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Mammoth Cave: A Hotspot of Subterranean Biodiversity in the United States

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Abstract: The Mammoth Cave System in the Interior Low Plateau karst region in central Kentucky, USA is a global hotspot of cave-limited biodiversity, particularly terrestrial species. We searched the literature, museum accessions, and database records to compile an updated list of troglomorphic and stygobiotic species for the Mammoth Cave System and compare our list with previously published checklists. Our list of cave-limited fauna totals 49 species, with 32 troglomorphic and 17 stygobiotic species. Seven species are endemic to the Mammoth Cave System and other small caves in Mammoth Cave National Park. The Mammoth Cave System is the type locality for 33 cave-limited species. The exceptional diversity at Mammoth Cave is likely related to several factors, such as the high dispersal potential of cave fauna associated with expansive karst exposures, high surface productivity, and a long history of exploration and study. Nearly 80% of the cave-limited fauna is of conservation concern, many of which are at an elevated risk of extinction because of small ranges, few occurrences, and several potential threats.

Keywords: checklist; karst; species richness; stygobiont; troglomorphic



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1. Introduction

The Mammoth Cave System in central Kentucky, USA is the most extensive cave system in the world with over 663 km (412 miles) of mapped passages, including 27 entrances and 10 significant caves that have been connected since explorations began in the late 1700s: Colossal, Crystal (=Floyd Collins' Crystal), Donkey, Hoover, Mammoth, Morrison, Proctor, Roppel, Salts, and Unknown caves. Colossal, Crystal, Salts, and Unknown caves comprise the 206 km (128 mile) Flint Ridge Cave system (Figure 1). Mammoth Cave National Park was created in 1941 and includes two-thirds of the Mammoth Cave System [1]. The Mammoth Cave System was recognized as a UNESCO World Heritage Site in 1981 because of its uniqueness as the world's longest cave system as well as its extensive geological, mineral, and biological resources. The region was recognized as the core of an UNESCO Biosphere Reserve—Mammoth Cave Biosphere Region—in 1990.

The Mammoth Cave System is developed in three major limestone layers at the northwestern extent of the Pennyroyal Plateau, an expansive flat karst plain within the Interior Low Plateau physiographic province. The limestone layers include, from youngest to oldest, the Girkin Formation (40 m thick), Ste. Genevieve Limestone (35 m thick), and St. Louis Limestone (53–60 m thick) [2–5]. The Girkin Formation is capped by resistant sandstone and shale of the Big Clifty Formation that form the Mammoth Cave, Flint, Joppa, and Toohey Ridges. Most of the cave system is developed in the Ste. Genevieve Limestone and the upper 40 m of St. Louis Limestone [5]. The limestone strata gently slope from the southeast to the northwest. The Pennyroyal Plateau is exposed at the surface to the

southeast, while insoluble strata of the Chester Upland, including the Big Clifty Formation, form a rugged hilly terrain that overlies the cave system to the northwest. The Green River, a tributary of the Ohio River, has cut into the Pennyroyal Plateau about 60 m such that most of the Mammoth Cave watershed now occurs underground [6]. The karst watershed of Mammoth Cave includes seven groundwater basins (Pike Spring, Great Onyx, Echo River, Double Sink, River Styx, Floating Mill Hollow, and Turnhole Bend); in addition, flood overflow occurs into an eighth basin (Sand Cave). These basins encompass 317 km² and ultimately drain at springs at base level into the Green River [7,8].

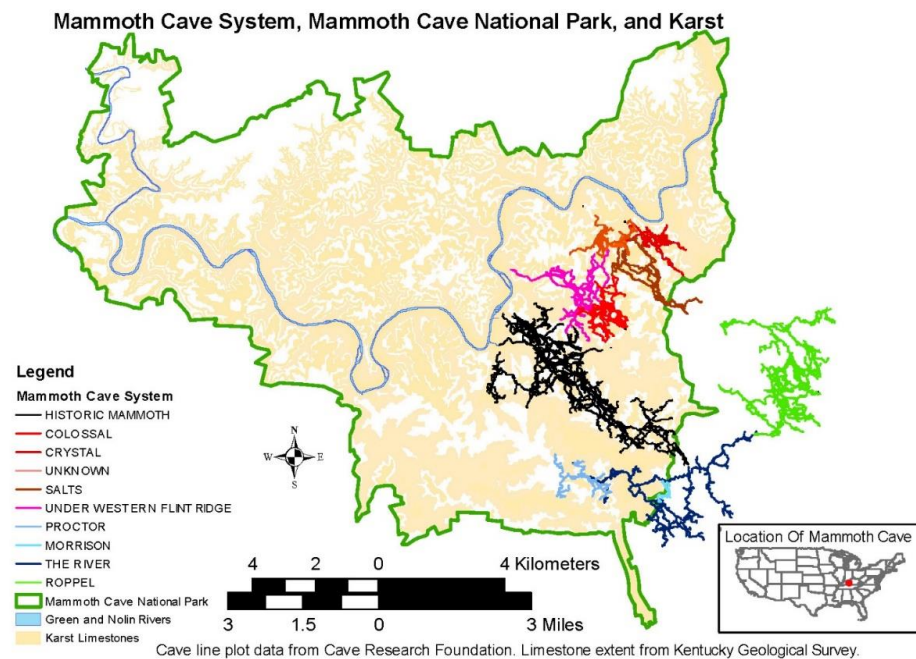


Figure 1. Map showing the location of Mammoth Cave National Park (MCNP) and the extent of the Mammoth Cave System in and adjacent to MCNP. The major segments of the Mammoth Cave System are shown as line plots in various colors. The different segments explored from different entrances (27 total). Line plot data from Cave Research Foundation. MCNP also contains over 500 smaller caves developed in various karstified limestones that are not attached to the Mammoth Cave System. These are grouped on the map, but include the St. Louis, Ste. Genevieve, Haney, Glen Dean and Girkin Formations. These smaller caves contain a variety of habitats from epikarst to base-level streams.

The Mammoth Cave System is characterized by a complex network of vadose and phreatic passages with at least five primary horizontal levels of passages (four fossil stream levels and the modern base level) representing distinct stages of development in association with past periods of water table stability and intervening periods of downcutting of the Green River valley through the resistant caprock into the soluble limestone layers below [1,6]. The evolution of the Mammoth Cave system is linked to the incision history of the Green River, drainage reorganizations, and significant climatic changes from the Pliocene through the Pleistocene, with the oldest upper-level passages dating to 3.2 Mya and the lower levels developing over the past 2 Mya [9].

Mammoth Cave has long been a focal region of study for North American subterranean biodiversity and for advancing our foundational knowledge of the ecology and evolution of cave fauna. Studies of the biodiversity in the Mammoth Cave System have an extensive history dating back to the 1820s (see [10]) when Constantin S. Rafinesque first visited Mammoth Cave [11]. Darwin [12] even mentions cave life from the Mammoth Cave region in *On the Origin of Species by Means of Natural Selection*. Much of our early knowledge of the North American cave fauna was derived from visits and studies by biologists to Mammoth Cave in the 1800s, such as DeKay [13], Wyman [14–19], Tellkamp [20–22], Agassiz [23–25], Von Mutschulsky [26,27], Call [28], and Packard [29–36] (reviewed in [10] and [37]).

Additional significant early publications on the fauna and ecology of Mammoth Cave include Putnam [38], Eigenmann [39–42], Bolivar and Jeannel [43], Bailey [44], Buchanan [45], Park [46], Dearolf [47], Hubricht [48–53], Jeannel and Henrot [54], and Barr [55–60]. Barr [10] provided the first comprehensive review of the fauna of the Mammoth Cave system. More recently, Poulson [61,62] and Helf and Olson [63] provided reviews of terrestrial and aquatic ecosystems in Mammoth Cave. Culver and Hobbs [37] comprehensively reviewed the obligate cave fauna of the Mammoth Cave system and compared the fauna with other global hotspots of terrestrial cave biodiversity. Toomey et al. [1] presented a general review of the Mammoth Cave system that included a checklist of cave obligate fauna.

Herein we present an updated list of terrestrial and aquatic cave obligate fauna (i.e., troglobionts and stygobionts, respectively) of the Mammoth Cave system. Our goal is not to duplicate recently published checklists by Culver and Hobbs [37] and Toomey et al. [1] but rather complement these works by including a comprehensive bibliography on the cave obligate fauna of Mammoth Cave. In addition, we compare our list with past checklists from Mammoth Cave and comment on the exceptional biodiversity of this North American and global hotspot of subterranean biodiversity.

2. Materials and Methods

We conducted a search of the scientific literature to compile an updated list of troglobiont and stygobiont species for the Mammoth Cave System. For an overview of taxa that are not cave-limited, we refer readers to Barr [10], Culver and Hobbs [37], Helf and Olson [63], and Poulson [62]. Scientific literature sources included journal articles, book chapters, books, conference proceedings, theses and dissertations, and government reports. Searches of literature sources included keyword queries of ISI Web of Science, Google Scholar, and Zoological Record. In addition, we also searched biodiversity databases including the Global Biodiversity Information Facility (GBIF; Available online: <https://gbif.org> (accessed on 28 June 2021)), VertNet (Available online: <http://www.vertnet.org> (accessed on 28 June 2021)), Symbiota Collections of Arthropods Network (SCAN; Available online: <https://scan-bugs.org/portal/> (accessed on 28 June 2021)), and InverteBase (Available online: <http://www.invertebase.org/portal/index.php> (accessed on 28 June 2021)). The list of cave obligate fauna includes the scientific name, authority, and conservation status of each species. Taxonomic nomenclature followed primarily the Integrated Taxonomic Information System (ITIS; Available online: <http://itis.gov> (accessed on 28 June 2021)). For conservation status, we include the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Available online: <http://www.iucnredlist.org> (accessed on 28 June 2021)) and NatureServe (Available online: <http://www.natureserve.org> (accessed on 28 June 2021)) conservation statuses when available. The status of a species according to the United States list of threatened and endangered species under the U.S. Endangered Species Act is included (Available online: <http://www.fws.gov/endangered> (accessed on 28 June 2021)), as well its status (endangered, threatened, or of greatest conservation need) under the latest Kentucky State Wildlife Action Plan (Available online: <https://fw.ky.gov/WAP/Pages/default.aspx> (accessed on 28 June 2021)).

3. Results

Packard [36] summarized the North America cave fauna, which at that time was primarily limited to the fauna of Mammoth Cave. He reported 31 permanent cave species, 18 of which we recognize as cave-limited species today, including 12 troglobionts and six stygobionts (Table 1). Barr [10] reported 44 cave-limited species (28 troglobionts and 16 stygobionts). More recently, Culver and Hobbs [37] listed 48 species (32 troglobionts and 16 stygobionts, 11 of which (nine troglobionts and two stygobionts) are endemic to the Mammoth Cave System, while Toomey et al. [1] reported 50 cave-limited species (32 troglobionts and 18 stygobionts). The authors also included two springtails not yet identified to species (*Willemia* sp. and *Onychiurus* sp.) on their list of cave-limited taxa, which were also reported by Barr [10].

Table 1. Troglobionts and stygobionts of the Mammoth Cave System, Kentucky, USA. NatureServe conservation ranks include Secure (G5), Apparently Secure (G4), Vulnerable (G3), Imperiled (G2), Critically Imperiled (G1), Possibly Extinct (GH), Presumed Extinct (GX), Unranked (GNR), and Unrankable (GU). IUCN Red List categories include Least Concern (LE), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW), and Extinct (EX). Kentucky State Nature Preserves Commission statuses include Endangered (E), Threatened (T), Special Concern (S), Historic (H), and Extirpated (X). Federal conservation status under the U.S. Endangered Species Act includes Listed Endangered (LE) and Listed Threatened (LT).

Taxon	Authority	Cons. Status	Packard [36]	Barr [10]	Culver and Hobbs [37]	Toomey et al. [1]	This Study
TROGLOBIONTS			13 Species	28 Species	32 Species	32 Species	32 Species
Phylum Arthropoda							
Class Arachnida							
Order Araneae							
Family Linyphiidae							
<i>Anthrobia monmouthia</i> ^T	Tellkamp, 1844	G5	X	X	X	X	X
<i>Bathypantes weyeri</i>	(Emerton, 1875)	G4		X	X	X	X
<i>Phanetta subterranea</i>	(Emerton, 1875)	G5		X	X	X	X
<i>Porhomma cavernicola</i>	(Keyserling, 1886)	G5		X	X	X	X
Family Zoropsidae							
<i>Liocranoides unicolor</i> ^T	Keyserling, 1881	GU	X				X
Order Opiliones							
Family Phalangodidae							
<i>Phalangodes armata</i> ^T	Tellkamp, 1844	G3	X	X	X	X	X
Order Pseudoscorpiones							
Family Chernetidae							
<i>Hesperochernes mirabilis</i>	(Banks, 1895)	G5		X	X	X	X
Family Chthoniidae							
<i>Kleptochthonius cerberus</i> ^{T,E}	Malcolm and Chamberlin, 1961	G1		X	X	X	X
<i>Kleptochthonius hageni</i> ^T	Muchmore, 1963	G1	X	X	X	X	X
<i>Tyrannochthonius hypogeus</i> ^{T,E}	Muchmore, 1996	G1			X		X
Order Acari							
Family Belbidae							
<i>Daneus bulbipedata</i> ^{T,E}	(Packard, 1888)	G1	X		X	X	X
Family Cocceupodidae							
<i>Linopodes mammothia</i> ^T	Banks, 1897	GNR		X	X	X	X
Family Galumnidae							
<i>Galumna alata</i>	(Hermann, 1804)	G1			X	X	X
Family Laelapidae							
<i>Laelaps cavernicola</i> ^T	Packard, 1888	GNR	X	X	X	X	X
Family Macrochelidae							
<i>Macrocheles troglodytes</i> ^T	(Packard, 1888)	G1			X	X	X
Family Rhagidiidae							
<i>Traegaardhia holsingeri</i> ^T	(Zacharda, 1980)	GNR	X	X	X	X	X
Class Collembola							

Table 1. Cont.

Taxon	Authority	Cons. Status	Packard [36]	Barr [10]	Culver and Hobbs [37]	Toomey et al. [1]	This Study
TROGLOBIONTS			13 Species	28 Species	32 Species	32 Species	32 Species
Order Entomobryomorpha							
Family Entomobryidae							
<i>Pseudosinella espanita</i> ^{T,E}	Christiansen and Bellinger, 1996	G1			X	X	X
Order Symphypleona							
Family Arrhopalitidae							
<i>Pygmarrhopalites altus</i> ^{T,E}	(Christiansen, 1966)	G2		X	X	X	X
Class Diplura							
Order Rhabdura							
Family Campodeidae							
<i>Litocampa cookei</i> ^T	(Packard, 1871)	G5	X	X	X	X	X
Class Diplopoda							
Order Chordeumatida							
Family Trichopetalidae							
<i>Scoterpes copei</i> ^T	(Packard, 1871)	G3	X	X	X	X	X
Order Polydesmida							
Family Macrosternodesmidae							
<i>Chaetaspis fragilis</i> ^T	(Loomis, 1943)	GNR		X	X	X	X
Class Insecta							
Order Coleoptera							
Family Carabidae							
<i>Neaphaenops tellkampfi</i> ^T	(Erichson, 1844)	G3	X	X	X	X	X
<i>Pseudanopthalmus audax</i>	(Horn, 1883)	G1		X	X	X	X
<i>Pseudanopthalmus inexpectatus</i> ^{T,E}	Barr, 1959	G1		X	X	X	X
<i>Pseudanopthalmus menetriesi</i> ^T	(Motschulsky, 1862)	G3	X	X	X	X	X
<i>Pseudanopthalmus pubescens</i>	(Horn, 1868)	G3		X	X	X	X
<i>Pseudanopthalmus striatus</i> ^T	(Motschulsky, 1862)	G2	X	X	X	X	X
Family Leiodidae							
<i>Ptomaphagus hirtus</i> ^T	(Tellkamp, 1844)	G4	X	X	X	X	X
Family Staphylinidae							
<i>Batrisodes henroti</i>	Park, 1956	G2		X	X	X	X
Order Diptera							
Family Phoridae							
<i>Megaselia cavernicola</i>	(Brues, 1906)	GNR				X	
Family Sphaeroceridae							
<i>Spelobia tenebrarum</i>	(Aldrich, 1897)	G5			X	X	X
Order Psocodea							
Family Psyllipsocidae							
<i>Psyllipsocus ramburii</i>	Selys-Longchamps, 1872	GNR		X			

Table 1. Cont.

Taxon	Authority	Cons. Status	Packard [36]	Barr [10]	Culver and Hobbs [37]	Toomey et al. [1]	This Study
TROGLOBIONTS			13 Species	28 Species	32 Species	32 Species	32 Species
Phylum Mollusca							
Class Gastropoda							
Order Basommatophora							
Family Carychiidae							
<i>Carychium stygium</i> ^T	Call, 1897	G3		X	X	X	X
Order Stylommatophora							
Family Helicodiscidae							
<i>Helicodiscus hadenoecus</i>	Hubricht, 1962	G3		X			
<i>Helicodiscus punctatellus</i> ^T	Morrison, 1942	G1		X	X	X	
Family Zonitidae							
<i>Glyphyalinia specus</i>	Hubricht, 1965	G4		X	X	X	X
STYGOBIONTS			6 species	16 species	16 species	18 species	17 species
Phylum Platyhelminthes							
Class Turbellaria							
Order Tricladida							
Family Kenkiidae							
<i>Sphalloplana buchmanani</i> ^T	(Hyman, 1937)	G1		X	X	X	X
<i>Sphalloplana percoeca</i> ^T	(Packard, 1879)	G5	X	X	X	X	X
Phylum Arthropoda							
Class Malacostraca							
Order Amphipoda							
Crangonyctidae							
<i>Crangonyx barri</i> ^T	Zhang and Holsinger, 2003	G5		X	X	X	X
<i>Stygobromus exilis</i>	Hubricht, 1943	G5		X	X	X	X
<i>Stygobromus vitreus</i> ^T	Cope, 1872	G4; S	X	X	X	X	X
Order Decapoda							
Family Atyidae							
<i>Palaemonias ganteri</i> ^T	Hay, 1901	G1; VU; E; LE		X	X	X	X
Family Cambaridae							
<i>Orconectes pellucidus</i> ^T	(Tellkamp, 1844)	G4; LC; S	X	X	X	X	X
Order Isopoda							
Family Asellidae							
<i>Caecidotea bicrenata</i>	Lewis and Bowman, 1981	G5				X	X
<i>Caecidotea stygia</i> ^T	Packard, 1871	G5	X	X	X	X	X
Class Maxillopoda							
Order Cyclopoida							

Table 1. Cont.

Taxon	Authority	Cons. Status	Packard [36]	Barr [10]	Culver and Hobbs [37]	Toomey et al. [1]	This Study
TROGLOBIONTS			13 Species	28 Species	32 Species	32 Species	32 Species
Family Cyclopidae							
<i>Megacyclops donaldsoni</i>	(Chappuis, 1929)	G3		X	X	X	X
Order Harpacticoida							
Family Canthocamptidae							
<i>Attheyella pilosa</i> ^T	Chappuis, 1929	GNR		X	X	X	
<i>Bryocamptus morrisoni</i>	(Chappuis, 1928)	G3		X	X	X	X
Order Siphonostomatoida							
Family Lernaepodidae							
<i>Cauloxenus stygius</i>	Cope, 1872	G1				X	X
Class Ostracoda							
Order Podocopida							
Family Entocytheridae							
<i>Sagittocythere barri</i>	(Hart and Hobbs, 1961)	G5		X	X	X	X
<i>Sagittocythere stygia</i> ^{T,E}	Hart and Hart, 1966	G1		X	X	X	X
Phylum Mollusca							
Class Gastropoda							
Order Neotaenioglossa							
Family Hydrobiidae							
<i>Antroselates spiralis</i> ^T	Hubricht, 1963	G3		X	X	X	X
Phylum Chordata							
Class Actinopterygii							
Order Percopsiformes							
Family Amblyopsidae							
<i>Amblyopsis spelaea</i> ^T	DeKay, 1842	G2; NT; S	X	X	X	X	X
<i>Typhlichthys subterraneus</i>	Girard, 1859	G4; NT; S	X	X	X	X	X

^T Type locality in Mammoth Cave National Park; ^E Mammoth Cave National Park endemic.

Our list of cave-limited fauna includes 49 species, with 32 troglobionts and 17 stygobionts (Table 1; Figure 2). Both Culver and Hobbs [37] and Toomey et al. [1] included the snail *Helicodiscus punctatellus* and copepod *Atteyella pilosa* in their respective lists of cave-limited taxa. *Helicodiscus punctatellus* is known from surface collections [64]. *Atteyella pilosa* is a facultative associate of several species of surface and cave-limited crayfishes and is also known from surface collections [65]. Culver and Hobbs [37] did not include the isopod *Caecidotea bicrenata*, which was included in our list and that of Toomey et al. [1]. Lewis [66] reported several collections of *C. bicrenata* from the Mammoth Cave System where it predominately occurs in lower-level aquatic habitats. Toomey et al. [1] included the phorid fly *Megaselia cavernicola* in their list of cave-limited taxa. *Megaselia cavernicola* is a widely occurring species in caves on eastern North America that lacks obvious troglomorphic characters, is known from surface collections [67], and has been treated as a troglophile (i.e., non-obligate) by most past authors (e.g., [68,69]).

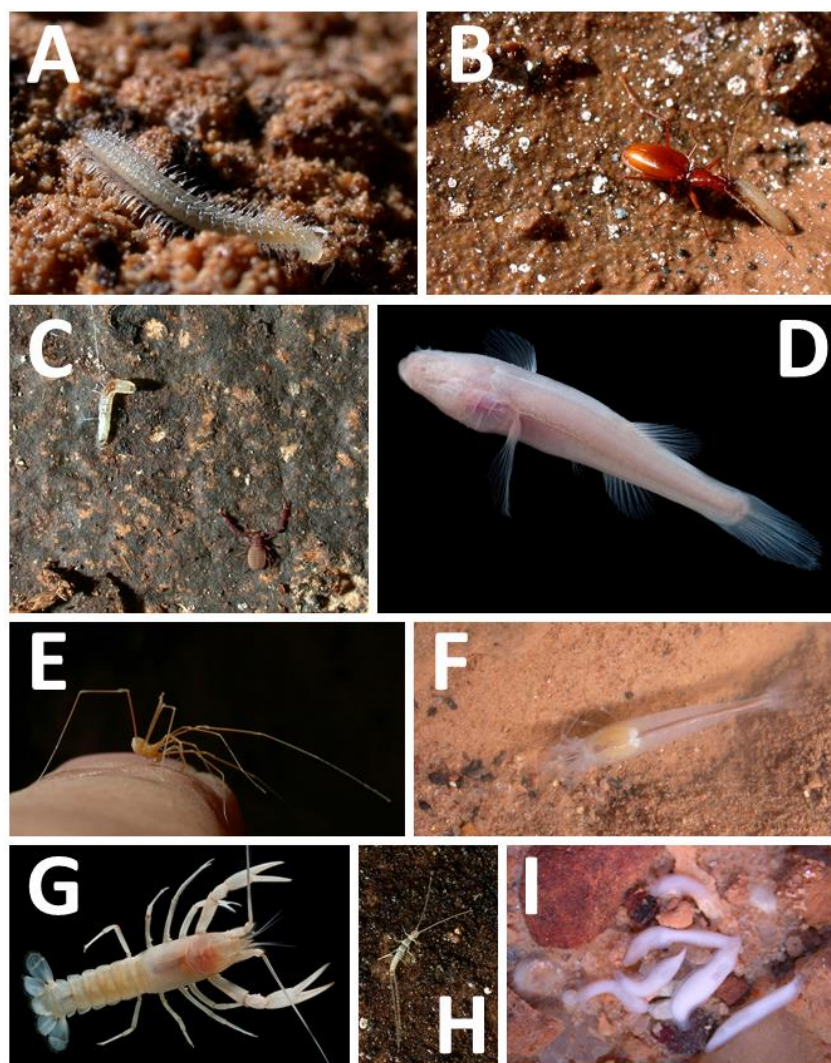


Figure 2. Representative cave-limited fauna from the Mammoth Cave System, Kentucky, USA: (A) *Scoterpes copei* (photo by Rickard A. Olson); (B) *Neaphaenops tellkampfi* feeding on the egg of the *Hadenoeus subterraneus* (photo by Rickard A. Olson); (C) *Hesperochnes mirabilis* with *Macrocera nobilis* larva (photo by Rickard A. Olson); (D) *Amblyopsis spelaea* (photo by Dante B. Fenolio); (E) *Phalangodes armata* (photo by Rickard A. Olson); (F) *Palaemonias ganteri* (photo by Rickard A. Olson); (G)—*Orconectes pellucidus* (photo by Dante B. Fenolio); (H) *Litocampa cookei* (photo by Rickard A. Olson); (I)—*Sphalloplana buchanani* (photo by Rickard A. Olson).

Mammoth Cave is the type locality for 33 cave-limited species (Table 1). Seven species are endemic to the Mammoth Cave system and other smaller caves in Mammoth Cave National Park (Table 1).

3.1. Terrestrial Fauna

Two troglobiotic snails have been documented in the Mammoth Cave System. *Carychium stygium* is found in association with cricket guano and is the most common of the two species [37]. Weigand et al. [70,71] suggest *C. stygium* may be an ecotype of the troglophile *C. exile*, as *C. stygium* shows limited mitochondrial COI sequence divergence from and is nested within a clade containing *C. clappi* and *C. exile*. However, this inference is based on a single locus and only two populations of *C. stygium* were included in analyses. Alternative hypotheses such as incomplete lineage sorting and mitochondrial introgression cannot be ruled out at present and warrant study. Regardless, these studies suggest that it is likely that *C. stygium* has recently colonized caves. *Glyphyalinia specus* is a wide-ranging snail known from 27 occurrences in five states [72]. Significant publications include Call [28], Hubricht [49,50,52,53], Barr [10], Poulson et al. [73], Dourson [74], Poulson [62], and Gladstone et al. [72].

Troglobiotic spiders documented in the Mammoth Cave System include four linyphiids and one zoropsid. All four linyphiids have broad distributions in caves of the eastern United States [75]. *Bathyphantes weyeri* is predominantly known from caves but has rarely been collected from surface habitats in Canada [75–77]. Holsinger et al. [78] hypothesized that the species may be troglobiotic in the southern parts of its range and troglophilic in the northern areas. Moreover, *B. weyeri* may represent a species complex. Most authors, including herein, still treat this species as a troglobiont [1,37,76,78,79]. *Liocranoides unicolor* was described by Keyserling [80] from Mammoth Cave. This species is pale in coloration but does not possess other troglomorphic characters [81]. Significant publications include Packard [29,32,33,36], Emerton [82], Hubbard [83], Keyserling [80], Call [28], McIndoo [84], Berland [85], Bailey [44], Barr [10], Poulson and Culver [86], Poulson [62,87], Platnick [81], and Miller [75].

A single troglobiotic opilionid (*Phalangodes armata*) is known from several areas in the Mammoth Cave System. Significant publications include Tellkamp [20,21], Packard [29,36], Hubbard [83], Call [28], Bailey [44], Goodnight and Goodnight [88], Barr [10], Poulson and Culver [86], Hedin and Thomas [89], and Poulson [62].

Four troglobiotic pseudoscorpions occur in the Mammoth Cave System. *Hesperochnes mirabilis* is a widely distributed species most abundant near entrances. It is often observed in and near rodent (*Neotoma* and *Peromyscus* sp.) nests, which may facilitate phoretic dispersal. The other three species are thought to be associated with deep cave habitats. *Kleptochthonius cerberus* was described from White's Cave in Mammoth Cave National Park [90] and has to date, only been found there. *Kleptochthonius hageni* was described from Mammoth Dome in Mammoth Cave [91]. *Kleptochthonius cereberus* is thought to be endemic to Mammoth Cave National Park. *Kleptochthonius hageni* is reported to occur in the Mammoth Cave System and possibly some nearby caves not on the park (C.D.R. Stephen, pers. comm.). *Tyrannochthonius hypogeus* is a small, eyeless species with attenuated appendages first collected from log litter in Bruce Hollow [92]. Muchmore [92] considered this species to be cave adapted and associated with the Mammoth Cave fauna. Notable publications include Hubbard [83], Packard [36], Banks [93], Malcolm and Chamberlin [90], Muchmore [91,92], and Barr [10].

The troglobiotic mite fauna is particularly diverse with six species but has been little studied since their descriptions [37]. Notable publications include Packard [36], Call [28], Vitzthum [94], Bailey [44], Holsinger [95], Barr [10], and Zacharda [96].

Two troglobiotic millipedes have been documented in the Mammoth Cave System. *Scoterpes copei* is a common trichopetalid distributed throughout the cave system where it can be found in moist habitats with organic matter (rotting wood, debris, and cricket guano). *Chaetaspis fragilis* is a small polydesmid infrequently encountered in the Mammoth Cave

System but more common in White Cave, Mammoth Cave National Park [10]. Significant publications include Packard [29,36], Cope [97], Hubbard [83], Loomis [98], Barr [10], Poulson and Culver [86], Poulson et al. [73], Shear [99], and Poulson [62].

Although more than 10 species of collembolans (i.e., springtails) have been documented in the Mammoth Cave System [10], just two taxa are considered troglobionts and both are endemic to the cave system. *Pygmarrhopalites altus* was described by Christiansen [100] from Eyeless Fish Trail in the Unkown Cave section of Mammoth Cave. *Pseudosinella espanita* was described by Christiansen and Bellinger [101] from Styx River near Charon's Cascade in Mammoth Cave. Notably absent from the fauna of the Mammoth Cave System are *P. hirsuta* and *Sinella cavernarum*, which have broad distributions that include the Western Pennyroyal Karst of nearby Barren County, Kentucky [102]. Barr [10] reported two undescribed collembolans as potential troglobionts from Mammoth Cave: *Willemia* sp. have been collected from rotting boards in the Roaring River section. This genus includes several edaphic species, but no troglobionts are known to date and it is unlikely that this taxon represents a true troglobiont. *Onychiurus* sp. also have been collected from Mammoth Cave. Four described species in this genus are considered troglobionts in caves of the eastern United States. Additional study is needed on the collembolans of the Mammoth Cave System. Significant publications include Packard [36], Call [28], Christiansen [97,103–105], Barr [10], Poulson and Culver [86], Christiansen and Bellinger [101], and Poulson [62].

A single troglobiotic dipluran occurs in the Mammoth Cave System. *Litocampa cookei* has the largest distribution of any troglobiotic dipluran in the United States [106] but may represent a cryptic species complex. It was described from Mammoth Cave [29]. Notable publications include Packard [29,30,36], Hubbard [83], Silvestri [107,108], Conde [109], Barr [10], Poulson and Culver [86], Ferguson [106,110], and Poulson [62].

The troglobiotic beetle fauna is the most well known and studied of all taxonomic groups in the Mammoth Cave System. Eight species have been documented, namely six carabids, one leiodid, and one staphylinid species. *Neaphaenops tellkampfi* is the largest troglobiotic carabid species in Mammoth Cave and is also the first troglobiotic trechine beetle discovered in North America [111]. It was described from Mammoth Cave [112]. This species is found in silty habitats, where it feeds mostly on the eggs of the cave cricket *Hadenoeus subterraneus* [111,113]. Five species in the genus *Pseudanophthalmus* occur in a variety of habitats throughout the Mammoth Cave System. Three species were described from Mammoth Cave and one species (*P. inexpectatus*) is endemic to MCNP. All six species are blind and wingless. In some locations in the cave system, all six carabid species can be found but appear to have different microhabitat preferences and can be readily distinguished morphologically [59,60,113]. *Ptomaphagus hirtus* is an abundant small carrion beetle that is becoming an important model for studying the genetics of circadian rhythms [114,115]. *Batrisodes henroti* is a small rove beetle that has been infrequently collected in the Mammoth Cave System. Relevant publications include Erichson [112], Tellkampff [20,21], Von Motschulsky [26,27], Horn [116,117], Packard [29,31,34,36], Hubbard [83], Jeannel [118–121], Valentine [122,123], Hatch [124], Jeannel and Henrot [54], Park [125–127], Barr [10,55–60,128–131], Poulson and Culver [86], Barr and Kuehne [132], Peck [133–137], Kane et al. [138], Norton et al. [139], Kane and Poulson [140], Laing et al. [141], Giuseffi et al. [142], Kane and Ryan [143], Barr and Holsinger [144], Kane and Brunner [145], Poulson et al. [73], Friedrich et al. [115], Friedrich [114], Helf [146], Poulson [62], and Leray et al. [147].

The only other troglobiotic insect documented from Mammoth Cave is the dipteran *Spelobia tenebrarum*, a widely distributed species in caves of eastern North America [148]. Notable publications include Barr [10], Marshall and Peck [148], and Poulson [62].

3.2. Aquatic Fauna

Two cave flatworms occur in and were described from the Mammoth Cave System. *Sphalloplana percoeca* occurs primarily in epikarst-fed drip pools in upper-level passages,

while *S. buchanani* is associated with stream gravels [37]. Significant publications on cave flatworms include Packard [29,36], de Beauchamp [149], Buchanan [45], Hyman [150], Barr [10], Carpenter [151,152], Barr and Kuehne [132], Kenk [153], Lewis [66], Pearson and Boston [154], and Helf and Olson [63].

A single groundwater snail has been documented in the Mammoth Cave System. *Antroselates spiralis* occurs in base-level streams in cave system. It was described from Echo River Spring, a major drain of the Mammoth Cave System. Notable publications include Hubricht [51], Barr [10], Barr and Kuehne [132], Hershler and Hubricht [155], Lewis [66], Pearson and Boston [154], and Helf and Olson [63].

The copepods of the Mammoth Cave System have not been well studied [37]. Three stygobionts have been documented—*Megacyclops donaldsoni*, *Bryocamptus morrisoni*, and *Cauloxenus stygius*. *Cauloxenus stygius* is an ectoparasite of the cavefish *Amblyopsis spelaea* [156]. Notable publications include Cope [97], Kofoid [157], Chappuis [158], Barr [10], Barr and Kuehne [132], Whitman [159], Lewis [160], Niemiller and Poulson [156], and Helf and Olson [63].

Two ostracods are ectocommensals primarily of the stygobiotic crayfish *Orconectes pellucidus*—*Sagittocythere barri* and *S. stygia*. *Sagittocythere stygia* was described from River Styx in Mammoth Cave. Significant publications include Kofoid [157], Klie [161], Hart and Hobbs [162], Hart and Hart [163], Barr [10], Barr and Kuehne [132], Hart and Hart [164], and Helf and Olson [63].

Isopods are represented by two aquatic stygobionts—*Caecidotea stygia* and *C. bicrenata*. *Caecidotea stygia* was described from Mammoth Cave by Packard [29] and is more abundant in upper to mid-levels of the cave system, whereas *C. bicrenata* is more common in low to mid-levels [66]. Significant publications include Packard [29,35,36], Hubbard [79], Garman [165], Hay [166], Giovannoli [167], Dearolf [47], Chappuis [168], Barr [10], Barr and Kuehne [132], Lewis and Bowman [169], Lewis [66], Helf and Olson [63], and Helf et al. [170].

Three species of stygobiotic amphipods have been reported from the Mammoth Cave System. *Stygobromus vitreus* is more common in upper levels of the cave system, while *S. exilis* is more common in low to mid-levels [66,132]. *Stygobromus vitreus* was described from Richardson Spring within Mammoth Cave. Cathedral Domes in Mammoth Cave is the type locality of *Crangonyx barri*, an inhabitant of small cave streams and drip pools [171]. Significant publications include Cope [97], Packard [36], Giovannoli [167], Hubricht [48], Barr [10], Barr and Kuehne [132], Holsinger [172], Lewis [66], Zhang [173], Zhang and Holsinger [171], Helf and Olson [63], and Helf et al. [170].

Two stygobiotic decapods occur in the Mammoth Cave System. *Palaemonias ganteri* is a federally endangered atyid shrimp found in slow-flowing base-level streams of eleven groundwater basins in the Mammoth Cave System ([174]; updated by R. Toomey with new data). Significant publications on *P. ganteri* include Hay [166], Fage [175], Giovanoli [167], Barr [10], Barr and Kuehne [132], Hobbs et al. [176], Holsinger and Leitheuser [177–179], Lisowski [180,181], Lisowski and Poulson [182], Leitheuser and Holsinger [183], Leitheuser et al. [184,185], Lewis [66], USFWS [174,186], Pearson and Boston [154], Pearson and Jones [187], Cooper and Cooper [188], Helf and Olson [63], and Stump [189]. *Orconectes pellucidus* was described from Mammoth Cave and is the only stygobiotic crayfish in the cave system. While *O. pellucidus* is a ubiquitous stygobiont in the Mammoth Cave System, it is more abundant in mid- and base-level streams and pools. Notable publications include Tellkamp [20,21], Hagen [190,191], Packard [29,36], Cope [97], Garman [192], Fage [175], Bailey [44], Park et al. [193], Rhoades [194], Hobbs and Barr [195,196], Brown [197], Wolfe and Cornwell [198], Barr [10], Hobbs et al. [176], Pearson and Boston [154], Pearson and Jones [187], Compson [199], Taylor and Schuster [200], Helf and Olson [63], and Helf et al. [170].

The only cave-limited vertebrates known from the Mammoth Cave System are the amblyopsid cavefishes *Amblyopsis spelaea* and *Typhlichthys subterraneus*. *Amblyopsis spelaea* was described from River Styx in Mammoth Cave by Dekay [13] and represents the

first cave-adapted fish formally described [156,201]. Mammoth Cave is one of only a handful of cave systems globally with two or more syntopic cavefish species [156,201]. *Typhlichthys subterraneus* are more abundant in upstream sections of streams that drain vertical shafts, whereas *A. spelaea* are more common in deeper pools at base level [61,156]; both are top predators. It remains unclear whether *A. spelaea* outcompetes *T. subterraneus* in base-level habitats. Significant publications on cavefishes of Mammoth Cave include Davidson [202], DeKay [13], Wyman [14–19], Thompson [203], Tellkamp [21,22], Agassiz [23–25], Girard [204], Putnam [38], Packard [36], Eigenmann [39–42], Bailey [44], Woods and Inger [205], Poulson [61,206–208], Barr and Kuehne [209], Rosen [210], Barr [10], Poulson and White [211], Barr and Kuehne [132], Clay [212], Swofford et al. [213], Lisowski and Poulson [182], Swofford [214], Burr and Warren [215], Lewis [66,160,216], Keith [217], Branson [218], Pearson and Boston [154], Pearson and Jones [187], Romero [219], Romero and Bennis [220], Compson [199], Proudlove [201], Niemiller and Poulson [156], Niemiller [221], Niemiller and Fitzpatrick [222], Niemiller et al. [223], Helf and Olson [63], Helf et al. [170], and Hart et al. [224].

4. Discussion

The Mammoth Cave obligate cave fauna is exceptionally rich with 49 troglobionts and stygobionts, making it one of the most diverse systems globally [37,225,226]. The terrestrial fauna is particularly diverse—tied for the third richest cave system in the world behind the Postojna Planina Cave System (36 species) in Slovenia and Cueva de Felipe Reventon (34 species) in the Canary Islands [226]. With respect to stygobiotic fauna, the Mammoth Cave System ranks second in North America behind San Marcos Artesian Well in San Marcos, Texas (55 taxa, 39 described and 16 undescribed; [227]).

Several hypotheses have been proposed [10,61,127,224,228] to explain the high species richness in the Mammoth Cave System (recently reviewed in [37]). First, high species richness in the Mammoth Cave System may reflect the long history of more intensive sampling and study compared to other cave systems in the region [37]. While sampling intensity and bias may partially explain the high species richness at Mammoth Cave, several other biogeographical hypotheses warrant mention. The Mammoth Cave System is developed within a thick, continuous karst exposure over a large area in the Interior Low Plateau, which supports larger and more stable population sizes, more complex communities, and greater dispersal potential [113,129,130]. Moreover, the Mammoth Cave System is located at an intersection of hypothesized dispersal routes for cave-limited species from other karst areas, such as the Pennyroyal Karst Plain, Cumberland Saddle, and Bluegrass Region, and its cave fauna includes not only endemic species but also taxa also found in these adjacent regions [10,37,66,130]. The Mammoth Cave System lies within a hypothesized ridge of high troglobiont diversity found in temperate North America and Europe identified by Culver et al. [228]. This ridge corresponds to a general region of high surface primary productivity, which provides higher levels of allochthonous input into cave systems [228]. Mammoth Cave is noted for having high levels of allochthonous productivity but also chemoautotrophic productivity [37,63,229]. However, whether chemosynthesis subsidizes troglobiont communities or contributes significantly to the high troglobiont diversity found in the Mammoth Cave System remains speculative, as it is not well supported by empirical evidence.

The obligate fauna of the Mammoth Cave System is diverse and includes 39 cave-limited species (18 troglobionts and 11 stygobionts) of conservation concern, highlighted by the federally endangered cave shrimp *Palaemonias ganteri*. Most of these species are at an elevated risk of extinction due to their limited distributions and/or are known from few occurrences. For example, the cave pseudoscorpion *Tyrannochthonius hypogeus* is known from just two specimens collected from a single locality [92]. Cave-limited fauna face many threats, such as habitat loss and degradation, groundwater overexploitation and contamination, and climate change [230,231].

Although much of the Mammoth Cave System lies within the boundaries of Mammoth Cave National Park, the cave system is not immune to direct and indirect threats to its biodiversity, particularly those stressors that originate from outside of the park, such as industrial and tourism development, oil and gas drilling, runoff from agriculture, residential areas, and highways, and emergent diseases [63,232–236]. For example, sewage from the town of Park City was previously known to drain into the headwaters of the Echo River basin potentially impacted the stygobiotic fauna [130], including *Typhlichthys subterraneus*, *Amblyopsis spelaea*, *Palaemonias ganteri*, *Orconectes pellucidus*, and *Antroselates spiralis*. A hydrocarbon spill along Interstate 65 was responsible for a significant die-off of aquatic cave life [232,236]. Flow reversals and back-flooding from the Green River into cave springs also may transport sediment, potential contaminants, pathogens, and invasive aquatic species into base level streams in the Mammoth Cave System [237–239].

Great potential still exists to discover new taxa and add to the list of obligate species at Mammoth Cave. Two potentially cave-limited springtails that we do not include in our checklist (*Willemia* sp. and *Onychiurus* sp.) are known from Mammoth Cave and have not been identified to species [1,10]. Terrestrial woodlice are notably absent from the troglobiotic fauna of Mammoth Cave and may be discovered in the future. Seven troglobiotic trichoniscids (Isopoda, family Trichoniscidae) are known caves of the Interior Low Plateau and Appalachians karst regions [240], including *Miktoniscus barri* known from several caves of Indiana and Kentucky [241]. A troglophilic species, *Miktoniscus mammothensis*, occurs in cave and surface habitats at MCNP [242]. Other taxonomic groups have not been particularly well studied in the Mammoth Cave System, such as flatworms, copepods, springtails, and mites. More intensive work on these groups may uncover additional taxa. With more than 651 km of passage, much of the Mammoth Cave System has not been comprehensively bioinventoried, and some habitats, such as epikarst, have been disproportionately under-sampled and may harbor undescribed taxa [37]. In addition, over 500 other caves occur in MCNP, including several biologically rich sites, such as White and Great Onyx caves. These cave systems also may harbor undocumented diversity. Finally, few genetic studies to date have incorporated samples from the Mammoth Cave System. Comprehensive sampling within the Mammoth Cave System has the potential to uncover cryptic diversity in some taxonomic groups, which is an increasingly common discovery of genetic and phylogenetic studies in cave-limited taxa [223,243–245].

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