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COMMENSAL OSTRACOD (OSTRACODA: ENTOCYTHERIDAE) PROVIDES EVIDENCE FOR THE POSTGLACIAL DISPERSAL OF THE BURROWING CRAYFISH, *CAMBARUS DIOGENES* (DECAPODA: CAMBARIDAE), INTO WESTERN NEW YORK

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Abstract: The burrowing crayfish, *Cambarus* (*Lacunicambarus*) *diogenes*, reaches the northeastern edge of its relatively extensive North American range in northwestern New York. This paper documents the distribution of this crayfish in New York for the first time since it was initially collected there in 1980. Currently *C. diogenes* is known in New York from only seven sites in Erie, Genesee, and Niagara counties. State or provincial records are also reported for the commensal ostracod, *Rhadinocythere serrata*, from Arkansas, Iowa, New York, Ontario, and Wisconsin; *C. diogenes* is its only known host. The distribution of *R. serrata* is concordant with morphological features of the crayfish chela that suggest a faunal relationship among populations of *C. diogenes* in northwestern New York, southern Ontario, and the upper Midwest. *Cambarus diogenes* most likely reached northwestern New York as a result of postglacial dispersal via the northern margin of the Lake Erie basin. Diagrams of the burrows and photographs of the "chimneys" that typically cap at least one passageway of the burrow of *C. diogenes* from northwestern New York are also presented.

The burrowing crayfish, *Cambarus* (*Lacunicambarus*) *diogenes* (Girard) (Decapoda: Cambaridae; Fig. 1), has fascinated generations of naturalists who have observed its "chimney" of excavated pellets of soil protruding above the banks of rivers and streams, the shorelines of ponds and lakes, and in fields, roadside ditches, and wetlands (Crocker and Barr 1968; Grow 1981; Grow and Merchant 1980; Harris 1903; Hobbs 1981; Hobbs and Jass 1988; Ortmann 1906; Page 1985; Phillips 1980; Tarr 1884; Williams and Leonard 1952). Figures 2–5 illustrate how these chimneys actually vary in shape from cylindrical (parallel-sided shafts) to conical (volcano-shaped) to low, amorphous piles (see also Tarr 1884). These structures are a consequence of the fact that *C. diogenes* spends most of its life in individually excavated underground chambers where ground water collects (Grow 1981; Grow and Merchant 1980; Hobbs 1969). This burrow-dwelling habit contrasts sharply with that of more familiar species of crayfishes that live in surface waters, although the latter typically conceal themselves during daylight hours beneath stones, in beds of aquatic plants, or in organic debris.

The systematic and zoogeographic relationships of *C. diogenes* have also attracted recent interest. Hobbs (1972, 1974, 1981, 1989) repeatedly emphasized that this taxon is actually a species complex that needed considerable attention. After studying the complex for 12 years, Jezerinac (1993) made significant progress toward resolving its systematic relationships by erecting the subgenus *Tubericambarus* to accommodate the following three species: *acanthura* Hobbs, 1981 (previously assigned to the subgenus *Lacunicambarus*); a new species, *thomai* Jezerinac, 1993; and one undescribed species designated as "species A" (Fig. 6). The subgenus *Lacunicambarus*, sensu Jezerinac (1993), hence now contains three species: *diogenes* Girard, 1852; *ludovicianus* Faxon, 1884; and *miltus* Fitzpatrick, 1978 (Fig. 7). Jezerinac (1993) also stated that the complex represented by these two subgenera contained "at least five additional species or subspecies," including the species he described therein, *C.* (*T.*) *thomai*. See Jezerinac (1993) for further details on the taxonomic history of the *C. diogenes* complex.

Cambarus diogenes, as currently defined, has one of the most extensive ranges of any North American crayfish (Fig. 7), thus reflecting a wide ecological tolerance, and morphological innovations (e.g., enlargement of the gill chambers) that allow it to exist in a broad spectrum of ecological conditions (Hobbs and Jass 1988). Although Crocker (1957) did not find this species while examining 5712 crayfishes in 710 collections from New York, he stated that *C. diogenes* may occur there since it had been reported within 48–121 km of the New York State border in New Jersey, Ohio, and Pennsylvania [see note added in proof at end of this article]. Thus it was significant when one of us (WKG) excavated the first New York specimens of this complex in 1980 (Pickett, Nasca and Gall 1982), extending the northeastern edge of its range by about 130 km from Turkey Point, Ontario. Recently the disjunction of Ontario and New York populations decreased when Guiasu, Barr and Dunham (1996) reported specimens of *C. diogenes* from two sites on the Niagara Peninsula of

[1]Deceased, 21 April 1996.

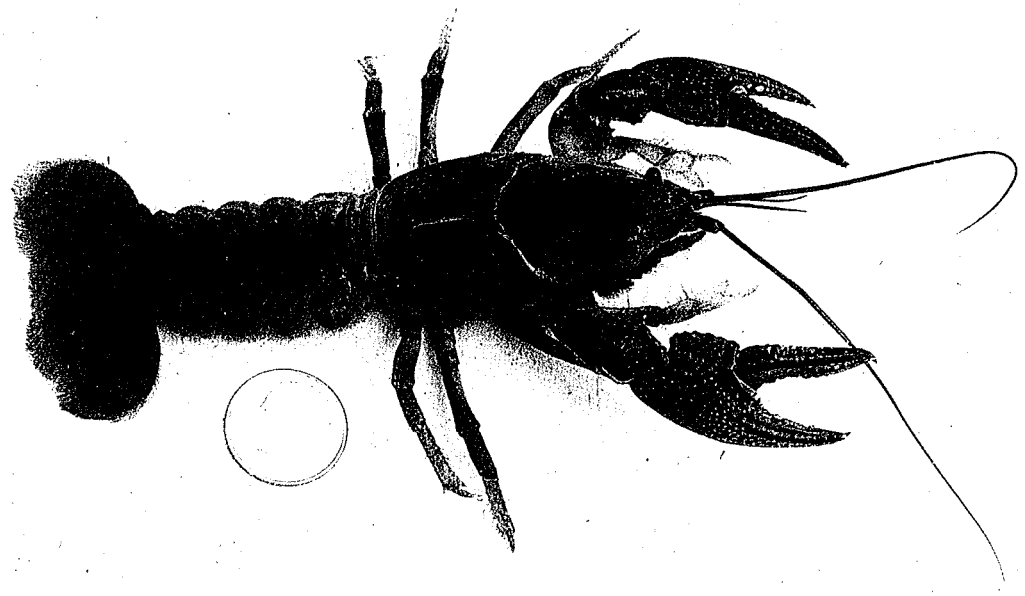

Fig. 1. Female *Cambarus diogenes* excavated from burrow, Strawberry Island, Erie County, New York (BMS-1995.347c).

Ontario: Wainfleet Marsh near Welland in Niagara County, and Binbrook in Hamilton-Wentworth County (Fig. 8).

Further interest was added to the discovery of *C. diogenes* in New York by the late Horton H. Hobbs, Jr., who identified the commensal ostracod, *Rhadinocythere serrata* (Hoff) (Ostracoda: Entocytheridae), infesting populations of this crayfish from northwestern New York as well as from Long Point, Ontario. This host-specific ostracod had not previously been reported any further east than northwestern Indiana (Hart and Hart 1974).

The purpose of this article is to document the distribution of *C. diogenes* in New York; provide new records for *R. serrata* in Arkansas, Iowa, New York, Ontario, and Wisconsin; and discuss the systematic and biogeographic implications of these findings.

Materials and Methods

Because of the burrowing habit of *C. diogenes*, specialized techniques were used to collect them relative to the techniques used to collect crayfishes that inhabit open water (Hobbs 1972). The chimney was removed, the burrow opened to the water table using a shovel or trowel, and the opening sufficiently enlarged so that the collector's hand could be thrust below the water surface. The water in the burrow was thoroughly roiled by hand or by stirring with a stick, and left undisturbed for a few minutes. When the occupant would come to the opening of the burrow, its presence was first indicated by gentle undulation of its antennae at the surface of the turbid water while the remainder of the crayfish generally remained submerged. The open hand of the collector was then thrust into the opening to "pin" the crayfish against the wall of the burrow. When this technique was unsuccessful, the burrow had to be laboriously excavated with shovel and trowel. In these situations the crayfish was usually "cornered" somewhere in the passageways of the burrow system as the collector probed with a bare hand.

Coincident with a broader study by the second author (Jezerinac 1993), crayfishes representing the subgenera *Cambarus* (*Lacunicambarus*) and *Cambarus* (*Tubericambarus*) were examined from the collections of the following institutions: Buffalo Museum of Science, Buffalo, New York (8 collections); Illinois Natural History Survey, Champaign, Illinois (55); National Museum of Natural History, Smithsonian Institution, Washington D.C. (59); The Ohio State University-Museum of Biological Diversity, Columbus, Ohio (34); The Ohio State University at Newark Crayfish Museum, Newark, Ohio (173); and the Royal Ontario Museum, Toronto, Canada (3). Persons who assisted in collecting crayfishes in the field are cited in the Acknowledgments.

Cambarus diogenes

Data for specimens of *Cambarus* (*Lacunicambarus*)

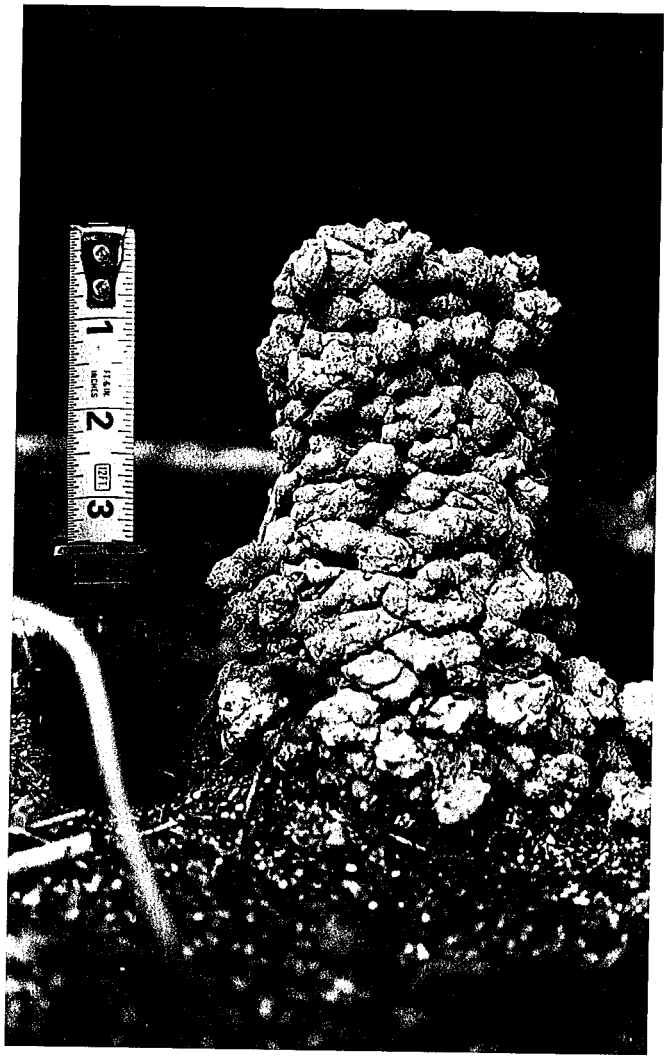

Fig. 2. Cylindrical chimney capping burrow of juvenile male *Cambarus diogenes*, Strawberry Island, Erie County, New York (BMS-1995.347e).

diogenes collected through 1995 by the authors at seven sites in northwestern New York are provided below. These data rigorously document the distribution of this burrowing crayfish in New York for the first time (cf. Pickett, Nasca and Gall 1982). The distributional records of *C. diogenes* in New York, as well as those reported by Guiasu, Barr and Dunham (1996) in the Niagara Peninsula of Ontario, are plotted in Fig. 8. These records define the extreme northeastern edge of the range of *C. diogenes* in North America (Fig. 7).

Acronyms for the institutions where these specimens are deposited are as follows: BMS = Buffalo Museum of Science, Buffalo, NY; NYSM = New York State Museum, Albany, NY; USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC; OSU-MBD = The Ohio State University-Museum of Biological Diversity, Columbus, OH; ROMCN = Royal Ontario Museum, Toronto. Catalogue numbers of the specimens deposited in the respective institutions follow the acronym of each institution.

NEW YORK, Erie County: City of Buffalo. Tifft Nature Preserve. Five collections: (1) In burrow along boardwalk to viewing blind at Lisa Pond. 9 JUL 1983. BMS-1996.035. WK Gall. 1♀. (2) In burrows, southeast corner Beth Pond. 18 SEP 1988. BMS-1988.022a&b. WK Gall. 1 ♂I, 1 ♂II. (3) In burrow, southwest shore Beth Pond. 20 MAY 1989. BMS-1989.003. WK Gall, ST Hasiotis. 1 ♂I. (4) In bentonite/concrete slurry poured in burrow, south shore Beth Pond. 21 MAY 1989. BMS-1989.004a. WK Gall, ST Hasiotis. 1 ♂II. (5) In burrow, south shore Beth Pond. 21 MAY 1989. BMS-1989.004b,c&d. WK Gall, ST Hasiotis. 1 ♂II, 2 ♀♀.

NEW YORK, Erie County: Town of Grand Island. Buckhorn Island State Park. Eight collections: (1) In burrow, 11 cm. from south bank of Woods Creek, approx. 45 m upstream from its mouth at the Niagara River. 12 SEP 1980. NYSM-C875. WK Gall, JA Nasca. 1 ♂I. (2) Dipnetted at edge of bed of *Vallisneria* in Woods Creek, 1.5–2 m from excavated (unoccupied) burrow on south bank, approx. 35 m upstream from its mouth at the Niagara River. 16 SEP 1980. NYSM-C876 (1 ♂I transferred to Dr. Alan Devcich, Waikato University, New Zealand, 15 DEC 1980). NYSM-C874 (1 juvenile ♀). WK Gall, JA Nasca. (3) In burrow, approx. 3.2 m from south bank of Woods Creek, approx. 48.5 m upstream from its mouth at the Niagara River. 16 SEP 1980. USNM-208707. WK Gall, JA Nasca. 1 ♂I. (4) In burrow, 64 cm from south bank of Woods Creek, approx. 60.4 m upstream from its mouth at the Niagara River. 16 SEP 1980. USNM-208708. WK Gall, JA Nasca. 1 ♂II, 2 ♀♀, 5 juvenile ♂♂, 3 juvenile ♀♀. (5) 8 NOV 1980. NYSM-C1407. WK Gall. 1 ♂I. (6) 8 NOV 1980. NYSM-C1408. WK Gall. 1 ♂II, 1 juvenile ♀. (7) 8 NOV 1980. NYSM-C1409. WK Gall. 1 ♂I, 1 ♀. (8) In burrow capped by a chimney along south bank of Woods Creek. 7 NOV 1981. NYSM-C1411. WK Gall. 1 ♀.

NEW YORK, Erie County: Town of Grand Island. In burrows, Ransom Road ditch in front of Grand Island High School. 7 JUL 1983. BMS-1996.036. WK Gall, DW Rowe. 2 ♂♂I, 2 ♀♀.

NEW YORK, Erie County: Town of Tonawanda. In burrows, Strawberry Island (upper Niagara River), northeast shore of bay on downstream side of island. Two collections: (1) 1 SEP 1995. BMS-1995.347a-e. WK Gall. 1 juvenile ♂, 4 ♀♀. (2) 2 OCT 1995. BMS-1995.303a-c. WK Gall. 3 ♀♀.

NEW YORK, Genesee County: Town of Alabama. Iroquois National Wildlife Refuge. Two collections: (1) In burrows, backwater 2 m south of Oak Orchard Creek,

Fig. 3. Low, broad, amorphous chimney capping burrow of female *Cambarus diogenes*, Strawberry Island, Erie County, New York (BMS-1995.347d).

approx. 0.4 km east of Sour Springs Road. 13 AUG 1980. USNM-177378. WK Gall. 1 ♂I, 1 ♀. (2) In burrows, three backwaters 6–30 m south of Oak Orchard Creek, 0.1–0.4 km east of Sour Springs Road. 5 SEP 1980. NYSM-C873. WK Gall, JA Nasca, and JF Pickett, Sr. 1 ♂I, 1 ♂II, 1 ♀, 7 juvenile ♀♀ (1 ♂II and 3 juvenile ♀♀ transferred to Dr. Alan Devcich, Waikato University, New Zealand, 15 DEC 1980).

NEW YORK, Genesee County: Town of Alabama. Along Lewiston Road [Roberts Road?], 0.3 km east of Sour Springs Road, 2 km northeast of Alabama. 5 JUL 1987. RF Jezerinac. 1 ♂II, 2♀♀. OSU-MBD-J-87-37.

NEW YORK, Niagara County: City of Niagara Falls. In burrows, wet meadow south of LaSalle High School athletic field, north of Mooradian Drive, east of Third Avenue. 8 NOV 1994. BMS-1994.464. WK Gall, KJ Roblee. 3 ♂♂I, 1 ♀.

Populations of *C. diogenes* were not found by WKG in late summer-early fall, 1980, during searches of suitable habitat along Conewango Creek in the Conewango Swamp southeast of Cherry Creek and southwest of Frewsburg (Chautauqua County). Thus there is currently no available evidence that this crayfish occurs in the Allegheny River drainage of southwestern New York. In addition, cursory searches for *C. diogenes* by WKG were unsuccessful at Irondequoit Bay (east of Rochester, Monroe County), on 25 September 1980, as were searches by WKG, J.F. Pickett, Sr., and J.A. Nasca at Cicero Swamp (northeast of Syracuse, Onondaga County), on 13 June 1981. Available data suggest that the distribution of *C. diogenes* in New York may be limited to the Lake Erie-Lake Ontario lowlands west of the Genesee River.

The populations of *C. diogenes* from northwestern New York and southern Ontario are most similar to populations of *C. diogenes* occurring from Auglaize County, Ohio, westward to Denver, Colorado, and from Pemiscot County, Missouri, northward into northern Wisconsin. The diagnostic features of these populations (see Fig. 1 in Jezerinac 1993) is the presence of two well defined rows of tubercles on the dorsomesial surface of the palm of the chela; an additional row of tubercles on the dorsal surface of the palm of the chela running from the articulation knob on the base of the chela to the articulation knob at the base of the dactyl; a few tubercles between the dorsomesial rows and the dorsal row; and one to three subpalmar tubercles. In contrast, *Cambarus* (*Tubericambarus*) spp. has multiple rows of tubercles covering the dorsal surface of the palm of the chela, and no subpalmar tubercles.

We conclude that these morphological features of the chela serve to distinguish the New York and Ontario populations of *Cambarus* (*Lacunicambarus*) *diogenes* from those of *Cambarus* (*Tubericambarus*) spp. (cf. Figs. 6 and

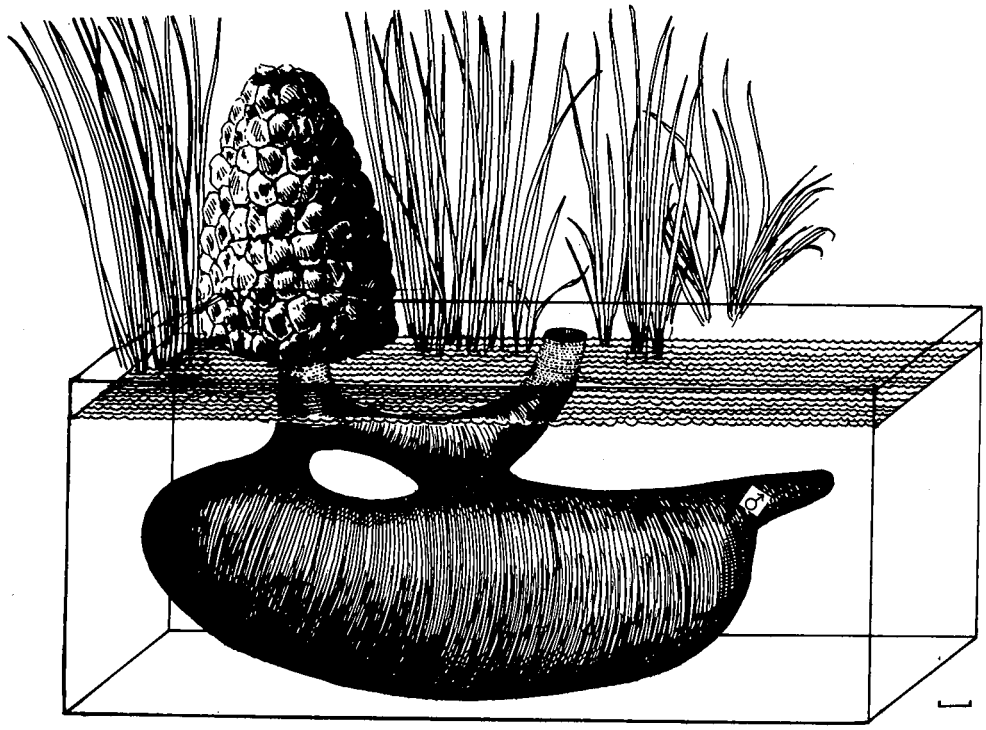

Fig. 4. Burrow of *Cambarus diogenes* capped by conical chimney, Buckhorn Island State Park, Erie County, New York; form I male (♂) collected in pocket on right (NYSM-C875). Scale = 1 cm.

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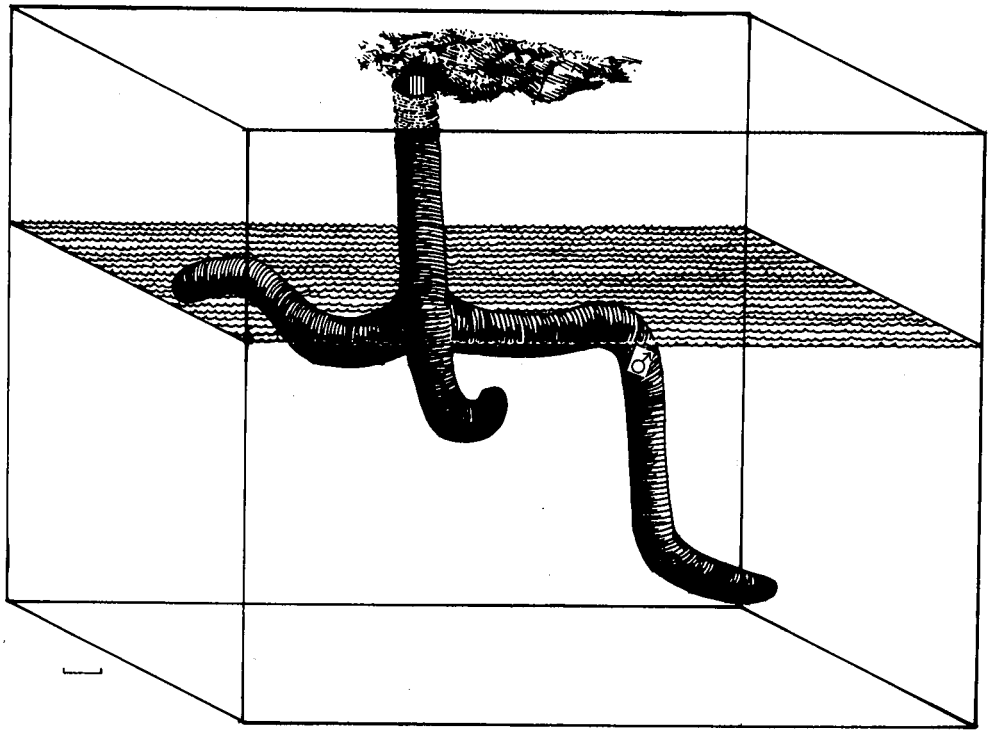

Fig. 5: Burrow of *Cambarus diogenes* capped by low, broad, amorphous chimney, Buckhorn Island State Park, New York; form I male (♂) collected in right passageway just below water level (USNM-208707). Scale = 1 cm.

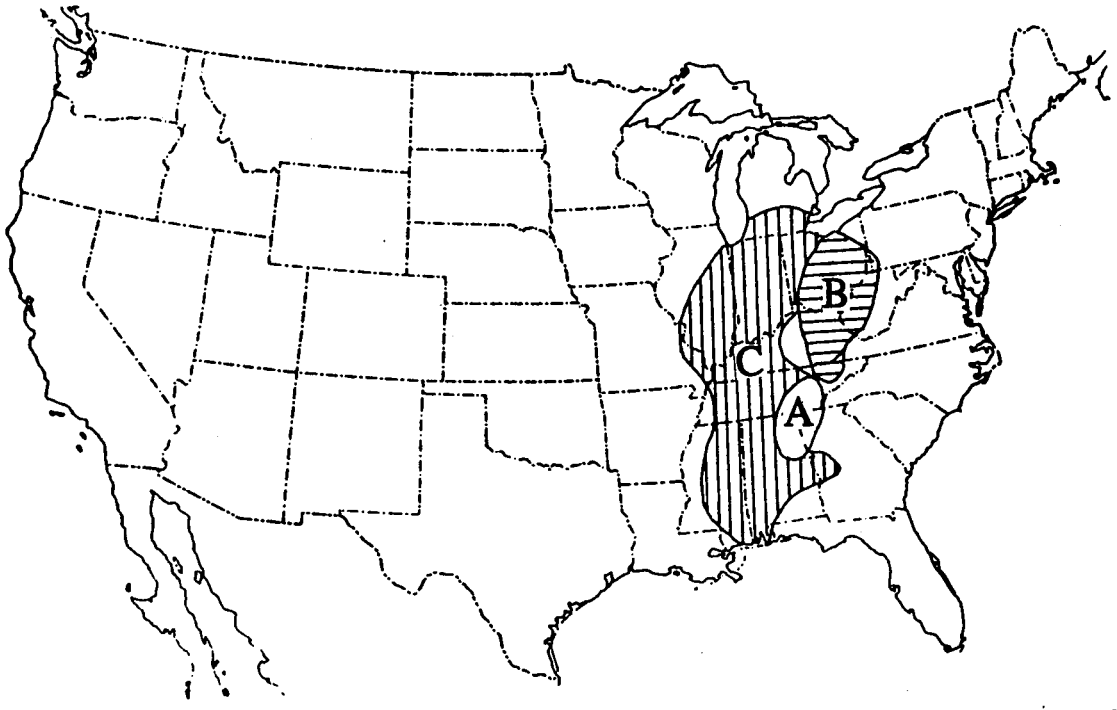

Fig. 6. Range of the subgenus, *Cambarus* (*Tubericambarus*): A = *C.* (*T.*) *acanthura*; B = *C.* (*T.*) *thomai*; C = *C.* (*T.*) sp. A. From Jezerinac (1993).

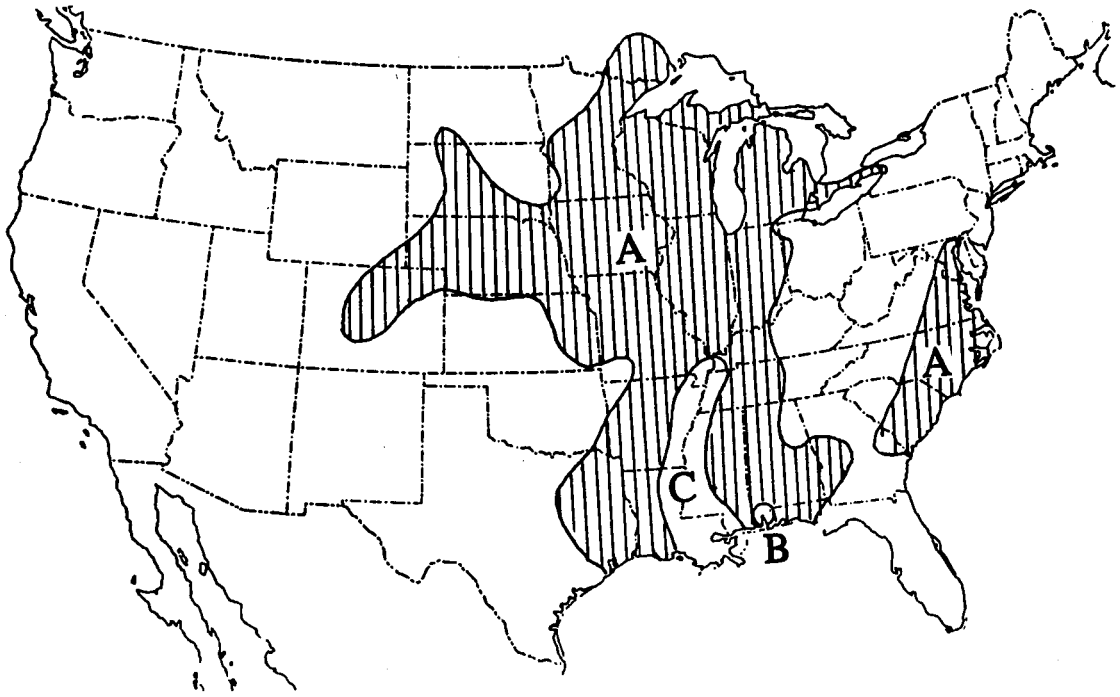

Fig. 7. Range of the subgenus, *Cambarus* (*Lacunicambarus*): A = *C.* (*L.*) *diogenes*; B = *C.* (*L.*) *miltus*; C = *C.* (*L.*) *ludovicianus*. From Jezerinac (1993).

7). We also conclude that the New York and Ontario populations of *Cambarus* (*Lacunicambarus*) *diogenes* are most similar to populations of the same taxon in the upper Midwest.

However, the taxonomic status of populations of *Cambarus* (*L.*) *diogenes* from New York, Ontario, and the upper Midwest, relative to populations east of the Appalachians (Fig. 7), is unclear and requires further study (cf. Ortmann 1906, pp. 407–409). Referring to the Genesee County specimens (USNM-177378), Hobbs stated (letter to Joseph F. Pickett, Sr., 21 August 1980):

> "I question the subspecific designation [*Cambarus* (*Lacunicambarus*) *diogenes* Girard] because they, like most populations of the species occurring in the upper Mississippi and Great Lakes basins, are easily distinguished from the typical form that frequents the area east of the Appalachians from New Jersey to Georgia and throughout much of the southern United States. The study that was made by Marlow (1960) represents a very unsatisfactory treatment of the species, and I look forward to the time when someone makes a careful analysis of the complex, employing both morphological and morphometric data. Until our understanding is more refined I suppose the conservative designation for your population is *Cambarus* (*L.*) *diogenes* subsp., for these specimens from New York are far from typical of either the nominate subspecies or of *C.* (*L.*) *diogenes ludovicianus* Faxon. I hope that no one places a name on it until the hoped-for study mentioned above has been completed."

In another letter to Pickett (28 August 1980), Hobbs added:

> "You are correct in assuming that the specimens of *C.* (*L.*) *diogenes* that you sent me [USNM 177378] are perhaps members of an undescribed subspecies, but it is equally likely that they represent a variant at the end of a cline and that subspecies should not be recognized. It is also not impossible that they should be assigned to a new species, for I am virtually sure that Faxon's variety '*ludovicianus*' should be elevated to specific status. Name shifting, however, should be supported by convincing data, and such have not yet been compiled."

Rhadinocythere serrata

Upon examining the first specimens of the *C. diogenes* complex ever collected in New York (Genesee County, USNM 177378), Horton H. Hobbs, Jr. reported (letter to Pickett, 18 September 1980) that they were infested with the entocytherid ostracod, *Rhadinocythere serrata* (Hoff). Previously this commensal had not been reported any further east than Lake Maxinkuckee and the Kankakee River in northwestern Indiana, where the host crayfish was reported as "*Cambarus d. diogenes*" (Hart and Hart 1974). In subsequent letters to WKG, Hobbs (9 November 1988, 24 January, and 6 February 1989), reported other unpublished records for *R. serrata* associated with *C. diogenes* from other localities: in marsh at Long Point, Ontario (Royal Ontario Museum, Toronto, ROMCN L2157 and 2158); Tifft Nature Preserve, Erie Co., New York (BMS 1988.022a&b); Buckhorn Island State Park, Erie Co., New York (USNM 208707 or 208708); Independence Co., Arkansas; Cherokee Co., Iowa; and Buffalo, Brown and Racine counties, Wisconsin. Hobbs further reported to WKG (letter of 6 February 1989) that the ostracods reported above were mounted on slides by him and retained in the collection of the USNM, with the exception of three slides of entocytherids associated with *C. diogenes* from Long Point, Ontario, that were sent to the Royal Ontario Museum (ROMCN L2738).

Hobbs also reported that the USNM collection contains specimens of *R. serrata* retrieved from *C. diogenes* and *Orconectes immunis* (Hagen) collected by the senior author, J.F. Pickett, Sr., and J.A. Nasca on 5 September 1980 on the floodplain of Oak Orchard Creek, Genesee Co. (NYSM-35912). However these two species of crayfish were collected from adjacent burrows and most likely shared the same container(s) of preservative (entocytherid ostracods are pipetted from the detritus in the bottom of the container after their crayfish hosts are preserved). Under these circumstances, and in view of the fact that *C. diogenes* has served as host to *R. serrata* in all other known localities where the latter has been reported, it is unlikely that *O. immunis* served as host to *R. serrata* at this site (letter from Hobbs to WKG, 6 February 1989).

The distribution of the commensal ostracod, *R. serrata*, is mapped on the range of its host crayfish, *C. diogenes*, in Fig. 9. Note that *R. serrata* has not been reported in association with the disjunct population of *C. diogenes* that occurs east of the Appalachians, in spite of surveys for entocytherid ostracods there (e.g., Hobbs and Peters 1977).

Postglacial Dispersal

Burrows containing *C. diogenes* in northwestern New York were excavated in wetland remnants of glacial Lake Tonawanda (Muller 1977) at the Niagara Falls, Buckhorn Island, Iroquois Refuge and Lewiston Road (Roberts Road?) sites; a remnant of a lacustrine wetland at the eastern end of Lake Erie (Tifft Preserve site); and wetlands associated with the Niagara River and its tributaries (Strawberry Island and the Ransom Road sites).

Morphological features of the crayfish chela, and the distributional pattern of its host-specific ostracod, suggest that populations of *C. diogenes* in northwestern New York are derived from populations in the upper Midwest. Perhaps the application of the techniques of molecular systematics may some day shed light on the relationships

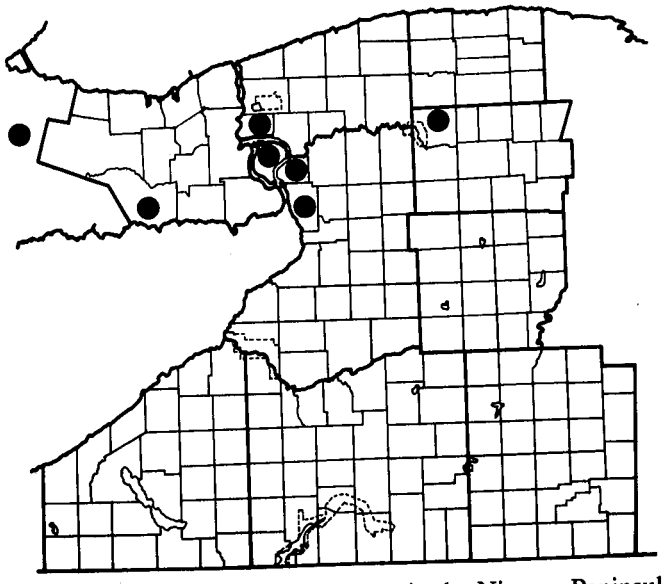

Fig. 8. Distribution of *C. diogenes* in the Niagara Peninsula of Ontario (Guiasu, Barr, and Dunham 1996), and in northwestern New York.

between these populations. If this inferred faunal relationship is indeed correct, what was the migratory pathway utilized by this crayfish during dispersal from the upper Midwest into northwestern New York? Isolated populations of *C. diogenes* similar to the New York specimens are found on the northern shore of Lake Erie in Ontario, Canada. No such populations have been found on the southern shore in Ohio (where *C. thomai* occurs) or Pennsylvania. This suggests dispersal along the northern shore of the Lake Erie basin one or more times since the retreat of the Wisconsin ice sheets (Fig. 10). The xerothermic, or hypsithermal, interval (Sears 1942; Ogden 1965) which occurred about 4,000 to 3,500 years before present (Forsyth 1973) may have provided excellent ecological conditions for the range expansion of this taxon. It is possible that competitive interactions with *C. thomai* on the Lake Erie lowlands of northern Ohio prevented the northeastward dispersal of *C. diogenes* along the southern shore of Lake Erie. This hypothesis suggests that *C. thomai* may have dispersed into glaciated northern Ohio from the unglaciated Allegheny Plateau to the south before the northeastward dispersal of *C. diogenes* along the northern shore of Lake Erie from the upper Midwest.

Orconectes immunis is a crayfish associate of *C. diogenes* in the Midwest (Hobbs and Jass 1988; Page 1985). Jezerinac (1982) has suggested that *O. immunis* may have dispersed northeastward during this same xerothermic period. How or when either taxon crossed the Niagara River, however, is unclear.

Conservation Considerations

Rarity of a species may be interpreted as few or widely scattered populations relative to a given geographic area (Mitchell and Sheviak 1981). Rarity of *C. diogenes* in New York can clearly be attributed to the occurrence of this taxon at the edge of its much broader range in North America.

The first step in establishing some level of regulatory protection (i.e., formal listing) of this crayfish would be to determine more precisely its status in New York. In this regard, a comprehensive survey should be undertaken to estimate the number and sizes of populations of *C. diogenes* in northwestern New York. Applying the criteria for protected native plants promulgated by the New York State Department of Environmental Conservation (NYSDEC 1995), *C. diogenes* could be listed as threatened and likely to become endangered within the foreseeable future in New York, because the preliminary data reported here suggest that it may be known from six to fewer than 20 sites, or 1,000 to fewer than 3,000 individuals.

Concerns for the conservation of this crayfish are further heightened by the fact that four of the seven known sites for *C. diogenes* in northwestern New York are vulnerable to various disturbances. The Ransom Road ditch in front of the Grand Island High School is subject to the vagaries of highway maintenance (e.g., ditching to improve drainage, runoff of road-salt and/or petroleum products from Ransom Road and the adjacent school parking lot, etc.). While it is likely that *C. diogenes* is more widely distributed on Grand Island, this insular town also has experienced an accelerated rate of residential and commercial development in recent years. The site along Lewiston Road (Roberts Road?) in Genesee County, although in a rural setting, may also be subject to disturbance from highway maintenance. Regarding the site in the City of Niagara Falls, a permit application for new construction in the adjacent upland of this wet meadow (designated as protected wetland TW-3 by the NYSDEC) was under review by the NYSDEC in 1996. However, mitigative measures (e.g., construction of a berm) were incorporated into the development plan for this site to protect the habitat of the population of *C. diogenes* occurring there (Kenneth J. Roblee, NYSDEC, pers. comm. to WKG, 31 December 1996). The fourth vulnerable site, Strawberry Island in the upper Niagara River, has been under the jurisdiction of the New York State Office of Parks, Recreation and Historic Preservation only since 1989. Unfortunately, commercial dredging of gravel prior to 1960 greatly reduced the surface area of Strawberry Island, and continuing shoreline erosion threatens its very existence (Virgilio and Spencer 1990).

The remaining three sites harboring populations of *C. diogenes* offer relatively more stable or protected habitat: Buckhorn Island State Park, the Iroquois National Wildlife

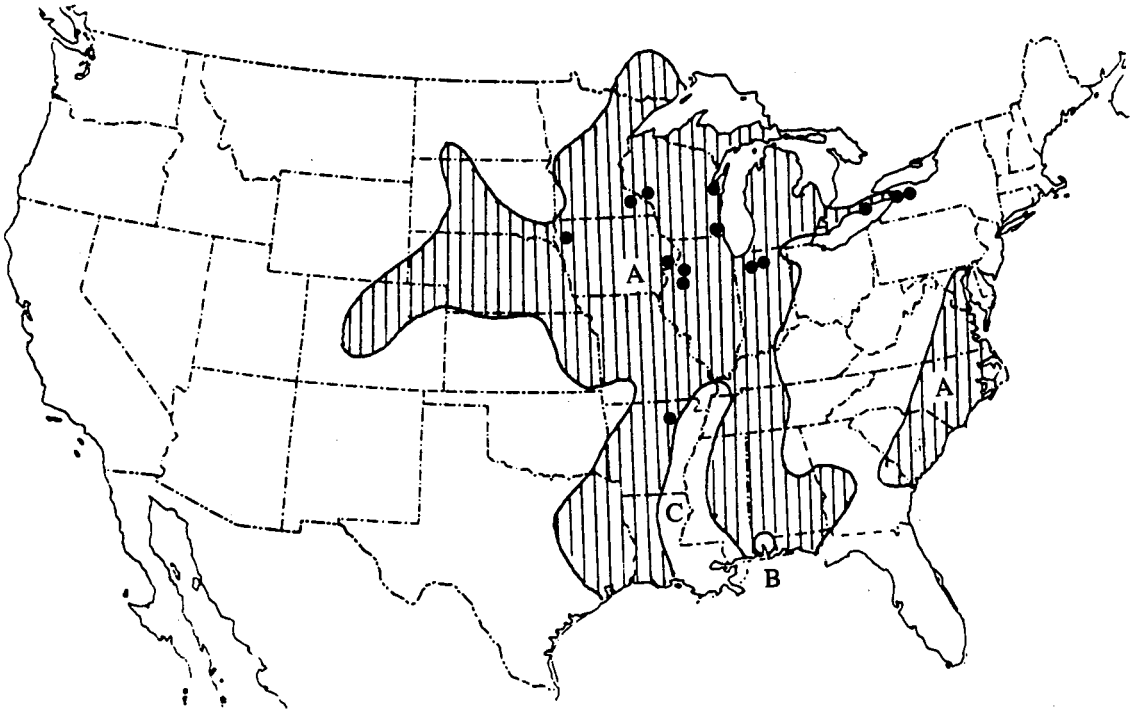

Fig. 9. Distribution of the commensal ostracod, *R. serrata*, mapped on the distribution of its host crayfish, *C. diogenes* [A]. Modified from Jezerinac (1993).

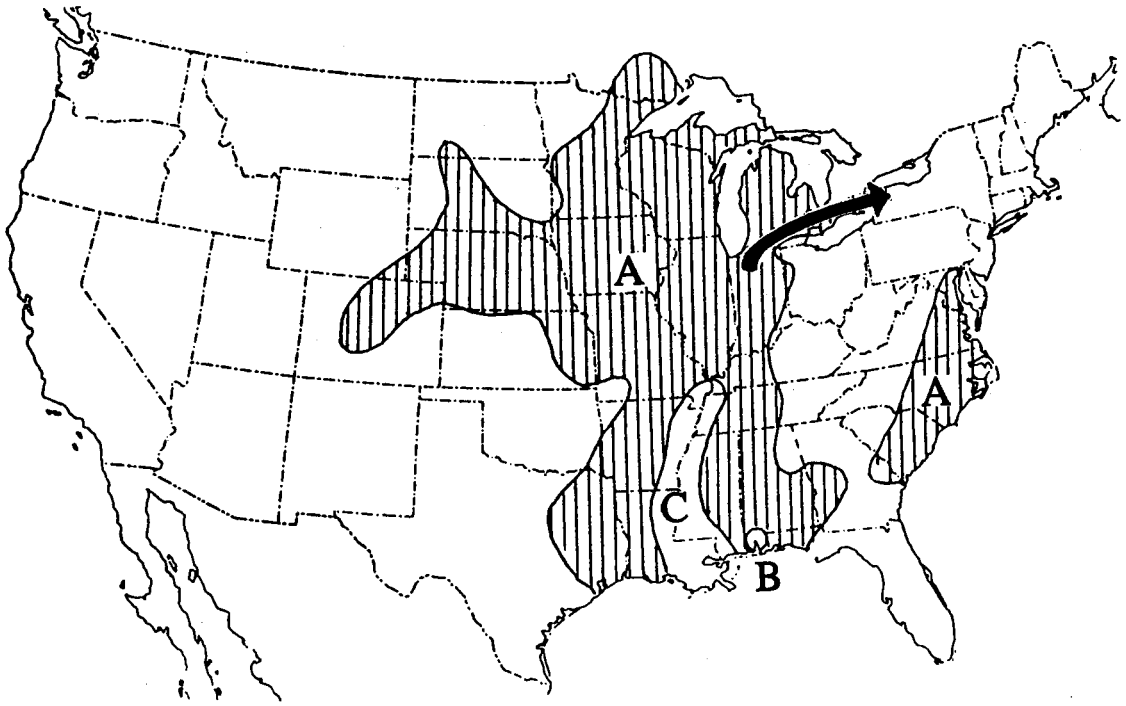

Fig. 10. Postglacial dispersal route (arrow) inferred for *C. diogenes* [A] into southern Ontario and northwestern New York. Modified from Jezerinac (1993).

Refuge, and Tifft Nature Preserve.

Conclusions

Two independent lines of evidence provide support for the relationship between populations of *Cambarus* (*Lacunicambarus*) *diogenes* in northwestern New York, southern Ontario, and the upper Midwest: concordance in meristic features of the chelae of the respective populations, and the distributional pattern of its host-specific entocytherid ostracod, *Rhadinocythere serrata*. The distribution of *R. serrata* also suggests postglacial dispersal of *C. diogenes* from the upper Midwest along the northern margin of the Lake Erie basin into northwestern New York.

A comprehensive revision is still needed to resolve remaining taxonomic problems within the *C. diogenes* complex (Hobbs 1972, 1974, 1981, 1989; Jezerinac 1993), particularly the relationship between populations east and west of the Appalachians. Phylogenetic analysis of the crayfishes within this complex, as well as a parallel analysis of the entocytherid ostracods associated with these crayfishes, not only may provide further insights into biogeographic patterns, but also may reveal coevolutionary relationships between crayfish host and ostracod symbiont.

Such analyses may shed light on several questions. For example, Horton H. Hobbs, Jr. did not find *R. serrata* associated with "*Cambarus* (*Lacunicambarus*) *diogenes*" from Beaver Co., Pennsylvania, and from Erie, Franklin, Jackson, Licking, Perry and Sandusky counties, Ohio (letter to WKG, 24 January 1989; letter to Pickett, 5 May 1981). Could it be more than fortuitous that the distribution of the subgenus erected by Jezerinac (1993), *Cambarus* (*Tubericambarus*), includes these counties of Ohio and Pennsylvania where the subgenus, *Cambarus* (*Lacunicambarus*) sensu Jezerinac (1993), is not found (cf. Figs. 6 and 7)? Also, Hart and Hart (1974) and Hobbs and McClure (1983) reported only the entocytherid ostracod, *Dactylocythere crawfordi* Hart, associated with "*Cambarus* (*Lacunicambarus*) *diogenes*" from Decatur, Marion, and White counties, Indiana, and from Clinton, Franklin, Licking, and Logan counties, Ohio. Could it be that the crayfish hosting *D. crawfordi* at these sites is actually *Cambarus* (*Tubericambarus*) *thomai* or *C.* (*T.*) sp. A (Fig. 6)? Putting these seemingly disparate questions together, is it possible that entocytherid ostracods could effectively serve as biological markers or tags, i.e., little free-loaders that ultimately might help reveal the phyletic affinity and/or biogeographic relationships of crayfishes in the *Cambarus* (*Lacunicambarus*) *diogenes* complex?

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Note added in proof by WKG: Figs. 7, 9 and 10 here, and Fig. 2 in Jezerinac (1993), err in not including extreme southeastern Pennsylvania and parts of New Jersey in the range of the eastern population of *C. diogenes* (cf. Francois 1959, Fig. 8; Hobbs and Jass 1988, Fig. 29; Ortmann 1906, Pl. XLIII). The range of *C. diogenes* no longer includes southwestern Pennsylvania and northern Ohio because the taxon in these areas is now referable to *C. thomai* (cf. Figs. 6 and 7).