Review of Studies of the Subterranean Faunal Studies of the Appalachians and a Review of Models of Subterranean Species Richness

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Historically, the cave fauna, and any biota for that matter, were largely studied from a taxonomic perspective. Papers focused on a lineage or a set of closely related lineages because of the strictures of taxonomic expertise, the difficulty in collating and summarizing information for a variety of taxonomic groups, and because, until relatively recently, there was no research agenda that emphasized patterns of species richness. With the advent of interest in species diversity *per se* in the late 1960's and especially with the interest in biodiversity and biodiversity hotspots in the late 1980's, the focus changed. Studies of cave fauna reflected the changing research agendas. In this bibliographic review, we examine five areas of interest:

1. National cave fauna studies
2. Regional and local cave fauna studies in the Appalachians
3. A summary of the major taxonomic studies
4. Previous mapping of biodiversity in the region and the techniques employed
5. Models for explaining subterranean biodiversity patterns, both in the Appalachians and elsewhere.

National cave fauna studies

Studies of the cave fauna of the Appalachians date back to Packard (1888), who summarized all available information on the cave fauna of the U.S., together with species lists for all sampled caves. Of course the number of sampled caves was quite small (approximately 20); it included several caves in the study area, *e.g.,* Luray Caverns in Virginia, Mammoth Cave in Kentucky, and Wyandotte Caves in Indiana. Packard emphasized the widespread presence of cave-limited species in U.S. caves and did not speculate on patterns of species richness, except to point out the extraordinary species richness in Mammoth Cave.

In 1960, Brother G. Nicholas published a checklist of cave-limited species in the U.S., the majority of which are within the Appalachian LCC. He enumerated more than 300 species, but provided no summaries of species richness by state or region. Indeed, such summaries would have been difficult and tedious without the aid of computer spreadsheets.

In 1998, Peck provided a taxonomic and biogeographic summary of subterranean species richness, and reported a total of 425 aquatic and 928 terrestrial species. He provided a list of aquatic (stygobiotic) and terrestrial (troglobiotic) genera for the U.S. and Canada. He also analyzed the state distributions of stygobiotic and troglobiotic genera separately. For troglobionts, Appaalchian LCC states ranked first (Alabama), third (Tennessee), and fourth (Kentucky). Among stygobionts, Kentucky ranked third, and Alabama, Indiana, and West Virginia tied for fourth.

Rather than analyzing genera as Peck did, Culver *et al.* (2000) looked at species richness patterns by county. They found that subterranean species richness was concentrated in a relatively few counties, and in general less than one percent of the land area accounted for over 50 percent of the species, both aquatic and terrestrial. Jackson County, Alabama, had the highest number of troglobionts, and two other Alabama Counties —Marshall and Madison— had the third and fourth highest number of troglobionts. Edmonson County, Kentucky, had the third highest number of stygobionts, and Jackson County had the fourth highest. Using the same dataset, Culver *et al.* (2003) compared different karst regions, *e.g.,* Interior Low Plateau and the Ozarks, and found that the Interior Low Plateau had the most troglobionts, followed by the Appalachians. For stygobionts, the order of the two regions was reversed. Both regions are within the Appalachian LCC They also provided a species list by region.

There were several studies that compared global patterns of subterranean species richness that included information from the Appalachian LCC. Culver and Sket (2000) listed all the hotspots of subterranean biodiversity known to them that had 20 or more stygobionts and troglobionts. Two Appalachian LCC sites were on Culver and Sket's list of 20 sites—Mammoth Cave in Kentucky and Shelta Cave in Alabama. Culver and Pipan (2013) updated the list, separating stygobionts and troglobionts. In the updated list, only Mammoth Cave remained a global hotspot of troglobionts (26 species compared to a maximum of 36 in Postojna Planina Cave system in Slovenia) and no sites were global hotspots of stygobionts. While there are many limitations to this approach, e.g. it did not take into account β-diversity which is many times higher than α-diversity in cave regions (Gibert and Deharveng 2002), it provides the only truly global comparison of subterranean species richness. Gibert *et al.* (2009) compared aquatic subterranean biodiversity at the regional level (approximately the size of US counties) for European and North American sites, including Jackson County (AL), Pocahontas County (WV), Edmonson County (KY), and Crawford County (IN). Europe generally had higher aquatic subterranean species richness than North American ones. Several important factors related to geology and hydrology were important for explaining the observed patterns.

The most detailed meso-scale comparative studies are those that utilize samples from large numbers of caves in relative small areas (approximately 10,000 km^2) and analyze species richness using two powerful techniques. The first is the species accumulation curve, where number of species is related to the amount of sampling (as number of sampled caves). A bootstrapping technique can be used to obtain a confidence band around the accumulation curve; this band is useful for testing and interpretation of the curve. If the accumulation curve reaches an asymptote, then an estimate (with standard errors) of species richness results. The second method is the set of measures that estimate the number of "missing" species. The best known of these are due to Anne Chao, and estimate the number of species not observed by extrapolating a curve that runs through the number of species observed exactly once (i.e. in a single cave) and the number observed exactly twice. These techniques have been used with the highly diverse subterranean beetle fauna of the Balkans (Zagmajster *et al.* 2010), European subterranean species (Dole-Olivier *et al.* 2009), and terrestrial cave biodiversity in Europe and North America (Culver *et al.* 2006). Culver *et al.* (2006) found that troglobiotic species richness in Jackson County in northeast Alabama rivaled troglobiotic species richness in the most diverse European areas—south-central Slovenia and the Pyrenees in France.

Regional and Local Cave Faunal Studies in the Appalachian LCC Study Area by State

Introduction

The study of cave fauna in the sense of inventory and biodiversity studies, dates back to Packard (1888). Some states, especially Alabama and Virginia, have a rich history of study, while others, especially the cave fauna-depauperate states of New York, Ohio, and Pennsylvania, have been little studied. At present, the cave fauna is tracked by state Natural Heritage programs, and most of these programs have a relatively up to date inventory. However, common stygobiotic and troglobiotic species, *e.g.,* those known from more than 50 caves, are typically not included in the natural heritage program's inventories of "species of concern." We briefly review the major biodiversity and inventory studies for each state in the Appalachian LCC area in this section.

Alabama

The first large scale inventory of the Alabama cave fauna was that of Peck (1989, 1995) for terrestrial species. No equivalent published list exists for the aquatic fauna, but Cooper (1975) produced a list of species in Shelta Cave, the richest aquatic cave in the U.S. (the Edwards Aquifer has more species, but the primary access points are wells [Culver and Sket 2000]). Culver *et al.* (1999) summarize the evidence that northeast Alabama is a biodiversity hotspot.

Georgia

Holsinger and Peck (1971) provided an inventory of the obligate cave fauna of Georgia. More recent inventories include Reeves et al. (2000) and Buhlmann (2001). Niemiller et al. (2012a) provided an updated review of the obligate cave fauna of Georgia that included 47 described species (31 troglobionts and 16 stygobionts).

Illinois

Peck and Lewis (1977) provide a comprehensive inventory of the cave fauna of Illinois, supplemented by the study of Lewis *et al.* (2003) of the fauna of southwest Illinois.

Indiana

Cope (1872) documented the cave fauna of Wyandotte Cave. Packard (1873) provided a general synopsis of cave fauna of Indiana. Packard (1888) included a list of cave fauna throughout North America, including those from accounts of the faunas from Wyandotte and Little Wyandotte caves. Blatchley (1897) reported on the fauna of several caves in Indiana and compared his faunal list with that of Cope (1872). Banta (1907) reported on the fauna of Mayfield's Cave in Monroe County. Much of our modern knowledge of cave fauna in Indiana is based on the impressive bioinventories of Jerry Lewis. Lewis (1983) listed the obligate cave fauna of southeastern Indiana. Other significant bioinventory studies include Lewis (1993, 1994, 1995, 1996, 1998, 2005a), Lewis and Rafail (2002), Lewis et al. (2004) and Lewis and Lewis (2006).

Kentucky

There has been no comprehensive published inventory of the obligate cave fauna of Kentucky. Barr (1967) and Barr and Kuehne (1971) provide a detailed fauna inventory of Mammoth Cave, one of the world's most diverse caves. There have been a large number of ecological and evolutionary studies in Mammoth Cave National Park (*e.g.,* Poulson 1992). Harker and Barr (1979, 1980) provide the most comprehensive list of cave fauna in Kentucky in two unpublished technical reports for the Kentucky Nature Preserves Commission.

Maryland

There has been no published inventory of the obligate cave fauna of Maryland. Most of the records of stygobionts (troglobionts are rare) are for non-cave subterranean habitats such as seepage springs, springs, etc. (Feller 1997, 2005, Culver *et al.* 2012), a situation unique to Maryland within the Appalachian LCC study area. This is most likely a result of more intensive collecting in these habitats (especially by D. Feller) than elsewhere. A major component of the fauna, the isopod genus *Caecidotea,* was reviewed by Lewis *et al.* (2011).

New Jersey

As far as we know, no stygobionts or troglobionts are known from New Jersey.

New York

Most records of stygobionts from caves (troglobionts are very rare) are for the amphipod genus *Stygobromus.* While the records are not organized by state, most records can be found in Holsinger's (1978) monographic treatment of the genus.

North Carolina

No statewide inventory of cave-dwelling species in North Carolina exists but Reeves (2000) provides a list of species (obligate and non-obligate) found in caves in the Great Smoky Mountains National Park.

Ohio

Hobbs and Hazleton (2010) provide an inventory of obligate and non-obligate species found in Ohio caves.

Pennsylvania

Holsinger (1976) reviews the largely stygobiotic fauna of Pennsylvania caves.

South Carolina

No statewide inventory of the cave fauna of South Carolina has been published, but Reeves (2001) provides an inventory of the invertebrate fauna of Santee Cave, developed in limestone in the Coastal Plain.

Tennessee

Several significant cave bioinventories studies have occurred in Tennessee, including Cope and Packard (1881), Hay (1902), Lewis (2001, 2002, 2004, 2005b), Lewis and Lewis (2005, 2007) and Lewis et al. (2010). These studies provide species lists at local (Cope and Packard 1881; Hay 1902) to regional scales (Lewis 2001, 2002, 2004, 2005; Lewis et al. 2010). The most extensive statewide inventory and analysis is that of Niemiller and Zigler (2013). At present, Tennessee has more reported troglobiotic species (160) than any other state. Niemiller and Zigler demonstrate that the terrestrial biodiversity hotspot previously identified from northeast Alabama (Culver *et al.* 2000) extends along the Cumberland Escarpment into southcentral Tennessee. Their analysis includes not only patterns of species richness but also endemism. Dixon and Zigler (2011) and Wakefield and Zigler (2012) provide fine-scale analyses of species richness in two small regions—Carter State Natural Area and the University of the South campus—and demonstrate remarkably small scale differences in species composition and richness.

Virginia

Holsinger has provided the impetus for three biological inventories of Virginia caves (Holsinger 1963; Holsinger and Culver 1988; Holsinger *et al.* 2013). The numbers of described troglobionts and stygobionts from caves increased from 45 in 1963 to 102 in 1988 to 168 in 2013. The last two publications include range maps for all species.

West Virginia

Holsinger *et al.* (1976) published an inventory of all West Virginia cave species, including stygobionts, stygophiles, troglobionts, and troglophiles. Fong *et al.* (2007) updated the list of stygobionts and troglobionts. Schneider and Culver (2004) did a detailed analysis of species composition and richness in a small cave-rich area in northern Greenbrier County.

Regional and Local Cave Faunal Studies in the Appalachian LCC Study Area by Taxonomic Group

Introduction

Rather than broad inventories and biodiversity studies at regional or national scales, most studies on cave fauna focus on specific taxonomic groups particularly with regard to distribution, biogeography, systematics and phylogenetics. Here we briefly review the major distributional, biogeographical, systematics and molecular studies for each taxonomic group of obligate cave fauna found in the Appalachian LCC area.

Phylum Platyhelminthes (Flatworms)

Major systematic treatments of stygobiotic flatworms (Order Tricladida) found in the Appalachian LCC area are limited to Carpenter (1970b) and Kenk (1977). Other studies include Buchanan (1936), Hyman (1937, 1939, 1945, 1954), Carpenter (1970a), Kenk (1970) and Chandler and Darlington (1984).

Phylum Mollusca, Class Gastropoda (Snails)

Significant studies on cave snails in the Appalachian LCC area include Hubricht (1960, 1962, 1963, 1964, 1965) and Hershler and Thompson (1990).

Phylum Arthropoda, Class Crustacea, Order Amphipoda (Amphipods)

Major systematic treatments of cave amphipods include Holsinger (1967, 1969, 1978; *Stygobromus*), Koenemann and Holsinger (2001; *Bactrurus*) and Zhang and Holsinger (2003; *Crangonyx*). Other significant studies include Hubricht and Mackin (1940) and Hubricht (1943).

Phylum Arthropoda, Class Crustacea, Order Cyclopoida (Copepods)

Significant studies on cave copepods in the Appalachian LCC area include Chappuis (1929, 1931), Yeatman (1964), Reid (2004) and Lewis and Reid (2007).

Phylum Arthropoda, Class Crustacea, Order Decapoda (Decapods)

Hobbs and Barr (1960, 1972) and Hobbs et al. (1977) reviewed the systematics and compiled records of cave decapods in the U.S. Other significant studies on cave decapods in the Appalachian LCC area include Cooper and Cooper (1997), Buhay and Crandall (2005, 2008, 2009), Buhay et al. (2007) and Cooper and Cooper (2011).

Phylum Arthropoda, Class Crustacea, Order Isopoda (Isopods)

The species descriptions of cave isopods from the Appalachian LCC area are scattered across two dozen papers. Recent work includes that of Lewis and Bowman (1977, 1981) and Lewis (1982, 1988, 2009a).

Phylum Arthropoda, Class Crustacea, Order Podocopida (Ostracods)

Significant studies on cave ostracods in the Appalachian LCC area include Hart and Hobbs (1961), Hart and Hart (1966, 1974) and Lewis and Lewis (2009).

Phylum Arthropoda, Class Arachnida, Order Acari (Mites)

The literature on cave mites in the Appalachian LCC is mostly limited to species descriptions by Packard (1888), Zacharda (1985), and Zachard et al. (2010).

Phylum Arthropoda, Class Arachnida, Order Araneae (Spiders)

Significant studies on cave spiders in the Appalachian LCC area include those by Gertsch (1984), Hedin (1997a; 1997b), Hedin and Dellinger (2005), and Snowman, Zigler and Hedin (2010) (all on *Nesticus*). Other studies on genera with only one or two cave species include Platnick (1999; *Liocranoides*), Miller (2005a; *Anthrobia*), Miller (2005b; *Porrhomma*), Paquin et al. (2009; *Oreonetides*), Gertsch (1992; *Cicurina*), Millidge (1984; *Phanetta*), Gertsch (1974) and Platnick (1986; *Neoleptoneta* and *Appaleptoneta*), Emerton (1875, *Bathyphantes*) and Ivie (1969a, 1969b; *Islandiana* and *Bathyphantes*).

Phylum Arthropoda, Class Arachnida, Order Opiliones (Harvestmen)

Significant studies focused on cave harvestmen in the Appalachian LCC area include Goodnight and Goodnight (1942, 1960), Hedin and Thomas (2010), and Shear (2010)..

Phylum Arthropoda, Class Arachnida, Order Pseudoscorpionida (Pseudoscorpions)

Studies of cave pseudoscorpions in the Appalachian LCC area include those by Muchmore (1965, 1966a, 1966b, 1967, 1974, 1976, 1996) and Malcolm and Chamberlin (1960, 1961). The widespread species *Hesperochernes mirabilis* was described by Banks (1895).

Phylum Arthropoda, Class Diplopoda (Millipeds)

Early studies on the speciose genus *Pseudotremia* include those by Loomis (1939, 1943). Shear's (1972) monograph is the central resource on the genus. Additional cave species of *Pseudotremia* were described by Lewis (2005c, 2009b) and Shear (2008, 2011). Shear (2010) revised the cave millipede genera *Scoterpes* and *Zygonopus*. Studies on millipede genera with one or a few cave species include Lewis (2002b, *Chaetapsis*), Causey (1959; *Chaetaspis*, *Ameractis* and *Tetracion*) and Hoffman (1956; *Tetracion*).

Phylum Arthropoda, Subphylum Hexapoda, Class Collembola (Springtails)

The central resource for springtail taxonomy in United States is Christiansen and Bellinger (1998). Studies on springtails in the Appalachian LCC include Delamare (1949), Christiansen (1960, 1961), Christiansen and Culver (1968), Christiansen and Bellinger (1980, 1996), Zeppelini and Christiansen (2003), Zeppelini et al. (2009), and Soto-Adames (2010). A number of other papers describe single Collembola species.

Phylum Arthropoda, Subphylum Hexapoda, Class Diplura (Diplurans)

The first treatment of cave diplurans found in the Appalachian LCC area was Conde (1949). Ferguson's (1981) dissertation on systematics, evolution and zoogeography is the most general treatment but most of these species were never described. .

Phylum Arthropoda, Subphylum Hexapoda, Class Insecta, Order Coleoptera (Beetles)

The cave beetles of the Appalachian LCC area are highly diverse. The speciose genus *Pseudanophthalmus* was reviewed by Barr (2004). Peck (1973) revised the cave *Ptomaphagus* of the southern Appalachians. Numerous species of cave staphylinids were described by Park (1951, 1956, 1958, 1960, 1965), Barr (1974, 1987), Besuchet (1982) and Carlton (2008). Genera with one or a few cave species include *Anillinus, Darlingtonea* and *Nelsonites* (Valentine, 1952; Jeannel 1963; Sokolov, 2012).

Phylum Arthropoda, Subphylum Hexapoda, Class Insecta, Order Diptera (Flies)

A single troglobiont fly (*Spelobia tenebrarum*) is known from the Appalachian LCC area. Marshall and Peck (1985a) reviewed the distribution of this and other species of sphaerocerid flies, while Marshall and Peck (1985b) discussed the origins and relationships of populations.

Phylum Chordata, Class Actinoptergyii (Ray-finned Fishes)

Three stygobiotic fishes occur in the Appalachian LCC area, all in the family Amblyopsidae). Significant studies on amblyopsid cavefishes include Eigenmann (1897, 1909), Woods and Inger (1957), Poulson (1960, 1963, 1969), Cooper and Beiter (1972), Cooper and Kuehne (1974), Bechler (1976), Keith (1988), Pearson and Boston (1995), Romero (1998a,b), Kuhajda and Mayden (2001), Proudlove (2006), Niemiller and Fitzpatrick (2008), Niemiller and Poulson (2010), Niemiller et al. (2010b), Dillman et al. (2011) and Niemiller et al. (2012, 2013a,b,c,d). Proudlove (2006) included species accounts of cave amblyopsids. Niemiller and Poulson (2010) reviewed the systematics, distribution, biology and conservation of all amblyopsids. Niemiller et al. (2013b) conducted a conservation assessment on cryptic lineages of *Typhlichthys subterraneus*.

Phylum Chordata, Class Amphibia, Order Caudata (Salamanders)

Three obligate cave-dwelling salamanders occur in the Appalachian LCC area. Major literature reviews include Brandon (1967), Niemiller and Miller (2010) and Miller and Niemiller (2012). Miller and Niemiller (2008) conducted the most in depth inventory of *Gyrinophilus palleucus* and *G. gulolineatus* to date. Systematic and molecular studies include Brandon (1962, 1966) and Niemiller et al. (2008, 2009). Other significant studies include McCrady (1954), Lazell and Brandon (1962), Brandon (1965, 1971), Cooper (1968), Cooper and Cooper (1968), Simmons (1975, 1976), Besharse and Holsinger (1977), Yeatman and Miller (1985), Caldwell and Copeland (1992), Hollingsworth et al. (1997), Godwin (2000), Osbourn (2005), Niemiller (2006), Niemiller et al. (2010a,c) and Huntsman et al. (2011).

Techniques for Mapping Subterranean Biodiversity

In order to graphically represent the spatial pattern of subterranean species richness, the area under study needs to be subdivided into either naturally occurring units such as drainage basins or in equally sized areas, typically quadrilaterals or sometimes hexagons (White 2000). For equal sized areas, Zagmajster *et al.* (2008a) and Christman and Zagmajster (2012) point out that there is an optimum sized quadrat, one that does not combine very different areas, but also one that does not have gaps in coverage. In the case of subterranean beetle diversity in the Balkans, this size was 100 km^2.

One result of their studies and that of Niemiller and Zigler (2013), is that a large number of caves need to be sampled in order to produce a credible map. For their study of Tennessee cave faunas, Niemiller and Zigler (2013) had cave fauna data for 661 caves. Their study also points out that even intensively studied regions are not completely sampled. While 661 sampled caves is an impressive sample, it is less than ten percent of the known caves in Tennessee (9517). Culver *et al.* (2004) report similar frequencies of sampling in Slovenia, arguably the best studied country in the world in terms of subterranean fauna.

Although contoured maps of biodiversity (generally produced by the technique of kriging) are available for many groups, the only one produced so far for subterranean fauna is that of Zagmajster *et al.* (2008b) and Christman and Zagmajster (2010) for the subterranean beetle fauna of the Balkans.

Models for Explaining Biodiversity Patterns

There have been two approaches to explaining subterranean biodiversity patterns. One, exemplified by the European PASCALIS project ((<u>P</u>rotocols for the <u>AS</u>sessment and <u>C</u>onservation of <u>A</u>quatic <u>L</u>ife In the <u>S</u>ubsurface), utilizes multivariate statistical techniques to identify physico-chemical variables that are associated with species richness. In particular, canonical correlation analysis (CCA) and outlying mean indices (OMI) were utilized to look for correlates explaining the differences in species richness (Dole-Olivier *et al.* 2009, Galassi *et.al.* 2009, Martin *et al.* 2009). Their approach is non-spatial in the sense that the spatial relationship among sites is not used in the analysis. The second approach is an explicitly spatial one exemplified by the work of Christman and colleagues (Christman and Culver 2001, Christman *et al.* 2005). They used a single measure of habitat availability—number of caves—to estimate species richness but modeled both local and regional effects. They found that the number of species (and the number of endemic species) depend not only on the number of caves in the immediate area but also on the number of caves in adjoining quadrats. The important take home message from these analyses is that the subterranean system is interconnected, and cannot be understood in isolation.

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