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Distribution of Indiana Cavernicolous Crayfishes and their Ecto-Commensal Ostracods

by

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The first report of crayfishes inhabiting Indiana caves appeared in The Indianapolis Journal in 1871 when Cope listed *Astacus pellucidus* (= *Orconectes inermis inermis* Cope, 1872) from Wyandotte Cave, Crawford County. The description of the cave however indicates that this was not Wyandotte Cave but was in all probability Sibert's Well Cave, a small cave located approximately 300 meters SW of the entrance to Wyandotte Cave. Ostracods were not known from caves until 1931 when Klie described an entocytherid, *Entocythere donnaldsonensis* (= *Donnaldsoncythere donnaldsonensis*), from Donaldson's Cave, Lawrence County. Although he made no reference to this ostracod being associated with a crayfish host, it is probable that an ecto-commensal-host relationship existed with the crayfishes *Cambarus (Erebicambarus) laevis* Faxon, 1914 and *Orconectes inermis inermis*. Thus, error and incomplete sampling seem to have played a hand in the beginnings of our knowledge of these two groups of spelean crustaceans in Indiana.

Investigators of the late 1800's and the early years of the 20th century visited numerous caves within the State, compiling lists of cavernicolous organisms (Hobbs III and Krantz, in preparation). These important studies added greatly to our knowledge of not only what kinds of creatures inhabit the stygian corriders but also provided observations concerning their behavior, habits, physical and physiological adaptations to the environment and theories of the evolution of troglobites.

Recent efforts to obtain a better understanding of the distribution of cave crayfishes and their ecto-commensals began in September 1969. This work has continued to the present with trips to over 100 caves in the southern part of the State and also includes extensive population studies in two caves (fig. 1): Mayfield's Cave, Monroe County [*Orconectes inermis testii* (Hay, 1891)] and Pless Cave, Lawrence County (*Orconectes inermis inermis*). Results of investigations in these two caves will be reported in a subsequent paper. From this work and from pre-existing efforts (see Hobbs and Barr, 1972) a better understanding is attained of the species composition of crayfishes and ostracods and their distribution in Indiana caves.

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METHODS AND MATERIALS

Cave streams were carefully searched for organisms. Often crayfishes and other crustaceans were observed in pools along the streams' length. Commonly, however, tedious examination of rocks, leaf litter or other materials which could be used for cover was required.

Crayfishes, as collected, were individually placed in plastic bags containing a small amount of cave-stream water. Immediately after removal from the cave, each specimen was placed in a separate jar containing a 5% formalin-70% ethyl alcohol solution (25-75% respectively). This procedure allowed for precise determinations of host-commensal associations. The crayfishes were then removed and thoroughly washed to detach any symbionts, passing the wash water through two sieves (nos. *20*, *140*). Then the solution in which they were killed was poured through the same sieves. The jars were rinsed and the rinse water likewise passed through the sieves which were then rinsed, and the debris trapped in the larger meshed sieve, discarded. Sediments from the smaller sieve were transferred to a small Stender dish, from which the ostracods were removed with forceps and the aid of a stereomicroscope. The ostracods were dehydrated in two rinses of glacial acetic acid and cleared with methyl salicylate. Using "Permount*R*" as the mounting medium, they were transferred to microscope slides. The animals were examined and identification was made with the aid of a compound microscope.

CAVES OF INDIANA

Two distinct karst areas occur in the State of Indiana (fig. 1). The smaller lies in the southeastern part of the State and occupies parts of Clark, Decatur, Jefferson, Jennings and Ripley Counties, where at least 80 caves are known to be present in these upper Silurian and lower Devonian limestone deposits.

The larger and more notable cave region lies in the south-central portion of the State between Putnam County and the Ohio River. More than 1300 caves have been discovered in this Mississippian limestone belt. Within the streams in them, crayfishes constitute a more conspicuous element of the fauna than in the subterranean waters of the eastern karst zone.

Many of the caves visited during this study were traversed by stream(s), which coursed through the lower levels. Not all of the caves with streams, however, harbored crayfishes, and in some instances no living aquatic animals were observed.

THE CRAYFISHES

Evolution: Hobbs (1967, 1969) and Hobbs and Barr (1972) have postulated that the extant crayfishes of North America east of the Continental Divide (except for one member of the genus *Pacifastacus* Bott, 1950, which occurs in the headwaters of the Missouri River) were probably derived from a *Procambarus*-like ancestor,

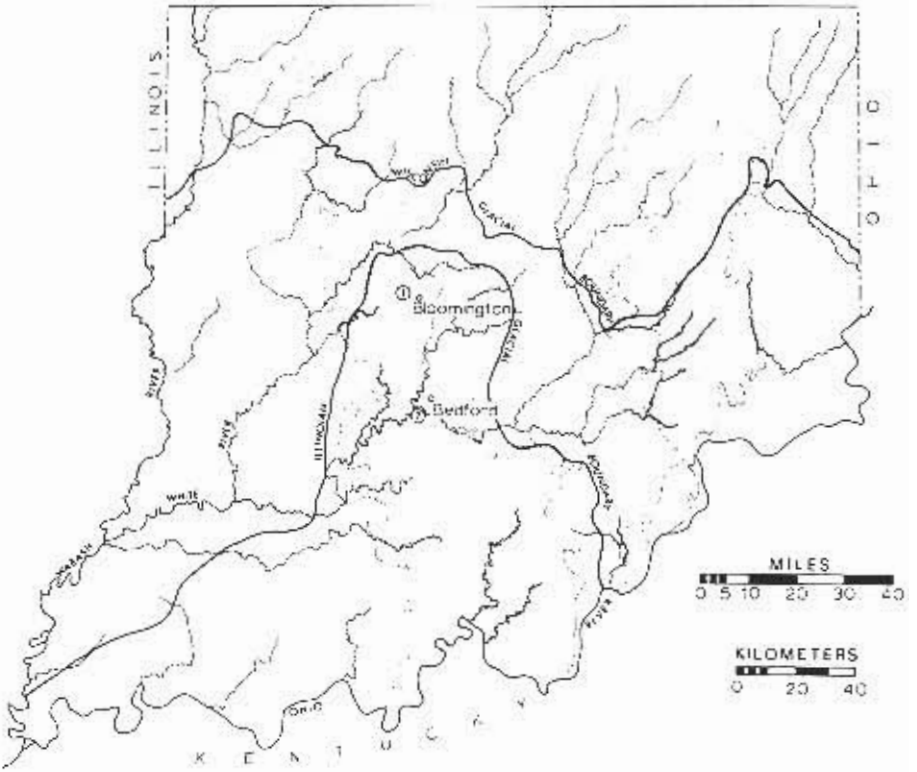

Fig. 1. Map of southern Indiana showing two major karst areas (larger – Mississippi limestone; smaller – Silurian and Devonian limestones – this eastern limestone unit continues to the north but no caves are known north of that shown on map. Numbers 1 and 2 indicate the locations of Mayfield's and Pless Caves, respectively (modified from Powell 1961).

which is believed to have occupied the coastal region of Alabama and Georgia. It then moved northward to the Cumberland Plateau, where, in the mid-Tertiary, ancestors of two major stocks of the subfamily Cambarinae probably became differentiated. In this region, much of the primary divergence between the two genera *Orconectes* Cope, 1872 and *Cambarus* Erichson, 1846 occurred, with stocks radiating from the center. *Orconectes* dispersed principally to the north and west and *Cambarus* to the east and south (with several stocks moving westward). It was postulated that some of the stream dwelling ancestors of *Orconectes* in the karst region moved into spelean habitats long ago (Eberly 1960, and Hobbs 1948). The troglobitic *Orconectes* do not appear to be closely related to any extant surface form. Either the epigean stock from which they originated has become further

diversified, departing considerably from the ancestral type, or the cave forms have evolved from an epigean ancestral stock that is no longer extant. The latter possibility is favored by Hobbs and Barr (1972). Since cave populations are often as isolated from each other as they are from the surface crayfish, one might anticipate that the crayfishes of the different cave systems would differ at least as significantly as do the various surface populations. On the contrary, however, there is great similarity among the different cave populations. Rather than being products of convergent evolution, the crayfishes demonstrate a channelizing effect of the spelean environment together with the retention of certain primitive characters (Hobbs and Barr 1972).

Cave Crayfishes of North America: Currently, there are 287 recognized species and subspecies of crayfishes representing 9 genera (Cambaridae) within North and Middle America (Hobbs 1974a, b). Only 24 of these are classified as troglobites, inhabiting the streams of numerous caves located in nine of the United States, Mexico and Cuba. The taxonomic outline presented below indicates the known troglobitic crayfishes, their distribution and relationships (modified from Hobbs and Barr 1972).

Cambaridae – Northern Hemisphere
Cambarinae – North America east of the Rocky Mountains

Cambarus Erichson, 1846 – United States east of the Rocky Mountains (Midwest and Southeast)
C. (Aviticambarus) hamulatus (Cope, 1881) – Alabama and Tennessee

C. (Aviticambarus) jonesi Hobbs and Barr, 1960 – Alabama
C. (Erebicambarus) hubrichti Hobbs, 1952 – Missouri
C. (Jugicambarus) cryptodytes Hobbs, 1941 – Florida and Georgia
C. (Jugicambarus) setosus Faxon, 1889 – Missouri
C. (Jugicambarus) tartarus Hobbs and Cooper, 1972 – Oklahoma
C. (Jugicambarus) zophonastes Hobbs and Bedinger, 1964 – Arkansas

Orconectes Cope, 1872 – United States east of the Rocky Mountains (Midwest and Southeast)

O. australis australis (Rhoades, 1941) – Alabama and Tennessee
O. australis packardi (Rhoades, 1944) – Kentucky
O. incomptus Hobbs and Barr, 1972 – Tennessee
O. inermis inermis Cope, 1872 – Indiana and Kentucky
O. inermis testii (Hay, 1891) – Indiana
O. pellucidus (Tellkampf, 1844) – Kentucky and Tennessee

Procambarus Ortmann, 1905 – Mexico, Cuba and the southeastern United States

P. (Austrocambarus) niveus Hobbs and Villalobos, 1964 – Cuba
P. (Austrocambarus) rodriguezi Hobbs, 1943 – Veracruz, Mexico
P. (Leonticambarus) mulleri Hobbs, 1971b – Florida
P. (Lonnbergius) acherontis (Lonnberg, 1895) – Florida
P. (Ortmannicus) horsti Hobbs and Means, 1972 – Florida
P. (Ortmannicus) lucifugus lucifugus (Hobbs, 1940) – Florida
P. (Ortmannicus) lucifugus alachua (Hobbs, 1940) – Florida
P. (Ortmannicus) orcinus Hobbs and Means, 1972 – Florida
P. (Ortmannicus) pallidus (Hobbs, 1940) – Florida
P. (Remoticambarus) pecki Hobbs, 1967 – Alabama

Troglocambarus Hobbs, 1942 – Peninsular Florida
T. maclanei Hobbs, 1942 – Florida

Indiana Cave Crayfishes: The troglobitic species of the genus *Orconectes* are found within caves of northeastern Alabama, central Tennessee and Kentucky, and south-central Indiana (see fig. 2 for geographic distribution). Two subspecies of *Orconectes inermis* including intergrade populations, are found within the cave systems of northern Kentucky and southern Indiana. The nominal subspecies inhabits caves in the southern part of the range, *Orconectes inermis testii*, the northernmost part of the range in Monroe County, and intergrading populations occur between the extremes. *O. i. testii* has been observed in 18 caves from Monroe County (fig. 3). Two

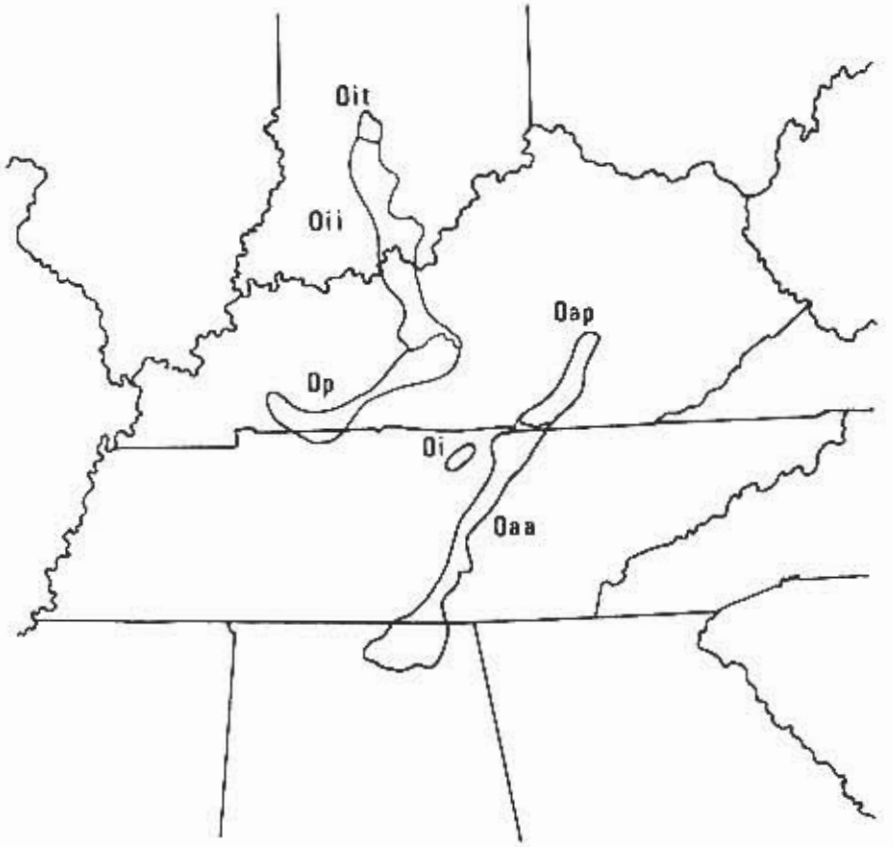

Fig. 2. Geographic distribution of the subterranean species of the crayfish genus *Orconectes* (modified from Hobbs and Barr, 1972). Oii – *Orconectes inermis inermis* Oit – *Orconectes inermis testii* Op – *Orconectes pellucidus* Oaa – *Orconectes australis australis* Oap – *Orconectes australis packardi* Oi – *Orconectes incomptus*

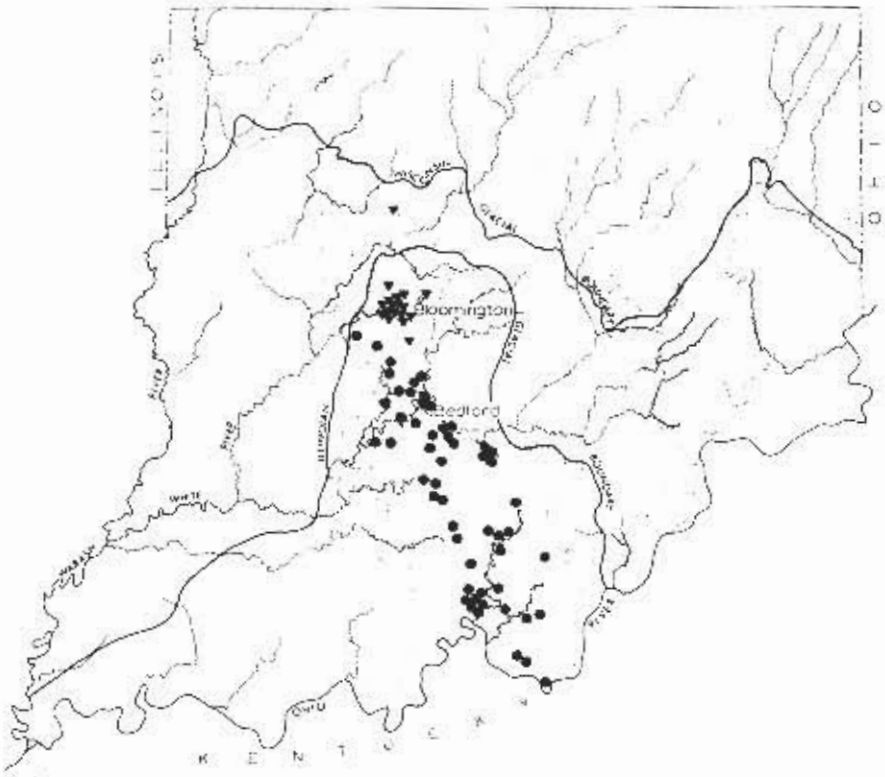

Fig. 3. Distribution map of *Orconectes inermis inermis* (circles) and *Orconectes inermis testii* (triangles) in southern Indiana caves (location for Down's Cave in Lawrence County is unknown).

locality records appear in the literature that perhaps should be verified: Porter's Cave,Owen County (Cox, 1973) and Ray's Cave, Greene County (Moore, 1967). The author has visited both caves on several occasions and was unable to find crayfish of this species. However, his failure to locate these crayfish does not dictate that these reports are incorrect, only that the caves need further examination in order to determine whether or not this crayfish still frequents them. Fifty-six caves from eight counties support populations of *O. i. inermis* (fig. 3).

Numerous studies of the troglobitic *Orconectes* "complex" have contributed to the knowledge of these crayfishes (see Hobbs and Barr 1972 for discussion); however, many facets of their biology are still completely unknown or inadequately understood. Considerably less in known about the troglophilic associate *C. (E.) laevis*, which is found in the streams of epigean and cavernous habitats in southern Indiana and Ohio. Although originally described from an epigean environment, several investigators have noted its occurrence in caves (Hay 1896; Banta 1907; Eberly 1960;

Hobbs 1969; and Hobbs 1974b). Apparently a stenothermal species, it occurs in both subterranean and spring-fed surface streams having temperatures not exceeding 20° C. It has the largest range of any of the cave-dwelling crayfishes in the State, being known from the streams of 58 caves in 10 counties (fig. 4). This species is more "ubiquitous" than *O. inermis* in that substrate types do not appear to limit its occurrence and/or abundance within or among caves. In contrast, *O. inermis* is not likely to be found in streams with bedrock or compact gravel bottoms but is usually observed in deeper, more slowly moving water, with mud or silt substrates. Both species are commonly found near debris clusters (often the debris is concentrated into "mats" which may be trapped under flat rocks or situated on the silt substrate of pools characterized by slowly moving water) or in areas where organic matter may accumulate following spates (i.e., eddies at the junction of the two streams).

A third species, *Orconectes immunis* (Hagen, 1870), is only an occasional inhabitant of caves. Typically, it is an inhabitant of lenitic or sluggish lotic epigean

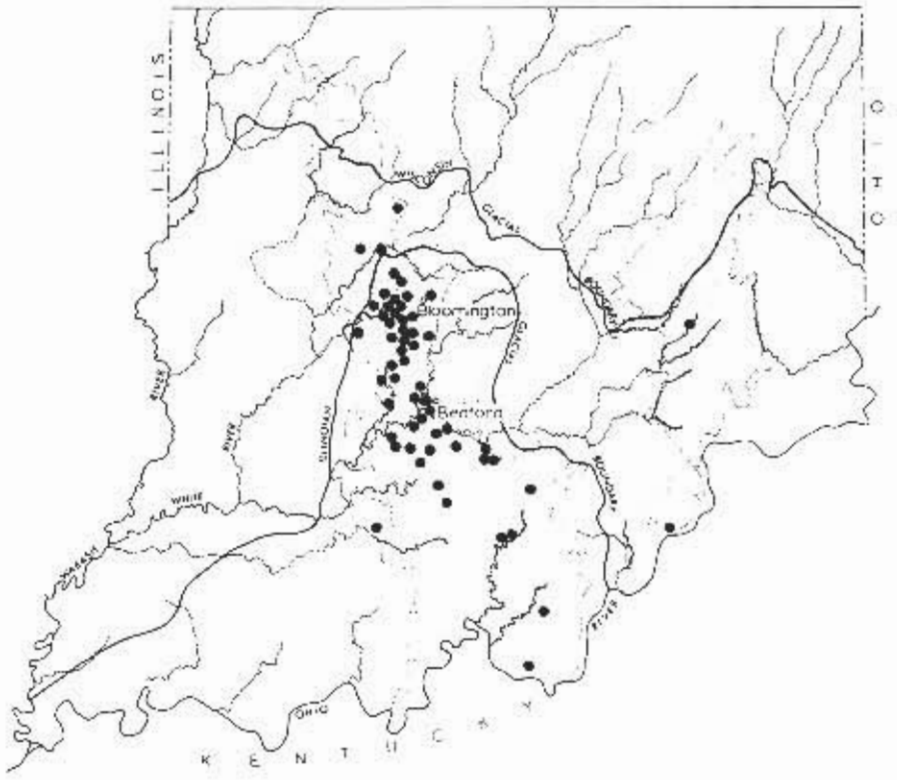

Fig. 4. Distribution map of *Cambarus (Erebicambarus) laevis* in southern Indiana caves (location for Down's Cave in Lawrence County is unknown).

environments (see Tack 1941 and Hobbs and Marchand 1943). This species, like *C. laevis*, is pigmented and possesses fully developed eyes. *O. immunis* has been observed only in Blue Spring and Pless Caves, where it is probably an "accidental" (although it may prove to be a trogloxene) in both localities. A sinkhole pond overlies a section of the south passages of Pless Cave and apparently feeds a small tributary into it. Possibly *O. immunis* enters the cave system at the source of this tributary.

Orconectes sloanii (Bundy, 1876) is found commonly in surface streams in southern Indiana and southwestern Ohio. A single specimen was collected within Pless Cave near the entrance, the only record of the occurrence of this species in a spelean habitat.

A fifth species, *O. propinquus* (Girard, 1852), which has not been reported from caves previously, has been observed in Pless Cave. It is also present in the surface effluent waters exiting the cave. The highest density -- twenty-seven individuals -- was observed within 160 m of the entrance, and very few individuals were noted in the farther recesses of the cave.

Most literature concerning cave crayfishes has dealt with taxonomic problems and the distribution and evolution of the various species. As early as 1877, however, Putnam published an article concerning the habits and replacements of lost appendages of *Cambarus pellucidus* (= *Orconectes pellucidus*) and Banta (1907), in his classical study of the fauna of Mayfield's Cave, described in detail his observations of the activity of both *Cambarus pellucidus* (= *O. i. testii*) and *C. bartonii* [= *C. (E.) Laevis*] found within that cave. Emphasis on the classification of these organisms continued, but some individuals also began to investigate aspects of the biology of the cavernicoles. For additional information concerning previous work, refer to Hobbs and Barr 1972.

THE OSTRACODS

Marshall (1903), in describing the first known entocytherid ostracod, erroneously called them parasites and haemophages. Since that time, several other workers have concerned themselves with the taxonomy and ecology of these animals. In 1962, Hart revised the family Entocytheridae Hoff, 1942, and Hart and Hart (1974) presented a monograph of the family. Currently, five subfamilies are recognized: Entocytherinae (Hoff, 1942 -- North America), Sphaeromicolinae (Hart, 1962 -- North America and Europe), Notocytherinae (Hart and Hart, 1967 -- Australia, Tasmania, New Zealand and New Guinea), Microsyssitrinae (Hart, Nair and Hart, 1967 -- Asia) and the Hartiellinae (Danielopol, 1971 -- Italy and France). All know species of these subfamilies are found in a commensal association with other crustaceans: Entocytherinae -- freshwater crabs, crayfishes; Sphaeromicolinae -- freshwater isopods, marine amphipods; Notocytherinae -- crayfishes, freshwater isopods; Microsyssitrinae -- wood-boring marine isopods; Hartiellinae -- marine amphipods.

Evolution: The evolutionary history of entocytherid ostracods is not so well established as that of the crayfishes. Hart and Hart (1969) postulated that the known freshwater entocytherids in Australia, North America and Europa represent at least three separate invasions from the sea. The representatives in New Zealand and New Guinea also probably represent separate invasions. The ostracods were at the mercy of their hosts and were carried along the dispersal paths of the latter.

Cave Entocytherid Ostracods of North America: All Entocytherinae are ectocommensal on freshwater crayfishes except a single species found on freshwater crabs of the family Pseudothelphusidae in Mexico (Hobbs and Villalobos 1958 and Hobbs 1971a). There are now 146 recognized species representing 20 genera of entocytherines within North America. Of these, only 19 species have been observed in association with crayfishes inhabiting caves. Too little is known about the relationship of the ostracods with their hosts (and in some instances even too little is known concerning the host) to determine accurately if the species is a troglobite, a troglophile, a trogloxene or an "accidental". The taxonomic outline presented below indicates the ostracod species reported from caves and their distribution.

Entocytheridae Hoff, 1942 – North America, Europe, Australia, Tasmania, New Zealand, New Guinea, Asia.

Entocytherinae Hoff, 1942 – North America

Ankylocythere Hart, 1962 – United States east of Rocky Mountains, Mexico, Cuba

A. sinuosa (Rioja, 1942) – Mexico,
A. tolteca Hobbs, 1971a – Mexico

Dactylocythere Hart, 1962 – United States east of Rocky Mountains (Midwest and Mideast)

Dt. arcuata (Hart and Hobbs, 1961) – Alabama,
Dt. prionata (Hart and Hobbs, 1961) – Kentucky
Dt. steevesi (Hart nd Hobbs, 1961) – Alabama, Tennessee,
Dt. susanae Hobbs III, 1971 – Indiana, Kentucky,
Dt. ungulata (Hart and Hobbs, 1961) – Tennessee

Donnaldsoncythere Rioja, 1942 – United States east of Rocky Mountains (Midwest, Southeast, Northeast)

Dn. donnaldsonensis (Klie, 1931) – Indiana,
Dn. tuberosa (Hart and Hobbs, 1961) – Tennessee

Phymocythere Hobbs and Hart, 1966 – United States east of Rocky Mountains (East)

Ph. phyma Hobbs and Hart, 1966 – Virginia and West Virginia

Entocythere Marshall, 1903 – United States east of Rocky Mountains (North-central, South, Southeast), Mexico

E. claytonhoffi Rioja, 1942 – Mexico,

E. reddelli Hobbs and Walton, 1968 – Texas

Sagittocythere Hart, 1962 – United States east of Rocky Mountains (Midwest, Southeast)
S. barri (Hart and Hobbs, 1961) – Alabama, Tennessee, Kentucky, Indiana,
S. stygia Hart and Hart, 1966 – Kentucky

Uncinocythere Hart, 1962 – United States

Un. ambophora (Walton and Hobbs, 1959) – Florida,
Un. lucifuga (Walton and Hobbs, 1959) – Florida,
Un. pholetera (Hart and Hobbs, 1961) – Missouri,
Un. warreni (Hobbs and Walton, 1968) – Georgia,
Un. xania (Hart and Hobbs, 1961) – Missouri, Indiana

Ostracods Associated with Indiana Cave Crayfishes: Table 1 lists the four species of entocytherid ostracods known to occur in southern Indiana caves, their hosts, entocytherid associates, and names of caves and counties from which collections were made. All except two collections (Thomas Crews Cave, Clark County, and an unnamed cave in Jennings County, both in Silurian limestone) were from caves developed in the Mississippian limestones. *Sagittocythere barri* was found in 22 caves in seven counties (fig. 5) and is hosted by *O. i. inermis*, *O. i. testii*, and *C. (E.)*

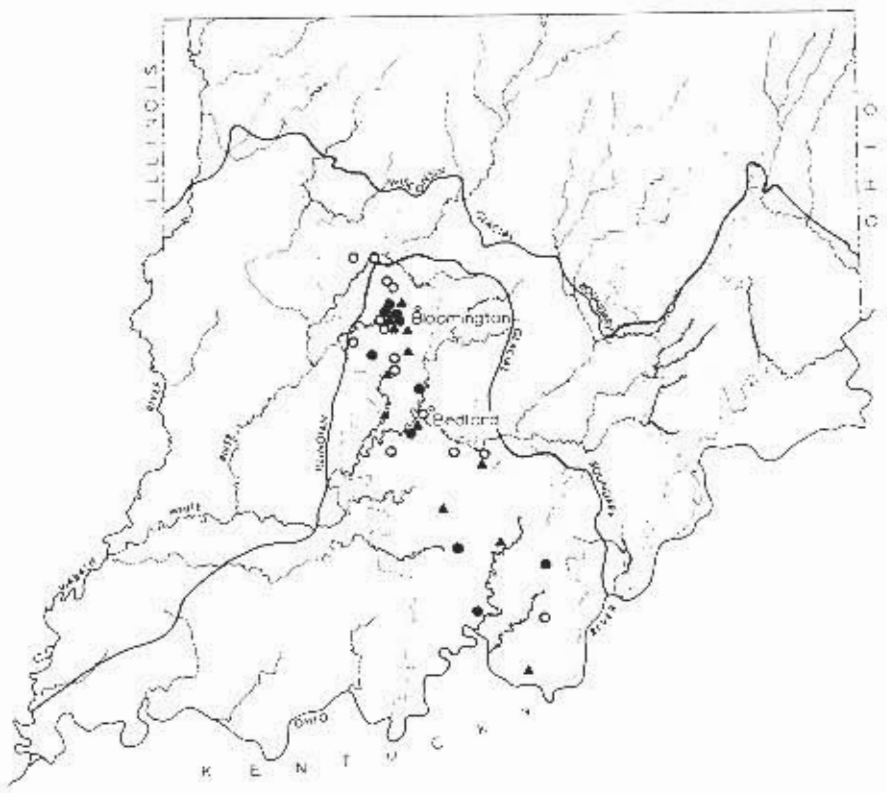

Fig. 5. Distribution map of *Sagittocythere barri* (closed circles) and *Donnalsonsythere donnaldsonensis* (open circles) in southern Indiana caves. Closed triangles represent caves from which both species were collected.

laevis. *Donnaldsoncythere donnaldsonensis* was collected from 27 caves in eight counties (fig. 5) and was associated with *O. i. inermis*, *O. i. testii* and *C. (E.) laevis*. *Uncinocythere xania* is known to occur in 22 caves in seven counties (fig. 6) and has been found in association with *O. i. inermis*, *O. i. testii* and *C. (E.) laevis*. These same three species of crayfishes plus *O. immunis* were hosts to *Dactylocythere susanae* in 22 caves in six counties (fig. 6).

Few observations have been reported on the ecology of these animals. As mentioned previously, Marshall (1903) erroneously described them as parasites and haemophages. Hobbs, Holt and Walton (1967) stated that the animals apparently feed on small particles of detritus encrusting the exoskeleton of the host. They appear to be limited to those anatomical regions of the crayfish where there are setae to which they cling or grooves in which they can obtain support. The crayfish apparently gains benefit from the association only in having its own "house cleaner". Hobbs III (1968, 1969) discussed host specificity in entocytherines and its

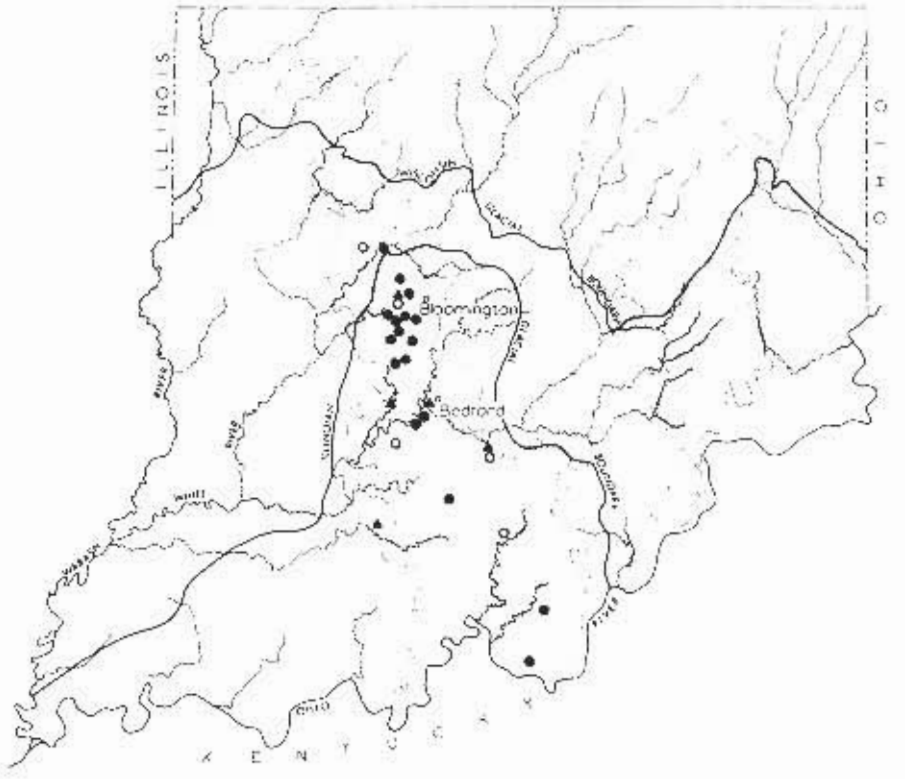

Fig. 6. Distribution map of *Uncinocythere xania* (closed triangles) and *Dactylocythere susanae* (open circles) in southern Indiana caves. Closed circles are localities from which both species were collected.

Table 1. List of caves visited during study or caves from which crayfishes and ostracods are reported. Caves supporting populations of crayfishes and ostracods are so indicated: + = crayfish species present based on author's observations or confirmation; * = crayfish species reported but not confirmed by author; 0 = ostracods associated with *O. i. inermis*; T = ostracods associated with *O. i. testii*; P = ostracods associated with *O. p. propinquus*; M = ostracods associated with O. immunis, X = ostracods associated with *C. laevis*. No ostracods were found to exhibit the few species of *O. sloanni* so this species is omitted from the Table. The column headed "Crayfishes" represents reports from the literature where no precise species determinations were made.

	CRAYFISHES						OSTRACODS			
CAVES	*Orconectes inermis inermis*	*Orconectes inermis testii*	*Orconectes immunis*	*Orconectes propinquus*	*Cambarus (E.) laevis*	"Crayfish"	*Sagittocythere barri*	*Donnaldsoncythere donnaldsonensis*	*Uncinocythere xania*	*Dactylocythere susanae*
CLARK CO.										
Thomas Crew's					*					
CRAWFORD CO.										
Archibald	+									
B-B Hole	*					*				
Carter Byrnes	*									
Christmas Pit						*				
Everton	+									
Marengo	+									
Sibert's Well	+						O*			
Wildcat	+									
Wyandotte	+									
DECATUR CO.										
Decatur										
Dud										
Hole										

	CRAYFISHES						OSTRACODS			
	Orconectes inermis inermis	*Orconectes inermis testii*	*Orconectes immunis*	*Orconectes propinquus*	*Cambarus (E.) laevis*	"Crayfish"	*Sagittocythere barri*	*Donnaldsoncythere donnaldsonensis*	*Uncinocythere xania*	*Dactylocythere susanae*
Horsethief										
Penther										
Scripture										
DUBOIS CO.										
Vowell					+				X	
GREENE CO.										
Batey's					+					
John's					+					
Ray's		*			+			X		
Sexton Sp.	+						O			
HARRISON CO.										
Baker Hollow	*									
Binkley's	*									
Boone's Mill	+				+		O	X	X	X
Borden's Pit										
Bradford	+						O*			
Cave near Mauckport	*									
King's	+				+			X	X	X
Parker Pit										
Rhoade's	+									
Wallier's	*									
Widewater	*									
JEFFERSON CO.										
Caves near Madison	*									
JENNINGS CO.										
Cave					+			X		

	CRAYFISHES						OSTRACODS			
	Orconectes inermis inermis	*Orconectes inermis testii*	*Orconectes immunis*	*Orconectes propinquus*	*Cambarus (F.) laevis*	"Crayfish"	*Sagittocythere barri*	*Donnaldsoncythere donnaldsonensis*	*Uncinocythere xanla*	*Dactylocythere susanae*
LAWRENCE CO.										
Avoca Sp.	+				+					
Bedford	*									
Blue Sp.	+		+		+		O,X		X	X
Cedar Pit										
Christmas Pit	+				+					
Connerly's	+				+			X		X
Crying	+									
Donaldson's	+				+			O		
Donnehue's	+				+			O,X	X	
Down's	*				*					
Eversole						*				
4-H										
4-Pit					+			X	X	X
Gollum's Crypt										
Gory Hole										
Gyger Bend I	*				+					
Hamer's	*					*				
Harrison	+				+					
Hugh's Christian Annex	*									
Ilco	+						O			
Indian Pipe										
Kern's Pit	*									
Linden Pit										
Lost Lamp Pit										
Mitchell	*									
Mitchell Crushed Stone Co.					*					

	CRAYFISHES						OSTRACODS			
	Orconectes inermis inermis	*Orconectes inermis testii*	*Orconectes immunis*	*Orconectes propinquus*	*Cambarus (E.) laevis*	"Crayfish"	*Sagittocythere barri*	*Donnaldsoncythere donnaldsonensis*	*Uncinocythere xania*	*Dactylocythere susanae*
Pless	+		+	+	+		O	O,X	X,O,P	X,M
Pless Cave Annex										
Popcorn Sp.	+				+		O	X	X	X
Post										
Rainey										
Ray Sp.					+					
Rock Lick					+					
Shiloh	+				+					
Siebolt Quarry Pit										
Storm's Pit										
Sullivan	+				+					
Sweet Potato										
Telephone Pit										
Valley Cathedral										
Wagoner	+				+		O	O	O	
MARTIN CO.										
Chapman Rizer	*									
Garbage Dump Pit										
MONROE CO.										
Abbott Pit										
Abbott Pit II					+			X		
Anderson Pit						*				
Bauer's					+					
Bone										
Brinegar's		*			*					
Broken Axe										
Buckner's		+			+		T	X	X	X

	CRAYFISHES					OSTRACODS			
	Orconectes inermis inermis	*Orconectes inermis testii*	*Orconectes immunis*	*Orconectes propinquus*	*Cambarus (E.) laevis*	"Crayfish"	*Sagittocythere barri*	*Donnaldsoncythere donnaldsonensis*	*Uncinocythere xania*	*Dactylocythere susanae*
Carmichael	+			+		T	T,X	T,X	T	
Coon's										
Duncan's Pit										
Dupe's Folley										
Eller's	+					T				
Freeman's Pit										
Goode's	+			+				X	X	
Green Eye I Pit										
Green Eye II Pit										
Grotto										
Hell's Kitchen Pit										
Hendrick's	+					T				
Hymen Hole										
Matlock's	*			+						
Mayfield's	+			+		T	X	X	X	
May's	+			+		T	X	X	X	
Oliver Pit										
Oliver Sp.				+						
Ord's				+			X	X		
Parrott Sp.				+						
Queen Blair				+			X	X	X	
Ranard School	*									
Reeve's	+			+						
Reeve's School				+			X	X	X	
Rice										
Richwine										
Salamander	+			+		T	T		T	
Saltpeter	+					T				

	CRAYFISHES						OSTRACODS			
	Orconectes inermis inermis	*Orconectes inermis testii*	*Orconectes immunis*	*Orconectes propinquus*	*Cambarus (E.) laevis*	"Crayfish"	*Sagittocythere barri*	*Donnaldsoncythere donnaldsonensis*	*Uncinocythere xania*	*Dactylocythere susanae*
Shaft		+			+					
Shirley Sp.										
Smith Sp.		*								
Strong's		*				*				
Studebaker Pit										
Teague Pit										
Trap Door										
Truitt's		+								
Turtle						▪				
Voorhie's Vat					+			X		
Wayne's		+			+		T		X	X
Weaver's Sp.					+				X	X
ORANGE CO.										
Aldrin						*				
Blackman					*	*				
Boiling Sp.										
Elrod										
Hudelson	*				*					
Murray Sp.	+				+		O	X	X	X
Orleans	*									
Paoli	*									
Riverside						*				
Stroud						*				
Wells	*									
Wesley Chapel	*									
Wildcat	+						O			
OWEN CO.										
Christmore Sp.					+			X	X	X
Lost Boy					+					
Porter's		▪								

	CRAYFISHES						OSTRACODS			
	Orconectes inermis inermis	*Orconectes inermis testii*	*Orconectes immunis*	*Orconectes propinquus*	*Cambarus (E.) laevis*	"Crayfish"	*Sagittocythere barri*	*Donnaldsoncythere donnaldsonensis*	*Uncinocythere xania*	*Dactylocythere susanae*
Texas Bear					+			X		X
Wolf										
WASHINGTON CO.										
Beck's Mill	*					*				
Endless	+				+		O	X		X
Fredericksburg	+				+		O	O,X		O,X
Glen Freed						*				
Greene					+			X	X	
Joy										
Lamplighter	*									
Nicholson										
River	+				+					
Russel										
Trappers	+				+					
Zinc					+					
Sinking Cr. Syst.	*									
Stillhouse Syst.	*									

relationship to ecological requirements, Walton and Hobbs (1971) studied the microhabitats of certain species on their crayfish hosts. Young (1971) presented the results of an ecological study conducted on *Ankylocythere sinuosa*, commensal on *Procambarus (Girardiella) simulans simulans* (Faxon, 1884).

Cave-dwelling entocytherines have received no attention beyond the recognition of species and their ranges. The first description of a spelean entocytherine was that of Klie (1931), previously mentioned. Subsequently, Hart and Hobbs (1961) described *Entocythere barri* from Cave Springs Cave, Alabama. In Hart's revision of the family (1962), this species was placed in the genus *Sagittocythere*. Later, Hart and Hobbs (1961), Hart and Hart (1966), Hobbs and Hart (1966), Hobbs and Walton (1968) and Hobbs III (1971) described ostracods associated with cave-

dwelling crayfishes. The only contributions not primarily taxonomic, zoogeographic, morphologic or developmental are those of Hobbs, Holt and Walton (1967), Baker (1969), Young (1971) and Walton and Hobbs (1971). None of these studies treats cave-dwelling organisms.

Table 1 sumarizes data obtained from this study. Caves visited but from which no crayfishes or ostracods were observed are also included. Localities and species marked with an asterisk indicate that a particular species of crayfish was *reported* from the caves indicated. Many of these reports were made by spelunkers having little or no biospeleological training, and others taken from the literature are based on collections no longer available for verification.

Tubes 2 – 4 present data of crayfishes and ostracods from caves within the State (biunguis female = female in penultimate molt stage; triunguis female - female in final molt stage).

DISCUSSION

From the data presented it becomes evident that considerable field work is required before a full understanding of distribution and host-commensal relationships is attained. Of the five species of crayfishes known from Indiana caves, *Cambarus (Erebicambarus) laevis* appears to have the broadest geographic distribution. Surface populations of this species occur sympatrically (syntopically?), thus enabling widespread distribution and genetic exchange of epigean and hypogean populations. The troglobitic crayfish populations of *Orconectes inermis* are predominately intergrading populations of the two geographic races, *O. inermis inermis* and *O. inermis testii*. The extreme morphological variations exhibited by these troglobitic populations within the State indicate a continuous exchange of genes within the "gene pool" of the species. Perhaps surprisingly, this dictates population interactions across (beneath) the Ohio River into Kentucky. Thus, even though surface populations of crayfishes or other forms may be geographically isolated, this gives credence to the theory that deep lying aquifers exist as pathways for dispersal of the subterranean fauna.

Verbal reports of "blind crayfishes" from the eastern karst area occasionally are received; however these have not been substantiated. This is an area which has received little work and until the faunas of more caves are carefully surveyed, one can only speculate that since this limestone unit is not contiguous with "troglobitic crayfish-bearing" areas, albinistic members of the genus *Orconectes* would not be expected to be present.

The three remaining species of crayfishes (*O. immunis, O. propinquus* and *O. sloanii*) are rarely observed in caves and thus are classified as trogloxenic or accidental cave forms. Since they seem to be restricted to parts of the streams near entrances, they probably have little effect upon cave ecosystems except in these areas.

Observing Table 1, certain relationships between hosts and commensals can be interpreted. Ninety-six percent of the populations of *Sagittocythere barri* examined

Table 2. Population structure of ostracods infesting 27 individuals of *Orconectes inermis inermis* in southern Indiana caves; ♀B = Biunguis female, ♀T = Triunguis female, J = Juvenile.

CAVE	HOST		NUMBER OF OSTRACODS																					
			S. barri				*Dn. donnaldsonensis*				*Un. xania*				*Dt. susanae*				Unidentified	Date	Total
	Sex	Carapace Length (mm)	♂	♀B	♀T	J	♂	♀B	♀T	J	♂	♀B	♀T	J	♂	♀B	♀T	J	juveniles		
Blue Spring	♂I	20.5			1															25/10/69	1
Boone's Mill	♂I	25.1	7	3	5	16														12/03/72	31
Donnehue	♂I	21.9					2	1		1										25/10/69	4
Endless	♂II	22.2			1	3														28/02/70	4
Fredericksburg	♂I	?	10	7	3	11	1	2								1				27/08/70	35
Fredericksburg	♀	?	16	6	13	19														27/08/70	54
Ilco	♀	32.5	5	4	3	7														17/07/71	19
Murray Spring	♂I	31.4	10	10	5	13														26/04/72	38
Pless	♀	23.6			1	3				2										10/02/73	7
Pless	♂I	23.1	7	9	4	18	1	1												10/02/73	40
Pless	♂II	18.7			1			1												10/02/73	2
Pless	♂J	15.3	2	1	1				1											18/09/72	5
Pless	♂II	23.0	1	1	1	10														18/09/72	13
Pless	♂II	29.8		1	1	4														18/09/72	6
Pless	♀	26.0	4	1	4	13	2	1	1	2									7	18/09/72	34
Pless	♀	19.3	3	2	1	5														18/09/72	11
Pless	♂II	20.4			1	2	1			1										18/09/72	5
Pless	♂II	20.5	3	2	1	5														18/09/72	11
Pless	♀	19.2	3	3	2	11						2		11						18/09/72	32
Pless	♂I	28.7	1		6	11														18/09/72	18
Pless	♀	25.0	9		2						1									18/09/72	12
Pless	♂II	22.8	2		1	2														18/09/72	5
Pless	♂I	26.0	1			1														18/09/72	2
Popcorn Spring	♂I	27.8			2	17														06/12/70	19
Sexton Spring	♂I	26.0	11	9	7	24														29/11/70	51
Wagoner	♀	22.6	1		1	3			1				1						4	21/02/70	11
Wildcat	♂I	22.5	5		6	7														28/02/71	18
Wildcat	♀	33.4	1	6	2	29														28/02/71	38
Totals			102	65	75	234	8	6	3	6	1	2	1	11	1				11		526
Grand Totals			476				23				15				1				11		526
% of Grand Totals			91.4%				4.4%				2,8%				0,2%				2.1%		

Table 3. Population structure of ostracods infesting 12 individual *Orconectes inermis testii* in southern Indiana caves; ♀B = Biunguis female, ♀T = Triunguis female, J = Juvenile.

CAVE	HOST		NUMBER OF OSTRACODS																			
			S. barri				*Dn. donnaldsonensis*				*Un. xania*				*Dt. susanae*				Unidentified	Date	Total
	Sex	Carapace Length (mm)	♂	♀B	♀T	J	♂	♀B	♀T	J	♂	♀B	♀T	J	♂	♀B	♀T	J	juveniles		
Buckner's	♂II	20.5	6		3	4														?/04/72	13
Carmichael	♂I	?	3	36	3	20			1				2		3				15	04/10/69	83
Eller's	♂I	25.2	4	4		7														21/10/69	15
Eller's	♀	19.2	1	1		5														21/10/69	7
Hendrick's	♀	29.2	6	2	2	31														02/10/72	41
Mayfield's	♂II	22.9	1	5	1	1														20/09/69	8
May's	♀	19.5	1		2	9														26/09/69	12
Salamander	♂I	25.1	5	4	4	3	1	1	1											08/10/69	19
Salamander	♀	18.2		2		2		1								1	1		1	08/10/69	8
Saltpeter	♂II	19.8			3	3														03/07/72	6
Wayne's	♀	18.3	1		7	2														07/02/71	10
Totals			28	54	25	87	1	2	2				2		4	1			16		222
Grand Totals					194				5				2				5		16		222
% of Grand Totals					87.3%				2.2%				0.9%				2.2%		7.2%		

Table 4. Population structure of ostracods infesting 36 individual *Cambarus (Erebicambarus) laevis* in Southern Indiana caves; ♀B = Biunguis female, ♀T = Triunguis female, J = Juvenile.

CAVE	HOST		NUMBER OF OSTRACODS																			
			S. barri				*Dn. donnaldsonensis*				*Un. xania*				*Dt. susanae*				Unidentified	Date	Total
	Sex	Carapace Length (mm)	♂	♀B	♀T	J	♂	♀B	♀T	J	♂	♀B	♀T	J	♂	♀B	♀T	J	juveniles		
Abbot Pit II	♀	31.2					2	1	6	7										30/10/70	16
Blue Spring	♂I	51.3	1		2	4					1	2	1				1		27	28/02/70	39
Boone's Mill	♀	?					2	1	4		1	2	1		4	2	3		26	12/03/72	46
Buckner's	♀	37.3					1	1	1		1	1			2				14	21/10/69	21
Carmichael	♂II	38.2					2				3		5						16	04/10/69	26
Cave	♂II	?					4	1	2										3	29/07/72	10
Connerly	♀	?					2		1						2	2	2		5	25/10/69	14
Connerly	♂II						2	6	4						1		4		7	25/09/70	24
Donnehue's	♂II	33.9					3		3		5	1	2						19	25/10/69	33
Endless	♂II	22.2					3	3	1							1	1		9	28/02/70	18
4-Pit	♂II	?						1	1		5		1		2		2		13	?/06/71	25
Fredericksburg	♀	?					2	1							8	3	2		16	27/08/70	32
Goode's	♀	32.5									1	1	1		1		3		11	03/10/69	18
Greene	♀	?						1	2		2		2						17	14/07/72	24
King's	♂II	35.4					2	4	1		1				3				14	11/06/70	25
Mayfield's	♂II	28.2					1				1				2		3		9	20/09/69	16
May's	♀	36.0					2	3	3		1	1			4		8		12	26/09/69	34
Murray Spring	♂II	48.5					1				1								23	28/02/70	25
Murray Spring	♂I	56.5					2									1	7		20	28/02/70	30
Ord's	♂II	25.9					1	1	1		1								16	10/06/70	20
Pless	♀	35.8					3	17	5		4		4						16	10/02/73	49
Pless	♂I	42.4						6	1		5	1							28	18/10/72	41
Pless	♂II	41.2					1				1								23	18/10/72	25

Pless	♂II	26.2						4	2		2						3	18/10/72	11
Pless	♂II	45.2							1		1			4		5	18	18/10/72	29
Popcorn Sp.	♀	44.5					2	1			5	2		4	1		53	06/12/70	68
Queen Blair	♂I	40.1						1	1		1			4		6	14	18/10/69	27
Ray's	♂II	40.1					1	5	1	8								04/07/70	15
Reeve's School	♂II	32.0					2	5	5		2			1	2	1	22	01/10/69	40
Texas Bear	♂J	14.5					3	1	1							1	9	18/07/70	15
Voorhie's Vat	♀	29.6					1	2	2	10								11/12/70	15
Vowell	♀	?									4	3	1	9				17/09/72	17
Buckner's	♂II	20.5	6		3	4												?/04/72	13
Carmichael	♂I	?	3	36	3	20			1				2		3		15	04/10/69	83
Eller's	♂I	25.2	4	4		7												21/10/69	15
Eller's	♀	19.2	1	1		5												21/10/69	7
Hendrick's	♀	29.2	6	2	2	31												02/10/72	41
Mayfield's	♂II	22.9	1	5	1	1												20/09/69	8
May's	♀	19.5	1		2	9												26/09/69	12
Salamander	♂I	25.1	5	4	4	3	1	1	1									08/10/69	19
Salamander	♀	18.2		2		2		1							1	1	1	08/10/69	8
Saltpeter	♂II	19.8			3	3												03/07/72	6
Wayne's	♀	18.3	1		7	2												07/02/71	10
Totals			28	54	25	87	1	2	2				2		4	1	16		222
Grand Totals				194				5				2			5		16		222
% of Grand Totals				87.3%				2.2%				0.9%			2.2%		7.2%		

was found to infest troglobitic crayfishes (*O. i. inermis* and *O. i. testii*) in 22 of the caves sampled, indicating a high degree of preference for these hosts. Only a single specimen of *C. (E.) laevis* from Blue Spring Cave (Lawrence County) harbored *S. barri*. These observations suggest that this ostracod has been associated with the troglobitic crayfishes for a long period of time, and that adaptations to the spelean mode of existence could well have progressed in the host and commensal concurrently. In Alabama, Kentucky and Tennessee, *S. barri* is associated with three additional troglobitic species, *O. australis*, *O. incomptus* and *O. pellucidus* as well as with the troglophile *C. (E.) tenebrosus* Hay, 1902. Thus if Hobbs and Barr (1972) are correct in their hypothesis of the independent allopatric origin of the four troglobitic crayfishes, one must conclude one of two possibilities. Either the ostracod infesting these crayfishes (except for loss of eyes) has remained virtually unchanged since their hosts introduced them to a spelean existence *or* that it became differentiated on one of the four troglobites and was transported from one cave system to another either on the troglobites or on the two troglophilic crayfishes.

Donnaldsonecythere donnaldsonensis was associated with *C. (E.) laevis* in 77% of the crayfish populations examined, again indicating a host preference by ostracods. Using these data, one may postulate something about host interactions. The troglobitic crayfishes are more acutely aware of chemical and physical changes that occur in the water. If an individual of *C. (E.) laevis* were to die, this would be a ready food source for any cavernicole. The more highly adapted forms would be first to locate the crayfish and begin to feed. The ostracods, in all probability would not die with the dead host, and thus as the troglobitic crayfish fed on the dead animal, ostracods would come in contact with its gnathal appendages, and thus would infest the feeding animal. Not only is the troglobitic *Orconectes* very sensitive to food but also is highly aware of the presence of other living crayfishes. Hence the spindly cave form avoids contacts with the more robust *Cambarus* and is not likely often preyed upon by the latter. Thus, its more acute senses allow *Orconectes inermis* not only to avoid contacts and be eaten (thus transferring ostracods to another host) but also enables it to find food more readily (becoming infested by these ostracods living on the crayfish upon which it feeds). Such possibilities are consistent with the observations that in the Indiana caves few *S. barri* are found except on *Orconectes inermis* and they also offer an explanation as to why specimens of *Dn. donnaldsonensis* are found on the troglobitic crayfishes in so many of the cave samples (23%).

In this survey, *Uncinocythere xania* infested only *C. (E.) laevis*, occurring in 86% of the populations of this host examined; and 82% of the infestations of *Dactylocythere susanae* were restricted to this troglophilic crayfish. These figures suggest a near-host-specific relationship between these symbionts and *C. (E.) laevis*.

To substantiate these conclusions, Tables 2 – 4 allow for a more precise evaluation of data. Of the 1674 individual ostracods recovered (slides containing specimens from Donnaldson's and Cristmore Spring Caves were damaged and thus data are not included in Tables 2 – 4) from cave crayfishes throughout southern Indiana, 670 specimens of *S. barri* (40%) were found associated with *O. i. inermis* and *O. i. testii* and only 7(0,4%) with *C. (E.) laevis*. Tables 2 – 4 show that 91, 87 and

0,8% of the ostracods on *O. i. inermis*, *O. i. testii* and *C. (E.) laevis*, respectively, are *S. barri*. These data further support the idea that this ostracod is predominantly restricted to the troglobitic crayfishes *O.i. inermis* and *O.i. testii* (and intergrades) in Indiana, *Sagittocythere barri* has probably been associated with the troglobitic species of *Orconectes* since their initial advent into caves. Like their crayfish hosts, they lack eyes. This species is relatively rare on other crayfishes and when present, the populations are small.

S. barri has never been recovered from any pigmented crayfish in Indiana other than *C. (E.) laevis*.

Of the 214 *Donnaldsoncythere donnaldsonensis* (12,7% of all the ostracods) recovered from *C. (E.) laevis*, *O. i. inermis* and *O. i. testii*, only 23 (10,7%) infested *O. i. inermis* and 5(2,4%) *O. i. testii*. This distribution demonstrates a definite host-preference of *Dn. donnaldsonensis* for *C. (E.) laevis* (88%).

Uncinocythere xania was associated with *O. i. inermis*, *O. i. testii* and *C. (E.) laevis*. Of the 114 specimens recovered (6,9% of the total number) 15, 2, and 97, respectively, came from these species, showing a strong preference for *C. (E.) laevis*. In surface water this species is commonly associated with *C. (E.) laevis* and *O. propinquus*. The surface streams from which the crayfishes were collected had predominately gravel or bedrock substrates with relatively steep gradients and were fed by springs. It is believed that the distribution of *Un. xania*, although certainly controlled by that of its hosts [*O. propinquus* and *C. (E.) laevis* in surface waters and the latter within subterranean streams], is also limited, at least to some extent, by ecological specificity (cool, aerated streams).

For *Dactylocythere susanae*, 123, 1 and 5 specimens, respectively, were recovered from *C. (E.) laevis*, *O. i. inermis* and *O. i. testii*. In addition, 12 specimens were obtained from *O. immunis* from Pless Cave. Approximately 95% of the specimens obtained from caves were recovered from *C. (E.) laevis*, indicating another near-specific relationship there between ostracod and crayfish host. In Indiana, this species also infests *C. (E.) laevis* in surface streams.

Juvenile ostracods occurring in the subterranean waters of Indiana cannot be identified to species or even to genus, except those of *S. barri* in which eyes, if present, lack pigment. When the adults of only one species infests a host, presumably the juveniles occurring on it are members of this species, but when more than one species is present, the juveniles of only *S. barri* can be recognized. Thus, 513 juvenile specimens (31% of those examined) associated with *C. (E.) laevis* could not be identified. This increases the difficulty of detecting any specific or dominant ostracod-host relationship (Tables 2-4).

The mean numbers of ostracods found in association with individual adult crayfishes (calculated from Tables 2 – 4) demonstrate that *C. (E.) laevis* is the most heavily infested of the cave crayfishes, 26.46 ± 3.70 (95% confidence limits) ostracods per individual crayfish. *O. i. inermis* supports a mean number of 18.78 (± 3.59) and *O. i. testii* 20.18 (± 13.58). Occasional individuals were examined that hosted no ostracods. In all instances thy were either very small (less than 15 mm carapace length) or had recently molted.

Walton and Hobbs (1971) reported much larger populations of entocytherids

associated with epigean crayfishes [as large as 119±17.5 individuals per female *Cambarus (Cambarus) bartoni bartonii* (Fabricus, 1798)]. The differences in ostracod population densities between surface and cave crayfishes may be species-specific in nature, or due to host size differences (surface crayfishes generally larger), may be a result of environmental pressures, or may be due to some unknown intrinsic agent(s). Considerable research is required before an understanding of the factors controlling entocytherid population structure and density is attained.

SUMMARY

Six species and subspecies of crayfishes and four species of entocytherid ostracods are known to inhabit the subterranean streams of southern Indiana. *Cambarus (E.) laevis* (troglophile) appears to be the most widely distributed crayfish and occurs in both karst areas within the State. The troglobite, *Orconectes inermis* (2 subspecies), is restricted to the larger karst area in solution cavities of Mississippian carbonate rocks. The remaining crayfishes, *Orconectes immunis*, *Orconectes propinquus* and *Orconectes sloanii*, are not common inhabitants of cave waters and are probably trogloxenes.

All of the crayfishes except *O. sloanii* were found to host at least one species of ostracod. From data presented, *Sagittocythere barri* might be expected to be found commonly in association with *Orconectes inermis*. *Donnaldsoncythere donnaldsonensis*, *Uncinocythere xania* and *Dactylocythere susanae*, however, are more commonly associated with *C. (E.) laevis*, indicating a near host-specific relationship among these taxa. Whether these are hostspecific associations or ones imposed by certain ecological parameters will require additional investigations.

Although a fair understanding of the distribution of these crustaceans in the larger, Mississippian limestone belt has been obtained, additional field work on the perimeter of the spelean ranges of the several species will probably prove productive. Furthermore, considerable cave exploration and biospeleological surveys are needed in the Silurian-Devonian limestones of southeast Indiana before our knowledge of these crayfishes, entocytherids and other cave-dwelling species approaches that for the Mississippian karst of the State.

RESUME

Six espèces et sous-espèces d'écrevisses et quatre espèces d'Ostracodes Entocythérides sont connues pour habiter les rivières souterraines du Sud de l'Indiana. *Cambarus* (E.) *laevis* (troglophile) est l'écrevisse qui semble avoir la plus vaste répartition: on la rencontre dans les deux régions karstiques de l'Etat. La répartition du troglobie *Orconectes inermis* (2 sous-espèces) se limite aux grottes creusées dans le calcaire Mississipien de la plus grande région karstique. Les autres écrevisses, *Orconectes immunis*, *Orconectes propinquus* et *Orconectes sloanii*, qui ne vivent pas dans les eaux souterraines, sont probablement trogloxènes.

Toutes les écrevisses, sauf *O. sloanii*, sont les hôtes d'au moins une espèce d'Ostracode commensal. D'après les données, on pouvait s'attendre à trouver *Sagittocythere barri* généralement associé à *Orconectes inermis*. Toutefois, *Donnaldsoncythere donnaldsonensis*, *Uncinocythere xania* et *Dactylocythere susanae* sont souvent associés à *C.* (E.) *laevis*, ce qui montre une étroite relation hôte-spécifique dans ces groupes. Il faudra faire des recherches supplémentaires pour déterminer si de telles associations sont du type hôte-spécifique, ou si elles sont imposées par certains paramètres écologiques.

Bien que l'on soit arrivé à une bonne compréhension de la répartition de ces crustacés dans la plus grande zone de calcaire Mississipien, un travail de terrain supplémentaire sur les nombreuses espèces du pourtour des régions caverneuses sera probablement fructueux. En outre, l'exploration des grottes et les études biospéléologiques des calcaires du Silurien-Dévonien du Sud-Est de l'Indiana s'avèrent nécessaires, avant que notre connaissance de ces écrevisses, entocythérides et autres espèces cavernicoles, n'atteigne celle que nous avons du karst Mississipien de cet Etat.

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