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The North American obligate cave fauna: regional patterns

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Abstract. The obligate cave faunas of nine regions of the United States - Florida Lime Sinks, Appalactians, Interior Low Plateaus, Ozarks, Driftless Area, Edwards Aquifer/Balcones Escarpment, Guadalupe Mountains, Black Hills, and Mother Lode - are described and compared. The number of aquatic (stygobitic) species ranged from zero (Black Hills) to 82 (Appalachians), and the number of terrestria (troglobitic) species ranged from zero (Florida Lime Sinks) to 256 (Interior Low Plateau). Even at the level of genus, overlap between regions is low. Several predictor variables (karst area, number of caves, number of long caves, number of deep caves, distance from the Pleistocene ice margin, distance from the late Cretaceous Sea, and vegetation type - a surrogate for productivity) were assessed using rank order statistics, especially rank order multiple regression with a backward elimination procedure. For both stygobites and troglobites, only number of caves was a significant predictor. The absence of a karst area effect suggested that the degree of karst development is better described by the number of caves rather than area of karst. There was no evidence that distance to Pleistocene glacial boundaries was important, but there was some support for the importance of distance from late Cretaceous sea margins, a potential source of aquatic subterranean colonists. Finally, there was no indication that surface productivity had an effect on species richness. Analysis was complicated by correlations among predictor variables.

Introduction

There are nearly 1000 described species and subspecies of animals that are obligate inhabit ants of caves within the 48 coterminous states of the United States (Culver et al. 2003). Most, if not all of these species are the product of independent invasion and isolation of past surface-dwelling populations, and their taxonomic range is large – 210 genera in 96 families in 38 orders. As a result, most of these species have highly restricted ranges – more than half are known from a single county. The obligate cave fauna has the highest reported level of endemism of any taxonomic or ecological group of organisms in the United States (L. Master, personal communication). It is this highly vulnerable, ecologically uniform, but evolutionarily diverse, fauna that is the focus of the present study.

Within North America, the appropriate habitat for subterranean faunas is found in distinct regions that are, in some cases, widely separated. Not surprisingly, there appear to be substantial differences in the fauna from region to region. Barr and Reddell (1967) noted the depauperate nature of the fauna of the Carlsbad Caverns region in New Mexico, which they attributed to the aridity of the region. Peck and Christiansen (1990) noted a similar pattern for the Driftless Area, covering parts of Iowa, Illinois, Wisconsin, and Minnesota (Figure 1). They attributed the low diversity to lack of time for colonization and isolation due to the area having been glaciated during the Pleistocene. Barr (1967) compared the beetle fauna of the Appalachians and Interior Low Plateaus and suggested that cave connectivity (and its converse, isolation) explained differences between the two areas.

All of the previous studies of regional differences have been piecemeal and for good reason. Until very recently there has been no comprehensive list of stygobites and troglobites for any area in sufficient detail for such an analysis. In this contribution, we take advantage of the list of stygobites and troglobites for each county in the US that is now available on the world-wide web at www.karst-waters.org/trogslist (Culver et al. 2000). Our focus here is on the regional differences in the cave faunas in the coterminous states of the USA. Our previous work has looked at a much smaller scale, that of the county. But patterns at one scale are not necessarily preserved at other, larger or smaller scales. The analysis of cave regions is important because each region, such as the Florida Lime Sinks, has a unique geology, a unique history, and a distinct climate. These kinds of regional scale differences may in turn explain differences in stygobitic and troglobitic richness among the regions.



Figure 1, Map of the karst regions considered in this paper. The Interior Low Plateau is shown in stippling to differentiate it from the Appalachians and the Ozarks.

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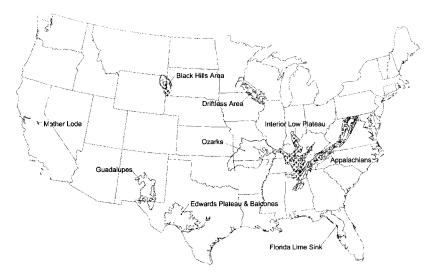


Figure 1. Map of the karst regions considered in this paper. The Interior Low Plateau is shown in stippling to differentiate it from the Appalachians and the Ozarks.

Simply put, our goal is to document the faunal differences among nine major cave regions in the United States and to propose historical and ecological explanations for these quantitative differences among cave regions.

Methods and materials

While there are a significant number of caves in lava flows in the western United States and additional mechanically formed sea caves, we focused only on regions where caves are formed in soluble rock, especially limestone. While lava tubes have an interesting fauna (Peck 1982), they have been very poorly studied in the continental US. Sea caves are unlikely to harbor stygobites and troglobites and in any case have not been studied biologically.

We relied on geological boundaries to define cave regions. In the central and eastern US there are six major cave-bearing (karst) regions:

- Florida Lime Sinks, with flat-bedded limestones of Tertiary age.
- Appalachians, with greatly folded and faulted limestones of Paleozoic age.
- Interior Low Plateaus, with flat-bedded limestones of Paleozoic age.
- Ozarks, with flat-bedded limestones of Paleozoic age.
- Drift ess Area, with flat-bedded limestones of Paleozoic age modified by glacial cover.
- Edwards Aquifer and Balcones Escarpment, with flat-bedded limestones of Mesozoic age.

There are three western karst areas of significant size that have been biologically investigated:

- Guadalupe Mountains, with Paleozoic reef limestone.
- Black Hills, with mildly folded limestones of Paleozoic age.
- Mother Lode karst of California, in tectonically modified Paleozoic limestones.

There are additional smaller karst areas, particularly in the west (Davies et al. 1984; Culver 1999). Except for the Mother Lode, none of these smaller areas has received the level of biological attention the nine just mentioned have. While the boundaries of these nine areas are straightforward (cf. Barr and Reddell 1967), several conventions were followed. The Appalachians, which extend into Canada, were truncated at the Maryland-Pennsylvania border. Thus constituted, the Appalachians include nearly the entire region south of the Pleistocene glaciation, and are a much more homogeneous region than would be the case if the northern part were included. Second, the Interior Low Plateaus is actually a complex of plateaus (e.g., Barr 1967), and we have narrowly defined the region as including only the Cumberland Escarpment, Central Basin, Pennyroyal Plateau (and Mitchell Plain), and Inner Bluegrass, excluding the Outer Bluegrass and smaller outlying regions

A series of physical and geographic characteristics was determined for each region:

- Are i (km²) of the karst region was determined from a digitized version of the mar in Culver (1999).
- The number of reported caves in each region was estimated from the number of caves in counties that are wholly or in part within the region. Original data were from the files of various state cave surveys affiliated with the National Spe eological Society.
- 3. The number of caves longer than 1.67 km (1 mile) from the list of long caves maintained by Robert Gulden at www.pipeline.com/~caverbob.
- 4. The number of caves deeper than 120 m (400 feet) from the list of deep caves maintained by Robert Gulden at www.pipeline.com/~caverbob.
- 5. The ranks of the distance from the maximum extent of Pleistocene glaciation, using the map in Dawson (1992).
- 6. The ranks of the distance from the edge of the maximum extent of the southern lobe of the late Cretaceous Seas using the map in Holsinger and Longley (1980).
- 7. Major habitat zone based on the habitat map of the World Wildlife Fund (Ricketts et al. 1999), including (a) temperate broadleaf and mixed forests, (b) temperate coniferous forests, (c) temperate grasslands, and (d) xeric shrublands.

The first four characteristics (karst area, number of caves, number of long caves, and number of deep caves) are measures of habitat availability. The next characteristic (rank distance from the Pleistocene ice margin) is a measure of the intensity of climate change that may have forced and/or isolated pre-adapted or exapted surface-dwelling terrestrial populations into caves. The sixth characteristic (rank distance from the southern lobe of the Cretaceous Sea) measures opportunity for invision of aquatic species into caves as a result of receding Cretaceous seas (Holsir ger and Longley 1980). Since the Florida Lime Sinks were completely inundated by Cretaceous Seas, it was given a rank of one, while the partially inundated Edwards Plateau/Balcones Escarpment was given a rank of two. Finally the habitat categories were ranked in the order given, which roughly corresponds to productivity differences. Higher productivity on the surface results in more food entering caves and thus may allow for more species.

The basic format of statistical analysis is a multiple regression with area, number of caves, long caves, deep caves, Cretaceous embayment distance, Pleistocene glaciation distance, and habitat zone as independent variables. The dependent variables were number of stygobites and number of troglobites. Aquatic and ter estrial species were analyzed separately because they appear to have quite different patterns (Christman and Culver 2001). Both because of the small number of regions analyzed and uncertainties in the data, rank order statistics methods were used — Spearman's correlation and a rank order multiple regression with a backward elimination procedure (Iman and Conover 1979). The procedure fits the full model with all of the explanatory variables. It then determines which variable contributes least to the predictive capability of the model. If it is not statistically significant, that variable is eliminated. The model is then refitted with all variables but that one and repeats the same procedure with the remaining variables. The

Table 1. Summary of species richness and geophysical parameters for each region (ranks are given in parentheses).

Region	Number of stygobites	Number of troglobites	Total species	Number of caves	Area of karst (km ²)	No. of long caves (>1 mile)	No. of deep caves . (>400')	Cretaceous rank	Pleistocene rank	Habitat
Florida Lime Sinks	20 (5)	0 (9)	20 (6)	627 (6)	27338 (6)	17 (5)	0 (6)	1	7	5
Appalachians	80 (1)	181 (2)	261 (2)	7441 (2)	37268 (5)	222 (2)	27 (2)	5	3	7
Interior Low Plateau	62 (2)	257 (1)	319 (1)	11928 (1)	60612 (3)	389 (1)	64 (1)	3	2	7
Ozarks	46 (4)	31 (4)	77 (4)	6964 (3)	110125(1)	84 (3)	0 (6)	4	4	7
Edwards/Balcones	55 (3)	108 (3)	163 (3)	2011 (4)	65586 (2)	19 (4)	1 (5)	2	6	2
Guadalupes	1 (8)	13 (6)	14 (7)	1379 (5)	43522 (4)	16 (6)	6 (3)	6	9	1
Mother Lode	3 (6)	20 (5)	23 (5)	179 (8)	390 (9)	1 (9)	0 (6)	9	8	5
Black Hills	0 (9)	2 (8)	2 (9)	160 (9)	7272 (8)	6 (8)	2 (4)	8	5	5
Driftless	2 (7)	11 (7)	13 (8)	615 (7)	25 222 (7)	7 (7)	0 (6)	7	1	2

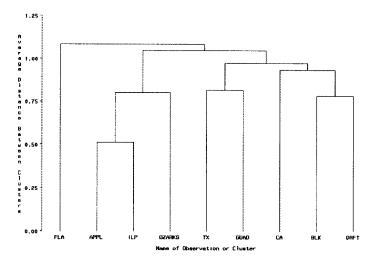


Figure 2 UPGMA of generic differences between regions (see Table 2). Regions are abbreviated as follows: Florida Lime Sinks (FLA); Appalachians (APPL); Interior Low Plateaus (ILP); Ozarks (OZARKS); Edwards Plateau/Balcones Escarpment (TX); Guadalupe Mountains (GUAD); Mother Lode (CA); Black Hills (BLK); and Driftless Area (DRFT).

Table 2. Proportion of genera that overlap between regions.

Region	1	2	3	4	5	6	7	8	9
1	8	0.250	0.500	0.375	0.125	0	0	0	0
2	0.030	67	0.612	0.254	0.149	0.045	0.060	0.030	0.090
3	0.048	0.494	83	0.181	0.121	0.036	0.048	0.024	0.048
4	0.083	0.472	0.417	36	0.194	0.056	0.111	0.028	0.167
5	0.017	0.170	0.170	0.119	59	0.136	0.051	0.017	0.068
6	0	0.231	0.231	0.154	0.615	13	0.154	0	0.077
7	0	0.308	0.308	0.308	0.231	0.154	13	0	0.231
8	0	1.000	1.000	0.500	0.500	0	0	2	0.500
9	0	0.545	0.364	0.545	0.364	0.091	0.273	0.091	11

The diagonal is the number of genera found in the region. Each row contains the proportion of genera in the region associated with that row, and which also are found in the region associated with the column.

procedure is repeated until only statistically significant variables are left in the model. Rank regression is well suited to analyze data that have monotonic, but non-linear, relationships.

Since most species have very small ranges – over half are known from a single county (Culver et al. 2000) – and those species with large ranges were described prior to 1900, suggesting that a taxonomic re-examination is in order (Christman and Culver 2001), we compared faunas at the level of genus by computing the fractior of each region's taxa shared with the region being compared. We also ran a cluster analysis using the unweighted pair-group method with arithmetic averages (UPGMA, Sneath and Sokal 1973) for genera among regions.

Results

The list of species and subspecies for each region is given in Appendix 1. Only described species and subspecies are included in the analysis. The number of stygobites and troglobites in each region is given in Table 1. The number of troglobites ranged from zero in the Florida Lime Sinks to 261 in the Interior Low Plateau. The median number of troglobitic species was 20. The number of stygobites ranged from zero in the Black Hills to 80 in the Appalachians. The median number of stygobitic species was also 20.

Overlap of genera is summarized in Table 2. Even those regions that are contiguous or nearly so (Appalachians, Interior Low Plateau, and Ozarks) share less than 62% of their genera. For many geographically distant regions, overlap is less than 10%. The UPGMA diagram (Figure 2) indicates that the Appalachians and Interior Low Plateaus are most closely related and that they are in turn most closely related to the Ozarks. The Edwards Plateau/Balcones Escarpment in Texas also shows overlap with the fauna of the Guadalupe Mountains in New Mexico, as does the Black Hills and Driftless Area fauna. In both of these comparisons the overlap is largely among terrestrial genera. The most distinct region is the Florida Lime Sinks, in part because it has no terrestrial fauna. All in all, the UPGMA of genera reflects geographic distance between regions.

Rank order correlations between stygobite and troglobite richness and a variety of potential predictor variables are shown in Table 3. We note in passing that stygobi e and troglobite numbers are themselves significantly correlated, although there are obvious differences in the pattern between the two. For example, the Florida Lime Sinks has no troglobites and the Black Hills has no stygobites. Stygobites show a significant pairwise correlation with two of the seven variables – number of caves and number of long caves. In addition, the habitat zone (ranked by relative dryness) and distance from the southern lobe of the Eocene embayment are marginally correlated (0.05 < P < 0.10) with stygobite numbers. Troglobites also showed a significant correlation with both number of caves and number of long caves. In this case there were no marginally significant correlations.

There were numerous significant correlations among the predictor variables. In particular the number of caves, karst area, number of long caves, and rank distance from Eocene embayment were themselves all significantly correlated (Table 3), with the absolute value of the correlations ranging from 0.62 to 0.97.

The rank order regression with backward elimination yielded very similar results for both stygobites (Table 4) and troglobites (Table 5). In both cases only one variable was found to be a significant predictor of species number, i.e., number of caves. Because of the strong correlation among variables (Table 3), this is not surprising, but it also means that it is difficult to disentangle the separate effects of the independent variables.

The high variability of number of stygobites and number of troglobites suggests another way to analyze the data. Stygobite numbers fall into two very distinct groups: 0-3 and 19-82; and troglobite numbers also fall into two very distinct groups: 0-29 and 105-256 (Table 1). Two-sample Mann-Whitney U tests (Table 6) indicated significant differences between low and high diversity stygobite

Table 3. Spearman correlation coefficients (P-values italicized and below the estimated correlation).

	Stygo- bites	Troglo- bites	Caves	Karst area	Long caves	Deep caves	Cretaceous rank	Pleistocene rank	Habitat class
Stygobites	1.00								
Troglobite:	0.80	1.00							
	0.01								
Caves	0.85	0.82	1.00						
	< 0.01	0.01							
Karst area	0.55	0.57	0.80	1.00					
	0.13	0.11	0.01						
Long cave;	0.85	0.72	0.97	0.78	1.00				
	< 0.01	0.03	< 0.01	0.01					
Deep cave;	0.33	0.56	0.54	0.25	0.52	1.00			
	0.38	0.11	0.13	0.51	0.15				
Eocene rank	-0.60	-0.22	-0.62	-0.68	-0.72	-0.10	1.00		
	0.09	0.58	0.08	0.04	0.03	0.81			
Pleistocene rank	-0.38	-0.35	-0.37	-0.15	-0.45	-0.17	0.07	1.00	
	0.31	0.36	0.33	0.70	0.22	0.65	0.86		
Habitat class	0.62	0.48	0.51	0.20	0.58	0.21	-0.18	-0.46	1.00
	0.07	0.19	0.16	0.61	0.10	0.58	0.64	0.21	

Table 4. Results of the rank regression backward elimination procedure for stygobites as the response variable.

Step	Model adj.	Estimated coefficients for the independent variables								
	R^2	Caves	Karst area	Cretaceous rank	Habitat class	Long caves				
0	0.594.3	1.476 (0.2983)	-0.399 (0.4309)	-0.466 (0.3813)	0.331 (0.4490)	-0.782 (0.6255)				
1	0.6659	0.892 (0.1065)	-0.399(0.3746)	-0.287 (0.3697)	0.203 (0.4961)					
2	0.6954	1.085 (0.0216)	-0.508(0.2122)	-0.278(0.3515)						
3	0.6926	1.139 (0.0130)	-0.361 (0.3114)							
4	0.6829	0.850 (0.0037)								

Independent variables were chosen based on Spearman's correlation coefficients for pairwise dependence. P-values for testing the null hypothesis that the coefficient is zero are given in parentheses.

Table 5. Results of the rank regression backward elimination procedure for troglobites as the response variable.

Step	Model adj.	Estimated coefficients for the independent variables							
	R^2	Caves	Long caves	WWF class	Deep caves	Karst area			
0	0.5254	1.942 (0.1540)	-1.556 (0.2491)	0.337 (0.4439)	0.244 (0.5258)	0.108 (0.8486)			
1	0.6389	1.997 (0.0815)	-1.484(0.1755)	0.294 (0.3544)	0.212 (0.4685)				
2	0.6€49	2.089 (0.0520)	-1.455(0.1549)	0.272 (0.3583)					
3	0.6637	1.890 (0.0563)	-1.110(0.2150)						
4	0.6194	0.817 (0.0072)	,						

Independent variables were chosen based on Spearman's correlation coefficients for pairwise dependence. P-values for testing the null hypothesis that the coefficient is zero are given in parentheses.

regions with respect to number of caves, karst area, number of long caves, and Eocene distance. There were significant differences between low and high diversity troglobite regions with respect to number of caves, number of long caves,

Table 6. "wo sample Mann-Whitney U test probabilities for differences between two categories of regions in terms of stygobites and troglobites (see text for details).

	Number of caves	Karst area	No. of long caves	No. of deep caves	Cretaceous distance	Pleistocene distance	Habitat
Stygobites	0.025	0.05	0.01	ns	0.025	ns	ns
Troglobites	0.025	ns	0.025	0.05	ns	ns	ns

and number of deep caves. Again, these numbers must be interpreted with caution because of the confounding nature of the correlation among the independent variables.

Discuss on

As is the case with any invertebrate fauna, the question must be raised about the quality of the data on species richness, and whether patterns are the result of sampling intensity. The cave faunas are probably better known than any other group of USA invertebrates, with the exception of butterflies and longhorn beetles (Culver et al. 2000). Nevertheless, new species are being described every year, and some genera, such as Pseudanophthalmus carabid beetles and Pseudotremia millipedes, are known to have many undescribed species (Peck 1998). In addition, one region - the Edwards Plateau/Balcones Escarpment - may have a higher percentage of undescribed species than other regions (Reddell 1994). It is of course difficult to predict the pattern of description of new species, but recent descriptions of species have been from the 'well-known' regions of the Appalachians and the Interior Low Plateau (Lewis 2000) as well as from 'poorly known' regions such as the Edwards Plateau (Lewis and Bowman 1996). All regions have been intensively sampled, but we have no direct quantitative measure of sampling intensity. Because we used ranks in our analysis, our results will change only if the ranks of species diversity change among the regions. It seems unlikely that the Edwards Plateau/Balcones Escarpment will surpass the Appalachians and Interior Low Plateau, since species numbers are much greater in the latter (Table 1) and species are being described from all regions. The most likely situation where ranks will change is in the number of stygobites in the western and upper Midwestern areas (Black Hills, Guadalupes, Driftless Area, and the Mother Lode). Each of these regions has fewer than four stygobitic species (Table 1). We believe that the potential for new stygobitic species in these areas is not great, but the discovery of even one or two new species will change their ranks.

The clearest pattern to emerge from the analysis is that for both stygobites (Table 4) and troglobites (Table 5) the rank order number of caves in a region is the best predictor of the rank order of the number of species. Conversely, karst area is not a good predictor, even when considered separately (Table 3). The only suggestion that karst area was important was the difference in karst area between high and low diversity stygobite regions (Table 6). This suggests that it is not size

but rather the degree of karst development that is an important determinant of species number. One measure of karst development – number of long caves – was found to be correlated with both the number of stygobites and troglobites, while yet another measure – the number of deep caves – was not (Table 3). This was somewhat surprising, since the extent of vertical development is possibly more likely to reflect higher habitat diversity than the extent of horizontal development. For example, even in very long caves such as Mammoth Cave, habitats differ most noticeably by their vertical position within the cave rather than distance from the entrance. Examples would include high level sandy floored passages and base level vertical shaft drains. When troglobites and stygobites were divided into two groups, a similar pattern was obtained except that the number of deep caves did significantly differ between low- and high-diversity troglobite areas (Table 6).

A scmewhat surprising result is the lack of any evidence that proximity to Pleistocene glacial boundaries was an important factor in determining species numbers, especially for troglobites. We certainly do not claim that the Pleistocene was unimportant in forcing species underground, it is just that distance from the Pleistocene margin showed no significant correlation. Part of the problem may be in the definition of distance from the Pleistocene ice sheet. We used the distance from the main lobe of the Wisconsin glaciation, but actual distance of each region from some ice sheet is quite different given the earlier glaciation and the smaller, isolated glaciers in the American West (Brouillet and Whetstone 1993).

There was weak support for the importance of the Cretaceous Embayment in determining the number of stygobites. Considered in isolation, distance to the Eocene Sea was marginally correlated with stygobite number (Table 3), and low stygobite diversity regions were farther from the Eocene boundary than high stygobite diversity regions (Table 6).

The historical patterns of glaciation and sea embayment may be relatively unimportant in determining species numbers but very important in determining species composition. The aquatic fauna of the Edwards Plateau/Balcones Escarpment is a good example. It is the only area at the margin of Cretaceous Seas (Florida was submerged), but it does not have the most stygobites (Table 1). However, the stygobites present reflect a marine ancestry (Holsinger and Longley 1980), inlike nearly all other stygobites in all other regions. That is, the source of stygobi es is different, but not necessarily their number.

The final variable we considered was major habitat zone. The four categories (temperate broadleaf forest, temperate coniferous forest, temperate grasslands, and xeric shrublands) provide a ranking of the productivity of different areas. Since the food in a cave results from secondary production of the surrounding surface area (Rouch 1982), there might be a correlation between the two, because amount of food in a cave may set a limit on the number of species present. In other words, resource level may affect extinction rates just as proximity to the Eocene Sea or the Pleistocene ice sheet may affect colonization rates. However, no relationship was found.

When viewed from the perspective of the individual region, there are plausible explanations for the patterns seen in each. We use Florida as an example. It is close to the late Cretaceous embayment and far from the Pleistocene ice margin, and so

we would expect few troglobites and many stygobites. This is what we observe (Table 1). It is just that, for the most part, these idiopathic explanations do not fit into a coherent whole when viewed from a larger perspective. Only the degree (or quality) of karstification as measured by the number of caves offers a general explanation of differences in species richness. This suggests that habitat constraints (number of caves in particular) are more important than opportunities for colonization in determining species richness. Species composition, on the other hand, may have a stronger historical component.

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Append:x 1

List	of	species	and	subspecies	by	region.

Class/phylum order		Species
Region 1: Florida Lime Si	nks	
Crustacea	Amphipoda	Crangonyx grandimanus
	• •	C. hobbsi
	Decapoda	Palaemonetes cummingi
	•	Procambarus acherontis
		P. attiguus
		P. delicatus
		P. erythrops
		P. franzi
		P. horsti
		P. leitheuseri
		P. lucifugus alachua
		P. lucifugus lucifugus
		P. morrisi
		P. orcinus
		P. pallidus
		Troglocambarus maclanei
	Isopoda	Caecidotea hobbsi
		Remasellus parvus
	Podocopida	Uncinocythere ambophora
Oligochaeta	Branchiobdellida	Cambarinicola leoni
Region 2: Appalachians		
Amphibia	Urodela	Gyrinophilus palleucus gulolineatus
		G. palleucus palleucus
		G. subterraneus
Arachnida	Acari	Foveacheles paralleloseta
		Poecilophysis wolmsdorfensis
		Rhagidia cavernarum
		R. varia

Araneae Anthrobia mammouthia Bathyphantes weyeri Islandiana muma I. speophila Liocranoides unicolor Nesticus barri N. barrowsi N. dilutus N. furtivus N. georgia N. holsingeri N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola Pseudoscorpiones Apochthonius coecus	
Islandiana muma I. speophila Liocranoides unicolor Nesticus barri N. barrowsi N. dilutus N. furtivus N. georgia N. holsingeri N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
I. speophila Liocranoides unicolor Nesticus barri N. barrowsi N. dilutus N. furtivus N. georgia N. holsingeri N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
Liocranoides unicolor Nesticus barri N. barrowsi N. dilutus N. furtivus N. georgia N. holsingeri N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
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N. barrowsi N. dilutus N. furtivus N. georgia N. holsingeri N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
N. dilutus N. furtivus N. georgia N. holsingeri N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
N. furtivus N. georgia N. holsingeri N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
N. furtivus N. georgia N. holsingeri N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
N. georgia N. holsingeri N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
N. holsingeri N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
N. paynei N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
N. tennesseensis Phanetta subterranea Porrhomma cavernicola	
Phanetta subterranea Porrhomma cavernicola	
Porrhomma cavernicola	
rseudoscorpiones Apoeninonius coecus	
A. holsingeri	
A. paucispinosus	
Chitrella regina	
Ch. superba	
Hesperochernes mirabilis	
Kleptochthonius affinis	
K. anophthalmus	
K. binoculatus	
K. gertschi	
K. henroti	
K. hetricki	
K. infernalis	
K. lutzi	
K. orpheus	
K. proserpinae	
K. proximosetus	
K. regulus	
K. similis	
Microcreagris subatlantic	а
M. valentinei	
Mundochthonius holsinger	ri
Tyrannochthonius chambe	
Chilopoda Geophilomorpha Nampabius turbator	
Crustacea Amphipoda C. antennatus	
C. dearolfi	
Stygobromus abditus	
S. ackerlyi	
S. allegheniensis	
S. baroodyi	
S. barryi	
S. biggersi	
S. conradi	
S. cooperi	
S. culveri	
S. cumberlandus	
S. dicksoni	
S. emarginatus	
S. ephemerus	
S. estesi	
S. exilis	
S. fecundus	

Class/phylum order		Species		
.7		S. fergusoni		
		S. finleyi		
		S. franzi		
		S. gracilipes		
		S. grandis		
		S. hoffmani		
		S. inexpectatus		
		S. interitus		
		S. leensis		
		S. mackini		
		S. minutus		
		S. morrisoni		
		S. mundus		
		S. nanus		
		S. nortoni		
		S. parvus		
		S. pollostus		
		S. pseudospinosus		
		S. redactus		
		S. sparsus		
		S. spinatus		
		S. stegerorum		
	Decapoda	Cambarus nerterius		
	2	Orconectes australis australis		
Isopoda	Amergoniscus curvatus			
	150poun	Am. georgiensis		
		Am. henroti		
		Am. nicholasi		
		Am. paynei		
		Am. proximus		
		Antrolana lira		
		Ca. cannula		
		Ca. circulus		
		Ca. cyrtorhynchus		
		Ca. franzi		
		Ca. henroti		
		Ca. holsingeri		
		Ca. incurva		
		Ca. meurva Ca. nortoni		
		Ca. norioni Ca. pricei		
		Ca. pricei Ca. recurvata		
		Ca. recurvata Ca. richardsonae		
		Ca. scypha		
		Ca. simonini		
		Ca. sinuncus		
		Ca. vandeli		
		Ligidium elrodii chatoogaensis		
		L. elrodii hancockensis		
		L. elrodii leensis		
		L. elrodii scottensis		
		Lirceus culveri		
		Lir. usdagalun		
		Miktoniscus racovitzai racovitzai		

Appendix 1. (continued)

Class/phylum order		Species
Crustacea	Podocopida	Donnaldsoncythere tuberosa
Diplopod 1	Callipodida	Tetracion jonesi
	Chordeumatida	Pseudotremia aeacus
		Ps. cavernarum
		Ps. deprehendor
		Ps. eburnea
		Ps. fulgida
		Ps. lusciosa
		Ps. nodosa
		Ps. tuberculata
		Ps. valga
		Scoterpes austrinus austrinus
		Trichopetalum krekeleri
		T. packardi
		T. weyeriensis
		T. whitei
	Julida	Ameractis satis
Imagata	Collembola	
Insecta	Collembola	Arrhopalites caedus
		Ar. carolynae
		Ar. clarus
		Ar. commorus
		Ar. lacuna
		Ar. marshalli
		Ar. pavo
		Ar. sacer
		Ar. silvus
		Oncopodura hubbardi
		Onychiurus janus
		Pseudosinella bona
		Pse. certa
		Pse. christianseni
		Pse. erehwon
		Pse. extra
		Pse. gisini gisini
		Pse. gisini virginia
		Pse, granda
		Pse. hirsuta
		Pse. orba
		Pse. spinosa
		Pse. testa
		Schaefferia hubbardi
		Sinella agna
		Sinena ugna Si. barri
		Si. cavernarum
		Si. hoffmani
		Si. krekeleri
	D: 1	Typhlogastrura valentini
	Diplura	Litocampa cookei
		Lit. fieldingi
		Lit. pucketti
		Lit. valentinei
	Coleoptera	Batriasymmodes greeveri
	-	B. parki
		B. spelaeus
		Batrisodes clypeospecus
		Darlingtonea kentuckensis kentuckensis

lass/phylum order	Species
	Horologion speokoites
	Nelsonites walteri
	Pseudanophthalmus alabamae
	Pseu. assimilis
	Pseu. avernus
	Pseu. beakleyi
	Pseu. cordicollis
	Pseu. deceptivus
	Pseu. delicatus
	Pseu. digitus
	Pseu. egberti
	Pseu. engelhardti
	Pseu. fastigatus
	Pseu. fulleri
	Pseu. fuscus
	Pseu. georgiae
	Pseu. gracilis
	Pseu. grandis
	Pseu. hadenoecus
	Pseu. higginbothami
	Pseu. hirsutus
	Pseu. hoffmani
	Pseu, holsingeri
	Pseu, hortulanus
	Pseu, hubbardi
	Pseu. hubrichti
	Pseu. hypertrichosis
	Pseu, intersectus
	Pseu. jonesi
	Pseu. krekeleri
	Pseu. lallemanti
	Pseu. limicola
	Pseu. longiceps
	Pseu, montanus
	Pseu. nelsoni
	Pseu, nortoni
	Pseu. pallidus
	Pseu. paradoxus
	Pseu. parvicollis
	Pseu. paynei
	Pseu. petrunkevitchi
	Pseu. pontis
	Pseu. potomaca potamaca
	Pseu, potomaca senecae
	Pseu. praetermissus
	Pseu. punctatus
	Pseu. pusillus
	Pseu. pusio
	Pseu. quadratus
	Pseu. robustus
	Pseu. rotundatus
	Pseu. sanctipauli
	Pseu. scutilus
	т зен. эсиниз

Class/phylum order		Species
		Pseu. seclusus
		Pseu. sequoyah
		Pseu. sericus
		Pseu. sidus
		Pseu. tennesseensis
		Pseu. thomasi
		Pseu. unionis
		Pseu. vicarius
		Pseu. virginicus
		Pseu. wallacei
		Ptomaphagus fiskei
		Pt. whiteselli
		Troglanillus valentinei
	Diptera	Spelobia tenebrarum
Mollusca	Mesogastropoda	Antrorbis breweri
Monusca	Mesogastropoda	Fontigens tartarea
		F. turritella
	Chalananata har	Holsingeria unthanksensis
	Stylommatophora	Helicodiscus barri
O11 1		Glyphyalinia specus
Oligochae a	Lumbriculida	Haplotaxis brinkhursti
		Spelaedrilus multiporus
		Stylodrilus beattiei
		Trichodrilus culveri
Pisces	Percopsiformes	Typhlichthys subterraneus
Turbellaria	Alloeocoela	Geocentrophora cavernicola
	Tricladida	Macrocotyla hoffmasteri
		Phagocata angusta
		Sphalloplana chandleri
		Sp. consimilis
		Sp. culveri
		Sp. georgiana
		Sp. percoeca
		Sp. virginiana
Region 3: Interior Low	Plateaus	
Amphibia	Urodela	G. palleucus necturoides
•		G. palleucus palleucus
Arachnida	Acari	Belba bulbipedata
		Galumna alata
		Hamohalacarus subterraneus
		Macrocheles troglodytes
		R. cavernarum
		Soldanellonyx chapuisi
		So. morardi
		Veigaia bakeri
		V. wyandottensis
	Araneae	An. mammouthia
	Attaileac	Bat. weyeri
		Cicurina wiltoni
		I. muma
		Leptoneta serena
		Lio. unicolor
		N. barri
		N. jonesi
		N. stygius N. valentinei
		iv vaieninei

Class/phylum order		Species
		Pha. subterranea
		Po. cavernicola
	Opiliones	Bishopella jonesi
		Erebomaster flavescens
		Hesperonemastoma pallidimaculos
		Phalangodes appalachius
		Ph. armata
	Pseudoscorpiones	Alabamocreagris mortis
,		Al. pecki
		Aphrastochthonius pecki
		Ap. tenax
		A. indianensis
		A. russelli
		Chitrella archeri
		He. mirabilis
		K. attenuatus
		K. barri
		K. cerberus
		K. charon
		K. daemonius
		K. erebicus
		K. hageni
		K. hubrichti
		K. krekeleri
		K. magnus
		K. microphthalmus
		K. myopius
		K. packardi
		K. pluto
		K. rex
		K. stygius
		K. tantalus
		M. eurydice
		M. nickajackensis
		M. persephone
	•	M. pluto
		M. subatlantica
		Ty. aladdinensis
		Ty. aralu
		Ty. archeri
		Ty. attenuatus
		Ty. avernicolus
		Ty. barri
		Ty. binoculatus
		Ty. charon
		Ty. diabolus
		Ty. erebicus
		Ty. felix
		Ty. fiskei
		Ty. gnomus
		Ty. halopotamus
		Ty. hypogeus
		Ty. infernalis
		Ty. jonesi

Class/phylum order		Species
		Ty. nergal
		Ty. orpheus
		Ty. osiris
		Ty. parvus
		Ty. pecki
		Ty. pholeter
		Ty. pluto
		Ty. satan
		Ty. sheltae
		Ty. skeletonis
		Ty. steevesi
		Ty. stygius
		Ty. tartarus
		Ty. tenuis
		•
0	A bi d	Ty. torodei
Crustace 1	Amphipoda	C. antennatus
		C. packardi
		S. dicksoni
		S. exilis
		S. nortoni
		S. smithi
		S. vitreus
	Copepoda	Bryocamptus morrisoni elegans
		Br. morrisoni morrisoni
	Cyclopoida	Diacyclops clandestinus
		D. jeanneli jeanneli
		Megacyclops donnaldsoni donnaldsoni
	Decapoda	Cam, hamulatus
	•	Cam. jonesi
		Cam. veitchorum
		O. australis australis
		O. australis packardi
		O. incomptus
		O. inermis inermis
		O. inermis testii
		O. pellucidus
		O. sheltae
		Palaemonias alabamae
		Pa. ganteri
	Y	P. pecki
	Isopoda	Am. nicholasi
		Ca. bicrenata bicrenata
		Ca. bicrenata whitei
		Ca. circulus
		Ca. jordani
		Ca. nickajackensis
		Ca. nortoni
		Ca. richardsonae
Lemaeonodoida	Ca. stygia	
		Ca. whitei
		Mik. alabamensis
		Mik, barri
	Lernaeopodoida	Cauloxenus stygius
	Podocopida	Dactylocythere arcuata

Class/phylum order		Species
	. <u></u>	Da. steevesi
		Da. susanae
		Pseudocandona jeanneli
		Pseud. marengoensis
		Sagittocythere barri
		Sa. stygia
		Do. tuberosa
Diplopoc a	Callipodida	Te. jonesi
	Callipodida	Te. tennesseensis
	Chordeumatida	Conotyla bollmani
		Ps. acheron
		Ps. blacki
		Ps. burnsorum
		Ps. cercops
		Ps. conservata
		Ps. cookorum
		Ps. eburnea
		Ps. indianae
		Ps. lethe
		Ps. lictor
		Ps. merops
		Ps. minos
		Ps. nyx
		Ps. purselli
		Ps. rhadamanthus
		Ps. salisae
		Sc. copei
		Sc. ventus
		T. syntheticum
Diplopoda	Julida	Amer. satis
Insecta	Collembola	Ar. altus
		Ar. bimus
		Ony. paro
		Pse. christianseni
		Pse. espanita
		Pse. fonsa
		Pse. hirsuta
		Pse. nata
		Pse. pecki
		Pse. spinosa
		Sch. alabamensis
		Sch. christianseni
		Si. alata
		Si. avita
		Si. barri
		Si. basidens
		Si. cavernarum
		Si. hoffmani
		Tomocerus missus
	Diplura	Lit. cookei
	•	Lit. henroti
		Lit. jonesi
		Lit. valentinei
	Coleoptera	B. jeanneli
	•	B. quisnamus
		B. spelaeus
		Ba. barri

Class/phy lum order	Species
	Ba. cavernosus
	Ba. clypeospecus
	Ba. ferulifer
	Ba. gemmoides
	Ba. gemmus
	Ba. henroti
	Ba. hubrichti
	Ba. jocuvestus
	Ba. jonesi
	Ba. pannosus
	Ba. specus
	Ba. subterraneus
	Ba. tumoris
	Ba. valentinei
	Dar. kentuckensis kentuckensis
	Neaphaenops tellkampfi henroti
	Ne. tellkampfi meridionalis
	Ne. tellkampfi tellkampfi
	Ne. tellkampfi viator Ne. walteri
	Pseu. acherontis
	Pseu, alladini
	Pseu. audax
	Pseu. bandermani
	Pseu. beakleyi
	Pseu. bloomi
	Pseu, catherinae
	Pseu. cerberus cerberus
	Pseu. cerberus completus
	Pseu, ciliaris ciliaris
	Pseu. ciliaris colemanensis
	Pseu, ciliaris orlindae
	Pseu. cumberlandus
	Pseu. darlingtoni darlingtoni
	Pseu. darlingtoni persimilis
	Pseu. distinguens
	Pseu. emersoni
	Pseu. eremita
	Pseu. farrelli
	Pseu. fluviatalis
	Pseu. fowlerae
	Pseu. globiceps
	Pseu. humeralis
	Pseu. illinoisensis
	Pseu. inexpectatus inexpectatus
	Pseu. inquisitor
	Pseu. insularis
	Pseu. leonae
	Pseu. loedingi
	Pseu. loganensis
	Pseu. macradei
	Pseu. menetriesii campestris
	Pseu. menetriesii menetriesii
	Pseu. meridionalis

Class/phy um order	Species
	Pseu. nickajackensis
	Pseu. occidentalis
	Pseu. pilosus
	Pseu. princeps
	Pseu. productus
	Pseu. profundus
	Pseu, pubescens intrepidus
	Pseu. pubescens pubescens
	Pseu. robustus
	Pseu. shilonensis mayfieldensis
	Pseu. shilonensis shilonensis
	Pseu. simplex
	Pseu. simulans
	Pseu, steevesi
	Pseu. striatus
	Pseu. templetoni
	Pseu. templetoni Pseu. tenuis blatchleyi
	Pseu, tenuis bidictieși Pseu, tenuis jeanneli
	Pseu, tenuis jeunnett Pseu, tenuis morrisoni
	Pseu, tenuis morrisoni Pseu, tenuis stricticollis
	Pseu, tenuis stretteonis Pseu, tenuis tenuis
	Pseu, tiresias
	Pseu. transfluvialis Pseu. tullahoma
	Pseu. valentinei
	Pseu. vanburensis
	Pseu. ventus
	Pseu. youngi donaldsoni
	Pseu. youngi youngi
	Pt. barri
	Pt. chromolithus
	Pt. episcopus
	Pt. fecundus
	Pt. hatchi
	Pt. hazelae
	Pt. hirtus
	Pt. hubrichti
	Pt. julius
	Pt. laticornis
	Pt. loedingi
	Pt. longicornis
	Pt. solanum
	Pt. torođei
	Pt. valentinei
	Pt. walteri
	Speleobama vana
	Spe. croceus
	Spe. stygicus
	Spe. synstygicus
	Subterrochus eurous
	Su. ferus
	Su. steevesi
	Tichobythinus hubrichti
	Ti. jonesi

Class/phylum order		Species
		Ti. strinatii
		Tro. valentinei
	Diptera	Spel. tenebrarum
Mollusca	Mesogastropoda	Antroselates spiralis
	Stylommatophora	Carychium stygium
		Gl. pecki
		Gl. specus
		Hel. barri
Oligochaeta	Branchiobdellida	Camb. alienus
2		Camb. dubius
		Camb. marthae
		Camb. sheltensis
		Camb. steevesi
	Lumbriculida	Tri, allegheniensis
Pisces	Percopsiformes	Amblyopsis spelaea
1 isces	rereopsitorines	Speoplatyrhinus poulsoni
		Tunkl subtamenana
Turbellaria	Tricladida	Typhl. subterraneus
rurbena ia	Triciadida	Sp. buchanani
		Sp. chandleri
		Sp. percoeca
		Sp. pricei
Destruction Const.		Sp. weingartneri
Region 4: Ozarks Amphibia	Urodela	Typhlotriton spelaeus
Arachnida	Araneae	Bat. weyeri
Aracillina	Araneae	I. speophila
		Pha. subterranea
		Po. cavernicola
	0	
	Opiliones	Crosbyella distincta
	B 1 1 11	Cr. roeweri
	Pseudoscorpionida	He. occidentalis
		A. colecampi
		A. diabolus
		A. mysterius
		A. titanicus
		A. typhlus
		Mu. cavernicola
Crustace a	Amphipoda	Allocrangonyx hubrichti
		Bactrurus brachycaudus
		Ba. hubrichti
		C. packardi
		S. clantoni
		S. onondagaensis
		S. ozarkensis
		S. subtilis
		Gammarus acherondytes
	Cyclopoida	D. clandestinus
	Decapoda	Cam. aculabrum
	Decapoda	Cam. hubrichti
		Cam. setosus
		Cam. subterraneus
		Cam. tartarus
		Cam. zophonastes
		O. stygocaneyi
	Isopoda	Ca. ancyla

Class/pl ylum order		Species
		Ca. antricola
		Ca. bicrenata whitei
		Ca. dimorpha
		Ca. fustis
		Ca. macropropoda
		Ca. packardi
		Ca. salemensis
		Ca. serrata
		Ca. spatula
		•
		Ca. steevesi
		Ca. stiladactyla
		Ca. stygia
		Ca. whitei
	Podocopida	U. pholetera
		U. xania
Diplopoda	Chordeumatida	Sc. dendropus
		Tingupa pallida
		Trigenotyla parca
	Julida	Zosteractis interminata
Insecta	Collembola	Ar. clarus
		Ar. jay
		On. hoffi
		On. iowae
		Ony. obesus
		Pse. dubia
		Pse. espana
		r se. espana Si. avita
		Si. barri
		Si. cavernarum
		To. missus
	Coleoptera	Xenotrechus condei
		X. denticollis
	Diptera	Spel. tenebrarum
Mollusca	Mesogastropoda	Amnicola cora
		Amn. stygia
		Antrobia culveri
		F. antroecetes
		F. proserpina
Pisces	Percopsiformes	Amb, rosae
1 13003	1 0.00psorm.us	Typhl. subterraneus
Turbellaria	Tricladida	Dendrocoelopsis americana
i ui ociia. ia	Titeladida	Ma. glandulosa
		Ma. lewisi
		Sp. evaginata
		Sp. hubrichti
	teau/Balcones Escarpment	
Amphibia	Urodela	Eurycea latitans
		E. neotenes
		E. tridentifera
		E. troglodytes
		Typlomolge rathbuni
		Typ. robusta
Arachnica	Araneae	Ci. bandida
		Ci. barri
Arachnic a	Araneae	E. troglodytes Typlomolge rathbuni Typ. robusta Ci. bandida

Class/phylum order	Species
	Ci. cueva
	Ci. elliotti
	Ci. ezelli
	Ci. gruta
	Ci. holsingeri
	Ci. medina
	Ci. menardia
	Ci. orellia
	Ci. pablo
	Ci. patei
	Ci. porteri
	Ci. rainesi
	Ci. reddelli
	Ci. reyesi
	Ci. russeli
	Ci. selecta
	Ci. serena
	Ci. sheari
	Ci. sprousei
	Ci. suttoni
	Ci. travisae
	Ci. ubicki
	Ci. uvalde
	Ci. venii
	Ci. vespera
	Ci. vibora
	Ci. wartoni
	Ci. watersi
	Eidmannella delicata
	Ei. nasuta
	Ei. reclusa
	Ei. rostrata
	I. unicornis
	Neoleptoneta anopica
	Neo. coeca
•	Neo. concinna
	Neo. devia
	Neo. microps
	Neo. myopica
	Neo. valverde
Opiliones	Hoplobunus madlae
Spinone.	H. madlae
	H. russelli
	Texella brevidenta
	Te. brevistyla
	Te. cokendolpheri
	Te. diplospina
	Te. grubbsi
	Te. hardeni
	Te. mulaiki
	Te. reddelli
	Te. renkesae
	Te. reyesi

Appendix 1. (continued)

Class/pt ylum order		Species
	Pseudoscorpiones	Apocheiridium reddelli
	•	Cheiridium reyesi
		Ch. elliotti
		Ch. major
		Dinocheirus cavicola
		He. occidentalis
		Leucohya texana
		Mexichthonius exoticus
		Neoallochernes stercoreus
		Neoa. stercoreus
		Tartarocreagris comanche
		Tariarocreagns comanche Ta. infernalis
		Ta. intermedia
		Ta. reddelli
		Ta. texana
G1 /1		Ty. texanus
Chilopoc a	Scolopendromorpha	Theatops phanus
Crustace 1	Amphipoda	Allotexiweckelia hirsuta
		Artesia subterranea
		Holsingerius samacos
		Hol. smaragdinus
		Mexiweckelia hardeni
		Parabogidiella americana
		Paramexiweckelia ruffoi
		Seborgia hershleri
		Se. relicta
		S. balconis
		S. bifurcatus
		S. dejectus
		S. flagellatus
		S. hadenoecus
		S. longipes
		S. pecki
		S. russelli
		Texiweckelia texensis
		Texiweckeliopsis insolita Texi, insolita
	Daniel I	
	Decapoda	Pal. antrorum
		Pal. holthuisi
	Isopoda	Brackenridgia cavernarum
		Br. reddelli
		Ca. bilineata
		Ca. reddelli
		Cirolanides texensis
		Lirceolus bisetus
		Lirc. hardeni
		Lirc. pilus
		Lirc. smithii
		Speocirolana hardeni
	Podocopida	Sphaeromicola moria
	Thermosbaenacea	Monodella texana
Diplopoda	Polydesmida	Speodesmus bicornourus
Diproporta	Loryaconna	Speod. echinourus

Appendix 1. (continued)

Class/phylum order		Species
Insecta	Collembola	Ar. texensis
		On. fenestra
		Si. baca
	Diplura	Mixojapyx reddelli
	Thysanura	Texoreddellia texensis
	Coleoptera	Ba. grubbsi
		Ba, revesi
		Ba. texanus
		Ba. venyivi
		Haideoporus texanus
		Rhadine austinica
		Rh. exilis
		Rh. infernalis ewersi
		Rh. infernalis ewerst Rh. infernalis infernalis
		Rh. insolita
		Rh. koepkei koepkei
		Rh. koepkei privata
		Rh. noctivaga
		Rh. persephone
		Rh. russelli crinicollis
		Rh. speca gentilis
		Rh. speca speca
		Rh. subterranea mitchelli
		Rh. subterranea subterranea
		Rh. tenebrosa mckenziei
		Rh. tenebrosa tenebrosa
		Stygoparnus comalensis
		Texamaurops reddelli
Mollusca	Mesogastropoda	Balconorbis uvaldensis
	2 1	Phreatoceras conica
		Phr. imitata
		Phr. taylori
		Phreatodrobia coronae
		Phre. micra
		Phre. nugax inclinata
		Phre. nugax nugax
		Phre. plana
		Phre. punctata
		Phre. rotunda
		Stygopyrus bartonensis
D '	Ci-ic	
Pisces	Cypriniformes	Satan eurystomus
		Trogloglanis pattersoni
Turbellar a	Tricladida	Sp. mohri .
Region 6 Guadalupe Mo		
Arachnid ı	Acari	Ceuthothrombium cavaticum
	Araneae	Ei. bullata
	Opiliones	Te. longistyla
		Te. welbourni
	Pseudoscorpiones	Ap. pachysetus
	-	Archeolarca guadalupensis
		Ch. welbourni
		Neoa. incertus
Chilopoda	Scolopendromorpha	Thalkethops grallatrix
Crustacea	Amphipoda	Ar. welbourni
C. 4	Polydesmida	Speod. tuganbius

Appendix 1. (continued)

Class/ph/lum order		Species
	Spirostreptida	Camb. speobia
Insecta	Collembola	Pse. vita
n : 2 M d		On. prietoi
Region 7: Mother Lode Arachnida	Acari	Fo. titanica
Aracilliui	Opiliones	Banksula elliotti
	Opiniones	Ban, grahami
		Ban. martinorum
		Ban. melones
		Ban, tuolumne
	Pseudoscorpiones	Ap. grubbsi
	rocudoscorpiones	Ap. similis
		A. grubbsi
		Australinocreagris grahami
		Larca lacevi
		Neochthonius troglodytes
		Neoc. troglodytes
		Pseudogarypus orpheus
Crustacea	Amphipoda	S. gradyi
		S. grahami
		S. harai
Diplopod 1	Chordeumatida	Speoseya grahami
		Striaria eldora
Insecta	Collembola	On. mala
		On. tunica
		Si. baca
		Si. tecta
Region 8: Black Hills		
Insecta	Collembola	Ar. clarus
D		Entomobrya troglodytes
Region 9 Driftless area		D 1 . 1 1 . 1.
Arachnid ı	Acari	Robustocheles occulta
	Araneae	Po. cavernicola
Countries	A	Bat. weyeri
Crustace:	Amphipoda Chordeumatida	S. iowae Achemenides pectinatus
Diplopoda Insecta	Collembola	Ar. bimus
Insecta	Concinodia	Ar. dubius
		On, iowae
		Onychiurus gelus
		Ony. obesus
		Si. barri
		Tullbergia hades

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