DISTRIBUTION AND EVOLUTION OF FLORIDA'S TROGLOBITIC CRAYFISHES

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ABSTRACT: The current knowledge of Florida's troglobitic crayfish fauna is discussed, interpretations of distributional and ecological patterns are reviewed, and an explanation of their evolutionary history is attempted.

These crayfishes are restricted to certain geological formations that have light to nonexistent clastic overburdens. Areas with moderate to heavy accumulations over the carbonate rocks lack these crustaceans. The Crystal River Formation, a group of highly soluble Eocene limestones, is the most important geological element influencing the distribution of most Florida cave-dwelling crayfishes. Members of the *Procambarus lucifugus* complex (with the possible exception of an undescribed species from Lake County), *Procambarus pallidus*, *Troglocambarus maclanei*, and *Cambarus cryptodytes*, are apparently confined to this formation. The remaining species are confined to other limestones (*Procambarus acherontis* and *Procambarus* species from Lake County in the Hawthorne Formation, *Procambarus milleri* in the Miami Oolite, *Procambarus horsti* and *Procambarus orcinus* in the St. Marks Formation).

Field observations suggest that available sources of food energy dictate which species groups inhabit particular cave systems. Species complexes that are most restricted to environments which provide large accumulations of organic detritus become ecologically and geographically isolated from other populations and exhibit increased speciation. For example, members of the *Procambarus lucifugus* complex seem to have demanding energy budgets and occur only in localized karst areas exhibiting mature features and high energy input. Dependency on constant energy supplies provided by large sinkhole entrances and/or bat roosts probably limits their dispersal ability. In contrast, members of the *Procambarus pallidus* complex inhabit systems with limited energy inputs, such as springs and sinkholes with small openings. *Troglocambarus maclanei* occurs syntopically with members of the *Procambarus lucifugus* and *Procambarus pallidus* complexes and may be capable of interstital movements from one cave to another. This may help to explain its extensive distribution.

SUMARIO: El corriente conocimiento de la fauna del ástaco troglobitico de Florida es tratado; las interpretaciones de los modelos ecológicos y de distribución son revisados, y se intenta dar una explicación de su historia evolutiva.

Estos ástacos están restringidos a algunas formaciones geológicas que son muy poco o nada clásticas. Las áreas con acumulaciones moderadas a pesadas sobre las rocas carbónicas carecen de estos ástacos. La formación de Crystal River, un grupo de piedras calizas del Eoceno, es el elemento geológico más importante que influye en la distribución de la mayoriá de los ástacos habitantes de las cuevas en Florida. Los miembros del complejo de *Procambarus lucifugus* (con la posible excepción de una especie que no está descrita para el Lago County), *Procambarus pallidus*, *Troglocambarus maclanei*, y *Cambarus cryptodytes* paracen estar confinados a ésta formación. Las especies restantes están confinadas a otras piedras calizas

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(*Procambarus acherontis* y la especie de *Procambarus* del Lago County en la formación Hawthorne; *Procambarus milleri* en el oolito de Miami, *Procambarus horsti* y *Procambarus orcinus* en la formación St. Marks).

Las observaciones de campo indican que la fuente de energía alimenticia disponible determina cuales grupos de especies viven en sistemas particulares de cuevas. Los complejos de especies más restringidas a grandes acumulaciones de detrito orgánico llegan e estar aisladas ecológica y geográficamente de las otras poblaciones y exhiben frecuente especiación. Por ejemplo, miembros del complejo *Procambarus lucifugus* parencen tener ciertas demandas de energía por lo que occurren solamente en áreas localizadas de Karst, exhibiendo estructuras maduras y gran gasto de energía. La dependéncia de un constante suplemento de energía provista por grandes entradas a hundimientos y/o perchas de murciélagos problemente limita su poder de dispersión.

En cambio, miembros del complejo de *Procambarus pallidus* habitan en sistemas con limitada energía, como manantiales y hundimientos con pequeñas aberturas. *Troglocambarus maclanei* ocurre sintópicamente con miembros de los complejos de *Procambarus lucifugus y Procambarus pallidus* y pueden moverse intersticialmente de una cueva a otra. Esto puede ayudar a explicar su extensa distribución.

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INTRODUCTION

Florida has the most diverse troglobitic crayfish fauna in the world. In this paper we will attempt to document their zoogeographic and ecological relationships and explain the reasons for the presence of this unusually rich fauna. The information presented here is based partly on existing literature, which is mostly of a taxonomic-distributional nature, and on our 17 years of field observations.

Our interest in the problems regarding the distributional patterns in Florida's troglobitic crayfishes was brought into sharp focus in 1964 while collecting *Procambarus* in northcentral Alachua County. We found that two caves, less than one kilometer apart, were inhabited by different species. These species, *Procambarus pallidus* and *P. lucifugus*, occurred in different densities, were distributed distinctly within the caves, and their populations were composed of proportionately different age classes. It is fortunate that our investigations started in these particular caves, for as our interest and area of field activities expanded we found ourselves comparing later observations to these two contrasting populations.

Through the efforts of Horton H. Hobbs, Jr., the Florida troglobitic crayfish fauna is now well known. Prior to his monumental works on Florida crayfishes in the late 1930's, only one troglobitic species, *Cam-*

barus (= *Procambarus*) *acherontis* Lonnberg, was known from the state. Between 1940 and 1942, Hobbs described five additional cave forms—*Cambarus* (= *Procambarus*) *lucifugus lucifugus*, *Cambarus* (= *Procambarus*) *lucifugus alachua*, *Cambarus* (= *Procambarus*) *pallidus*, *Troglocambarus maclanei*, and *Cambarus cryptodytes*. In 1971 and 1972, three additional cave species were described from the peninsula: *Procambarus milleri* Hobbs (1971), *Procambarus orcinus* Hobbs and Means (1972), and *Procambarus horsti* Hobbs and Means (1972). These discoveries brought about renewed interest in sinkhole and spring crayfishes. As a result, three other troglobitic species were recently discovered. Of these, *Procambarus erythrops* Relyea and Sutton (1975) and *Procambarus franzi* Hobbs and Lee (1976) are formally named; the other must await the discovery of Form I males before it can be described. In this paper we summarize previously published information, present additional data gathered by us and others, and provide an analysis of the accumulated distributional and ecological data.

ACKNOWLEDGEMENTS

Much of the information presented in this report was obtained through the generosity of others. Cavers and cave divers, particularly Paul Heinerth, Brian Houha, the late Bill Hurst, Buford Pruitt, and Paul Smith, provided invaluable observations and occasional specimens. Mr. Heinerth enthusiastically collected numerous specimens and detailed field notes from important and often dangerous cave systems. We also wish to thank: Patricia Ashton, Ray Ashton, Jon Baskin, Lea Franz, Michael Frazier, Barbara Lee, A.T. Leitheuser, and numerous other friends who assisted us in the field; land owners, particularly Mr. and Mrs. Marion Bishop of Newberry and Mr. Junior Kelly of Bell, for their hospitality while working on their properties; Thomas Scott, Bureau of Geology in Tallashassee, Florida, for well-core data and general help with local geology; Rhoda J. Bryant, Carter R. Gilbert, Bruce J. MacFadden, Fred G. Thompson, and S. David Webb, Florida State Museum, for guidance in the preparation of the manuscript; Helen S. Bates, Nancy R. Halliday, Eugene Hanfling, and M. Glen Rogers, Florida State Museum, for help in the preparation of the figures; and William Young, Altamonte Springs, and Walter Wood, U.S. Geological Survey, for data on *Procambarus acherontis*. We are grateful to John E. and Martha R. Cooper, North Carolina State Museum, for their enthusiasm and guidance of our crayfish studies. We especially thank Horton H. Hobbs, Jr., for openly sharing his ideas with us, providing identifications, and encouraging our activities from their earliest stages.

Field work was, in part, sponsored through a contract from the U.S. Fish and Wildlife Service (#SFWB 115344) to study the impact of phosphate mining on the Osceola National Forest and the upper Suwannee River. We wish to acknowledge the late Howard W. Campbell, former Chief of the Gainesville Lab, and Steven P. Christman, Project Leader, of the U.S. Fish and Wildlife Service, for their assistance and support during this phase of the project.

FLORIDA'S TROGLOBITIC CRAYFISH FAUNA

Eleven troglobitic crayfishes belonging to the genera *Cambarus*, *Procambarus*, and *Troglocambarus* are reported from the state, representing the most diverse, known troglobitic crayfish fauna. The general distribution of each species is shown in Figures 1-4. For convenience we have

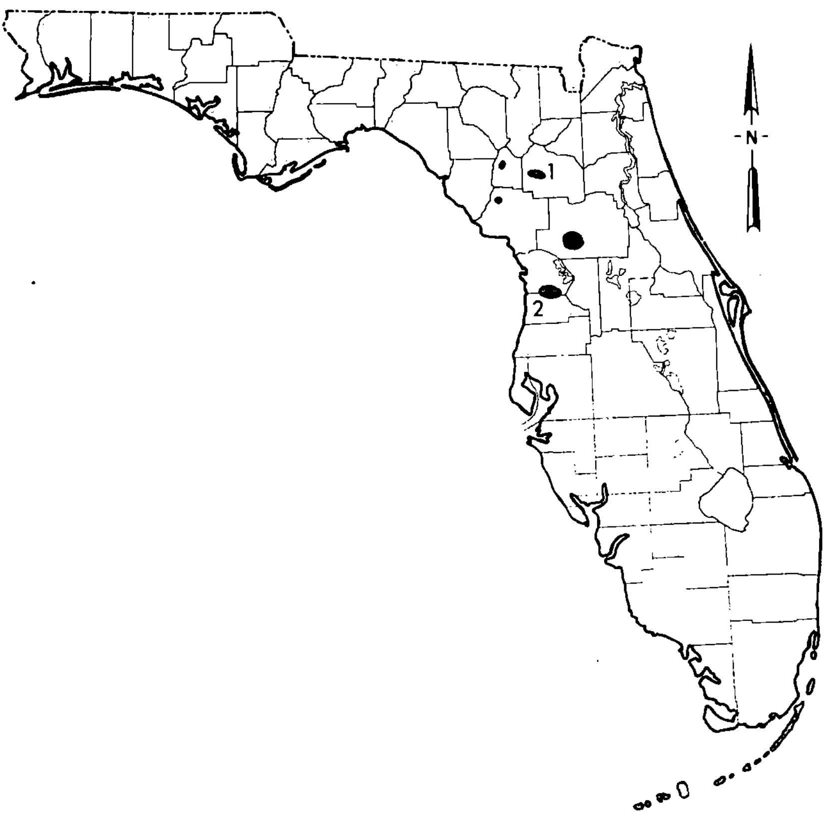

FIGURE 1. Distribution of (1) *Procambarus lucifugus alachua*, (2) *Procambarus lucifugus lucifugus*. Unnumbered populations are considered intergrades.

organized them into six groups (in part following Hobbs et al. 1977). The following list shows the species included in each group, attempts to briefly illustrate their relationships with other crayfishes, discusses their general distributions, and gives a list of additional localities not found in Hobbs et al. (1977).

GROUP A.—The genus *Cambarus* is represented by *Cambarus (Jugicambarus) cryptodytes* Hobbs. Hobbs and Barr (1960) and Hobbs et al. (1977) considered this a relict species, with its closest relatives occurring in Tennessee and the Ozark Mountain areas.

Cambarus cryptodytes is the only Florida troglobitic crayfish known to occur outside the state. This species has been observed at 15 localities in Jackson County, Florida, and one in Decatur County, Georgia (Fig. 5). Its range may extend farther northward in Georgia along the Flint River to the vicinity of Albany, Dougherty County, but no specimens are available from this area. This presumption is based on the occurrence of

FIGURE 2. Distribution of (1) *Cambarus cryptodytes*, (2) *Procambarus erythrops*, (3) *Procambarus franzi*, (4) *Procambarus* species.

the cave salamander *Haideotriton wallacei* at Albany (Carr 1939). This salamander is associated with *C. cryptodytes* at practically all known localities in Jackson and Decatur counties.

In Florida the distribution of *C. cryptodytes* lies entirely within the northern two-thirds of Jackson County in a physiographic unit, the Marianna River Valley Lowlands, of the Coastal Plain Province (as shown in Moore 1955). All populations occur within the Chipola River drainage, except the Graceville site (type locality) which is in the Holmes Creek basin of the Choctawhatchee River drainage. All but the Graceville population were found in caves; the series from Graceville was taken from an open well (Hobbs et al. 1977).

ADDITIONAL RECORDS: JACKSON COUNTY—Cave in the Woods (Sec. 22, T.5N, R.11W), Hole in Wall (Sec. 5, T.4N, R.9W), Twin Cave (Sec. 6, T.4N, R.9W).

GROUP B.—One species, *Procambarus (Lonnbergius) acherontis*

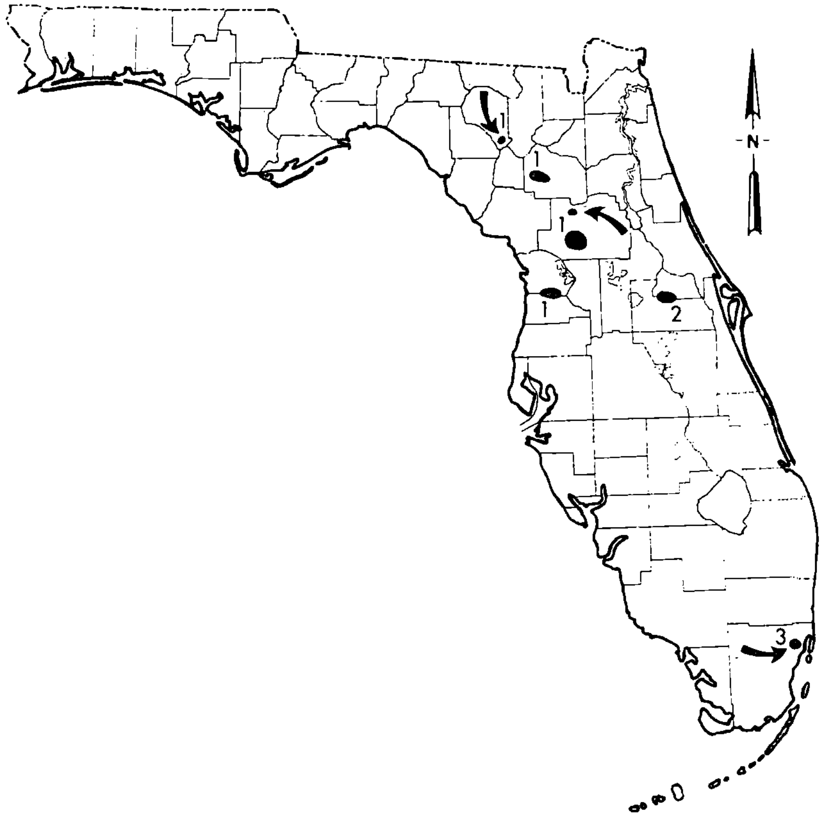

FIGURE 3. Distribution of (1) *Troglocambarus maclanei*, (2) *Procambarus acherontis*, (3) *Procambarus milleri*.

described by Lonnberg in 1894, is apparently unrelated to any other living species of the genus (Hobbs 1972; Hobbs et al. 1977). It is known from one site in Orange County and three in Seminole County. The Altamonte Springs specimen (Form II male, carapace length [CL] 24 mm) was examined by R. Franz (December 1977); however, the specimen was retained by Mr. William Young, Young's Well Drilling, Altamonte Springs, Florida.

ADDITIONAL RECORDS: ORANGE COUNTY—Long Lake well (Sec. 36, T.21S, R.28E); SEMINOLE COUNTY—Altamonte Springs well (Sec. 13, T.21S, R.29E).

GROUP C.—This group contains one species, *Procambarus (Leconticambarus) milleri* Hobbs, which is closely related to the epigean species, *Procambarus alleni* (Faxon). It is the only known troglobite in this subgenus (Hobbs, 1971) and is only recorded from the type locality, a well

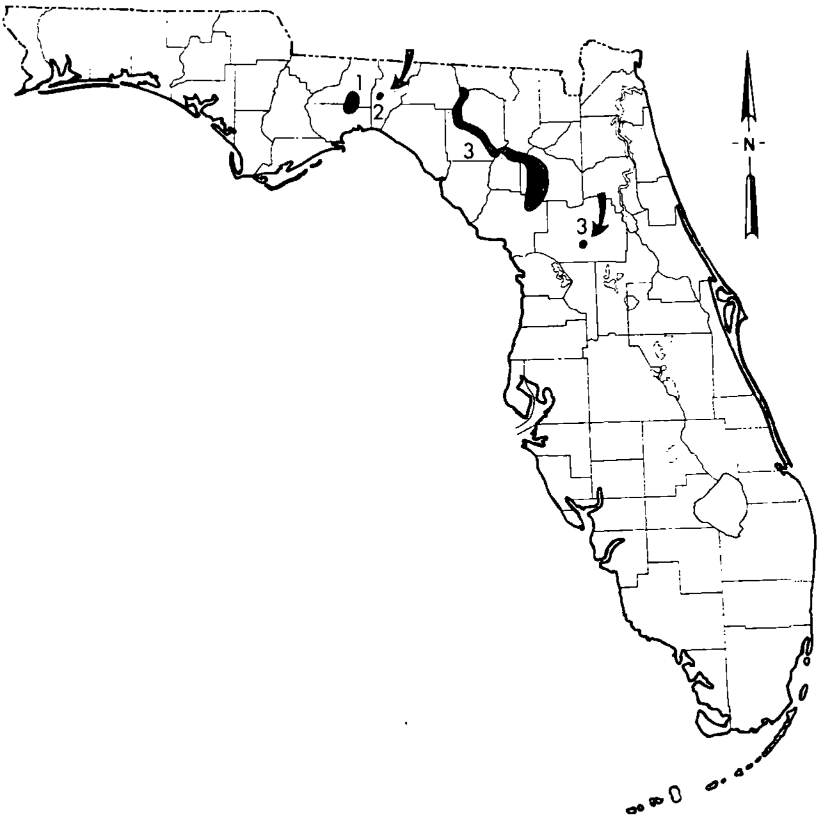

FIGURE 4. Distribution of (1) *Procambarus orcinus*, (2) *Procambarus horsti*, (3) *Procambarus pallidus*. Locality 3 with arrow is a questionable record for *Procambarus pallidus* from Eickelburger Cave, Marion County.

in Miami, Dade County. No additional information is available beyond the original description.

GROUP D.—Five members of the *P. lucifugus* complex of the subgenus *Ortmannicus* (Pictus Group, as defined by Hobbs, 1942) make up this group. Species in the complex appear closely related to *Procambarus pictus* Hobbs, a stream-inhabiting species endemic to the Black Creek drainage of northeastern Florida (Hobbs et al., 1977; Franz and Franz, 1979). The group includes *Procambarus lucifugus lucifugus* (Hobbs), *P. lucifugus alachua* (Hobbs), *P. erythrops* Relyea and Sutton, *P. franzi* Hobbs and Lee, and one undescribed species, *Procambarus* sp. (Hobbs and Lee, 1976; Hobbs et al., 1977; Hobbs, pers. comm.). The five members of the *lucifugus* complex occur mostly in small, well-defined geographical areas with no overlap in their ranges (Figs. 1-2).

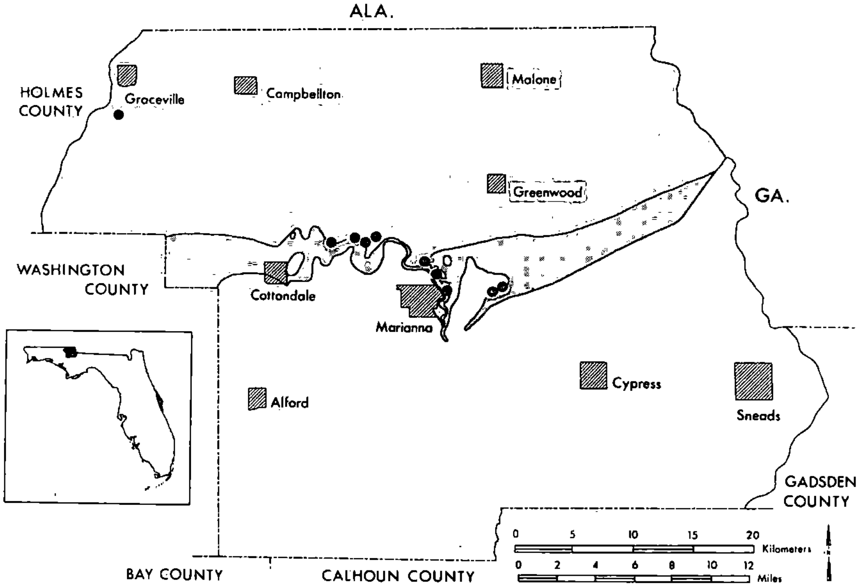

FIGURE 5. Specific records (solid circles) of *Cambarus cryptodytes* in Jackson County showing its relationship with the Marianna Limestone (darker band) and the Crystal River Formation (lighter band). Circles may represent more than one site. Geological features are from Moore (1955).

Procambarus lucifugus, as presently understood, has the largest range of any member in the *lucifugus* complex, extending from western Levy, Gilchrist, and Alachua counties, southward through Marion County to Citrus and Hernando counties. This seemingly large range, however, is not continuous, but consists of five apparently isolated populations. Populations 1 and 2, known from three caves near Bell in western Gilchrist County and one cave in Levy County, appear to be isolated from the population in adjacent Alachua County. After examination of several females, Hobbs (pers. comm.) believes them to be more similar to the nominate subspecies than to the adjacent *P. l. alachua* populations. Resolution of their affinities must await the collection of Form I males. In Alachua County population 3 (or *Procambarus lucifugus alachua*) is confined to a small area extending a few kilometers north and south of a line drawn between Gainesville and Newberry. Population 4 lies in southwestern Marion County, approximately 50 km south of the Alachua population. Hobbs (1942) suggested that this Marion population is intermediate between that in Alachua County and those in Citrus and Hernando counties. His taxonomic decision was tentative, awaiting the collection of Form I males from the intermediate area (Hobbs, 1942). Collections made by us at Sunday Sink and Ocala Caverns include many Form I males, and examination of these by Hobbs bears out his original conclusion. The intermediate population is completely allopatric and lies between *P. l. alachua* and *P. l. lucifugus*. Population 5 (or *P. l. lucifugus*) occurs in Citrus and Hernando counties, west of the Withlacoochee River and southwest of the Marion County population. Our knowledge of this population is limited. The original accounts were provided by Hobbs (1940, 1942), and we can only add that Paul Heinerth (pers. comm.) observed small crayfishes, presumably this form, in a sinkhole near Weekiwachee Springs, Hernando County.

In addition to *Procambarus lucifugus*, four other species belong to the *P. lucifugus* complex. *Procambarus erythrops* is endemic to a small area in southern Suwannee County. Only four sites have been located, although several dozen sinks in the area have been examined by us for crayfish. This population lies in a small karsted pocket north of the Santa Fe River, east of the Suwannee River, and west of the Ichetucknee Springs Run. Thus, *P. erythrops* is 14 km north of the Gilchrist population of *P. lucifugus*. *Procambarus franzi* occurs in northern Marion County between two populations of *P. lucifugus*, and Hobbs and Lee (1976) suggested a close kinship between the two species. The two known sites are separated by 7 km. Only two specimens of *Procambarus* sp. are available at this time, both from Alexander Springs, Lake County (see Relyea and Sutton, 1976, for the history of their discovery).

ADDITIONAL RECORDS: *Procambarus franzi:* MARION COUNTY—Hell Hole (Sec. 6, T.12S, R.21E). *Procambarus lucifugus:* ALACHUA COUNTY—Tusk Cave (Sec. 27, T.9S, R.18E); GILCHRIST COUNTY—Kelly Sinks (Sec. 34, T.8S, R.14E), Old Walker Farm Sinks (Sec. 35, T.8S, R.14E); LEVY COUNTY—Manatee Springs (Sec. 26, T.11S, R.13E); MARION COUNTY—Ocala Caverns (Sec. 23, T.16S, R.22E), Redding Catacombs (Sec. 20, T.16S, R.22E).

GROUP E.—Three species, also in the subgenus *Ortmannicus* of the Pictus Group, comprise this group. Hobbs et al. (1977) believed that members of the *Procambarus pallidus* complex are closely related to *Procambarus lepidodactylus* Hobbs, a stream-inhabiting species that occurs in northeastern South Carolina and adjacent North Carolina. The two species, *Procambarus horsti* Hobbs and Means and *Procambarus orcinus* Hobbs and Means, are more closely related to each other than to *Procambarus pallidus* (Hobbs and Means, 1972). The three together, however, form a natural group (Hobbs, pers. comm.).

Procambarus horsti and *Procambarus orcinus* are completely allopatric to each other and to all other troglobitic crayfishes and occur in the area south of Tallahassee (in Jefferson, Leon, and Wakulla counties). *P. orcinus* is known from five localities within the Woodville Karst, while

P. horsti has been found in only one site, Big Blue Spring, on the Wacissa River. The range of *P. pallidus* includes western Alachua County, one cave just south of the Alachua-Levy county line, in Levy County, and the karst following the Santa Fe and upper Suwannee rivers. Its range overlaps with members of the *lucifugus* complex and with *Troglocambarus maclanei* in Alachua and Suwannee counties (Fig. 6). It has also been reported from one cave in southwestern Marion County (listed by Hobbs et al., 1977), but we question this record (Fig. 4). The specimen was supposedly collected by Richard Warren in Eickelburger Cave, a site which has since been destroyed by quarrying activities (Florida Speleological Society, pers. comm.). Hobbs (pers. comm.) has recently reexamined this specimen at our request and has found it indeed to be *Procambarus pallidus*. We question the record because it is 40 km south of the closest known locality (Archer Caves), and because no additional specimens have been collected from caves close to the Eickelburger Cave locality, even though there has been extensive sampling in that area. We assume that the specimen was collected elsewhere and was inadvertently placed with the Eickelburger Cave samples.

ADDITIONAL RECORDS: *Procambarus pallidus:* ALACHUA COUNTY—Alachua Sink (Sec. 10, T.8S, R.18E), 32 Foot Cave (Sec. 18, T.10S,R.19E); GILCHRIST COUNTY—Devil's Eye Spring (Sec. 34, T.7S, R.16E), Jinnie Spring (Sec. 34, T.7S, R.16E); LAFAYETTE COUNTY—Troy Springs (Sec. 34, T.5S, R.13E); LEVY COUNTY—Archer Caves (Sec. ?, T.11S, R.17E); MADISON COUNTY—Thunderhole (Sec. 10, T.1N, R.10E); SUWANNEE COUNTY—Little River Spring (Sec. 1, T.6S, R.13E).

GROUP F.—*Troglocambarus maclanei* Hobbs is a highly specialized troglobitic species derived from the Pictus Group and thought to be closely related to *Procambarus ancylus* of the *seminolae* subgroup (Hobbs et al., 1977). *P. ancylus*, a lentic species, presently occurs in southeastern North Carolina and adjacent South Carolina (Hobbs, 1974).

Troglocambarus maclanei is known from seven localities in Alachua, Citrus, Marion, and Suwannee counties (Fig. 3). Its range spans both the Santa Fe and southern Withlacoochee River basins and completely overlaps the range of the *lucifugus* complex and a portion of the *pallidus* complex. There is no morphological evidence of differentiation.

ADDITIONAL RECORDS: MARION COUNTY—Sunday Sink (Sec. 24, T.6S, R.22E), Orange Lake Cave (Sec. 34, T.12S, R.21E).

DISTRIBUTIONAL PATTERNS

The distributional patterns of Florida troglobitic crayfishes have been

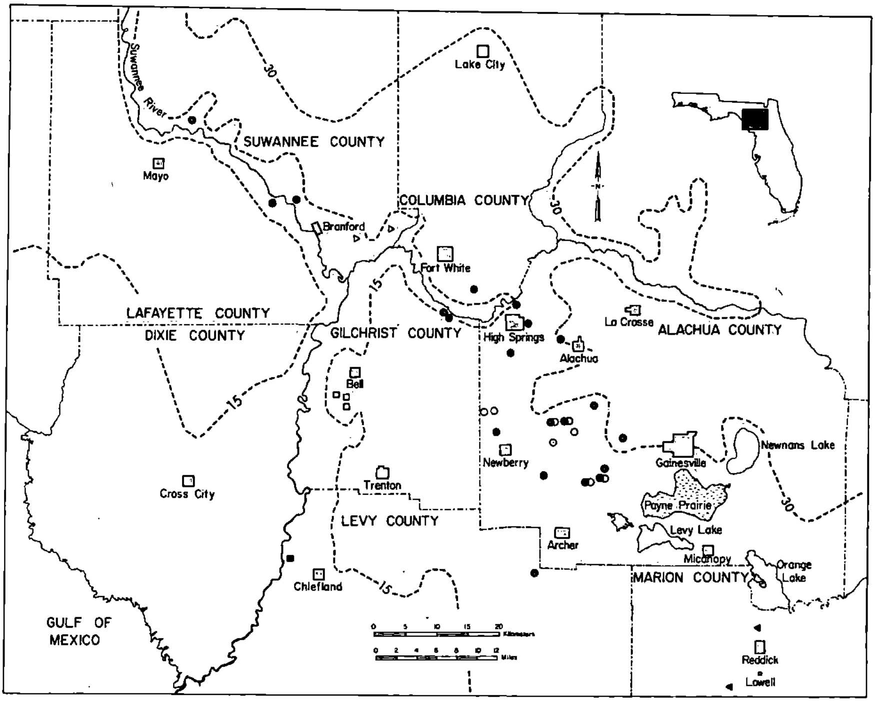

FIGURE 6. Specific records for cave crayfishes in the Suwannee River basin, showing their relationship to the 15 and 30m contours. Solid circles = *Procambarus pallidus*, hollow squares = *Procambarus lucifugus* (population 1), solid triangles = *Procambarus franzi*, hollow triangles = *Procambarus erythrops*, hollow circles = *Procambarus lucifugus alachua* (population 2).

the subject of portions of several papers (Hobbs 1942, 1958; Hobbs et al. 1977; Caine 1974; Relyea et al. 1976). However, we can now make additional interpretations, based on particular geological features and certain ecological factors.

EFFECTS OF OVERBURDEN

An important distributional phenomenon is the lack of troglobitic crayfishes in areas where moderate to heavy accumulations of unconsolidated sediments overlie the limestone (Fig. 7). This affects all of the troglobitic species by preventing the penetration of organic matter to the aquifer. Sediments, even coarse sands, filter detritus, and only through cave entrances and sinkholes is trophic input possible. Subterranean areas covered with thick accumulations of clastic overburden are thus severely energy limited.

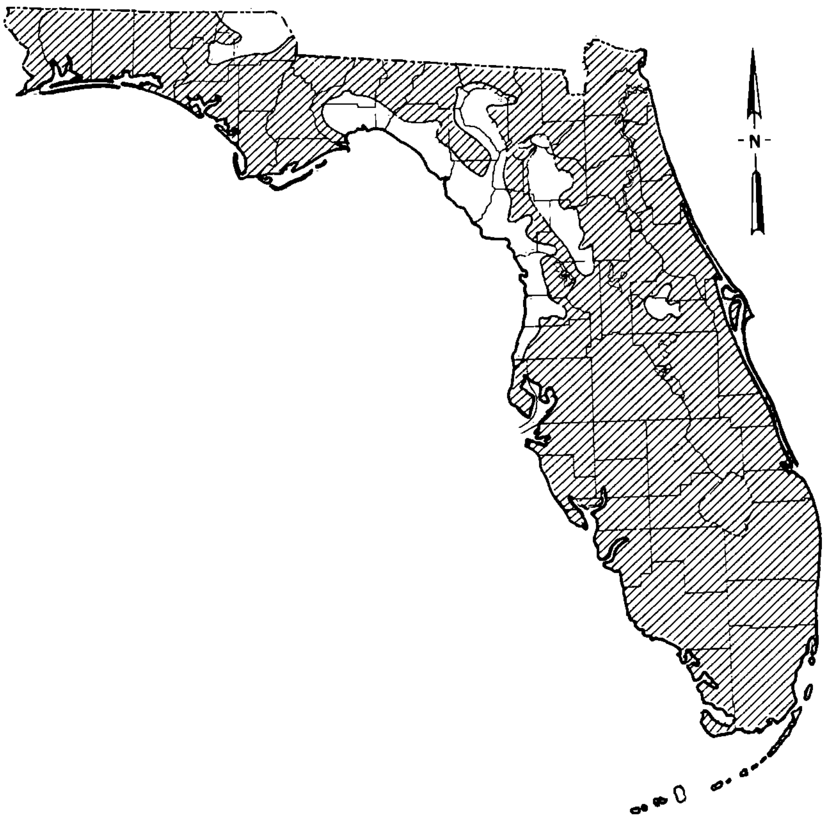

FIGURE 7. Distribution of moderate to heavy accumulations of clastic materials overlying carbonate rocks (hatched areas on map).

PHYSIOGRAPHIC FEATURES

Local distributions of certain crayfishes can be related to the escarpment of the Northern Highlands, low hills composed of residual clastics and rivers. The escarpment of the Northern Highlands runs roughly northwest to southeast, from near Tallahassee to Gainesville, and approximates the 30 m contour. It is a narrow band of rolling hills composed of clastics and characterized by extensive sinkhole activity. Streams flowing west from the Northern Highlands are quickly swallowed by these sinkholes (Williams et al. 1977). The most spectacular example in the northern peninsula is the disappearance of the Santa Fe River into a large sinkhole at Oleno State Park and its resurgence some 5 km away. West of the escarpment are karsted regions (e.g. western Alachua County and southern Columbia and Suwannee counties) inhabited by cave crayfishes (Fig. 6). In western Alachua County, *Procambarus pallidus* and *P.*

lucifugus alachua appear to inhabit different portions of this karst plain with respect to the escarpment. *P. pallidus* occurs primarily in "newly" developing cave systems along the escarpment (Warrens Cave, Fort Clark Church, and sites along the Santa Fe and Suwannee rivers), although it is found in other systems, including three sites where it occasionally has been known to occur with *P. l. alachua*. *P. l. alachua*, on the other hand, appears to be primarily restricted to more mature systems below the escarpment.

Southwest of the Northern Highlands are several series of low hills that are apparently remnants of a once more extensive highland. They resemble the Northern Highlands escarpment in that they are composed of similar sediments and have similar sinkhole activity. *Procambarus franzi* is associated with a set of hills south of Orange Lake in northern Marion County, and the intergrade population 3 of *P. lucifugus* with the hills of southern Marion County.

Caine (1974) attempted to show a correlation between the distribution of Florida troglobitic crayfishes and elevation, in particular the 15 m contour. However, after plotting crayfish localities, we found them to be between 3 m elevation at Manatee Springs and 46 m at Fort Clark Church.

Rivers may play a role in the distribution of Florida's troglobitic crayfishes, although it is not a direct relationship as implied in Relyea (1976). Rivers are the erosional agents that expose additional limestone. A species like *P. pallidus* prefers caves in the "newly" emerging karst, as seen in its distribution along the Suwannee and Santa Fe River basins (Fig. 6).

Geological Formations

Florida troglobitic crayfishes are confined to carbonate rocks, but not all aquifers in carbonate rocks are inhabited. We can only speculate as to the factors controlling this apparent selectivity.

Of the geological facies influencing the distribution of these crayfishes, the Crystal River Formation, a series of highly soluble Eocene limestones forming the upper portion of the Ocala Group, is the most important (Fig. 8). *Procambarus lucifugus*, *P. erythrops*, *P. franzi*, *P. pallidus*, and *Troglocambarus maclanei* are almost completely confined to it. However, under special conditions *P. pallidus* is occasionally found associated with additional limestones. At Thunder Hole, Suwanacoochee Springs, and Peacock Slough, *P. pallidus* is associated in part with the Suwannee limestone. These three cave systems lie along contacts between the Suwannee Limestone and the Crystal River Formation. *Cambarus cryptodytes* mostly occurs in caves lying near the contact between the Marianna Limestone and the Crystal River Formation, although the

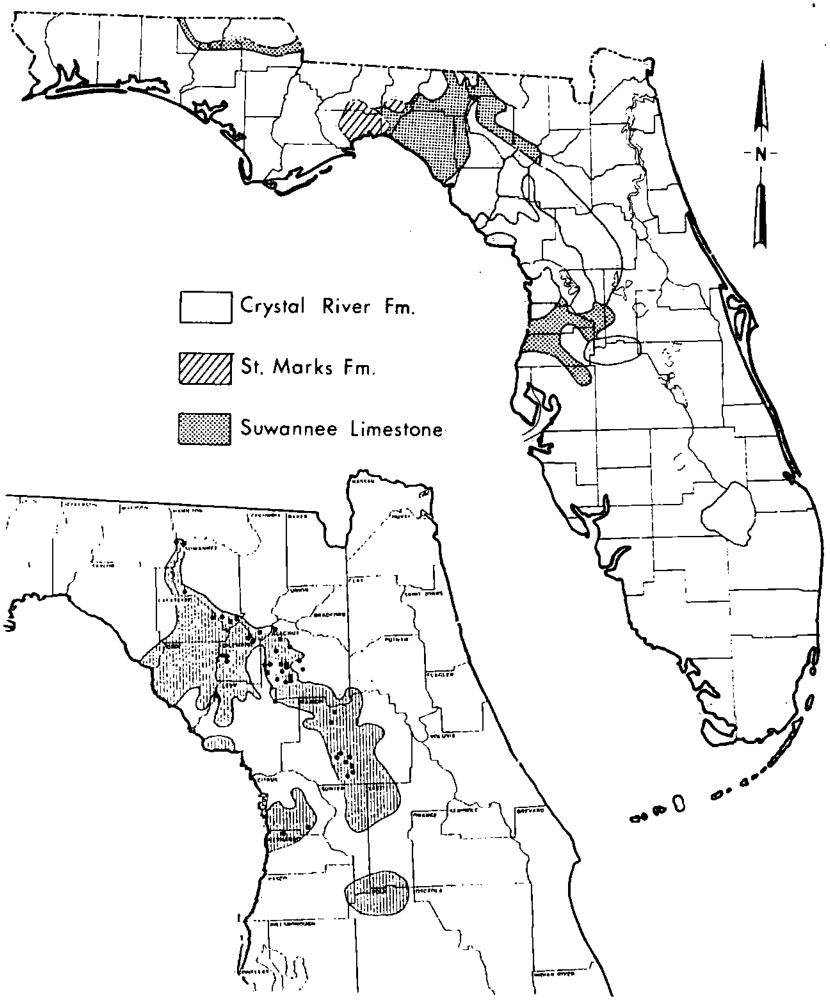

FIGURE 8. Distribution of certain carbonate rocks in Florida. Solid circles on insert map are crayfish localities. Geological features based on the map by Vernon and Puri (1964).

Graceville and Geromes Cave records are wholly within the latter formation (Fig. 5). *P. acherontis* and *P.* sp. are known from sites in the Hawthorne Formation, although they may ultimately be found associated with the Ocala Group (Crystal River and Williston formations). *P. acherontis* exists in the Palm Springs-Lake Brantley-Altamonte Springs region, a karsted area in southwestern Seminole County and adjacent Orange County. Wells drilled in the Palm Springs-Lake Brantley area show profiles consisting of varying amounts of Plio-Pleistocene terrace deposits covering 15-18 m of Hawthorne Formation, underlain with limestone of the Williston and Inglis formations (lower members of the Ocala Group). The Crystal River Formation is available here as thin beds in some wells, but is otherwise absent. Water from Palm Springs issues from two intersecting joints, each less than a meter wide in the Hawthorne. Crayfishes brought up from the Geological Survey's well at Long Lake and a private well at Altamonte Springs probably originated in the Ocala Group, since both of these wells are over 30 m deep. *Procambarus orcinus* and *P. horsti* are associated with the St. Marks Formation. The five known sites for *P. orcinus* are clustered about the town of Woodville, an area referred to as the Woodville Karst. *P. horsti* is known from a single locality, Big Blue Spring on the Wacissa River, which is developed as a deep shaft penetrating the St. Marks at the surface and the Suwannee Limestone below. The karst area around Woodville is extensive and separated from that at Big Blue Spring by a wide gap composed of Suwannee Limestone (Fig. 8). In the area about Big Blue Spring, the St. Marks occurs as a thin, crescent-shaped band lying adjacent to the Cody Scarp. We hypothesize that at one time the St. Marks Formation was continuous but, because much of the region was eroded by the Wacissa River, the formation has been divided. With this division we believe that a widespread subterranean crayfish population became fragmented, eventually differentiating into the two present-day species. Hobbs and Means (1972) suggested a very close relationship between these forms, and their distribution supports this hypothesis. *P. milleri* is known from one site in the Miami oolite, but its range remains a mystery.

Although certain geological formations that appear suitable for occupation by troglobitic crayfishes lie at the surface, none is known from these formations. The most obvious are the Suwannee and Tampa limestones. Large areas of the state have exposures of these formations (Fig. 8), and solution features such as caves, sinks, and springs are common to them. The lack of troglobitic crayfishes here is intriguing. Banks (1976) showed these limestones to be generally harder than the Crystal River and Williston formations, with zones of extremely hard (or dense) dolomite, breccia, shell, and clay beds. These hard zones may limit solubility and the extent to which cave systems can develop, and may restrict sinkhole formation. The latter would prevent access by crayfishes into the heart of the geological formation; the former would discourage the downward movement of detritus, and without food the crayfishes would be unable to survive. Other factors, like the chemical properties of the waters in the uninhabited aquifers of these rocks, would be worthy topics of investigation.

ECOLOGICAL FACTORS

Caine (1978) presented the only ecological data available for a few species of Florida troglobitic crayfishes. This information has been incorporated into our interpretation. As we have no personal field experiences with either *Procambarus acherontis* (Group B) or *P. milleri* (Group C), our discussion is limited to those in other groups, but we suspect that many of our observations may also apply to these two species.

The distribution of Florida's cave crayfishes within cave systems is clearly related to the availability of food. This food consists of either plant or animal debris washed in through sinks from surface ecosystems or guano under bat roosts.

Two bats, *Myotis austroriparius* and *M. grisescens*, use Florida caves in sufficient numbers to accumulate guano deposits. Estimates of nursery colonies of *M. austroriparius* at Sunday Sink and Orange Lake Cave indicate populations of 14,000 and 17,000, respectively (Zinn, 1977; pers. comm). The bats are present for several months in late spring and summer before the young can fly, after which the caves are usually vacated. At Sunday Sink, the crayfish, estimated at more than 1000 in number, continue to congregate under the bat roost for approximately two months after the bats have left. They eventually disperse into deep recesses of the cave, suggesting that bat guano may be a short term resource. These bats normally limit their nursery areas to portions of the cave directly over water, and, since suitable maternity caves are limited, it is reasonable to assume that the dependence of certain crayfish populations on bat activity may have been continuous for a long period.

Crayfish distributions fall into two basic patterns with respect to the dispersal of organic food matter. First, in caves where there is considerable subterranean water movement, incoming food is carried great distances from the input source, and populations of crayfishes in these caves appear to be widely, and more or less uniformly, distributed throughout the aquifer. Second, in areas where water movement and the energy source is more static, populations are clustered around the limited organic source.

In the Florida panhandle, *Cambarus cryptodytes* is known from one well and 14 caves. Although small to moderate numbers of these crayfishes concentrate around accumulated organic debris, individuals can be expected throughout the aquifer. Here the karst is characterized by shallow meandering cave systems occasionally penetrating below the water table. Since lateral transport of detritus is much more extensive than in the peninsular karst, crayfishes are not concentrated at the input areas but are more widely distributed. Seasonal flooding (usually in spring) causes ground water to flood otherwise dry caves, and *Cambarus cryptodytes* appears to take advantage of rising waters to temporarily move into recently flooded areas for exploitation of newly submerged food resources. In many caves there is a slow but regular flow of water throughout most of the year. This movement provides a dependable method of dispersal for organic matter.

Cambarus cryptodytes does not appear to thrive in aquatic systems rich in nutrients. In Geromes Cave, where there is an extremely large guano deposit and little lateral water movement, we only encountered two *Cambarus cryptodytes* in 20 visits. However, we found moderate numbers of a surface-dwelling species, *Procambarus paeninsulanus*. This is the only site in Florida where both troglobitic and epigean species were found together. In Bat Cave there is also an extremely rich supply of organic material, and *Cambarus cryptodytes* has never been found here.

Procambarus pallidus, and apparently *Procambarus horsti* and *Procambarus orcinus* (Group E), occur under conditions similar to those associated with *Cambarus cryptodytes*. Relatively few individuals (<50) are found at energy input areas (small sinks, solution pipes, and springs). To our knowledge, no population of Group E species has been found under bat roosts. These crayfishes seem to be unaffected by light and commonly occur in "blue hole" sinks, and occasionally in the open, outside of spring mouths. Within cave systems, *Procambarus pallidus* is typically found where potential food accumulates in small, often isolated pockets. Occasionally, these pockets are in protected areas within major conduits where strong water currents occur.

Members of the *Procambarus lucifugus* complex (Group D) occur most often in collapse sinks and under bat roosts, where large amounts of organic material are available (Fig. 9). Probably because of the large food resources, this group maintains the largest populations of the Florida troglobitic species. The *Procambarus erythrops* population at Sims Sink is estimated at 400-500 individuals, and the intergrade *Procambarus lucifugus* population at Sunday Sink at more than 1000. In most caves we studied, the largest populations were in more stagnant portions where much detritus accumulated and the energy source remained relatively stable.

Based on these observations we conclude that *Procambarus pallidus* is the most competitive and the most successful colonizer of low energy systems. There are few cases where members of the "pallidus" and "lucifugus" groups occur together, even though their overall geographic distributions indicate that there is considerable opportunity to do so. We know of only three cases of reported syntopic occurrence: *P. pallidus* outnumbers *P. lucifugus* in Squirrel Chimney and *P. lucifugus* outnumbers *P. pallidus* in Goat and Hog sinks. In each case the rarer species is known only from one or two individuals that we assume represent vagrants. This, along with the distribution of *Troglocambarus*, *Crangonyx*, and *Caeci-*

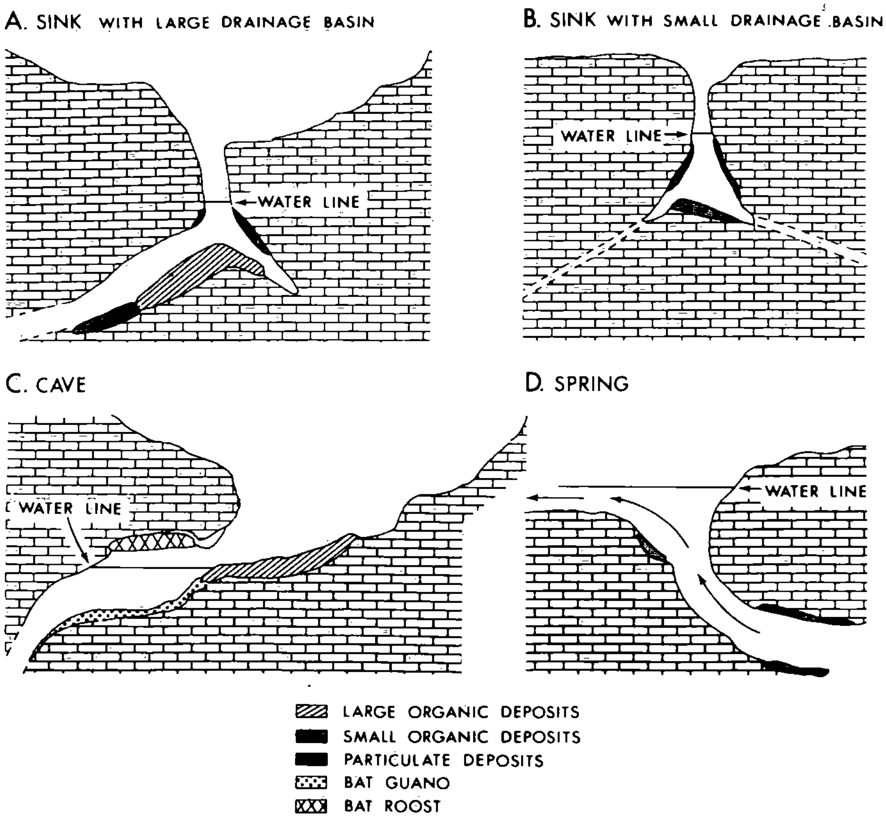

FIGURE 9. Types of openings to aquifers inhabited by Florida cave crayfishes, showing the distributions of organic debris. Type A and C entrances represent examples of high energy input sources; Type B and D, low energy input sources. When water levels occur close to the surface in Type A and B sinkholes, the ambient light causes the water to appear blue. Under these conditions, the sinkholes are locally referred to as "blue holes."

dotea in north-central Florida, suggests that subterranean routes for dispersal are open but that the amount of incoming energy clearly dictates which of these species groups will be successful in colonizing a given system. The presence of populations of the cave-dwelling fish, yellow bullheads, *Ictalurus natilis* (Relyea and Sutton 1973), and *Notropis harperi* (Marshall 1947, Hubbs 1956), in north-central Florida caves, often many kilometers from the nearest epigean habitats, suggests that much of the aquatic subterranean system is interconnected.

The distribution of *Troglocambarus maclanei*, a small species, seems to be related to the size of organic particles, and it is usually found in zones of lowest energy concentrations (Fig. 9). Hobbs (1942) described their "peculiar habit of clinging ventral-side-up to the submerged ceilings" of the flooded cave passage in Squirrel Chimney. Sutton (pers. comm.) observed that *Troglocambarus maclanei* in Sims Sink were concentrated on the lower portions of the detrital cone where the particle size was small. He also noted that there was little overlap of the areas in which this crayfish and the larger *Procambarus erythrops* occurred. The two species seem to be distributed along an energy gradient that occurs outward from these energy islands. There is apparently little competition between *Troglocambarus maclanei* and the larger species since, at each *Troglocambarus maclanei* locality, there occurs a member of the *lucifugus* or *pallidus* complex. Conversely it is exceptional to find any of the other species living sympatrically.

Troglocambarus appears to exist at much lower densities than any of the species discussed above, although it is not clear whether this is simply because of their low visibility or whether it is indicative of actual numbers.

Caine (1978) and Dickson and Franz (1980) demonstrated that certain hypogean Florida crayfishes (including members of both the *pallidus* and the *lucifugus* groups) have lower metabolic rates than related surface species. In addition, data on whole body respiration rates (Baskin, unpubl. manuscript) and on respiration rates, ATP turnover, and adenylate energy charge in excised gills suggests that *P. pallidus* exhibits a greater physiological adjustment to low energy cave environments than do *P. erythrops*, *P. franzi*, and *P. lucifugus*, which parallels the observed habitat differences between these two groups. No similar data are available for *Troglocambarus maclanei*.

SUGGESTED EVOLUTIONARY HISTORY OF CERTAIN TROGLOBITIC SPECIES

Hobbs (1942) originally visualized two separate invasions of crayfishes into Florida aquifers, and attempted to relate them to peninsular submergence during the Pleistocene. He later inferred a third invasion with the discovery of *Procambarus milleri* in South Florida (Hobbs 1971). Mohr and Poulson (1966) speculated that north-central Florida cave crayfish evolved primarily through avoidance of competition with the larger and more recent invaders dominating areas of food abundance.

Caine (1974) discussed cave crayfish distributions in relation to maximum sea level stands and suggested that all cave *Procambarus*, except *P. milleri* and *P. acherontis*, invaded subterranean habitats in the Pleistocene. He considered *P. milleri* to be recently derived, stating that "this species may have been isolated after the aquifer was lowered in southern Florida in the 1920's." Caine suggested that *P. acherontis* arose after flooding above the 15 m level in the early Pleistocene. We believe most of these statements to be incorrect.

Recent reinterpretation of Florida's Tertiary and Quaternary history and the correlation of certain geological features with present troglobitic crayfish distributions allow us to reevaluate the evolutionary history of these crustaceans. One of the major conflicts of earlier attempts at explanations was the concept of drastic eustatic fluctuations during the Pleistocene. Newer interpretations indicate that rises in sea levels during this period probably never exceeded 20 meters above present m.s.l. and maybe much less (E.S. Deevey, pers. comm.; Alt and Brooks 1965; Alt 1968). Geological and paleontological evidence also suggests the presence of at least a short, truncated Florida peninsula since at least the Pliocene (S.D. Webb, pers. comm.). These two concepts provide us with a persistent land mass, and a large span of time in which crayfishes could enter Florida and invade spelean habitats.

The ancestral forms essentially entered the particular geological formations where their modern counterparts exist today (i.e. Crystal River, Hawthorne and St. Marks formations). We should also point out that many present sinks are probably ancient. Webb (1974) documents that some have existed at their present locations and remained open for at least 2,000,000 years. Other sinkholes having terrestrial Miocene and even late Oligocene fossils associated with them suggest that sinkholes have characterized Florida for millions of years.

Remains of bats that are indistinguishable from present day *Myotis austroriparius* are known from several Northcentral Florida fossil deposits of middle to late Pleistocene age (Martin 1974, Webb 1974). This implies that many of the bat/crayfish colonies now present in this area may have been more or less continuous at many sites. Because of this we suggest the strong possibility of extremely protracted histories of particular crayfish colonies.

Hobbs (1958) postulated "that the Propictus Stock had gained a foothold in at least some streams of the southeast not later than the Pliocene—probably much earlier—and that their migrations from one river system to another were largely dependent upon stream piracy." We suspect that at least some members of this stock entered Florida shortly after the establishment of the peninsula. Only a small group of this once important faunal element exists in Florida today, represented by *Procambarus pictus* (Hobbs), *P. youngi* Hobbs, *P. seminolae* Hobbs and the troglobitic members of the *P. pallidus* and *P. lucifugus* complexes and *Troglocambarus maclanei*. The first two species show a relictual distribution, being endemic to a few isolated creek systems associated with old landforms. *P. pictus* is on the southeastern flank of the Northern Highlands and *P. youngi* on the southern escarpment of the Appalachicola Highlands. *P. seminolae*, a flatwoods species, is perhaps a later migrant to Florida, but at least one member of this subgroup must have reached Florida earlier to account for the existence of *T. maclanei*.

The drainage pattern of the ancestral peninsula was probably one of short streams draining flatwoods and flowing directly into the sea. The occurrence of fossil streams like those of the Love Bone Bed and McGeehee Farm sites in western Alachua County, which date from the late Miocene (latest Clarendonian to early Hemphillian) (Webb et al. 1981), helps substantiate this pattern. The coalescing of several headwater streams probably gave rise to the precursor of the Suwannee River, at a somewhat later time. Sediment analysis and bone orientation studies at Love Bone Bed reveal that this ancient stream had a sufficient current to support a stream fauna, including stream-dwelling crayfishes. Unfortunately crayfishes are rarely fossilized, but some plate-like carbonate structures collected at the Love Site suspiciously resemble crayfish gastroliths. These stream faunas probably moved from one creek system to another through stream piracy. Thus, *P. pictus* could have arrived in Black Creek (suggested as a Pliocene relict by Burgess and Franz 1978) and *P. youngi* in the Wetappo-St. Marks systems in this way. The elimination of other surface *pictus*-like populations from intermediate areas can be explained by the disappearance of the small stream systems along the western margin of the ancestral peninsula. This occurred as the large expanses of karst west of the Northern Highlands and south of the Appalachicola Highlands were exposed. Streams flowing off these highlands were captured by sinks, as they are today; the Santa Fe, Aucilla, and Chipola rivers disappear into sinks for varying distances. We see this as an excellent opportunity for surface crayfishes to gain entrance to the aquifer, and propose that multiple invasions of the aquifers account for the number of modern troglobitic species and their varying degrees of specialization.

There are numerous documented accounts of recent "overnight" captures of central Florida lakes by sinks during periods when lowered water tables were unable to provide support for time-eroded limestone (Lakeland-Bartow Ridge in Polk County). These captures would certainly pour tremendous quantities of organic debris into the aquifer and perhaps provide enough food to sponsor colonizing surface crayfishes through generations of early adaptations.

It is unfortunate that it is not possible to reconstruct the exact sequence of invasion of crayfishes into subterrean habitats. Mohr and Poulson (1966) suggested that the most specialized species entered the system first and adapted into its present form because of competitive pressure from larger species, which later invaded the underground habitats. Although this may well be the case, it could be argued with equal vigor that the earliest invader would already be specialized enough to have a competitive edge over later invaders. The amount of time available for evolution and development is certainly sufficient for almost any sequence of events.

It is probable that two ancestral forms may have entered at different points and at different times. This may account for the existence of the multispecies in the *P. pallidus* and *P. lucifugus* complexes. The modern range of *P. lucifugus* consists of five allopatric populations. We believe that these populations were continuous with one another, and that certain barriers arose to effectively impede gene flow. Some of these barriers can be tentatively identified. The western Gilchrist population appears to be isolated from that in adjacent Alachua County by a system of north-south trending ridges and the floodplain of an extinct river. The combination of deep terrace sands and dense floodplain sediments is probably enough to discourage the entry of detritus into, and the movement of crayfish within, the aquifer. No obvious barriers separate the Alachua population from the intermediate one in southwestern Marion County. However, a second closely related species, *P. franzi*, fills the gap. This species may have competitively excluded *P. lucifugus* in that area by exerting some biological influence that caused or initiated its extirpation. The barrier between the intermediate and the Citrus-Hernando populations, the Withlacoochee River, is more obvious. This river removed the Crystal River Formation from a wide band, exposing the Williston and Inglis formations, which are less soluble lower members of the Ocala Group.

It is perhaps worth speculating on the origins of the north-central Florida cave crayfish populations in view of their ecological distributions. *Troglocambarus maclanei* is the most widespread Florida cave crayfish species, yet exhibits no morphological differentiation (or variation). Since this species is ostensibly the least dependent on north-central Florida energy islands, it has apparently retained a more or less constant gene flow between colonies by following interstitial routes. *P. pallidus*, which has an intermediate dependency on energy islands, has colonized a relatively large area, and *pallidus*-like stocks have given rise to two additional species. The *P. lucifugus* complex, composed of the largest group of taxonomically distinct populations, has the greatest dependency on energy islands and therefore experiences less gene interchange than do other north-central Florida crayfishes. Thus it is reasonable to assume that the degree of ecological dependence on energy islands has, in varying degrees, dictated the ability to disperse, limited the gene flow, and resulted in the diverse speciation of central Florida's cave crayfishes.

At least three different life styles evolved. *P. pallidus*, and possibly *P. horsti* and *P. orcinus*, had more efficient metabolisms and were able to occupy caves, springs and solution tube sinkholes where only limited amounts of detrital energy were available. Members of the *P. lucifugus* complex, on the other hand, capitalized on the greater amounts of energy associated with collapse sinks and bat caves. The peculiar feeding modifications and life style of *Troglocambarus maclanei* may have developed to allow coexistence with the larger species, as suggested by Mohr and Poulson (1966) or developed independently in caves with modest energy availability. Changing sea levels, undulating water tables, and shifts in major areas of energy input may have secondarily forced species to coexist, and at times could have either united or further isolated closely related stocks.

P. milleri is known from a single well in southeast Florida. It is apparently derived from a parental stock of *P. alleni*, an epigean species that is common in south Florida. We have observed *P. alleni* living in water-filled limestone sinks on Big Pine Key, Monroe County, Florida. Caine (1974) theorized that the ancestral form burrowed into subterranean habitats or entered through exposures of oolitic limestone. The seasonal fluctuation of surface waters in south Florida would certainly provide numerous opportunities for crayfishes to move into karst areas and then become at least seasonally confined to solution pools and sinks. Caine (1974) suggested that *P. milleri* is not as old as other troglobitic cambarids, and that the species may have evolved after the aquifer was lowered in south Florida in the 1920's. That this form retains some black pigment and facets in the eye was his only apparent evidence of this (yet various populations of the *lucifugus* complex also have eye spots), although he was certainly led to a conclusion of recent evolution based on the supposed submergence of south Florida in the Pleistocene.

Although geologic evidence is lacking, zoogeographic patterns indicate that the most recent submergence of south Florida may not have occurred as recently as believed. Telford (1966) surmised that an endemic species of snake, *Tantilla oolitica*, in south Florida may have lived on high ground in Dade County during the Peorian interglacial. A diverse tropical element, with no apparent endemics is limited to a narrow strip of south coastal Florida and the Keys (see Neill 1957), which includes the area inhabited by *P. milleri.* Also known from this general area are numerous recognized races and/or disjunct populations of terrestrial vertebrates. All this suggests that some type of refugium persisted in this region for a considerable period. Although the exact age of the area is not clear, it certainly existed for a long enough period to suggest that *P. milleri* could have appeared prior to the 1920's.

In contrast to the energy island species assemblages of troglobitic crayfishes in peninsula Florida, a single, apparently wide ranging species, *Cambarus cryptodytes*, occurs in west Florida and southwest Georgia. We attribute this distribution and the lack of defined populations to the ample lateral transport of detritus throughout the aquifer. Although individuals will congregate around available food sources, they freely disperse once the food source is exhausted.

In summary, the specious nature of Florida's troglobitic crayfish fauna resulted from the invasion of the aquifer by at least 6 different surface crayfishes, possibly beginning as early as the late Miocene or Pliocene. They probably gained access to the subterranean environment when surface streams were captured by sinkholes. Multiple invasions of single species at different times and in different areas could account for the occurrences of multi-species in both the *Procambarus lucifugus* and *P. pallidus* complexes. Once underground, certain crayfishes, possibly resulting from sympatry, engaged in occupying different parts of the inhabitable cave environment. Some species (e.g. members of the *P. lucifugus* complex) inhabited the energy rich areas (i.e. in large sinks and under bat roosts), while others were not as dependent on these accumulations. The low energy species (e.g. members of the *P. pallidus* complex and *Troglocambarus maclanei*) had greater dispersal abilities, and today occupy the greatest geographic ranges.

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