THE CAVE FAUNA OF TEXAS
WITH SPECIAL REFERENCE TO THE WESTERN EDWARDS PLATEAU

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INTRODUCTION

Texas contains a rich but still poorly known cavernicole fauna. Approximately 1,040 terrestrial and 150 aquatic species have been recorded from the state. This number will doubtless greatly increase when large collections, especially of mites, centipedes, and miscellaneous insects, are identified and described. An estimated 81 aquatic and 161 terrestrial species are believed to be sufficiently cave-adapted in appearance to indicate that they are troglobites (restricted to caves). Additional troglobites probably exist in several groups not yet adequately studied taxonomically. The number of species, including troglobites, will also increase as additional caves are investigated. The degree of our ignorance of the state's cave fauna is well illustrated by the discovery in the last few years of several additional species of troglobite in Travis, Williamson, Hays, and Bexar Countiesthe most intensively studied counties in the state.

Stejneger's 1896 description of *Typhlomolge rathbuni*, the Texas blind salamander, from the artesian well in San Marcos, inspired several important studies of the cave and phreatic fauna of the San Marcos area. Additional random collections in Texas resulted in the discovery of several additional troglobites and troglophiles of interest. No systematic survey of the cave fauna of the state, however, existed prior to the formation of the Texas Speleological Survey (TSS) in 1961. The TSS began an active program of collection in all caves visited, with several trips specifically designed to sample cave fauna. The early results of these studies were published by Reddell (1965, 1966, 1967, 1970a, 1970b, 1970c). Mitchell and Reddell (1971) summarized the invertebrate cave fauna. Despite these efforts, the cave faunas of many areas remain extremely poorly known. Several counties known to contain caves have received no attention, while others have been only scantily surveyed. The poorest known parts of the state are parts of the Llano Region, the northern outliers of the Lampasas Cut Plains, and the isolated mountain ranges of West Texas (see Smith and Veni's "Karst Regions of Texas" chapter in this volume). The endangered species listing of seven species of cave arthropod in Travis and Williamson Counties has led to the most intensive investigation of any part of the state and perhaps the United States. Hundreds of new caves have been excavated or located and biologically studied to date, with studies continuing.

Caves occur in all parts of Texas, but the few known caves south and east of the Balcones Fault Zone appear to be too recent to harbor terrestrial troglobites. The discovery of the eyeless planarian *Dendrocoelopsis americana* (Hyman) in Rockwall County, a record of asellid isopods of the genus *Caecidota* (not represented by existing specimens) in a cistern in Panola County, and recent discoveries of eyeless amphipods and asellid isopods in coastal areas of the eastern United States indicate that these parts of the state may harbor an interesting groundwater fauna.

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The most remarkable aquatic fauna in the United States and the world exists in the vast underground Edwards (Balcones Fault Zone) Aquifer (Longley, 1981). Sampling of cave, well, spring, and interstitial habitats has resulted in the discovery of at least 50 species in this vast aquatic system. Doubtless, many more species await discovery. Aquatic species have also been found in other parts of the state, but these studies have been sporadic and probably represent only a small percentage of the fauna.

By far the most diverse terrestrial fauna occurs in the Balcones Fault Zone. This faunal region constitutes a transitional zone between the Coastal Plain and the Edwards Plateau. River and canyon incision and complex faulting have resulted in isolated exposures of cavernous limestone. As a result several groups have speciated to form numerous closely related species within a comparatively short distance. Of particular interest are spiders of the genera *Cicurina*, *Neoleptoneta*, and *Eidmannella*; pseudoscorpions of the genus *Tartarocreagris*; harvestmen of the genus *Texella*; millipedes of the genus *Speodesmus*; ground beetles of the genus *Rhadine*; and mold beetles of the genus *Batrisodes*.

The Llano Region continues to be poorly known with respect to its cavernicole fauna, but given the geologic complexity of this region it should produce numerous new locally endemic species. The few collections made in this extensive area indicate that each major outcrop will produce its own distinct suite of species.

The Edwards Plateau is an extensive area of flat-lying limestones dissected by stream channels. Deep stream incisions along the southeastern margins of the plateau have resulted in similar isolation of limestone areas. The resulting isolation speciation, albeit on a lesser scale, is similar to that seen along the Balcones Fault Zone. The western Edwards Plateau is discussed in more detail below.

The gypsum karst region of northwestern Texas contains a depauperate (relatively low species diversity) cave fauna with only two or possibly three troglobites known. This is probably indicative of the recent age of this karst.

By contrast, the gypsum karst of Culberson County contains several distinctive troglobites, including the isopod *Brackenridgia* new species, spider *Eidmannella bullata* Gertsch, the millipedes *Speodesmus tuganbius* (Chamberlin) and *Cambala reddelli reddelli* Causey, and an undescribed genus and species of the dipluran family Campodeidae.

ENDANGERED SPECIES

The extremely limited distributions of many troglobites make them particularly susceptible to extinction. This is especially true in areas undergoing rapid urbanization. The first species to be placed on the U.S. Fish and Wildlife Service endangered species list was the Texas blind salamander *Typhlomolge rathbuni* in 1967. This salamander, restricted to the San Marcos Pool of the Edwards (Balcones Fault Zone) Aquifer, is threatened by pollution as the city of San Marcos, lying directly above the aquifer continues to grow. It is also theatened by declining water levels in the Edwads Aquifer. Longley (1978), in a review of the status of the species, indicated that he did not feel the species was endangered. Recent declines in the water levels and several incidents of pollution from sewer leaks have led him to believe now that the species is in fact endangered (Longley, pers. comm.).

Five species of troglobitic invertebrates were listed by the U.S. Fish and Wildlife Service as endangered in 1988. These five species are the Tooth Cave spider *Neoleptoneta myopica* (Gertsch), the Tooth Cave pseudoscorpion, *Tartarocreagris texana* (Muchmore), the Bee Creek Cave harvestman *Texella reddelli* Goodnight and Goodnight, the Tooth Cave ground beetle *Rhadine pesephone* Barr, and the Kretschmarr Cave mold beetle *Texamaurops reddelli* Barr and Steeves. All were known from one or a few caves in and near Austin. Elliott (1989, 1990, 1993b) discussed the background leading to their listing and the subsequent studies resulting from that listing. Subsequent taxonomic study of *Texella reddelli* found that the original listing included populations properly assigned to a second species, later described as *Texella reyesi* by Ubick and Briggs (1992). It was also found that two of the populations originally listed as being *Texamaurops reddelli* were in fact an undescribed species that now bears the name *Batrisodes* (*Excavodes*) *texana* Chandler (1992). Since these populations were considered in the original listing and therefore the intent of the ruling was to protect them, *Texella reyesi* and *Batrisodes* (*Excavodes*) *texana* were also determined in 1993 to be properly considered endangered. The ranges of most of these species remain extremely limited despite the most intensive study of any cave area in the state. *Texella reyesi* has proven to be present in almost 100 caves, but its actual range has not been significantly increased. The discovery of this species in so many caves has been the direct result of surveys conducted on property proposed for development and thus every new population is protected only by the endangered status of the species (Elliott, 1991; Elliott

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and Reddell, 1989; Reddell and Elliott, 1991; Reddell, 1992).

The most immediate threat to the karst invertebrate fauna in the Austin area (and in fact throughout the Balcones Fault Zone and adjacent Edwards Plateau) is development. With the revitilization of the real estate market in the 1990s thousands of acres are being considered for housing and commercial sites in Travis and Williamson Counties. Similar development projects are proposed throughout the Central Texas area. Another major threat to the cave fauna is the red imported fire ant *Solenopsis* (*Solenopsis*) *invicta* Buren. This species has now invaded hundreds of caves in Central Texas. The disturbance caused by construction increases the habitat for fire ants and as urbanization progresses so has the intensity of fire ant activity in caves.

The fact that only seven species of cave invertebrate are presently considered endangered in Texas is no indication of the severity of the problem. Many additional species, described and undescribed, in the greater Austin area are protected only by the presence of the listed species in the caves. It is probably safe to say that there is no troglobitic species with a limited distribution in the area from the greater Austin area to San Antonio that is not equally endangered.

Intensive development in the San Antonio region led to a petition to the U.S. Fish and Wildlife service in 1992 by several environmental groups to list nine troglobites (one with two subspecies) as endangered. These include the spiders *Cicurina* (*Cicurella*) *baronia* Gertsch, *Cicurina* (*Cicurella*) *madla* Gertsch, *Cicurina* (*Cicurella*) *venii* Gertsch, *Cicurina* (*Cicurella*) *vespera* Gertsch, and *Neoleptoneta microps* (Gertsch); the harvestman *Texella cokendolpheri* Ubick and Briggs; the ground beetles *Rhadine exilis* (Barr and Lawrence), *Rhadine infernalis infernalis* (Barr and Lawrence), and *Rhadine infernalis ewersi* (Barr); and the mold beetle *Batrisodes* (*Excavodes*) *venyivi* Chandler. All of these species are restricted to Bexar County and most are known from only one or a few localities. Subsequent studies have not significantly extended the range of these species.

The listing and proposed listing of the "cave bugs" has created intense controversy in the Austin and San Antonio areas. A petition in 1993 by Williamson County was submitted to the U.S. Fish and Wildlife Service to delist the species on the grounds that they should never have been listed in the first place. In 1994 this petition was found to be without sufficient basis for acceptance and was rejected (Fish and Wildlife Service, 1994). A lawsuit by Williamson County has been filed in U.S. District Court against the U.S. Fish and Wildlife Service to remove *Rhadine persephone* and *Texella reyesi* from the endangered species list.

Despite the necessity by the land owner to conduct studies of caves on land proposed for large-scale development and to set aside preserves for protection for the caves and karst features, virtually every development has been approved once there is a guarantee that the caves are protected. Numerous examples of this exist in the Austin area and demonstrate that responsible development and the protection of the cave fauna can coexist.

CAVE FAUNA OF THE WESTERN EDWARDS PLATEAU

The first species encountered (at least in the summer months) in a typical cave in the Edwards Plateau is likely to be the daddy longlegs harvestman *Leiobunum townsendii*. This scavenging species forms enormous colonies on the walls and ceiling of caves. Farther into the cave one may encounter two large, impressive species on cave walls: spiders of the genus *Ctenus* and "whipless whipscorpions" or "scorpion spiders" of the genus *Phrynus*. A third large arachnid found on walls, floor, and ceilings is the black scorpion *Vaejovis reddelli*. In caves with large entrances cave swallows, *Hirundo fulva pallida*, may form sizable colonies. Their nests are open-top mud constructions on the cave walls. Farther back in the cave animal life typically becomes sparse. *Cambala* millipedes, which coil up in response to light even though they are eyeless, and the eyed, red, ant-like *Rhadine* beetles are frequently found on bat guano. Wet flowstone may be the home to orange *Hoplobunus* cave harvestmen, white *Speodesmus* millipedes, and white *Texoreddellia* silverfish *Brackenridgia* isopods are more likely to be found on rotting wood than anywhere else. Rocks hide small blind spiders and mold beetles, along with other secretive fauna. The centipede *Theatops phanus* is most common on clay banks bordering streams, but may occur on moist flowstone.

Large freetail bat caves, such as Fern Cave in Val Verde County, present their own biological challenge to exploration. In addition to the millions of bats, the cave will harbor an even larger population of annoying invertebrates. Mites rain, along with bat urine and guano, from the ceiling to cover the explorer. The air is filled with small gnats that seem to have a particular affinity for the nose, eyes, and mouth. The guano literally moves with the activity of untold millions of mites, ticks, pseudoscorpions, dermestid and other beetles, and fleas. This is a fascinating habitat, but one not for the squeamish. Some caves harbor the old man

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bat *Moormoops megalophylla*, a tropical species that barely ranges into Texas (see description of Webb Cave in "Texas Wild Caves" in this volume).

The cave fauna of the western Edwards Plateau is apparently far less diverse than that of the Balcones Fault Zone. There are several possible explanations for this. One, of course, is that the area has received far less attention than has the more easily accessible caves of the Balcones Fault Zone and certainly more species await discovery. It is more likely, however, that the reduced fauna in this region is real and reflects the past history of the region.

Caves along the Balcones Fault Zone and in the deeply incised margins of the eastern Edwards Plateau certainly became available for colonization earlier than have the caves of the comparatively flat uplands of the western plateau. Ancestral species along the Balcones Fault Zone may have survived longer in the mesic habitats along streams emptying into the coastal plain, thus existing long enough to invade caves when they became accessible. In contrast, earlier drying of the western Edwards Plateau may have led to the extinction of many possible colonizers prior to development of openings in the karst.

Several genera that have speciated abundantly to the east have produced few or no troglobites in the western Edwards Plateau. These include *Neoleptoneta* and *Eidmannella* spiders, *Tartarocreagris* pseudoscorpions, *Texella* harvestmen, *Speodesmus* millipedes, *Rhadine* ground beetles, and *Batrisodes* mold beetles. This is partly the result of the isolation of populations by stream incision and faulting, resulting in distinct, closely related species in nearby caves. Cavernous limestone extends across virtually the entire western Edwards Plateau with comparatively little faulting. Furthermore, streams have usually not completely dissected the cavernous strata, thus allowing migration under dry canyon bottoms.

Only two aquatic troglobites are known from the western Edwards Plateau. The amphipod *Stygobromus hadenoecus* has been found only in the Devil's Sinkhole, Edwards County. The only other aquatic species is the isopod *Cirolanides texensis*. This species is known from O-9 Well, Crockett County; Cave Y, Scheicher County; and Devil's Sinkhole, Edwards County. It probably will be found in most deep caves containing permanent streams and lakes.

The terrestrial fauna includes 21 species, of which nine are *Cicurina* (*Cicurella*) spiders. Other species endemic to the caves of this region include an undescribed schizomid of the family Protoschizomidae, an undescribed species of the spider genus *Neoleptoneta*, two undescribed species of the milliped genus *Speodesmus*, and an undescribed species of mold beetle of the genus *Batrisodes*. The isopod *Brackenridgia cavernarum* is known only from the western Edwards Plateau and along the Balcones Fault zone. The range of the harvestman *Hoplobunus madlae* extends west to the southern edge of the Balcones Fault Zone. The range of the centipede *Theatops phanus*, as presently defined extends to the Balcones Fault Zone but probably this species is restricted to the Crockett, Schleicher, and Sutton counties. The millipedes *Cambala speobia* and *Speodesmus echinourus* and the silverfish *Texoreddellia texensis* are widely distributed throughout Central Texas.

REVIEW OF THE TEXAS CAVE FAUNA

Space does not permit a full discussion of the cave fauna of Texas. The following discussion emphasizes the troglobites, with reference only to those troglophiles (somewhat cave-limited species) and trogloxenes (species that roost in caves) of unusual interest (see Appendix D at the back of this volume for a list of Texas troglobites).

Phylum Platyhelminthes
Order Tricladida (flatworms)

Two genera of flatworms are represented in Texas caves by troglobites. An eyeless population of *Dendrocoelopsis americana* (Hyman) (Dendrocoelopsidae) has been reported from Soda Water Well in Rockwall County (Kawakatsu and Mitchell, 1984). This species is also known from eyed populations in caves and springs in Arkansas and Oklahoma. Five species of *Sphalloplana* have been described from single caves in Hays, Kendall, Travis, San Saba, and Mason counties (Mitchell, 1968). Without discussion, Kenk (1972) placed the four species described by Mitchell in the synonymy of *Sphalloplana mohri* Hyman from Ezell's Cave, Hays County. Given the isolation of each cave population and the absence of supporting evidence by Kenk, all of these species names probably should be considered valid.

Phylum Mollusca
Class Gastropoda (snails)

No terrestrial snails are troglobites in Texas. The only undisputed troglophilic snail is *Helicodiscus eigenmanni* Pilsbry. This species is abundant in caves

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throughout Texas. Twelve species of troglobitic snails (Hydrobiidae) have been reported from cave and phreatic waters in Texas (Hershler and Longley, 1986a, b). This may represent only a small percentage of the species that exist in the Edwards and associated aquifers.

Phylum Annelida
Class Hirudinea (leeches)

A single undescribed species of the leech genus *Mooreobdella* is apparently troglobitic in Texas caves. It has only been found in Ezell's Cave and the artesian well at San Marcos. This appears to be the only troglobitic leech in the United States.

Phylum Arthropoda
Class Crustacea
Subclass Eucopepoda (copepods)

Two species of tiny, eyeless copepods of the genus *Cyclops* were described by Ulrich (1902) from the artesian well at San Marcos. The descriptions are inadequate for determination of the species. Two species of eyeless copepod have been found in the artesian wells near San Antonio but remain undetemined.

Subclass Podocopa (ostracods)

One or more undescribed, troglobitic ostracods of the genus *Candona* have been found in Texas caves. Of special interest is an undescribed species of the genus *Prionocypris* from Salamander Cave, Travis County. This genus is otherwise known from Canada. The tiny, commensal *Sphaeromicola moria* was described by Hart (1978) from specimens attached to the isopod *Cirolanides texensis* in Rambie's Cave, Uvalde County. This is the only record for this genus in the United States.

Subclass Malacostraca
Order Bathyllenacea

The only species of this order in Texas is *Iberobathynella bowmani* (Delamare Deboutteville, Coineau, and Serban, 1975). It has been found in Roaring Spring, Dickens County, and in deep gravel deposits in Gorman Cave, San Saba County.

Order Thermosbaenacea

Maguire (1965) described *Monodella texana* from Ezell's Cave, Hays County, as the first representative of the order in the Western Hemisphere. It has since been found in artesian wells in Hays and Bexar counties (Stock and Longley, 1981). Numerous species in the order have since been described from many parts of the Caribbean.

Order Amphipoda (amphipods)

Texas contains a remarkable diversity of amphipods (shrimp-like crustaceans) in its underground waters, with 21 species having thus far been described. Several additional species await description. Ten species of the genus *Stygobromus* have been described from Texas caves (Holsinger, 1967). At least two additional new species are known. Most have fairly limited distributions, but *S. russelli* (Holsinger) ranges widely throughout the Balcones Fault Zone and eastern Edwards Plateau. Of great interest is the appearance of ten species in five families in the artesian well at San Marcos (Holsinger and Longley, 1980). Four additional species have been described from caves and springs (Holsinger, 1992).

Order Isopoda (isopods)

Troglobitic aquatic and terrestrial isopods occur in Texas caves. The terrestrial fauna includes three species in the family Trichoniscidae (Vandel, 1965). The terrestrial *Amerigoniscus gipsicolus* Vandel is known only from a gypsum cave in King County. Two species of *Brackenridgia* are known from the Balcones Fault Zone and Edwards Plateau. A third species of *Brackenridgia* from the gypsum plain of Culberson County awaits description. One or more minute species have been found in caves in Bexar, Travis, and Williamson counties, but have yet to be studied. The aquatic fauna includes species of Asellidae, Stenasellidae, and Cirolanidae. Two genera of asellid isopods have been found in Texas caves (Steeves, 1968; Bowman and Longley, 1976; Lewis, 1983). *Caecidotea* includes two described and at least two undescribed species, while *Lirceolus* contains two species. The Stenasellidae is represented only by *Mexistenasellus coahuila* Cole and Minckley. This species, described from springs at Cuatro Ciénegas de Carranza, Coahuila, México, was recently reported from springs and artesian wells in Bexar County and the hyporheic habitat in Medina County (Bowman, 1992). The family Cirolanidae includes two species. *Cirolanides texensis* Benedict is widespread in Texas cave and phreatic waters (Bowman, 1964, 1992). *Speocirolana hardeni* was described by Bowman (1992) from artesian wells in Bexar County and from Emerald Sink and springs in

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Val Verde County. The genus *Speocirolana* is otherwise known only from cave and phreatic habitats in Mexico.

Order Decapoda (shrimps, crayfish, and crabs)

Only two decapod crustaceans, both shrimp, are troglobitic in Texas caves. *Palaemonetes antrorum* Benedict is known from artesian wells and caves in Bexar and Hays counties, while *P. holthuisi* Strenth has been found only in Ezell's Cave (Strenth, 1976). It is notable that no troglobitic crayfish occur in the state, although several species are present as troglophiles. Of some interest is the appearance in Estelline Salt Spring, a deep artesian salt spring in Hall County, of an endemic crab species, *Hemigrapsis estellinensis* Creel, of the otherwise marine family Grapsidae (see the spring description in "Unusual Texas Caves and Karst" in this volume).

Class Arachnida
Order Scorpiones (scorpions)

The only scorpion regularly found in Texas caves is the troglophilic *Vaejovis reddelli* Gertsch and Soleglad (1972). This large (55 mm or more in adults) brown to black scorpion is widely distributed throughout the Balcones Fault Zone and Edwards Plateau. It is present in some caves in considerable numbers and it is frequently found on the cave ceiling. It is known to feed on cave crickets, who also roost on the ceiling. An immature has been observed feeding on a small blind spider. Although not dangerous, its sting can cause considerable discomfort (Reddell, 1988).

Order Schizomida

The largely tropical order Schizomida is represented in Texas caves by an undetermined species of the family Protoschizomidae (Cokendolpher and Reddell, 1992). A single immature was found in Seminole Sink, Val Verde County. Schizomids, which are small, ant-like relatives of the large "vinegaroon", are otherwise known only from eastern and southern Mexico.

Order Amblypygida (whipless whipscorpions)

The order Amblypygida is largely tropical in distribution but reaches the southwestern United States. They are also known as "scorpion spiders," which better describes their apperance. They have a flattened body with segmented abdomen and long legs. The pedipalps are raptorial and the first legs are long and antenna-like. They are nonvenomous and shy. An apparently undescribed species of the genus *Phrynus* has been found in several caves in the western Edwards Plateau. This species roams actively over the cave walls. The presence of females bearing young in the dark zone clearly indicates that this is a troglophile.

Order Araneae (spiders)

The spider fauna of Texas caves is remarkably rich with four families having contributed troglobites. Gertsch (1992) in a brief review of the North American fauna reports 61 species of troglobitic spider in Texas. The family Linyphiidae is represented only by *Islandiana unicornis* Ivie from caves in Childress and Wheeler counties in the northwestern Texas gypsum karst. Five species of the family Nesticidae, all in the genus *Eidmannella* have been described from caves in Texas. Most are extremely limited in distribution. The family Leptonetidae includes seven described and at least two undescribed species of *Neoleptoneta* from Texas caves. Each species is limited to one or a few nearby caves. However, the most remarkable assemblage of troglobitic spiders belongs to the family Dictynidae. Forty-six eyeless species of *Cicurina* (*Cicurella*) are known from Texas caves. Most of these appear to be restricted to a single cave, with a few occurring in small clusters of associated caves. Preliminary analysis indicates that these distributions fit well with geologic barriers also of significance to other groups. *Cicurina* (*Cicurella*) has been observed feeding on an immature *Speodesmus* millipede. It is worth noting a few common troglophilic spiders in Texas caves. *Achaearanea porteri* Banks (Theridiidae), *Eidmannella pallida* Emerton (Nesticidae), and *Cicurina* (*Cicurusta*) *varians* Gertsch and Mulaik are virtually omnipresent in Texas caves. *Eidmannella pallida*, however, is usually absent from caves containing the eyeless species.

Order Pseudoscorpionida (pseudoscorpions)

Muchmore (1992) in a review of the cavernicolous pseudoscorpions of Texas caves reports 24 species, of which nine appear to be troglobitic. Three or four additional species have been found since that report. The family Chthoniidae includes one described troglobite in Texas caves, *Tyrannochthonius troglodytes* Muchmore, from Rock Slab Cave, a granite cave in Llano County. An additional species of *Tyrannochthonius* from a cave in Bexar County and one or more species of *Aphrastochthonius* from caves in Travis and Williamson counties appear to be undescribed troglobites. The family Neobisiidae

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includes five described and two undescribed species of the genus *Tartarocreagris*. These species are all highly localized and known only from one or a few nearby caves in Bexar, Burnet, Travis, and Williamson Counties. The family Bochicidae is represented only by *Leucohya texana* Muchmore from Frio Queen Cave, Uvalde County. This genus includes two other species, both from Nuevo León, México. *Tartarocreagris* has been observed feeding on nymphs of *Ceuthophilus* cave crickets.

Order Opiliones (harvestmen)

Two genera, both in the family Phalangodidae, contain troglobites in Texas caves. The tropical genus *Hoplobunus* includes two described species from caves in the southern Balcones Fault Zone and Edwards Plateau (Goodnight and Goodnight, 1968). These two species probably do not belong in *Hoplobunus*, but are clearly closely related to the Mexican fauna. It is also likely that the species now described actually include a complex of closely related species. The genus *Texella* was revised by Ubick and Briggs (1992). They report 13 species from Texas caves. These range from species with short legs and well-developed eyes to highly troglomorphic eyeless species. The genus ranges from California into eastern Texas and includes both epigean and cavernicole populations throughout its range. The common daddy-long-legs harvestman *Leiobunum townsendii* Weed, a scavenger, forms enormous colonies in the entrance area of most caves in Texas during the summer months, but disappears in the winter. They emerge at night to feed and, like cave crickets, probably are a significant source of nutrient input into caves.

Class Chilopoda (centipedes)
Order Geophilomorpha

The long slender centipedes of the order Geophilomorpha are an abundant element of the soil fauna. Two Texas cavernicole species, probably of the family Himantariidae, are of unusual interest in that they have much longer legs than epigean species and have been observed crawling across clay banks in direct association with other highly cave-adapted species. This behavior is quite unlike other members of the order, which normally burrow in silt, and indicates that they are troglobitic. One species is known from Harrell's Cave, San Saba County, and the other from two caves in Williamson County.

Order Lithobiomorpha

Lithobiomorph centipedes are frequently encountered as accidentals and troglophiles in Texas caves. Two species of the order in Texas caves appear to be troglobitic. Both are totally eyeless, largely depigmented, and have extremely long, slender legs. One from O-9 Well, Crockett County, is as yet undetermined. An undescribed species of the genus *Neolithobius* is abundant on clay banks along the stream passage in Powell's Cave, Menard County.

Order Scolopendromorpha

A single species of the family Cryptopidae is described from Texas caves. *Theatops phanus* Chamberlin was described from Stephenson Sinkhole, Sutton County. It was later recorded from caves in Menard and Williamson counties. This species is totally eyeless, depigmented, and with extremely long appendages and is certainly troglobitic. Recent collections of the genus from Bexar, Crockett, Schleicher, Travis, and Williamson counties indicates that what was previously considered to be a single species is in fact a complex of closely related species. It is of interest that more eastern species are less highly troglomorphic than western species. Shelley (pers. comm.) reports that this species occurs on the surface in eastern Texas but that there it is dark and with short appendages. There is little question that the highly troglomorphic populations are genetically distinct from these surface forms.

Class Diplopoda (millipedes)
Order Spirostreptida

Two species of *Cambala* are known from Texas caves (Causey, 1964). *Cambala speobia* (Chamberlin) is an eyeless species ranging from the Balcones Fault Zone to the western edges of the Edwards Plateau. It is a recent troglobite as evidenced by its retention of pigment and reaction to light—it coils up though it is eyeless. *Cambala reddelli* Causey includes two subspecies. *C. reddelli reddelli* Causey is known from caves in the gypsum plain of Culberson County and from caves in New Mexico. *C. reddelli inornatus* Causey is known only from caves in the northwest Texas gypsum karst. Both subspecies retain small ocelli. Shelley (1979) placed *C. reddelli* in the synonymy of *C. speobia* and reported populations of the species from epigean localities in New Mexico. The two nominate species are allopatric in their distribution and are easily separable by several morphological characters. Their

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close relationship is obvious, but it is thought here that they should be considered distinct species.

Order Siphonophorida

The millipede order Siphonophorida is a primarily tropical group with two epigean species known from southern Texas. Recent collections in several Texas caves have included specimens of at least two species. These were found crawling on clay banks in total darkness in direct association with other troglobites, indicating that these species may be troglobitic. Further study is necessary to determine the ecological status of these populations but they represent the only North American cave representatives of the order.

Order Polydesmida

Three genera of polydesmid millipede are of interest in the Texas cave fauna. The hot house millipede, *Oxidus gracilis* (Koch), is frequently present in vast numbers in caves in urban areas. The appearance of this exotic species in caves is of concern because of its breeding success and the likelihood that it may be able to successfully out-compete the troglobitic millipede fauna. A second introduced species, also present in Texas caves as a troglophile, is *Myrmecodesmus formicarius* Silvestri. This species was described from fire ant nests in Veracruz. It apparently has moved north from tropical America with the fire ants and is now established in some Texas caves. Three species of the exclusively troglobitic genus *Speodesmus* have been described from Texas caves, but several additional species await study (Elliott, 1976). *Speodesmus bicornourus* Causey is a large species known with certainty only from caves in Travis and Williamson counties. *Speodesmus echinourus* Loomis is a smaller, less troglomorphic species distributed from southern Travis County south to Bexar County and into the Edwards Plateau to the west. *Speodesmus tuganbius* (Chamberlin) is found in the gypsum plain of Culberson County and many caves in New Mexico. At least six new species have been found in Texas caves, most restricted to one or a few nearby caves in isolated areas. However, one undescribed species, is sympatric with *S. bicornourus* in southern Travis County (Elliott, 1976).

Class Insecta
Order Collembola (springtails)

Springtails are tiny, hopping insects. Only one species is probably troglobitic in Texas caves. *Pseudosinella violenta* Folsom is omnipresent in Texas caves, frequently in vast numbers. This is certainly an extremely important element in the cave ecosystems as they are consumed by many small predators. An undescribed species of the largely tropical genus *Oncopodura* has been found in caves in Travis and Williamson counties.

Order Entotrophi (Diplura)

Diplurans are small, wingless insects with a double tail. Two families of entotroph contain troglobites in Texas caves. The family Campodeidae, with two long tails, is frequently found and troglobites belonging to two or more genera are known, but none have received taxonomic study. Of great interest is the presence of a highly troglomorphic species of the family Iapygidae in Texas caves. Iapygids have claw-like tails. This is only the third known species of troglobite in the family, the other two occurring in Africa and Europe. *Mixojapyx reddelli* Muegge (1992) was described from caves in Uvalde, Kimble, Travis, Menard, Bexar, and Comal counties. The body length may reach 48 mm, appendages are extremely elongate, and it contains enormous numbers of setae. Additional specimens probably belonging to this species have been found in caves in Crockett and Schleicher counties. The species is extremely rare with only one specimen found in most caves. As in the case of the centipede genus *Theatops*, this species is probably a complex of closely related species.

Order Thysanura (silverfish)

The only unquestioned troglobitic thysanuran in the United States is *Texoreddellia texensis* (Ulrich) from numerous caves in Texas (Wygodzinsky, 1973). It is a white, elongated insect with three long tails.This species ranges from the western edge of the Edwards Plateau to the Balcones Fault Zone. Considerable variation exists between different cave populations and it is possible that this is a complex of closely related species. What appears to be an undescribed species of troglobitic Nicoletiidae has been found in Rattlesnake Cave, Ward County.

Order Saltatoria

The only genus of cave cricket in Texas caves is *Ceuthophilus*, with numerous described and undescribed species known. Three species occur sympatrically in caves along the Balcones Fault Zone. *Ceuthophilus* (*Geotettix*) *cunicularis* Hubbell, *C.* (*C.*)

secretus Scudder, and *C.* (*C*). new species. The first species is usually found on the cave floor while the others roost on the ceiling. Two other described species are common in Texas caves. *Ceuthophilus* (*C*). *conicaudus* Hubbell is abundant in caves on the Edwards Plateau, where it is frequently found with one or more undescribed species. *Ceuthophilus* (*Geottettix*) *carlsbadensis* Caudell is a frequent inhabitant of caves in the gypsum plain of Culberson County. Cave crickets are a critical element in the Texas cave ecosystems, emerging at night to feed and returning to the caves to roost during the day. They lay eggs in cave sediments and the nymphs emerge. At least two species of troglobitic *Rhadine* beetles prey on cricket eggs, and the cricket nymphs serve as prey items for other active predators. Their droppings serve either directly as food or as a medium for the growth of fungus on which millipedes, collembolans, and other species feed.

Order Coleoptera (beetles)

Four families of beetles include troglobites in Texas caves, while several families contribute a significant number of troglophiles. Two families of aquatic beetles have each contributed one species to the fauna of the Edwards Aquifer. The dytiscid *Haideoporus texanus* Young and Longley (1976) was described from the artesian well at San Marcos, and it also has been found in Ezell's Cave in San Marcos, Hays County. This is the only troglobitic predaceous diving beetle known in the United States. Barr and Spangler (1992) described a remarkable aquatic beetle from Comal Springs, Comal County. *Stygoparnus comalensis* is the first troglobitic species of the family Dryopidae. Its occurrence in Comal Springs is especially interest- ing since the larvae of this family are terrestrial. The adults were collected in the spring mouth, presumably because of the concentration of food there. It is likely that their normal habitat is open caverns farther back in the system that feeds the springs.

The family Carabidae is represented in Texas caves by several genera, but only *Rhadine* contains troglobites. This genus includes both eyed and blind species in Texas, with all of the eyed species belonging to the *subterranea* group (Barr, 1974). Eyed species of interest include *R. babcocki* (Barr), known only from caves in the western Edwards Plateau, and *R. howdeni* (Barr and Lawrence), known from caves throughout the Edwards Plateau and along the Balcones Fault Zone. Both species are frequently found associated with bat guano. The *subterranea* group includes 13 described species, five of which have subspecies. With the exception of two species from caves in northern Mexico, all are endemic to Texas. Two undescribed species have recently been found from caves in Hays and Coryell counties. The troglobites are restricted to the Balcones Fault Zone and eastern edge of the Edwards Plateau. Sympatry occurs in several areas, with one species in a pair being slender and the other robust. Mitchell (1971a, b, c) has discussed in detail the distribution and dispersion, preference responses and tolerances, and feeding habits of *Rhadine subterranea subterranea* (Van Dyke). He discovered that in Beck Ranch Cave, Williamson County, the species feeds almost exclusively on the eggs of cave crickets (*Ceuthophilus* spp.) buried in fine-grained, white, calcareous deposits. This study demonstrated the importance of cave crickets to the cave ecosystem. *Rhadine noctivaga* Barr has also been observed exhibiting similar behavior in similar deposits in caves in northern Williamson County. The frequency with which beetles have been noted on cave walls and ceilings indicates that they are probably searching for cricket eggs in caves where these deposits do not occur.

The family Pselaphidae is well-represented in Texas caves, but rare in numbers. Given the small size of these beetles they are probably more common than presently known. *Texamaurops reddelli*, the first troglobitic pselaphid from Texas, was described by Barr and Steeves (1963) from Kretschmarr Cave, Travis County. It remains an extremely rare species known from only a few nearby caves. Chandler (1992) in a review of the pselaphid fauna of Texas caves records 12 species, of which five (including *T. reddelli*) are troglobitic. The remaining four troglobites belong to *Batrisodes* (*Excavodes*) and all are known only from the Balcones Fault Zone. An undescribed blind species of *Batrisodes* (*Babnormodes*) has recently been found in Tippit Cave, Coryell County. Nothing is known of the feeding habits of these species. All are extremely rare and occur only on the underside of rocks buried in silt.

Troglophiles in the families Leiodidae, Ptinidae, Staphylinidae, and Tenebrionidae are frequently encountered in Texas caves. The rove beetle *Eustilicus condei* (Jarrige) (Staphylinidae), is abundant in Texas caves and has never been found on the surface, indicating it may be an incipient troglobite. Records of the species from caves in Mexico (Herman, 1970) are in error and the species remains known only from Texas (Herman, pers. comm.). *Ptomaphagus* (*Adelops*) *cavernarum* Schwarz (Leiodidae) is known from numerous caves (Peck, 1973). The spider beetle *Niptus abstrusus* Spilman (Ptinidae) was described from bat guano deposits in Fern Cave, Val Verde County (Spilman, 1968). This species has also been found in fossil packrat middens in Big Bend National Park

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(Ashworth, 1973). Numerous species of large, black, tenebrionid ("darkling") beetles are known from Texas caves. *Eleodes*, *Embaphion*, and other genera are frequently found in bat guano deposits.

Order Hymenoptera

The only hymenopteran of significant interest to the Texas cave fauna is the red imported fire ant *Solenopsis* (*Solenopsis*) *invicta* Buren. Infestations of this species were first noted in Texas caves in 1988. As the range of the species has increased and as urbanization has encroached onto the karst along the Balcones Fault Zone, fire ants have placed increased pressure on the cavernicole fauna. Elliott (1992b, 1993a) has detailed control measures and the impact of fire ants on the cave ecology. Next to actual destruction of caves during quarrying and urban construction, fire ants probably constitute the greatest threat to cave ecosystems.

Phylum Chordata
Class Teleostomi
Order Siluriformes (catfish)

Two species of blind catfish have emerged from deep artesian wells in the San Antonio area of Bexar County. These remarkable fish are known from depths as great as 582 m. *Trogloglanis pattersoni* Eigenmann, the Toothless blindcat, apparently feeds by scraping organic material from the walls of the cavernous openings intersected by the wells. *Satan eurystomus* Hubbs and Bailey, the widemouth blindcat, feeds on crustaceans and other arthropods inhabiting the deep wells. The status of these two species has been studied by Longley and Karnei (1979a, b).

Class Amphibia
Order Urodela (salamanders)

The first troglobite to be described from Texas was the blind salamander *Typhlomolge rathbuni* Stejneger. This species emerged from an artesian well in San Marcos, Hays County. The unusual nature of the species inspired additional work in caves in the area and additional populations were discovered in the immediate vicinity. The species remains known only from the San Marcos Pool of the Edwards (Balcones Fault Zone) Aquifer (Russell, 1976). Smith and Potter (1946) described *Eurycea latitans* from Cascade Caverns, Kendall County. This species is now known from a few nearby caves. The third troglobitic species to be described was *E. troglodytes* Baker (1957) from Valdina Farms Sinkhole, Medina County. A fourth species, *Eurycea tridentifera*, was added by Mitchell and Reddell (1965) from Honey Creek Cave, Comal County. This species has since been reported from several other caves in Comal and one in Bexar County. Potter (1963) included the description of *Typhlomolge robusta* from a water-filled crevice in the bed of the Blanco River in an unpublished thesis. Longley (1978) in a review of the status of *T. rathbuni* used the name with a brief diagnosis, thus inadvertently validating the name. The species, still known only from the original specimen, was redescribed by Potter and Sweet (1981). Mitchell and Reddell (1965) and Mitchell and Smith (1972) considered the genus *Typhlomolge* to be invalid, but Sweet (1977) provided evidence that the two genera are in fact distinct. Sweet (1984) also considered *E. latitans* and *E. troglodytes* to represent hybrid populations of *E. tridentifera* and the spring salamander *E. neotenes* Bishop and Wright. Recent studies of all of the spring and cave salamanders of Texas by Paul Chippendale, David Hillis, and Andy Price in Austin indicate that the taxonomic status of these salamanders is far more complex that has previously been thought and that several species are represented in the Texas cave and surface fauna.

Any final decision on the described species and the generic status of all of the species must await completion of their genetic studies.

Two other species of salamander are frequent inhabitants of Texas caves. The white-throated slimy salamander *Plethodon albagula* Grobman is common in entrance areas of caves along the Balcones Fault Zone. The tiger salamander *Ambystoma tigrinum* Green is found in caves in the northwest Texas gypsum karst.

Order Anura (frogs)

Two species of cave-dwelling frog in Texas are of sufficient interest to warrant mention. The tiny cliff frog *Syrrhophus marnocki* Cope is frequently found in caves along the Balcones Fault Zone and Edwards Plateau. The barking frog *Hylactophryne latrans* (Cope) is occasionally seen in caves along the Balcones Fault Zone.

Class Reptilia
Order Serpentes

Non-poisonous snakes are occasionally found in the entrance area of caves, but none are closely associated with caves. The only poisonous species of concern are copperheads, *Agkistrodon contortrix* (Linnaeus), and rattlesnakes of the genus *Crotalus*. Copperheads are occasionally found in entrance areas in caves along the

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Balcones Fault Zone. By far the most dangerous snake likely to be found in Texas caves is the western diamondback rattlesnake, *Crotalus atrox* Baird and Girard. It has been found in numerous caves throughout the state and anyone entering caves should take extra care.

Class Aves
Order Passeriformes

The only bird closely associated with Texas caves is the cave swallow *Hirundo fulva pallida* Nelson. This species forms large colonies in caves from the Edwards Plateau west to New Mexico. The species has been studied in some detail by Selander and Baker (1957) and Martin et al. (1977).

Class Mammalia
Order Chiroptera

Numerous species of bat have been found in Texas caves, but five are of special significance. Townsend's big-eared bat, *Plecotus townsendii pallecens* (Miller), hibernates in caves in the northwestern gypsum karst. The species has also been seen in caves in Kinney, Terrell, and Val Verde counties (George Veni, pers. comm.). The old man bat *Mormoops megalophylla* Peters reaches its northern distributional limit in Texas. Several populations in the thousands occur in caves of the Stockton and western Edwards Plateau. The eastern pipistrelle *Pipestrellus subflavus* (F. Cuvier) sometimes roosts near cave entrances as a solitary bat or in small clusters. The two most significant bats in Texas caves are the Mexican free-tailed bat *Tadarida brasiliensis mexicana* (Saussure) and the cave myotis *Myotis velifer incautus* (J. A. Allen). Freetails, though occasionally present in small colonies, are most noted for their enormous matenity colonies. Estimates of population size extend into the tens of millions. This species has been extensively studied, including a pioneering study by Eads, Wiseman, and Menzies (1957). Mitchell (1970) has studied the unique fauna inhabiting freetail bat guano in Fern Cave, Val Verde County. He demonstrates the enormous number of carabid, dermestid, and ptinid beetles, pseudoscorpions, fleas, and other species inhabiting the guano. The most commonly encountered bat in Texas caves is the cave myotis, or Mexican brown bat. This species is found in caves throughout the state. Colony size may range from a few dozen to thousands of individuals. Hibernating colonies are known from caves in the northwestern gypsum karst. The guano of this species is an important source of nutrient input in many caves.

Order Carnivora

Skunks, ringtails, raccoons, and bobcats have been observed in Texas caves. The raccoon *Procyon lotor* (Linnaeus), is the only species that appears to make a significant contribution to nutrient input in the caves. Some caves are frequented by large numbers of raccoons and their droppings may be found well back into the dark zone. The droppings are fed on directly, but more importantly fungus growing on the droppings provides food for springtails and other species which are in turn prey items for the predatory troglobites.

ZOOGEOGRAPHY

The cave fauna of Texas includes representatives of several different ancestral lineages. The history of the various groups is a reflection of past climatic and geologic events, time of availability of caves for colonization, and the ancestral fauna inhabiting the surface.

The aquatic fauna is derived both from freshwater and marine ancestors. The flatworms, snails, leeches, bathynellacean, *Candona* and *Prionocypris* ostracods, copepods, *Stygobromus* amphipods, asellid isopods, shrimp, beetles, fish, and salamanders are derivates of freshwater ancestors. The ostracod genus *Sphaeromicola* is known only from cirolanid isopods and has apparently evolved with those species after invasion of freshwater. The thermosbaenaceans; artesiid, bogidiellid, and hadziid amphipods; and cirolanid and stenasellid isopods exhibit a "Tethyan" distribution. These all belong to groups known from subterranean waters around the Mediterranean Sea and Caribbean Sea and apparently represent relicts of the ancient Tethys Sea prior to the breakup of Gondwanaland. Invasion into the caves of Texas from marine waters had to have occurred in the Cretaceous or early Cenozoic at the time when uplift caused the Cretaceous seas to retreat. Some species at least probably entered caves via interstitial spaces along the margins of the limestone. The discovery of amphipods and isopods in this habitat reinforces this assumption. Holsinger and Longley (1980) and Holsinger (1992) discuss in detail the zoogeography of the Texas amphipod fauna.

The terrestrial fauna includes species derived, some probably very recently, from surface ancestors still occupying the surface in, or recently extinct from, the same area. These include all of the spiders, *Tyrannochthonius* pseudoscorpions, *Texella* harvestmen, *Theatops* centipedes, ground beetles, and mold beetles. The presence of small eyes in some

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species of *Tartarocreagris* pseudoscorpions indicates that a surface ancestor of the cave species will be found on the surface.

The millipede genus *Cambala* does not occur on the surface in the areas where troglobitic species occur, but is known from eastern Texas and from the mountains of New Mexico, indicating that these recent troglobites have become cave isolates as a result of the drying of the karst areas of Texas.

Species with affinities to the western fauna include the isopods *Brackenridgia cavernarum* and the pseudoscorpions *Aphrastochthonius* new species and *Archeolarca guadalupensis.*

The isopod *Brackenridgia* new species, the milipedes *Cambala reddelli reddelli* and *Speodesmus tuganbius*, and the entotroph Campodeidae new genus and species inhabit the gypsum karst of Culberson County. This karst is only a few kilometers from the vast limestone reef of the Guadalupe Mountains. Canyons in the mountains have deposited deep accumulations of gravels that extend from the base of the mountains to partially overlie the gypsum karst. Since the same troglobitic species are also found in the Guadalupe Mountains, it is likely that these species have migrated through the deep gravel deposits into the caves of the gyspum karst.

Of special interest are several species that are most closely related to tropical species and are now relicts in Texas caves. These include the isopod *Brackenridgia reddelli*, the schizomid of the family Protoschizomidae, the pseudoscorpion *Leucohya texana*, the harvestmen of the genus *Hoplobunus*, the collembolan *Oncopodura* new species, the earwiglike entotroph *Mixojapyx reddelli*, and the silverfish *Texoreddellia texensis*.

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