Proceedings of the United States National Museum

SMITHSONIAN INSTITUTION • WASHINGTON, D.C.

Volume 123 | 1967 | Number 3602

The Crayfishes and Their Epizoötic Ostracod and Branchiobdellid Associates Of the Mountain Lake, Virginia, Region [1]

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The Mountain Lake Region, as here considered, comprises approximately 500 square miles (1290 square km) in Craig, Giles, and Montgomery Counties, Va., and Monroe County, W. Va. Here the altitude varies from 396 m (1300 ft) at New Castle, Craig County, to 1329 m (4363 ft) at Bald Knob on Salt Pond Mountain in Giles County. Waters draining from the area contribute to three major river systems—the New River flowing to the Ohio and Mississippi Rivers, the James River to Chesapeake Bay, and the Roanoke River to Albemarle Sound, N.C.

Except for a few sphagnum bogs, sinkhole ponds, and impounded streams, the only lentic habitat larger than a few feet in diameter is the oligotrophic Mountain Lake situated at an elevation of 1180 m,

[1] A contribution from the Mountain Lake Biological Station of the University of Virginia and the Department of Biology of the Virginia Polytechnic Institute. The branchiobdellid studies were supported by grants (NSF G-4439, G-9828, GB-372) from the National Science Foundation.

[2] Hobbs: Smithsonian Institution; Holt: Virginia Polytechnic Institute; Walton: Mountain Lake Biological Station.

with a surface area of 0.2 square km and a maximum depth of 31.5 m (Roth and Neff, 1964, pp. 5, 8). Of these, collections were made only in Mountain Lake.

The streams vary in size from tiny spring rills cascading over rocky and sandy bottoms to the 161-meter-wide New River, which courses with a moderate current over bedded limestone and discharges from 1186 to 35,228 cubic feet per second at the Eggleston Gauging Station (average annual minimum and flood flows from 1930 to 1958) (Ross and Perkins, 1959, p. 6).

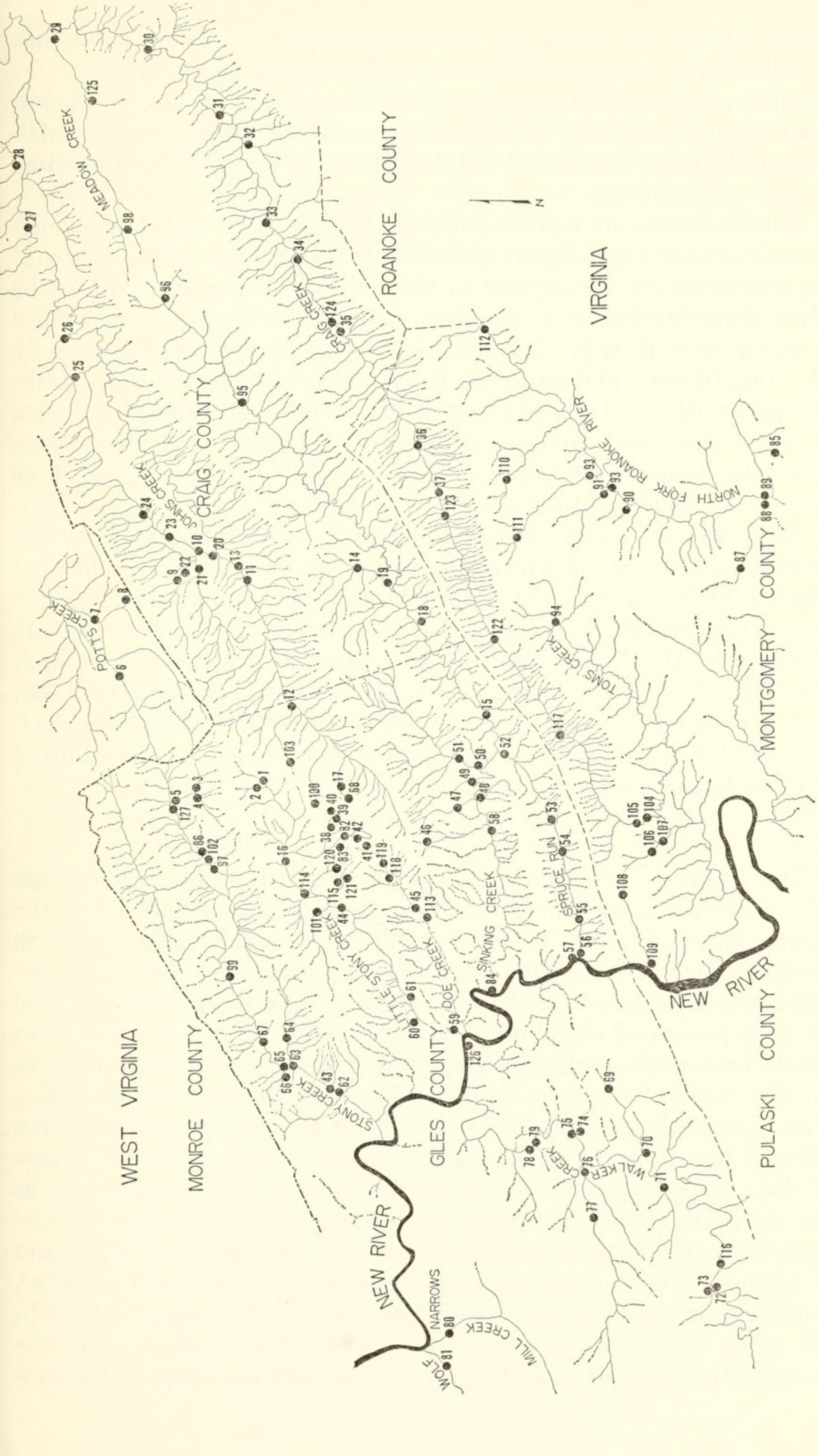
In much of the area, sandstones of the Silurian Age overlie Ordovician limestones and shales, and at higher elevations the waters flowing over the exposed sandstones have a total hardness of as little as 4 ppm. Some streams at lower elevations, passing over and through channels in calciferous rocks, accumulate soluble carbonates to the extent that in the larger valley streams the total hardness may attain concentrations of as much as 142 ppm (Shoup, 1948). In one stream (sta. 85) the M.O. alkalinity reaches 350 ppm.

The midsummer temperature of one of the springs (sta. 68) located at an elevation of 1219 m is 13° C, and that of the valley streams may rise to 26.7° C (Shoup, 1948).

Physiographic, hydrographic, and ecological data for several of the streams sampled in this study may be found in Burton and Odum (1945), Ross and Perkins (1959), and Shoup (1948).

Precise numbers of specimens examined during the course of the survey are not available; however, records include some 2700 crayfishes, 5200 ostracods, and 1600 branchiobdellids.

Collection techniques and disposition of specimens.—This study was initiated during the summer of 1960 and collections have been amassed during each of the succeeding summers through 1965. One hundred and twenty-seven stations (see map 1) were established in the area, and collections of the crayfishes were made by hand from open water or burrows and with the aid of minnow seines. In most instances all of the crayfishes collected from one station on a given day were killed in 6 to 10 percent formalin in a single container. In the laboratory, the ostracods and branchiobdellids were recovered from the bottom of the container and prepared for identification. All of the species (crayfish, ostracods, and branchiobdellids) found in that collection were considered to be associated and were so recorded. In instances wherein there was a question as to whether or not a particular ostracod species actually lived upon the exoskeleton of a particular species of crayfish, that species of crayfish was recollected, preserved alone, and the ostracods recovered from that collection were then known as associates. In that manner it was determined that the assumed associations were highly probable. In order to determine the abundance and distribution of certain sym-



Map 1.—The Mountain Lake, Virginia, Region with drainage systems and collecting stations referred to in this study.

bionts on the crayfish host, the crayfish was killed, dissected into units, and the specimens from each unit separately preserved.

Most of the crayfishes and ostracods on which this study is based are in the collections of the U.S. National Museum; the branchiobdellids are in the collection of Holt, but most of these will be deposited in the same museum.

Presentation of data.—Brief discussions of the habitat, population sizes and fluctuations, and food habits of each of the three groups precede the sections devoted to the individual species. Within the discussions devoted to each group, brief accounts of the anatomical features utilized in the identification of the species are followed by illustrated keys and generic diagnoses. For each species, a diagnosis, the range, the distribution in the area, and the drainage systems, range of elevations, and associates are presented. Data relative to associations are summarized in table 1, and a discussion of those associations concludes the study.

Acknowledgments.—We should like to express our appreciation to the following persons who assisted us on one or more of our collecting trips in the Mountain Lake region: Messrs. Paul Buhan, J. E. Carico, C. J. Freeman, R. H. Gilpin, H. H. Hobbs, III, H. A. James, E. P. McConnell, Dr. F. A. Marland, Mr. Homer Mumaw, Dr. John J. Neal, Jr., Dr. Jean E. Pugh, Miss Lucile Walton, Mrs. Shirley Wells, and Miss Mary Lou Wood. Also, we are grateful to Dr. Robert D. Ross for his discussions of stream piracy and problems of distribution of fishes in the area.

The Habitats

The crayfishes.—Of the six species and subspecies of crayfishes in the area, four vie for the habitats provided by tributaries of the James River (Hobbs, 1951). In the uppermost reaches of both headwaters and lateral tributaries, almost without respect to altitude, *Cambarus b. bartonii* is the sole inhabitant and utilizes cover provided by rocks, roots of shoreline plants exposed in the water, and most debris occurring within the stream bed. As the stream begins to exhibit alternating riffles and pools, in contradistinction to cascading areas and pools, *C. l. longulus* takes over the major portions of the riffles while *C. b. bartonii* occupies the pools and takes advantage of the rock cover along the margins of the riffles. Downstream, as the alternating pool and riffle areas become more pronounced and more extensive, *C. acuminatus* replaces *C. b. bartonii* in the pools and is frequently abundant immediately above and below the riffles, utilizing, for the most part, cover provided by the larger rocks. In the areas where the three may be found, *C. b. bartonii* seeks the marginal portions of both the riffles and pools and frequently constructs tunnels in the bordering banks. As might be expected, none of the three recognizes any absolute limits such as suggested, and occasional individuals of each may invade the ecological niche of the other two. To what extent these invasions are due to individual wanderings, intraspecific population pressures, or interspecific pressures, is not known. Of the three there seems to be little doubt that *C. l. longulus* is ecologically more restricted than either of the other two. At lower elevations, particularly in the larger streams in which there are larger rocks in the riffle areas, *C. acuminatus* not only appears to compete with *C. l. longulus* but frequently replaces it. *C. b. bartonii* undoubtedly has the broadest ecological tolerance, and in the New River drainage, where it is not in competition with *C. l. longulus*, it is as abundant in the riffle areas as in the pools and marginal portions of the stream. Furthermore, in the tidewater areas of Virginia, *C. b. bartonii* is found not only living in the smaller streams but also burrowing in swampy areas along the margins of streams. In the Roanoke drainage system, the ecological distribution of *C. b. bartonii*, *C. l. longulus*, and *C. acuminatus* is not unlike that indicated in the James River drainage above; however, the headwater streams are not at such high elevations.

The fourth species, *Orconectes juvenilis*, occurs in two quite dissimilar habitats in the Mountain Lake area. At the present time it is the only crayfish found in Mountain Lake itself, and apparently it is found in most of the littoral zone, where adequate cover exists in the form of stones and rubble. In the single Potts Creek locality, it occurs primarily in precisely the same types of habitats in which *C. acuminatus* is found elsewhere in the James drainage, and in addition it has invaded the riffle zones frequented by *C. l. longulus*. In the portion of the New River system treated here, *O. juvenilis* is restricted to Mountain Lake, having been introduced there in 1933 (Hobbs and Walton, 1966a). *Cambarus b. bartonii* and *C. sciotensis* share the remainder of the watershed in the area. As in the James drainage, *C. b. bartonii* is the sole inhabitant of the headwater streams, and downstream, where it encounters populations of *C. sciotensis*, it is confined to the marginal regions, but even there, apparently it competes for cover with the latter. In Little Stony Creek, both species occur up to the level of station 44, where the cascades serve as a barrier to *C. sciotensis* (and probably to the upstream migration of *C. b. bartonii* as well); above the cascades, *C. b. bartonii* is the sole crayfish inhabitant and it occupies all portions of the stream bed. In accessible areas of the New River system, it appears that *C. sciotensis* vicariates for *C. acuminatus* and in part for *C. l. longulus*.

While all the crayfishes of the area demonstrate some burrowing tendencies, only *C. carolinus* spends the greater part of its life living in burrows or wandering over land on humid evenings. In all of our collections no specimen has been collected from a stream, pond, or puddle, and most were found at night either wandering above ground or were taken from the mouths of their burrows. A few were dug from their branching burrows.

In the smaller creeks, *C. b. bartonii*, *C. l. longulus*, and *C. acuminatus* all burrow in the stream beds during the winter months as they do if the water level in the streams becomes low at other seasons. Seldom does *C. b. bartonii* seem to be content simply to crawl beneath a rock unless it is a rather large one. Even then evidence of excavation may be seen. *Cambarus sciotensis*, *C. acuminatus*, and *O. juvenilis* apparently exert far less effort in digging than do *C. b. bartonii* and *C. l. longulus*, but neither of the latter is so typically associated with burrows as is *C. carolinus*.

The ostracods.—With only one exception (*Uncinocythere biscuspide* on a freshwater crab of the genus *Pseudothelphusa* in Mexico: Hobbs and Villalobos, 1958, p. 395), ostracods of the subfamily Entocytherinae seem to be confined to the exoskeleton of crayfishes. Marshall (1903) reported *Entocythere cambaria* from the gill chamber of a crayfish collected at Madison, Wisc. In 1926, Sars described *Cytherites insignipes* (the second known member of the subfamily) from three female specimens collected in Canada but had no further data for them. Klie (1931) described *E. donnaldsonensis* (=*Donnaldsoncythere donnaldsonensis*) from Donaldson's Cave, Lawrence County, Ind., but did not indicate that it was associated with a crayfish. Rioja (1940a, pp. 593, 594; 1941, pp. 193, 194) indicated that the habitat of *E. heterodonta* (=*Ankylocythere heterodonta*) is quite different from that of Marshall's species inasmuch as the animals are found rarely in the branchial chamber; instead, most of them occur on the outer surface, clinging to the setae. Dobbin (1941, p. 185) reported her *E. columbia* (=*Uncinocythere columbia*) "from crayfish branchiae." Hoff (1942, pp. 63–65) implied that the primary infestation of the ostracods is in the gill chambers of the crayfish, for, in his "Methods," he indicated that "the ostracods will leave the gills of the host if the crayfishes are placed in a vessel containing 95% ethyl alocohol." He did not indicate that he found them elsewhere on the crayfish, but he did state that he found them "in the water of crayfish burrows." Kozloff and Whitman (1954, p. 159) reported that *E. columbia* and *E. occidentalis* (=*U. columbia* and *U. occidentalis*) "occur principally among the cuticular hairs on the ventral side of the thorax of the host, but a few are found among the mouth parts and on the branchiae." Kozloff (1955, p. 156) indicated that *E. erichsoni* and *E. caudata* (=*U. erichsoni* and *U. caudata*) that remained on their hosts after preservation "were found primarily among the cuticular hairs on the ventral side of the thorax. A few were taken from the mouth parts." In studying the incubation and hatching of the eggs of *E. illinoisensis*, Stamper (1957, p. 50) reported that 90 percent of the crayfishes examined carried eggs of the ostracod "attached to the hooked setae and/or the coxal filaments. Both of these structures are located underneath the carapace of the crayfish." Westervelt and Kozloff (1959, p. 239) stated that *E. neglecta* (=*U. neglecta*) occurs principally on the same areas of the crayfish as *U. erichsoni* and *U. caudata*.

Two of us (Walton and Hobbs) have attempted to discover whether or not several of the species in the Mountain Lake area are limited to certain anatomical regions of their crayfish host. As might be expected, they are not found on exposed surfaces except where there are setae to which they may cling or grooves in which they may obtain support. Particularly do they seem to congregate on the gnathal appendages, where, on occasional crayfishes, scores of them may be found moving about or clinging to the setae. Far fewer individuals are found among the articular membranes and setae associated with the ambulatory appendages, but certain species are more abundant on the abdomen. Not one ostracod has been observed in the branchial chambers of the crayfishes examined! There seems to be no absolute specificity of microhabitat on the crayfish for any of the ostracods observed although if two or more species occur on the same crayfish, as they frequently do, one may be found more abundantly in one area than elsewhere. We have found, for example, that in the associations of *Ascetocythere asceta* and *Dactylocythere chalaza* on *Cambarus carolinus*, the latter is more abundant on the abdomen and *As. asceta* among the gnathal appendages.

None of the ostracods in the Mountain Lake area occurs in all parts of any of the drainage systems and, although they are obviously subject to restrictions, no analytical data are available to demonstrate the nature of these limiting factors. Two of the species, *As. asceta* and *Dt. chalaza* are confined to the exoskeletons of the burrowing crayfish, *C. carolinus*, which tunnels its way to ground water. Whether it is the absence of competition with other ostracods, the groundwater habitat, an obligate relationship with the crayfish, or a combination of, or none of, these factors that is restricting these ostracods remains to be demonstrated. Altitudinal correlations exist with at least two of the species—*Donnaldsoncythere scalis* has not been found below approximately 670 m, and *Ankylocythere ancyla* above 475 m; however, it is unlikely that altitude is serving directly as a barrier to them. To our knowledge, not a single limiting factor in the ecological distribution of any entocytherid has been identified.

If, as generally conceded at the present time, the ostracods of the

Entocytherinae are not parasitic on their crayfish hosts, there seem to be few reasons why one might expect host specificity to have developed. Nevertheless, there are a few species that have been found only on one host. This apparent specificity is more probably related to the the habitat of the crayfish than to other factors, for in most of these associations a burrowing crayfish is involved, either *C. carolinus* or *C. d. diogenes*. Of the nine species of the genus *Ascetocythere* (see Hobbs and Hart, 1966), five of them have been found only on *C. carolinus;* both species of the genus *Plectocythere* are restricted to the same crayfish; and the three species of the genus *Geocythere* (see Hart, 1959, 1965) and the monotypic *Rhadinocythere* (see Hart, 1965) have been found only on *C. d. diogenes*. In the Mountain Lake region, *As. asceta* and *Dt. chalaza* share a single host, *C. carolinus*.

THE BRANCHIOBDELLIDS.—The branchiobdellids are epizoites known from several holarctic freshwater crustaceans, principally decapods of the family Astacidae, but they have been recorded from freshwater crabs (Hobbs and Villalobos, 1958, p. 395; Holt, 1964, p. 2), freshwater shrimp (Liang, 1963, pp. 569, 570), and a cave isopod (Holt, 1963, p. 99). All attach to the exterior surface of the host by means of a posterior sucker and move from place to place on the host's body in a leechlike fashion, using the peristomium as an anterior sucker. All of the branchiobdellids considered here are from crayfishes.

Most species of branchiobdellids are not found in all parts of the streams of a drainage system in which they occur. There are, presumably, ecological factors regulating such distributional patterns; but in general it is not known what these factors are, though Berry and Holt (1959, p. 7) showed a difference in the temperature responses of *Xironogiton instabilius* and *Xironodrilus formosus,* which suggests that an intolerance of high temperatures may operate in confining *Xg. instabilius* to the colder streams of higher elevations.

The occurrence of several species of branchiobdellids (as many as six) on the same host animal has raised the question as to whether or not a particular species is confined to a specific part of the body of the host. Holt (1954, p. 170) first called attention to the problem presented by the possible existence of microhabitats for branchiobdellids on the crayfish hosts. McManus (1960, p. 422) studied three species of branchiobdellids, *Xg. instabilius, Cambarincola philadelphica,* and *C. fallax,* all of which occur in the Mountain Lake area) from Fall and Cascadilla Creeks in New York, and his observations are in accord with those of Brown (1961, p. 25), who has studied, from Sinking Creek, the microhabitats of 6 of the 12 species of branchiobdellids that occur in the Mountain Lake area. Though a more rigorous control of his statistical procedures would have been desirable, there is no reason to doubt his general conclusions: (1) the microhabitat of *C. branchiophila* is within the gill chambers of the crayfish; (2) *Ankyrodrilus koronaeus* (his species X) is primarily an inhabitant of the chelipeds; (3) *Pterodrilus alcicornus* is randomly distributed over the ventral surface of the crayfish; (4) *C. fallax* is essentially confined to the basal segments of the pereiopods and antennae; (5) *C. ingens* occurs principally upon the ventral surface of the abdomen and along the cervical groove, but competes with *C. fallax* so that, when one species is common upon a crayfish, the other is rare; (6) *Xg. instabilius* is found almost always on the chelipeds. Of the other species included in this study, *Bdellodrilus illuminatus* is known beyond doubt to be a gill-inhabiting form; it is assumed that the microhabitat of *A. legaeus* is that of its congener and that these two species are allopatric; *Xd. formosus*, on the basis of our field experience, is a species of the exterior surface of the branchiostegites of the crayfish; and little or nothing can be said of the microhabitats of the remaining species (*C. heterognatha*, *C. philadelphica*, and *C. holostoma*), though we suspect that *C. philadelphica* and C. *holostoma* may occupy essentially the same microhabitats as *C. fallax* and *C. ingens*.

Goodnight (1940, p. 65) and McManus (1960, pp. 424–427) have, among others, considered the question of host specificity among the branchiobdellids. Goodnight reviewed the host records presented by previous workers and said, "In short, within the limits of the range of any branchiobdellid any crayfish may serve as host." McManus found it surprising that branchiobdellids should have the broad ecological tolerances attributed to them and attempted to study this problem in New York from an area where there are three species of branchiobdellids and four of their crayfish hosts. He found very few worms and no cocoons on *Orconectes p. propinquus*, confirmed by experimental procedures that *O. immunis* is an unsatisfactory host for *Cambarincola philadelphica* and *C. fallax* (lumped together by him as *Cambarincola* species), noted that all subadults and adults of *Cambarus robustus* carried either worms or cocoons, and observed that *C. b. bartonii* is very commonly infested. Lytle (pers. comm.) reports a similar finding for branchiobdellids from central Pennsylvania.

Populations

The crayfishes.—No quantitative data on crayfish populations in the area are available, but it is readily apparent that population sizes vary tremendously from stream to stream and even from year to year in corresponding seasons. Unfortunately, in this study observations were largely confined to the summer months, and most seasonal fluctuations, if they occurred, might well have escaped detection. Admittedly, in certain instances the fluctuations are more apparent than real; for example, it is highly unlikely that there are fewer individuals of *Cambarus l. longulus* in a given riffle area in January than in April. Utilizing the usual collecting techniques, however, it is very difficult to obtain even a dozen specimens during the winter months; in the early spring the collectable individuals are mostly males and yearling females; a little later in the spring the adult females appear in the population so that an approximation of the population size cannot be obtained until late spring. In late fall the population begins to diminish in size and by winter it has almost disappeared. This fluctuation is obviously a result of the habits of the species in burrowing below the frostline before the stream freezes and, although the males and yearling females emerge in early spring, the adult females remain in the burrows until their eggs (laid in late winter or early spring) have hatched and the young have left or are ready to leave their mothers. Although year-round data are not available on any of the crayfishes in the Mountain Lake area, Smart (1962) and one of us (Hobbs) have not observed appreciable changes in populations in Swift Run in Greene County, Va., over a 10-year period.

In contrast to the seasonal fluctuation of populations of *C. l. longulus*, the collectable population of *C. sciotensis* in Sinking Creek exhibits little fluctuation throughout the year and from year to year, and the same is true for many populations of *C. b. bartonii*.

Adequate data are not available to assess the population sizes in various localities, but possible effects of competition are emphasized in (1) the natural experiment in Little Stony Creek above the Cascades, which *C. sciotensis* has not been able to ascend (here, without competition, *C. b. bartonii* occurs in much larger numbers than in similar streams where it occurs with *C. sciotensis*), and in (2) Mountain Lake, where the introduced *O. juvenilis* has displaced the introduced *C. acuminatus* and the native *C. b. bartonii* (Hobbs and Walton, 1966a).

Perhaps the most exciting observations of competition between species in the area are those that are in progress in Potts Creek. In 1960, two of us (Hobbs and Walton), together with several others whose help has been acknowledged above, visited station 7 and within a few minutes collected 12 specimens of *C. b. bartonii*, 10 of *C. l. longulus*, and 12 of *O. juvenilis*. In 1965, one of us (Walton) returned to this locality and this time collected 94 specimens of *O. juvenilis* and a single specimen of *C. b. bartonii;* not one individual of *C. l. longulus* was to be found! There is no record of *O. juvenilis* having been intentionally introduced into the headwaters of Potts Creek and presumably fishermen collecting their "crawfish bait" in West Virginia released excess animals in the creek, thus stocking a population that not only has become successfully established but is in the process of replacing the native species as it has done in Mountain Lake. In an earlier draft of this paper, we wrote concerning the Potts Creek locality, "Here, in the single known locality, it [*O. juvenilis*] was found with *C. b. bartonii* and *C. l. longulus* but occurring in an area that might well have been inhabited by *C. acuminatus*. This is perhaps significant in light of the account of the occurrence of *O. juvenilis* in Mountain Lake." With the apparent expulsion of most of the *C. l. longulus* population by 1965, the supposed eradication of *C. acuminatus* prior to 1960, and the apparent inroad on the *C. b. bartonii* population during the intervening 5-year period, the possibility of a rapid spread of *O. juvenilis* in the James drainage system might well be anticipated. Also worthy of note is the fact that, as in Mountain Lake, *C. acuminatus* was supposedly supplanted first, and *C. b. bartonii* is now very poorly represented in the crayfish population. (See further remarks under *O. juvenilis*.)

In 1966, Hobbs and Walton again visited this locality and collected 71 specimens of *O. juvenilis*, 6 of *C. l. longulus*, and 2 of *C. b. bartonii*. Concentrated efforts in selected riffle areas were required to obtain the specimens of *C. l. longulus*, and it seemed obvious to the two of us that there can be no question that the *C. l. longulus* population has been reduced and that the *C. b. bartonii* population has either been reduced or has largely retreated to burrows along the banks of the creek. We do not yet know the range of *O. juvenilis* within Potts Creek but 10 miles downstream from Waiteville, where Route 17 crosses the Creek, the large riffle area there is largely populated by *C. l. longulus*, but *O. juvenilis* is also present. *Cambarus b. bartonii* and *C. acuminatus* were not found. With the absence of the latter, it is probable that even that far downstream, *O. juvenilis* is vicariating for *C. acuminatus*.

It seems unlikely that in any part of the region a lack of food is responsible for depauperate populations, and even in waters low in calcium the crayfishes do not seem less abundant than in those high in calcium. One of the chief limiting factors seems rather to be available cover in the way of loose rocks (as opposed to bedrock), debris, and suitable banks into which the crayfish may burrow. For example, in suitable riffle areas within the range of *C. l. longulus* (James and Roanoke drainages), populations proportional to the size of the riffle and number of rocks of diameters greater than 10–100 mm have been invariably encountered. In contrast, in areas where the water flows rapidly over scoured bedrock, not a specimen of *C. l. longulus* or any other crayfish is to be found. Except in the upper portions of streams that are subject to being converted to a series of pools in dry seasons (such as the upper portion of Craig Creek, sta. 122), the oxygen content (sometimes a limiting factor) of most of the streams in this area approaches saturation throughout the summer.

The only known instance of actual fluctuation of a population in the area is one of *C. sciotensis*, which occupied the riffle area on Sinking Creek just below the bridge on State Route 700. Since this is a readily accessible area for obtaining crayfishes for experimental work at the Mountain Lake Biological Station, hundreds of specimens were removed during one summer, and the following spring, hours of work in the riffle revealed very few adult individuals. It was not until early fall that the population seemed to have recovered.

THE OSTRACODS.—Although the population size of ostracods on a single crayfish is unpredictable, there are few crayfishes in this area that do not harbor a number of ostracods. A single female specimen of the burrowing crayfish, *Cambarus carolinus*, was infested with 238 ostracods (*Dactylocythere chalaza* and *Ascetocythere asceta*); however other individuals of the same species from the same locality had as few as a dozen. Thirty-five ostracods were recovered from a specimen of *C. b. bartonii* with a carapace length of only 14 mm.

It is not known at what age the young crayfish may become infested but apparently they are susceptible to harboring the ostracods within a short time after leaving the parent. The smallest crayfish observed to be infested was *C. b. bartonii* with a carapace length of 12 mm carrying a single individual of *Donnaldsoncythere scalis*.

Repeated observations of infestations of "soft" crayfishes examined shortly following a molt indicate that the ostracods respond to the molt by leaving the old exoskeleton and making their way to the new one. This reinfestation is undoubtedly more nearly assured because of the fact that in this area most of the crayfishes devour their old exuviae, thereby bringing any ostracod remaining on it close to the vulnerable gnathal appendages of the freshly molted host.

It is not known how crayfishes become infested nor are data available to indicate that the population of ostracods increases with time following a molt or that population size diminishes with a molt.

In some portions of the area, a single crayfish may be infested with only one species of ostracod, but, more frequently, at least two species, and often more, occur on a single host; in such instances, they may tend to be concentrated on one area of the host's exoskeleton but there are other associations in which one of the ostracods may occur with equal frequency on the setae of the gnathal, ambulatory, or natatory areas.

Many of the ostracods are infested with peritrichous ciliates; colonial (Epistylidae) and solitary stalked forms are found on the appendages between the valves, and the external surfaces of the valves are often inhabited by members of the family Urceolariidae.

THE BRANCHIOBDELLIDS.—Branchiobdellids may occur in large numbers on a single adult crayfish and there are few crayfish in the area that do not carry at least a few worms. Brown (1961, p. 7, table IV) collected 100 crayfish from Sinking Creek and recovered from them an average of 106 worms of all species per crayfish. This is, by far, too high an average for all the crayfish in the stream since Brown chose only large and not recently molted crayfish for his studies.

In this study, we present under "Specimens Examined" the number of animals actually studied, selected in most cases from much larger numbers. The collecting methods we used were not such as to allow us readily to determine the number of worms per crayfish, but several times one of us (Holt) has counted over 200 worms from a single crayfish from other areas.

Little is known as to seasonal fluctuations in branchiobdellid populations. Young (1966, p. 576) has found that branchiobdellid populations decline in the winter, which is in agreement with our experience that, when crayfish can be taken, branchiobdellids and their cocoons are almost always present. Some exceptions to this are known: in streams polluted with waste from coal mines, branchiobdellids disappear before crayfish do; although crayfish (*C. b. bartonii*) are present in the upper reaches of Little Stony Creek above the Cascades, branchiobdellids are often rare, perhaps because of the effect of severe winter temperatures or of lowered pH values in the boggy headwaters of the stream; and branchiobdellids are usually absent from recently molted crayfish and almost invariably so from very small animals. The scanty available evidence, then, is not adequate to form a basis for statements about fluctuations of branchiobdellid populations.

Little is known likewise about methods of infestation, and what is known is due mostly to the efforts of McManus (1960, pp. 422–424). He found that the worms apparently do not move to the host when the old exoskeleton is shed in molting and that the young crayfish are not infested with worms for some time after leaving their mother, conclusions supported by our observations and those of Young (1966, pp. 573–574). Apparently crayfish obtain worms when they come in contact with another animal bearing them. It must be noted, however, that these conclusions are not in accord with ours concerning the infestation of crayfishes by ostracods. Especially striking is the presence of ostracods and the absence of branchiobdellids on freshly molted hosts.

As is true of the ostracods, the epizoic branchiobdellids carry in turn their burden of epizoites: peritrichous protozoans. In addition, some of the larger branchiobdellids of the area are parasitized by an unidentified organism, which is found usually as a spherical mass embedded in the worm's body wall tissues. Protozoologists who have seen this parasite think it may be a fungus; mycologists have shown a preference for regarding it as a protozoan. Nothing else is known of it.

Food Habits

The crayfish.—No concentrated effort has been made to determine what the crayfishes of the area feed upon, but on the basis of a few observations it seems that the chief item of their diet is decaying plant fragments. Both in the laboratory and in the streams, the crayfish seem readily to accept whatever animal material becomes available; occasional individuals have been observed feeding on fish and insect larvae and not a few on crayfish of the same or different species. In the laboratory, they do not scorn fresh plant material such as lettuce. Crayfishes are as nearly omnivorous as any animals ever observed by us.

The ostracods.—Marshall (1903, p. 118), who described the first known member of the family, *Entocythere cambaria*, was of the opinion that this ostracod lived in the gill chamber of the crayfish host, where it fed on the readily accessible blood flowing through the branchiae. In contrast, Rioja (1940a, p. 593) indicated in connection with his description of *E. heterodonta* (=*Ankylocythere heterodonta*) that this ostracod is rarely found in the gill chamber of the host and that he considered the members of this genus to be "simple epizoario," taking issue with Marshall's belief that *E. cambaria* is a parasite. Rioja (1940b, p. 58) reiterated the opinion that *An. heterodonta* is an epizoötic commensal. In 1941 (p. 194) Rioja, in discussing the same species, indicated that he had observed the feeding process, which involved the use of the terminal claws of the feet and the apical claws of the second antenna in passing "detritus diversos" to the mouth. Hoff (1942, p. 64) also questioned the fact that Marshall's species was parasitic, indicating that Marshall's deduction "based on the belief that the homogeneous mass of material in the intestine of the ostracod is the blood of the host . . . is not valid proof . . . since a homogeneous food mass is found as well in many free-living ostracods." He summarized the situation as follows:

> That the Entocythere species do feed on material in the water is evidenced by the finding of diatoms and other particulate organic materials in the gut. That the organisms are not strictly parasitic is also shown by the fact that they often for some reason leave the host. Individuals have been found by the writer in the water of crayfish burrows and by Klie (1931) in Indiana cave waters. All of the Entocythere species are probably commensal, but at the very most, if parasites at all, are only facultative.

Our observations support Hoff's conclusions and those of Rioja: in living animals both the mandibles and maxillae with their branchial plates seem constantly to be in motion receiving finely divided particles passed to them by the second antenna. The terminal claws of the latter collect the particles entrapped by the setae of the host. Fecal pellets contain mostly a finely divided brown material (the origin of which is not known), small translucent refractive fragments, portions of diatoms, small rods (presumably bacilli), and what are believed to be spore cases. Furthermore we have not observed a single ostracod among the gill filaments, where, were they parasitic, they would most likely occur.

THE BRANCHIOBDELLIDS.—There is a persistent tradition that branchiobdellids are parasitic; this is certainly not true of most species, but almost surely it is true of the gill-inhabiting forms. Smallwood (1906, p. 100) found the gut of *Xironogiton instabilius* always full of algae and thought he found the same for *Bdellodrilus illuminatus.* Since the latter is confined to gill chambers, Smallwood probably was dealing instead with a species of *Cambarincola* that is not gill-inhabiting. Hall (1914, p. 189), on the basis of pieces of striated muscle fibers found in the lumen of the intestine, reported that adults of *Ceratodrilus thysanosomus* are parasitic. These fibers, however, probably were derived from ingested insect larvae rather than from the hosts. Goodnight (1940, p. 66) reviewed these and other similar comments and added his opinion that diatoms are the "favorite" food of most species. The truth is that no careful studies of the food and feeding habits have been made. It can, nevertheless, be said of the species encountered in the present study that *Bdellodrilus illuminatus* is parasitic, feeding on the gill filaments of the host; probably the same is true of *Cambarincola branchiophila. Pterodrilus alcicornus* is particularly partial to diatoms, which constitute the vast bulk of the food of this species. The larger species of *Cambarincola* show carnivorous and cannibalistic tendencies as well. Whether or not the other species of the area have a specialized diet cannot be said, for all branchiobdellids, except the gill-inhabiting parasites, appear to feed simply by grazing on the unicellular algae, bacterial gloea, and the animals, except the ostracods, that make up the flora and fauna that are borne by crayfishes.

The Crayfishes

The key that is provided for the identification of the crayfishes of the region can be used reliably only in the immediate area. In order to facilitate the rapid identification of specimens of both sexes, the secondary sexual characters that are definitive for generic determinations, and some specific ones as well, have been disregarded.

The male crayfishes of the area, like all members of the subfamilies of the Astacidae except the Astacinae, exhibit a cyclic dimorphism

(Hagen, 1870, p. 21) affecting principally the first pair of pleopods, the hooks on the ischiopodites of the third pereiopods, and the cheli-peds. In the breeding males, "Form I," the first pleopod has one corneous terminal element, and the hook of the ischiopodite of the third pereiopod is developed more strongly and usually more acutely; the cheliped is usually more robust and frequently the crayfish is more vividly colored (ignoring the fact that all freshly molted crayfishes are more brightly colored than at any other time.) The nonbreeding males are designated "Form II."

The life cycle of *Cambarus l. longulus* (see Smart, 1962) is better known than that of any of the other species in the area, and it appears that it does not differ, except perhaps in details, from that of *C. acuminatus* (see Word and Hobbs, 1958, p. 436) and *O. juvenilis*. The young of *C. l. longulus* hatch from the egg in early spring, undergo a series of molts through the summer and fall but cease to grow through-out the winter. The following spring, growth resumes and in Septem-ber juvenile males molt to the breeding stage (Form I). The first breeding season extends from late fall to spring when the male molts to the nonbreeding stage (Form II). In September it again molts to the first form and passes its second breeding season, molting to the second form in the spring. Most of the males die after the second breeding season but a few undergo one additional molt to the first form in the fall and die in the spring. Females carry their eggs during the late winter and early spring; however, an occasional female will be found in midsummer with a full complement of eggs on the pleopods. It is obvious, on the basis of this brief account, that first form males of *C. l. longulus*, *C. acuminatus*, and *O. juvenilis* are abundant in the late fall, winter, and early spring but are rare at other seasons.

In contrast, first form males of *C. sciotensis*, *C. b. bartonii*, and *C. carolinus* may be collected at almost any time during the year, and females with eggs occur, for the most part, during the summer and fall months. Almost no life history data are available for *C. carolinus* and *C. sciotensis*.

Additional data for all of the crayfishes treated here may be found in the indispensable contributions of Ortmann (1905, 1931).

Key to Crayfishes

1 Rostrum with marginal spines; first pleopod of male terminating in two straight rami . . . . **Orconectes juvenilis**

1′ Rostrum without marginal spines; first pleopod of male terminating in two short rami that are recurved at angles of approximately 90°. **Cambarus** . . 2

2(1′) Fingers of chela with weak longitudinal ridges above, broadly gaping and with a conspicuous tuft of setae in gap; rostrum with much thickened, convergent margins; areola with crowded, deep punctations. **C. l. longulus**

2′ Fingers of chela with well-defined longitudinal ridges above and fingers seldom broadly gaping; if so, then no conspicuous tuft of setae between them; rostral margins may or may not be thickened but, if so, never strongly convergent; areola usually with scattered punctations, if crowded, never deep 3

3(2′) Lateral surfaces of carapace with a strong spine on each side immediately posterior to cervical groove; rostrum with margins gently converging mesially along almost entire length; postorbital ridges with spines. **C. acuminatus**

3′ Lateral surfaces of carapace with or without a well-developed tubercle on each side immediately posterior to cervical groove but never with a strong spine; margins of rostrum always suddenly contracted at base of short acumen; postorbital ridges never with spines at anterior extremities. 4

4(3′) Rostrum with thickened subparallel margins suddenly contracting to form right angles (in mature specimens) at base of acumen . . **C. sciotensis**

4′ Rostrum with slender or moderately thickened margins that never form right angles at base of acumen, angles obtuse or contractions rounded . 5

5(4′) Areola at least eight times longer than broad; inner margin of palm of chela with cristiform row of tubercles flanked above by at least one or two additional tubercles; color red; and seldom found outside of complex burrows except in evenings after heavy rains when they wander over land . . . . **C. carolinus**

5′ Areola never so much as eight times longer than broad; inner margin of palm of chela with single row of appressed tubercles with occasional two or three scattered tubercles flanking it above; color shades of tan, green, or blue but never red; usually found in flowing water under stones or debris or in burrows along banks of streams or ponds. **C. b. bartonii**

Genus *Cambarus* Erichson, 1846

DIAGNOSIS.—Hobbs (1965, p. 267) stated:

First pleopod of first form male symmetrical and terminating in two or three distinct parts, usually only two (mesial process and central projection) bent caudally or caudolaterally with principal axes of shaft and each ramus forming angles of approximately 90 degrees; if mesial process and central projection directed at angles of less than 90 degrees to main shaft, central projection never comprising more than ⅛ of total length of appendage or bent at angle of less than 45 degrees; central projection corneous and flattened laterally; mesial process mostly non-corneous, frequently inflated; caudal process, when present, forming knob-like prominence at caudolateral base of central projection. Hooks present on ischiopodites of third pereiopods only except in *Cambarus dissitus* Penn (1955, p. 73) in which also present on those of fourth pereiopods. Opposable margins of ischiopodites of third maxillipeds with teeth.

Cambarus acuminatus Faxon

FIGURE 1

Cambarus acuminatus Faxon, 1884, p. 113.

DIAGNOSIS.—Margins of rostrum gently converging from base to apex, not thickened, and without marginal spines; areola never more than six, usually three or four, times longer than broad with many shallow punctations; suborbital angle acute. Chela with subovate fingers bearing distinct median longitudinal ridges on upper surfaces; fingers not conspicuously gaping and never provided basally with conspicuous tuft of setae; inner margin of palm with two well-defined rows of prominent tubercles.

RANGE.—Atlantic watershed from southern Maryland to South Carolina in the lower mountains, piedmont, and upper coastal plain.

SPECIMENS EXAMINED.—Approximately 235 specimens in 25 collections from tributaries of the James River and North Fork of the Roanoke River in Craig and Montgomery Counties, respectively (sta. 20, 27, 29–33, 35, 87–93, and 112) at altitudes from 402 to 535 m.

ASSOCIATES.—*Cambarus acuminatus* was collected with *C. l. longulus* at all of the stations except 87 and with *C. b. bartonii* except at 20, 27, 30, 31, 33, 88, 112.

In the James drainage, ostracod associates include *Dn. ardis* at stations 20, 27, 30–33, 35; *Dn. ileata* at 20, 29, 31–33, 35; *Dt. suteri* at 27, 30, 31, 33, 35; *E. internotalis* at 30, 31, 35; and in the Roanoke drainage the latter at 88, 90; *An. ancyla* at 88, 89, 92, 93; *Dn. truncata* at 87, 88, 90, 91, 93; and *Dt. falcata* at 87–93, 112.

In the James drainage branchiobdellid associates include *C. philadelphica* at stations 20, 27, 29, 32, 33, 35; *A. koronaeus* at 29, 30; *C. branchiophila* at 20, 29; *B. illuminatus* and *C. holostoma* at 20; and in the Roanoke drainage *A. koronaeus*, *C. branchiophila*, and *C. philadelphica* at 87–93, 112; *B. illuminatus* at 87; *C. fallax* at 87–89, 91, 92; and *Xd. formosus* at 88–92, and 112.

REMARKS.—This species is more abundant in the larger streams in the Roanoke and James drainages, where it occurs in pools, under larger stones, in debris among the marginal vegetation, and in submerged tangles of roots along the banks. It is also found in tunnels along the shore, particularly in areas where there are steep clay banks on the outer sides of bends in the stream. In the Mountain Lake area it shares such habitats with *C. b. bartonii*.

Like *C. l. longulus*, most of the population of *C. acuminatus* disappears from the shallow water of streams in November and does not reappear until spring. Most, if not all, of the individuals retreat into burrows that presumably they construct with the onset of cold weather.

In Virginia, first form males have been found every month of the year; however, from late September to May, most of the adult male population is in the first form, whereas such males are much rarer from June through August. Females with eggs occur from March to July, although they are very rare after mid-June.

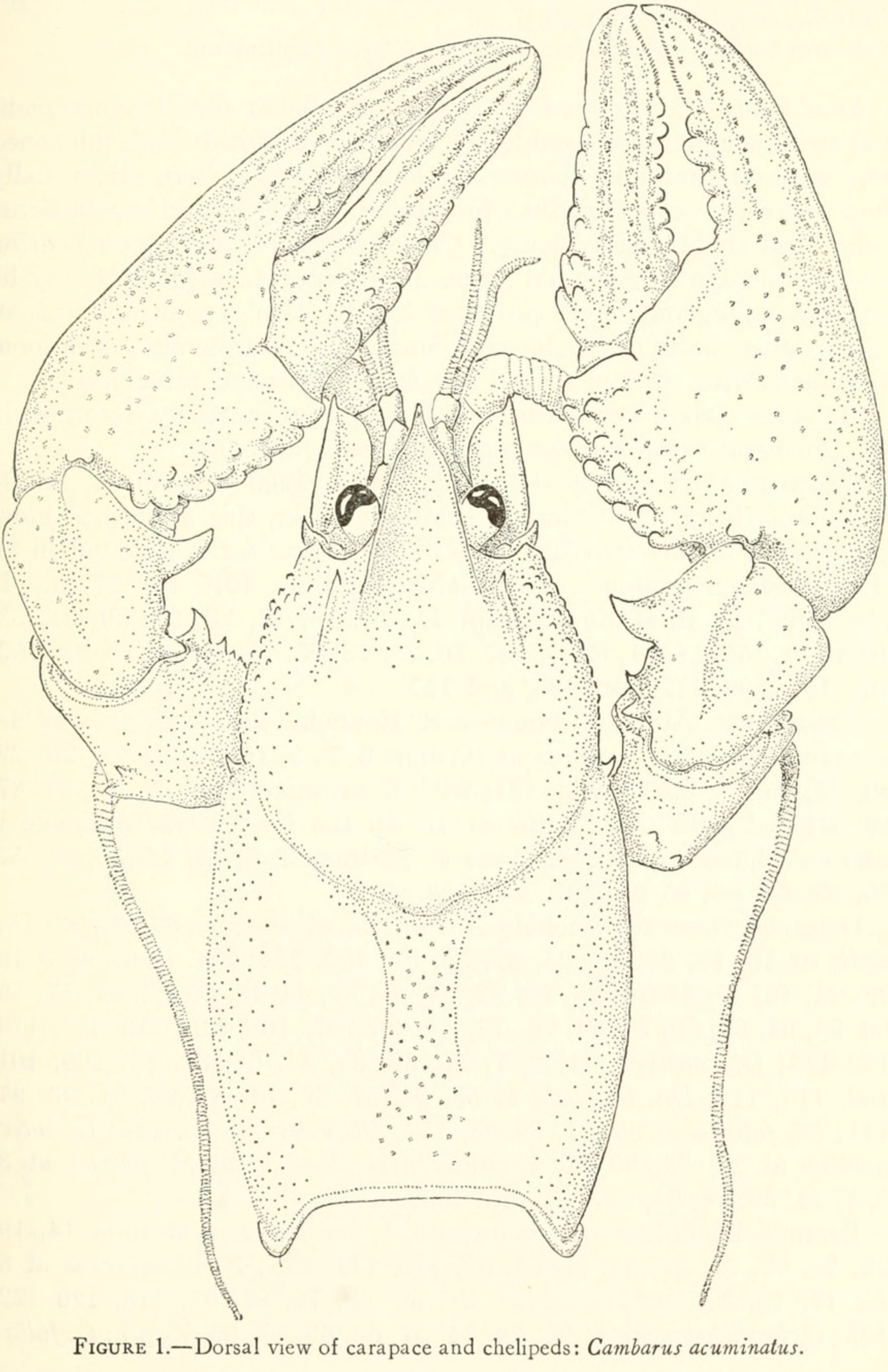


FIGURE 1.—Dorsal view of carapace and chelipeds: *Cambarus acuminatus.*

Cambarus bartonii bartonii (Fabricius)

FIGURE 2

Astacus bartonii Fabricius, 1798, p. 407.
Astacus (*Cambarus*) *bartonii* Erichson, 1846, p. 97.
Cambarus bartonii Girard, 1852, p. 88.
Cambarus bartonii bartonii Faxon, 1890, p. 622 [by implication].

DIAGNOSIS.—Margins of rostrum subparallel or slightly convergent to base of acumen where suddenly contracted (but rounded), thickened but without marginal spines; areola never more than six, usually four or five, times longer than broad with widely spaced punctations; suborbital angle usually acute. Chela with subovate fingers bearing distinct median longitudinal ridges on upper surfaces; fingers may be slightly gaping but never provided basally with conspicuous tuft of setae; inner margin of palm with single row of tubercles, occasional specimens with trace of second row or few scattered tubercles.

RANGE.—From New Brunswick, Canada, to northern Georgia; in the southeast mostly in the mountains and piedmont.

SPECIMENS EXAMINED.—Approximately 1200 specimens in 97 collections from 87 stations. Unquestionably this species is more widespread in this area than any of the others for it is found in all three drainage systems and at altitudes from 1219 to 427 m. It was found at all stations except 11, 13, 15, 18, 20, 27, 30, 31, 33, 40–43, 55, 56, 58, 61, 62, 65, 67, 70, 72, 73, 75, 78–81, 84, 86, 88, 102, 104–106, 109, 112, 116, 126, and 127.

ASSOCIATES.—In the James and Roanoke drainages it was associated with *C. l. longulus* at stations 6, 7, 9, 10, 12, 21–23, 25, 29, 32, 34, 35, 37, 89–93, 123, 124; with *C. acuminatus* at 29, 32, 35, 87, 89–93; and with *O. juvenilis* at 7. In the New River drainage it was associated with *C. sciotensis* at Stations 3, 5, 19, 44, 50, 54, 57, 59, 63, 64, 66, 95–97, 107, and 108.

Ostracod associates include *An. ancyla* at stations 89, 92, 93; *Dn. ardis* at 10, 12, 21, 23, 25, 32, 35, 37, 123, 124; *Dn. ileata* at 3–10, 12, 14, 16, 19, 21–26, 28, 29, 32, 34, 35, 37, 44–48, 50–52, 54, 57, 59, 60, 63, 64, 66, 69, 71, 74, 76, 77, 94–99, 107, 108, 110, 113, 117, 119, 122–125; *Dn. scalis* at 1, 2, 7, 17, 38, 39, 44, 68, 82, 83, 100, 101, 103, 114, 115; *Dn. truncata* at 53, 54, 57, 69, 71, 87, 90, 91, 93, 94, 111; *Dt. falcata* at 85, 87, 89–93, 111; *Dt. suteri* at 35, 124; *E. internotalus* at 23, 35, 90; *E. kanawhaensis* at 44; and *P. phyma* at 3, 5, 7, 24, 38, 44, 64, 82, 101, and 103.

Branchiobdellid associates include *A. koronaeus* at stations 14, 19, 29, 52, 69, 71, 77, 87, 89–93, 98, 110, 111, 125; *B. illuminatus* at 5, 16, 17, 19, 22, 34, 44, 45, 48, 51, 59, 68, 76, 87, 97, 115, 120–122, 125; *C. branchiophila* at 24, 29, 34, 57, 63, 66, 87, 89–93, 97; *C. fallax* at 3, 5, 24, 49, 54, 57, 63, 66, 71, 87, 89, 91, 92, 95–97; *C. holostoma* at 7, 10, 19, 21–23, 25, 37; *C. ingens* at 5, 54, 64, 95, 97; *C. philadelphica* at 3, 5, 8–10, 12, 14, 16, 17, 19, 21, 22, 24–26, 28, 29, 32, 34–37, 39, 44–46, 48, 50–54, 59, 60, 66, 68, 69, 71, 74, 76, 77, 87, 89–94, 98, 107, 108, 110, 111, 113, 115, 118, 119–125; *P. alcicornus* at 3–5, 19, 24,

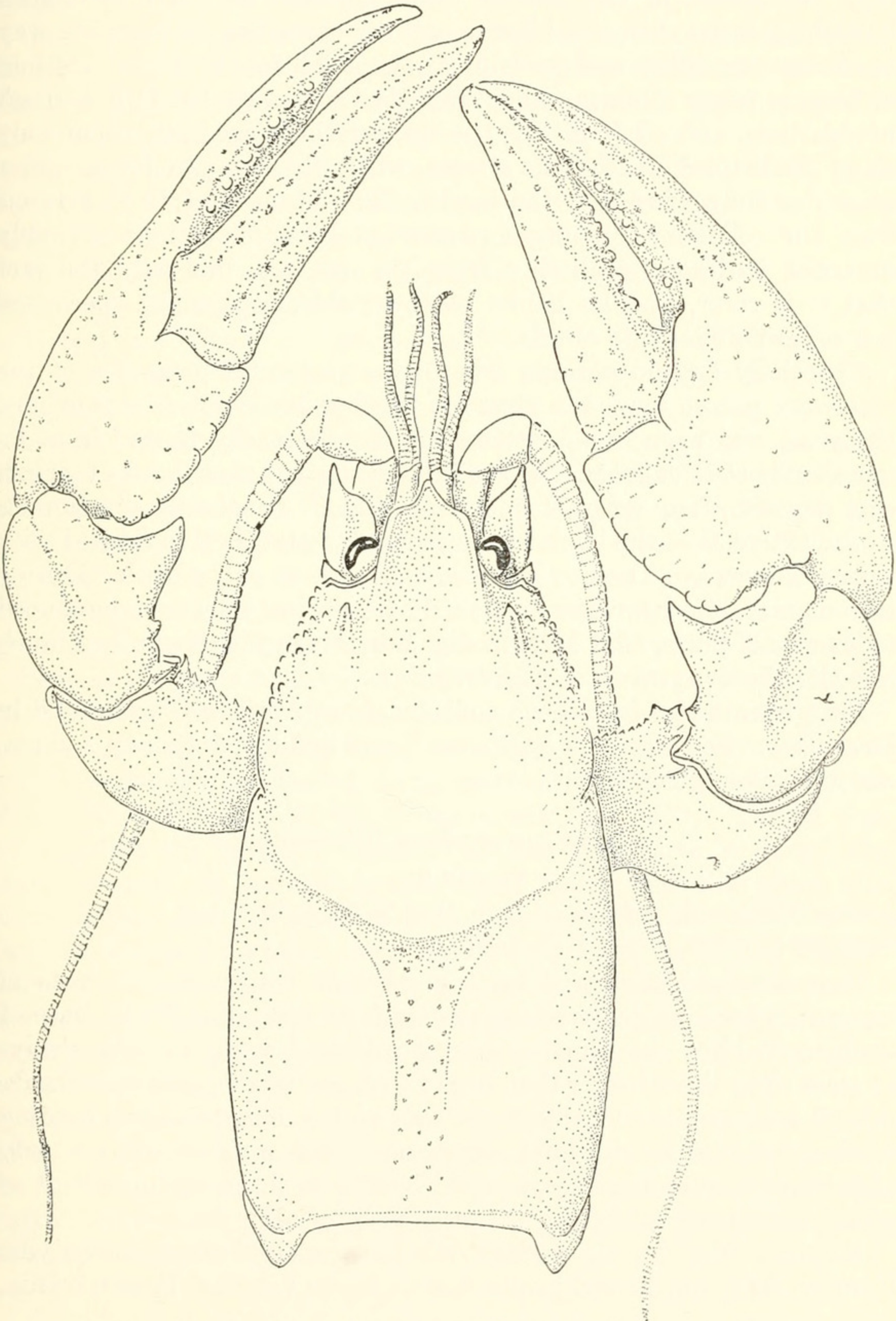


FIGURE 2.—Dorsal view of carapace and chelipeds: *Cambarus b. bartonii.*

25, 63, 64, 66, 74, 76, 95, 97; *Xd. formosus* at 10, 21, 89–92; and *Xg. instabilius* at 3–5, 7, 9, 12, 21, 22, 24, 37, 44, 46, 53, 54, 60, 64, 56, 97, 121, and 123.

REMARKS.—As indicated above, *C. b. bartonii* is the most widely distributed crayfish in the area, abounding in mountain brooks at high elevations; in the smaller feeder streams at lower elevations it is the sole crayfish inhabitant. As the cascading waters give way to alternating riffles and pools or as the small feeder tributaries join or become larger streams, other crayfishes encounter the *C. b. bartonii* populations, and adult of this species, for the most part, occur only along the littoral areas of the stream, where they may be found under stones or burrowing into the banks. The absence of *C. b. bartonii* from the collections in larger streams at lower elevations probably does not indicate its absence from the streams, but only the fact that it is rarer, and its habits at these elevations make specimens much more difficult to obtain.

Especially around springs, where the winter temperatures of the water are not so low as in streams, this species is active throughout the year, and even in the streams it is more easily routed from its lair than is *C. l. longulus*. Where the streams cut steep banks through clay deposits, frequently *C. b. bartonii* and *C. acuminatus* dig tunnels to the extent that the bank below the high water level is riddled with their passageways, thereby hastening the erosion of the bank. During the summer months, when some of the headwater streams are reduced to a series of pools, *C. b. bartonii* digs burrows in the stream bed much like the winter retreats of *C. l. longulus*.

First form males have been collected from April to October and in December. Females with eggs were found in June, July, and August, and with young in August.

Cambarus carolinus (Erichson)

FIGURE 3

Astacus (*Cambarus*) *carolinus* Erichson, 1846, p. 96.
Cambarus carolinus Girard, 1852, p. 88

DIAGNOSIS.—Margins of rostrum slightly convergent to base of acumen, where suddenly contracted to form obtuse angles at base of acumen, neither thickened nor with marginal spines; areola always at least eight times longer than broad with scattered punctations; suborbital angle weak and obtuse. Chela with subovate fingers bearing distinct median longitudinal ridges on upper surfaces; fingers only slightly gaping and never provided basally with conspicuous tuft of setae; inner margin of palm with two rows of tubercles.

RANGE.—Not at all understood but reported from Greenville County, S.C., northward in the mountains to Virginia, Pennsylvania, and Kentucky. At least two color phases are involved, and perhaps two or more races should be recognized.

Specimens examined.—135 specimens in 12 collections from the following stations: 8, 22, 40, 41, and 127, at elevations of 585 to 1250 meters. Three of these lie in the New and two in the James drainage systems.

Associates.—*Cambarus carolinus* was collected with no other crayfish, for it is the only primary burrowing species in the area. There is little likelihood of its being found with any other species in the region except possibly *C. b. bartonii.*

Ostracod associates include *As. asceta* and *Dt. chalaza*, which have been found with no other crayfish except *C. carolinus* and which were with it in all five of the localities in which it was collected.

Branchiobdellid associates include *B. illuminatus* and *C. fallax* at station 40, and only the former at 41.

Remarks.—While our knowledge of all of the crayfishes in the region is limited, data on *C. carolinus* is almost totally lacking. The rocky soil in the area makes digging for these animals highly impracticable, and most of our specimens were collected on foggy or rainy evenings when the crayfishes had left their burrows and were crawling about in the grass on the golf course (sta. 41) and in the road (sta. 40).

Cambarus carolinus seldom invades bodies of open water. In some 12 years of observing the streams in the area, we have seen only one individual (juvenile) in such a habitat—at Hunters Branch on the grounds of the Biological Station one evening following a heavy rain.

Several attempts to extricate individuals of this species from burrows in the vicinity of the Mountain Lake Biological Station proved totally unsuccessful. The same technique used there, however, was most successful in a cleared, grass-covered area near the junction of White Rock Branch and Big Stony Creek (sta. 127). Taking care not to allow the burrow to become clogged with earth, a shovel was used to open the burrow to the water table, and the water was thoroughly roiled. Within a short time, the crayfish came to the exposed area and its antennae could be seen whipping to and fro just below the surface film. Making a quick grab, the observer caught the animal. In the area of the Biological Station, the crayfish were never observed coming to the exposed opening as they characteristically did here.

The depths of the burrows at station 127 were not determined, but at about 60 cm below the surface some of them contained chambers 15 to 20 cm in diameter. From one large chamber, 12 juveniles (with carapace lengths ranging from 11 to 18 mm) and an adult female, presumably the mother, were taken.

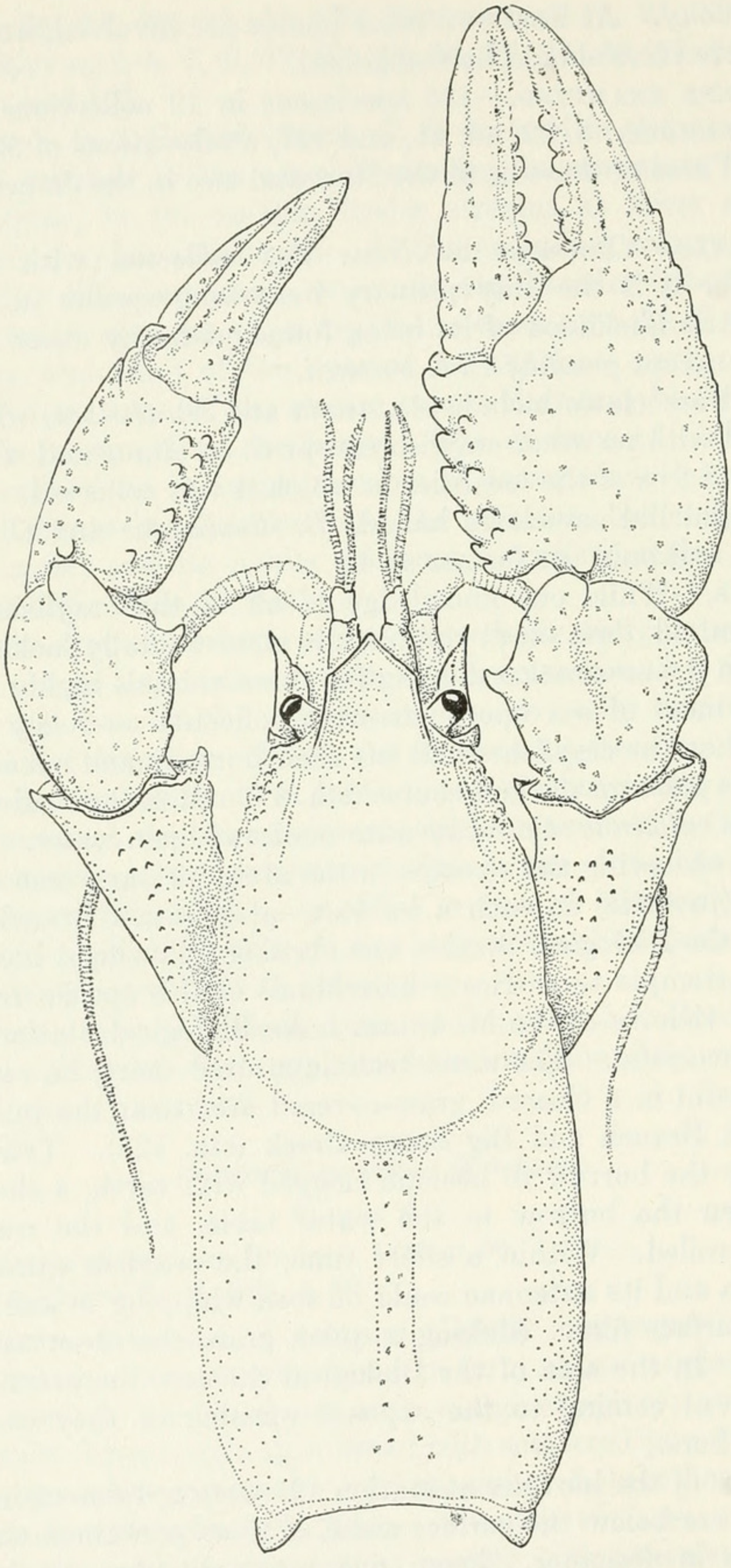


FIGURE 3.—Dorsal view of carapace and chelipeds: *Cambarus carolinus*.

First form males of *C. carolinus* have been collected in the Mountain Lake area in June, July, and August (elsewhere also in April and September through December). A female with eggs was found in June, and the young mentioned above in July.

Cambarus longulus longulus Girard

FIGURE 4

Cambarus longulus Girard, 1852, p. 90.
Cambarus longulus longulus Hay, 1899, p. 959 [by implication].

DIAGNOSIS.—Margins of rostrum gently convergent from base to apex, distinctly thickened and without marginal spines; areola never more than six times longer than broad, usually about three and a half, with crowded deep punctations; suborbital angle lacking. Chela with subcylindrical fingers lacking distinct median longitudinal ridges on upper surfaces; fingers gaping and usually provided basally with conspicuous tuft of setae; inner margin of palm with single, strongly depressed, row of tubercles (frequently scarcely rising above contour of palm).

RANGE.—In the Atlantic watershed from the James River in Virginia to the Yadkin River in North Carolina in the low mountains and upper piedmont provinces. Details of range and variation of this and the other two subspecies of *C. longulus* are discussed by James (1966).

SPECIMENS EXAMINED.—Approximately 450 specimens in 35 collections from the following stations: 6, 7, 9–13, 20–23, 25, 27, 29–35, 37, 88–93, 112, 123, and 124 in tributaries of the James River and North Fork of the Roanoke River in Craig, Giles, and Montgomery Counties, Va., and from tributaries of Potts Creek, Monroe County, W. Va. These stations lie at altitudes between 402 and 686 m.

ASSOCIATES.—Crayfish associates include *C. acuminatus* at stations 20, 27, 29–33, 35, 88–93, 112; *C. b. bartonii* at 6, 7, 9, 10, 12, 21–23, 25, 29, 32, 34, 35, 37, 89–93, 123, 124; and *O. juvenilis* at 7.

In the 23 localities in the James drainage, *C. l. longulus* was found with *Dn. ardis* at stations 10–13, 20, 21, 23, 25, 27, 30–33, 35, 37, 123, 124; *Dn. ileata* at 6, 7, 9–12, 20–23, 25, 29, 31–35, 37, 123, 124; *Dt. suteri* at 27, 30, 31, 33, 35, 124; and *E. internotalus* at 23, 30, 31, and 35. In the seven localities in the North Fork of the Roanoke River, *C. l. longulus* was associated with *Dt. falcata* at all stations (88–93, 112); *Dn. truncata* at 88, 90, 91, 93; and *An. ancyla* at 88, 89, 92, and 93.

Branchiobdellid associates in the James drainage include *A. koronaeus* at stations 29, 30; *B. illuminatus* at 20, 22, 34; *C. branchiophila* at 20, 29; *C. heterognatha* at 34, 123; *C. holostoma* at 7, 10, 11, 13, 20–23, 25, 37; *C. philadelphica* at 9, 10, 12, 20–22, 25, 27, 29, 32–35, 37, 123, 124; *P. alcicornus* at 25; *Xd. formosus* at 10, 21; and *Xg. instabilius* at 7, 9, 11–13, 21, 22, 37, 123. In the Roanoke drainage, *A. koronaeus*, *C. branchiophila*, and *C. philadelphica* were found at stations 88–93, 112; *Xd. formosus* at 88–92, 112; and *C. fallax* at 88, 89, 91, and 92.

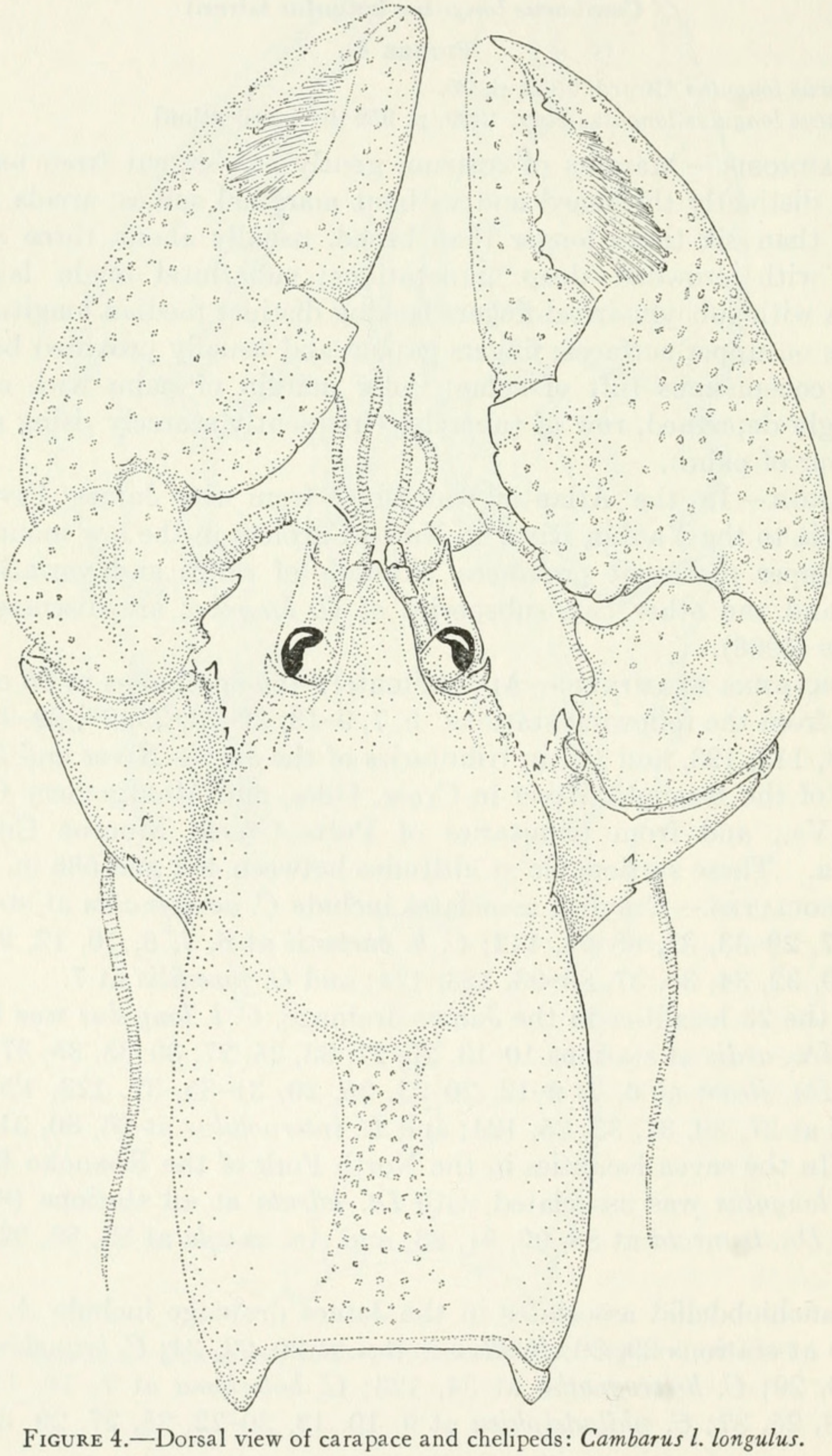


FIGURE 4.—Dorsal view of carapace and chelipeds: *Cambarus l. longulus.*

Remarks.—This crayfish is the dominant decapod inhabitant of the riffle areas in the James and Roanoke river systems. Except from November to April, this small crayfish can be found in almost every riffle in the lower mountains and piedmont. During the colder months, individuals retreat to their burrows beneath stones in the riffles. At least some of the tunnels descend to depths greater than 30 cm. Because of the sand, gravel, and interlocking stones submerged in the current, it is exceedingly difficult to dissect a burrow. Even though we have removed specimens from such burrows, we are not at all certain that we determined the full extent of the excavations. In the spring, the adult males and juveniles leave the burrows first; the females remain in their tunnels, where presumably they lay and hatch their eggs before venturing into open water. Not until mid-May can one sample the riffle and expect to obtain a knowledge of all the components of the *C. l. longulus* population.

The life history of this crayfish has been briefly outlined above; for details, see Smart (1962).

Cambarus sciotensis Rhoades

Figure 5

Cambarus bartoni sciotensis Rhoades, 1944, p. 96.
Cambarus sciotensis Hobbs, 1964, p. 189.

Diagnosis.—Margins of rostrum subparallel or slightly convergent to base of acumen where suddenly contracted to form angles of approximately 90° (or with slightly protruding knobs), thickened but without marginal spines; areola never more than six, usually about four and a half times longer than broad with deep, but not crowded, punctations; suborbital angle obtuse. Chela with subovate fingers bearing distinct median longitudinal ridges on upper surfaces; fingers may or may not be gaping but never provided basally with conspicuous tuft of setae; inner margin of palm with two rows of tubercles.

Range.—Apparently discontinuous; in the Scioto River in Ohio and in the New River system in Virginia and southeastern West Virginia (both areas in the Ohio drainage system).

Specimens examined.—Approximately 450 specimens in 43 collections from the following stations: 3, 5, 15, 18, 19, 43, 44, 50, 54–59, 61–67, 70, 72, 73, 75, 78–81, 84, 86, 95–97, 102, 104–109, 116, and 126. All of them are in the New River drainage system at elevations of 427 to 899 m.

Associates.—The only crayfish associate was *C. b. bartonii*, which was found at the following stations: 3, 5, 19, 44, 50, 54, 57, 59, 63, 64, 66, 95–97, 107, and 108.

Ostracod associates include *Dn. ileata* at all stations except 70 and 78; *Dn. scalis* at 44; *Dn. truncata* at 54–57; *Dt. daphnioides* at 70, 72,

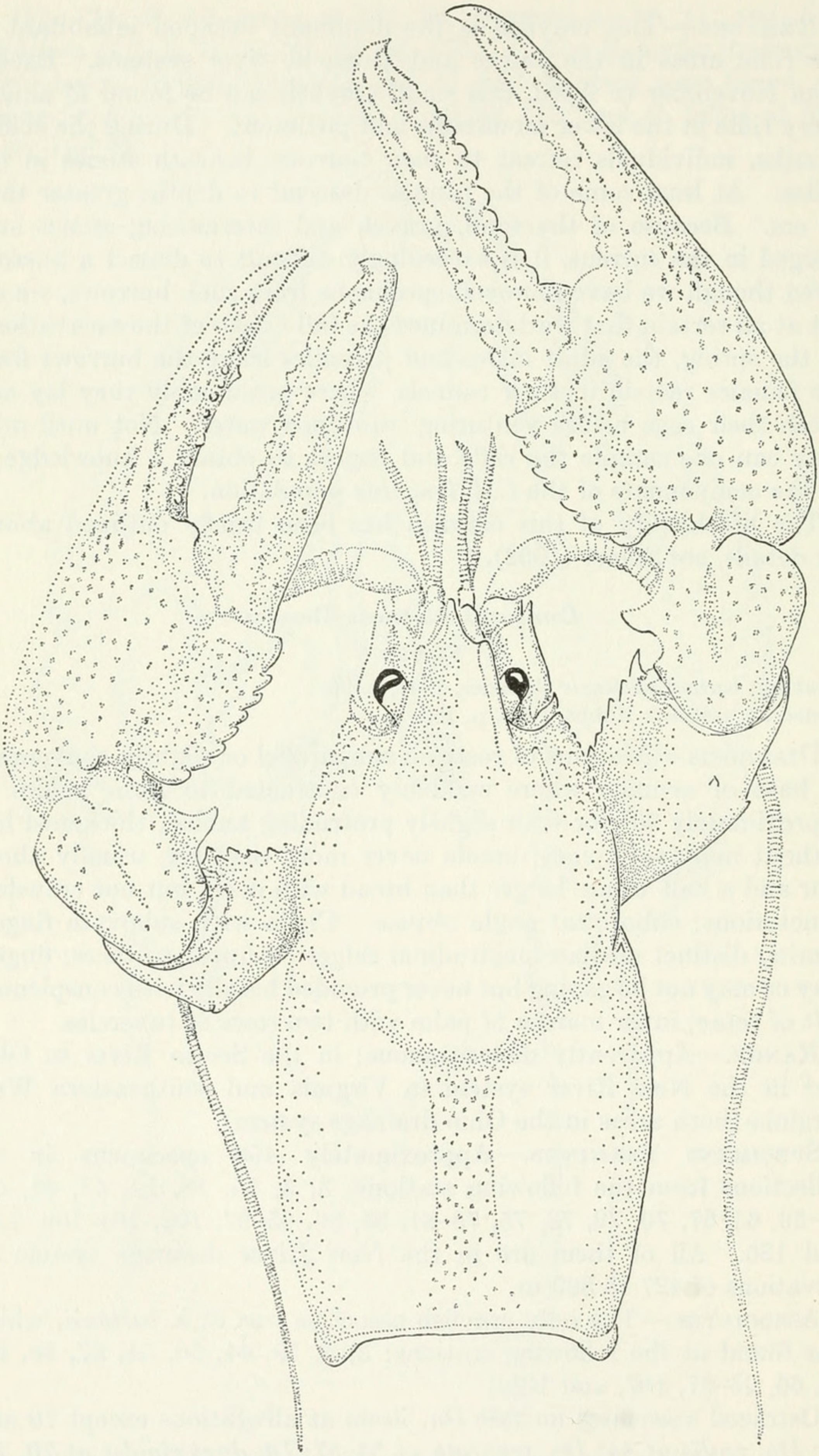


Figure 5.—Dorsal view of carapace and chelipeds: *Cambarus sciotensis.*

73, 75, 79–81, 116; *E. kanawhaensis* at 44, 126; and *P. phyma* at 3, 5, 44, and 64.

Branchiobdellid associates include *A. koronaeus* at stations 18, 19, 72; *A. legaeus* at 81; *B. illuminatus* at 5, 19, 44, 59, 86, 97; *C. branchiophila* at 15, 18, 43, 55, 57, 58, 63, 65–67, 72, 73, 75, 79, 81, 86, 97, 104, 116, 126; *C. fallax* at 3, 5, 15, 18, 43, 54–58, 61, 63, 65–67, 70, 72, 75, 78, 79, 81, 86, 95–97, 126; *C. heterognatha* at 3, 5, 61, 63–67, 70, 72, 78–81, 86, 97, 105, 106, 116, 126; *C. holostoma* at 18, 19; *C. ingens* at 5, 15, 18, 54, 58, 61, 64, 67, 70, 72, 73, 75, 79–81, 86, 95, 97, 104, 116; *C. philadelphica* at 3, 5, 19, 44, 50, 54–56, 59, 66, 106–109; *P. alcicornus* at 3, 5, 15, 18, 19, 43, 58, 61, 63–67, 70, 72, 73, 75, 79, 81, 86, 95, 97, 104, 105; and *Xg. instabilius* at 3, 5, 44, 54, 61, 64, 86, 95, and 97.

Remarks.—In the New River system, this crayfish vicariates for *C. acuminatus* of the Roanoke and James drainages, and with the absence of the riffle-inhabiting *C. l. longulus* invades such habitats to a greater extent than does *C. acuminatus*. In marked contrast to *C. l. longulus*, *C. sciotensis* seems to be active throughout the year, never burrowing except to excavate shallow depressions beneath rocks.

First form males have been collected in March, April, and June to October. Females with eggs were found in July and August, and with young in August.

Genus *Orconectes* Cope, 1872

Diagnosis.—First pleopod of first form male terminating in two parts, which may be straight or gently curved, short or long spines, blades, or subspatulate projections. If terminals bent so much as at right angle, bend never accomplished adjacent to shaft. Male with hooks on ischiopodites of third pereiopods and occasionally on those of fourth. Third maxillipeds not conspicuously elongate and ischiopodite with row of teeth along mesial margin.

Orconectes juvenilis (Hagen)

Figure 6

Cambarus juvenilis Hagen, 1870, p. 66, figs. 29–33, 157.
Orconectes juvenilis Hobbs, 1942, p. 352 [by implication].

Diagnosis.—Margins of rostrum subparallel or slightly convergent, not thickened, and with pair of marginal spines at base of acumen, upper surface provided with distinct, median, longitudinal carina. Lateral surfaces of carapace with pair of spines immediately caudal to cervical groove; postorbital ridges terminating cephalically in spines; suborbital angles lacking. Inner margin of palm of chela with two closely appressed rows of tubercles with others above. First pleopod of first form male extending cephalad to base of first pereiopod when abdomen is flexed; central projection spiculiform and both it and mesial process straight, the former slightly curved caudally near tip; cephalic surface of shaft with prominent shoulder just proximal to base of central projection. Annulus ventralis with transversely oval depression extending cephalically beneath cephalic wall, latter bearing median cleft.

RANGE.—From Ohio and Kentucky southward to northwest Georgia west of the Alleghenies, and in the headwaters of the James River in Craig County, Va.

SPECIMENS EXAMINED.—300 specimens in 22 collections from stations 7 and 42. The occurrence of *O. juvenilis* in the Mountain Lake area represents two probable introductions (see p. 10 and below), and that at station 7 is the first record of the presence of this species on eastern slopes of the Allegheny Mountains. These stations are located at elevations of 671 and 1180 m respectively.

After this manuscript had been completed, two specimens of *O. juvenilis* were found in the New River, 500 m south of the mouth of Spruce Run in the vicinity of a fishing camp.

ASSOCIATES.—At station 7, *O. juvenilis* was found with *C. b. bartonii* and *C. l. longulus;* in Mountain Lake (sta. 42) it is not accompanied by any other crayfish at the present time.

In station 42, neither ostracods nor branchiobdellids infest the members of this population. At station 7, the ostracod associates include *Dn. ileata*, *Dn. scalis*, and *P. phyma;* the branchiobdellid associates, *C. holostoma* and *Xg. instabilius*.

REMARKS.—With regard to the population of *O. juvenilis* in Mountain Lake (see Hobbs and Walton, 1966a), it is perhaps of interest that in 1933 *C. b. bartonii* was the only crayfish inhabiting it. The latter was, and is still, the only crayfish in the small stream, "Pond Drain," flowing from the Lake. In 1933, members of one of the classes in aquatic biology at the Biological Station brought collections of animals from the vicinities of their homes and released them in the Lake. In 1947, three species were found to be present and with few exceptions were restricted to different regions of the Lake. *Orconectes juvenilis* occurred along the east and to a lesser degree along the south side; *C. acuminatus*, never observed by us to be abundant, was found only along the north side and never closer than 100 yards from the outlet; *C. b. bartonii* was found in the area of the outlet, at the northwest corner. According to our observations, crayfishes have never been abundant along the west side (perhaps they are inaccessible because of the greater depth of the water), and we have no records of what species, if any, frequent this area. By 1954, there were no *C. acuminatus* to be found in any of the littoral areas, and it seemed that *O. juvenilis* was invading the north side;

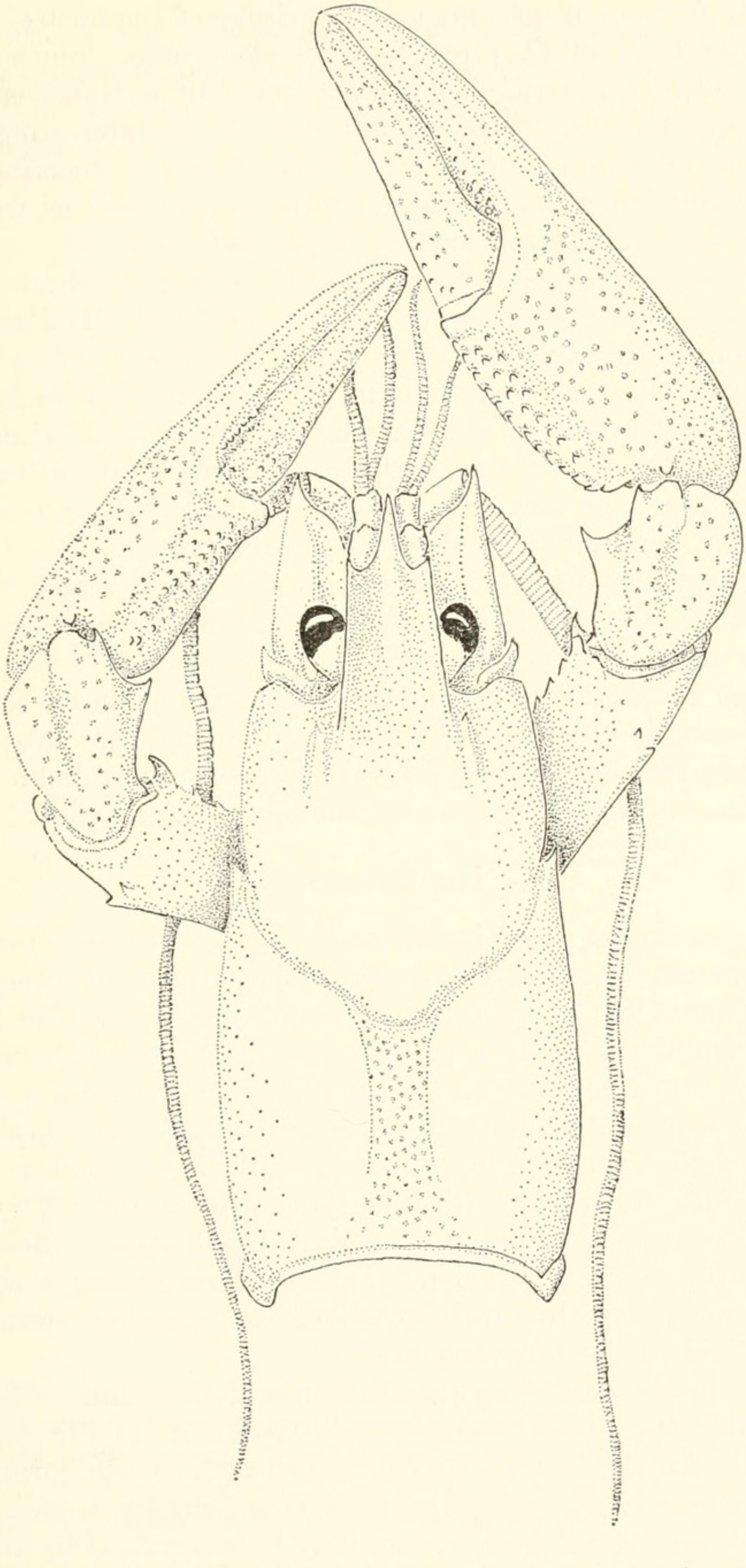


FIGURE 6.—Dorsal view of carapace and chelipeds: *Orconectes juvenilis*.

C. b. bartonii was still present in the vicinity of the outlet, but occasional individuals of *O. juvenilis* were also there. Since 1957, no crayfish except *O. juvenilis* has been observed by us in the entire lake. We have not done any trapping, and it would be interesting to know whether or not populations of *C. b. bartonii* and *C. acuminatus* have found congenial niches at greater depths or whether, as we believe, they have been totally replaced by *O. juvenilis*.

The presence of *O. juvenilis* in New River is possibly due to very recent migrations upstream from West Virginia. Had it been in this portion of the river for some years, it is likely that with all of the collecting that has been done in the river in the Mountain Lake area, it would have been encountered by one of us. While natural migration might furnish an entirely plausible explanation for its occurrence here, the fact that the two specimens came from near a fishing camp does not strengthen the possibility.

Throughout the range of the species, first form males have been collected in January and from April through November. Females with eggs were found only in April.

Although three ostracods and two branchiobdellids are associated with *O. juvenilis* at station 7, it seems unlikely that any of them reached this area on this crayfish. It seems more probable that the infestations occurred after the introduction of the crayfish.

The Ostracods

It is necessary in most instances to rely on the structure of the copulatory complex of the male for the indentification of entocytherids, and this cannot be satisfactorily done unless the specimen has been cleared (temporary mounts in glycerine or permanent mounts in balsam or some comparable medium).[3] The copulatory complex consists of a pair of modified appendages that during amplexus are so arranged that the clasping apparatus (fig. 7*a*) of each is directed anteriorly but which at most other times are rotated 180° with the clasping apparatus directed posteriorly. Orientation in descriptions is that of the clasping position. Figure 7*a* represents a composite copulatory complex that includes all of the secondary sexual characters utilized in the following key.

Whereas in the crayfishes it is the male that is dimorphic, in the entocytherids the female exists in two "forms": (1) the copulatory or biunguis female, which, to our knowledge, is the form that is always the partner in amplexing pairs (and perhaps should be considered the last "larval instar") and may be recognized by the 4-seg-

[3] Most of our specimens have been prepared by dehydrating them with glacial acetic acid—transferring the specimen from formalin, water, or alcohol directly to the acid—clearing them in methyl salicylate and mounting them in balsam.

mented second antenna bearing only two terminal claws; (2) the gravid or triunguis female, which frequently contains eggs and may be recognized by the apparently 5-segmented antenna bearing three terminal claws.

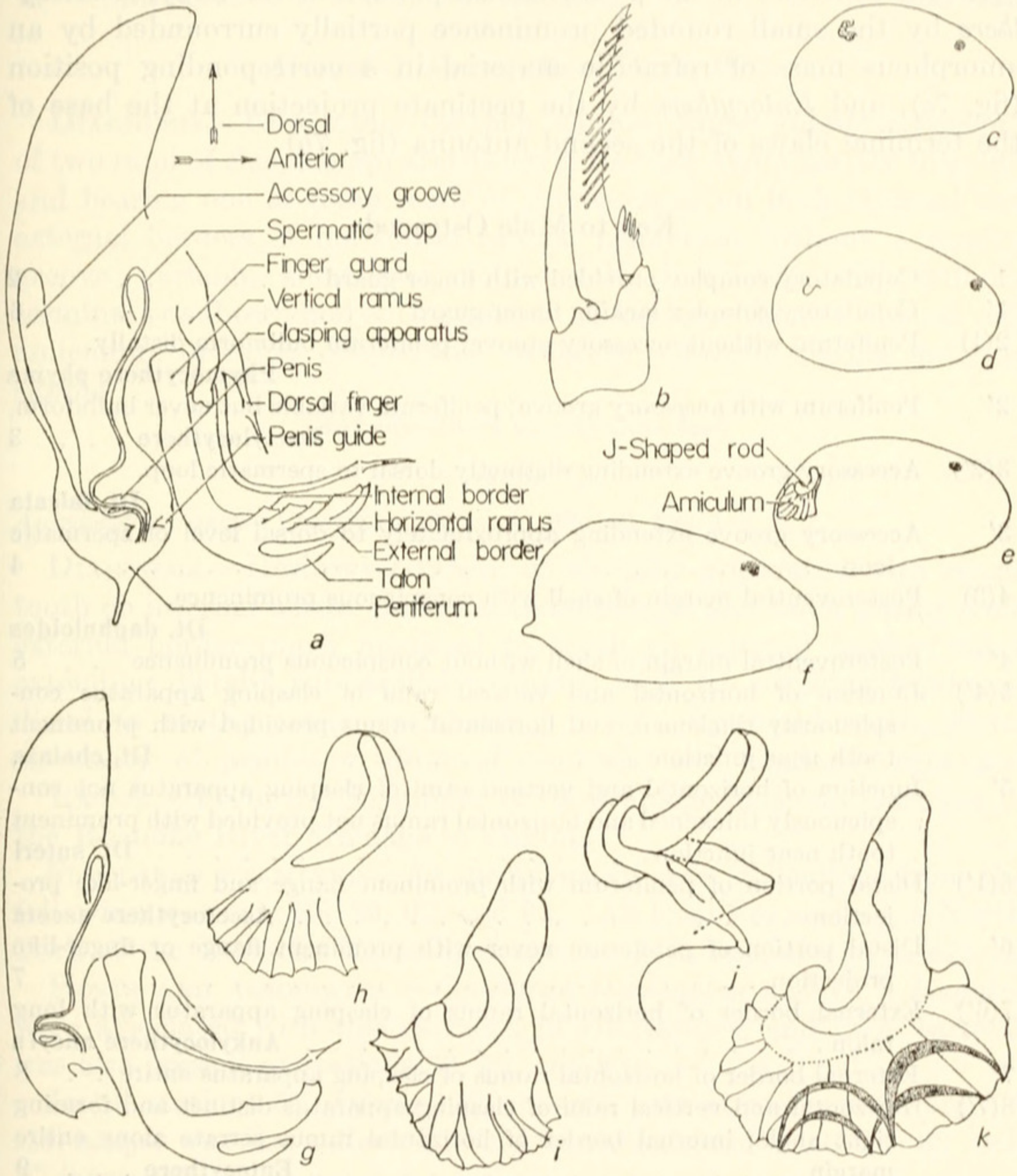


FIGURE 7.—Entocytherids: *a*, generalized peniferum illustrating structures mentioned in key; *b*, terminal claws of antenna of female *Entocythere internotalus*. Lateral views of shells: *c*, female *Ascetocythere asceta; d*, female *Donnaldsoncythere scalis; e*, female *Dactylocythere chalaza; f*, male *Dt. daphnioides*. Peniferum: *g*, *Ankylocythere ancyla*. Amicula and J-shaped rods: *h*, *Dt. suteri; i*, *Dt. chalaza; j*, *Dt. falcata; k*, *Dt. daphnioides*.

Unfortunately, few female entocytherids can be identified unless they are found in amplexus or can definitely be associated with the male. Few generic determinations of females are possible; however, in the Mountain Lake region, the triunguis females of the four species of the genus *Dactylocythere* may be recognized by the presence of an amiculum (figs. 7*e*, *h–k*) and the posteroventral projection on the shell of *Dt. daphnioides* (fig. 7*f*), *Donnaldsoncythere* by the small corneous tubercles in the posterodorsal portion of the body, *Ascetocythere* by the small rounded prominence partially surrounded by an amorphous mass of refractile material in a corresponding position (fig. 7*c*), and *Entocythere* by the pectinate projection at the base of the terminal claws of the second antenna (fig. 7*b*).

Key to Male Ostracods

1 Copulatory complex provided with finger guard 2

1′ Copulatory complex lacking finger guard 6

2(1) Peniferum without accessory groove; peniferum bulbiform distally. **Phymocythere phyma**

2′ Peniferum with accessory groove; peniferum variable but never bulbiform. **Dactylocythere** . . . 3

3(2′) Accessory groove extending distinctly dorsal to spermatic loop. **Dt. falcata**

3′ Accessory groove extending approximately to dorsal level of spermatic loop 4

4(3) Posteroventral margin of shell with conspicuous prominence. **Dt. daphnioides**

4′ Posteroventral margin of shell without conspicuous prominence . . 5

5(4′) Junction of horizontal and vertical rami of clasping apparatus conspicuously thickened, and horizontal ramus provided with prominent tooth near junction . . . . **Dt. chalaza**

5′ Junction of horizontal and vertical rami of clasping apparatus not conspicuously thickened and horizontal ramus not provided with prominent tooth near junction . . . . **Dt. suteri**

6(1′) Distal portion of peniferum with prominent flange and finger-like projection . . . . **Ascetocythere asceta**

6′ Distal portion of peniferum never with prominent flange or finger-like projection 7

7(6′) External border of horizontal ramus of clasping apparatus with long talon . . . . **Ankylocythere ancyla**

7′ External border of horizontal ramus of clasping apparatus entire . . 8

8(7′) Horizontal and vertical rami of clasping apparatus distinct and forming right angle; internal border of horizontal ramus serrate along entire margin . . . . **Entocythere** . . . 9

8′ Horizontal and vertical rami of clasping apparatus not distinct and joining in angle greater than right angle; internal border of horizontal ramus never with more than three teeth. **Donnaldsoncythere** . . . 10

9(8′) Mesial surface of junction of horizontal and vertical rami of clasping apparatus thickened and armed with one or more teeth or ridges. **E. internotalus**

9′ Mesial surface of junction of horizontal and vertical rami of clasping apparatus not thickened and without teeth or ridges. **E. kanawhaensis**

10(8′)	Distal extremity of peniferum acuminate	**Dn. ardis**
10′	Distal extremity of peniferum truncate, rounded, or scooplike . . .	11
11(10′)	Distal extremity of peniferum scooplike	**Dn. scalis**
11′	Distal extremity of peniferum truncate or rounded	12
12(11′)	Distal extremity of peniferum truncate	**Dn. truncata**
12′	Distal extremity of peniferum rounded	**Dn. ileata**

Genus *Ankylocythere* Hart, 1962

Diagnosis.—Copulatory complex without finger guard; extensions of two rami of clasping apparatus never forming angle greater than 90° and bearing one or more teeth or excrescences on both internal and external borders of horizontal ramus; peniferum without accessory groove, variable, sometimes cleft distally but never with bulbous terminal or subterminal enlargement. Females without J-shaped rod, amiculum, or other comparable structure; claws of second antenna simple.

Ankylocythere ancyla Crawford

Figure 7*g*

Ankylocythere ancyla Crawford, 1965, pp. 148–149, figs. 1–3, 6, 7.

Diagnosis.—Horizontal ramus of clasping apparatus with single tooth on internal border proximal to midlength and talon arising from external border much proximal to tooth on internal border; talon extending distally subparallel to ramus with tip reaching level just distal to tooth; ramus terminating in two upturned teeth; distal extremity of peniferum directed ventrally and shallowly excavate.

Range.—From the Savannah River drainage in South Carolina to the Roanoke River drainage in Virginia.

Specimens examined.—60 specimens in eight collections from the following stations: 88, 89, 92, and 93. All localities are in the North Fork of the Roanoke River drainage, at elevations of 439 to 475 m.

Hosts and associates.—*Cambarus acuminatus* and *C. l. longulus* were associated with this ostracod in all stations, and *C. b. bartonii* was also present at stations 89, 92, and 93.

In all stations *Dt. falcata* was present, and at stations 88 and 93 *An. ancyla* was also collected with *Dn. truncata* and at station 88 with *E. internotalis*.

Branchiobdellid associates include *A. koronaeus*, *C. branchiophila*, *C. philadelphica* at stations 88, 89, 92, 93; and *C. fallax* and *Xd. formosus* at 88, 89, and 92.

Genus *Ascetocythere* Hart, 1962

Diagnosis.—Hobbs and Hart (1966, p. 37) stated:

Terminal tooth of mandible with cusps. Copulatory complex without finger guard; peniferum extending ventrally much beyond clasping apparatus, elongate, comparatively slender, with subterminal bulbous enlargement bearing one (anterior) or several projections; penis complex consisting of separate dorsal spermatic and ventral prostatic elements; spermatic element always shorter than clasping apparatus; accessory groove lacking. Clasping apparatus well developed, not always clearly divisible into vertical and horizontal rami; external border of horizontal ramus entire, internal border with two, three, or no teeth along apical half, if present often grouped far distally with three apical denticles.

Ascetocythere asceta (Hobbs and Walton)

Figures 7*c*, 8*a*

Entocythere asceta Hobbs and Walton, 1962, pp. 43–44, figs. 1–4.
Ascetocythere asceta Hart, 1962, p. 128.

Diagnosis.—Hobbs and Hart (1966, p. 39) stated:

Peniferum with three prominences extending from subterminal bulbous expansion—anterior process delicate, club-shaped, extending anteroventrally, from cephalic surface; ventral process large, finger-like, with distinct angular flange near its midlength, and directed ventrally; posterior process small, rounded, and situated at posterior base of ventral process; prominent penis guide (acute projection) lying between flange and anterior process; penis reaching surface anteriorly dorsal to flange. Vertical ramus of clasping apparatus less than ⅓ of total length of apparatus; internal border of horizontal ramus with two teeth along distal third with distal tooth almost midway between proximal tooth and apex.

Range.—Known from crayfish burrows in the James and New river systems in Craig and Giles Counties, Va., and from Monroe County, W. Va.

Specimens examined.—275 specimens in 12 collections from the following stations: 8, 22, 40, 41, and 127, at elevations of 585 to 1250 m.

Host and associates.—*Ascetocythere asceta* is apparently restricted to the single host *Cambarus carolinus*.

Ostracod associates include but one species, *Dt. chalaza*, with which it was found in all five localities.

Branchiobdellid associates include *B. illuminatus* at stations 40, 41, and 127; and *C. fallax* at 40.

Genus *Donnaldsoncythere* Rioja, 1942

Diagnosis.—Copulatory complex without finger guard; clasping apparatus frequently not divisible into vertical and horizontal rami and angle formed by extensions of two always greater than 90°; external border of horizontal ramus (or distal half of apparatus) entire and internal border never with more than three teeth near distal end, distal extremity terminating in from 3 to 10 serrations or emarginations; peniferum lacking accessory groove; corneous penis curved at almost right angle near midlength with proximal extremity level, or almost level, with base of clasping apparatus. Length of penis greater than half that of clasping apparatus. Female without J-shaped rod or amiculum but with small corneous tube directed ventrally or posteroventrally in corresponding position; claws of second antenna simple.

Donnaldsoncythere ardis Hobbs and Walton

FIGURE 8*b*

Donnaldsoncythere ardis Hobbs and Walton, 1963, pp. 364–368, figs. 6–9, 10, 26.

DIAGNOSIS.—Copulatory complex with peniferum terminating ventrally in conspicuously slender, pointed extension; clasping apparatus only slightly curved along shaft, not divisible into vertical

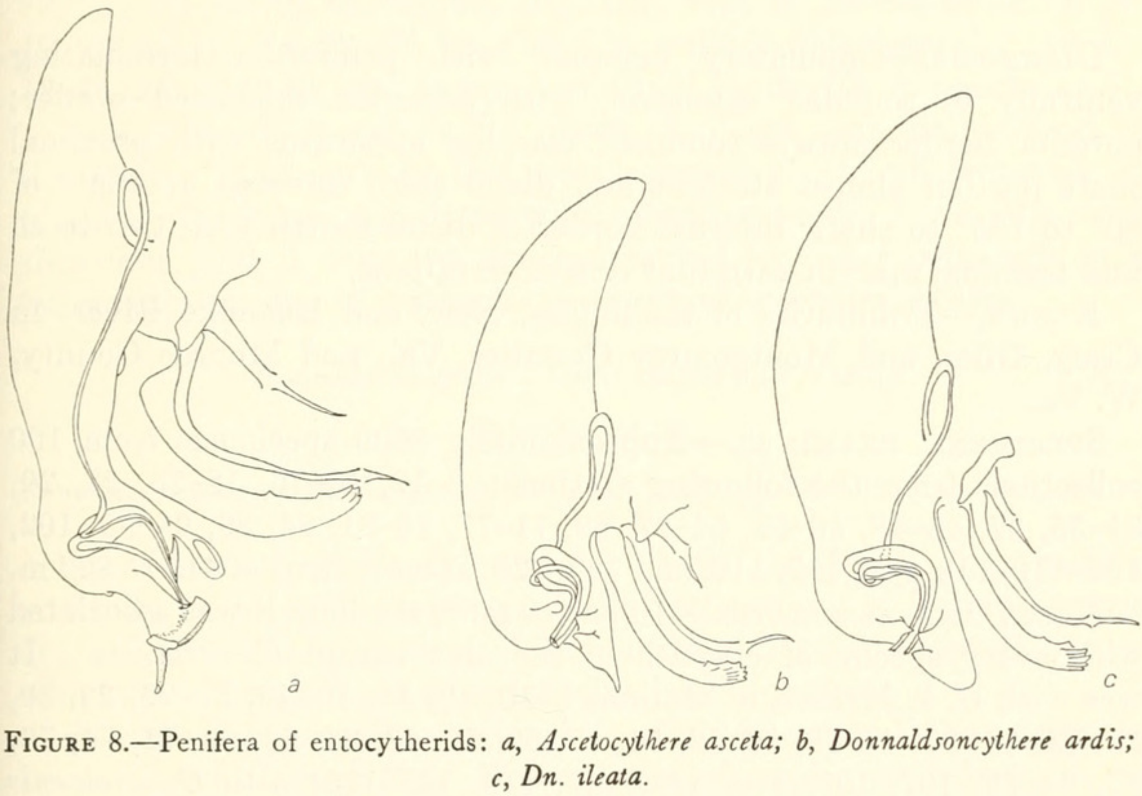


FIGURE 8.—Penifera of entocytherids: *a*, *Ascetocythere asceta;* *b*, *Donnaldsoncythere ardis;* *c*, *Dn. ileata.*

and horizontal rami, distal portion slightly enlarged and directed anteroventrally, internal border with two teeth and apical border with four serrations.

RANGE.—The James River drainage in Craig, Giles, and Montgomery Counties, Va.

SPECIMENS EXAMINED.—Approximately 175 specimens from 18 collections in the following stations: 10–13, 20, 21, 23, 25, 27, 30–33, 35, 37, 123, and 124, at elevations from 402 to 622 m.

HOSTS AND ASSOCIATES.—*Donnaldsoncythere ardis* was associated with *Cambarus l. longulus* in all stations; with *C. b. bartonii* at stations 10, 12, 21, 23, 25, 32, 35, 37, 123, 124; and with *C. acuminatus* at 20, 27, 30–33, and 35.

Ostracods with which it was associated include *Dn. ileata* at all stations except 13, 27, 30; *Dt. suteri* and *E. internotalus* at 30, 31, 35; *Dt. suteri* at 27, 33, 124; and *E. internotalus* at 23.

Branchiobdellid associates include *C. philadelphica* at stations 10, 12, 20, 21, 25, 27, 32, 33, 35, 37, 123, 124; *C. holostoma* at 10, 11, 13, 20, 21, 23, 25, 37; *Xg. instabilius* at 11–13, 21, 37, 123; *Xd. formosus* at 10, 21; *A. koronaeus* at 30; *B. illuminatus* and *C. branchiophila* at 20; *C. heterognatha* at 123; and *P. alcicornus* at 25.

Donnaldsoncythere ileata Hobbs and Walton

FIGURE 8c

Donnaldsoncythere ileata Hobbs and Walton, 1963, pp. 364, 368, figs. 11–15, 23.

DIAGNOSIS.—Copulatory complex with peniferum terminating ventrally in rounded extension, with posterior thickened border; anterior border always rounded; clasping apparatus with proximal shaft portion almost straight and distal third directed at angle of 90° to 135° to shaft; internal border of distal fourth with two teeth and terminal margin with four or five serrations.

RANGE.—Tributaries of the James, New, and Roanoke Rivers in Craig, Giles, and Montgomery Counties, Va., and Monroe County, W. Va.

SPECIMENS EXAMINED.—Approximately 3000 specimens from 100 collections from the following stations: 3–12, 14–16, 18–26, 28, 29, 31–35, 37, 43–48, 50–52, 54–67, 69, 71–77, 79–81, 84, 86, 94–99, 102, 104–110, 113, 116, 117, 119, and 122–126, at elevations of 415 to 899 m.

HOSTS AND ASSOCIATES.—In one or more stations, it was associated with every species of crayfish in the area except *C. carolinus*. It was with *C. b. bartonii* at stations 3–10, 12, 14, 16, 19, 21–26, 28, 29, 32, 34, 35, 37, 44–48, 50–52, 54, 57, 59, 60, 63, 64, 66, 69, 71, 74, 76, 77, 94–99, 107, 108, 110, 113, 117, 119, 122–125; with *C. sciotensis* at 3, 5, 15, 18, 19, 43, 44, 50, 54–59, 61–67, 72, 73, 75, 79–81, 84, 86, 95–97, 102, 104–109, 116, 126; with *C. l. longulus* at 6, 7, 9–12, 20–23, 25, 29, 31–35, 37, 123, 124; with *C. acuminatus* at 20, 29, 31–33, 35; and with *O. juvenilis* at 7.

Although in 52 stations *Dn. ileata* was the only ostracod present, it was found with *P. phyma* at stations 3, 5, 7, 24, 44, 64; with *E. internotalus* at 23, 31, 35; with *Dt. suteri* at 31, 33, 35, 124; with *Dt. daphnioides* at 72, 73, 75, 79–81, 116; with *Dn. ardis* 10–12, 20, 21, 23, 25, 31–33, 35, 37, 123, and 124; with *Dn. truncata* at 54–57, 69, 71, 94; with *Dn. scalis* at 7, 44; and with *E. kanawhaensis* at 44, and 126.

Branchiobdellid associates include all 12 species known from the area. It was with *C. philadelphica* at stations 3, 5, 8, 9, 10, 12, 14, 16, 19–22, 24–26, 28, 29, 32–35, 37, 44–46, 48, 50–52, 54–56, 59, 60, 66, 69, 71, 74, 76, 77, 94, 98, 106–110, 113, 119, 122–125; with *C. heterognatha* at 3–5, 24, 28, 34, 45, 48, 61, 63–67, 72, 79-81, 86, 97, 105, 106, 116, 122, 123, 125, 126; with *C. fallax* at 3, 5, 15, 18, 24, 43, 54–58, 61, 63, 65–67, 71, 72, 75, 79, 81, 86, 95–97, 126; with *P. alcicornus* at 3–5, 15, 18, 19, 24, 25, 43, 58, 61, 63-67, 72, 76, 79, 81, 86, 95, 97, 104, 105; with *C. branchiophila* at 15, 18, 20, 24, 29, 43, 55, 57, 58, 63, 65–67, 72, 73, 75, 79, 81, 86, 97, 104, 116, 126; with *Xg. instabilius* at 3–5, 7, 9, 11, 12, 21, 22, 24, 37, 44, 46, 54, 60, 61, 64, 86, 95, 97, 123; with *B. illuminatus* at 5, 16, 19, 20, 22, 34, 44, 45, 48, 51, 59 76, 86, 97, 122, 125; with *C. ingens* at 5, 15, 18, 54, 58, 61, 64, 67, 72, 73, 75, 79–81, 86, 95, 97, 104, 116; with *A. koronaeus* at 14, 18, 19, 29, 52, 69, 71, 72, 77, 98, 110, 125; with *C. holostoma* at 7, 10, 11, 18–23, 25, 37; with *Xd. formosus* at 10, 21; and with *A. legaeus* at 81.

Remarks.—Not only is *Dn. ileata* the most variable ostracod in the region, it is perhaps the most aggressive. In all instances in which it was found associated with other ostracods, it was the most abundant, and it occurred unaccompanied by other ostracods in a far greater number of instances than any of the other species.

Donnaldsoncythere scalis Hobbs and Walton

Figures 7*d*, 9*a*

Donnaldsoncythere scalis Hobbs and Walton, 1963, pp. 364–366, figs. 1–5, 25.

Diagnosis.—Copulatory complex with peniferum terminating ventrally in scooplike expansion; clasping apparatus forming gentle arc, not divisible into vertical and horizontal rami, internal border with two teeth and apical border with four serrations.

Range.—Apparently restricted in the Mountain Lake region to Little Stony Creek (New River drainage) and two tributaries to Johns Creek and Potts Creek (James River drainage) in Giles County, Va., and Monroe County, W. Va.; elsewhere in the Susquehanna River drainage system in Luzerne and Wyoming Counties, Pa., and in a tributary of Lake Cayuga, Cayuga County, N.Y.

Specimens examined.—Approximately 325 specimens from 16 collections in the following stations: 1, 2, 7, 17, 38, 39, 44, 68, 82, 83, 100, 101, 103, 114, and 115, at elevations of 671 to 1219 m.

Hosts and associates.—*Donnaldsoncythere scalis* was associated with *Cambarus b. bartonii* at all stations, with *C. sciotensis* at 44, and with *O. juvenilis* at 7.

Except at stations 7, 38, 44, 82, 101, and 103, it had no ostracod associates; at these it was accompanied by *P. phyma; Dn. ileata* and *E. kanawhaensis* were also present at 44.

Branchiobdellid associates include *C. philadelphica* at stations 17, 39, 44, 68, 115; *C. holostoma* at 7; *B. illuminatus* at 17, 44, 68, 115; and *Xg. instabilius* at 44.

Donnaldsoncythere truncata Hobbs and Walton

FIGURE 9*b*

Donnaldsoncythere truncata Hobbs and Walton, 1963, pp. 364–366, 369, figs. 16–20, 24.

DIAGNOSIS.—Copulatory complex with peniferum terminating ventrally in broad short terminal extension with subangular distal corners; neither corner conspicuously thickened; clasping apparatus with proximal shaft portion only slightly curved and distal third directed at angle of about 90° to proximal third; internal border of

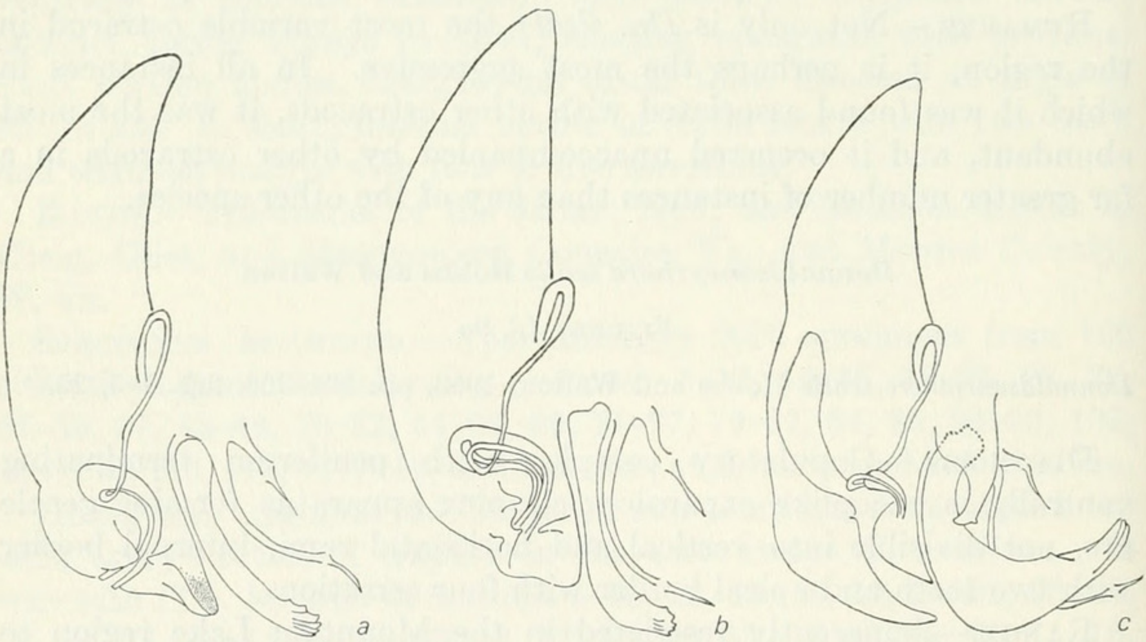


FIGURE 9.—Penifera of entocytherids: *a*, *Donnaldsoncythere scalis;* *b*, *Dn. truncata:* *c*, *Dactylocythere chalaza.*

distal fifth with six serrations, proximal three toothlike. Distal end of penis situated above terminal extension rather than posterodorsal to it as in other species of genus.

RANGE.—Tributaries of the New and Roanoke Rivers in Montgomery and Giles Counties, Va.

SPECIMENS EXAMINED.—Approximately 325 specimens from 17 collections from the following stations: 53–57, 69, 71, 87, 88, 90, 91, 93, 94, and 111. These are situated on tributaries to Walker Creek, Spruce Run, and Toms Creek (New River drainage) and from tributaries of the North Fork of the Roanoke River at elevations ranging from 445 to 625 m.

Hosts and associates.—In the Roanoke River drainage, *Dn. truncata* was associated with *Cambarus acuminatus* at stations 87, 88, 90, 91, 93; with *C. b. bartonii* at 87, 90, 91, 93, 111; and with *C. l. longulus* at 88, 90, 91, and 93. In the New River drainage, it was with *C. b. bartonii* and *C. sciotensis* at 54 and 57; with the former at 53, 69, 71, 94; and with *C. sciotensis* at 55 and 56.

Ostracod associates include *Dt. falcata* at stations 87, 88, 90, 91, 93, 111; *An. ancyla* at 88, 93; *E. internotalus* at 88, 90; *Dn. ileata* at 54–57, 69, 71, and 94. No ostracod associates were with it at 53.

Branchiobdellid associates include *C. philadelphica* at stations 53–56, 69, 71, 87, 88, 90, 91, 93, 94, 111; *A. koronaeus* at 69, 71, 87, 88, 90, 91, 93, 111; *C. branchiophila* at 55, 57, 87, 88, 90, 91, 93; *C. fallax* at 54–57, 71, 87, 88, 91; *Xd. formosus* at 88, 90, 91; *Xg. instabilius* at 53, 54; *B. illuminatus* at 87; and *C. ingens* at 54.

Genus *Dactylocythere* Hart, 1962

Diagnosis.—Copulatory complex with finger guard; two rami of clasping apparatus never forming angle greater than 90° and usually (except in *Dt. striophylax* Crawford and *Dt. falcata* Hobbs and Walton) bearing teeth or serrations on internal border; peniferum provided with accessory sperm groove but never terminating in "barbed terminal extension" (Hart, 1962, p. 129). Females with J-shaped rod (except in *Dt. leptophylax* Crawford) and amiculum; claws of second antenna simple.

Dactylocythere chalaza (Hobbs and Walton)

Figures 7*e*, *i*, 9*c*

Entocythere chalaza Hobbs and Walton, 1962, p. 45, figs. 6–9.
Dactylocythere chalaza Hart, 1962, p. 129.

Diagnosis.—Posteroventral margin of shell without conspicuous prominence. Accessory groove extending dorsally to level of spermatic loop; clasping apparatus with junction of horizontal and vertical rami forming angle of less than 90°, distinctly thickened at junction, and internal border of horizontal ramus with single tooth and three distal serrations. Female with J-shaped rod and amiculum.

Range.—Drainage systems of the James and New Rivers in Craig and Giles Counties, Va., and Monroe County, W. Va.

Specimens examined.—Approximately 775 specimens in 12 collections from the following stations: 8, 22, 40, 41, and 127, at elevations of 585 to 1250 m.

Hosts and associates.—*Dactylocythere chalaza*, like *As. asceta*, seems to be restricted to a single host *Cambarus carolinus*.

At each station *Dt. chalaza* was associated with *As. asceta*.

Branchiobdellid associates include *B. illuminatus* at stations 40, 41, 127; and *C. fallax* at 40.

Dactylocythere daphnioides (Hobbs)

FIGURES 7*f*, *k*, 10*a*

Entocythere daphnioides Hobbs, 1955, p. 325, figs. 1, 2, 5–9.
Dactylocythere daphnioides Hart, 1962, p. 130.

DIAGNOSIS.—Posteroventral margin of shell with conspicuous prominence. Accessory groove extending dorsally to level of spermatic loop; clasping apparatus with junction of horizontal and vertical rami forming angle less than 90°, somewhat thickened at junction, and internal border of horizontal ramus with proximal tooth and four or five distal serrations. Female with J-shaped rod and amiculum.

RANGE.—From the Watauga drainage system in Avery and Watauga Counties, N.C.; the New River system from Alleghany and Ashe Counties, N.C., to Pocahontas County, W. Va.; and the Pound drainage system in Dickerson County, Va.

SPECIMENS EXAMINED.—Approximately 100 specimens in eight collections from the following stations: 70, 72, 73, 75, 79–81, and 116. All localities are in the New River drainage in Walker, Mill, and Wolf Creeks at elevations of 488 to 561 m.

HOST AND ASSOCIATES.—In all stations listed *Dt. daphnioides* was found on *Cambarus sciotensis*.

Donnaldsoncythere ileata was the only ostracod associate and was present in all stations except 70.

Branchiobdellid associates include *C. ingens* at all stations; *P. alcicornus* at 70, 72, 73, 75, 79, 81; *C. fallax* at 70, 72, 75, 79, 81; *C. branchiophila* at 72, 73, 75, 79, 81, 116; *C. heterognatha* at 70, 72, 79–81, 116; *A. koronaeus* at 72; and *A. legaeus* at 81.

Dactylocythere falcata (Hobbs and Walton)

FIGURES 7*j*, 10*b*

Entocythere falcata Hobbs and Walton, 1961, p. 379, figs. 2, 3, 7, 8.
Dactylocythere falcata Hart, 1962, p. 130.

DIAGNOSIS.—Posteroventral margin of shell without conspicuous prominence. Accessory groove extending dorsally beyond spermatic loop; clasping apparatus scythelike usually without teeth or serrations along internal border of horizontal ramus, although some specimens with single tooth near midlength. Female with J-shaped rod and amiculum.

RANGE.—The Hiwassee drainage system in North Carolina, Georgia, and Tennessee (Hobbs and Walton, 1961, p. 381) and from the Roanoke River and its tributaries in Montgomery County, Va.

SPECIMENS EXAMINED.—Approximately 90 specimens in 14 collections from the following stations: 85, 87–93, 111, and 112, at elevations of 439 to 597 m.

HOSTS AND ASSOCIATES.—*Dactylocythere falcata* was associated with *Cambarus l. longulus* and *C. acuminatus* at stations 88, 112; with *C. b. bartonii* at 85, 111; with *C. acuminatus* and *C. b. bartonii* at 87; and with the three at 89–93.

Entocytherid associates include *Dn. truncata* at stations 87, 88, 90, 91, 93, 111; *An. ancyla* at 88, 89, 92, 93; and *E. internotalus* at 88 and 90.

Branchiobdellid associates include *A. koronaeus*, which was present at all stations except 85, where no branchiobdellids were found; *C. branchiophila* at all except 85 and 111; *C. philadelphica* at all except 85; *C. fallax* at 87–89, 91, 92; *Xd. formosus* at 88–92, 112; and *B. illuminatus* at 87.

Dactylocythere suteri (Crawford)

FIGURES 7*h*, 10*c*

Entocythere suteri Crawford, 1959, p. 162, pl. 3.
Dactylocythere suteri Hart, 1962, p. 131.

DIAGNOSIS.—Posteroventral margin of shell without conspicuous prominence. Accessory groove extending dorsally to level of sper-

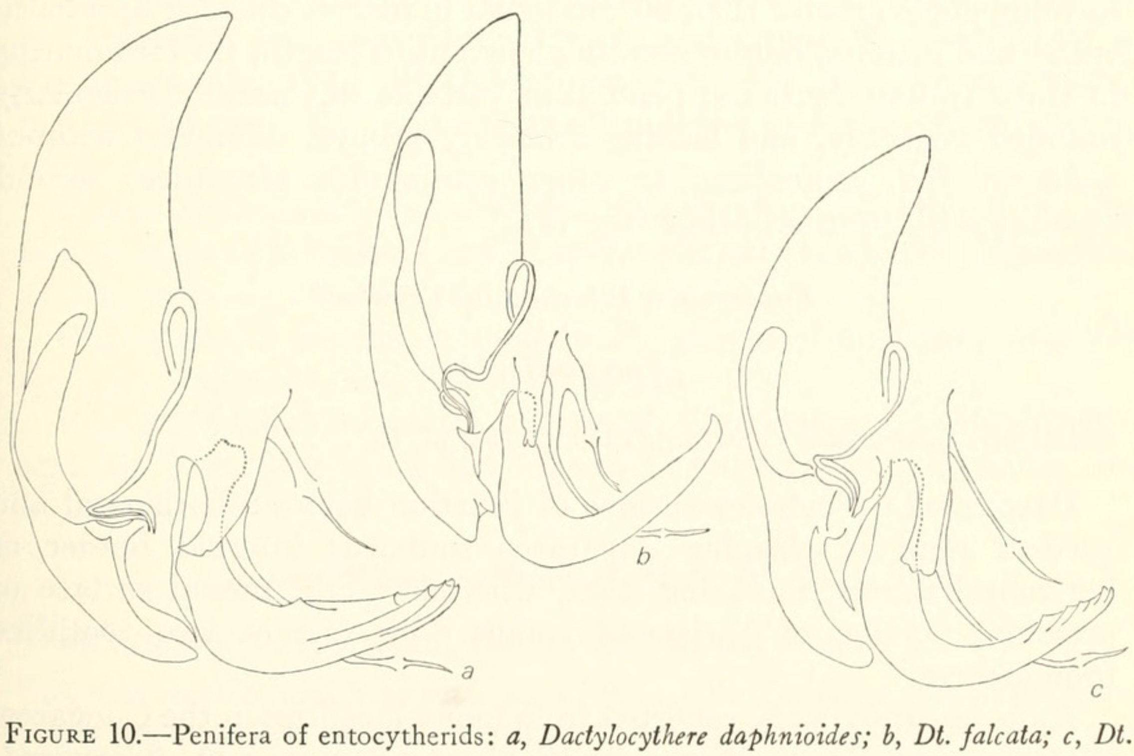


FIGURE 10.—Penifera of entocytherids: *a*, *Dactylocythere daphnioides;* *b*, *Dt. falcata;* *c*, *Dt. suteri.*

matic loop; clasping apparatus with junction of horizontal and vertical rami rounded but extensions forming angle of less than 90°, with no thickening at junction, and internal border of horizontal ramus without proximal tooth but with series of five distal serrations. Female with J-shaped rod and amiculum.

RANGE.—Previously recorded from the drainage systems of the Wateree and Congaree Rivers in Richland County, S.C. (Crawford, 1959, p. 166); in the Mountain Lake region in tributaries of the James River in Craig County, Va.

SPECIMENS EXAMINED.—30 specimens in six collections from the following stations: 27, 30, 31, 33, 35, and 124 in Craig and Johns Creeks, at elevations of 402 to 482 m.

HOSTS AND ASSOCIATES.—In all stations it was associated with *Cambarus l. longulus* and *C. acuminatus* except at 124; and in 35 and 124 with *C. b. bartonii.*

Entocytherid associates include *Dn. ileata*, *Dn. ardis*, and *E. internotalus* at stations 31, 35; *Dn. ardis* and *E. internotalus* at 30; *Dn. ardis* and *Dn. ileata* at 33, 124; and *Dn. ardis* at 27.

Branchiobdellid associates include *C. philadelphica* at stations 27, 33, 35, 124; and *A. koronaeus* at 30.

Genus *Entocythere* Marshall, 1903

DIAGNOSIS.—Copulatory complex without finger guard; clasping apparatus extending ventrally beyond peniferum; extensions of two rami of clasping apparatus seldom (only in *E. dorsorotunda* Hoff, 1944) forming angle greater than 90°; external border of clasping apparatus entire and internal border serrate along entire length, tip terminating in three to five denticles; peniferum variable but usually irregularly rounded ventrally, and lacking accessory groove. Females without J-shaped rod, amiculum, or other comparable structure; second antenna with pectinate claw (fig. 7*b*).

Entocythere internotalus Crawford

FIGURES 7*b*, 11*a*

Entocythere internotalus Crawford, 1959, p. 152, pl. 1.

DIAGNOSIS.—Posterior surface of junction between horizontal and vertical rami of clasping apparatus rounded; internal border of horizontal ramus, including apex, with six teeth; mesial surface of proximal portion of horizontal ramus with one or two toothlike prominences.

RANGE.—Previously reported from many localities in the Congaree, Wateree, and Broad Rivers in Richland County, S.C. (Crawford, 1959, p. 156); in the Mountain Lake region present in tributaries of the James River in Craig County and in the North Fork of the Roanoke River, Montgomery County, Va.

SPECIMENS EXAMINED.—20 specimens in six collections from the following stations: 23, 30, 31, 35, 88, and 90 on tributaries of the James and Roanoke Rivers at elevations of 402 to 475 m.

HOSTS AND ASSOCIATES.—This ostracod was associated with *Cambarus acuminatus* and *C. l. longulus* at stations 30, 31, 35, 88; with *C. b. bartonii* and *C. l. longulus* at 23; and with the three at 35 and 90.

Ostracod associates include *An. ancyla* at station 88; *Dn. ardis* at 23, 30, 31, 35; *Dn. ileata* at 23, 31, 35; *Dt. falcata* and *Dn. truncata* at 88, 90; and *Dt. suteri* at 30, 31, and 35.

Branchiobdellid associates include *A. koronaeus* at stations 30, 88, 90; *C. branchiophila* at 88, 90; *C. philadelphica* at 35, 88, 90; *Xd. formosus* at 88, 90; *C. holostoma* at 23; and *C. fallax* at 88.

Entocythere kanawhaensis Hobbs and Walton

FIGURE 11*b*

Entocythere kanawhaensis Hobbs and Walton, 1966b, Proc. U.S. Nat. Mus., vol. 119, no. 3542, p. 6, figs. 1*l-o*.

DIAGNOSIS.—Posterior surface of junction between horizontal and vertical rami of clasping apparatus subangular; internal border of horizontal ramus, including apex, with nine teeth; mesial surface of horizontal ramus without teeth or emarginations.

RANGE.—Known only from the two localities cited below.

SPECIMENS EXAMINED.—4 specimens in two collections from station 44, Cascades on Little Stony Creek, and from the New River at Pembroke (sta. 126). Both stations are in the New River drainage in Giles County, Va., and are at altitudes of 500 and 899 m, respectively.

HOSTS AND ASSOCIATES.—Within the crayfish collection from station 44 were *C. b. bartonii* and *C. sciotensis;* only the latter was present at 126.

Entocytherid associates include *P. phyma*, *Dn. ileata*, and *Dn. scalis* at station 44, and *Dn. ileata* at 126.

Branchiobdellid associates include *B. illuminatus*, *C. philadelphica*, and *Xg. instabilius* at station 44, and *C. branchiophila*, *C. fallax*, and *C. heterognatha* at 126.

Genus *Phymocythere* Hobbs and Hart, 1966

DIAGNOSIS.—Hobbs and Hart (1966, p. 48) stated:

Terminal tooth of mandible with cusps. Copulatory complex with finger guard; periferum extending ventrally much beyond clasping apparatus, elongate, comparatively slender, entirely corneous with terminal bulbous enlargement lacking superficial extensions; penis complex consisting of separate dorsal spermatic and ventral prostatic elements; spermatic element longer than clasping apparatus: accessory groove lacking. Clasping apparatus reduced, not clearly divisible into vertical and horizontal rami; external border of horizontal ramus entire, internal border also entire except at apex, latter may be expanded and bear three to six denticles.

Phymocythere phyma (Hobbs and Walton)

Figure 11c

Entocythere phyma Hobbs and Walton, 1962, p. 44, figs. 10–13.
Cymocythere phyma Hart, 1962, p. 129.
Phymocythere phyma Hobbs and Hart, 1966, p. 48.

Diagnosis.—Length of penis greater than longitudinal diameter of bulbiform portion of peniferum; clasping apparatus small and with distal margin not extending anterior to anterior margin of peniferum. Female unknown.

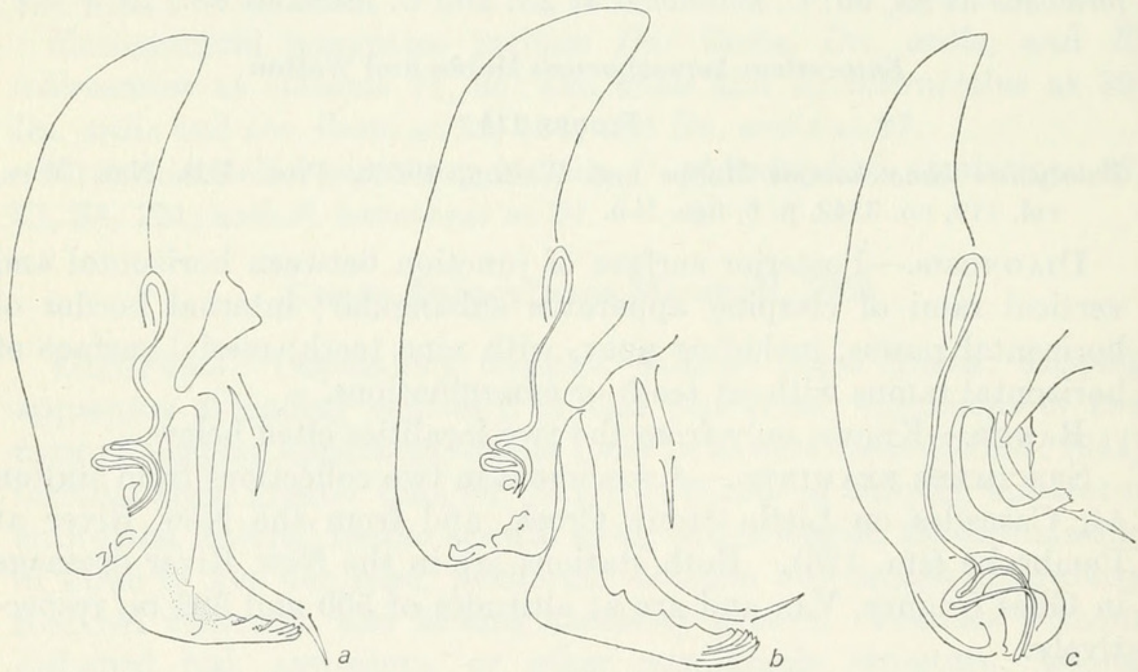


Figure 11.—Penifera of entocytherids: *a*, *Entocythere internotalus;* *b*, *E. kanawhaensis;* *c*, *Phymocythere phyma.*

Range.—Tributaries of the James, Potomac, New, and Tygart Rivers in Virginia and West Virginia. (See Hobbs and Hart, 1966, p. 48.)

Specimens examined.—85 specimens in 12 collections from the following stations: 3, 5, 7, 24, 38, 44, 64, 82, 101, and 103. Represented are tributaries of Johns and Potts Creeks (James River drainage) and Big Stony and Little Stony Creeks (New River drainage), at elevations of 610 to 1143 m.

Hosts and associates.—*Phymocythere phyma* was associated with *Cambarus b. bartonii* at all stations; with *C. sciotensis* at 3, 5, 44, 64; and *O. juvenilis* and *C. l. longulus* at 7.

Entocytherid associates include *Dn. ileata* at stations 3, 5, 7, 24, 44, 64; *Dn. scalis* at 7, 38, 44, 82, 101, 103; and *E. kanawhaensis* at 44.

Branchiobdellid associates include *B. illuminatus* at stations 5, 44; *C. branchiophila* at 24; *C. heterognatha* and *P. alcicornus* at 3, 5, 24, 64; *C. holostoma* at 7; *C. ingens* at 5, 64; *C. philadelphica* at 3, 5, 24, 44; and *Xg. instabilius* at 3, 5, 7, 24, 44, and 64.

The Branchiobdellids

The epizoites that compose the clitellate order Branchiobdellida are annelids with leechlike suckers and a short body of 15 segments of which the first four form a "head." Segmentation is obscured by coalescence in the head and also posteriorly in the formation of the posterior sucker, so that usually only the trunk segments are numbered; e.g., the anterior nephridia are said to open on segment III, but actually this is segment VII. The conventional system of designating the first trunk segment as I will be followed here. The body is cylindrical (terete) in most species, but members of three genera (*Ankyrodrilus*, *Xironodrilus*, and *Xironogiton*) are variously dorsoventrally flattened (depressed) in body form.

The trunk segments, marked internally by distinct muscular septa anterior to the sucker, are further subdivided into annuli, normally only two, of which the anteriormost (prosomite) is longer and often greater in diameter than the posterior annulus (metasomite). Some branchiobdellids possess dorsal projections of various types on the prosomites of some trunk segments (fig. 20).

A prostomium, common among the annelids, is absent in the branchiobdellids. The mouth is surrounded by a peristomium (the first head segment) that is set off by a sulcus and may be entire (not divided into lobes or provided with tentacles) or variously lobed or tentaculate, but most often the peristomium forms dorsal and ventral lips. The buccal cavity of all branchiobdellids, presumably in the second head segment, is armed with sclerotized "jaws": one dorsal, one ventral. These jaws are usually provided with denticles ("teeth": figs. 12*c*, *f*). The number of teeth is often expressed by a "dental formula" in which the teeth of the upper jaw are enumerated first.

The reproductive systems have been found to provide the most reliable taxonomic characters. The components of these systems may best be understood by reference to figures 12*b*, 14*a*, and 15*a*. Testes, not patent in mature animals, are found in segments V and VI, ovaries in segment VII. Spermatogenic cells and spermatozoa fill the coelomic spaces of the testicular segments and the spermatozoa are conveyed to the outside by a series of ducts, beginning in the male funnels (f), which are the ental ends of the efferent ducts. The efferent ducts (ed) unite in each testicular segment to form the deferent ducts (dd), which enter a glandular organ, the spermiducal gland (sg). The deferent ducts may enter the ental end of the spermiducal gland, with or without a previous thickening of the ducts, forming deferent lobes of the gland (dl), or they may enter the gland near its midlength. In some genera, an accessory gland, the prostate (pr), is given off as a blindly ending sac, at the ectal part of the spermiducal gland, where it narrows to form the muscular ejaculatory duct (ejd). The latter, in turn, joins the bursa (b), the muscular eversible sac (in the species considered here) enclosing the penis in its ental portion, which may be considerably elongated (as in *Ankyrodrilus*) or a short, pyriform organ (as in *Cambarincola*). Of these components of the male efferent apparatus, the spermiducal gland is always present but may vary in shape, in the presence or absence of deferent lobes and in the point of entry of the deferent ducts; the prostate may be present or absent and, if present, may be histologically similar to or different from the spermiducal gland and of varying proportional lengths and diameters; the ejaculatory duct may be either present or absent and of varying lengths, and the bursa of varying shapes. The other male parts exhibit little variation of taxonomic importance.

The female system is much simpler in arrangement and composition. There is little variation in the arrangement of the ovaries and ovipores in segment VII. The spermatheca (fig. 18) in segment V is an unpaired sac (but bifid in *Bdellodrilus*) that may vary from species to species in such features as the length and diameter of the ectal spermathecal duct, the diameter and length of the spermatozoa-storing spermathecal bulb, and the presence or absence of an ental process.

Key to Branchiobdellids

1	Body terete	2
1′	Body depressed, at least in part.	9
2(1)	With bifurcate spermatheca; without prostate .	**Bdellodrilus illuminatus**
2′	Spermatheca not bifurcate; prostate present	3
3(2′)	Trunk segments III, IV, V, and VIII with fanlike dorsal projections.	**Pterodrilus alcicornus**
3′	Trunk segments without dorsal projections . . **Cambarincola** . .	4
4(3′)	Jaws similar in size and shape, both upper and lower jaws with odd number of teeth	5
4′	Jaws dissimilar in at least shape, upper jaw with odd number, lower jaw with even number of teeth	7
5(4)	With peristomial tentacles, dental formula 5/5	**C. fallax**
5′	Without peristomial tentacles, dental formula may or may not be 5/5	6
6(5′)	Prostate histologically similar to spermiducal gland, spermiducal gland with deferent lobes, dental formula 5/5	**C. branchiophila**
6′	Prostate and spermiducal gland histologically dissimilar; dental formula often 3/3	**C. holostoma**

7(4′) Jaws grossly unequal in size . . . . **C. heterognatha**
7′ Jaws similar in size 8
8(7′) Prostate longer than slender spermiducal gland . . . . **C. ingens**
8′ Prostate shorter and lesser in diameter than spermiducal gland. **C. philadelphica**
9(1′) Anterior body segments terete, fifth through eleventh segments depressed (tennis racquet shaped) . . . . . **Xironogiton instabilius**
9′ Body uniformly depressed, spatulate 10
10(9′) Deferent ducts enter ental end of spermiducal gland. **Xironodrilus formosus**
10′ Deferent ducts enter midlength of T-shaped spermiducal gland. **Ankyrodrilus** . . 11
11(10′) Dental formula 3/4 . . . . **A. koronaeus**
11′ Dental formula 5/4 or 5/5 . . . . **A. legaeus**

Genus *Ankyrodrilus* Holt, 1965

Diagnosis.— Holt (1965, p. 10) stated:

Branchiobdellid worms with two pairs of testes; paired nephridiopores on the dorsum of segment III; at least nine distinct segments visible in dorsal view; gut straight, with sacculations in segments II, III, IV, those of segments III and IV the larger; aggregations of gland cells present in lateral portions of segments VIII and IX; caudal sucker ventral; body depressed and tapering gradually from anterior end to its greatest width in segment VI, VII or VIII; spermiducal gland large with blindly ending bifurcated proximal portion, vasa deferentia entering the median portion of the organ; bursa constricted between atrial and penial sheath portions, giving the organ as a whole a reduplicated aspect; ejaculatory duct absent; spermatheca composed of ectal duct, bulb and ental process.

Ankyrodrilus koronaeus Holt

Figures 12*a–d*

Ankyrodrilus koronaeus Holt, 1965, p. 11.

Diagnosis.—"Upper jaw with three large teeth, subequal in length; lower jaw convex, rounded at tooth-bearing border, carrying four small, subequal teeth" (Holt, 1965, p. 11).

Range.—Tributaries of the Roanoke, James, and New Rivers in Montgomery, Giles, Craig, and Botetourt Counties, Va.

Specimens examined.—More than 160 specimens in 22 collections from the following stations: 14, 18, 19, 29, 30, 52, 69, 71, 72, 77, 87–93, 98, 110–112, and 125. These are in all the major drainages of the area at elevations ranging from 402 to 750 m.

Host and associates.—*A. koronaeus* was associated with *Cambarus acuminatus* at stations 29, 30, 87–93, 112; with C. *b. bartonii* at all stations except 18, 30, 72, 88, 112; with *C. l. longulus* at 29, 30, 88–93, 112; and with *C. sciotensis* at 18, 19, and 72.

Ostracod associates include *An. ancyla* at stations 88, 89, 92, 93; *Dn. ileata* at 14, 18, 19, 29, 52, 69, 71, 72, 77, 98, 110, 125; *Dn. truncata* at 69, 71, 87, 88, 90, 91, 93, 111; *Dt. daphnioides* at 72; *Dt. falcata* at 87–93, 111, 112; *Dn. ardis* and *Dt. suteri* at 30; and *E. internotalus* at 30, 88, and 90.

Branchiobdellid associates include *B. illuminatus* at stations 19, 87, 125; *C. branchiophila* at 18, 29, 72, 87–93, 112; *C. fallax* at 18, 71, 72, 87–89, 91, 92; *C. heterognatha* at 72, 125; *C. holostoma* at 18, 19; *C. ingens* at 18, 72; *C. philadelphica* at all stations except 18, 30, 72; *P. alcicornus* at 18, 19, 72; and *Xd. formosus* at 88–92, and 112.

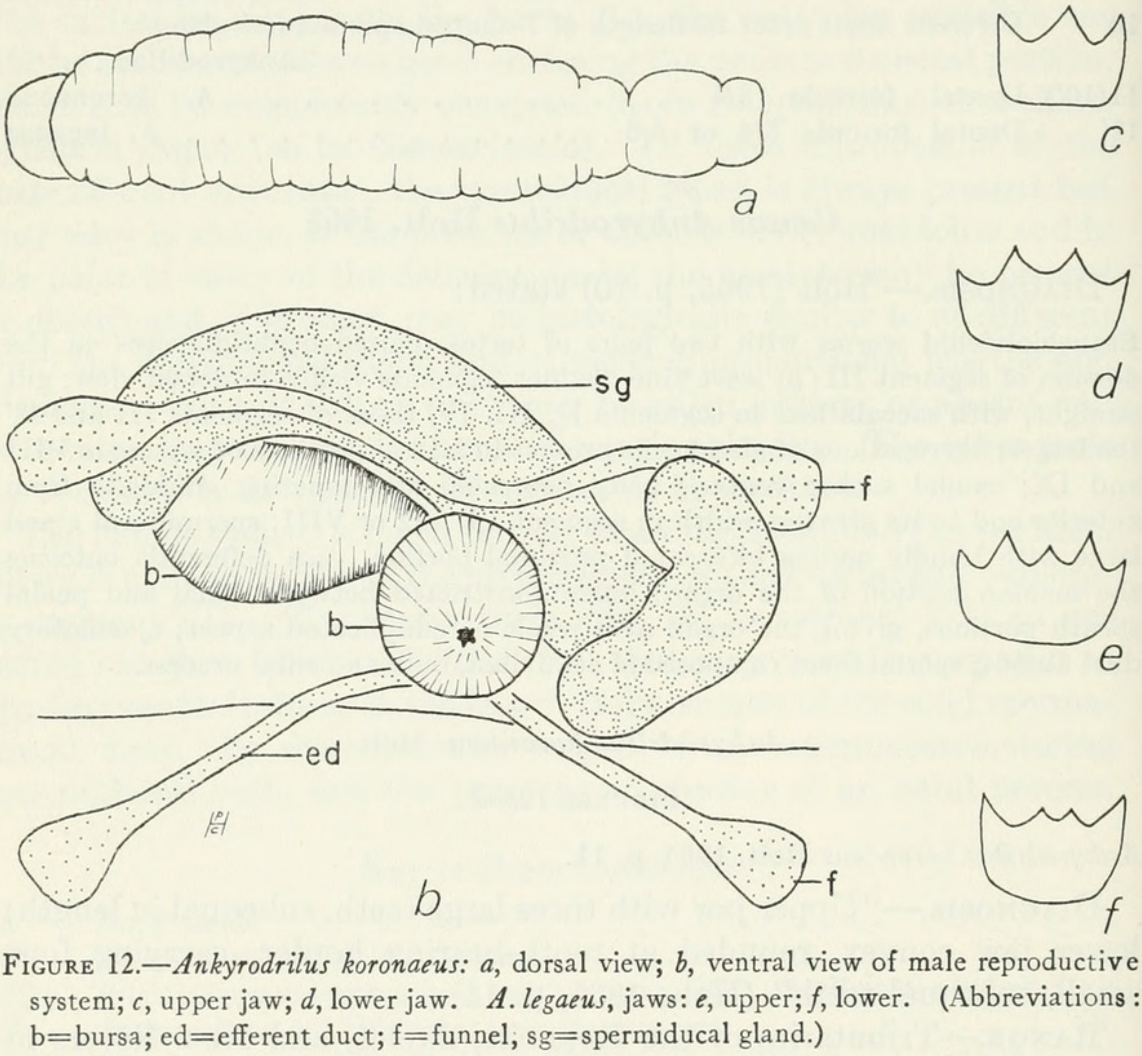


FIGURE 12.—*Ankyrodrilus koronaeus: a*, dorsal view; *b*, ventral view of male reproductive system; *c*, upper jaw; *d*, lower jaw. *A. legaeus*, jaws: *e*, upper; *f*, lower. (Abbreviations: b=bursa; ed=efferent duct; f=funnel, sg=spermiducal gland.)

REMARKS.—Present distribution records indicate that *A. koronaeus* and its congener, *A. legaeus*, are allopatric. Both species of *Ankyrodrilus* are inhabitants of middle altitude streams and may vicariate there for *Xg. instabilius* as inhabitants of the chelipeds of the host.

Ankyrodrilus legaeus Holt

FIGURES 12*e–f*

Ankyrodrilus legaeus Holt, 1965, p. 12.

DIAGNOSIS.—"Upper jaw with five teeth; lower jaw with four—five teeth; teeth of upper jaw of unequal length, lateral teeth and median teeth shorter than others; lateral teeth of lower jaw longer than median teeth" (Holt, 1965, p. 12).

RANGE.—From Overton County, Tenn., sporadically to the New River drainage in Giles County, Va.

SPECIMENS EXAMINED.—7 specimens from station 81 in the New River drainage at an elevation of 488 m.

HOST AND ASSOCIATES.—*Ankyrodrilus legaeus* was associated with *Cambarus sciotensis* at station 81.

Ostracod associates include *Dn. ileata* and *Dt. daphnioides.*

Branchiobdellid associates include *C. branchiophila, C. fallax, C. heterognatha, C. ingens,* and *P. alcicornus.*

REMARKS.—*Ankyrodrilus legaeus* has been found associated with eight other species or subspecies of crayfishes; its single occurrence on *C. sciotensis* in the Mountain Lake region is no indication of host specificity.

Genus *Bdellodrilus* Moore, 1895

DIAGNOSIS.—Head elongated and less in diameter than anterior body segments; peristomium without lobes, body wall thin and glandular (parasitic facies); posterior sucker small and weak; two pairs of testes, no prostate, penis eversible; spermatheca bifid; lateral glands present in trunk segments I through IX; anterior nephridia open by common pore; upper jaw longitudinal ridge bearing three teeth, lower jaw deep trough in which dorsal one fits; inhabitants of gill chambers. Monotypic.

Bdellodrilus illuminatus (Moore)

FIGURES 13*a–b*

Branchiobdella illuminata Moore, 1894, p. 421.
Bdellodrilus illuminatus Moore, 1895b, p. 498.

DIAGNOSIS.—As above for the genus.

RANGE.—Eastern North America.

SPECIMENS EXAMINED.—Approximately 50 specimens in 24 collections from the following stations: 5, 16, 17, 19, 20, 22, 34, 40, 41, 44, 45, 48, 51, 59, 68, 76, 86, 87, 97, 115, 120–122, 125, and 127. All of the major drainage areas are represented among these stations. Elevations range from 518 to 1250 meters.

HOSTS AND ASSOCIATES.—*Bdellodrilus illuminatus* was associated with *Cambarus acuminatus* at stations 20, 87; with *C. b. bartonii* at all stations except 20, 40, 41, 86, 127; with *C. carolinus* at 22, 40, 41, 127; with *C. l. longulus* at 20, 22, 34; and with *C. sciotensis* at 5, 19, 44, 59, 86, and 97.

Ostracod associates include *As. asceta* and *Dt. chalaza* at stations 22, 40, 41, 127; *Dn. ardis* at 20; *Dn. ileata* at 5, 16, 19, 20, 22, 34, 44, 45, 48, 51, 59, 76, 86, 97, 122, 125; *Dn. scalis* at 17, 44, 68, 115; *Dn. truncata* and *Dt. falcata* at 87; *E. kanawhaensis* at 44; and *P. phyma* at 5 and 44.

Branchiobdellid associates include *A. koronaeus* at stations 19, 87, 125; *C. branchiophila* at 20, 86, 87, 97; *C. fallax* at 5, 40, 86, 87, 97; *C. heterognatha* at 5, 34, 45, 48, 86, 97, 122, 125; *C. holostoma* at 19, 20, 22; *C. ingens* at 5, 86, 97; *C. philadelphica* at all stations except 40, 41, 86, 97, 127; *P. alcicornus* at 5, 19, 76, 86, 97; and *Xg. instabilius* at 5, 22, 44, 86, 97, and 121.

Remarks.—*Bdellodrilus illuminatus* is an indisputable gill-inhabiting species. Often it is the only branchiobdellid associate of the burrowing *C. carolinus*, the only crayfish species with which it was found to occur more often than would be expected by chance.

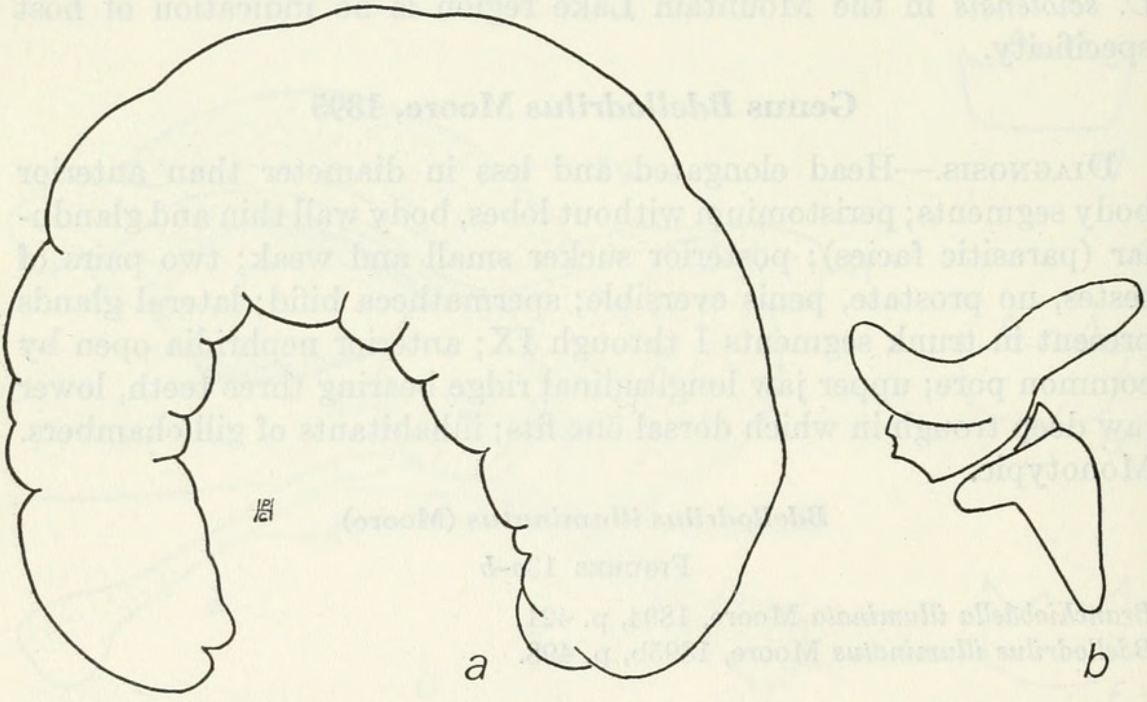


Figure 13.—*Bdellodrilus illuminatus*, lateral views: *a*, entire animal; *b*, jaws.

Genus *Cambarincola* Ellis, 1912

Diagnosis.—Body terete without specialized projections; anterior nephridia opening through common pore on dorsum of segment III; deferent ducts entering ental end of spermiducal gland; prostate and ejaculatory duct both present; penis noneversible; bursa subpyriform to obcordate; spermatheca never bifid.

Cambarincola branchiophila Holt

Figures 14*a–c*

Cambarincola branchiophila Holt, 1954, p. 168.

Diagnosis.—Gill-inhabiting branchiobdellid; lips entire; dental formula 5/5, with lateralmost teeth longer than teeth between them and median teeth; prosomites not raised; spermiducal gland with deferent lobes; prostate shorter than spermiducal gland and histologically similar; relatively large, stout (to about 3.5 mm in length).

RANGE.—Known only from the Mountain Lake area, *C. branchiophila* has been found in the major streams of all the drainage systems of the area.

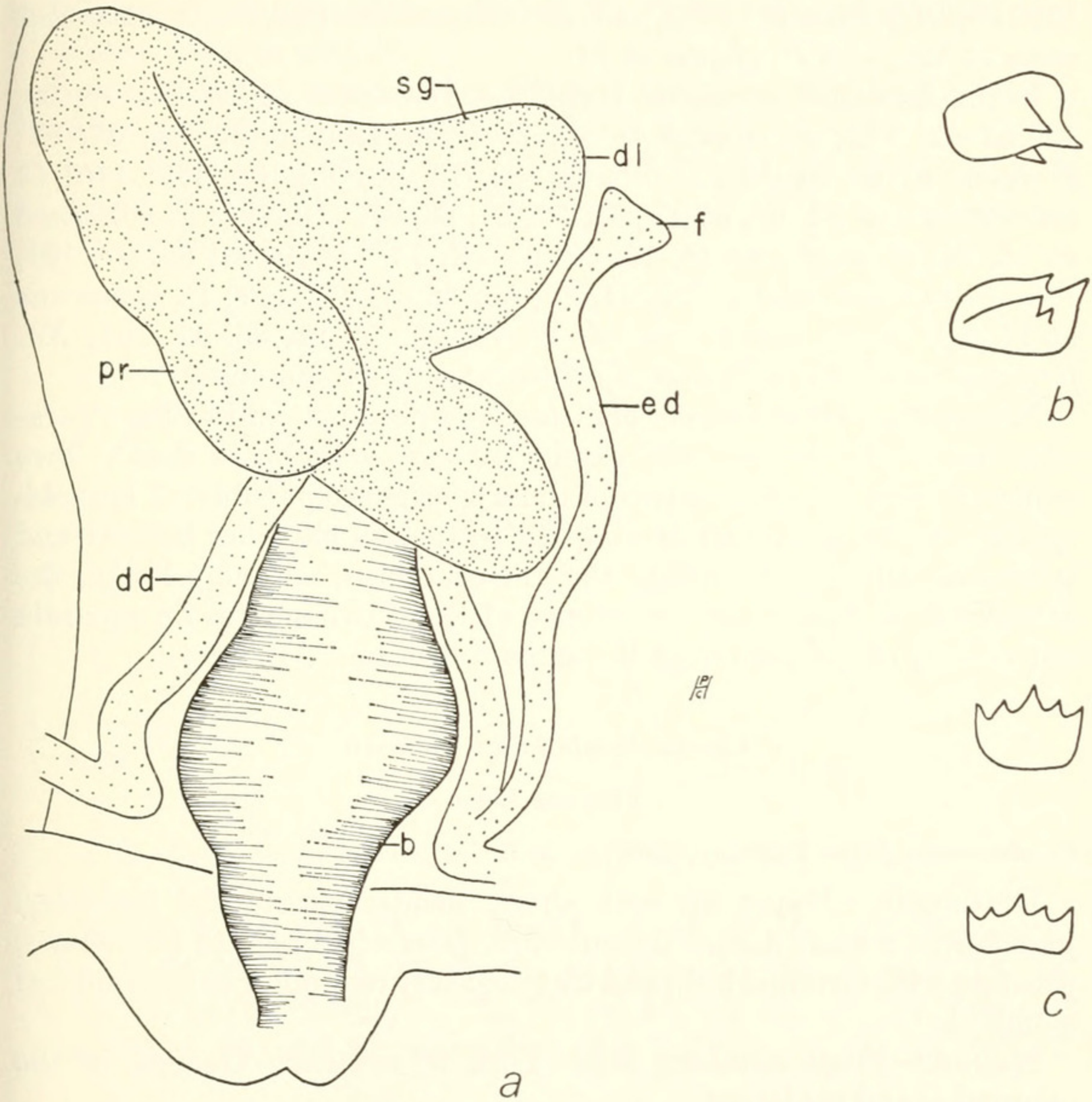


FIGURE 14.—*Cambarincola branchiophila*, lateral views: *a*, male reproductive system; *b*, jaws. En face view: *c*, jaws, upper uppermost. (Abbreviations: b=bursa; dd=deferent duct; dl=deferent lobe; ed=efferent duct; f=funnel; pr=prostate; sg=spermiducal gland.)

SPECIMENS EXAMINED.—More than 150 specimens in 31 collections from the following stations: 15, 18, 20, 24, 29, 43, 55, 57, 58, 63, 65–67, 72, 73, 75, 79, 81, 86–93, 97, 104, 112, 116, and 126. Elevations range from 427 to 762 m.

HOSTS AND ASSOCIATES.—*Cambarincola branchiophila* was associated with *Cambarus acuminatus* at stations 20, 29, 87–93, 112; with *C. b.*

bartonii at 24, 29, 57, 63, 66, 87, 89–93, 97; with *C. l. longulus* at 20, 29, 88–93, 112; and with *C. sciotensis* at all stations except 20, 24, 29, 87–93, 112.

Ostracod associates include *An. ancyla* at stations 88, 89, 92, 93, *Dn. ardis* at 20; *Dn. ileata* at all stations except 87–93, 112; *Dn. truncata* at 55, 57, 87, 88, 90, 91, 93; *Dt. daphnioides* at 72, 73, 75, 79, 81, 116; *Dt. falcata* at 87–93, 112; *E. internotalus* at 88, 90; *E. kanawhaensis* at 126; and *P. phyma* at 24.

Branchiobdellid associates include *A. koronaeus* at stations 18, 29, 72, 87–93, 112; *A. legaeus* at 81; *B. illuminatus* at 20, 86, 87, 97; *C. fallax* at all stations except 20, 29, 73, 90, 93, 104, 112, 116; *C. heterognatha* at 24, 63, 65–67, 72, 79, 81, 86, 97, 116, 126; *C. holostoma* at 18, 20; *C. ingens* at 15, 18, 58, 67, 72, 73, 75, 79, 81, 86, 97, 104, 116; *C. philadelphica* at 20, 24, 29, 55, 66, 87–93, 112; *P. alcicornus* at 15, 18, 24, 43, 58, 63, 65–67, 72, 73, 75, 79, 81, 86, 97, 104; *Xd. formosus* at 88–92, 112; and *Xg. instabilus* at 24, 86, and 97.

REMARKS.—*Cambarincola branchiophila* does not exhibit the "parasitic facies" to the extreme extent that *B. illuminatus* does. Two explanations of the association of these species are possible: *C. branchiophila* may be incompletely adapted to the gill chamber habitat and is occasionally found outside the gill chambers, or, more likely, the association is due to the occurrence of these two species on separate individuals of the host from the same collection.

Cambarincola fallax Hoffman

FIGURES 15*a*–*b*

Cambarincola fallax Hoffman, 1963, p. 356.

DIAGNOSIS.—Upper lip with short, slender peristomial tentacles; prosomites raised; dental formula 5/5, jaws of same size and shape; prostate with terminal bulb and histologically dissimilar to spermiducal gland.

RANGE.—From northern New York to northern Georgia in the mountains and piedmont.

SPECIMENS EXAMINED.—More than 300 specimens in 35 collections from the following stations: 3, 5, 15, 18, 24, 40, 43, 49, 54–58, 61, 63, 65–67, 70–72, 75, 78, 79, 81, 86–89, 91, 92, 95–97, and 126 at elevations from 439 to 1158 m. This species, common to the three drainage systems of the area, appears to be somewhat less common in the James than in the others: it was taken twice (sta. 11 and 24) from Johns Creek.

HOSTS AND ASSOCIATES.—*Cambarincola fallax* was associated with *Cambarus acuminatus* at stations 87–89, 91, 92; with *C. b. bartonii* at 3, 5, 24, 49, 54, 57, 63, 66, 71, 87, 89, 91, 92, 95–97; with *C. carolinus* at 40; with *C. l. longulus* at 88, 89, 91, 92; with *C. sciotensis* at 3, 5, 15, 18, 43, 54–58, 61, 63, 65–67, 70, 72, 75, 78, 79, 81, 86, 95–97, and 126.

Ostracod associates include *An. ancyla* at stations 88, 89, 92; *As. asceta* at 40; *Dn. ileata* at 3, 5, 15, 18, 24, 43, 54–58, 61, 63, 65–67, 71, 72, 75, 79, 81, 86, 95–97, 126; *Dn. truncata* at 54–57, 71, 87, 88, 91; *Dt. chalaza* at 40; *Dt. daphnioides* at 70, 72, 75, 79, 81; *Dt. falcata* at 87–89, 91, 92; *E. internotalus* at 88; *E. kanawaensis* at 126; and *P. phyma* at 3, 5, and 24.

Branchiobdellid associates include *A. koronaeus* at stations 18, 71, 72, 87–89, 91, 92; *A. legaeus* at 81; *B. illuminatus* at 5, 40, 86, 87, 97; *C. branchiophila* at 15, 18, 24, 43, 55, 57, 58, 63, 65–67, 72, 75, 79, 81, 86–89, 91, 92, 97, 126; *C. heterognatha* at 3, 5, 24, 61, 63, 65–67; 70, 72, 78, 79, 81, 86, 97, 126; *C. holostoma* at 18; *C. ingens* at 5, 15,

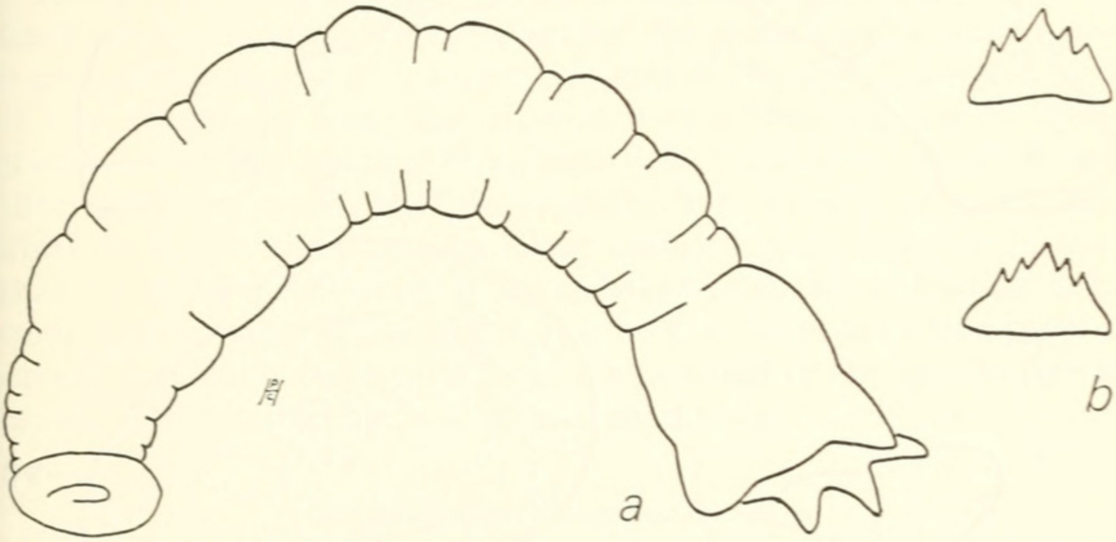


FIGURE 15.—*Cambarincola fallax: a*, lateral view of entire animal; *b*, en face view of jaws.

18, 54, 58, 61, 67, 70, 72, 75, 79, 81, 86, 95, 97; *C. philadelphica* at 3, 5, 24, 54–56, 66, 71, 87–89, 91, 92; *P. alcicornus* at 3, 5, 15, 18, 24, 43, 58, 61, 63, 65–67, 70, 72, 75, 79, 81, 86, 95, 97; *Xd. formosus* at 88, 89, 91, 92; and *Xg. instabilius* at 3, 5, 24, 54, 61, 86, 95, and 97.

Cambarincola heterognatha Hoffman

FIGURES 16*a–c*

Cambarincola heterognatha Hoffman, 1963, p. 362.

DIAGNOSIS.—Without peristomial tentacles; prosomites not distinctly raised; dental formula 1/4 (usually), upper jaw strikingly larger than lower; prostate half or less length of spermiducal gland and dissimilar histologically.

RANGE.—In the mountainous regions of West Virginia, Virginia, North Carolina, Tennessee, and Kentucky (Adair County).

Specimens examined.—Approximately 100 specimens in 28 collections from the following stations: 3, 4, 5, 24, 28, 34, 45, 48, 61, 63–67, 70, 72, 78–81, 86, 97, 105, 106, 116, 122, 123, 125, and 126. These stations are in the New and James river systems at elevations from 451 to 838 m.

Hosts and associates.—*Cambarincola heterognatha* was associated with *Cambarus b. bartonii* at stations 3–5, 24, 28, 34, 45, 48, 63, 64, 66,

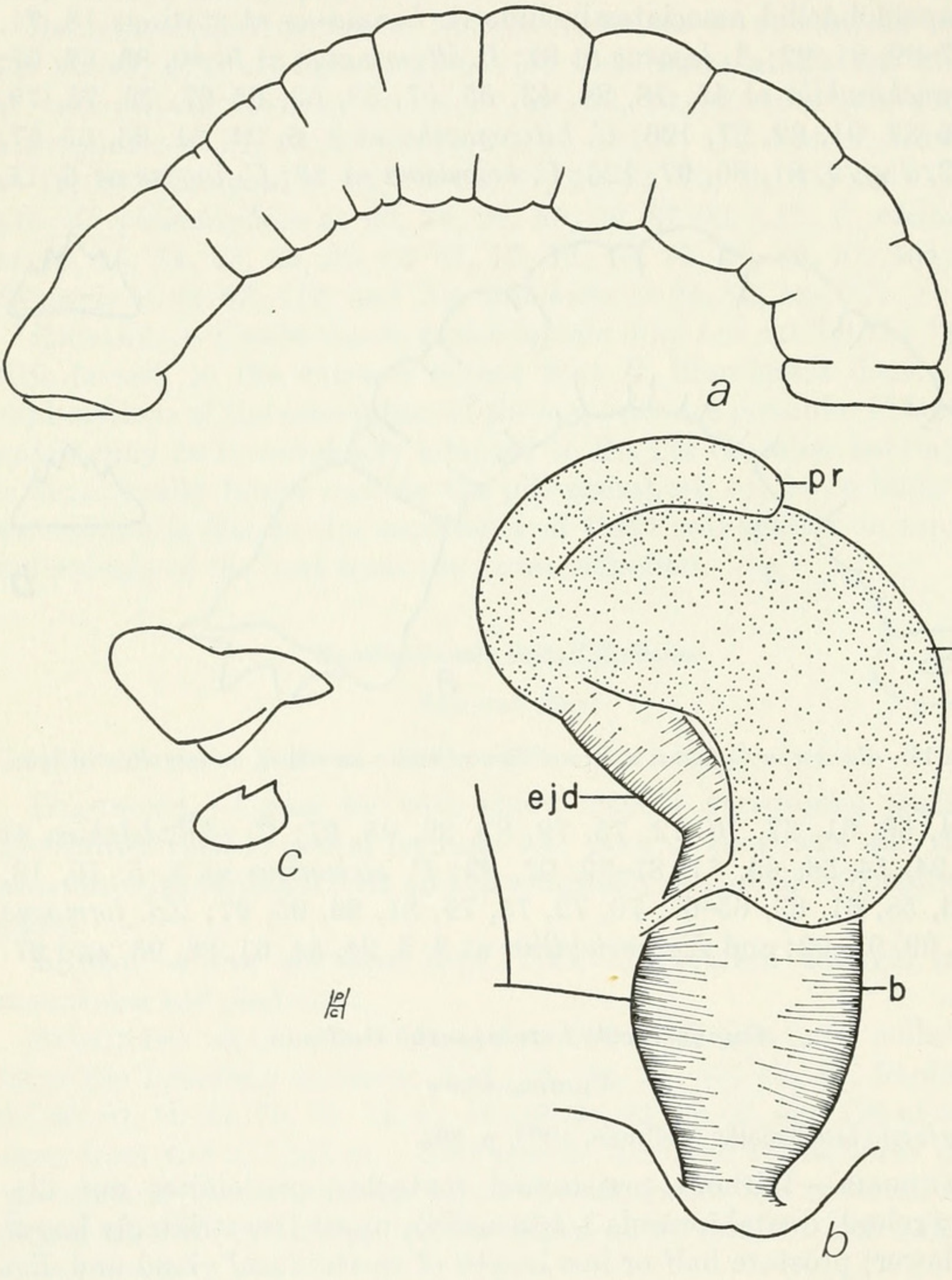


Figure 16.—*Cambarincola heterognatha*, lateral views: *a*, entire animal; *b*, male reproductive system; *c*, jaws. (Abbreviations: b=bursa; ejd=ejaculatory duct; pr=prostate; sg= spermiducal gland.)

97, 122, 123, 125; with *C. l. longulus* at 34, 123; with *C. sciotensis* at 3, 5, 61, 63–67, 70, 72, 78–81, 86, 97, 105, 106, 116, and 126.

Ostracod associates include *Dn. ardis* at station 123; *Dn. ileata* at all stations except 70 and 78; *Dt. daphnioides* at 70, 72, 79–81, 116; *E. kanawhaensis* at 126; and *P. phyma* at 3, 5, 24, and 64.

Branchiobdellid associates include *A. koronaeus* at stations 72, 125; *A. legaeus* at 81; *B. illuminatus* at 5, 34, 45, 48, 86, 97, 122, 125; *C. branchiophila* at 24, 63, 65–67, 72, 79, 81, 86, 97, 116, 126; *C. fallax* at 3, 5, 24, 61, 63, 65–67, 70, 72, 78, 79, 81, 86, 97, 126; *C. ingens* at 5, 61, 64, 67, 70, 72, 79–81, 86, 97, 116; *C. philadelphica* at 3, 5, 24, 28, 34, 45, 48, 66, 106, 122, 123, 125; *P. alcicornus* at 3–5, 24, 61, 63–67, 70, 72, 79, 81, 86, 97, 105; and *Xg. instabilius* at 3–5, 24, 61, 64, 86, 97, and 123.

Remarks.—The absence of *C. heterognatha* in our collections from the Roanoke drainage is surprising; but the species, in our experience, is predominantly one of tributary streams of the mountains and most of our collections from the Roanoke were from regions of lower gradient and fair volume of stream flow. There exists (Hoffman, 1963, p. 364) a record of *C. heterognatha* from Franklin County, Va., which is within the Roanoke River system. Only a more detailed analysis of the distribution of the species will enable a decision to be made as to whether the species is just now, at some favorable areas of stream capture, invading the Roanoke or whether the distribution as known is determined by local stream conditions.

Cambarincola holostoma Hoffman

Figures 17*a–d*

Cambarincola holostoma Hoffman, 1963, p. 359.

Diagnosis.—Peristomium entire without lobes or tentacles; prosomites not of greater diameter than metasomites; dental formula 3/3; reproductive systems similar to those of *C. philadelphica*.

Range.—*Cambarincola holostoma* is known only from western Virginia in the headwaters of the Potomac and James Rivers with an isolated occurrence in Sinking Creek (sta. 18, 19) of the New River drainage.

Specimens examined.—Approximately 80 specimens in 12 collections from the following stations: 7, 10, 11, 13, 18–23, 25, and 37. These stations are in the James River drainage (Potts, Johns, and Craig Creeks) except 18 and 19 which are in the New River drainage (Sinking Creek). The elevations of these stations range from 512 to 671 m.

Hosts and associates.—*Cambarincola holostoma* was associated with *Cambarus acuminatus* at station 20; with *C. b. bartonii* at 7, 10, 19, 21–23, 25, 37; with *C. carolinus* at 22; with *C. l. longulus* at 7, 10, 11, 13, 20–23, 25, 37; with *C. sciotensis* at 18, 19; and with *O. juvenilis* at 7.

Ostracod associates include *As. asceta* and *Dt. chalaza* at station 22; *Dn. ardis* at 10, 11, 13, 20, 21, 23, 25, 37; *Dn. ileata* at 7, 10, 11, 18–23, 25, 37; *Dn. scalis* and *P. phyma* at 7; and *E. internotalus* at 23.

Branchiobdellid associates include *A. koronaeus* at stations 18, 19; *B. illuminatus* at 19, 20, 22; *C. branchiophila* at 18, 20; *C. fallax* and *C. ingens* at 18; *C. philadelphica* at 10, 19–22, 25, 37; *P. alcicornus* at 18, 19, 25; *Xd. formosus* at 10, 21; and *Xg. instabilius* at 7, 11, 13, 21, 22, and 37.

Remarks.—*Cambarincola holostoma,* on the basis of present knowledge, appears to be a highly localized species that has recently invaded the headwaters of Sinking Creek from the nearby tributaries of the James River.

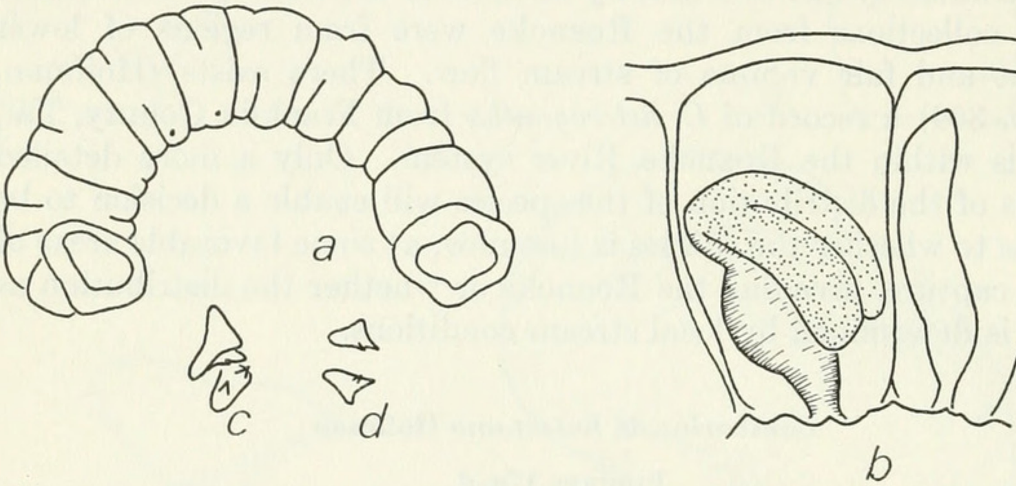


Figure 17.—*Cambarincola holostoma: a,* lateroventral view of entire animal; *b,* lateral view of male reproductive system and spermatheca; *c,* dorsolateral view of jaws; *d,* lateral view of jaws. (After Hoffman, 1963.)

Cambarincola ingens Hoffman

Figures 18*a–d*

Cambarincola ingens Hoffman, 1963, p. 333.

Diagnosis.—Upper lip of peristomium with four long lobes or short tentacles; prosomites only moderately greater in diameter than metasomites; dental formula 5/4 or 3/4; prostate longer than spermiducal gland and bent back upon itself; large worms, to 6 mm after preservation.

Range.—Blue Ridge and Valley and Ridge physiographic provinces of the southern Appalachians, in the New and Tennessee river drainage systems of West Virginia, Virginia, North Carolina, and Tennessee and the Roanoke (Smith River) drainage in Patrick County, Va.

Specimens examined.—Approximately 80 specimens in 20 collections from the following stations: 5, 15, 18, 54, 58, 61, 64, 67, 70, 72, 73, 75, 79-81, 86, 95, 97, 104, and 116. All of these stations are in the New River drainage at elevations from 488 to 777 m.

Hosts and associates.—*Cambarincola ingens* was associated with *Cambarus b. bartonii* at stations 5, 54, 64, 95, 97; and with *C. sciotensis* in all stations.

Ostracod associates include *Dn. ileata* at all stations except 70; *Dn. truncata* at 54; *Dt. daphnioides* at 70, 72, 73, 75, 79-81, 116; and *P. phyma* at 5, and 64.

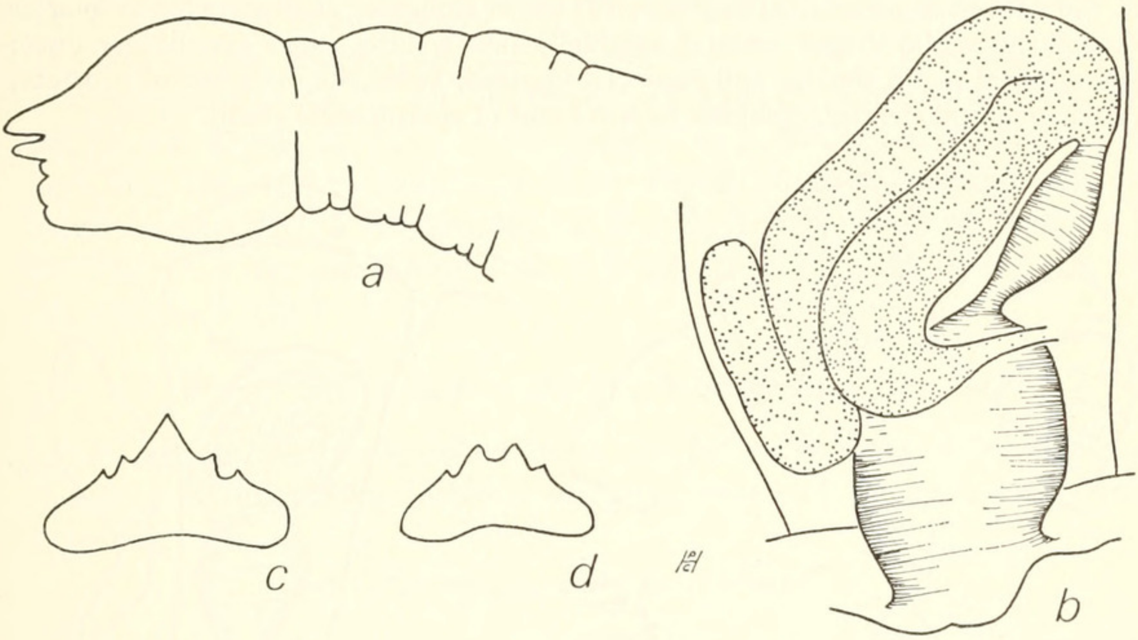


Figure 18.—*Cambarincola ingens*, lateral views: *a*, anterior portion of entire animal; *b*, male reproductive system. En face views: *c*, upper jaw; *d*, lower jaw.

Branchiobdellid associates include *A. koronaeus* at stations 18, 72; *A. legaeus* at 81; *B. illuminatus* at 5, 86, 97; *C. branchiophila* at 15, 18, 58, 67, 72, 73, 75, 79, 81, 86, 97, 104, 116; *C. fallax* at 5, 15, 18, 54, 58, 61, 67, 70, 72, 75, 79, 81, 86, 95, 97; *C. heterognatha* at 5, 61, 64, 67, 70, 72, 79-81, 86, 97, 116; *C. holostoma* at 18; *C. philadelphica* at 5, 54; *P. alcicornus* at 5, 15, 18, 58, 61, 64, 67, 70, 72, 73, 75, 79, 81, 86, 95, 97, 104; and *Xg. instabilius* at 5, 54, 61, 64, 86, 95, and 97.

Remarks.—On the basis of presently known distribution records, *C. ingens* is a native of the New River that has spread to only a few other drainage systems, notably the Tennessee. Our data positively associates *C. ingens* only with *Cambarus sciotensis* as a host, but it is known that other crayfishes serve as hosts for this branchiobdellid. (Hoffman, 1963, p. 336.)

Cambarincola philadelphica (Leidy)

FIGURES 19*a–d*

Astacobdella philadelphica Leidy, 1851, p. 209.
Branchiobdella philadelphica Moore, 1894, p. 427.
Bdellodrilus philadelphicus Moore, 1895b, p. 498.
Cambarincola philadelphica Ellis, 1912, p. 485.

DIAGNOSIS.—Hoffman (1963, p. 346) stated:

Peristomium divided into dorsal and ventral lobes, the dorsal larger and with four low marginal lobations; jaws relatively large and subrectangular in lateral aspect, the dorsal jaw usually a little larger than the ventral [and the dental formula 5/4 to 3/2]; male reproductive system moderate in size, filling from half to two-thirds of the coelom of one side of segment VI; bursa elongate, at least twice as long as broad, the penial sheath merging gradually into a fairly short ejaculatory duct; spermiducal gland slender and recurved ventrad, twice the diameter of prostate, latter long and slender, reaching to ental end of spermiducal gland.

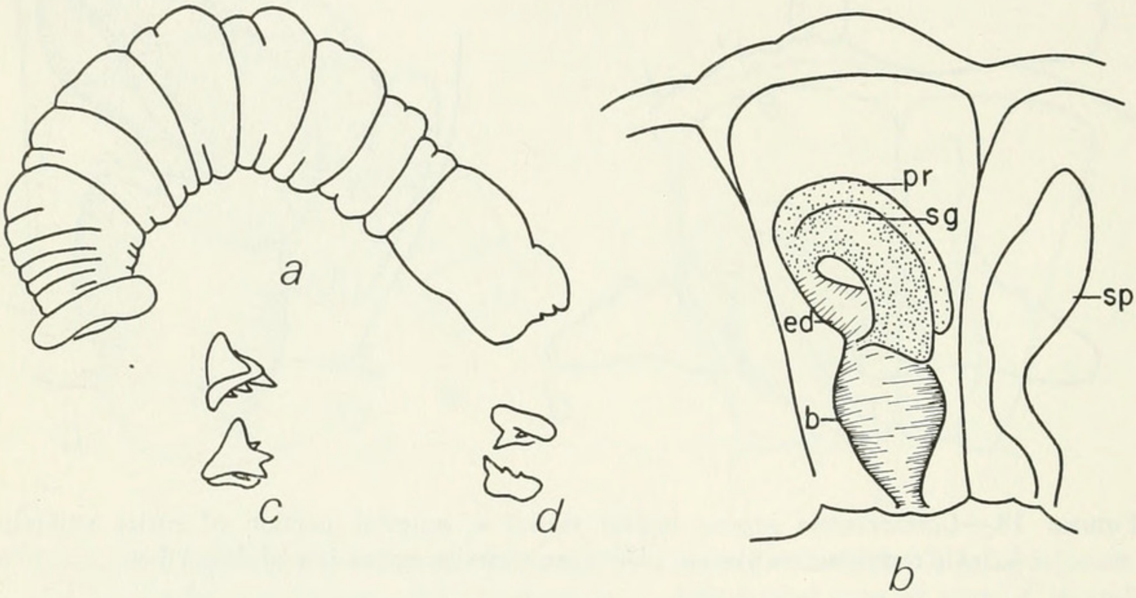


FIGURE 19.—*Cambarincola philadelphica*, lateral views: *a*, entire animal; *b*, male reproductive system and spermatheca; *d*, jaws. Dorsolateral view: *e*, jaws. (Abbreviations: b=bursa; ed=ejaculatory duct; pr=prostate; sp=spermatheca; sg=spermiducal gland. After Hoffman, 1963.)

RANGE.—Eastern North America, from southern Canada south to South Carolina and west to Wisconsin (Hoffman, 1963).

SPECIMENS EXAMINED.—More than 500 specimens in 72 collections from the following stations: 3, 5, 8–10, 12, 14, 16, 17, 19–22, 24–29, 32–37, 39, 44–46, 48, 50–56, 59, 60, 66, 68, 69, 71, 74, 76, 77, 87–94, 98, 106–113, 115, and 118–125. These specimens came from all drainage systems of the area and from elevations of 427 to 1170 m.

HOSTS AND ASSOCIATES.—*Cambarincola philadelphica* was associated with *Cambarus acuminatus* at stations 20, 27, 29, 32, 33, 35, 87–93, 112; with *C. b. bartonii* at all stations except 20, 27, 33, 55, 56, 88, 106, 109, 112; with *C. carolinus* at 8, 22; with *C. l. longulus* at 9, 10, 12, 20–22, 25, 27, 29, 32–35, 37, 88–93, 112, 123, 124; and with *C. sciotensis* at 3, 5, 19, 44, 50, 54–56, 59, 66, and 106–109.

Ostracod associates include *An. ancyla* at stations 88, 89, 92, 93; *As. asceta* and *Dt. chalaza* at 8, 22; *Dn. ardis* at 10, 12, 20, 21, 25, 27, 32, 33, 35, 37, 123, 124; *Dn. ileata* at all stations except 17, 27, 36, 39, 53, 68, 87–93, 111, 112, 115, 118, 120, 121; *Dn. scalis* at 17, 39, 44, 68, 115; *Dn. truncata* at 53–56, 69, 71, 87, 88, 90, 91, 93, 94, 111; *Dt. falcata* at 87–93, 111, 112; *Dt. suteri* at 27, 33, 35, 124; *E. internotalus* at 35, 88, 90; *E. kanawhaensis* at 44; and *P. phyma* at 3, 5, 24, and 44.

Branchiobdellid associates include *A. koronaeus* at stations 14, 19, 29, 52, 69, 71, 77, 87–93, 98, 110–112, 125; *B. illuminatus* at 5, 16, 17, 19, 20, 22, 34, 44, 45, 48, 51, 59, 68, 76, 87, 115, 120–122, 125; *C. branchiophila* at 20, 24, 29, 55, 66, 87–93, 112; *C. fallax* at 3, 5, 24, 54–56, 66, 71, 87–89, 91, 92; *C. heterognatha* at 3, 5, 24, 28, 34, 45, 48, 66, 106, 122, 123, 125; *C. holostoma* at 10, 19–22, 25, 37; *C. ingens* at 5, 54; *P. alcicornus* at 3, 5, 19, 24, 25, 66, 74, 76; *Xd. formosus* at 10, 21, 88–92, 112; and *Xg. instabilius* at 3, 5, 9, 12, 21, 22, 24, 37, 44, 46, 53, 54, 60, 121, and 123.

Genus *Pterodrilus* Moore, 1895

Diagnosis.—Distinguished from *Cambarincola* by smaller size and presence of dorsal projections on prosomites of at least one trunk segment.

Pterodrilus alcicornus Moore

Figure 20

Pterodrilus alcicornus Moore, 1895a, p. 449.

Diagnosis.—With fanlike and cylindrical processes on dorsum of prosomites of segments iii, iv, v, viii.

Range.—Southern Appalachians from Virginia southward to North Carolina and Tennessee (principally in the New and Tennessee Rivers).

Specimens examined.—Approximately 125 specimens in 29 collections from the following stations: 3–5, 15, 18, 19, 24, 25, 43, 58, 61, 63–67, 70, 72–76, 79, 81, 86, 95, 97, 104, and 105. All but two of these stations are in the New River drainage; stations 24 and 25 are in the James (tributaries of Johns Creek) drainage. Elevations range from 488 to 838 m.

Hosts and associates.—*Pterodrilus alcicornus* was associated with *Cambarus b. bartonii* at stations 3–5, 19, 24, 25, 63, 64, 66, 74, 76, 95, 97; with *C. l. longulus* at 25; and with *C. sciotensis* at 3, 5, 15, 18, 19, 43, 58, 61, 63–67, 70, 72, 73, 75, 79, 81, 86, 95, 97, 104, and 105.

Ostracod associates include *Dn. ardis* at station 25; *Dn. ileata* at all stations except 70; *Dt. daphnioides* at 70, 72, 73, 75, 79, 81; and *P. phyma* at 3, 5, 24, and 64.

Branchiobdellid associates include *A. koronaeus* at stations 18, 19, 72; *A. legaeus* at 81; *B. illuminatus* at 5, 19, 76, 86, 97; *C. branchiophila* at 15, 18, 24, 43, 58, 63, 65–67, 72, 73, 75, 79, 81, 86, 97, 104; *C. fallax* at 3, 5, 15, 18, 24, 43, 58, 61, 63, 65–67, 70, 72, 75, 79, 81, 86, 95, 97; *C. heterognatha* at 3–5, 24, 61, 63–67, 70, 72, 79, 81, 86, 97, 105; *C. holostoma* at 18, 19, 25; *C. ingens* at 5, 15, 18, 58, 61, 64, 67, 70, 72, 73, 75, 79, 81, 86, 95, 97, 104; *C. philadelphica* at 3, 5, 19, 24, 25, 66, 74, 76; and *Xg. instabilius* at 3–5, 24, 61, 64, 86, 95, and 97.

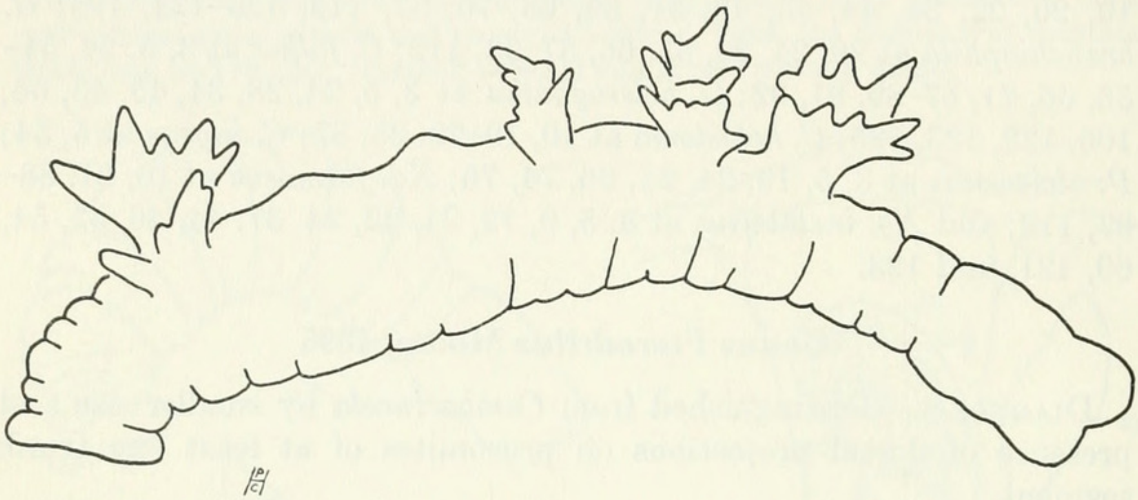


FIGURE 20.—*Pterodrilus alcicornus*, lateral view.

Genus *Xironodrilus* Ellis, 1918

DIAGNOSIS.—Body depressed, widening gradually from segment I to segment VII; deferent ducts entering ental end of spermiducal gland; prostate absent; bursa spherical.

Xironodrilus formosus Ellis

FIGURES 21*a–d*

Xironodrilus formosus Ellis, 1918, p. 49.

DIAGNOSIS.—Dental formula 4/3 to 6/5, teeth subequal in size with lateral teeth somewhat shorter than median ones; spermathecal duct distinct, bulb of spermatheca globose or cylindrical; spermiducal gland simple U-shaped tube, less than twice diameter of vasa deferentia; ejaculatory duct absent.

RANGE.—Michigan, Indiana, Kentucky, Virginia. The range of *Xd. formosus* appears to be discontinuous; it is present in the James and Roanoke Rivers but apparently absent in the New River.

SPECIMENS EXAMINED.—Approximately 30 specimens in 8 collections from the following stations: 10, 21, 88–92, and 112. Of these stations 10 and 21 are on Johns Creek at elevations of 549 and 561 m, and the remainder are on the Roanoke River and the lower reaches of its tributaries at elevations from 439 to 543 m.

HOSTS AND ASSOCIATES.—*Xironodrilus formosus* was associated with *Cambarus acuminatus* at stations 88–92, 112; with *C. b. bartonii* at 10, 21, 89–92; and with *C. l. longulus* at all stations.

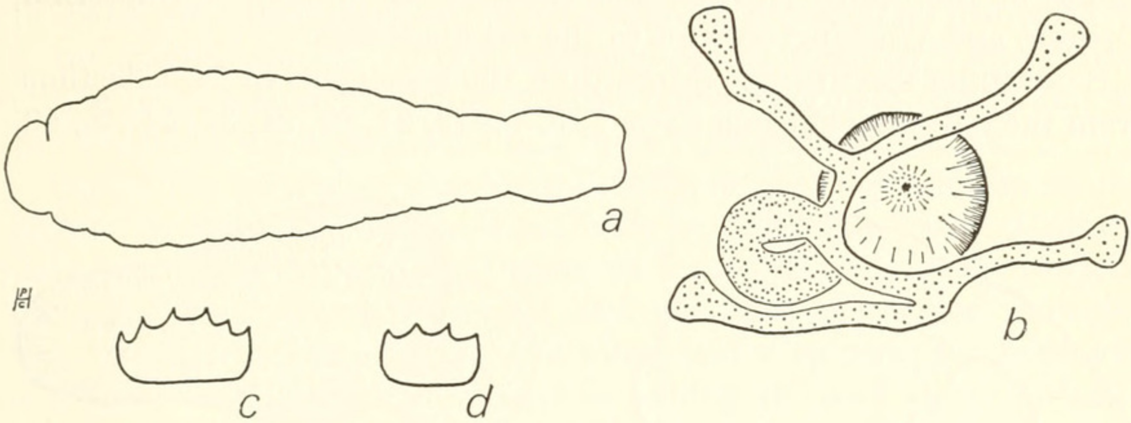


FIGURE 21.—*Xironodrilus formosus*: *a*, dorsal view of entire animal; *b*, ventral view of male reproductive system; *c*, upper jaw; *d*, lower jaw.

Ostracod associates include *An. ancyla* at stations 88, 89, 92; *Dn. ardis* and *Dn. ileata* at 10, 21; *Dn. truncata* at 88, 90 91; *Dt. falcata* at 88–92 112; and *E. internotalus* at 88 and 90.

Branchiobdellid associates include *A. koronaeus* and *C. branchiophila* at stations 88–92, 112; *C. fallax* at 88, 89, 91, 92; *C. holostoma* at 10, 21; *C. philadelphica* at all stations; and *Xg. instabilius* at 21.

REMARKS.—*Xironodrilus formosus* was associated with the riffle-inhabiting *Cambarus l. longulus* in every locality that this worm occurred and may be ecologically restricted to much the same habitat. No conclusions as to host specificity should be drawn from this association, however, for most of the range of *Xd. formosus* is outside that of *C. l. longulus*.

Genus *Xironogiton* Ellis, 1919

DIAGNOSIS.—Body terete anteriorly, depressed posteriorly ("tennis racquet-shaped"); peristomium entire; posterior sucker ventral; spermiducal gland long and tubular, deferent ducts entering near its midlength, prostate absent; bursa large and asymmetrical; spermatheca very small.

Xironogiton instabilius (Moore)

Figures 22*a–d*

Branchiobdella instabilia Moore, 1894, p. 425.
Bdellodrilus instabilius Pierantoni, 1912, p. 22.
Xironogiton instabilius Ellis, 1919, p. 252.
Xironogiton instabilius instabilius Goodnight, 1940, p. 45.

Diagnosis.—Dental formula 5/5 or 4/4, teeth irregular in shape with some median teeth shorter than lateral ones on both jaws.

Range.—Swift, colder streams of the mountains from Ontario to Georgia; a form at present indistinguishable from *Xg. instabilius* is the most common branchiobdellid in the streams of the western slopes of the Sierra Nevada and Cascade Mountains of California, Oregon, and Washington west to the Pacific Ocean.

Specimens examined.—More than 100 specimens in 24 collections from the following stations: 3–5, 7, 9, 11–13, 21, 22, 24, 37, 44, 46, 53,

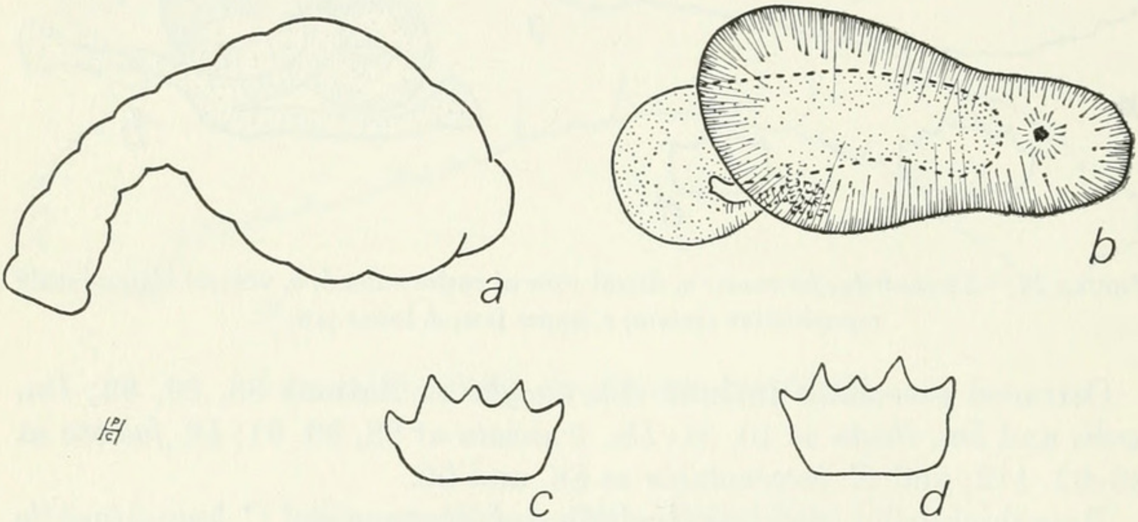


Figure 22.—*Xironogiton instabilius*: *a*, dorsal view of entire animal; *b*, ventral view of bursa and spermiducal gland; *c*, upper jaw; *d*, lower jaw.

54, 60, 61, 64, 86, 95, 97, 121, and 123. These stations are in the headwaters or swifter tributaries of the James and New river drainages at elevations of 512 to 1097 m.

Hosts and associates.—*Xironogiton instabilius* was associated with *Cambarus b. bartonii* at all stations except 11, 13, 61, 86; with *C. carolinus* at 22; with *C. l. longulus* at 7, 9, 11, 12, 13, 21, 22, 37, 123; with *C. sciotensis* at 3, 5, 44, 54, 61, 64, 86, 95, 97; and with *O. juvenilis* at 7.

Ostracod associates includes *As. asceta* and *Dt. chalaza* at station 22; *Dn. ardis* at 11–13, 21, 37, 123; *Dn. ileata* at all stations except 13, 53, 121; *Dn. scalis* at 7, 44; *Dn. truncata* at 53, 54; *E. kanawhaensis* at 44; and *P. phyma* at 3, 5, 7, 24, 44, and 64.

Branchiobdellid associates include *B. illuminatus* at stations 5, 22, 44, 86, 97, 121; *C. branchiophila* at 24, 86, 97; *C. fallax* at 3, 5, 24, 54, 61, 86, 95, 97; *C. heterognatha* at 3–5, 24, 61, 64, 86, 97, 123; *C. holostoma* at 7, 11, 13, 21, 22, 37; *C. ingens* at 5, 54, 61, 64, 86, 95, 97; *C. philadelphica* at 3, 5, 9, 12, 21, 22, 24, 37, 44, 46, 53, 54, 60, 121, 123; *P. alcicornus* at 3–5, 24, 61, 64, 86, 95, 97; and *Xd. formosus* at 21.

Discussion

Since the crayfishes in the area serve as hosts to the epizoötic ostracods and branchiobdellids and since, in this area, neither of the latter is known to occur independently of their hosts, it seems highly probable that they reached the Mountain Lake region on one or more of the crayfish stocks. If this likelihood can be accepted, a knowledge of the probable origin of the crayfish fauna may help to explain, in part, some of the associations that have been recorded above.

One of the crayfishes, *Cambarus b. bartonii,* is at home in the Appalachian Mountain system, and probably had its origin in the southern part, migrating in postglacial times as far north as New Brunswick, Canada. This crayfish ascends the smallest headwater streams, burrows in seepages, springs, and along water courses; furthermore, it is not averse to leaving the aquatic habitat to crawl about on land. These habits would, of course, enable it to ignore narrow terrestrial barriers between headwater streams, and, consequently, it is not surprising that it occurs in all three river systems in the Mountain Lake Region.

Cambarus sciotensis, a not-so-distant relative of *C. b. bartonii,* appears to be confined to the Ohio drainage system in the Kanawha and Scioto tributaries, where it seeks cover beneath stones or in vegetation throughout most of the stream bed. Its range is not adequately known, but it seems probable that it reached this area through migrations up the Kanawha and New Rivers, and here it is confined to the New River drainage.

Cambarus l. longulus, probably the most primitive member of the genus in the area, almost certainly has reached its present range by the migration of its ancestors from the southwest (Coosa-Tennessee drainage systems) leaving populations in the Tennessee (*C. l. longirostris* Faxon) and New (*C. l. chasmodactylus* James) systems. The typical subspecies is found in the lower mountains and Piedmont provinces from the James River to the Yadkin River in Virginia and North Carolina. Although perhaps exhibiting a larger number of generalized characteristics than other members of the genus in the area, it is almost as ecologically restricted as *C. carolinus* in that here it is confined to riffles in tributaries of the James and Roanoke Rivers.

The range of *Cambarus acuminatus* and its relatives forms an asymmetrical U around the Appalachian Mountains, extending from the eastern Great Lakes area southward along the western slopes, eastward around the southern portion of the Blue Ridge, and northward to Maryland. The ancestors of this stock probably arose from a southern Appalachian *C. extraneus* stock and spread northward on both sides of the mountains. There is little doubt that *C. acuminatus* arose in the foothills of the southern Blue Ridge and spread northward along the Atlantic slopes to southern Maryland, an area in which it is characteristic of the nonriffle portions of most of the lower mountain and piedmont streams. In areas of the northern part of its range, it even frequents streams in the lower coastal plain. In the Mountain Lake area it occurs, like *C. l. longulus*, in the James and Roanoke drainage systems.

Cambarus carolinus is, in another way, equally as restricted in its ecological requirements as is *C. l. longulus*, frequenting ground water which it reaches through burrowing. Like the latter, it gained access to the area along the western slopes of the Appalachian system, if not from the south then from an original home to the west, probably not far from this area. This crayfish habitually leaves its burrows after dark following or during rains and often wanders some distance from its tunnels. Not infrequently it has been seen crossing roads and crawling about open areas where there are few or no obvious burrows; consequently, an absence of standing surface water is not a serious deterrent to the migration of this crayfish, and, therefore, it is not surprising to find that it has crossed the divide into both the New and James watersheds.

Although *Orconectes juvenilis* is native to the Ohio drainage system, its presence in the Mountain Lake area is almost certainly attributable to introductions. It has demonstrated a remarkable vigor both in Mountain Lake proper, where it has apparently brought about the expulsion of other crayfishes, and in Potts Creek, where it seems to be making notable progress in taking over most of the crayfish niches. The sources of the introduced stocks have not been ascertained, but it is highly probable that the animals were obtained from either (or both) the New or Tennessee systems in West Virginia and Virginia, respectively. To summarize briefly, the presence of the crayfishes in the Mountain Lake region may be explained as follows:

Cambarus acuminatus—by migrations along the Atlantic slope from the southeast.
Cambarus b. bartonii—originated in or near the area.
Cambarus carolinus—originated in the area or by migrations from the southwest.
Cambarus l. longulus—by migrations from the southwest via the Tennessee and New Rivers to the Atlantic slope, probably along the James, and from it to the Roanoke.

Cambarus sciotensis—by migrations from the west along the New River.
Orconectes juvenilis—by introductions in Potts Creek and in Mountain Lake proper and by recent migrations from the west in New River.

Despite overwhelming evidence for a lack of host specificity for most of the ostracod and branchiobdellid symbionts, it is highly probable that all of them or their ancestors have reached the area as passive migrants on one or more of the crayfish stocks presently represented in the area. Too, it is scarcely to be denied that the association of certain ostracods with a particular crayfish is in a few instances apparently absolute, and most of the ostracods tend to "favor" one or two crayfish species. Among the ostracods that have evolved nearby or within the Mountain Lake area are the monotypic *Phymocythere phyma,* and three species of the genus *Donnaldsoncythere: Dn. ardis, Dn. ileata,* and *Dn. truncata.* As nearly as can be ascertained at the present, the genus *Donnaldsoncythere* has as its center of distribution the Appalachian Mountains, and *Dn. ardis* and *Dn. truncata* are confined to the general Mountain Lake region. *Dn. scalis,* which is also known from two localities in Pennsylvania and one in New York, is largely restricted in the Mountain Lake area to the higher altitudes in the James and New drainages, where *Cambarus b. bartonii* is the usual host. *Dn. ardis,* endemic in the James drainage, occurs at lower altitudes primarily on *Cambarus l. longulus. Dn. truncata* appears to be confined to lower elevations in the Roanoke and New drainage systems, where the principal hosts are *C. acuminatus, C. b. bartonii,* and *C. sciotensis. Dn. ileata,* known from a number of localities in the New River (Kanawha) system to the west of the Mountain Lake area, occurs in all three drainage systems and on all the species of crayfishes in the area except *C. carolinus.* In this group of four closely related ostracods it seems likely that three of them might well have evolved from a common stock that became, for a time, isolated in the three drainage systems studied here: *Dn. ardis* in the James, *Dn. ileata* in the New, and *Dn. truncata* in the Roanoke. *Dn. scalis* probably arose in some stream to the north (its range is too poorly known at present to be more specific), and it has been introduced by *C. b. bartonii* into the Mountain Lake area at higher elevations, apparently first reaching the James drainage and later being transported, presumably by the same crayfish, to the headwaters of the New River. The absence of *Dn. scalis* from the Roanoke River can perhaps be explained by the fact that the headwater streams occur at too low an elevation for the species—certainly the maximum elevation of the system in the area under consideration is marginal for the species. With *Dn. scalis* occupying the smaller tributaries at higher elevations (even now, except in one locality on Potts Creek, above 890 m), the ancestors of *Dn. ardis* had access to the lower elevations (below 625 m) in the James River drainage. Through migrations of *C. b. bartonii* overland between headwater streams, *Dn. ileata* was introduced from the New River into the James River, where it is widespread in the Mountain Lake area, and, although less well established in the Roanoke River, it has been found in one locality there. Two sources of evidence provide the basis for the hypothesis that *Dn. truncata* originated in the Roanoke River and later reached the New River, because (1) only *Dn. truncata* and *Dn. ileata* (the latter of which is abundant in the New and James drainages but represented in only one station in the Roanoke) are found in the Roanoke, and (2) Burton and Odum (1945, pp. 192–193) indicated that two "Atlantic coast" fishes are found in the New River system, suggesting that streams of the New River system had pirated tributaries of the James. Now there are data that support equally well a tapping of the Roanoke River by the New River (R. D. Ross, pers. comm.). Even if stream piracy were highly improbable, there is no reason why *C. b. bartonii*, one of the principal hosts of the species, could not cross the relatively low divide between tributaries of Indian Run or Cedar Run (to Roanoke) and Slate Branch or Toms Creek (to New).

The monotypic *Phymocythere phyma*, the closest relatives of which are members of the genus *Ascetocythere*, is probably a somewhat degenerate offshoot (reduced clasping apparatus and unadorned swollen subterminal area of the peniferum) from the *Ascetocythere* stock that has forsaken the groundwater environment and ventured into competition with other ostracods frequenting lotic surface habitats. In terms of numbers of individuals, it does not appear to have been spectacularly successful. Supporting the assumption of the close relationship of *Phymocythere* to *Ascetocythere* is their apparent commonly shared preference for living among the setiferous areas of the mouthparts of their hosts.

The single ostracod that seems to have been derived from a stock reaching the area from the west is *Entocythere kanawhaensis*, which probably arrived on *Cambarus sciotensis;* close relatives of this ostracod are known from the west and south.

Four species apparently are derived from stocks that have moved into the area from the southwest although the ancestral home of the two genera is in the southern Appalachians and Cumberland Plateau; thus, any of them conceivably might have had their origin in this region. Ancestors of *Ascetocythere asceta* undoubtedly arrived in the area on the *C. carolinus* stock, the range of which is almost congruent with that of the genus *Ascetocythere;* furthermore, *As. asceta* is not known to occur on any other host. Also sharing the same host is *Dactylocythere chalaza*, which, in contrast to *Phymocythere phyma*, was derived from a stock that is primarily associated with lotic habitats but which invaded the groundwater in adopting *C. carolinus* as a host; it is not improbable that this crayfish brought the progenitors of *Dt. chalaza* with it when it moved into the area. The third species postulated to have arrived in the area from the southwest is *Dt. daphnioides*, which, in the Mountain Lake region, is associated with only one crayfish, *C. sciotensis*, but outside of the area (in the New, Watauga, and Pound drainages) it infests several species, including *C. b. bartonii*. The fourth species, *Dt. falcata*, insofar as is presently known, has a discontinuous distribution and probably reached the Roanoke River from the southwest, perhaps following the same route as proposed for *Dn. truncata* in getting from the New into the Roanoke basin. The perplexing problem of *Dt. falcata* not having been found in the New River leads to speculation that it may have been routed by other species there, perhaps one or more of its close relatives.

Southeastern components of the entocytherine fauna of the region include *Entocythere internotalus*, *Dt. suteri*, and *An. ancyla*. The principal hosts of all three of these species are *C. acuminatus* and *C. l. longulus*, and it is likely that *C. acuminatus* has been more important in the dispersal of these three than has *C. l. longulus*, not only because of its larger surface area and broader ecological tolerance, but also because its range far exceeds that of the smaller species. In summary, the presence of the ostracods in the Mountain Lake region may be explained as follows:

Ascetocythere asceta, *Dactylocythere chalaza*, *Dt. daphnioides*, and *Dt. falcata*—by migrations from the southwest along the Tennessee and New drainage systems.

Ankylocythere ancyla, *Entocythere internotalus*, and *Dt. suteri*—by migrations along the Atlantic slope from the southeast.

Donnaldsoncythere ardis, *Dn. ileata*, *Dn. truncata*, and *Phymocythere phyma*—originated in or near the area.

Donnaldsoncythere scalis—by migrations from the north into the James drainage.

Entocythere kanawhaensis—from the west along the Kanawha and New rivers.

Two-thirds of the branchiobdellids of the Mountain Lake area are endemic to the southern Appalachians. Of the remainder, *Xg. instabilius* is confined to mountain streams, at relatively high elevations throughout the Appalachians, but it is indistinguishable from the western *Xg. oregonensis*. The greater number of species of *Xironogiton* are found to the west of the continental divide, and one must assume that the present disjunct distribution of the genus is a relict of a former continuous range. The monotypic *Bdellodrilus illuminatus* is widely distributed over North America. At this time few inferences can be drawn as to place of origin, migration routes, or evolution of this species, which, in some respects, is the most primitive of North American branchiobdellids, and, in other respects (its parasitic habitus), among the more highly specialized. Probaby an early branchiobdellid stock acquired the parasitic habit, is now widely distributed, and has undergone (because of its confinement to branchial chambers of the various hosts [?]) little or no evolutionary diversification. A possible caveat to this conclusion must be entered because of the lack of taxonomic studies of *B. illuminatus;* further study may show that some of the widely disjunct populations (e.g., those from the Pacific drainage in Mexico and California) assigned to this species are actually other disjunct species. *Xd. formosus* is more common in the Ohio drainage in Kentucky, Tennessee (Cumberland drainage), Ohio, and West Virginia than in Virginia, but the greatest number of the species are from the Great Lakes region, primarily in Michigan. Yet the genus, with the exception of *Xd. formosus,* appears to be confined to the southern Appalachians and the Ozarks. *Xironodrilus formosus* is a primitive species within the genus (and the order), and one must postulate a post-Pleistocene invasion of the Great Lakes from the South and attribute a relict status to the populations in the James and Roanoke Rivers. This conclusion has been reached because (1) the distribution of the species (and the genus) is such that we can only assume that it reached the Roanoke and James by way of the New, and (2) that the genus originated within either the New or Tennessee systems, most likely the New, since the ancient Teays River and the Illinois Ozarks would link the Appalachian and Ozarkian progenitors of the modern species and leave relict populations along the present Ohio as a source for the invasion of the Great Lakes. The remaining widespread species, *C. philadelphica,* is clearly one of Appalachian origin that has spread from the mountains into the piedmont and, to the north, the coastal plain; the western limits of *C. philadelphica* are in the interior plateau regions of Tennessee, Kentucky, and Ohio, although there is evidence here that it intergrades with the Ozarkian *C. chirocephala,* and there is one anomalous record from Wisconsin. It is futile to speculate about the origins of *B. illuminatus* and *Xg. instabilius;* they are bound to the ancient invasion of the continent by the ancestors of the order. *Cambarincola philadelphica* and *Xd. formosus,* the former the dominant branchiobdellid species of eastern North America and the latter a primitive species fragmented into disjunct populations, are, however, derived from early inhabitants of either the Tennessee or New Rivers, more likely the New.

The remaining two-thirds of the species are at home in the area. *C. branchiophila* is a gill-inhabiting branchiobdellid known only from the Mountain Lake area, where it is found associated with all the crayfishes except the burrowing *C. carolinus* and the introduced *Orconectes* *juvenilis*. *Cambarincola branchiophila* is apparently more common in the New River system, 18 occurrences as compared to 4 in the James and 9 in the Roanoke, but this may be a sampling artifact (table 1). The species appears to belong to a primitive section of the genus, and its closest relative is *C. shoshone* Hoffman (1963, p. 319) from the Snake River drainage in Idaho. As a putatively relict species that has survived in the area as a consequence of the adoption of the gill-parasitic habit, the only clue as to its origin is the general importance of the New River as the source of the branchiobdellid fauna of the region from which the invasion of the upper reaches of the James and Roanoke is easily understandable either through stream captures, which have indubitably occurred, or the overland wandering of *C. b. bartonii*.

Ankyrodrilus koronaeus is likewise confined to the streams in the area, occurring in all three of the drainages, but it has been found outside the area in Botetourt County, Va., in the Roanoke drainage. But *A. legaeus*, with only one record in the area from Wolf Creek of the New River, is really a species of the Tennessee drainage, extending from southwest Virginia to middle Tennessee, where it is found in the Cumberland River drainage. At this time, the phylogenetic position of *Ankyrodrilus* is obscure: one of us(Holt, 1965, p. 10) has pointed out previously the similarities, mostly in body form, of the genus to *Xironodrilus* and *Xironogiton*, yet a further consideration of the male reproductive system leads to the tentative conclusion that *Ankyrodrilus* may be most closely related to the eastern Asian *Cirrodrilus*. The genus would appear to be a survival in the southern Appalachians of a formerly more widespread group and has reached the Mountain Lake area from the Tennessee and Cumberland systems by way of the Clinch or Holston Rivers.

Pterodrilus alcicornus is a member of a genus, clearly an offshoot of *Cambarincola*, that is centered in the southern Appalachian-Ozark region with an outlier, *P. distichus*, which is found primarily in the glaciated areas around the Great Lakes, and possibly another, *P. mexicanus*, in southeastern Mexico. *Pterodrilus alcicornus* is a species of the Tennessee system and has reached the New River from the southwest and hence to the James. The species is not known from the Roanoke.

Of the remaining species of the genus *Cambarincola*, *C. holostoma* is known only from the James, Potomac, and New river basins. But it is most common in the James system (Potts, Craig, and Johns Creeks), with two records from Sinking Creek and one record (Hoffman, 1963, p. 360) from the Potomac drainage. The conclusion that *C. holostoma* is a specialized derivative of a *C. philadelphica* stock that arose in the upper tributaries of the James River is inescapable. *Cambarincola ingens*, common in the Tennessee drainage southward to northeastern

TABLE 1.—*Summary of geographical and altitudinal distribution and associations of the crayfishes, entocytherids, and branchiobdellids of the Mountain Lake Region* (J=James; N=New; R=Roanoke)

Animal	Drainage systems	Altitude (meters)	Crayfishes	Ostracods	Branchiobdellids
I. *C. acuminatus*	JR	402–535	II, IV	1, 3, 4, 6, 9, 10, 11	acdegik
II. *C. b. bartonii*	JNR	427–1219	I, IV, V, VI	1, 3, 4, 5, 6, 9, 10, 11, 12, 13	acdefghijkl
III. *C. carolinus*	JN	585–1250		2, 7	ce
IV. *C. l. longulus*	JR	402–686	I, II, VI	1, 3, 4, 6, 9, 10, 11	acdefgijkl
V. *C. sciotensis*	N	427–899	II	4, 5, 6, 8, 12, 13	abcdefghijl
VI. *O. juvenilis*	JN	671–1180	II, IV	4, 5, 13	gl
1. *An. ancyla*	R	439–475	I, II, IV	6, 9, 11	adeik
2. *As. asceta*	JN	585–1250	III	7	ce
3. *Dn. ardis*	J	402–622	I, II, IV	4, 10, 11	acdfgijkl
4. *Dn. ileata*	JNR	415–899	I, II, IV, V, VI	3, 5, 6, 8, 10, 11, 12, 13	abcdefghijkl
5. *Dn. scalis*	JN	671–1219	II, V, VI	4, 9, 12, 13	cil
6. *Dn. truncata*	NR	445–625	I, II, IV, V	1, 4, 9, 11	acdebikl
7. *Dt. chalaza*	JN	585–1250	III	2	ce
8. *Dt. daphnioides*	N	488–561	V	4	abdefhj
9. *Dt. falcata*	R	439–597	I, II, IV	1, 6, 11	acdeik
10. *Dt. suteri*	J	402–482	I, II, IV	3, 4, 11	ai
11. *E. internotalus*	JR	402–475	I, II, IV	1, 3, 4, 6, 9, 10	adegik
12. *E. kanawhaensis*	N	500–899	II, V	4, 5, 13	cdefil
13. *P. phyma*	JN	610–1143	II, V, VI	4, 5, 12	cdefghijl
a. *A. koronaeus*	JNR	402–750	I, II, IV, V	1, 3, 4, 6, 8, 9, 10, 11	cdefghijk
b. *A. legaeus*	N	488	V	4, 8	defhj
c. *B. illuminatus*	JNR	518–1250	I, II, III, IV, V	2, 3, 4, 5, 6, 7, 9, 12, 13	adefghijl
d. *C. branchiophila*	JNR	427–777	I, II, IV, V	1, 3, 4, 6, 8, 9, 11, 12, 13	abcefghijkl

TABLE 1.—*Summary of geographical and altitudinal distribution and associations of the crayfishes, entocytherids, and branchiobdellids of the Mountain Lake Region* (J=James; N=New; R=Roanoke)—Continued

Animal	Drainage systems	Altitude (meters)	Crayfishes	Ostracods	Branchiobdellids
e. *C. fallax*	JNR	439–1158	I, II, III, IV, V	1, 2, 4, 6, 7, 8, 9, 11, 12, 13	abcdfghijkl
f. *C. heterognatha*	JN	451–838	II, IV, V	3, 4, 8, 12, 13	abcdehijl
g. *C. holostoma*	JN	512–671	I, II, IV, V, VI	2, 3, 4, 5, 7, 11, 13	acdehijkl
h. *C. ingens*	N	488–777	II, V	4, 6, 8, 13	abcdefgijl
i. *C. philadelphica*	JNR	427–1170	I, II, III, IV, V	1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12, 13	acdefghjkl
j. *P. alcicornus*	JN	488–838	II, IV, V	3, 4, 8, 13	abcdefghijl
k. *Xd. formosus*	JR	439–561	I, II, IV	1, 3, 4, 6, 9, 11	adegil
l. *Xg. instabilius*	JN	512–1097	II, IV, V, VI	2, 3, 4, 5, 6, 7, 12, 13	cdefghijk

Georgia and confined to the New River and its tributaries in the area, is another specialized offshoot of the *C. philadelphica* stock that has reached the Mountain Lake region from the south. There is one record from Patrick County, Va., in the Roanoke drainage (Hoffman, 1963, p. 335); the remaining records from outside the area are from the mountain streams of the New and Tennessee drainages. *Cambarincola ingens* is a Blue Ridge species, but it is impossible to decide whether it evolved in the headwaters of the New River in North Carolina or in those of the Tennessee River in the same region. *Cambarincola heterognatha* is known from the Potomac southeastward through the mountains in the New, Cumberland, and Tennessee river systems, with one isolated record in the Roanoke drainage (Franklin County, Va.). Again, we are dealing with a species, widespread in the mountains, that appears to have spread into the Tennessee drainage. The alternative possibility of an origin in the Tennessee may be as likely, and there is no way now to decide between these choices. Finally, *C. fallax* is not quite so widespread as *C. philadelphica*, but it is abundant throughout the southern Appalachians. Our information suggests that *C. fallax* has reached the James and Roanoke from the New, but it does not indicate any choice between the New or the Tennessee as the ancestral home of the species. In summary, the presence of the branchiobdellids in the Mountain Lake region may be explained as follows:

Ankyrodrilus koronaeus—originated in or near the area, but derived from a Cumberland Plateau group by way of the Tennessee drainage.
Ankyrodrilus legaeus—by migrations from the Cumberland Plateau region by way of the Tennessee drainage.
Bdellodrilus illuminatus—unknown origin (ancient, widespread).
Cambarincola branchiophila—New River endemic, relict survivor of a once wider range.
Cambarincola fallax—a southern Appalachian species (now widespread in eastern highlands) that reached James and Roanoke from New.
Cambarincola heterognatha—New River native.
Cambarincola holostoma—James River native, evolved from *C. philadelphica* stock.
Cambarincola ingens—by migrations from the south, headwaters of New or Tennessee.
Cambarincola philadelphica—Appalachian (widespread).
Pterodrilus alcicornus—Tennessee drainage.
Xironodrilus formosus—relict of ancient Teays River fauna.
Xironogiton instabilius—unknown origin (ancient relict).

It has been pointed out above that evidence exists that most of the ostracods tend to favor one or more crayfish hosts. The extreme of this favoritism is demonstrated in the relationship between *C. carolinus* and its two "riders," *As. asceta* and *Dt. chalaza*, in which the associations appear to be absolute for the ostracods. (As has already been suggested, the "favoritism" probably has more to do with the environment of the host than with physiological relationships usually associated with "host specificity.") The opposite extreme is demonstrated in an apparent lack of discrimination on the part of the ostracod *Dn. ileata* that infests all the crayfishes in the area except *C. carolinus* and is associated with it in other areas. The affinities of other ostracods for one or two particular hosts seem to lie somewhere between these two extremes.

What the nature of the ties is between the ostracod symbionts and the crayfish hosts and between the branchiobdellid symbionts and the crayfish hosts has not been critically analyzed. It cannot be said that the ostracod relationship is parasitic even in the sense that they have free transportation and pasturage, for they might well be paying a service charge in ridding the crayfish of foreign organic matter that adheres particularly to the setiferous areas of the exoskeleton. While they may not do a thorough cleaning job, the accumulation of such matter is probably retarded.

There are instances of branchiobdellids known from only one host species, but these are associations in which the worm is known from only one or a few collections. The one such association of this type from our collections (*A. legaeus* on *Cambarus sciotensis*) clearly does not indicate host-species specificity since *A. legaeus* is known from other species of crayfishes outside of the Mountain Lake area (Holt, 1965, p. 12) Similarly, the associations (table 1) in which it might appear that there is a "preference" by a branchiobdellid species for one or another host species are surely to be interpreted as the consequence of the ecological relationships of hosts and worms or as the product of the migration (distribution) patterns of the two. Host specificity in the sense of host-species specificity is not an important feature of the relationship between the annelids and the crustaceans; yet, the relationship is an obligate one for the branchiobdellids.

In occupying the exoskeleton of the crayfish host, the ostracods and branchiobdellids have found niches that remind one of the occupation of a stream by two or more species of crayfishes. Although detailed observations on the distribution of the ostracods on their hosts are limited to those that are reported above, it is reasonable to assume that most multiple infestations result in a partial segregation of the species on different areas of the host, similar to that exemplified by *As. asceta* and *Dt. chalaza* on *C. carolinus*, in which the former is concentrated among the setae of the gnathal appendages and the latter on the setiferous portions of the abdomen. In terms of obvious morphological adaptations to microhabitats on the crayfishes, the ostracods have not approached the refinements exhibited by some of the branchiobdellids (see p. 8). The contrast in body form of the vermiform, gill-inhabiting *B. illuminatus*, the plumose, venter-dwelling *P. alcicornus*, and the depressed, tennis-racquet-shaped, chela-dwelling *Xg. instabilius* reflect the extreme conspicuous adaptive modifications accomplished by the members of this order in becoming specialized for a particular microhabitat on the crayfish host. Even in the absence of such adaptive features, there must be equally strong as yet unrecognized ones that are in effect in the ostracods, for in the associations just mentioned the gnathal areas of all specimens of *C. carolinus* examined were dominated by *As. asceta* and the abdominal region by *Dt. chalaza*.

While the adaptations of the crayfishes to riffles and pools are not so conspicuous as those among the branchiobdellids in their modifications for living on different body regions of the crayfish, the riffle-dwelling *C. l. longulus* is smaller, less spiny, and has smoother chelae than the pool-dwelling *C. acuminatus*. The burrowing *C. carolinus*, in contrast to *C. l. longulus*, has a compressed rather than depressed thorax, a longer, narrower areola signifying a more spacious gill chamber, a less pointed rostrum, and more tuberculate and sharper-tipped chelae.

Although a number of references have been made by us to the associations between the epizoites and their hosts, it is not an omission on our part that we have scarcely alluded to the relationships existing between the branchiobdellids and the entocytherids. It seems probable that the gill-inhabiting branchiobdellids, *B. illuminatus* and *C. branchiophila,* probably have few contacts with the entocytherids for, as pointed out, we have not encountered a single ostracod within the gill chamber of the crayfish. Furthermore, contacts between *Xg. instabilius,* the branchiobdellid that is almost confined to the chela of the host, would also have little cause for encountering an ostracod, for the latter has not been observed to inhabit the chelae of the hosts. In contrast, most of the members of the genus *Cambarincola,* the two members of *Ankyrodrilus, P. alcicornus,* and *Xd. formosus* do undoubtedly encounter the ostracods in the course of their moving about the ventral part of the thoracic and abdominal areas of the crayfish. Even though the methods of feeding of the branchiobdellids and ostracods may be different, in view of the fact that they share the same source of food scraped from the exoskeleton of the host, there must be some degree of competition between them, however slight the intensity of the competition might be. Furthermore, inasmuch as several of the branchiobdellids are known to feed on other animals, even other branchiobdellids, that dwell on the crayfish, it is a bit surprising that there is no record of their having ingested an entocytherid ostracod. One cannot help posing the question as to the nature of the immunity of the entocytherids from the apparently voracious appetite of their fellow epizoites! There are some data that indicate that crayfishes heavily infested with branchiobdellids seldom, if ever, have large numbers of ostracods.

Two studies have been made elsewhere that are similar to that undertaken here. Crawford (1959) treated the crayfishes and their ostracod associates of Richland County, S.C., and Simonds [4] conducted a study of the crayfishes and their ostracod and branchiobdellid symbionts of the Hiwassee drainage system in Georgia, North Carolina, and Tennessee. In both studies, only a single drainage system was involved, the former dealing with the Santee river system and the latter with a major tributary of the Tennessee-Ohio river system.

Crawford found that within Richland County there were 11 species

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[4] Kenneth W. Simonds conducted this survey of the Hiwassee drainage system in the late 1950s; however, a final report was not completed and no publications have been derived from the survey except the descriptions of new species of ostracods by Hobbs and Walton (1960, 1961).

of crayfishes belonging to three genera, *Procambarus* (4 species), *Cambarus* (6 species, 2 of which, *C. b. bartonii* and *C. acuminatus*, are also present in the Mountain Lake region), and *Orconectes clypeatus* (=*Faxonella clypeata*). Infesting these crayfishes were six species of entocytherids (the first two of the following list occur also in the Mountain Lake region): *Entocythere internotalus*, *Dactylocythere suteri*, *Dt. striophylax*, *Ankylocythere telmoecea*, *An. tiphophyla*, and *An. hobbsi* (Hoff)—all except the latter described as new in his report. The most outstanding difference between the faunas of the Santee River and the Mountain Lake region is the number of species of each

Table 2.—*Major streams, altitude ranges, stations, and numbers of species in the Mountain Lake Region*

Streams	Altitudes (meters)	Stations	Cray-fishes	Ostra-cods	Branchi-obdellids	Totals
James River						
Craig Creek	384–853	30, 31, 32, 33, 34, 35, 36, 37, 122, 123, 124	3	4	6	13
Johns Creek	384–1219	9, 10, 11, 12, 13, 17, 20, 21, 22, 23, 24, 25, 26, 27, 28, 68, 100, 103	4	8	9	21
Meadow Creek	390–811	29, 98, 125	3	1	5	9
Potts Creek	671–1085	6, 7, 8	4	5	3	12
New River	384–524	26, 57	2	3	3	8
Doe Creek	500–1067	45, 113, 118, 119	1	1	3	5
Big Stony Creek	488–1067	3, 4, 5, 43, 62, 63, 64, 65, 66, 67, 86, 97, 99, 102, 127	3	4	8	15
Little Stony Creek	500–1250	1, 2, 16, 38, 39, 40, 41, 42, 44, 59, 60, 61, 82, 83, 101, 114, 115, 120, 121	4	6	7	17
Sinking Creek	518–1067	14, 15, 18, 19, 46, 47, 48, 49, 50, 51, 52, 58, 84, 95, 96	2	1	10	13
Spruce Run	506–671	53, 54, 55, 56	2	2	5	9
Toms Creek	524–738	94, 104, 105, 106, 107, 108, 109, 117	2	2	5	9
Wolf and Mill Creeks	472–1067	80, 81	1	2	6	9
Roanoke River						
North Fork	411–756	85, 87, 88, 89, 90, 91, 92, 93, 110, 111, 112	3	5	6	14

group—in the Santee, there are 11 crayfishes, 6 ostracods, and 4 branchiobdellids; in the Mountain Lake region there are 6, 13, and 12, respectively (see table 3 for the numbers in the three river systems in the area). Both species of crayfishes common to the two areas occur in the Roanoke and James drainages, and *C. b. bartonii* is also present in the New; both of the ostracods common to the two occur in the James and one of them in the Roanoke drainage. Of the four species of branchiobdellids present in the Santee, two of them, *B. illuminatus* and *C. philadelphica*, occur in all three drainages of the Mountain Lake area.

Simonds has provided us with a summary chart of his findings and the numbers of species present are recorded in table 3. Two crayfish common to the two areas, *C. carolinus* and *C. b. bartonii*, are found in the James and New drainages and the latter also in the Roanoke. Of the two species of ostracods shared in common, *Dt. falcata* and *E. internotalus*, the former occurs in the Roanoke and the latter in the James and New drainages. Of the five branchiobdellids found in the two regions, *B. illuminatus*, *C. fallax*, and *C. philadelphica* occur in all three drainages of the Mountain Lake area, *C. heterognatha* in the James and New, and *C. ingens* in the New.

Only three of the animals mentioned above occur in all five drainage systems: one crayfish, *C. b. bartonii*, and two branchiobdellids, *B. illuminatus* and *C. philadelphica*.

The only comparative faunistic study of the drainage systems in the Mountain Lake area is that of Burton and Odum (1945), in which they compared the fish faunas of certain tributaries of the New and James Rivers. Table 5 presents one of their comparisons and summarizes our findings in the same streams. From the standpoint of the fishes, Craig and Sinking Creeks and Craig and Spruce Runs share the greatest number of species and Johns and Little Stony the least; in contrast, using the totals of the three groups studied by us, Johns and Little Stony have the most in common and Craig and Spruce Run the least. Similarities and differences in our findings may be found in the table. There is abundant evidence for multiple faunal interchanges between the three river systems in the Mountain Lake area but these data have never been brought together. Suffice it to say here that the New River fauna is the principal component of the crayfish-entocytherid-branchiobdellid fauna of the region as here defined, and the Tennessee basin has served as the chief pathway for the migrations of stocks into the region. The Roanoke basin apparently has contributed the least. Not only is the Roanoke the smallest and has the least ecological diversity of the three river systems in the region, but also there appear to have been fewer ancient ancestral stocks of crayfishes, entocytherids, and branchiobdellids in it.

TABLE 3.—*Numbers of species occurring in the major drainage systems of the Mountain Lake Region, the Santee (Richland County, S.C.) and Hiwassee (Georgia, North Carolina, and Tennessee) Rivers*

Drainage	Crayfishes	Ostracods	Branchiobdellids	Totals
James	5	8	10	23
New	4	8	11	23
Roanoke	3	5	6	14
Santee [1]	11	6	4	21
Hiwassee [2]	11	10	9	30

[1] Except for numbers of branchiobdellids (original data), from Crawford, 1959.
[2] From Simonds (see ftn., p. 76).

TABLE 4.—*Numbers of species restricted to the drainage system or combinations of systems indicated*

Drainage	Crayfishes	Ostracods	Branchiobdellids	Totals
James, New, Roanoke	1	1	5	7
James, New	2	4	4	10
James, Roanoke	2	1	1	4
New, Roanoke	0	1	0	1
James	0	2	0	2
New	1	2	2	5
Roanoke	0	2	0	2
Totals	6	13	12	31

TABLE 5.—*Summary of similarities and differences in the crayfish, entocytherid, branchiobdellid, and fish faunas in selected streams in the Mountain Lake Region* (S=number of species shared in common by the two streams; D=number of species found in both streams that are not shared in common)

Streams		Crayfishes		Ostracods		Branchiobdellids		Totals		Fishes [1]	
James Drainage	New Drainage	S	D	S	D	S	D	S	D	S	D
Craig	Sinking	1	3	1	3	6	4	8	10	8	27
Craig	Spruce Run	1	3	1	4	2	7	4	14	8	23
Johns	Sinking	1	4	1	7	7	3	9	14	7 [2]	23
Johns	Spruce Run	1	4	1	8	4	6	6	18	5	25
Craig	Little Stony	1	5	1	8	4	5	6	18	3	22
Johns	Little Stony	2	4	5	4	6	4	13	12	2	20

[1] Compiled from Burton and Odum, 1945, table VI.
[2] Given as 6 by Burton and Odum, p. 192, but according to table VI, 7 species are shared in common.

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U.S. GOVERNMENT PRINTING OFFICE: 1967

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