

## Biogeography of subterranean decapods in North and Central America and the Caribbean region (Caridea, Astacidea, Brachyura)\*

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### Abstract

A significant number of decapod crustaceans (81 troglobites and 58 other cavernicoles) has been described from various subterranean waters in North and Central America (United States south to Costa Rica) and from the islands in the western north Atlantic and the Caribbean Sea, posing puzzling questions concerning their evolution and biogeography. Of these troglobitic species, 36 are shrimps (1 procarid, 11 atyids, 2 agostocarids, 15 palaemonids, 2 alpheidids, 5 hippolytids), 35 are cambarid crayfishes, and 10 are crabs (1 grapsid, 7 pseudothelphusids, 2 trichodactylids). They are known to occur in caves, springs, cenotes, blue holes, anchialine environments, and various crevicular habitats in localized areas throughout the region. Many, if not the majority, of the troglobites appear to have arisen independently from epigeal progenitors rather than sharing common subterranean precursors.

### Introduction

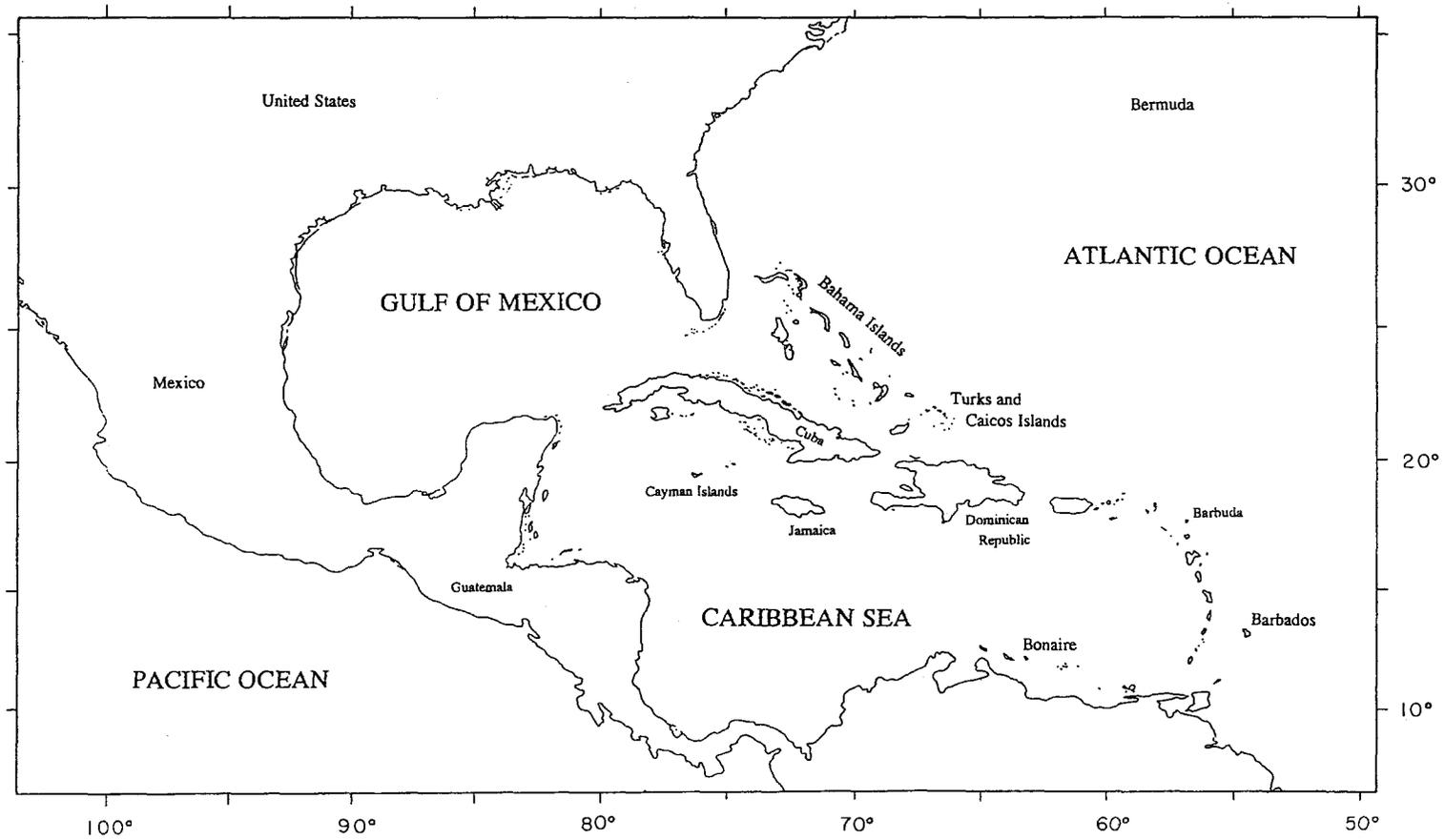
The decapod crustaceans of North America and Mesoamerica (Mexico, Central America, West Indies) are an extremely diverse group of arthropods of mixed geographical origin. A significant number of species has been discovered inhabiting various subterranean waters, the distribution of which often poses puzzling questions concerning their evolution and biogeography. In Mesoamerica, caves and other subterranean habitats have provided opportunities for marine stocks and refugia for others that invaded continental waters. Also there and in North America, representatives of several stocks that became established in fresh waters invaded subterranean waters opportunistically and became obligate cavernicoles. For many, if not most, of the decapods treated herein, the acquisition of troglomorphic characters associated with obligate subterranean life represents parallel development (convergence). Explanations for the disjunct distribution of related species in these crustaceans commonly have involved discussions concerning vicariance (e.g., con-

tinental drift) and dispersal biogeography as well as isolated dispersal phenomena. This paper represents an attempt to address briefly such explanations and to summarize the current knowledge of the distribution of the cavernicolous decapod species of 11 families (shrimps, crayfishes, crabs) in North America and Mesoamerica (see Fig. 1 and Table 1). No attempt is made to treat the possible origins and individual ranges of all members of these families.

### *List of cavernicolous decapods in North America and Mesoamerica*

The following is a list of shrimps, crayfishes, and crabs known to occur in caves, springs, cenotes, blue holes, anchialine, and crevicular habitats, distributed from the United States to Central America and on the islands of the western north Atlantic and Caribbean from Bermuda to Bonaire. All species listed are aquatic troglobites (stygiobionts) unless otherwise indicated.

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*Fig. 1.* Map of area treated in text, including parts of North America and Mesoamerica.

Table 1. Distribution by family of cavernicolous decapods of North America and Mesoamerica

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\* CARIDEA (Shrimps):  
 Procarididae (*Procaris*) - Bermuda, Mexico; (Ascension, Hawaii)  
 Atyidae (*Atya*, *Palaemonias*, *Typhlatya*, *Xiphocaris*)  
 Barbados, Jamaica, United States, Mexico, Cuba, Bahamas, Caicos Islands,  
 Bermuda, Barbuda, Isla Mona, Puerto Rico, Dominican Republic; (Ascension,  
 Galapagos)  
 Agostocarididae (*Agostocaris*) - Mexico, Bahamas, Turks Islands,  
 Caicos Islands  
 Palaemonidae (*Cryphiops*, *Creaseria*, *Macrobrachium*, *Neopalaemon*,  
*Palaemonetes*, *Troglocubanus*) - Mexico, Costa Rica, Jamaica,  
 United States, Bonaire, Curacao, Dominican Republic, Cuba, Puerto Rico,  
 Isla de Pinos  
 Alpheidae (*Alpheopsis*, *Potamalpheops*) - Mexico, Bermuda  
 Hippolytidae (*Barbouria*, *Calliasmata*, *Janicea*, *Somersiella*,  
*Yagerocaris*) - Bahamas, Caicos Islands, Cayman Islands, Bermuda,  
 Cuba, Dominican Republic, Antigua, Mexico

\* ASTACIDEA (Crayfishes):  
 Cambaridae (*Cambarus*, *Orconectes*, *Procambarus*, *Troglocambarus*)  
 Canada, United States, Mexico, Belize, Guatemala, Cuba

\* BRACHYURA (Crabs):  
 Gecarcinidae (*Cardisoma*, *Gecarcinus*) - Cuba, Jamaica, Puerto Rico  
 Grapsidae (*Sesarma*) - Jamaica, Cuba, Guatemala  
 Pseudothelphusidae (*Epilobocera*, *Isabellagordonia*, *Odontothelphusa*,  
*Phrygiopilus*, *Potamocarcinus*, *Pseudothelphusa*, *Ptychophallus*,  
*?Raddus*, *Srygothelphusa*, *Tehuana*, *Typhlopseudothelphusa*,  
*Zilchia*) - Mexico, Cuba, Puerto Rico, Guatemala, Belize, Costa Rica  
 Trichodactylidae (*Avotrichodactylus*, *Rodriguezia*, *Trichodactylus*) - Mexico

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## CLASS CRUSTACEA

### Order Decapoda

#### SUBORDER PLEYCYEMATA

##### Infraorder Caridea

#### Superfamily Procaridoidea

##### Family Procarididae

*Procaris chacei* Hart & Manning - Green Bay Cave  
 (anchialine habitat) - Bermuda

*Procaris* n.sp. - anchialine habitat - Mexico: Quintana  
 Roo

Two additional species are known from anchialine lava  
 pools: *P. ascensionis* Chace & Manning (1972), from  
 Ascension Island in the South Atlantic Ocean and  
*P. hawaiiiana* Holthuis (1973) on Maui and Hawaii,  
 Hawaiian Islands

#### Superfamily Atyoidea

##### Family Atyidae

*Atya brachyrhinus* Hobbs & Hart - cave - Barbados

*Atya innocous* (Herbst) - troglaxene - caves - Jamaica:  
 Saint Elizabeth and Saint Mary parishes

*Atya lanipes* Holthuis - troglaxene - caves - Jamaica:  
 Saint Mary Parish

*Palaemonias alabamae* Smalley - caves - USA: Madi-  
 son County, Alabama

*Palaemonias ganteri* Hay - caves - USA: Edmonson,  
 Hart counties, Kentucky

*Typhlatya campecheae* Hobbs & Hobbs - caves - Mex-  
 ico: Campeche

*Typhlatya consobrina* Botosaneanu & Holthuis - caves  
 - Cuba: Camaguey, Pinar del Río provinces

*Typhlatya garciai* Chace - caves, anchialine habitats - Cuba: Oriente, Pinar del Río provinces; Caicos Islands: Providenciales

*Typhlatya iliffei* Hart & Manning - Tucker's Town Cave (anchialine cave) - Bermuda

*Typhlatya mitchelli* Hobbs & Hobbs - caves, cenotes - Mexico: Quintana Roo and Yucatán

*Typhlatya monae* Chace - well, caves - Barbuda, Isla Mona, Puerto Rico, Dominican Republic

*Typhlatya pearsei* Creaser - caves, cenotes - Mexico: Campeche, Quintana Roo, Yucatán

*Typhlatya taina* Estrada and Gomez - Cueva de la India - La Habana, Cuba

*Typhlatya* n.sp. [Kensley 1988:688] - Mexico: Yucatán Peninsula

The genus is represented by two additional species: *T. galapagensis* Monod & Cals (1970), stygobiont from anchialine habitat on Isla Santa Cruz, Galapagos Islands and *T. rogersi* Chace & Manning (1972) from saline, anchialine pools on Ascension Island

*Xiphocaris elongata* (Guerin-Meneville) - troglone - caves - Jamaica, Puerto Rico

#### Superfamily Rhynchocinetoidae

##### Family Agostocarididae

*Agostocaris bozanici* Kensley - Xcan-ha Cenote - Mexico: Quintana Roo (Cozumel Island)

*Agostocaris williamsi* Hart & Manning - blue hole, anchialine caves - Bahamas: Cat and Grand Bahama Islands; Caicos Islands: Providenciales

#### Superfamily Palaemonoidea

##### Family Palaemonidae

*Cryphiops (Bithynops) luscus* (Holthuis) - Grutas del Arco - Mexico: Chiapas

*Cryphiops (Bithynops) perspicax* (Holthuis) Cenote La Cueva - Mexico: Chiapas

*Creaseria morleyi* (Creaser) - caves - Mexico: Yucatán, Quintana Roo

*Macrobrachium acherontium* Holthuis - caves - Mexico: Tabasco

*Macrobrachium carcinus* (Linnaeus) - troglone-caves and/or springs - Costa Rica: Puntarenas Province; Jamaica: Manchester and Saint Ann parishes; Mexico: Chiapas, San Luis Potosí; USA: Marion and Putnam counties, Florida

*Macrobrachium heterochirus* (Wiegmann) - troglone-cave - Jamaica: Saint Ann Parish

*Macrobrachium lucifugum* Holthuis - troglone-caves and anchialine habitats - Bonaire, Curacao, Dominican Republic, Jamaica: Saint Ann Parish,

Cuba: Oriente, Pinar del Río provinces; Puerto Rico

*Macrobrachium villalobosi* Hobbs - Cueva del Nacimiento del Río San Antonio - Mexico: Oaxaca

*Neopalaemon nahuatlus* Hobbs - Cueva del Guano - Mexico: Oaxaca

*Palaemonetes (Alaocaris) antrorum* (Benedict) - wells and caves - USA: Hays, Uvalde counties, Texas

*Palaemonetes (Alaocaris) holthuisi* (Strenth) - cave - USA: Hays County, Texas

*Palaemonetes (Palaemonetes) cummingsi* Chace - Squirrel Chimney - USA: Alachua County, Florida

*Palaemonetes (Palaemonetes) paludosus* (Gibbes) troglone-cave - USA: Leon County, Florida

*Troglocubanus calcis* (Rathbun) - caves - Cuba: Camagüey and La Habana provinces

*Troglocubanus eigenmanni* (Hay) - caves - Cuba: Pinar del Río, La Habana, Matanzas provinces; Isla de Pinos

*Troglocubanus gibarensis* (Chace) - caves - Cuba: Oriente and Las Villas provinces

*Troglocubanus inermis* (Chace) - caves - Cuba: Camagüey and La Habana provinces

*Troglocubanus jamaicensis* Holthuis - cave - Jamaica: Saint Mary Parish

*Troglocubanus perezfarfanteae* Villalobos F. - caves - Mexico: San Luis Potosí, Tamaulipas

#### Superfamily Alpheoidea

##### Family Alpheidae

*Automate dolichognatha* De Man - Tucker's Town Cave (anchialine cave) - Bermuda

*Potamalpheops stygicola* (Hobbs) - Cueva del Nacimiento del Río San Antonio - Mexico: Oaxaca

##### Family Hippolytidae

*Barbouria cubensis* (von Martens) - caves, blue holes, anchialine habitats - Bahamas: Abaco Island, San Salvador Island; Caicos Islands: Providenciales; Cayman Islands: Cayman Brac; Bermuda; Cuba: Habana, Matanzas, Oriente provinces

*Calliasmata rimolii* Chace - anchialine cave - Dominican Republic: Puerto Plata Province

*Janicea antiguensis* (Chace) - caves, anchialine caves - Antigua; Bahamas: Grand Bahama; Bermuda; Mexico: Quintana Roo (Cozumel Island)

*Somersiella sterreri* Hart & Manning - anchialine caves - Bermuda; Mexico: Quintana Roo (Cozumel Island)

*Yagerocaris cozumel* Kensley - cenote, anchialine cave  
- Mexico: Quintana Roo (Cozumel Island)

#### Infraorder Astacidea

#### Superfamily Astacoidea

#### Family Cambaridae

#### Subfamily Cambarinae

*Cambarus (Aviticambarus) hamulatus* (Cope) -caves -  
USA: Alabama, Tennessee

*Cambarus (Aviticambarus) jonesi* Hobbs & Barr -  
caves - USA: northeastern Alabama

*Cambarus (Cambarus) sp.* - troglophile? - caves -  
USA: southwestern Virginia; reported by Holsinger  
(1964:62) as '*Cambarus bartonii* ssp.'

*Cambarus (Cambarus) bartonii bartonii* (Fabricius)-  
troglophile - surface waters, springs, and caves - USA:  
Alabama, Georgia, Virginia, West Virginia

*Cambarus (Cambarus) bartonii cavatus* Hay -  
troglophile - surface streams and springs - USA: Geor-  
gia, Kentucky, Ohio, Tennessee, Virginia

*Cambarus (Depressicambarus) latimanus* (LeConte)  
- troglaxene? - surface burrows and streams, cave  
streams - USA: Chatooga, Dade, Walker counties,  
Georgia

*Cambarus (Depressicambarus) striatus* Hay - troglax-  
ene? - surface burrows and streams, cave streams -  
USA: Chatooga, Walker counties, Georgia

*Cambarus (Erebicambarus) hubbsi* Creaser - troglax-  
ene? - surface streams, burrows, caves - USA: north-  
eastern Arkansas and southeastern Missouri

*Cambarus (Erebicambarus) hubrichti* Hobbs - springs  
and caves - USA: Missouri

*Cambarus (Erebicambarus) laevis* Faxon - troglophile  
- surface streams, springs, and caves - USA: Indiana,  
Kentucky

*Cambarus (Erebicambarus) ornatus* Rhoades -  
troglaxene? - intermittent surface streams, springs,  
cave - USA: Kentucky

*Cambarus (Erebicambarus) tenebrosus* Hay -  
troglophile - surface streams, caves and springs - USA:  
Alabama, Kentucky, Tennessee

*Cambarus (Jugicambarus) aculabrum* Hobbs &  
Brown - caves - USA: Benton Co., Arkansas

*Cambarus (Jugicambarus) dubius* Faxon - troglaxene?  
- surface primary burrower, cave - USA: Russell Coun-  
ty, Virginia

*Cambarus (Jugicambarus) cryptodytes* Hobbs - caves  
- USA: Jackson and Washington counties, Florida and  
Decatur County, Georgia

*Cambarus (Jugicambarus) setosus* Faxon - caves -  
USA: Christian, Dade, Greene, Jasper, Lawrence,  
Newton, and Stone counties, Missouri; Delaware and  
Mayes counties, Oklahoma

*Cambarus (Jugicambarus) tartarus* Hobbs & Cooper  
- Stansberry-January Cave System, - USA: Delaware  
County, Oklahoma

*Cambarus (Jugicambarus) zophonastes* Hobbs &  
Bedinger - Hell Creek Cave - USA: Stone County,  
Arkansas

*Cambarus (Puncticambarus) nerterius* Hobbs - caves  
- USA: Greenbrier and Pocahontas counties, West Vir-  
ginia

*Cambarus (Puncticambarus) robustus* Girard -  
troglophile? - surface streams, cave streams - USA:  
New York

*Orconectes (Buannulifictus) meeki brevis* Williams -  
troglaxene? - surface streams, caves - USA: Arkansas,  
Oklahoma

*Orconectes (Buannulifictus) palmeri longimanus*  
(Faxon)-troglaxene? - surface lotic habitats; cave,  
spring - USA: Pontotoc County, Oklahoma

*Orconectes (Crockerinus) propinquus* (Girard) -  
troglaxene? - surface streams and rocky shores of  
lakes; cave - USA: Lawrence County, Indiana

*Orconectes (Gremicambarus) immunis* (Hagen) -  
troglaxene? - surface lentic and sluggish lotic habi-  
tats; cave - USA: Lawrence County, Indiana; Canada

*Orconectes (Gremicambarus) virilis* (Hagen) - troglax-  
ene? - surface lakes and streams - cave - USA: Alabama

*Orconectes (Orconectes) australis australis* (Rhoades)  
- caves - USA: Alabama, Tennessee,

*Orconectes (Orconectes) australis packardi* Rhoades  
caves - USA: Kentucky

*Orconectes (Orconectes) incomptus* Hobbs & Barr -  
caves - USA: Jackson County, Tennessee

*Orconectes (Orconectes) inermis inermis* Cope - caves  
USA: Indiana, Kentucky

*Orconectes (Orconectes) inermis testii* (Hay) - caves  
USA: Monroe County, Indiana

*Orconectes (Orconectes) pellucidus* (Tellkamp) -  
caves - USA: Kentucky, Tennessee

*Orconectes (Procericambarus) luteus* (Creaser) -  
troglaxene? - surface lotic habitats; cave - USA: Mis-  
souri

*Orconectes (Procericambarus) neglectus neglectus*  
(Faxon) - troglaxene? - surface rocky streams; caves -

USA: southwestern Missouri; Delaware County, Oklahoma

*Orconectes (Procericambarus) punctimanus* (Creaser) troglaxene? - surface lotic habitats; cave - USA: Missouri

*Orconectes* spp. - two undescribed troglobitic species from caves in northern Alabama

*Procambarus (Austrocambarus) mirandai* Villalobos-troglophile - caves - Mexico: Chiapas

*Procambarus (Austrocambarus) niveus* Hobbs & Villalobos - Cuevas de Santo Tomas - Cuba: Pinar del Río

*Procambarus (Austrocambarus) oaxacae oaxacae* Hobbs-Cueva del Guano - Mexico: Oaxaca

*Procambarus (Austrocambarus) oaxacae reddelli* Hobbs-caves - Mexico: Oaxaca, Veracruz

*Procambarus (Austrocambarus) pilosimanus* (Ortmann)-troglaxene? - surface waters and caves - Belize, Guatemala, and Mexico: Chiapas and Quintana Roo

*Procambarus (Austrocambarus) rodriguezi* Hobbs - Cueva de Ojo de Agua Grande - Mexico: Veracruz

*Procambarus (Austrocambarus) sbordonii* Hobbs - troglophile - Cueva del Nacimiento de Río S. Domingo - Mexico: Chiapas

*Procambarus (Girardiella) simulans* (Faxon) - troglophile - surface lotic, lentic, burrow habitats; caves - USA: Greer, Major, Murray, Washita, Woodward counties, Oklahoma; Burnet County, Texas

*Procambarus (Leonticambarus) milleri* Hobbs - well in Miami - USA: Dade County, Florida

*Procambarus (Lonnbergius) acherontis* (Lönnerberg)-springs and caves - USA: Orange and Seminole counties, Florida

*Procambarus (Lonnbergius) morrissi* Hobbs & Franz-Devil's Sink - USA: Putnam County, Florida

*Procambarus (Ortmannicus) acutus acutus* (Girard) troglaxene? - surface lentic, sluggish lotic habitats; caves - USA: Texas

*Procambarus (Ortmannicus) acutus cuevachicae* (Hobbs)-troglophile - surface waters and caves - Mexico: Hidalgo, Puebla, San Luis Potosí, Tamaulipas, and Veracruz

*Procambarus (Ortmannicus) delicatus* Hobbs & Franz-Alexander Spring and Cave - USA: Lake County, Florida

*Procambarus (Ortmannicus) erythropros* Relyea & Sutton-caves - USA: Suwannee County, Florida

*Procambarus (Ortmannicus) fallax* (Hagen) - troglaxene? - surface lotic, lentic environments, burrows, cave-USA: Florida

*Procambarus (Ortmannicus) franzi* Hobbs & Lee - caves USA: Marion County, Florida

*Procambarus (Ortmannicus) horsti* Hobbs & Means-springs and caves - USA: Jefferson, Leon, and Wakulla counties, Florida

*Procambarus (Ortmannicus) leitheuseri* Franz & Hobbs-caves - USA: Hernando and Pasco counties, Florida

*Procambarus (Ortmannicus) lucifugusalachua* (Hobbs) caves - USA: Alachua, Gilchrist, Levy, and Marion counties, Florida

*Procambarus (Ortmannicus) lucifugus lucifugus* (Hobbs) - caves - USA: Citrus, Hernando, Marion counties, Florida

*Procambarus (Ortmannicus) orcinus* Hobbs & Means-caves - USA: Leon and Wakulla counties, Florida

*Procambarus (Ortmannicus) pallidus* (Hobbs) - caves-USA: Alachua, Columbia, Suwannee counties, Florida

*Procambarus (Ortmannicus) toltecaae* Hobbs - troglaxene? - caves - Mexico: Hidalgo, San Luis Potosí, Tamaulipas

*Procambarus (Ortmannicus) villalobosi* Hobbs troglaxene? - surface lotic habitats; cave - Mexico: San Luis Potosí

*Procambarus (Ortmannicus) attiguus*. Hobbs and Franz (1992) - cave - USA: Marion County, Florida

*Procambarus (Remoticambarus) pecki* Hobbs - caves - USA: Colbert, Lauderdale, and Morgan counties, Alabama

*Procambarus (Scapulicambarus) clarkii* (Girard) - troglaxene? - surface lentic, lotic, burrow habitats; caves - USA: Texas

*Procambarus (Scapulicambarus) paeninsulanus* (Faxon) - troglophile? - surface lotic, lentic, burrow habitats; caves - USA: Florida

*Procambarus (Scapulicambarus) xilitlae* Hobbs & Grubbs - Hoya de las Guaguas - Mexico: San Luis Potosí

*Procambarus (Villalobosus) cuetzalanae* Hobbs - troglophile? - caves and springs - Mexico: Puebla

*Procambarus (Villalobosus) xochitlanae* Hobbs - caves - Mexico: Puebla

*Troglocambarus maclanei* Hobbs - caves - USA: Alachua, Citrus, Hernando, Marion, Suwannee counties, Florida

*Infraorder Brachyura**Superfamily Grapsidoidea**Family Gecarcinidae*

*Cardisoma guanhumi* Latreille - troglone? - cave  
- Cuba: La Habana, Las Villas, Oriente provinces;  
Jamaica: Clarendon Parish; Puerto Rico  
*Gecarcinus ruricola* (Linnaeus) - troglone - cave  
- Cuba: Las Villas and Oriente provinces; Jamaica:  
Clarendon Parish

*Family Grapsidae*

*Sesarma (Sesarma) verleyi* Rathbun - caves - Jamaica:  
Manchester, Saint Ann, Saint Catherine, Saint Elizabeth,  
Saint James, Saint Mary parishes  
*Sesarma* sp. - troglone? - cave - Cuba: Oriente  
Province  
*Sesarma (Holometopus) miersii* Rathbun - troglone?  
- cave - Jamaica  
*Sesarma (Holometopus) roberti* H. Milne Edwards-  
troglone? - cave - Guatemala  
*Sesarma (Sesarma) bidentatum* Benedict - troglone?  
- cave - Jamaica: Saint Ann, Saint Elizabeth parishes

*Family Pseudothelphusidae*

Pseudothelphusidae indet. species - troglone - cave  
- Mexico: Veracruz; reported by Rodriguez & Hobbs  
(1989:398)  
*Epilobocera armata* Smith - troglone? - cave - Cuba:  
Las Villas  
*Epilobocera gertraudae* Pretzmann - troglone? -  
cave - Cuba: Las Villas  
*Epilobocera sinuatifrons* (A. Milne-Edwards) -  
troglone? - cave - Puerto Rico  
*Isabellagordonia longipes* Pretzmann - troglone? -  
cave - Guatemala  
*Odontothelphusa monodontis* Rodriguez & Hobbs -  
troglone - cave - Mexico: Tabasco  
*Phrygiopilus acanthophallus* Smalley - troglone? -  
cave - Guatemala: Altaverapaz  
*Potamocarcinus aspoekorum* (Pretzmann) - troglone  
- cave - Belize  
*Potamocarcinus leptomelus* Rodriguez & Hobbs -  
troglone - cave - Mexico: Veracruz  
*Potamocarcinus maanus* (Rathbun) - troglone - cave  
- Costa Rica  
*Pseudothelphusa mexicana* Alvarez-Noguera - troglone  
- cave - Mexico: Guerrero

*Pseudothelphusa puntarenas* Hobbs III - troglone -  
cave - Costa Rica: Puntarenas Province  
*Pseudothelphusa sonora* Rodriguez & Smalley -  
troglone? - cave - Mexico: Sonora  
*Pseudothelphusa* sp. - cave - Mexico: Guerrero; reported  
by Hoffman *et al.* (1986:175,186,213,237)  
*Ptychophallus montanus* (Rathbun) - troglone - cave  
- Costa Rica: Puntarenas Province  
*?Raddus* sp. - cave - Mexico: Chiapas; reported by  
Rodriguez & Hobbs (1989:397)  
*Stygothelphusa lopezformenti* Alvarez and Villalobos  
- cave - Mexico: Oaxaca  
*Tehuana complanata* Rodriguez - troglone? - cave -  
Mexico: San Luis Potosí, Veracruz  
*Typhlopseudothelphusa acanthochela* Hobbs - cave -  
Belize  
*Typhlopseudothelphusa hyba* Rodriguez & Hobbs -  
caves - Mexico: Chiapas  
*Typhlopseudothelphusa iuberthiei* Deboutteville - cave  
- Guatemala: Alta Verapaz Province  
*Typhlopseudothelphusa mitchelli* Deboutteville - caves  
- Guatemala: Alta Verapaz Province  
*Typhlopseudothelphusa mocinoi* (Rioja) - caves - Mex-  
ico: Chiapas  
*Zilchia falcata* Rodriguez & Hobbs - cave - Guatemala

*Family Trichodactylidae*

*Avotrichodactylus bidens* (Bott) - troglone - cave -  
Mexico: Tabasco  
*?Avotrichodactylus constrictus* (Pearse) - troglone -  
cave - Mexico: Oaxaca  
*Rodriguezia mensabak* Cottarelli & Argano - cave -  
Mexico: Chiapas  
*Trichodactylus bidens* Bott - cave(s) - Mexico: Tabasco  
3.

**Biogeographical Considerations:**

The discussions of nearly a century concerning the evolution and biogeography of cave-dwelling decapods in the Americas and Caribbean region are reviewed in Hobbs *et al.* (1977). Some recent discoveries and hypotheses treating these crustaceans are summarized by Hart *et al.* (1985), Manning *et al.* (1986), Rodriguez (1986), and Hobbs (1988).

### Shrimps:

The diverse "cave" shrimp faunas found in the region covered in this discussion are polyphyletic in origin. Some are truly fresh water organisms while others are capable of tolerating wide variations in salinity, such as those species found in coastal anchialine and crevicular habitats. Certain genera and species are known from widely separated anchialine localities and pose puzzling questions concerning their biogeography. Hart *et al.* (1985) and Manning *et al.* (1986) address some of these questions and summarize similar distribution patterns for other groups of crustaceans. They present evidence to support the hypotheses that shrimps (and others) may have invaded crevicular and anchialine habitats in Bermuda and the Caribbean before the opening of the North Atlantic in the Jurassic and thus these habitats may have served as Mesozoic refugia for the ancestors of many extant species. Also they suggested that subterranean environments could have provided a continuum of habitats from the abyssal zone to above sea level fresh waters and that these could have been entered at virtually any level (depth) via marine crevicular habitats.

The procarid shrimps are represented by a single genus and four species that are disjunctly distributed in anchialine habitats in the western Atlantic Ocean, the western Caribbean Sea, and the eastern Pacific Ocean. This is one of the most primitive of all caridean shrimps and because of low variability among the species, Hart and Manning (1986) suggest that the genus demonstrates an extremely slow rate of evolution. *Procaris*, or its predecessors, may have been distributed widely throughout the oceans and survives today in cryptic habitats where environmental rigors are minimal.

The Atyidae is a successful group that is widespread in caves in the Atlantic, the Bahamas and West Indies, in North and Middle America, and in the southeastern Pacific Ocean. The genus *Atya* is found in caves only in the West Indies and only *A. brachyrhinus* demonstrates any recognized troglomorphic adaptations; the two additional species depict surface populations that have extended their distributions into subterranean waters. *Xiphocaris* is represented by a single species that is epigeic and occasionally enters caves in the Greater Antilles. The genus *Palaemonias* contains two disjunct species that are troglobitic in the southeastern United States. It is likely that they shared a common ancestor that was widely distributed in epigeic aquatic systems. Populations entered hypogean waters in different parts of the range and subsequent extinction of the surface

species resulted in isolation of these small gene pools. The genus *Typhlatya* is one of the most successful of all troglobitic shrimps and the current distribution of cavernicolous species is widely disjunct. The subterranean species live in cave, anchialine, or crevicular habitats in Mexico, the Caribbean, western Atlantic, as well as on the Galapagos Island of Santa Cruz and Ascension Island. Manning *et al.* (1986) suggest that the ancestors of extant *Typhlatya* may have frequented crevicular habitats along the Mid-Atlantic Ridge prior to major plate tectonic activity and argued against the derivation of today's species from possible pelagic larvae of ancestral forms.

The family Agostocarididae is represented by a single genus and two disjunct species in the western Atlantic and the western Caribbean Sea. Hart and Manning (1986) and Kensley (1988) point out similarities with the bresiliids and atyids but the phylogeny of this group is unclear.

Palaemonid shrimps have invaded caves in the United States, Mexico, Central America, and in many Caribbean islands. It is likely that the genera *Cryphiops*, *Creaseria*, *Neopalaemon* (all inhabiting caves and anchialine habitats in southern Mexico), and *Troglocubanus* (caves in Cuba, Jamaica, and Mexico) were derived from various marine ancestors. The species of *Palaemonetes* inhabiting fresh waters were derived from a widespread Mesozoic or early Cenozoic ancestor that gave rise to *P. cummingsi* in the east and to *P. antrorum* and *P. holthuisi* to the west. *Macrobrachium* is believed to have moved inland more recently and probably through competitive exclusion expelled *Palaemonetes* from the middle latitudes by the Miocene. Five species of *Macrobrachium* have invaded subterranean waters in this area of study, primarily in Mexico (see Strenth 1976 and Hobbs *et al.* 1977).

The family Alpheidae is represented by two genera and two species that are cavernicolous in Mexico (fresh water) and Bermuda (anchialine habitat). *Automate dolichognatha* is widely distributed in the western Atlantic and the Indo-West Pacific regions while *Potamalpheops stygicola* is known only from a single cave in Oaxaca, Mexico, and while sharing affinities with members of the widespread genus *Alpheopsis*, its congeners occur in West Africa.

Five genera and species constitute the hippolytid shrimps inhabiting caves and anchialine habitats in the area of study. All are of marine origin with *Yagerocaris cozumel* and *Calliasmata rimolii* having the most restricted ranges (Cozumel Island and Domini-

can Republic, respectively) and *Barbouria cubensis* demonstrating a markedly broader distribution (Bermuda, Bahamas, Caicos Islands, and West Indies). Like *B. cubensis*, *Janicea antiguensis* and *Somersiella sterreri* exhibit disjunct distributions and are derived from widely ranging marine stocks.

#### *Crayfishes:*

The most successful cambarid crayfishes in the Northern Hemisphere are those belonging to the subfamily Cambarinae and they have undergone an adaptive radiation that surpasses that of any other crayfish group (Hobbs 1988). Specifically, the cavernicolous cambarines represent a polyphyletic group that has undergone multiple colonizations of subterranean waters by ancestral epigeal species of the genera *Cambarus*, *Orconectes*, and *Procambarus*.

Hobbs, Jr. (1988) and Hobbs III (1991) summarized the arguments concerning the origin and dispersal of cambarid decapods and an abbreviation of those discussion is presented here (see also Hobbs *et al.* 1977). The ancestral cambarine stock entered fresh waters of southeastern North America no later than the Cretaceous or and perhaps earlier in the Mesozoic Era. Through adaptive radiation this ancestral *Procambarus* stock underwent differentiation into the genus *Procambarus* and two additional stocks, the orconectoid and cambaroid crayfishes. This highly variable *Procambarus* stock extended its range primarily to the west and south and during the early Cenozoic became widespread in the southern part of the United States and Mexico. During the Miocene the crayfish stock from which the Mexican and Cuban troglobites arose was isolated by a vicariance event. Probably competitive exclusion played a role in the resulting separation and slight overlap within the ranges of the pseudothelphusid crabs and the cambarid crayfishes (see Rodriguez 1986).

The monotypic *Troglocambarus* probably shared a common ancestry with several members of the subgenus *Ortmannicus* (genus *Procambarus*), the ranges of which it overlaps (see Hobbs and Franz 1986).

The orconectoid stock moved primarily to the north and west, giving rise predominantly to stream-dwelling species of the genus *Orconectes* (other genera also). The ancestors of the extant troglobitic members of the genus found refuge from Pleistocene rigors in subterranean waters on the Cumberland Plateau, the Pennyroyal Plateau, and on the Mitchell Plain. The current ranges of these blind, depigmented forms are, for the

most part, allopatric and these crayfishes have retained primitive characteristics (plesiomorphy).

The cambaroid stock spread mainly to the north and east [e.g., ancestor of *C. (P.) nerterius* entered caves in West Virginia] but also extended south and westward where different epigeal ancestors entered subterranean waters in the Tennessee Valley, the Florida Panhandle region, and in the Ozarks.

#### *Crabs:*

The present distribution of freshwater crabs (Trichodactylidae, Pseudothelphusidae) can be summarized in terms of vicariance, dispersal, and "various dispersion events" (Rodriguez 1986). The wide ranging, polyphyletic trichodactylids and other relatives (originally from Africa) generally occupy large rivers at low elevations, demonstrate plesiomorphy, and have comparatively fewer adaptations to terrestrial environments. The narrow ranging pseudothelphusids and other groups (originally from West Africa) and India are usually found in small streams at higher altitudes and show progressive adaptations to air breathing. The Neotropical/Paleotropical disjunct distribution of crabs sharing synapomorphies of the buccal area and branchial chamber implies that pseudothelphusid freshwater crabs are a monophyletic group that was separated by a vicariant event (the break up of Pangaea) during the mid-Cretaceous. The pseudothelphusid morphocline in southern Mexico, based on the structure of the gonopod, follows a general westward direction and suggests a series of allopatric speciation of primitive demes, encompassing a progressive immigration along the westward geographical axis. Chance dispersal after the Miocene played a role in the disjunct distribution of species in the Lesser Antilles and Guianas. Independent invasion of the spelean environment by trichodactylid and pseudothelphusid ancestors of extant cavernicolous species occurred in Belize, Costa Rica, Cuba, Guatemala, Mexico, and Puerto Rico.

The two species of gecarcinids inhabiting caves in Cuba and Jamaica are troglloxenes and are far more frequently found in burrows in epigeal habitats. Ancestors of both undoubtedly were marine forms that invaded fresh waters.

Except for the troglobitic *Sesarma* (*Sesarma*) *verleyi* the remaining grapsid cavernicolous crabs are troglloxenes found in Cuba, Guatemala, and Jamaica and all have marine ancestors that invaded freshwater environments. Although not known, it is likely that the

larva of the troglobitic *S. (S.) verleyi* may complete its metamorphosis in fresh water.

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