

WILLIAM B. MUCHMORE (1920–2017): HIS TAXONOMIC CONTRIBUTIONS AND A COMPLETE BIBLIOGRAPHY

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Abstract

William B. Muchmore (1920–2017) was the most influential worker on cave pseudoscorpions in North America and a globally-recognized expert on this arachnid order. Aside from brief stints in herpetological embryology and isopod taxonomy, he dedicated his 62-year career to the study of pseudoscorpions, focusing on their taxonomy. He described 278 new species, of which 167 were from caves. The majority of North American cave pseudoscorpions were either initially described or revised by him. He also wrote on the phoretic habits of pseudoscorpions, and speculated that cave pseudoscorpion distributions may be influenced by troglophilic rodents and bats. A complete bibliography of his scientific papers is provided.

William (“Bill”) Breuleux Muchmore (Fig. 1) was born in Cincinnati, Ohio, on May 20, 1920. He was the first child of Oliver Charles Muchmore (1892–1968) and Ruby Breuleux (1895–1958), both of Ohio. His family has a long history in the United States (U.S.), with ancestry on his mother’s side tracing to Philip Frederick Breuleux (born 1830, Busserel, Haute Saône, France; immigrated in 1860 to Sycamore, Ohio), and on his father’s side to John Muchmore (born 1692, Windsor, Connecticut Colony; now the State of Connecticut). He had two children with his wife Marjorie Murrin: Susan Muchmore (born 1947) and Patricia Muchmore (born 1950). Marjorie predeceased Muchmore in 2007 at the age of 85. He died May 11, 2017 at the age of 96. At the time of his death he was an author of 145 publications on pseudoscorpions and was internationally recognized as a global expert on this arachnid order.

In his youth, Muchmore achieved the status of Eagle Scout, a path that likely influenced his interest in biology and fostered his mind into becoming a broadly-trained naturalist. After completing a B.A. at Oberlin College, Oberlin, Ohio, in 1942, from 1943–1946 he served with the U.S. Army Medical Corps in the southwest Pacific theatre of World War II (NARA, 2005). After the war ended he returned to the U.S. and enrolled at Washington University, Saint Louis, Mo., where he received his Ph.D. in 1950. He then moved to New York, where he spent his entire academic career at the University of Rochester, going up the ranks from Instructor (1950–1952), to Assistant Professor (1952–1958), to Associate Professor (1958–1970), to Professor (1970–1988), and finally “retiring” as Professor Emeritus (1985). Muchmore ceased working independently on pseudoscorpions around 2009. Continuing collaborations produced three additional papers, with his last published at age 93 in 2013. In his later years, he became a local historian for the Rochester area, participated in local cultural centers, and was involved in wildlife conservation.

Muchmore’s career began as a herpetologist, not an arachnologist. His Ph.D. dissertation was on embryological development of the mesoderm germ layer in *Ambystoma maculatum* (Spotted Salamander). From 1947–1950, he collected this species and *Lithobates pipiens* (Northern Leopard Frog) egg masses from Missouri, New Hampshire, New York, and Tennessee. In his lab, he reared the eggs of these species into embryos and conducted his experiments with these developing embryos. His work followed two lines: (1) cell survival and differentiation of *A. maculatum* embryo mesoderm tissues, following experimental explantation into *L. pipiens* trunk mesoderm; and (2) cell survival and differentiation of *A. maculatum* embryo mesoderm tissues, following experimental removal of different ectodermal, mesodermal, and endodermal tis-

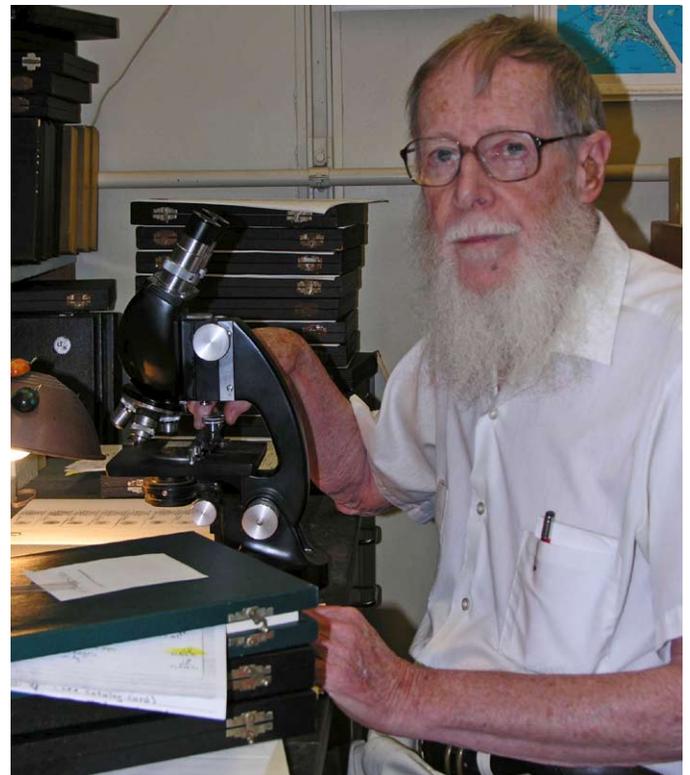


Figure 1. William B. Muchmore in his laboratory, June 11, 2006.

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sues from the developing embryo.

The central thesis of his dissertation was to test hypotheses developed by the Japanese herpetologist Tuneo Yamada that described how the mesoderm differentiates in the amphibian embryo. The meticulous nature of his dissertation engendered a familiarity with anatomy and esoteric nomenclature, taught him scientific illustration, and trained him in histological and embryological staining techniques. These skills were transferable to his later work with pseudoscorpions.

From 1951–1968, Muchmore authored seven papers that derived from his dissertation (Muchmore, 1951, 1957a, 1957b, 1958a, 1958b, 1964b, 1968). He never again published on embryology. Instead, he changed paths to become a highly productive taxonomist. In 1955, he authored his first taxonomic paper of any kind, in which he synonymized *Plethodon huldae* with northwestern New York populations of the nominate subspecies of the Red-backed Salamander (*Plethodon cinereus* (Green, 1818)) (Muchmore, 1955a). Also in this year, he published a taxonomic note motivated by a report of the Cave Salamander (*Eurycea lucifuga*) occurring in a hollow among bluffs of southern Ohio (Muchmore, 1955a, 1955b). He determined that the report of this species was, in fact, misidentified Longtail Salamander (*E. longicauda*), a troglomorphic species that is presently known to occur in caves of the Interior Plateau and Appalachian karst regions (Buhlmann, 2001; Garton et al., 1993; Niemiller et al., 2016).

In 1955, he was awarded a Summer Research Fellowship at Edmund Niles Huyck Preserve, Rensselaerville, N.Y. His interests branched into arthropods here. He spent a summer looking for exotic arthropods in greenhouses and turning over logs and rocks across northern New York. Under the mentorship of Kenneth Cooper at the University of Rochester, this resulted in new reports of populations of exotic isopod, harvestman, and pseudoscorpion species in New York (Muchmore, 1957, 1963, 1969b). It was also from these early collections that he later described the epigeal isopod *Miktoniscus ohioensis* and the epigeal pseudoscorpion *Serianus enhuycki* (Muchmore, 1964a, 1968f).

These first forays into arthropods began to establish a reputation that would serve to induce worldwide collectors to send him specimens. The first example of this is the hypogean isopod *Caucasonethes paynei*, which he described from specimens collected in Tennessee by J.A. Payne from Offutt's Cave, Anderson County (now Offutt Cave (TAN12)) and Melton Hill Cave #1, Roane County (now Melton Hill Spring Cave (TLN4) and actually located in Loudon County) (Muchmore, 1970). On dedicating his career to arachnids, Muchmore later remarked that he was greatly encouraged by the eminent pseudoscorpionologists, Joseph C. Chamberlin, Max Beier, and C. Clayton Hoff, in the study of "those fascinating little critters, the pseudoscorpions" (Muchmore, 1998a).

Muchmore (1963b, 2000b) credited Hermann A. Hagen with initiating the study of North American cave pseudoscorpions in 1879 with his description of *Blothrus packardi* (now *Kleptochthonius packardi*). However, Muchmore has overwhelmingly made the most significant contribution to the study of cave pseudoscorpions on this continent. He remains one of the major authors of North American biospeleological taxonomy. His first paper on pseudoscorpions (Muchmore, 1962) described the hypogean *Microcreagris grandis*. This initial paper was based on specimens that were collected at Lehman Caves National Monument, Nevada, and that were borrowed from the Yale Peabody Museum of Natural History. Following Mahnert's (1979) redefinition of *Microcreagris*, most North American species were transferred to newly erected genera (Ćurčić, 1981, 1984, 1989), but *M. grandis* was not included in these or later treatments.

Defining North America as including the Caribbean archipelago and Central America, from this continent, Muchmore described 157 new species, co-authored two species, transferred 12 species to different genera, described one subspecies, *Ideobisium puertoricense caviculum* (Muchmore, 1982e), and revised 19 taxa. These include 107 new species from the U.S.: in the Edwards Plateau and Balcones, Ozarks, Interior Low Plateau, and Appalachians karstic regions, as defined by Culver et al. (2003). Of the 151 pseudoscorpion species currently known from caves in the U.S. and Canada, 76 % have been either described or revised by Muchmore. South of the U.S., he increased the known cave pseudoscorpion fauna of Mexico from three species to 39, added three species to Belize, and two to Guatemala. From the Caribbean archipelago, he added eight cave-adapted species, including one new species from Antigua and Barbuda, one from the Bahamas, one from the Dominican Republic, and five from Jamaica. As of 2011, only five species that he authored have been synonymized with another species, and 15 have been transferred to a different genus (Harvey, 2013). Not only do these feats speak to his influence and the quality of his work, but also to the lack of any major pseudoscorpion taxonomist simultaneously based on the continent. Contemporaries of Muchmore, who were involved in taxonomy of North American cave pseudoscorpions, include James Cokendolpher, Bozidar Ćurčić, Ellen Benedict, Mark Harvey, and David Malcolm.

Muchmore contributed on a more minor level to biospeleology on other continents. He described five new cave-adapted species from Oceania (one from Australia and four from lava tubes on the Hawaiian archipelago), one new species from Africa, and two new species from South America. Additionally, he authored the first known troglitic species from Hawaii, *Tyrannochthonius howarthi* (Muchmore, 1979d), and contributed five papers to the series "Cavernicolous fauna of Hawaiian lava tubes," that was initiated by Francis Howarth (1973), expanding the series' scope to include pseudoscorpions. In 2000, he published what was envisioned to be the first in a series of papers summarizing

and describing all known Hawaiian pseudoscorpions, both epigeal and subterranean. In this paper, which focused on the superfamily Chthonioidea, he listed nine species, provided a regional key, described one new genus, referred a species to this new genus, and described two new species. New species included *Vulcanochthonius howarthi*, known exclusively from volcanoes, and *V. aa*, known only from milieu souterrain superficial (MSS) of 'a'a volcanic rock near a cave entrance. This paper also included the first plausible record from the North Pacific Rim of the synanthropic, globally distributed species *Chthonius tetrachelatus* (Preyssl, 1790). Unfortunately, subsequent papers in this series, meant to cover the remaining superfamilies, never made it to publication.

Muchmore's ideas on adaptation to cave life in pseudoscorpions included several morphological features, which are seen in other troglomorphic arthropods and expanded upon by other authors (e.g., Barr, 1961). These include absence or reduction of eyes, appendage attenuation, and reduction or absence of pigment. However, in several instances he noted that some of these features were found in species that had only been collected from epigeal habitats. Examples include elongate appendages in bark-dwelling species, such as *Bituberochernes mumae* (Muchmore, 1974d); eye loss in leaf litter-dwelling *Tyrannochthonius hypogeus*, a species known only from a sinkhole in Mammoth Cave National Park, Kentucky (Muchmore, 1996g); and depigmentation and eye reduction in *Apochthonius hypogeus*, a species known only from under rocks in the Appalachian Mountains of Virginia (Muchmore, 1976d). He struggled with explaining how troglobiotic species came to have disjunct distributions, as seen in *A. colecampi* (Muchmore, 1976d). In the first thorough review paper on phoresy in pseudoscorpions, he speculated that hypogean species of Chernetidae may be carried between caves via bats or rodents (Muchmore, 1971d, 1996b). However, molecular tools currently available for testing these ideas were either not yet invented or were, presumably, unavailable to him.

Despite much of his career having been dedicated to biospeleology (167 of 278 species he described or co-authored are hypogean), Muchmore rarely collected in caves himself. It is doubtful that he would have considered himself a caver. The only specimen from a cave that he both collected and used as material in a species description was *Apochthonius indianensis* from Donaldson-Bronson Cave, Indiana, which he collected in 1958 (Muchmore, 1967b). On one of the few subsequent occasions when he ventured into a cave with a fellow biologist, it was noted by his companion that he was both remarkably, and somewhat amusingly, unprepared for exploring the subterranean environment (Julian J. Lewis, pers. comm.). Instead, he relied on highly productive relationships with a wide assortment of cavers and biospeleologists. The most prolific collector from whom he received specimens was Stewart Peck, who contributed to 36 new species discoveries in caves of Belize, Jamaica, and the United States. In recognition of these survey efforts, he named six species in Peck's honor.

Although Muchmore collected extensively from epigeal localities, for type specimens he usually relied on material sent to him by other collectors. His preferred collection method for epigeal fauna was sampling leaf litter in bulk and then extracting animals using Berlese-Tullgren funnels. He did not throw away by-catch from this sampling; instead, he deposited non-pseudoscorpion specimens that he collected into museums or gave them directly to specialists. Muchmore's contributions to epigeal pseudoscorpion taxonomy is on par with those to subterranean taxa: he described 92 new species and co-authored 19 new species. As with cave-adapted fauna, his focus was mostly North America, although he also described new species from Africa, Asia, Australia, South America, and remote island archipelagos. Two notable epigeal species described by him include *Solinellus simberloffi* from Daniel S. Simberloff and Edward O. Wilson's famous defaunation and recolonization studies of Florida mangrove islands, that led to the formation of their theory of island biogeography (Simberloff and Wilson, 1969); and *Wyochernes asiaticus*, which is known from a higher latitude than any other pseudoscorpion species, at 69° N, in Yukon, Canada (Muchmore, 1979a, 1990b, 1996f).

In addition to describing new species and subspecies, Muchmore named several higher taxa that cannot be easily divided amongst epigeal or subterranean habitat. These include two subfamilies, 27 genera (three of which were co-authored), and one subgenus. Despite the common use of the subgenus rank in European pseudoscorpion taxonomy, as a rule Muchmore did not use this taxonomic rank. The only exception was the genus *Kleptochthonius*. In this genus, species only known from caves and with troglomorphic characters have been placed into the subgenus *Chamberlinochthonius*, while those collected exclusively from epigeal environments and lacking troglomorphic characters have been placed into the nominative subgenus. In one of his last papers, Muchmore (2000a) described two new species of *Kleptochthonius* without assigning them to either subgenus. In this paper he also mentioned that he was working on a revision of the genus, but he never subsequently published on *Kleptochthonius*. Consequently, there is now some ambiguity in *Kleptochthonius*, with all but two of the 39 species in the genus assigned to either *K. (Chamberlinochthonius)* or *K. (Kleptochthonius)*.

Muchmore was known for his kindness in assisting new students of pseudoscorpions, regardless of their country of origin or the seriousness of their interest in publishing on specimens they had collected (René Barba Díaz, pers. comm.; Christopher M. Buddle, pers. comm.; William A. Shear, pers. comm.). Despite serving on the Board of Directors of the American Arachnological Society, he was not known among his peers to attend many conferences. As such, most of his colleagues came to know him through correspondence. He also influenced many pseudoscorpion scholars through

his key to North American species, which remains the most comprehensive key for the continent (Muchmore, 1990c). Eighteen taxa have been named for Muchmore. These patronyms were given in respect of his being an international authority on pseudoscorpions, for his friendship, and in thanks for his personal collection efforts. One genus and six species of pseudoscorpions were named for him: *Muchmoreus* (Harvey, 2013), *Americhernes muchmorei* (Harvey, 1990), *Antillochernes muchmorei* (Dumitresco and Orghidan, 1977), *Austrochthonius muchmorei* (Harvey and Mould, 2006), *Ideoblothrus muchmorei* (Heurtault, 1983), *Pseudalbiorix muchmorei* (Harvey et al., 2006) and *Spelaeobochica muchmorei* (de Andrade and Mahnert, 2003). One pseudoscorpion species was named for Muchmore and his wife: *Tyrannochthonius muchmoreorum* (Cokendolpher, 2009). Patronyms in taxa other than pseudoscorpions include the edaphic minute brown scavenger beetle *Metophtalmus muchmorei* (Andrews, 1988); the eyeless weevil *Decuanellus muchmorei* (Howden, 1992); the edaphic unique-headed bug *Alienates muchmorei* (Wygodzinsky and Schmidt, 1991); the edaphic scolopendromorph centipede *Cryptops neocaledonicus muchmorei* (Lewis, 1989); the edaphic pauropod *Diplopauropus muchmorei* (Scheller and Muchmore, 1989); the epigeal scorpion *Heteronebo muchmorei* (Francke and Sissom, 1980); three epigeal spiders *Zimiromus muchmorei* (Platnick and Shadab, 1976), *Monoblemma muchmorei* (Shear, 1978), and *Khamisoides muchmorei* (Platnick and Berniker, 2015); and the epigeal whip spider *Charinus muchmorei* (Armas and Teruel Ochoa, 1997).

Pseudoscorpion anatomical nomenclature has been interpreted differently over the years and in different regions (e.g., Chamberlin, 1931; Harvey, 1992). Muchmore used the schema developed by Chamberlin (1931) and studied specimens through permanent slide mounts made with Canada Balsam. He used slide-mounting methods described by Joseph C. Chamberlin and C. Clayton Hoff (Chamberlin, 1923; Hoff, 1944). This meticulous technique involves dissecting the chelicerae, a pedipalp, and two legs from the body, clearing the body in potassium hydroxide or beechwood creosote, and then mounting all parts onto a slide in a medium of Canada Balsam sap, liquefied with xylene. This method allows specimens to persist essentially unchanged for centuries. The slide-mounting technique was a passion of Muchmore. He confided to the junior author that he enjoyed the process to such an extent that he made his own thin glass tubes, used to prop coverslips over the thousands of specimens that he mounted over the course of his career. These slide mounts allowed the detailed examination of the specimens, which is required for species description. Some of Muchmore's material is stored in alcohol, but the vast majority is mounted on slides. Each is labeled with his personal catalog number.

Over five decades Muchmore accumulated a large collection of specimens and built a personal catalog of all specimens that he examined. In a paper on the arachnid order Schizomida, Reddell and Cokendolpher (1995) referred to Muchmore's private collection as "WBMC--William B. Muchmore collection, Rochester." However, in his own papers Muchmore never referred to his private collection by any acronym. Following the cessation of his work on pseudoscorpions around 2009, this collection, which included several important pseudoscorpion paratypes, was moved to the Florida State Collection of Arthropods (FSCA), Gainesville, Fla. Muchmore was a Research Associate at FSCA and this institute holds the majority of his type specimens. Other type material, including holotypes, paratypes, and topotypic specimens, are stored at Instituto de Ecología y Sistemática, Havana, Cuba; American Museum of Natural History, New York, N.Y.; Auburn University Museum of Natural History, Auburn, Ala.; Bohart Museum of Entomology, University of California, Davis, Calif.; Bernice P. Bishop Museum, Honolulu, Hawaii; California Academy of Sciences, San Francisco, Calif.; Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada; Laboratorio de Acarología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico; Museum of Comparative Zoology, Cambridge, Mass.; Smithsonian Institution National Museum of Natural History (previously known as United States National Museum), Washington, D.C.; and Western Australian Museum, Perth, Western Australia, Australia.

Muchmore has left to future researchers a rich body of taxonomic literature on this rather poorly studied group of arachnids. This accumulation includes both the volume of publications he produced and the quality and quantity of specimens he has deposited into institutions situated worldwide. These treasures continue to be prized by pseudoscorpion researchers. The many insights he has provided into this arachnid order, through his meticulous scrutiny of the specimens coming under his microscope, will continue to influence pseudoscorpion researchers for many years to come.

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