spines in groups of 2-3. Telson much longer than broad, notched about 2/3 distance to base, each lobe with 3-4 apical spines and 1-3 mid-dorsal spines.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 5 segments of flagellum.

Propod of gnathopod 1 palm with 16 spine teeth on inside, 16 notched spine teeth on outside; defining angle with 3-4 notched and 1 serrate spine teeth on inside and 3 notched and 2 serrate spine teeth on outside. Propod of gnathopod 2: defining angle with 2 spine teeth on inside and 5 notched spine teeth on outside.

Uropod 2: inner ramus with 11 spines; outer ramus much smaller than inner ramus, deflected laterally, with about 9 spines, 4 or 5 closely spaced near apex; peduncle with 4 outer spines, 4 inner spines, and bearing bluntly rounded apical process.

Distribution and ecology.—The range of this species extends from Washington, DC south along the Coastal Plain to northern Florida (fig. 153). *Crangonyx serratus* is an inhabitant of small bodies of water, including ponds, streams, and drainage ditches. Ovigerous female are recorded from November to June (Holsinger, 1972).

*Crangonyx antennatus* Packard

Figures 154-157


Eucrangonyx antennatus Stebbing, 1899:423; 1906:388.

Siphargus antennatus Hay, 1902:430. fig. 6. --Weckel, 1907-36. fig. 6. --Schellenberg, 1936:33

Figure 154. *Crangonyx antennatus* Packard. Female (9.8 mm). Subers Cave, Hancock Co., Tennessee: a, b. antennae 1, 2; c, d. maxillae 1, 2; e, lower lip; f, left mandible; g, inner and outer plates and palp dactyl (greatly enlarged); h, i. gnathopods 1, 2 (palmar margins enlarged).
Figure 155. *Crangonyx antennatus* Packard. Female (9.8 mm). Subers Cave, Hancock Co., Tennessee: a, pereopod 3 (in part); b, c, pereopods 4, 7; d, pleonal plates; e, f, uropods 2, 3. Female (8.0 mm), Secret Cave, Lee Co., Virginia: g, head (in part); h, uropod 1; i telson.
Figure 156.—*Crangonyx antennatus* Packard. Male (10.0 mm). Subers Cave, Hancock Co., Tennessee: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7; e. g. uropods 1, 3; f. uropod 2 (apex of outer ramus enlarged); h. telson.

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Figure 157.--Distribution of _Crangonyx antennatus_ in North America. Solid circles represent 1-10 closely proximate localities.

Diagnosis.—A medium-sized cavernicolous species easily distinguished from other species in the genus by having weakly notched spine teeth on female gnathopods; strongly oblique palms of gnathopod
propods (especially in mature female); end of defining angle of propod of gnathopod 2 of both sexes with 1 very long, large unnotched spine tooth on the outside; pleonal plate 1 with 1-3 subventral spines; and outer ramus of male uropod 2 with 4-5 large comb-like spines on inner side. Largest male, 8.0 mm; largest female, 13.5 mm.

Female.—Eye greatly reduced to few black specks or absent. Antenna 1, about 60 percent length of body, about 1.7 times longer than antenna 2; primary flagellum with up to 29 segments. Antenna 2: flagellum with 8-10 segments, with small calceoli in some larger specimens. Mandibles subequal, spine row with 9 spines; segment 2 of palp with 10-13 long setae, segment 3 with 1 A seta, 5 C setae, 4-5 E setae, and a row of 16 D setae, lacking B seta. Maxilla 1: inner plate with 7-8 apical plumose setae; palp with 6-10 slender spines on apex. Maxilla 2, inner plate with oblique row of 8 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 3 naked setae, and about 8 plumose setae extending from inner margin to apex; outer plate with row of naked setae and about 3-4 slender pectinate spines on inner margin and 2-3 plumose long setae on apex; dactyl with 2 setae on inner margin near nail; dactyl nail long, about 1/3 of length dactyl.

Propod of gnathopod 1 more than 2 times longer than carpus; palm convex and strongly oblique, much longer than posterior margin, with 11 weakly notched long spine teeth on inside. 14 on the outside: defining angle with 1 notched and 3-4 notched-serrate spine teeth on inside, 1 large notched and 1 small simple spine teeth on outside; superior medial setae few in number and singly or doubly inserted: 10(-) inferior lateral setae, singly inserted; posterior margin with 6 sets of setae in groups of 2-4. Dactyl of gnathopod 1 with a row of short setae on inner margin, outer margin with 1-3 setae, nail short. Ventral margin of coxa 1 with 14-16 setae.

Propod of gnathopod 2 more than 2 times longer than carpus; palmar margin almost straight, strongly oblique, more than 2 times longer than posterior margin in mature specimens, with 13 weakly notched, long spine teeth on inside. 14 on outside: defining angle with 3-4 large notched spine teeth on inside, 4-5 small notched spine teeth and 1 very large, long unnotched spine tooth on outside: 8 sets of superior medial setae in groups of 1-3 but mostly with 1 seta each; 6 sets of inferior medial setae in groups of 1-2; posterior margin with 6 sets of setae in groups of 2-6. Dactyl with about 4 short setae along inner margin, up to 4 setae on outer margin. Ventral margin of coxa 1 with 11 setae.

Coxa of pereopod 3 with 14 marginal setae. Coxa of pereopod 4 with 24 marginal setae. Pereopod 5: basis with about 22 shallow serrations on posterior margin; 12 short spines on anterior margin; 3 long setae on the anteroproximal margin. Pereopod 6: basis with 24 shallow serrations along posterior margin; 9 short spines on anterior margin; 3 long setae on anteroproximal margin. Pereopod 7: coxa with 1 seta along the posterior margin; basis with 21 shallow serrations along posterior margin, deeper near apex; 10 short spines on anterior margin; 3 short setae on anteroproximal margin; dactyl about 33 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta. Distoposterior corner not
produced but acute, ventral margin with 1-3 (subventral) spines; posterior margin of plate 2 nearly straight with 1 seta. Distal posterior corner produced and acute. Ventral margin with 4-5 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta. Distal posterior corner small, rounded, not produced. Ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outer margin.

Uropod 1: inner ramus armed with about 13 spines; outer ramus with about 14 spines; peduncle with 9 outer and 1 inner spines. Uropod 2: inner ramus armed with 12 spines; outer ramus with about 10 spines; peduncle with 5 outer and 2 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.9 times longer than peduncle. Inner and outer margin each with 3-4 sets of spines in groups of 1-3. Telson broader than long, notched about 1/3 distance to base, each lobe with 3 apical spines; spines about 1.2 length of telson.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 1 or 2 segments of flagellum.

Uropod 2: inner ramus much wider than outer ramus, with about 13 spines; outer ramus deflected laterally, much smaller than outer ramus. Distal end with 4-5 large comb-like spines on inside and 4-5 short comb-like spines on outside, outside with 4-5 well spaced short spines also; peduncle with 4 outer and 2-3 inner spines. Telson much broader than long.

Variation.—The eye structure is somewhat variable. Eyes are greatly reduced to a few block specks or are completely absent. The presence or absence of eyes may be variable within or between two closely proximate populations. In juveniles and submature females the palmar margin of the gnathopod propods is not oblique and long, and the propod itself is not 2 times larger than the carpus. When specimens become mature, the palm becomes oblique and longer, and the propod becomes larger. The number of subventral spines on pleonal plate 1 varies from 1 to 3, but 1 spine is always present. The number of large comb-like spine on the end of the outer ramus uropod 2 varies, but the spines always appear comb-like.

Distribution and ecology.—This relatively common troglobitic species ranges from the upper Tennessee River drainage basin in Lee, Scott, and Wise counties, Virginia south-southwestward to northeastern Georgia (into the upper Alabama River basin) and west along the Tennessee River valley to northwestern Alabama and extreme southcentral Tennessee; it is also found in the Sequatchie River Valley in Tennessee (fig. 157).

Further details on ecology and natural history are found in Dickson (1977). Dickson and Holsinger (1981) and Dickson (1982).

Crangonyx specus, new species

Figures 158-161

Material examined (paratypes unless designated otherwise).—KENTUCKY. Pulaski Co.: Girdler Cave
Figure 158.—*Crangonyx specus*, new species. Female paratype (7.0 mm). Girdler Cave No.2, Pulaski Co., Kentucky: a, b, maxillae 1, 2; c, lower lip; d, left mandible; e, dentate part of right mandible; f, inner and outer plates and palp dactyl of maxilliped (greatly enlarged); g, h, gnathopods 1, 2 (palmar margins enlarged).
Figure 159. — *Crangonyx specus*, new species. Female paratype (7.0 mm), Girdler Cave No.2, Pulaski Co., Kentucky: a. head (in part); b. antenna 1; c, d, e, pereopods 3, 5, 6 (in part); f, pereopod 7; g. pleonal plates; h, i, uropods 2, 3; j, telson.
Figure 160.—*Crangonyx specus*, new species. Male paratype (4.5 mm). Girdler Cave No. 2, Pulaski Co., Kentucky: a, antenna 2; b, c, gnathopods 1, 2 (palmar margins enlarged); d, e, f, uropods 1, 2, 3; g, telson.
Figure 161.--Distribution of *Crangonyx specus* in North America. Solid circles represent 1-2 closely proximate localities.

Diagnosis.—A relatively small troglobitic species very similar to C. antennatus but distinguished from it by outer ramus of male uropod 2, which has only 1-2 short inner spines and 3 short setal-like outer spines: defining angle of gnathopods 1 and 2 of both sexes with very distinct notched-serrate spines: single seta on dactyl of outer margin of gnathopods: lacking subventral spines on pleonal plate 1: and proportionately shorter uropod 3 in female. Largest male, 4.5 mm; largest female 7.5 mm.

Female.—Eye absent or reduced to few tiny specks. Antenna 1, about 50 percent length of body, about 2 times longer than antenna 2; primary flagellum with about 20 segments. Antenna 2, flagellum with 6-8 segments. Mandibles subequal, spine row with 5-6 spines: segment 2 of palp with 6 long setae, segment 3 with 1 A seta, 2 C setae, 4 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 6 apical plumose setae; palp with 5-7 slender spines on apex. Maxilla 2, inner plate with oblique row of 6 plumose setae on inner margin. Maxilliped: inner plate apically with 3 bladelike spines, 3 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and about 2-3 pectinate slender spines on inner margin; dactyl with 2-3 short setae near nail; dactyl nail very long, about 1.3 length of dactyl.

Propod of gnathopod 1 about two times longer than carpus: palm slightly convex, slightly longer than posterior margin, with 6 notched spine teeth and 1 simple spine tooth on inside; 9 notched spine teeth and 3 simple spine teeth on outside: defining angle with 1 simple spine tooth and 4 notched-serrate spine teeth on inside, 1 large notched and 2 serrate spine teeth on outside: superior medial setae singly inserted; posterior margin with 5 sets of setae in groups of 2-5. Dactyl with 2-3 short setae on inner margin, nail about 1.4 length of dactyl. Ventral margin of coxa 1 with 7-8 setae, some very long.

Propod of gnathopod 2 much wider and more than 2 times longer than carpus: palm convex, oblique, longer than posterior margin, with 9 spine teeth on inside, 13 on outside; defining angle with 2 notched and 1 very long simple teeth and 3 serrate spine teeth on inside, outside with 3 notched and 1 very large simple spine teeth: superior medial setae singly inserted; posterior margin with 5 sets of setae in groups of 3-6. Dactyl lacking setae on inner margin. Ventral margin of coxa 2 with 7 setae.

Coxa of pereopod 3 with 7 marginal setae, 2 very long. Coxa of pereopod 4 with 11 marginal setae. Pereopod 5: basis with 11 very shallow serrations along posterior margin; 7 short spines on anterior margin: 2 long setae on the anteroproximal margin. Pereopod 6: basis with 10 shallow serrations along posterior margin; 7 short spines on anterior margin; 3 long setae on anteroproximal margin. Pereopod 7: coxa with 3 setae on the posterior margin; basis with 11 shallow serrations along posterior margin; 7 short spines on anterior margin; 2 short setae on anteroproximal margin; dactyl about 35 percent length of corresponding propod.

Pleonatal plates: posterior margin of plate 1 convex, with 1 seta, distoposterior corner not produced.
subacute; posterior margin of plate 2 nearly straight with 1-2 setae, distoposterior corner weakly produced and acute. Ventral margin with 3 (subventral) spines; posterior margin of plate 3 convex with 1 seta. Distoposterior corner recessed and indistinct, ventral margin with 2 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus 65 percent length of peduncle, armed with 12 spines; outer ramus with 11 spines; peduncle with 10 outer and 4 inner spines. Uropod 2: inner ramus armed with 12 spines; outer ramus with 10 spines; peduncle with 3 outer and 5 inner spines. Uropod 3: inner ramus with 1 large spine, outer ramus about 1.5 times longer than peduncle, inner and outer margin each with 2-3 set of spines in groups of 1-2. Telson broader than long, notched about 1/6 distance to base, each lobe with 3 apical spines.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 3 segments of flagellum.

Propod of gnathopod 1 palm convex, oblique, with 7 spine teeth on inside. 8 on outside, defining angle with 3 notched-serrate spine teeth on inside. 1 large notched and 2 serrate spine teeth on outside. Propod of gnathopod 2 palm oblique, with 7 spine teeth on inside. 10 on outside; defining angle with 3 notched and 1 notched-serrate spine teeth on inside. 3 notched and 1 very large simple spine teeth on outside.

Uropod 2: inner ramus with 10 spines; outer ramus weakly deflected laterally, with 1-2 short inner spines, and 3 short setal-like outer spines, apex with 5 spines; peduncle with 4 outer and 3-4 inner spines. Uropod 3: inner ramus with 1 spine; outer ramus about 2 times length of peduncle, inner and outer margins each with 3 sets of spines in groups of 1-3. Telson slightly longer than broad, notched about 1/4 distance to base; each lobe with 2 apical spines; spines about 1/2 length of the telson.

Type-locality.—Girdler Cave No. 2, located in Pulaski Co., Kentucky, is a stream passage cave developed in Mississippian-aged limstone. The type specimens were collected from mud-bottom stream pools, where they were relatively abundant (J. R. Holsinger, pers. comm.).

Distribution and ecology.—As presently known, the range of this species is limited to the extreme western margin of the Cumberland Plateau or the eastern margin of the Cumberland Saddle and occupies a small part of the Cumberland River drainage basin (fig. 161). The range, which covers a linear distance of approximately 50 km from north to south, extends from Pulaski County southward to Wayne County.

All collections made to date have been from stream pools except one from a drip/seep pool. In stream pools it was associated with a stygobiont isopod Caecidotea sp., while in drip pools it was taken with the stygobiont amphipod Stygobromus exilis and isopod Caecidotea sp. Ovigerous females have not been collected to date; however, females (size range, 6.5-7.5 mm) with setose brood plates have been collected in October.

Etymology.—The epithet specus is from Latin, meaning "cave" or "den."

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Crangonyx fontinalis, new species

Figures 162-165

Material examined (paratypes unless designated otherwise).—VIRGINIA. Bland Co.: spring on Walker Creek just NW of Hamilton Cave, 22 9, 25 ♂, J. R. Holsinger, 10 May 1965; spring, ca. 300 m N of Repass Salt peter Cave, holotype 9, 35 9, 16 ♂, J. R. Holsinger, 10 May 1965 and 50 ♀, 12 ♂, J. R. Holsinger, 28 Jan 1968.

Diagnosis.—A medium-sized species similar to C. orientalis but distinguished from it by having about 5 evenly distributed spines on inner margin of outer ramus of male uropod 2, lacking serrate spine teeth on propod of male gnathopod 2, setal-like spines on anterior margin of bases of pereopods of male. Largest male, 6.0 mm; largest female, 8.0 mm.

Female.—Eye large and ovate. Antenna 1, about 50 percent length of body, about 2 times longer than antenna 2: primary flagellum with about 22 segments. Antenna 2, flagellum with 8 segments. Mandibles subequal. spine row with 5-6 spines: segment 2 of palp with 7-9 long setae, segment 3 with 1 A seta, 2 C setae, 4-5 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 7-8 apical plumose setae; palp with 5-6 slender spines on apex. Maxilla 2, inner plate with oblique row of 8 plumose setae on inner margin. Maxilliped: inner plate apically with 4 bladelike spines, 3 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 4-5 slender pectinate spines on inner margin; dactyl with 2-3 setae near nail on inner margin; dactyl nail longer than 1:3 length of dactyl.

Propod of gnathopod 1 less than 2 times longer than carpus: palm almost straight, slightly shorter than posterior margin. with 8 spine teeth on inside, 9 on the outside: defining angle with 3 notched-serrate spine teeth on inside, 1 large notched and 1 small notched-serrate spine teeth on outside: superior medial setae singly inserted; posterior margin with 4-5 sets of setae singly inserted or in groups of 2-3. Dactyl with a row of 5 short setae on inner margin, nail long. Ventral margin of coxa 1 with 8 setae.

Propod of gnathopod 2: palm slightly convex, oblique, shorter than posterior margin, with 7 spine teeth on inside, 9 on outside: defining angle with 1 notched and 2 notched-serrate spine teeth on inside, 2 notched and 1 large simple teeth on outside: superior medial setae singly inserted; posterior margin with 5 sets of setae in groups of 2-6. Dactyl with row of 5 short setae on inner margin. Ventral margin of coxa 2 with 8 setae.

Coxa of pereopod 3 with 8 marginal setae. Coxa of pereopod 4 with 16 marginal setae, dactyl of pereopod 4 about 45 percent length of corresponding propod. Pereopod 5: basis with deep 10 serrations along posterior margin; 4 short spines on anterior margin; 3 long setae on the anteroproximal margin. Pereopod 6: basis with 11 deep serrations along posterior margin; 6 short spines on anterior margin; 3 short setae on anteroproximal margin. Pereopod 7: coxa with 3 setae on the posterior margin; basis with 14 deep
Figure 162.—*Crangonyx fontinalis*, new species. Female paratype (7.8 mm), spring N of Repass Saltpetre Cave, Bland Co., Virginia: a, head (in part); b, antenna 1; c, d, maxillae 1, 2; e, lower lip; f, left mandible; g, dentate part of right mandible; h, inner and outer plates and palp dactyl of maxilliped; i, j, gnathopods 1, 2 (palmar margins enlarged).
Figure 163.—Crangonyx fontinalis, new species. Female paratype (7.8 mm), spring N of Repass Saltpetre Cave, Bland Co., Virginia: a, c, d. pereopods 3, 5, 6 (in part); b. e. pereopods 4, 7; f. pleonal plates; g, h, i. uropods 1, 2, 3; j. telson.
Figure 164.—*Crangonyx fontinalis*, new species. Male paratype (5.0 mm), spring N of Repass Saltpetre Cave, Bland Co., Virginia: a. antenna 2; b. c. gnathopods 1, 2 (palmar margins enlarged); d. e. uropods 2, 3; f. telson; g. pereopods 7.
Figure 165.—Distribution of Crangonyx fontinalis in North America. Solid circles represent single localities.
serrations along posterior margin; 6 short spines on anterior margin; 2 long setae on anteroproximal margin; dactyl about 35 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner produced and acute; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner strongly produced and acute, ventral margin with 1 (subventral) spine; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner produced and acute, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus 70 percent length of peduncle, armed with 10 spines; outer ramus with 11 spines; peduncle with row of 5 outer and 1 inner spines. Uropod 2: inner ramus armed with 12 spines: outer ramus with 11 spines; peduncle with 4 outer spines, and 2 inner spines. Uropod 3: inner ramus lacking spines, outer ramus about 1.5 times longer than peduncle, inner and outer margin each with 3-4 sets of spines in groups 1-3. Telson slightly broader than long, notched about 1/2 distance to base, each lobe with 4 apical spines; spines less than 1/2 length of telson.

Male.— Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 2 segments of flagellum.

Propod of gnathopods 1 and 2 more than 2 times larger and longer than carpus, proportionately much broader. Palm of propod of gnathopod 1 with 6 spine teeth on inside, 6 on outside; defining angle with 3 notched-serrate spine teeth on inside and 3 notched and 1 serrate spine teeth on outside. Propod of gnathopod 2 palm margin oblique, with 7 spine teeth on inside, 8 on outside; defining angle with 4 spine teeth on inside and 4 on outside.

Pereopod 6-7: basis with about 10 prominent serrations along posterior margin, 6-7 short setal-like spines on anterior margin.

Uropod 2: outer ramus strongly deflected laterally, with about 5 short inner and 5 short outer spines on upper margin, apex with 3 spines; peduncle with 3 thin outer spines, 2 inner spines. Uropod 3: inner ramus with 1 spine; outer ramus about 2 times length of peduncle.

Type-locality.— Spring, approximately 300 m N of Repass Saltpetre Cave, Bland Co., VA.

Distribution and ecology.— The presently known range of this species is limited to Bland county, VA, and covers a linear distance of only about 20 km (fig. 165). This species is known only from two karst springs situated close to several caves. However, the populations appear to be epigean and superficially resemble Gammanus minus when alive in their natural setting. Specimens were abundant on roots and under leaves just beyond the spring outlets (J. R. Holsinger, pers. comm.).

Etymology.— The epithet fontinalis is from the Latin fontinalis, meaning "of a spring" and refers to the only known habitat of this new species.
Crangonyx cooperi, new species

Figures 166-169


Diagnosis.—A relatively small species morphologically similar to C. orientalis but distinguished easily from it by absence of comb spines on outer ramus of male uropod 2, which are replaced by thin spines (setal-like) instead. Largest male, 5.6 mm; largest female, 7.5 mm.

Female.—Eye large and ovate. Antenna 1, 50-55 percent length of body, about 1.8-2.0 times longer than antenna 2; primary flagellum with about 25 segments. Antenna 2, flagellum with 7 segments. Mandibles subequal. spine row with 4-6 spines; segment 2 of palp with 7-8 long setae, segment 3 with 1 A seta, 3 C setae, 5 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 8 apical plumose setae; palp with 9 slender spines on apex. Maxilla 2, inner plate with oblique row of 7-8 plumose setae on inner margin. Maxilliped: inner plate apically with 4 blade-like spines. 1 naked spine, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of 3-4 slender pectinate spines on inner margin; dactyl with 2 setae on inner margin near nail; dactyl nail very long, about 1/3 length of dactyl.

Propod of gnathopod 1 less than 2 times longer than propod: palm slightly convex, shorter than posterior margin, with 7 spine teeth on inside, 7 on outside; defining angle with 5 notched-serrate spine teeth on inside, 1 large notched and 2 serrate small spine teeth on outside; posterior margin with 5 sets of setae singly inserted or in groups of 2-5. Ventral margin of coxa 1 with 9 setae.

Propod of gnathopod 2 less than 2 times longer than carpus; palm slightly convex, much shorter than posterior margin, with 9 spine teeth on inside, 10 on outside; defining angle with 1 large notched spine tooth and 3 weakly notched-serrate spine teeth on inside. 1 large simple spine tooth and 1 small (simple or notched) spine tooth on outside; superior medial setae mostly singly inserted; posterior margin with 6 sets of setae in groups of 2-6. Ventral margin of coxa 2 with 10 setae.

Coxa of pereopod 3 with 9 marginal setae. Coxa of pereopod 4 with 21 marginal setae, dactyl of pereopod 4 about 35 percent length of corresponding propod. Pereopod 5: basis with 16 shallow serrations along posterior margin; 6 short spines on anterior margin; 2 long setae on the anteroproximal margin.
Pereopod 6: basis with 16 serrations along posterior margin; 5 short spines on anterior margin; 3 short setae on anteroproximal margin. Pereopod 7: coxa with 2-3 setae on the posterior margin; basis with 18 shallow serrations along posterior margin; 5 short spines on anterior margin; 3 short setae on proximal margin; dactyl about 33 percent length of corresponding propod.
Figure 166. *Crangonyx cooperi*, new species. Female paratype (7.7 mm). Roper Cave, Morgan Co., Alabama: a, maxillae 1, 2; b, lower lip; c, dentate part of left mandible; d, right mandible; e, inner and outer plates and palp dactyl of maxilliped (greatly enlarged); f, gnathopods 1, 2 (palmar margins enlarged).
Figure 167.—Crangonyx cooperi, new species. Female paratype (7.7 mm). Roper Cave, Morgan Co., Alabama: a, antenna 1; b, c, d, pereopods 3, 5, 6 (in part); e, pereopod 7; f, pleonal plates; g, h, i, uropods 1, 2, 3; j, telson.
Figure 168.—*Crangonyx cooperi*, new species. Male paratype (5.6 mm), Roper Cave, Morgan Co.,
Alabama: a, antenna 2; b, c, gnathopods 1, 2 (palmar margins enlarged); d, e, uropods 2, 3; f, telson.
Figure 169.--Distribution of Crangonyx cooperi in North America. Solid circles represent 1-2 closely proximate localities.
Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta. Distoposterior corner produced and acute; posterior margin of plate 2 nearly straight with 1-2 setae. Distoposterior corner strongly produced and acute, ventral margin with 5 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner weakly produced and acute, ventral margin with 3 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus 80 percent length of peduncle, armed with 13 spines; outer ramus with 12 spines; peduncle with 9 outer and 1 inner spines. Uropod 2: inner ramus armed with 12 spines; outer ramus with 11 spines; peduncle with 4 outer spines and 2 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 2 times longer than peduncle. Inner and outer margin each with 3-4 sets of spines in groups 1-3. Telson slightly broader than long, notched about 1/3 distance to base, each lobe with 3 apical spines; spines length less than 1/2 length of telson.

Male.—Differing from females as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 4 segments of flagellum.

Propod of gnathopod 1 more than 2 times longer than carpus; palm with 9 spine teeth on inside, 10 on outside. Defining angle with 1 notched and 4 notched-serrate spine teeth on inside, 1-3 small notched and 1 large notched and 1 serrate spine teeth on outside. Propod of gnathopod 2 more than 2 times longer than carpus; palm margin convex and oblique, with 12 spine teeth on inside, 13 on outside; defining angle with 1 notched and 2 weakly notched-serrate spine teeth on outside and 4 notched spine teeth on outside.

Uropod 2: outer ramus slightly deflected laterally and tapering distally, with 1 very thin inner and 4 very thin outer spines, apex with 3 spines; peduncle with 3 outer and 3 inner spines.

Type-locality.—Roper Cave, Morgan Co., Alabama, located 14.5 km SW of Decatur, contains a stream that flows to the surface through its mouth (Varnedoe, 1973).

Distribution and ecology.—Despite being found only in cave streams (at least to date), this species shows no obvious troglomorphic features (fig. 169). The range of the species, which lies within the Tennessee River drainage, covers a linear distance of approximately 120 km, and extends from Colbert County east to Morgan County. The August collection from Roper Cave contained two ovigerous females, 1 with 7 young in the brood pouch, the other with 23 eggs.

Etymology.—It is pleasure to name this species in honor of Dr. John E. Cooper, a biospeleologist whose extensive fieldwork in Alabama resulted in the discovery of this species.

*Crangonyx lewisi*, new species

Figures 170-173

Material examined (paratypes unless designated otherwise).—INDIANA. Clark Co.: Sunset Village Cave, 1 ♂, 4 juvs. J. J. Lewis, 26 Mar 1975; Jefferson Co.: Deputy Corner Cave, 6 ♂, 3 ♀, J. J. Lewis, 28.
Figure 170.—*Crangonyx lewisi*, new species. Female paratype (8.2 mm). Wilsons Cave. Jefferson Co., Indiana: a. antenna 1; b, c. maxillae 1, 2; d. lower lip; e. dentate part of left mandible; f. right mandible; g. inner plate and palp dactyl of maxilliped (greatly enlarged); h, i. gnathopods 1, 2 (palmar margins enlarged).
Figure 171.—Crangonyx lewisi, new species. Female paratype (8.2 mm), Wilsons Cave, Jefferson Co., Indiana: a. d. pereopods 3, 7; b, c. pereopods 4, 5 (in part); e. pleonal plates; f, g, h. uropods 1, 2, 3; i. telson.
Figure 172.—*Crangonyx lewisi*, new species. Male paratype (5.3 mm). Wilsons Cave, Jefferson Co., Indiana: a, antenna 2; b, c, gnathopods 1, 2 (palmar margin enlarged); d, pereopod 7; e, f, g, uropods 1, 2, 3; h, telson
Figure 173. -- Distribution of Crangonyx lorisii in North America. Solid circles represent 1-3 closely proximate localities.

Diagnosis.—A relatively small stygobiont species closely similar to C. housfieldi but distinguished from it by the outer ramus of male uropod 2, which has about 8 outer and 1-2 inner (short) spines; and having only 1 seta on the posterior margins of pleonal plates. Largest male, 6.0 mm; largest female, 8.5 mm.

Female.—Eye greatly reduced to several black specks. Antenna 1, about 50 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with 17 segments. Antenna 2. flagellum with 8-9 segments. Mandibles subequal, spine row with 4-5 spines; segment 2 of palp with 8 long setae, segment 3 with 1 A seta. 1 B seta. 4 C setae. 4-5 E setae and a row of D setae. Maxilla 1: inner plate with 9 apical plumose setae; palp with 4 slender spines and 4 plumose setae on apex. Maxilla 2, inner plate with oblique row of 8 plumose setae on inner margin. Maxilliped: inner plate apically with 4 bladelike spines. 3 naked spines, and 7-8 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 3-7 slender pectinate spines on inner margin; 4-5 setae on inner margin of dactyl; dactyl nail very long, about 2.5 length of dactyl.

Propod of gnathopod 1 less than 2 times longer than carpus; palm almost straight, shorter than posterior margin, with 8 spine teeth on inside, 8 notched and 2 simple spine teeth on the outside; defining angle with 5 notched-serrate spine teeth on inside, 1 large notched and 3 serrate spine teeth on outside; posterior margin with 4 sets of setae inserted in groups of 2-5. Dactyl with row of short setae on inner margin; dactyl nail very long. Ventral margin of coxa 1 with 17 setae.

Propod of gnathopod 2 less 2 times longer than carpus; palm almost straight, oblique, shorter than posterior margin, with 10 spine teeth on inside, 11 on outside; defining angle with 1 notched and 5 notched, serrate spine teeth on inside, 1 very large notched and 2 serrate spine teeth on outside; superior medial setae singly inserted; posterior margin with 6 sets of setae in groups of 3-5. Dactyl with row of short setae on inferior margin. Ventral margin of coxa 2 with 11 setae.

Coxa of pereopod 3 with 9 marginal setae. Coxa of pereopod 4 with 19 marginal setae. dactyl of pereopod 4 about 33 percent length of corresponding propod. Pereopod 5: basis with 12 very shallow serrations along posterior margin; 6-8 short spines on anterior margin; 2 long setae on the anteroproximal margin. Pereopod 6: basis with 13 very shallow serrations along posterior margin; 9 short spines on anterior margin; 2 long setae on anteroproximal margin. Pereopod 7: coxa with 4 setae on the posterior
margin: basis with 12 shallow serrations along posterior margin; 10 short spines on anterior margin; 2 long setae on anteroproximal margin; dactyl about 30 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 convex, with 1 seta, distoposterior corner recessed, neither produced nor acute; posterior margin of plate 2 slightly convex with 1 seta, distoposterior corner weakly produced and subacute, ventral margin with 3 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta, distoposterior corner recessed, almost indistinct, ventral margin with 4 (subventral) spines. Peduncle of pleopod 1 with 2 retinaculae, lacking setae on outside margin.

Uropod 1: inner ramus about 70 percent length of peduncle, armed with 9 spines; outer ramus with 11 spines; peduncle with 12 outer and 3 inner spines. Uropod 2: inner ramus armed with 13 spines; outer ramus with 9 spines; peduncle with 7 outer spines, 3 inner spines. Uropod 3: inner ramus lacking spines, outer ramus about 1.5 times longer than peduncle, inner and outer margins each with 2-3 set of spines in groups of 1-3. Telson broader than long, notched about 1/3 distance to base, each lobe with 3 apical spines: spines longer than 1/2 length of telson.

Male.—Differing from females as follows. Smaller with more slender, elongate body. Antenna 2: calceoli present on peduncular segments 4 and 5, and first 3 segments of flagellum.

Gnathopods 1 and 2: propod more than 2 times larger and longer than carpus. Propod of gnathopod 1 palm slightly concave, slightly longer than posterior margin, with 7 spine teeth on inside, 7 on outside: defining angle with 4 serrate spine teeth on inside and 2 serrate spine teeth on outside. Propod of gnathopod 2: palmar margin oblique, slightly concave, longer than posterior margin, with 11-12 spine teeth on inside, 12 on outside: defining angle with 3-4 spine teeth on inside and 3 on outside.

Uropod 2: inner ramus with 11 spines; outer ramus curved laterally to nearly right angle with peduncle, with 1-2 inner spines and about 8 short outer spines, apex with 3 spines; peduncle with 4 outer and 3 inner spines.

Type-locality.—Crosley Canyon Cave, 4 km S of North Vernon, is located in the Crosley State Fish and Wildlife area of Jennings County, Indiana.

Distribution and ecology.—The range of this species, which is limited to southeastern Indiana and north-central Kentucky, extends from Jennings County, Indiana southwest to Meade County, Kentucky and southeast to Owen County, Kentucky (fig. 173).

Ovigerous females are recorded from May, August and November collections and brood about 20 young each. In caves this species has been found together with the amphipods C. packardi, C. forbesi, and rarely Synurella dentata. The cave habitats include streams, stream pools, and drip pools. This species was also found in surface springs in Meade County, KY, where it was associated with the amphipods C. rivularis and C. packardi.

Etymology.—It is pleasure to name this species in honor of Dr. Julian J. Lewis, a biospeleologist whose diligent field work has led to the discovery of many records and new taxa of subterranean crustaceans in Indiana and elsewhere.
Crangonyx orientalis, new species

Figures 174-178

Material examined (paratypes unless designated otherwise).—MARYLAND. Dorchester Co.: swamp. 5.3 km W of Cambridge. 5 ♂, 1 ♀. R. W. Jackson, 20 Apr 1943 (USNM); NORTH CAROLINA. Carteret Co.: Bogue Banks, ca. 0.45 km SE of western bridge. 4 ♂, 4 ♀. R. E. Ashen and E. Van Riper, 16 Mar 1978; Hertford Co.: Winton. 1 ♂, 3 ♀. collector unknown, 23 Nov 1940 (USNM). VIRGINIA. Charlotte Co.: vernal pool. Keysville. 1 ♂. 28 Mar 1967. A. Weaner; Chesapeake (Norfolk County): roadside ditch. 1.6 km S of Walaceton, 20 specs (♀, ♂). J. R. Holsinger et al., 18 Apr 1971; Dinwiddie Co.: Belchers pond near Petersburg. 2 ♂, 2 ♀. R. Bray, 22 Mar 1940 (USNM); Elizabeth City Co.: small stream. 6.2 km NW of Hampton, 12 ♂. L. Hubricht. 23 Jan 1944 (USNM); Hampton (Elizabeth City County). ditch. NW of corner of NASA Langley Research Center. 1 ♂. R. Bedenbaugh et al., 30 Mar 1994; small pool in forested wetland, western side of NASA Langley Research Center. R. L. Bedenbaugh et al., 3 ♂, 17 Mar 1994; Henrico Co.: stagnant pond in Maymont Park. Richmond. 9 ♂. A. J. Seidenberg, 31 May 1973; seep on Sawmill Rd., ca. 5.6 km W of Richmond. 4 ♂, 3 ♀. W. C. Sears. Nov 1977: Isle of Wight Co.: outlet of drain tile on Taylor farm. 5.6 km N of Chuckatuck. 1 ♂, J. R. Holsinger, 24 Apr 1983; Mecklenburg Co.: pond at Oak Grove School. Chase city. 3♂, 6 May 1935 (USNM) and 3 ♀, 15 ♀, 11 May 1935 (USNM); Nansemond Co.: seep. 1.6 km S of Crittenden. 2 ♂, 1 ♀. L. Hubricht. 30 Jan 1944 (USNM); pool in Dismal Swamp near Washington Ditch. 8.0 km SE of Suffolk. 7 ♂, 1 ♀. L. Hubricht. 30 Apr 1944 (USNM); marsh-like pond. SW end of Dismal Swamp. 11 ♂, W. Priest. 2 Mar 1974: temporary pool in woods. 1.6 km E of Driver. 20 ♂. 15 ♀. L. Hubricht. 26 Mar 1944 (USNM); Parkers pond. Suffolk. 1 ♂. R. Bray, 24 Mar 1940 (USNM); roadside ditch near Suffolk airport. 1 ♀, 1 juv. K. Garrett. 6 May 1971: Whaleyville. Suffolk. 5 ♂, 5 ♀. R. Bray. 22 Mar 1940 (USNM); Norfolk Co.: temporary pool in Dismal Swamp. 3.2 km SSE of Bowers Hill. 1 ♀, 1 ♀. L. Hubricht. 14 Nov 1943 (USNM); roadside ditch. Bowers Hill. 9 ♂, L. Hubricht, 25 Feb 1945 (USNM); stream in swamp. 3.2 km S of North Landing, holotype ♀. 220 specs (♀. ♀, ♀, juvs). L. Hubricht, 9 Apr 1944 (USNM); Northampton Co.: small stream. 1 mi S of Capeville. 18 ♂. 5 ♀. L. Hubricht. 16 Apr 1944 (USNM); Pittsylvania Co.: swale. Motley's Mill. 14 ♂. 8 ♀. L. Hubricht, 5 Feb 1949 (USNM); Southampton Co.: Charles Plantation. Franklin. 8 ♀. 3 ♀. R. Bray. 22 Mar 1940 (USNM); Franklin. 6 ♂, 2 ♂. R. Bray. 22 Mar 1940 (USNM); Virginia Beach (Princess Anne County): Stumpy Lake. 8.0 km S of Kempsville near Golf Course. 50 specs (♀, ♂, juvs). J. R. Holsinger and C. H. Holsinger, 2 May 1971: Warwick Co.: pools in woods. 4.0 km NW of Newport News. 13 ♂. 7 ♀. L. Hubricht. 23 Jan 1944 (USNM); ditch. 2.4 NE of Morrison. 3 ♂. 2 juvs. L. Hubricht. 23 Jan 1944 (USNM); York Co.: pond. 1.0 km S of Grafton Church. 2 ♂. P. H. Stevenson and S. H. Holbrook. 13 Feb 1993: pond on Rt. 17 ca. 1.1 km S of Harris Grove. 1 ♂. J. R. Holsinger et al., 9 Mar 1994.

Diagnosis.—A small species morphologically similar to C. shoemakeri by possession of comb spines
Figure 174. *Cyclopoa orientalis*, new species. Female paratype (0.5 mm), whole animal from left side, stream in swamp 3.2 km S of North Landing, Norfolk Co., Virginia.
Figure 175.—Crangonyx orientalis, new species. Female paratype (8.5 mm), stream in swamp 3.2 km S of North Landing, Norfolk Co., Virginia: a. head (in part); b. c. antennae 1. 2; d. e. maxillae 1. 2; f. lower lip; g. dentate part of left mandible; h. right mandible; i. inner and outer plates and palp dactyl of maxilliped; j. k. gnathopods 1. 2 (palmar margins enlarged).
Figure 176.—*Crangonyx orientalis*, new species. Female paratype (8.5 mm), stream in swamp 3.2 km S of North Landing, Norfolk Co., Virginia: a, c, d, pereopods 3, 5, 6 (in part); b, e, pereopods 4, 7; f, pleonal plates; g, h, i, uropods 1, 2, 3; j, telson.
Figure 177.—*Crangonyx orientalis*, new species. Male paratype (6.4 mm), stream in swamp 3.2 km S of North Landing, Norfolk Co., Virginia: a, antenna 2; b, c. gnathopods 1, 2 (palmar margins enlarged); d. pereopod 7; e, g. uropods 1, 2, 3; f. uropod 2 (inner and outer rows of spines shown separately); h. telson.
Figure 178.--Distribution of *Crangonyx orientalis* in North America. Solid circles represent 1-4 closely proximate localities.
on male uropod 2, but distinguished from it by lacking spine teeth on dactyl of gnathopod propods. Largest
male, 6.0 mm; largest female, 10.0 mm.

Female.—Eye large and ovate. Antenna 1, 55-57 percent length of body, about 1.8 times longer than
antenna 2; primary flagellum with about 18 segments. Antenna 2, flagellum with 6-8 segments. Mandibles
subequal, spine row with 5-6 spines; segment 2 of palp with 8-9 long setae, segment 3 with 1 A seta, 3 C
setae, 4 E setae and a row of D setae, lacking B seta. Maxilla 1: inner plate with 5-7 apical plumose setae;
palp with 5-6 slender spines on apex. Maxilla 2, inner plate with oblique row of 5-7 plumose setae on inner
margin. Maxilliped: inner plate apically with 2 bladelike spines, 1 naked spine, and 5-7 plumose setae
extending from inner margin to apex; outer plate with row of naked setae and 3-4 slender pectinate spines
on inner margin and 1 apical plumose seta; dactyl with 3 setae on inner margin; dactyl nail very long, about
1.3 length of dactyl.

Propod of gnathopod 1 less than 2 times longer than carpus; palm straight or slightly concave, shorter
than posterior margin, with 7 spine teeth on inside, 10 on the outside; defining angle with 1 large notched
and 2 serrate spine teeth on inside, 3 small, notched-serrate and 2 serrate spine teeth on outside; posterior
margin with 4 sets of setae singly or doubly inserted. Dactyl with row of short setae on inner margin, nail
long. Ventral margin of coxa 1 with 9-11 setae.

Propod of gnathopod 2 less than 2 times longer than carpus; palm straight, shorter than posterior
margin, with 6 spine teeth on inside, 10 on outside; defining angle with 2 notched and 3 notched-serrate
spine teeth on inside, 2 notched and 1 serrate spine teeth on outside (1 larger); superior medial setae singly
inserted; posterior margin with 5 sets of setae in groups of 2-6. Dactyl with row of short setae on inner
margin. Ventral margin of coxa 2 with 9-11 setae.

Coxa of pereopod 3 with 12-14 marginal setae. Coxa of pereopod 4 with 20-22 marginal setae. Dactyl
of pereopod 4 about 35 percent length of corresponding propod. Pereopod 5: basis with 10 shallow
serrations along posterior margin; 9 sets of short spines on anterior margin; 3-4 long setae on the
anteroproximal margin. Pereopod 6: basis with 12-14 shallow serrations along posterior margin. 8 sets of
short spines on anterior margin; 3 short setae on anteroproximal margin. Pereopod 7: coxa with 3 setae
on the posterior margin; basis with 12-15 shallow serrations along posterior margin. 9 sets of short spines on
anterior margin; dactyl about 35 percent the length of corresponding propod.

Pleonal plates: posterior margin of plate 1 slightly convex, with 1 seta, distoposterior corner produced
and acute; posterior margin of plate 2 nearly straight with 1 seta, distoposterior corner slightly produced
and acute. Ventral margin with 5 (subventral) spines; posterior margin of plate 3 nearly straight with 1 seta.
distoposterior corner produced and acute, ventral margin with 4 (subventral) spines. Peduncle of pleopod 1
with 2 retinaculae: lacking setae on outside margin.

Uropod 1: inner ramus 80 percent length of peduncle, armed with 11 spines; outer ramus with 14
spines; peduncle with 5 outer and 5 inner spines. Uropod 2: inner ramus armed with 14 spines; outer ramus
with 13 spines; peduncle with 4 outer spines, and 4 inner spines. Uropod 3: inner ramus with 1 spine, outer
ramus about 2 times longer than peduncle, inner and outer margin each with 3–4 set of spines in groups of 1–3. Telson broader than long, notched about 1/3 distance to base, each lobe with 3–4 apical spines: spines about 1/2 length of telson.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2: flagellum with 6 segments, calceoli present on peduncular segments 4 and 5, and first 4 segments of flagellum.

Propod of gnathopod 1 more than 2 times larger and longer than carpus, and much broader: palm convex, oblique, 10 spine teeth on inside, 9 on outside: defining angle with 1 notched and 3 notched-serrate spine teeth on inside. 4 on outside.

Propod of gnathopod 2 more than 2 times longer and larger than carpus: palm margin convex, oblique, with 12 spine teeth on inside, 11 on outside: defining angle with 4 spine teeth on inside and 3 on outside.

Uropod 2: inner ramus with 11 spines; outer ramus deflected laterally, with inner row of comb spines on distal 3/4–2/3. 6 short spines on outer margin, 3 spines on apex; peduncle with 3 outer and 5 inner spines.

Type-locality.—Stream in swamp, 3.2 km S of North Landing, Norfolk County (now in the city of Chesapeake). This locality is close to the northern margin of the Great Dismal Swamp.

Distribution and ecology.—The range of this species extends from Dorchester Co., Maryland southward on the Coastal Plain to northeastern North Carolina and southwest into the Piedmont of southwestern Virginia (Fig. 178). It covers a linear distance of about 450 km north to south and about 300 km east to west.

The habitat of this species includes swamps, roadside ditches, small woodland ponds, seeps and outlets of drain tiles.

Crangonyx orientalis has been taken with other species of Crangonyx, including C. disjunctus, C. poliusris, and C. serratus. It is often associated with the first two species in the Grafton "sinkhole" ponds near Hampton, VA. Ovigerous females were collected in February, March, April and May.

Etymology.—The epithet orientalis is from Latin meaning "eastern." and refers to the distribution of this species in the eastern United States.

Crangonyx bousfieldi, new species

Figures 179-182

Material examined (paratypes unless designated otherwise).—INDIANA. Wayne Co.: spring between Dublin and Mt. Auburn, 2 ♀ (not paratypes), L. Hubricht, 17 Apr 1942 (USNM). KENTUCKY. Jefferson Co.: tiny stream, 3.2 km S of Thixton, 30 spec. (♀, ♂), N. Hynes, 6 Jan 1985 (USNM); spring 1.6 km E of Preston, holotype ♂, 8 ♀, 4 ♂, R. Fox, 12 Feb, 1971; Oldham Co.: tributary to Harrods Creek.
Figure 179.—*Crangonyx bousfieldi*, new species. Female paratype (7.8 mm), spring 1.6 km E of Preston, Jefferson Co., Kentucky: a, b, maxillae 1, 2; c, lower lip; d, right mandible; e, dentate part of left mandible; f, inner and outer plates and palp dactyl of maxilliped (greatly enlarged); g, h, gnathopods 1, 2 (palmar margins enlarged); i, pereopod 4.
Figure 180.—Crangonyx bousfieldi, new species. Female paratype (7.8 mm), spring 1.6 km E of Preston, Jefferson Co., Kentucky: a. antenna 1; b, c, d. pereopods 3, 5, 6 (in part); e. pereopod 7; f. pleonal plates; g, h. uropods 2, 3; i. telson.
Figure 181.—Crangonyx bousfieldi, new species. Male paratype (4.7 mm), spring 1.6 km E of Preston, Jefferson Co., Kentucky: a, antenna 2; b, c, gnathopods 1, 2 (palmar margins enlarged); d, pereopod 7; e, f, g, uropods 1, 2, 3; h, telson.
Figure 182.—Distribution of *Crangonyx houfieldi* in North America. Solid circles represent 1 or 2 closely proximate localities.
Diagnosis.—A small species very similar to *C. lewisi* but distinguished from it by having 2 setae on posterior margins of pleonal plates 1-3, (1 located just above the corner); well developed eyes; absence of notched-serrate spine teeth on propod of gnathopods of male; inner side of outer ramus of male uropod 2 with only 1 spine in the middle. Largest male, 5.1 mm; largest female, 8.2 mm.

Female.—Eye large and ovate. Antenna 1, 55-57 percent length of body, about 1.8 times longer than antenna 2; primary flagellum with about 21 segments. Antenna 2, flagellum with 7-9 segments. Mandibles subequal. spine row with 5 spines; segment 2 of palp with 8-9 setae. segment 3 with 1 A seta, 1 B seta, 2 C seta. 4-5 E setae and a row of D setae. Maxilla 1: inner plate with 7 apical plumose setae; palp with 10 slender spines on apex. Maxilla 2, inner plate with oblique row of 7 plumose setae on inner margin. Maxilliped: inner plate apically with 3 blade-like spines, 3 naked spines, and 5-6 plumose setae extending from inner margin to apex; outer plate with row of naked setae and 4-5 slender pectinate spines on inner margin; dactyl with 3 setae on inner margin; dactyl nail very long, 1/3 length of dactyl.

Propod of gnathopod 1 and 2 less than 2 times larger and longer than carpus; palm almost straight, shorter than posterior margin, with 8 spine teeth on inside, 12 on the outside; defining angle with 3 notched-serrate spine teeth on inside, and 1 large simple and 2 serrate spine teeth on outside; superior medial setae singly or doubly inserted; posterior margin with 6 sets of setae singly or doubly inserted. Dactyl with row of short setae on inner margin, nail long. Ventral margin of coxa 1 with 13 setae.

Propod of gnathopod 2 less than 2 times larger and longer than carpus; palm almost straight, shorter than posterior margin, with 8 spine teeth on inside, 10 on outside; defining angle with 1 notched, 1 large simple and 2 serrate spine teeth on outside, and 2 small notched and 1 large simple and 2 serrate spine teeth on outside; superior medial setae singly inserted; posterior margin with 4 sets of setae in groups of 1-5. Dactyl with row of short setae on inner margin. Ventral margin of coxa 2 with 13 setae.

Coxa of pereopod 3 with 12 marginal setae. Coxa of pereopod 4 with 16 marginal setae, dactyl of pereopod 4 about 33 percent length of corresponding propod. Pereopod 5: basis with 9 shallow serrations along posterior margin; 5 sets of short spines on anterior margin; 1 long seta on the anteroproximal margin. Pereopod 6: basis with 8-9 serrations along posterior margin, 9 short spines on anterior margin; 1 setae on anteroproximal margin. Pereopod 7: coxa with 2 setae on the posterior margin; basis with 9 shallow serrations along posterior margin; 12 sets of short spines on anterior margin; dactyl about 33 percent length of corresponding propod.

Pleonal plates: posterior margin of plate 1 convex, with 2 setae, 1 on distoposterior corner, distoposterior corner recessed and subacute; posterior margin of plate 2 weakly convex, with 2 setae, 1 on distoposterior corner, distoposterior corner recessed, rounded, indistinct, ventral margin with 3 (subventral)
spines: posterior margin of plate 3 nearly straight with 2 setae, 1 just on distoposterior corner.

distoposterior corner round and not produced, ventral margin with 3 (subventral) spines. Peduncle of
pleopod 1 with 2 retinaculae; lacking setae on outside margin.

Uropod 1: inner ramus 65 percent length of peduncle, armed with 10 spines; outer ramus with 12
spines: peduncle with 7 outer and 1 inner spines. Uropod 2: inner ramus armed with 10 spines; peduncle
with 5 outer and 2 inner spines. Uropod 3: inner ramus with 1 spine, outer ramus about 1.5 times longer
than peduncle. inner and outer margins each with 2-3 set of spines in groups of 1-3. Telson broader than
long, notched about 1/4 distance to base, each lobe with 3-4 apical spines: spines about 1/2 length of
telson.

Male.—Differing from female as follows. Smaller with more slender, elongate body. Antenna 2:
calceoli percent on peduncular segments 4 and 5, and first 3 segments of flagellum.

Propod of gnathopods 1 and 2 more than 2 times larger and longer than carpus and much broader.
Propod of gnathopod 1 palm convex: defining angle with 3-4 spine teeth on inside and 4 on outside.
Propod of gnathopod 2: palm oblique and convex: defining angle with 3-4 spine teeth on inside and 7 on
outside.

Uropod 2: inner ramus with 11 spines: outer ramus deflected laterally and slightly backward, upper
margin with 1 inner and 4 short outer spines, apex with 5 spines: peduncle with 4 outer spines and 2 inner
spines. Uropod 3: inner ramus lacking spines; outer ramus about 2 times length of peduncle. inner and
outer margin each with 2-3 set of spines in groups of 1-3.

Type-locality.—A spring located about 46 m S of state road 1003, about 1.6 km E of Preston Highway
in Jefferson County, Kentucky. The type-series consists of 13 specimens, which includes 3 ovigerous
females.

Distribution and ecology.—The range of this species covers a wide area but is represented by only a
few collections. It extends from middle Ohio on the north to northern Kentucky on the southwest, covering
a linear distance of about 300 km (fig. 182). The specimens from Indiana and central Ohio differ slightly
from those farther south and were not designated paratypes.

This species has been collected from small streams, one spring, one cave and one well. Ovigerous
females were found in collections form the months of January, February, and November.

Etymology.—It is pleasure to name this species in honor of Dr. Edward L. Bousfield, a world authority
on the systematics of the Amphipoda, who has contributed significantly to our knowledge of amphipod
crustaceans, both marine and freshwater.

*Crangonyx* species

The following 13 populations cannot be assigned to any known species. Some of them probably
represent distinct species but have not been described for lack of mature specimens or adequate material.
All of them, however, appear to belong to the *gracilis* group.

1. A single ovigerous female (5.6 mm), with small eyes, collected from Bear Creek at Oak Ridge, Anderson Co., Tennessee by J. A. Payne (14 April 1963).

2. Two immature males (4.0-4.5 mm), very similar to males of *C. gracilis*, collected from a spring 4.8 km SE of Sulphur, DeKalb Co., Alabama by S. B. Peck and A. Fiske (15 July 1967).

3. One immature male (3.9 mm) and 8 juveniles collected from J. E. Holt's well, 17.6 km E of Pittsboro, Chatham Co., North Carolina by L. Hubricht (27 May 1951). The male is similar to males of *C. stagnicolous*.

4. Five immature females (largest 4.5 mm), 1 mature male (4.5 mm) and 2 juveniles collected from small seep draining into Red River along Kentucky Hwy 715, about 7.2 km SW of Pomeroyton in Menifee Co., Kentucky by J. E. & M. R. Cooper (13 April 1968). The outer ramus of male uropod 2 has only 2 inner spines near its end.

5. Ten ovigerous female and 1 male collected from a seep 9 km E of Olive Hill, Carter Co., Kentucky by L. Hubricht (22 April 1949). The distoposterior corners of pleonal plates of the female bear 2 setae, one at the corner.

6. One female (5.7 mm), 2 males (largest, 5.5 mm) and 1 juvenile collected from Croxville Cave, Pike Co., Illinois by S. B. Peck (15 August 1968). Although these specimens are in poor condition, they are slender, eyeless and have elongate appendages and are very similar to *C. hobbsi*.

7. Six females and 6 males collected from a stream in Blount Co., Alabama by M. R. Cooper (31 December 1965). This species appears to be very similar to *C. rivularis*.

8. A single female (5.3 mm) collected from a small spring near Great Saltpeter Cave, Rockcastle Co., Kentucky by T. C. Barr, Jr (18 April 1964).

9. A single mature female (7.0 mm) collected from Patuxent River, Maryland (county not given) by Chu-Je Tsai (collection date not given). The telson has 1 lateral spine per lobe.

10. A single female collected from a spring beside US Rt. 441 ca. 1.6 km S of Anderson-Knox Co. line, Knox Co., Tennessee by R. Fox et al. (4 January 1971).

11. Eleven females and 2 males collected from springs 3.6 km NW of Lancaster, Garrard Co., Kentucky by L. Hubricht (24 April 1941).

12. Five females and 7 males collected from a spring 4.6 km E of Castalian Springs, Trousdale Co., Tennessee by L. Hubricht (1 June 1941).

13. Three immature females (one eyeless) and 3 mature males collected from a spring 1.0 km E of Clifton, Woodford Co., Kentucky by J. J. Lewis et al. (19 February 1995).

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CHAPTER V

FINDINGS AND INTERPRETATIONS

ORIGIN OF CRANGONYX

As discussed by Holsinger (1978, 1986) the family Crangonyctidae has an ancient freshwater ancestry probably dating back at least to the Mesozoic. Two lines of evidence support this theory: (1) the crangonyctids are exclusively freshwater and have no apparent relationship with any marine forms and (2) the three largest genera (Crangonyx, Stygobromus and Synurella) of the family Crangonyctidae have a Holarctic distribution, which suggests that they were well established on the Laurasian landmass prior to continental breakup in the late Mesozoic. Putative ancestors of the genus Crangonyx probably originated as a very old freshwater lineage dating back at least to the Mesozoic and possibly earlier.

From the discussions in the Phylogenetic Analysis Section, Crangonyx and Synurella are established as sister groups. Although hypothesized cladistic relationship (figs 1-3) cannot give us a clear picture of what the ancestor of Crangonyx looked like, they all clearly support a two lineage evolutionary scheme, one lineage being gracilis-like and the other forbesi- and richmondensis-like. Most of the species of Synurella have as many ancestral characters as the forbesi and richmondensis groups. Crangonyx chebnikovi and C. subterraneus from Europe are morphologically more similar to species of the forbesi and richmondensis group than to the gracilis group (C. chebnikov apparently belongs to the richmondensis group, at least on the basis of its description). Another European species, C. paxi, is a tiny interstitial species, apparently adapted for life in microspaces of the subterranean environment and has several autapomorphic characters. The only species of the gracilis group found in Europe is C. pseudogracilis, but it has been introduced there by human transport (see discussion later). From the above discussion, I suggest that the ancestor of Crangonyx resembled C. forbesi and separated from the common ancestor of Synurella and Crangonyx somewhere on Laurasia. Extensive diversification occurred in North America as more and more species of the gracilis group evolved after the break up of Laurasia. In Europe the surface species were probably driven out by Synurella, which is more common and widespread in Eurasia than North America, and other surface amphipods such as Gammarus spp. However, a few survived in the subterranean habitats, where they now probably represent relict species. The evolution of the species groups is discussed in the Phylogenetic Analysis Section.

HABITATS OF SPECIES

Species of Crangonyx have exploited a wide variety of surface and groundwater habitats in North
America. In an attempt to gain further insight into the biogeographic, phylogenetic, and ecological relationships among these species, I have compiled general descriptive data on the different freshwater biotopes inhabited by the species in this genus in Table 3. The data are from observations by the collectors, wherever that can be determined. The number of different habitats recorded for some species may not be complete, because in many cases only a few collections were available.

Species have been collected from basically five different habitat types: (1) subterranean waters, (2) seeps/springs, (3) surface streams/rivers, (4) wetland waters (e.g., bogs, swamps, ditches, etc.), and (5) large ponds/lakes. The most common habitat types are springs/seeps and wetland waters. A total of 36 species are found in one or both of these habitats. Only six species can be found in large ponds/lakes and these species are widely distributed and can be found in almost all the other habitats as well.

A total of 24 species are found in subterranean waters (primarily in caves), but only 11 of them are troglobites. An additional 16 species are found in springs/seeps habitats. Based on reduced eyes, light pigmentation and a strong association with secluded spots in cold spring waters, many of the spring seep dwellers are apparently preadapted to life in subterranean waters (Holsinger, 1994).

BIOGEOGRAPHY OF CRANGONYX

The world distribution of Crangonyx is shown in Figure 4 and distributions of species groups and individual species are shown in figures that accompany the species descriptions. Like the other members of the Crangonyctidae, the ranges of species of Crangonyx are quite variable but fall into one of the three basic patterns as described by Holsinger (1978): (1) distribution is localized and species are known only from a few localities; (2) distribution is restricted to a single major drainage system, and (3) distribution is very broad, covering parts of two or more major drainage systems.

Of the six species groups, only the richmondensis and gracilis groups are widely distributed in North America. These two groups also contain many species, with a total of about 66% of the recognized species. This broad distribution may indicate that some species in these two groups are highly vagile and have great dispersal capability. Ranges of members of the three large species groups (shoemakeri, richmondensis, gracilis), plus the forbesi group, all overlap in the middle-western region of North America. In the Origin of Crangonyx section, I concluded that the ancestor of Crangonyx might have been more forbesi-like. Here I suggest that the ancestor might have evolved in the middle-western region of North America and subsequently all species groups (and species) evolved as the ancestral species dispersed outward from this area. The alternative hypothesis is that the ancestor may actually have been widely distributed on Laurasia and species groups later evolved in place as the result of isolation and environmental changes and subsequent genetic differentiation.

Several aspects of distribution are noted for Crangonyx in North America. The first is that almost all species of the genus are distributed in the eastern part of North America, east of the Rocky Mountains. The
Table 3. Records of species of *Crangonyx* from five kinds of generalized habitats in North America.

<table>
<thead>
<tr>
<th>Species</th>
<th>Subterranean waters</th>
<th>Seeps/Springs</th>
<th>Surface Stream</th>
<th>Wetland Waters</th>
<th>Larger Ponds/Lakes</th>
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<td>x</td>
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<td>x</td>
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<tr>
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<tr>
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Table 3. continued

<table>
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<tr>
<th>Species</th>
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<th>surfaces stream</th>
<th>wetland waters</th>
<th>larger ponds/lakes</th>
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exceptions are *C. pseudogracilis*, *C. floridanus*, and *C. richmondensis*, which also have limited distributions in the west. The western part of North America may lack enough good habitats to support more than a few species of the genus, and the species found there, such as *C. pseudogracilis* and *C. floridanus*, were probably introduced recently by man (see Ecological Relationship section). However, as pointed out below, the very wide distribution of *C. richmondensis* needs further explanation and does not appear to have been affected by human introductions.

The second is that the species of *Crangonyx* with distributions in glaciated areas also have distributions south of the southern extent of Pleistocene glaciation. This is strong evidence that these species dispersed north after glaciation, expanding their ranges throughout several drainage systems. These species are all epigean forms. The subterranean species have limited dispersal ability and, in turn, the extent of subterranean drainage is generally restricted. In contrast to the large, exclusively subterranean amphipod genus *Stygobromus*, no surviving relics of subglacial refugia are found in North American *Crangonyx* (Holsinger, 1978).

The *shoemakeri* group has a disjunct distribution, with two species (*C. setodactylus* and *C. minor*) widely distributed in middle-western North America and the other two species (*C. shoemakeri* and *C. aberrans*) distributed east of the Appalachians. These two pairs are also separated from each other by a distance of about 900 km. One hypothesis to explain this disjunct distribution is that distributions of the two eastern species were reduced after speciation or that they moved further eastward to exploit new habitats that were developing on Coastal Plain terrains recently freed of marine/brackish transgressions in the middle to late Tertiary. The alternative hypothesis is that the *shoemakeri* group may not be a monophylegetic group as I suggested in the Phylogenetic Analysis section. If we accept the possibility that the principal diagnostic (apomorphic) character of this group, which is the possession of teeth along the inner margin of the dactyl of the female gnathopod, was independently derived in the two pairs, then this group as presently recognized cannot hold. I prefer the second hypothesis, since *Synurella dentata* also has this "apomorphic" character. Thus, according to the latter, this complex character may have been derived independently. And although these species have similar morphology, I find that *C. setodactylus* and *C. minor* also share apomorphic characters with the unassigned group species *C. lewisi* and *C. housfieldi*, which are also distributed in the middle-western region. It is possible that these species may all belong to one species group. *Crangonyx shoemakeri* is also very similar to *C. orientalis*, except the latter does not have teeth on the inner margin of the dactyl of the female gnathopods. These species overlap in part of their distribution, and moreover, they may be derived from a common ancestor. But as is often the case with analysis of species distributions in poorly known genera, many species distributions may not yet be completely known and only a few good characters are used in phylogenetic analysis. Thus, in the absence of contrary evidence, the *shoemakeri* group is at least tentatively regarded as monophyletic.

The geographic distributions of *C. setodactylus* and *C. minor* are also rather unusual. *Crangonyx minor* has a wider distribution, which surrounds that of *C. setodactylus*. Except in the middle of Kentucky
and in the vicinity of their type-localities, separated by just a few kilometers, where these two species overlap, they do not come in actual contact with each other. My hypothesis is that *C. minor* has greater dispersal ability and *C. setodactylus* has greater competition ability. Thus, after glaciation, they both dispersed northward and *C. setodactylus* replaced *C. minor* in the heart of the middle-western area.

*Crangonyx aberrans* is the only species of the *shoemakeri* group that is restricted to an area north of the southern limit of Pleistocene glaciation. It might be derived from an ancestral population that moved there from an area south of the glacial boundary after glaciation.

The *longicarpus* group is represented by only one species on the Coastal Plain of Virginia and North Carolina. In the Phylogenetic Analysis section, I suggested that this species may be an evolutionary intermediate between the ancestor and the *gracilis* group. If this is the case it should have a wider distribution. One interpretation is that the *longicarpus* group may have been represented by many species in the past but only *C. longicarpus* has survived until the present time. The Coastal Plain of eastern North America, occupied today by *C. longicarpus*, contains geologically younger freshwater habitats than inland areas to the west. Another explanation is that the ancestor of *C. longicarpus* moved to the east after being expelled by the newly evolved *gracilis* group species. Populations of *C. longicarpus* are also found on the eastern shore of Virginia, which is separated from the remainder of the species range by the Chesapeake Bay, suggesting that this species occupied what is now the eastern shore before the Chesapeake Bay was formed.

The *richmondensis* group is the second largest group of *Crangonyx* and is widely distributed in North America and may also occur in eastern Europe (see above). The phylogenetic analysis indicates three species clusters in North America constituted as follows (see fig. 3): (1) *C. obliquus* and *C. richmondensis* are closely similar sister species; (2) *C. anomalus*, *C. cornutus*, *C. dearolfi*, *C. grandimanus* and *C. hubrichti* cluster together but the analysis does not reveal more about the relationship among these species; and (3) *C. indianensis* and *C. disjunctus*, which are near the group ancestor. The actual distributional relationship of these species does to some extent correspond to their phylogenetic relationship. The distributions of *C. obliquus* and *C. richmondensis* do not overlap but they are near each other geographically in the southern part of North America. Although these two species are similar morphologically, their distribution indicates that they are geographically well separated from each other. After evolving from an immediate common ancestor, *C. obliquus* has come to occupy the middle and lower Mississippi River drainage basin, while *C. richmondensis* is widely distributed over large parts of North America and is the most widely distributed species of *Crangonyx*. Moreover, it is the only species that is widely distributed in the western part of North America. A hypothesis to explain its western distribution is that this species was already widely distributed across North America before Pleistocene glaciation. After glaciation, the western habitats changed and some become unsuitable. But some populations of *C. richmondensis* survived as relict populations on the humid western coast in isolated packets. *Crangonyx richmondensis* is the only species of the genus that occurs on Vancouver Island and it also occurs on two
islands in the Alexander Archipelago of southeastern Alaska. The occurrence of this species on these islands, which are separated from the mainland and each other by marine waters, is zoogeographically very interesting. One explanation is that this species reached these islands by way of land connection during lower sea levels at glacial maxima in the Pleistocene (Bousfield, 1970b; Holsinger et al., in press). *Crangonyx richmondensis* is also found in Newfoundland and on Sable Island (Bousfield, 1970b) off the eastern coast of North America. According to Steele's (1983) offshore survival hypothesis, the distribution on these islands suggests this species may have survived glaciation on the continental shelf when sea level was lower and then was able to move back onto the mainland when the ice retreated.

The next clade of the *richmondensis* group consists of the epigean species *C. cornutus, C. anomalus* and *C. hubrichti* and subterranean species *C. dearolfi* and *C. grandimanus*. Although the distributions of these five species do not overlap, the phylogenetic analysis does not resolve the relationship among them, inasmuch as their geographic relationship does not correspond with the phylogenetic analysis. *Crangonyx anomalus* is found only in springs and spring-fed streams and also rarely in caves. Of particular interest regarding the distribution of *C. anomalus* is an approximately 250 km disjunction between one locality in southern Illinois and the heart of its range in northern Kentucky. This large gap may indicate that this species was once widely distributed and inhabited a wider variety of habitats, but is now reduced in distribution and largely restricted to surface springs. Morphologically it has very small eyes and therefore, combined with its apparent restriction to spring waters and caves, there is a possible indication of evolution toward life in the subterranean environment.

At present, *C. indianensis* is found only in caves of Indiana but it is not troglomorphic. Why a species found only in caves is not troglomorphic remains unclear. Apparently this species evolved very recently from a surface ancestor, which would account for presence of eyes and some pigmentation. *Crangonyx disjunctus* is widely distributed on the eastern Coastal Plain of Virginia but one isolated population is found much farther west in the Appalachian mountains. This may indicate either the lack of adequate collections between these two areas or alternatively that *C. disjunctus* was widely distributed in the mountains and gradually moved to the east as Tertiary seas retreated. If this is the case, then the western mountain population(s) is a relict. Another possibility is that the Appalachian population(s) is genetically different and may not actually be the same species as the Coastal Plain *C. disjunctus*, despite morphological similarities.

The *forbesi* group, which contains one species, *C. forbesi*, is widely distributed in the east-central region of North America. Although its distribution is not completely continuous, this is probably due to lack of collection samples in some areas. There are many variations in certain characters, such as the telson shape, and this may indicate this species is very old. The present distribution may reflect an ancient distribution that originated by active dispersal of the ancestor. *Crangonyx forbesi* is morphologically similar to *C. insolitus* (of the *insolitus* group) and the two species may share a common ancestor (figs 1-2). But the distribution of *C. insolitus* is at present limited to a single cave in southern Missouri and lies within
the range of C. forbesi. If C. insolitus and C. forbesi do share a common ancestor, then the speciation of C. insolitus may have been sympatric or parapatric and occurred after its ancestor invaded a cave environment. But although C. insolitus is only found in a cave, it is not troglomorphic and has very special characters that are unique in the family Crangonyctidae (for example the short lateral spines on the peduncle of uropod I). This species may have evolved directly from the common ancestor of the richmondensis, forbesi and insolitus groups (fig. 3). It may have once been as widely distributed as C. forbesi and is now limited in distribution because of inability to compete with C. forbesi for habitat space. However, the actual distribution of this species will probably turn out to be larger than a single locality as more areas are explored and more collections are made.

Three species. -- C. antennatus, C. serratus and C. specus --, apparently have the same common ancestor as the richmondensis, forbesi and insolitus groups. Crangonyx antennatus is a cavernicolous species, distributed through a part of the Appalachians from southwest Virginia to northwestern Alabama and also found in the Sequatchie River Valley in Tennessee. It is known primarily from caves but is also found in karst springs associated with caves. It is a troglomorphic species, although the eyes of some populations are variable and in the form of a few black specks. It is clearly derived from a surface ancestor, probably originating in one area and gradually spreading through subterranean groundwater aquifers. Its large subterranean distribution is probably due to in part to active dispersal through shallow groundwater habitats (Holsinger, 1969, 1975, 1986). It is assumed that these subterranean amphipods inhabit an epikarstic zone saturated with groundwater above open cave passages and can pass downward into these passages by migration and/or accident (Holsinger, 1986). Crangonyx specus is also a cavernicolous species and to date is found only in four caves in eastern Kentucky, which is geographically not far away from the distribution of C. antennatus. One hypothesis for the distribution of this species is that C. specus evolved from C. antennatus by allopatric speciation after some populations of C. antennatus dispersed westward into the Cumberland River drainage and became isolated. Another hypothesis is that they are both from a single common ancestor, whereas C. specus is a poor disperser with a limited distribution, in contrast to C. antennatus which has gained a wide distribution by active dispersal in groundwater habitats.

Crangonyx serratus is widely distributed along the eastern Coastal Plain southward from Washington, DC to Florida. Like C. antennatus and C. specus, its phylogenetic position is unclear (figs. 1-3). Its wide distribution on the Coastal Plain, however, probably reflects a relatively recent event. After sea water recessions in the late Tertiary, the ancestor of this species moved onto the Coastal Plain from a western inland source area by dispersal. It should be noted that the distribution of C. serratus overlaps that of C. richmondensis on the Coastal Plain, but these two species are never found together in the same specific locality.

From the Phylogenetic Analysis section, five ungrouped species, including C. bousfieldi, C. Cooperi, C. fontinalis, C. lewisi, and C. orientalis, are seen to have a close relationship with the shoemakeri and gracilis groups, but the relationships among these species are not clear (figs 1-3). Except for C. orientalis.
which is known from many collections in the Piedmont and Coastal Plain from Maryland to North Carolina, the other four species are known only from a few collections, so it is difficult to explain their distributions at the present time. It is possible that they are all evolved from a single common ancestor. If this is the case, one scenario that explains the present distribution is that an ancestral species was widely distributed and then, through both physical and reproductive isolation of populations at different places, evolved into a suite of closely similar species.

The *gracilis* group is composed of 14 species and widely distributed in the eastern part of North America. Except for a few species such as *C. hobbsi* and *C. packardi*, which appear to be well adapted to the subterranean environment, all of the females look alike and in some species they cannot be told apart. The males also look alike but normally there are good differential diagnostic characters on uropod 2. However, except for a well defined *floridanus* subgroup, the phylogenetic analysis did not tell us much about the relationship among these species. The observations discussed above support the hypothesis that the ancestor of the *gracilis* group was widely distributed in the eastern part of North America. The individual species that have evolved within this group are morphologically not well separated. However, many of the species of this group may not be biological species by strict definition, but this cannot be tested with our limited morphological data. It also follows that the difficulty in differentiating the species may lead to some problems with interpretations of their distribution. Another difficulty is that more than one-half of the species are known from only a few collections and therefore appear to have very limited distributions. Thus, the distributions may be incorrect due to identification error. For example, some collections contain only female specimens and/or damaged males, making it very difficult to get a correct species identification. The following is a discussion of some of the interesting species of this group.

The *floridanus* subgroup is well defined and separated from all other members, although the phylogenetic relationship among the subgroup members is not clear (figs. 1-3). *Crangonyx floridanus* and *C. pseudogracilis* are morphologically closely similar and undoubtedly derived from a relatively recent common ancestor. *Crangonyx pseudogracilis* occurs primarily west of the Appalachian Mountains. In contrast, *C. floridanus* occurs generally east of the Appalachians, but several populations were also found on the western side. The distributions of *C. floridanus* and *C. pseudogracilis* overlap in the middle of the drainage basin of Mississippi River in Missouri and on the Coastal Plain in Mississippi. The overlap in these two places can be explained by dispersal of *C. floridanus* from the most western part of its range and dispersal of *C. pseudogracilis* from the most eastern part of its range. However, these species have never been found together in the same locality. The populations of *C. floridanus* found in Ohio and Kansas are very difficult to explain and the occurrences of *C. floridanus* in Colorado and Oregon may be due to accidental transports by man (discuss below).

*Crangonyx gracilis* is found mainly in the Great Lakes region but also found in the mountains of southeastern West Virginia and southwestern Virginia. The populations in the Virginias occur south of the southern extent of Pleistocene glaciation and may be relics of a former continuous distribution. The Great
Lakes populations are probably the result of dispersal to the north following the last glaciation. The above explanation can also be applied to the distribution of *C. rivularis*.

The distribution of the stygobiont *C. packardi* is also very interesting inasmuch as its range crosses three physiographic provinces and the Mississippi River, covering a distance of about 1000 km. This wide distribution suggests that the species might have evolved and spread before the Mississippi River developed into its present form. It might also explain some of the geographic variation of characters among different populations. However, it is very likely that genetic differences exist among some populations and some of them in turn probably represent different species. Their resolution, however, cannot be accomplished by morphological analysis alone.

*Crangonyx hobbsi* is one of the two subterranean species found in Florida, the other being *C. grandimanus*. These species are almost always found living together in the same caves. Additional discussion on these two species is included below in the Origin of Subterranean Species section.

**ORIGIN OF TROGLOBITES**

As seen from the habitat analysis, 24 species of *Crangonyx* have been found in caves or other subterranean habitats. Eleven are troglobites; the others may be found in cave environments but also have surface populations. Utilizing results of the biogeographic and cladistic analyses, I will attempt to draw a clear picture of the taxonomic and ecological relationships between the subterranean and surface species of *Crangonyx*. The principal questions are namely: how and when the surface ancestors invaded subterranean habitats and evolved into troglobites and what morphological changes were associated with these events?

From the cladograms (figs. 1-3), two troglobites are found in the *richmondensis* group (*C. deurolfi*, and *C. grandimanus*), six in the *gracilis* group (*C. packardi*, *C. hobbsi*, *C. barri*, *C. castellanum*, *C. caecus* and *C. ohioensis*) and three are unassigned to groups (*C. antennatus*, *C. specus* and *C. lewisi*). In addition four species (*C. indianensis*, *C. insolitus*, *C. fontinalis* and *C. Cooperi*) are almost always found in subterranean waters (caves, seeps and springs) but are not troglomorphic. Finally, eight other species are also recorded from caves but most of them are predominately epigean and, with the exception of *C. forbesi*, are far more common in surface habitats. The fact that more than half the species of *Crangonyx* have been reported from subterranean waters is a good indication that this genus has a strong association with the subterranean environment (see Holsinger, 1994). The existence of different subterranean species in different species group also indicates that cave species have evolved in different lineages at different times, and possibly under different conditions.

There are at least two acceptable theories that explain the evolution of subterranean species. One is the relict theory (Barr, 1968), which states that caves have served as refugia. Preadapted species invaded and colonized caves in order to survive harsh environmental conditions at the surface, such as glaciation. The
relict taxa left in the caves are then isolated reproductively from their epigean relatives and become increasingly adapted to cave environments by evolving a troglomorphic facies. Many of the troglobitic species of *Crangonyx* found in the Appalachians and Interior Low Plateaus regions, which are close to areas glaciated during the Pleistocene, could be explained by this theory. The theory may also give us a fairly good idea of the time of cave invasion (obviously sometime during the Pleistocene).

The second theory considers the active role of the animals themselves. Troglobites evolved by active or passive colonization of caves by preadapted epigean taxa without the constraint of climatic changes. Under this theory the factor that triggers troglobite evolution is not dependent on harsh environmental conditions but there is a tendency for the animals to exploit new niches with available food resources (Howarth, 1987). This theory can also be used to explain the troglobites of *Crangonyx* that are found far to the south in Florida, such as *C. hobbsi* and *C. grandimanus*, presumably in areas not drastically affected by climatic changes in the Pleistocene. But many species living in the north can also be explained by this theory. For example, *C. setodactylus*, an epigean species with well developed eyes is also represented by a population living in a cave in northern Ohio. It has reduced eyes, and a slight reduction in pigmentation but shows no other morphological changes for cave life. The reduction of eyes suggests that populations of this species can probably change rather quickly when they move into the cave environment. Since it is usually found in surface habitats, its occurrence in caves is best explained by active colonization. Under the second theory troglobite evolution may occur at any time, and populations that enter caves may adapt rather quickly to subterranean waters as they evolve into troglobites.

Another explanation for the evolution of troglobites in the genus *Crangonyx* is that some species may be evolved from ancestors that are already troglobitic. This may be the case of *C. specus*, which is morphologically similar to *C. antennatus* and distributed just beyond the range of *C. antennatus* in eastern Kentucky. These species appear to have a recent common troglobite ancestor, with *C. specus* possibly originating through peripheral isolation, possibly in subterranean waters.

In most troglobitic amphipods, the eyes are either reduced to a few black specks or are totally absent. The most striking troglomorphy can be found in *C. hobbsi*, which may be more specialized morphologically than any other species of *Crangonyx*. Eyes are lost completely, antennae are elongate, appendages are attenuate, and no calceoli are found on antennae 2 of the male. For the other troglobitic species in the *gracilis* group, the eyes are not completely lost, and all are morphologically similar to each other except for *C. packardi*. It is possible that *C. packardi* evolved earlier than the others, inasmuch as its range presently crosses three physiographic regions and extends both east and west of the Mississippi River. Unlike other members of the *gracilis* group, the gnathopods of this species lack notch-serrated spine teeth.

To date, *Crangonyx* is the only subterranean amphipod found in the karst regions of Florida, where it is represented by *C. hobbsi* of the *gracilis* group and *C. grandimanus* of the *richmondensis* group. Both
species are almost always found living together but both are absent in the middle region of Florida; they occur in the north, north-central and extreme south. No obvious morphological differences are found between the populations of either species in the north-central and south. An explanation for the disjunct distribution of these two species is that there may be subterranean links between the northern and southern areas, allowing species to move, at least to some extent, between these regions by subterranean dispersal. The occurrence of only two subterranean amphipods in Florida is also intriguing. Especially, since Stygobromus, the largest genus of Crangonyctidae with more than 100 species, has never been found in Florida. Holsinger (1986) suggested two possible explanations for the presence of troglobitic species of Crangonyx. and absence of Stygobromus. in the karst regions of Florida: (1) the limestone region of Florida is geologically much younger than in most of the other North American regions (Cenozoic in age) and Stygobromus was already widely distributed in other regions prior to the relatively recent development of subterranean freshwater aquifers on the Florida peninsula. (2) there are several Crangonyx spp. living on the Coastal Plain just north of the Floridian karst, which could account for the occurrence on or near the Florida peninsula of potential ancestors of troglobitic Crangonyx. Besides the two subterranean species, epigean C. richmondensis, C. floridanus and C. serratus are also found in Florida. From the above it seems reasonable to suggest that after karst habitats of Florida became available for amphipod colonization, species of Crangonyx were present in this region, and the ancestors of C. hobbsi and C. grandimanus invaded subterranean waters and evolved into troglobites. Some populations of C. floridanus are also found in the same cave habitats with C. hobbsi and C. grandimanus, both in the northern and southern part of the state. They have greatly reduced eyes, but no other troglomorphic features, suggesting that populations of C. floridanus have recently invaded caves and are adapting rather quickly to the subterranean environments.

INTRODUCTION OF C. PSEUDOGRAICILIS AND C. FLORIDANUS TO AREAS OUTSIDE THEIR ESTABLISHED RANGES

Crangonyx pseudogracilis was first found outside North America in the London area in the 1930s (Crawford, 1937; Tattersall, 1937). It then became widely distributed in British freshwaters through migration into central and southern England and Wales, eventually spreading northward through Scotland (Gledhill et al., 1993). It is thought that this species was brought to Europe unwittingly by man (Hynes, 1955). In 1975 it was also found in a pond in Dublin, Ireland (Holmes, 1975). In 1979 it was first found in inland waters in the Netherlands in a limited area of the province of Groningen. From here, it gradually extended its distribution in a western and southern direction (Hautus and Pinkster, 1987; Pinkster et al., 1992). In the Dutch inland waters it inhabits all kinds of habitats such as rivers, canals, ponds, lakes, and
reservoirs, tolerating both fresh and brackish, clean and polluted waters. The successful distribution of this species in Europe is thought to be because of its high fecundity as compared to local species (Pinkster et al., 1992).

*Crangonyx floridanus* was recorded from a freshwater pond of the Tone River in Chiba Prefecture, Japan (see notes under the species description section of *C. floridanus*). The specimens were collected in 1992 and the pond is not far away from sea water.

How did the populations of *C. pseudogracilis* in the Europe and the population of *C. floridanus* in Japan get there from their original ranges in North America? One explanation of this is the ballast water theory, which is the transport of organisms in ballast water by ocean-going ships (summarized by Carlton and Geller, 1993). In their survey it was found that a total of 367 taxa were found in Japanese ballast water released in Oregon (Carlton and Geller, 1993). These studies found that the ships can take up and release ballast water in bays, estuaries, and inland waters and then release this water into similar environments elsewhere. There are also freshwater ballasts transferred to other freshwater endpoints (such as from Europe to the Laurentian Great Lakes, or vice versa).

*Crangonyx pseudogracilis* is found near the Coastal Plain and also near the Great Lake region of North America, so it is possible that some specimens were carried in ballast water to Europe. According to Dirk Platvoet (pers. comm.) all localities where *C. pseudogracilis* was first found in the Netherlands are in connection with a canal on which several shipbuilding companies are located. He found that many ships returning from transoceanic trips empty their ballast tanks in the shipyards. Apparently the amphipods survive in the ballast water of ships successfully and extend their distribution from there. The ballast hypothesis also explains why *C. pseudogracilis* occurs in Britain and Ireland.

The same theory also explains why *C. floridanus* is found in a freshwater pond in Japan. This pond is connected to the Tone River which flows to the sea, thus *C. floridanus* could have migrated from the ballast water inland to the ponds by following the river. There is no other good explanation for the occurrence *C. floridanus* in Japan. Both *C. pseudogracilis* and *C. floridanus* occur on the Coastal Plain of North America and could be very easily picked up by ships when they take on ballast water.

In North America, populations morphologically very similar to *C. pseudogracilis* are found in Arizona and Nevada. If they are bona fide *C. pseudogracilis*, one explanation for their occurrence in western North America is that they were transported by man in fish containers or on aquarium vegetation from eastern localities. However, the population from Page Spring Fish Hatchery in Yavapai Co., Arizona is a more likely candidate for this kind of introduction than the population in the Trukey River in Nevada. The alternative hypothesis is that these western population may be a genetically different but morphologically similar species.

In North America, *C. floridanus* was recorded from Colorado and Oregon far away from its distribution in eastern North America. One or more of the populations of *C. floridanus* found in Colorado
may have also been transported by man in fish transplant containers (Pennak & Rosine, 1976). The population of *C. floridanus* found in Oregon could, however, be explained by the ballast theory because the collections were made near Portland, which is a large inland port near the western coast of North America. Alternatively, these populations may represent new undescribed species that are morphologically similar to but genetically different from *C. floridanus.*
LITERATURE CITED


Craig, J. L. 1977. Invertebrate Faunas of Caves to be inundated by the Meramec Park Lake in eastern

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Notenboom, J. 1988. Phylogenetic relationships and biogeography of the groundwater dwelling amphipod...
genus *Pseudoniphargus* (Crustacea), with emphasis on the Iberian species. *Bijdragen tot de Dierkunde* 58: 159-204.


Shoemaker, C. R. 1933. Amphipod from Florida and the West Indies. *American Museum Novitiates*, 598:1-
24.


Smith, D. G. 1981. Selected fresh-water invertebrates proposed for special concern status in Massachusetts. Massachusetts Department of Environmental Quality Engineering, Division of Water Pollution Control. Westborough, Massachusetts. 26pp


Smith, D. G. 1988. *Keys to the freshwater macroinvertebrates of Massachusetts* (No. 3): *Crustacea Malacostraca* (crayfish, isopods, amphipods). Department of Environmental Quality Engineering, Division of Water Pollution Control. Westborough, Massachusetts. 58pp


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