Stweard B. Peck-A Summary of Diversity and Distribtuion of the Obligate Cave-Inhabiting Faunas of the United States and Canada. *Journal of Cave and Karst Studies 60*(1): 18-26.

A SUMMARY OF DIVERSITY AND DISTRIBUTION OF THE OBLIGATE CAVE-INHABITING FAUNAS OF THE UNITED STATES AND CANADA

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A summary is given of families, genera, species numbers, and state distributions of the obligate subterranean (cave and groundwater) faunas of the contiguous United States and Canada. A total of 425 aquatic and 928 terrestrial species (1353 species in all) is now known. Total genus level diversity is greatest (in descending order) in the states of Texas, Alabama, Kentucky, Tennessee and Virginia. This genus and species richness is vulnerable to a variety of land use and pollution problems.

Nicholas (1960) provided the last complete list of the obligate subterranean fauna (troglobites and stygobites) of the United States. A total of 334 species and subspecies were then known. Since then, there has been much additional field work and taxonomic study on the U.S. cave fauna. Many taxonomic papers and state lists have been published, but they are too numerous to list here. No nationwide species-level list has been compiled since that of Nicholas. As a step towards this goal, I have compiled a summary list. This gives the taxonomic classification of obligate subterranean faunas to the genus level, and a numerical total of such species known in the genus, and the states or provinces in which they are known to occur. I believe this summary list to be a useful indicator of richness of subterranean faunas and their general areas of distribution. Reviews about the origin and ecology of this fauna are in Barr (1967, 1968), Barr, Culver and Kane (1995), Barr and Holsinger (1985), Culver (1982), Holsinger (1988) and Howarth (1983). In this paper I do not attempt to analyze the causes of the different state diversities.

METHODS

I started with the incomplete list in Barr et al. (1995) and worked to improve it. I then asked various taxonomic specialists to correct my preliminary summary lists. An attempt was made to exclude obvious troglophiles (species which may be known only from caves, but which show no morphological specializations for cave life). Troglobites (in terrestrial habitats) and stygobites (in aquatic habitats) are ecologically restricted to caves and subterranean groundwaters, and have usually had a long history of evolutionary specialization to these underground habitats. These animals usually have visibly distinctive cave-related body features (troglomorphies) and less evident physiological or behavioral specializations which restrict them to living only in pre-existing subterranean spaces and caves. These troglobites and stygobites are ecologically and evolutionarily the most interesting animals in caves and groundwaters. The faunas are here separated as terrestrial or aquatic in habitat because these two environments have entirely different faunas and environmental characteristics.

RESULTS

DIVERSITY

The list (Table 1) shows the genus and species level diversity and geographic occurrence by state and province of known troglobites and stygobites in the United States and Canada. This shows the extraordinary diversity of higher taxonomic categories, the species diversity, and geographic diversity of the USA cave fauna. Only one mite, one isopod, and two amphipods are cave-restricted in Canada. Note that the known total is now 425 aquatic species and 928 terrestrial species. Thus, at least 1353 animal species in the contiguous USA and Canada are restricted to cave and groundwater habitats, especially in the southeastern USA, Texas, and California.

DISTRIBUTION

In North America, cave-evolved species are mostly found to the south of the southern limits of the Pleistocene glacial ice sheet. But a few species were apparently able to survive subglacial conditions in the northern US and some parts of Canada. These are groundwater isopods and amphipods which now live in previously glaciated areas of New York, Vermont, Wisconsin, Alberta and British Columbia.

At the genus level, most USA cave fauna diversity occurs in the large limestone karst areas of Texas, the southeastern USA (Appalachian Mountains, Cumberland Plateau, Central Basin of Tennessee, the Bluegrass and Mammoth Cave regions of Kentucky), and the Sierra Nevada Mountain foothills of California. The states with the greatest total generic diversity are Texas, Alabama, Kentucky, Tennessee and Virginia (Fig. 1). The states with greatest troglobite (terrestrial) diversity are Alabama, Texas, Tennessee, Kentucky, California and Virginia (Fig. 2). The states with greatest stygobite (aquatic) diversity are Texas, Missouri, Kentucky, Virginia, Alabama, and West Virginia (Fig. 3). Northern and Central Florida, the Ozarks, southern Illinois, southern Indiana and other areas are secondary regions of medium level total diversity. Other smaller

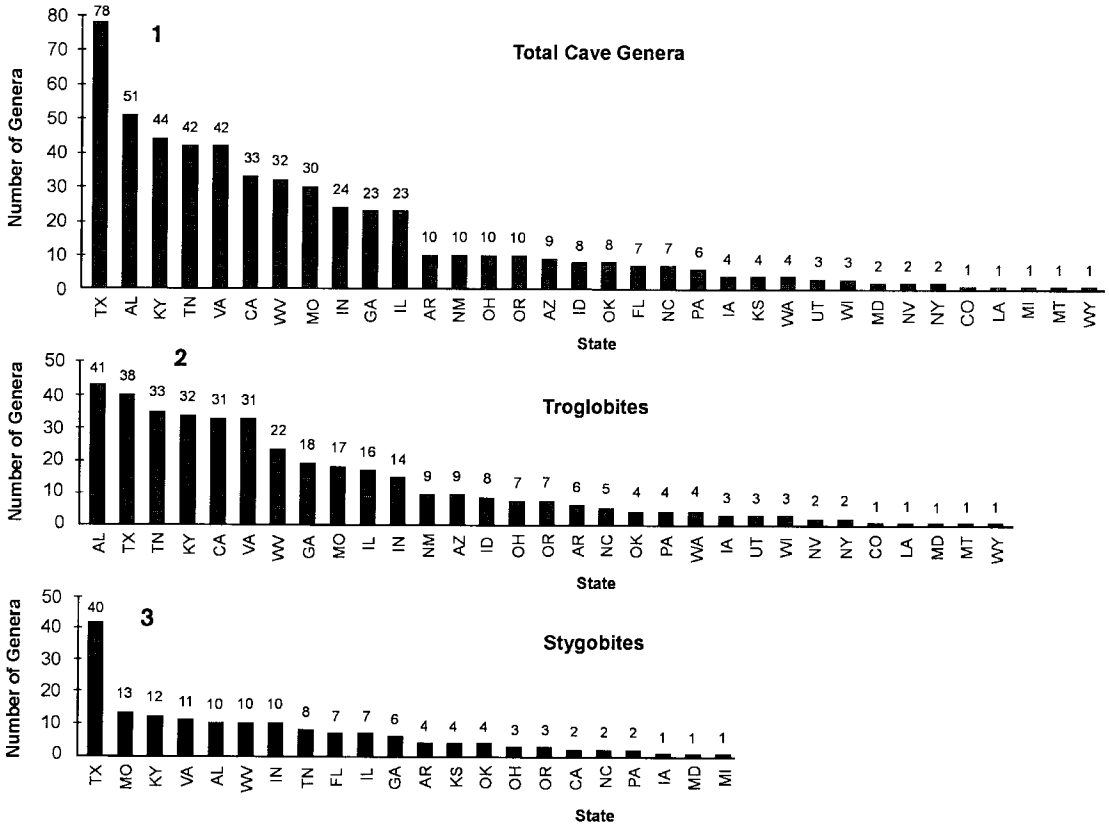
Figures 1-3.

Frequency histograms by state of minimum number of genera with obligate subterranean species.

1. Combined (total) generic diversity by state.

2. Troglobite (terrestrial) generic diversity by state.

3. Stygobite (aquatic) generic diversity by state; the amphipod genus *Stygobromus* occurs in 36 states (not all shown here).



limestone regions in the east and west also have a cave fauna but it is more limited. Volcanic landscapes of the western US (and Hawaii - data not included here) have troglobites in lava tube caves and the extensive system of cracks and crevices which exist in volcanic basalt rocks.

PROSPECT

This summary list cannot yet be considered as complete. Although the faunal exploration of United States caves may now possibly be considered to be at a mature level, some new species will still be found. Some groups are known to have many still undescribed species, such as *Pseudanophthalmus* carabid beetles and *Pseudotremia* millipeds. And, compared to Europe, some subterranean habitats have been poorly sampled. The superficial subterranean environment ("MSS"), which has a rich fauna in Europe (Juberthie et al. 1980) has not been explored in North America. The hyporheic environment (groundwater beyond caves) is virtually unexplored in North America (Camacho 1992, Juberthie 1983). The list is also based on the traditional morphological definition of a species. There may be more "sibling-species" complexes that can be detected with modern molecular techniques (Laing et al. 1976).

Although there are certainly more species yet to be discovered, it seems unlikely to me that there are as many as the 6000 USA troglobite-stygobite species predicted by Culver and Holsinger (1992). Nevertheless, the presently known diversity of at least 1353 species shows the remarkable tendency for a great many groups of very different animals to move into all the many bio-spaces of groundwater and caves; habitats which seem so hostile to us. All of these species are vulnerable to many human land-use activities, and especially to karst groundwater pollution. There is certainly a need to work towards the protection and conservation of this special part of the world's biodiversity. I hope this list will help to alert officials to the richness of subterranean faunas in various states.

ACKNOWLEDGEMENTS

I thank the organizers of the Karst Waters Institute Conference on Conservation and Protection of the Biota of Karst (13-16 February 1997, Nashville, TN) for the invitation which led to the construction of this faunal summary. Field research has been supported in part by grants from the Natural Sciences and Engineering Research Council of Canada. Generous help with checking Table 1 and in providing additional data came from T.C. Barr, Jr. (carabid and pselaphid beetles), D. Chandler (pselaphid beetles), K. Christiansen (collembola), J. Cokendolpher (spiders and harvestmen), D. Culver (general groups), L. Ferguson (Diplura), J. Holsinger

(amphipods and general faunas), J. Lewis (planaria and various aquatics), W.B. Muchmore (pseudoscorpions), W.A. Shear (millipeds), and J. Reddell (Texas faunas). I hope I have correctly summarised their information. Steve Goodacre, DeLancy Bishop, Jennifer Read, and Robert S. Anderson helped with data analysis and graphics.

Table 1. Summary of known (minimal) species diversity and state distributions of animals which are adapted for (and limited to) cavernous subterranean habitats in the contiguous United States and Canada. Both limestone karst and basaltic volcanic terrane faunas are combined here.

Higher Groups, families	Genera	Number of Species	States
I. AQUATIC HABITATS - Stygobionts			
PLATYHELMINTHES (flatworms)			
Lecithoepitheliata			
Prorhynchidae	*Geocentrophora cavernicola*	1	KY, VA
Tricladida			
Dendrocoelidae	*Dendrocoelopsis americana*	1	TX
Kenkiidae	*Kenkia* (= *Macrocotyla*)	4	MO, OR, WV
	Sphalloplana	14	AL, CA, GA, IN, KS, KY, MO, TN, TX, VA, WV
Planariidae	*Paraplanaria occulta*	1	VA
	Phagocata	6	IL, NC, PA, TN, WV
ANNELIDA			
Oligochaeta			
Haplotaxidae	*Haplotaxis brinkhursti*	1	WV
Lumbriculidae	*Spelaedrilus multiporus*	1	VA
	Stylodrilus beattiei	1	VA, WV
	Trichodrilus	2	TN, WV
MOLLUSCA			
Gastropoda			
Hydrobiidae (snails)			
Amnicolinae	*Amnicola*	4	AR, KY, MO
Emmericiinae	*Fontigens*	7	IL, MO, VA, WV
Lithoglypinae	*Balconorbis uvaldensis*	1	TX
	Holsingeria	2	VA
	Phreatoceras taylori	1	TX
	Phreatodrobia	9	TX
Littoridininae	*Antrobia culveri*	1	MO
	Antroselates spiralis	1	IN, KY
	Stygopyrus bartronensis	1	TX
Hirudinea			
Eropodbellidae	*Mooreobdella* n.sp.	1	TX
ARTHROPODA			
CRUSTACEA			
Eucopepoda			
Canthocamptidae	*Bryocamptus morrisoni*	1	IN, KY
Cyclopidae	*Cyclops* (?)	4	TX
	Diacyclops	2	IL, IN, TN
	Megacyclops	1	IN
Podocopa			
Entocytheridae	*Hobbsiella*	1	TX
	Sagittocythere	2	AL, IN, KY, TN
	Sphaeromicola moria	1	TX
	Uncinocythere	2	GA, MO

Candoniidae	*Candona* n.sp.	1	TX
	Prionocypris n.sp.	1	TX
Cyrididae	*Pseudocandona*	2	IN
Bathynellacea			
Parabathynellidae	*Iberobathynella bowmani*	1	TX
Thermosbaenacea			
Thermosbaenidae	*Monodella texana*	1	TX
Decapoda			
Astacidae (crayfish)	*Cambarus*	8	AL, AR, FL, GA, MO, OK, TN, WV
	Orconectes	4	AL, IN, KY, TN
	Procambarus	10	FL
	Troglocambarus maclanei	1	FL
Atyidae (shrimps)	*Palaemonias*	2	AL, KY
Palaemonidae (shrimps)	*Calathaemon holthuisi*	1	TX
	Palaeomonetes	2	FL, TX
Isopoda (isopods)			
Asellidae	*Caecidotea*	56+	AL, AR, FL, GA, IL, IN, KS, KY, MD, MO, OH, OK NC, PA, TN, VA, WV
	Calasellus	2	CA
	Lirceolus	5	TX
	Lirceus	2	VA
	Remasellus parvus	1	FL
	Salmasellus steganothrix	1	AB
Cirolanidae	*Antrolana lira*	1	VA
	Cirolanides texensis	1	TX
	Speocirolana hardeni	1	TX
Stenasellidae	*Mexistenasellus coahuila*	1	TX
Amphipoda (amphipods)			
Allocrangonyctidae	*Allocrangonyx*	2	MO, OK
Artesiidae	*Artesia*	2	TX
Bogidiellidae	*Parabogidiella*	2	TX
Crangonyctidae	*Bactrurus*	9	AL, AR, IA, IL, IN, KS, MI, MO, OH, OK, TN, VA
	Crangonyx	14	AL, FL, GA, IL, IN, KS, KY, MD, MO, OH, PA, TN, VA
	Stygobromus	180	in 36 states (not FL), AB, BC
	Stygonyx courtneyi	1	OR
Gammaridae	*Gammarus*	2	IL, VA, WV
Hadziidae	*Allotexiweckelia hirsuta*	1	TX
	Holsingerius	2	TX
	Mexiweckellia hardeni	1	TX
	Paramexiweckelia ruffoi	1	TX
	Texiweckelia texensis	1	TX
	Texiweckeliopsis insolita	1	TX
Sebidae	*Seborgia*	2	TX
INSECTA (insects)			
Coleoptera (beetles)			
Dytiscidae (water beetles)	*Haideporus texensis*	1	TX
	Stygoporus oregonensis	1	OR
Dryopidae (long-toed beetles)	*Stygoparnus comalensis*	1	TX
VERTEBRATA			
Pisces (fishes)			
Amblyopsidae	*Amblyopsis rosae*	1	MO

	Amblyopsis spelaea	1	KY
	Typhlichthys subterraneus	1	AL, KY, TN
	Speoplatyrhinus poulsoni	1	AL
Ictaluridae	*Satan eurystomus*	1	TX
	Trogloglanis pattersoni	1	TX
Amphibia (salamanders)			
Plethodontidae	*Eurycea latitans*	1	TX
	Eurycea neotenes	1	TX
	Eurycea tridentifera	1	TX
	Eurycea troglodyes	1	TX
	Eurycea n.sp.	2	TX
	Gyrinophilus subterraneus	1	WV
	Gyrinophilus palleucus	1	AL, TN
	Haideotriton wallacei	1	FL, GA
	Typhlomolge rathbuni	1	TX
	Typhlomolge robusta	1	TX
	Typhlotriton spelaeus	1	MO
	TOTAL AQUATIC SPECIES	**425**	

II. TERRESTRIAL HABITATS - Troglobites

MOLLUSCA			
Gastropoda (land snails)			
Ellobiidae	*Carychium stygium*	1	KY, TN
Endodontidae	*Helicodiscus barri*	1	AL, GA, TN
Zonitidae	*Glyphyalina*	2	AL, KY, TN, WV
	Ogaridiscus	?	?
	Spelaeodiscoides spirellum	1	CA
CRUSTACEA			
Isopoda, Oniscoidea (terrestrial isopods)			
Trichoniscidae	*Amerigoniscus*	8	GA, OK, TN, TX, VA
	Brackenridgia	3	TX
	Miktoniscus	2	AL, KY, OH, VA
ARACHNIDA			
Schizomida			
Protoschizomidae	gen & sp	1	TX
Araneae (spiders)			
Cybaeidae	*Cybaeus* n.sp.	1	CA
	Cybaeozyga n.spp.	3	CA
Dictynidae	*Blabomma* n.sp.	6	CA
	Cicurina	58	AL, GA, TX
Leptonetidae	*Appaleptoneta*	5	AL, GA
	Callileptoneta n.sp.	1	CA
	Neoleptoneta	15	AL, TX
Linyphiidae	*Anthrobia monmouthia*	1	KY, TN, VA, WV
	Bathyphantes weyeri	1	VA
	Erigone sp.	1	TX
	Islandiana	3	KY, VA, TX, WV
	Oreonetides n.sp	1	VA
	Phanetta subterranea	1	AL, KY, TN, VA, WV, etc.
	Porhomma cavernicolum	1	AL, AR, KY ,IL, TN, VA, WV, etc.
	Smilax n.sp	1	IA, WI
Nesticidae	*Eidmannella*	6	TX
	Nesticus	9	AL, CA, GA, NC, TN, VA
Telemidae	*Usofila* n.spp.	6	CA

Tetragnathidae	*Meta dolloffi*	1	CA
Theridiidae	*Thymoites*	3	AZ, NM
Pseudoscorpiones (pseudoscorpions)			
Superfamily Chthonioidea			
Chthoniidae	*Aphrastochthonius*	7	AL, CA, NM, TX
	Apochthonius	24	AL, AR, CA, GA, IL, IN, MO, NM, OH, OR, VA, WV
	Chthonius	2	AL, IL, IN, KY ,OH, TN, VA
	Kleptochthonius	40	AL, IN, KY, TN, VA, WV
	Mexichthonius n.sp.	1	TX
	Mundochthonius	2	IL, MO, VA
	Neochthonius	2	CA
	Tyrannochthonius	35	AL, KY, TN, TX
Superfamily Feaelloidea			
Pseudogarypidae	*Pseudogarypus*	3	AZ, CA
Superfamily Garypoidea			
Garypidae	*Archeolarca*	4	AZ, CA, TX
	Larca laceyi	1	CA
Superfamily Neobisioidea			
Bochicidae	*Leucohya texana*	1	TX
Ideoroncidae	*Albiorix* n.sp.	1	AZ
Neobisiidae	*Alabamacreagris*	2	AL
	Americocreagris colombiana	1	OR
	Australinocreagris grahami	1	CA
	Fissilicreagris imperialis	1	CA
	Lissocreagris	4	AL, GA, VA
	Minicreagris pumila	1	AL, GA, TN
	Parobisium charlottea	1	OR
	Setigerocreagris phyllisae	1	CA
	Tatarocreagris	10	TX
Syarinidae	*Chitrella*	7	TN, TX, VA, WV
	Chitrellina n.sp.	1	AZ
Superfamily Cheiridioidea			
Cheiridiidae	*Cheiridium* reyesi	1	TX
Superfamily Cheliferoidea			
Chernetidae	*Dinocheirus cavicolus*	1	TX
	Hesperochernes	3	AL, AR, GA, IN, KY, MO, OH, OK, TN, VA
	Neoallochernes stercoreus	1	TX
	Tuberochernes	2	CA, AZ
Acari (mites)			
Rhagidiidae	*Elliotta howarthi*	1	ID, WA
	Robustocheles occulata	1	AB, IA, WA
	Flabellorhagidia pecki	1	ID
	Foveacheles	2	CA
	Rhagidia varia	1	VA
Opiliones (harvestmen)			
Ceratolasmatidae	*Hesperonemastoma*	3	AL, ID, KY, UT
Cladonychiidae	*Speleomaster*	2	ID
Phalangodidae	*Banksula*	10	CA
	Bishopella jonesi	1	AL
	Calicinia cloughensis	1	CA
	Crosbyella	2	AR
	Hoplobunus	2	TX
	Phalangodes	2	AL, KY, TN

	Phalangomma virginicum	1	VA
	Texella	14	CA, NM, TX
Travuniidae	*Speleonychia sengeri*	1	WA
	Erebomaster flavescens	1	IN
Triaenonychidae	*Cryptobunus*	2	MT, NV, UT
ATELOCERATA (= "TRACHEATA")			
DIPLOPODA (millipeds)			
Callipodida			
Abacionidae	*Tetracion*	2	AL, TN
Dorypetalidae	*Colactis*	1	CA
Spirostreptida			
Cambalidae	*Cambala*	3	AL, FL, GA, KY, TN, TX, VA,WV
Chordeumatida			
Caseyidae	*Speoseya grahami*	1	CA
	Opiona siliquae	1	CA
Cleidogonidae	*Pseudotremia*	30	AL, GA, IN, KY, TN, VA, WV
Conotylidae	*Achimenides pectinata*	1	IL, WI
	Austrotyla specus	1	MO
	Conotyla	2	IN, MD, NY, PA
	Idagona westcotti	1	ID
	Lophomus	2	WA
	Macromastus	2	ID, OR
	Plumatyla humerosa	1	CA, OR
Striariidae	*Striaria*	2	CA, VA
	Speostriaria shastae	1	CA
Tingupidae	*Tingupa pallida*	1	IL, MO
Trichopetalidae	*Scoterpes*	30	AL, GA, IL, KY, MO, TN
	Trichopetalum	4	?KY, VA, WV
Polydesmida			
Fuhrmannodesmidae	*Speodesmus*	10	CO, NM, TX
	Tidesmus hubbsi	1	NV
Macrosternodesmidae	*Chaetaspis*	3	KY, TN
Nearctodesmidae	*Ergodesmus remingtoni*	1	IL
Polydesmidae	*Brachydesmus pallidus*	1	VA, WV
Xystodesmidae	gen.sp.	1	TX
Julida			
Zosteractinidae	*Ameractis*	2	AL, NC, TN
	Zosteractis interminata	1	IL, MO, NC?
CHILOPODA			
Scolopendromorpha			
Cryptopidae	*Theatops*	3+	TX
Geophilomorpha			
Himantariidae?	gen.sp.	3	TX
Lithobiomorpha			
Lithobiidae	gen. sp.	2	TX
HEXAPODA; PARAINSECTA			
Collembola (springtails)			
Sminthuridae	*Arrhopalites*	14	AR, KY, IL, IN, MO, OK, TX, VA, WI
Entomobryidae	*Entomobrya*	12	
	Pseudosinella	22	AL, GA, IN, KY, MO, NC, NM, OH, OK, TN, TX, VA, WV

	Sinella	8	CA, IN, KY, MO, OH, TN, VA, WV
Hypogastruridae	*Schaefferia*	5	AL, TX, VA
Oncopoduridae	*Oncopodura*	3	CA, MT, NM, OR, TX, VA, WY
Onychiuridae	*Onychiurus*	3	AL, IA, IL, IN, KY ,MD, MO, NC, OH, OR, PA, TX, VA, WA, WI, WV
Tomoceridae	*Tomocerus*	4	AL, CA, IL, KY, LA, MD, MO, NM, TN, VA, WV
INSECTA			
Diplura (bristletails)			
Campodeidae	*Allocampa*? n.sp.	1	TX
	Eumesocampa	2	IL, MO, WV
	Haplocampa	11	AZ, CA, ID, IL, MO, OR, UT, WA
	Litocampa	23	AL, AR, GA, IN, KY, MO, NC, NM, TN, VA, WV
	Genus A	1	NM, TX
	Genus B	1	TN
	Genus C	1	NV
Japygidae	*Mixojapyx reddelli*	1	TX
Thysanura (silverfish)			
Nicoletiidae	*Texoredellia texensis*	1	TX
Coleoptera (beetles)			
Carabidae	*Ameroduvalius*	5	KY
(ground beetles)	*Darlingtonea kentuckensis*	1	KY, TN
	Horologion speokoites	1	WV
	Neaphaenops	4	KY
	Nelsonites	5	KY, TN
	Pseudanophthalmus	250+	AL, GA, IL, IN, KY, MD, OH, PA, TN, VA, WV
	Rhadine	11	TX
	Xenotrechus	2	MO
Leiodidae	*Ptomaphagus*	19	AL, AZ, GA, KY, TN
(scavenger beetles)	*Glacicavicola bathyscioides*	1	ID, WY
Pselaphidae	*Arianops*	6	AL, TN, VA
(pselaphid beetles)	*Batriasymmodes*	4	AL, KY, TN, WV
	Batrisodes	19	AL, IN, KY, OH, TN, TX
	Tychobythinus (=*Bythinopsis)*	3	AL, KY, TN
	Speleochus (=Macherites)	12	AL, TN, GA
	Spelobama vana	1	AL
	Subterrochus	3	AL
	Texamaurops reddelli	1	TX
Diptera (flies)			
Sphaeroceridae	*Spelobia tenebrarum*	1	AL, AR, GA, IL, IN, KY MO, NY, PA, TN, VA, WV
(small dung flies)			

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