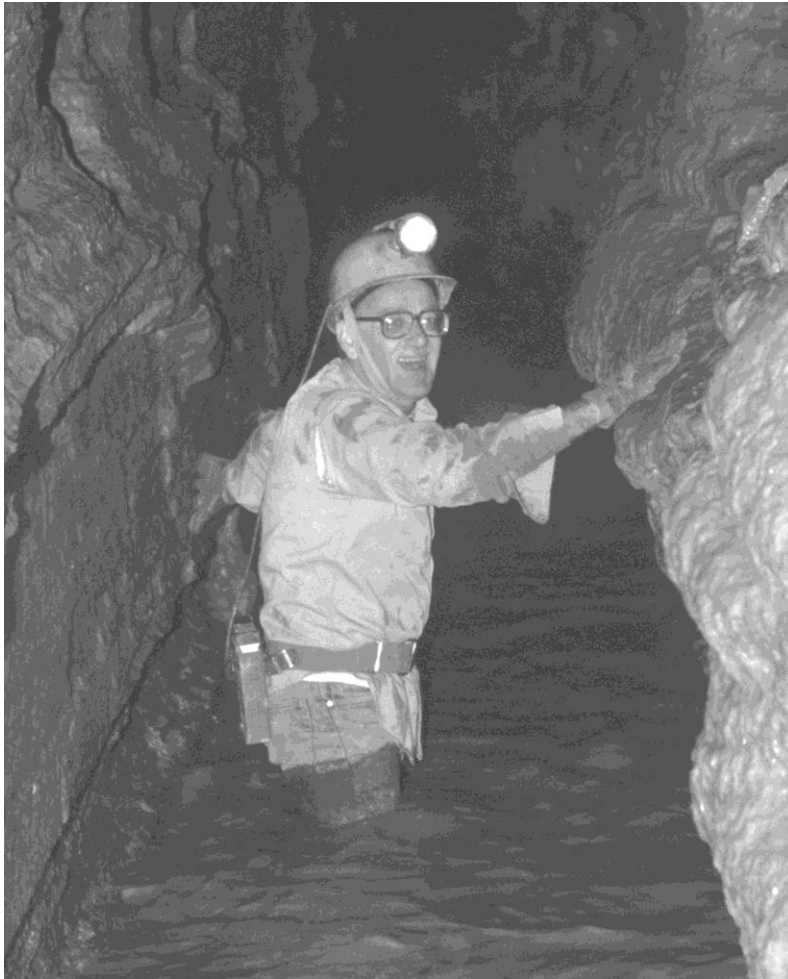


BANISTERIA

A JOURNAL DEVOTED TO THE NATURAL HISTORY OF VIRGINIA



John R. Holsinger
(1934-2018)

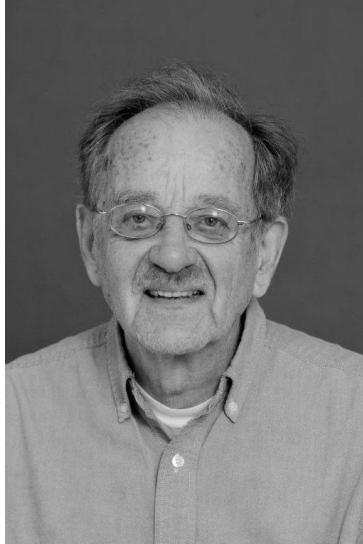
An obituary of this world renowned biospeleologist, cave conservationist, and freshwater amphipod systematist, who was a pioneering figure in the exploration and study of Virginia caves and their faunas, appears on pages 61-72 of this issue.

Miscellanea

Banisteria, Number 51, pages 61-72
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Obituary

John R. Holsinger
(1934-2018)



Dr. John Robert Holsinger, world renowned biospeleologist, cave conservationist, and amphipod crustacean systematist, died on November 10, 2018, at the age of 84 in Richmond, Virginia after a long illness. A longtime resident of Norfolk, Virginia, he was born on April 6, 1934, in Harrisonburg, Virginia, and grew up in the Shenandoah Valley. After graduating from Dayton High School in 1951, he attended Virginia Polytechnic Institute (Virginia Tech), where he served in the Corps of Cadets, was a member of the Hokie Cheerleading Squad, and was introduced to caving (in 1954) through the Virginia Tech cave club. He was a rabid fan of Hokie football for many years prior to his death. Following graduation (B.S., Biology) in 1955, John served in the US Army Security Agency in the Pacific Theater (Army Signal Corps in Hawaii), achieving the rank of Specialist 4th Class. After completion of his military service in 1958, John began what would become his lifelong passion for teaching others. He taught biological and earth sciences in the Fairfax County, Virginia public school system for the next five years (1958–1963) and pursued graduate studies at George Washington University and James Madison University (then Madison College), earning a Master of Science degree in biology from the latter institution in 1963.

Starting in late 1958 upon his return to Virginia from military duty, John became more seriously and permanently interested in caving and his biological sampling of caves during the next several years formed the basis for his Master's thesis research titled "Studies on the ecology and geographic distribution of macroscopic cavernicolous invertebrates of the central Appalachians." His thesis was the basis for the first (Holsinger, 1963) of his six papers published in the *Bulletin of the National Speleological Society* over the next three decades. In the fall of 1963, John began graduate studies at the University of Kentucky (UK) and earned a Ph.D. in evolutionary and systematic biology three years later. His dissertation, titled "Systematics, speciation, and distribution of the subterranean amphipod genus *Stygonectes* (Gammaridae)," was published in 1967 as *United States National Museum Bulletin* 259. Following graduation from UK, John was an assistant professor of biology at East Tennessee State University for two years. In 1968, he returned to his home state and joined the faculty of the Department of Biological Sciences at Old Dominion University (ODU) in Norfolk, where he remained for the rest of his career. John attained the rank of Full Professor a decade later and achieved the rare status of Eminent Scholar of Biological Sciences in August 1990.

John taught upper level undergraduate and graduate courses in invertebrate zoology, cave biology, biogeography, and systematics at ODU. His cave biology class included a weekend-long field trip to southwestern Virginia to visit several caves. Besides traditional students, several members of the Virginia Natural Heritage Program took this class because of John's reputation and his close association with the program. During his tenure at ODU, John directed the research of five Ph.D. and nine Master's degree students, co-chaired one Ph.D. student (Lynn Ferguson) at Virginia Tech, and also served on the committees of graduate students at several other institutions around the world. In 1995, John was one of the first recipients of a Partnerships for Enhancing Expertise in Taxonomy (PEET) grant from the National Science Foundation; these grants were established for the purpose of training a new generation of systematists. He also served one year (1972–1973) as a Visiting Curator at the U.S. National Museum of Natural History, Smithsonian Institution (NMNH). Upon his retirement from ODU at the end of 2008, John was named Eminent Scholar Emeritus and Professor Emeritus of Biological Sciences. In addition to his work at ODU, John was a research associate for several decades in the Department of Invertebrate Zoology at NMNH (appointed 1990) and the Virginia

Museum of Natural History (VMNH; appointed 1993). In 1992, he received the Thomas Jefferson Medal for outstanding contributions to the natural sciences in Virginia from VMNH, and also served on the museum's scientific advisory board beginning in 2006.

John was known both nationally and internationally for his lifetime work on the study and conservation of cave habitats and their faunas as well as the systematics and biogeography of freshwater amphipod crustaceans (see Culver [2018] for more details and a list of 135 of John's publications). John published numerous papers describing new species of amphipods, not only in the Appalachian region, but throughout North America, as well as other parts of the world. Especially during the latter half of his career, John frequently collaborated with colleagues in foreign countries to describe new species of amphipods. His publications also include significant summaries of the invertebrate cave faunas of Virginia (Holsinger & Culver, 1988; Holsinger et al. 2013), West Virginia (Holsinger et al. 1976), and several other states, as well as isopod systematics and ecology, cave conservation, and groundwater crustaceans (e.g., Edwards Plateau aquifer in Texas). He is also the author of "Descriptions of Virginia Caves" published in 1975 by the Virginia Division of Mineral Resources. John's scientific publications span more than 50 years (1963–2014; at least one more paper, containing descriptions of 22 new species of the subterranean amphipod genus *Stygobromus*, will be published posthumously). He also authored a semi-popular article on cave-dwelling organisms for *American Scientist* (Holsinger, 1988).

John was a pioneer in the exploration and documentation of the biological, geological, and historical significance of Virginia caves. He personally surveyed hundreds of caves in the Virginias, and many others elsewhere, and collected numerous biological specimens of all taxa from these habitats. John considered the discovery of new caves and extensive virgin passages in Lee, Scott, and Wise counties in southwestern Virginia during the 1960s and 1970s at or near the top of his most memorable caving experiences. Many of these early caving expeditions involved vertical caving techniques and were conducted with the late John Cooper (Figs. 1–2; retired from the North Carolina Museum of Natural Sciences); together they embarked on the "Biological Survey of Virginia Caves" project, which was affiliated with the National Speleological Society. John was director of the Virginia Cave Survey (since renamed Virginia Speleological Survey) from 1965 to 1974. Dr. Holsinger was also well versed in karst geology, and his biological sampling included groundwater organisms in non-karst habitats, especially *Stygobromus* amphipods (e.g., see Culver et al., 2012). In a paper presented at the 1993 International Congress



Fig. 1. John Holsinger and John Cooper at the entrance to Showalter's Cave, Rockbridge County, Virginia on a collecting trip in May 1961 that marked the beginning of the "Biological Survey of Virginia Caves" project. Photographer unknown.

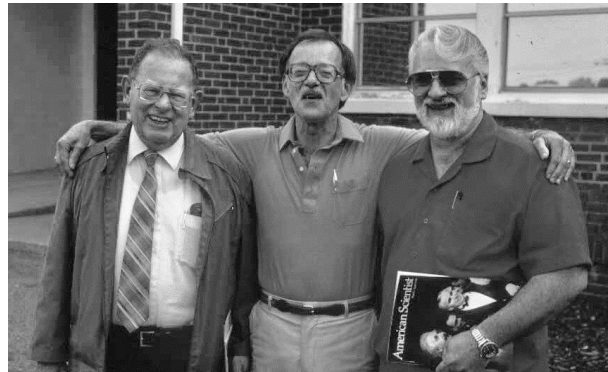


Fig. 2. Bill Davies, John Holsinger, and John Cooper at the Virginia Cave Board meeting held in May 1988 at the Virginia Museum of Natural History in Martinsville. Cooper is holding the latest issue of *American Scientist* containing Holsinger's paper on cave-dwelling organisms. Photo by Lynn Ferguson.

of Speleology in Beijing, China, he reported that about two-thirds of the species of *Stygobromus* inhabit caves (mostly pools and streams) and the remaining one-third inhabit springs, seeps, hyporheic zones, and phreatic waters (Holsinger, 1993a). Consequently, John was a strong advocate for groundwater protection, as well as cave and karst systems. He served as co-organizer/co-chairman of an international symposium on groundwater biology that was held in Blacksburg in 1978, and co-edited the proceedings published in *Crustaceana* and *International Journal of Speleology* in 1980 and 1981, respectively.

John knew many landowners in southwestern Virginia who had caves on their properties and had permitted him to explore them, often multiple times spanning decades. He could readily recall their names, locations, and what he found in each cave decades later. Beginning in 1961, John was a primary organizer of and regular participant in the more than half century-long “DOM” (Dirty Old Men) tradition of cave exploration trips that was held annually in southwestern Virginia (usually Lee County) over the Thanksgiving weekend. Numerous cavers convened to conduct biological monitoring and sampling as well as cave exploration and mapping activities in multiple caves. Among his fellow cavers, John was affectionately known as “Captain Karst” (see tribute by Culver et al., 2019).

John described more than 100 species and genera worldwide and established 4 new amphipod families. He coauthored the description of the West Virginia Spring Salamander (*Gyrinophilus subterraneus*), a single cave endemic (Besharse & Holsinger, 1977). With reference to the Virginia fauna, he described at least 40 species and one subspecies, including 37 amphipods, three isopods, and one freshwater snail (Table 1); among these, 26 species and one subspecies were amphipods of the genus *Stygobromus*, the taxonomic group of greatest interest and effort during his career. John had also provisionally recognized at least a dozen additional new species of *Stygobromus* from Virginia, but he did not prepare formal descriptions of them during his lifetime, primarily because he desired larger samples before the status of each could be properly evaluated. He described 21 new species of *Stygobromus* from states bordering Virginia, as well as dozens more from other parts of the United States, plus several species each from Canada and Siberia. In total, John described about 80 percent of the approximately 140 species of *Stygobromus* in the world.

John interacted with the leading taxonomists of his generation (most are now deceased) to obtain identifications of his cave invertebrate collections, including such prominent figures as Tom Barr (his Ph.D. mentor) and Stewart Peck (beetles), Willis Gertsch (spiders), Bill Muchmore (pseudoscorpions), Ken Christiansen (springtails), Lynn Ferguson (diplurans), Bill Shear (millipeds and harvestmen), Roman Kenk (flatworms), Leslie Hubricht and Bob Hershler (snails), Harrison Steeves and Tom Bowman (isopods), and Horton Hobbs (crayfish). He also maintained a close association spanning a half century with cave ecologist and evolutionary biologist Dave Culver (dates of their coauthored papers range from 1969–2013), and also retained close ties with isopod taxonomist Jerry Lewis, one of his former students, and Dan Fong (a Culver student), a cave ecologist and evolutionary biologist.

Dr. Holsinger was honored by various colleagues

through the description of patronyms for cave invertebrates in at least the following taxonomic groups: snails, spiders, pseudoscorpions, millipeds, beetles, isopods, amphipods, and flatworms (Table 2; additional patronyms may be forthcoming). In describing a new genus (*Holsingeria*) of freshwater snails in John’s honor, Hershler (1989) identified him as “a pioneering figure in North American cave biology.” In an interesting twist, Barnard & Karaman (1982) moved 2 of 3 subterranean amphipods from Texas that John had assigned to his new genus *Texiweckelia* just two years earlier (Holsinger & Longley, 1980) into their own monotypic genera, including one (*Holsingerius*) named in his honor. A decade later, John described a second member of this genus (Holsinger, 1992).

John attended many national and international conferences, congresses, and symposia concerning biospeleology, cave conservation and management, groundwater protection, and systematics, and regularly made presentations at those meetings, including giving plenary lectures at two International Symposia of Biospeleology (Italy, 2002; India, 2004). John was an Honorary Life Member (1980) and Fellow (1968) of the National Speleological Society (NSS; joined in 1959), served as Chairman of the 1963 NSS Convention at Mountain Lake, Virginia, was on the NSS Board of Governors (1962–1971), and chaired the NSS research advisory committee (1970–1975). In 1995, he received the NSS Science Award for lifetime contributions to the science of speleology. In 2007, John was honored by a special symposium at the annual NSS convention in Indiana (Fig. 3), and in 2014, he was invited to give the luminary talk at the NSS convention in Alabama.

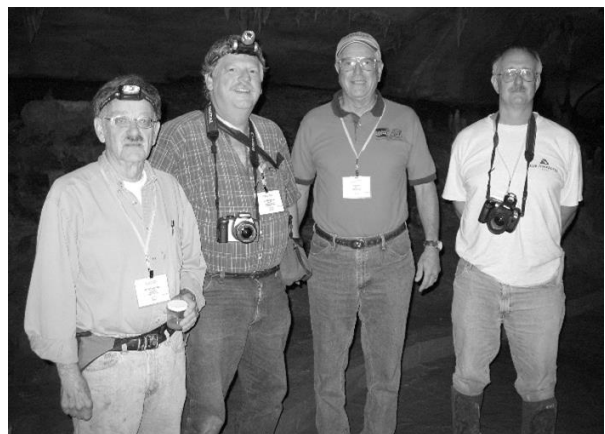


Fig. 3. John Holsinger, Bill Elliott, Gordon Smith (cave owner), and Jerry Lewis during a field trip to Marengo Cave, Indiana, held in conjunction with the 2007 annual convention of the National Speleological Society, at which Dr. Holsinger was honored for his lifetime contributions to cave biology and conservation. Photo by Lynn Ferguson.

Closer to home, John participated in the invertebrate portion of the 1968 symposium on Appalachian Biogeography held in Blacksburg and contributed a paper on amphipods to the proceedings (Holsinger, 1969). He also participated in the 1978 and 1989 symposia on threatened and endangered species of Virginia and contributed chapters containing species accounts on amphipods and isopods (also flatworms for the first symposium) to both proceedings volumes (Holsinger, 1979a-c, 1991b-c).

John was the longest serving member (30 years total [1978–1996, 2000–2012]) of the Virginia Cave Board (and its predecessor the Virginia Cave Commission), a governor-appointed citizen advisory board to the Virginia Department of Conservation and Recreation (and its predecessor agencies), and was its Chairman in 1982 and 1988–1994. In December 1976, he testified before the House Rules Committee of the Virginia General Assembly in support of a bill to create a Study Commission for Cave Protection in Virginia, which ultimately led to the creation of the Virginia Cave Commission. John developed the first list of “significant caves” for Virginia (Holsinger, 1980), one of the principal tasks of the Commission during its early years. The designation of “significant” was assigned to less than ten percent of the known caves in the state. A smaller subset of caves was designated as “very significant” (Fig. 4). Each cave was assessed for its potential significance based on the following criteria: archeological, biological, depth, economic, esthetic, geological, historical, hydrological, paleontological, length, and recreational. The initial list identified 220 caves and seven karst areas. John updated the list five years later (Holsinger, 1985), adding four more caves. The Significant Caves List continues to be updated periodically to the present day by the Virginia Speleological Survey based on new information obtained for previously known caves and the evaluation of newly discovered caves. Its main purposes are to identify the most important caves in the state and thus be more able to defend the need to protect them, specifically for the reasons defined by their significance criteria.

John was the leading early advocate for cave conservation in Virginia and the region, a cause to which he remained devoted throughout his career. He was a member of the Arthropod/Invertebrate Taxa Committee of the Virginia Department of Game and Inland Fisheries; in that role he provided advice to the agency concerning species worthy of conservation attention and state listing. John personally advocated for the federal listing (by the US Fish and Wildlife Service) of *Antrolana lira* (Madison cave isopod, listed as threatened in 1982) and *Lirceus usdagalun* (Lee County cave isopod; listed as endangered in 1992) because of



Fig. 4. John Holsinger examining biological samples in Madison Saltpetre Cave, Augusta County, Virginia, type locality of the Madison Cave Isopod (*Antrolana lira* Bowman, federally threatened) and the Madison Cave Amphipod (*Stygobromus stegerorum* Holsinger, state threatened). Dr. Holsinger and his students conducted several detailed studies of both species in this cave, which is considered one of the most significant caves in Virginia. Photo (1992) by Dave Hubbard.

threats to their habitats; the latter listing was controversial and John drew the ire of many local citizens as a result. He also recommended the Madison cave amphipod (*Stygobromus stegerorum*) and several cave beetles (*Pseudanophthalmus*) for state-listed status.

Beginning about 1970, and continuing for the rest of his career, John served as a consultant (often gratis) to many federal and state agencies and non-profit conservation organizations on matters related to cave, karst, and groundwater protection and threatened and endangered species biology and conservation. These agencies and groups included the US Fish and Wildlife Service, US Forest Service, US National Park Service, US National Marine Fisheries Service, US Natural Resources Conservation Service, Virginia Department of Transportation, Virginia Division of Mineral Resources, Virginia State Parks, the Natural Heritage Programs for Virginia, Maryland, Tennessee, Tennessee Valley Authority, Pennsylvania, California, Kansas, Michigan, Missouri, and Texas, The Nature Conservancy (multiple state chapters), World Wildlife Fund, and the Illinois Natural History Survey. He also consulted with media outlets such as National Geographic TV, Smithsonian World, Smithsonian Magazine, Time-Life Books, National Public Radio, and various newspapers on cave and endangered species-related issues. Among his many awards, John received the 2002 Karst Waters Institute Award in recognition of outstanding contributions to karst science.

John worked closely with the Virginia chapter of The Nature Conservancy to protect and ultimately purchase Unthanks Cave (now a dedicated state natural area

preserve), which he surveyed and studied periodically for 30 years (1961–1991), and other important karst habitats in Lee County in far southwestern Virginia. He also worked with the West Virginia chapter of The Nature Conservancy to purchase and permanently protect General Davis Cave in Greenbrier County, West Virginia. Beginning with its establishment as a state agency in 1986, John worked closely with the Virginia Department of Conservation and Recreation, Division of Natural Heritage (DCR-DNH), on cave conservation and groundwater protection issues, and is at least partly responsible for the current existence of a Karst Protection Program within that agency. In recent decades, DCR-DNH has purchased several additional caves in western Virginia that harbor rare species. The agency has also greatly expanded its holdings in “The Cedars” area of Lee County, the most significant karst landscape in Virginia. All of these properties are now protected as state natural area preserves.

A longtime supporter of the Virginia Natural History Society, John was a charter member (joined in its inaugural year, 1992) and published two papers that comprised a special cave issue of *Banisteria* (Holsinger, 2013; Holsinger et al., 2013). Besides those papers, I had the pleasure of editing John’s contribution to Richard Hoffman’s *Festschrift* volume (Holsinger, 2009) and served as guest editor of his coauthored paper on groundwater invertebrates that comprised an issue of *Northeastern Naturalist Monographs* (Culver et al., 2012). John also maintained longtime memberships in numerous other societies, including the National Speleological Society, International Society of Biospeleology, American Association for the Advancement of Science, Sigma Xi, Biological Society of Washington, Crustacean Society, Society for the Study of Evolution, Society of Systematic Biology, Willi Hennig Society, Association of Systematic Collections, American Association for Zoological Nomenclature, Cave Conservancy of the Virginias, and the American Cave Conservation Association. He served on the editorial boards of several of these societies.

In 2017, the Cave Conservancy of the Virginias and the Cave Conservancy Foundation provided funding to DCR-DNH to inventory Dr. Holsinger’s research collection of freshwater amphipods and other crustaceans in preparation for its subsequent permanent donation to the Smithsonian (NMNH). John’s collection was among the largest such collections in the world, but his failing health prevented him from completing this task himself. Less than a week after John’s death, his entire specimen collection was transferred to NMNH, where it will be an invaluable resource to current and future researchers of freshwater amphipod systematics. A portion of Dr. Holsinger’s research library now resides

at DCR-DNH, with the remainder currently in the custody of the Virginia Speleological Survey.

With the passing of John Holsinger, Virginia and the world has lost an irreplaceable giant in the fields of biospeleology, systematics, conservation, and natural history. He was buried in Harrisonburg, Virginia with military honors and is survived by his wife of 33 years, Linda Bogan Holsinger (a fellow caver) of Norfolk, stepchildren Charmaine Villa-Lobos, Robert Villalobos, Rebecca Villa-Lobos Davatellis, Danielle Villa-Lobos Hicks, and nine stepgrandchildren, and extended family of niece Kathy Hilbert, nephew J. Steven Hilbert, and great nephew Hunter Hilbert of Rockingham County, Virginia. He was preceded in death by his sister and brother-in-law Mary Ann and John Hilbert and nephew Gary Hilbert.

In 2018, DCR-DNH established a special fund to honor Dr. Holsinger’s contributions to cave conservation and research. All donations will be directed to the study, documentation, and protection of underground biodiversity. Persons wishing to contribute should make checks payable to the “Virginia Natural Area Preservation Fund” with “Holsinger Cave Conservation Fund” in the memo line and mail their donation to: Virginia Department of Conservation and Recreation, Division of Natural Heritage, 600 East Main Street, Richmond, VA 23219 (for questions call 804-786-7951).

I thank Lynn M. Ferguson for providing photos and information pertaining to the remarkable life and career of John R. Holsinger.

Literature Cited (excluding Holsinger publications)

Barnard, J. L., & G. S. Karaman. 1982. Classificatory revisions in gammaridean Amphipoda (Crustacea), Part 2. *Proceedings of the Biological Society of Washington* 95: 167–187.

Culver, D. C. 2018. In Memoriam – John R. Holsinger. *Subterranean Biology* 28: 53–56.

Culver, D., W. Orndorff, & C. Hobson. 2019. Remembering Captain Karst: Dr. John R. Holsinger. *NSS News* 77(1): 28-29.

Hershler, R. 1989. *Holsingeria unthinksensis*, a new genus and species of aquatic cavesnail from eastern North America. *Malacological Review* 22: 93–100.

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Table 1. Virginia species described by John R. Holsinger and coauthors, with original citation and known states of occurrence.

Snails

Fontigens morrisoni Hershler, Holsinger and Hubricht, 1990 VA

Hershler, R., J. R. Holsinger, & L. Hubricht. 1990. A revision of the North American freshwater snail genus *Fontigens* (Prosobranchia: Hydrobiidae). *Smithsonian Contributions to Zoology* 509: 1–50.

Isopods

Caecidotea phreatica Lewis and Holsinger, 1985 VA

Lewis, J. J., & J. R. Holsinger. 1985. *Caecidotea phreatica*, a new phreatobitic isopod crustacean (Asellidae) from southeastern Virginia. *Proceedings of the Biological Society of Washington* 98: 1004–1011.

Lirceus culveri Estes and Holsinger, 1976 VA

Estes, J. A., & J. R. Holsinger. 1976. A second troglobitic species of the genus *Lirceus* (Isopoda, Asellidae) from southwestern Virginia. *Proceedings of the Biological Society of Washington* 89: 481–490.

Lirceus usdagalun Holsinger and Bowman, 1973 VA

Holsinger, J. R., & T. E. Bowman. 1973. A new troglobitic isopod of the genus *Lirceus* (Asellidae) from southwestern Virginia, with notes on the ecology and additional cave records for the genus in the Appalachians. *International Journal of Speleology* 5: 261–271.

Amphipods

Bactrurus angulus Koenemann and Holsinger, 2001 TN, VA

Koenemann, S., & J. R. Holsinger. 2001. Systematics of the North American subterranean amphipod genus *Bactrurus* (Crangonyctidae). *Beaufortia (Bulletin Zoological Museum, University of Amsterdam)* 51(1): 1–56.

Crangonyx acicularis Zhang and Holsinger, 2003 TN, VA

Crangonyx baculispina Zhang and Holsinger, 2003 VA

Crangonyx disjunctus Zhang and Holsinger, 2003 NC, VA

Crangonyx fontinalis Zhang and Holsinger, 2003 VA

Crangonyx longicarpus Zhang and Holsinger, 2003 NC, VA

Crangonyx montanus Zhang and Holsinger, 2003 VA, WV

Crangonyx orientalis Zhang and Holsinger, 2003 MD, NC, VA

Crangonyx palustris Zhang and Holsinger, 2003 MD, NC, NJ, VA

Crangonyx stagnosticolous Zhang and Holsinger, 2003 MD, VA

Zhang, J., & J. R. Holsinger. 2003. Systematics of the freshwater amphipod genus *Crangonyx* (Crangonyctidae) in North America. *Virginia Museum of Natural History Memoir* 6. 274 pp.

Stygobromus conradi (Holsinger, 1967) VA

Stygobromus gracilipes (Holsinger, 1967) MD, PA, VA, WV

Stygobromus indentatus (Holsinger, 1967) MD, NC, VA

Stygobromus morrisoni (Holsinger, 1967) VA, WV

Stygobromus mundus (Holsinger, 1967) VA

Stygobromus tenuis potomacus (Holsinger, 1967) DC, MD, PA, VA, WV

Holsinger, J.R. 1967. Systematics, speciation, and distribution of the subterranean amphipod genus *Stygobromus* (Gammaridae). *Bulletin of the United States National Museum* 259: 1–176.

Stygobromus araeus (Holsinger, 1969) NC, VA

Stygobromus ephemerus (Holsinger, 1969) VA

Holsinger, J. R. 1969. The systematics of the subterranean amphipod genus *Apocrangonyx* (Gammaridae), with remarks on geography and zoogeography. *American Midland Naturalist* 81: 1–28.

Table 1 (continued).

<i>Stygobromus abditus</i> Holsinger, 1978	VA
<i>Stygobromus baroodyi</i> Holsinger, 1978	VA
<i>Stygobromus biggersi</i> Holsinger, 1978	MD, PA, VA, WV
<i>Stygobromus cumberlandus</i> Holsinger, 1978	VA
<i>Stygobromus estesi</i> Holsinger, 1978	VA
<i>Stygobromus fergusonii</i> Holsinger, 1978	VA
<i>Stygobromus finleyi</i> Holsinger, 1978	TN, VA
<i>Stygobromus hoffmani</i> Holsinger, 1978	VA
<i>Stygobromus interitus</i> Holsinger, 1978	VA
<i>Stygobromus kenki</i> Holsinger, 1978	DC, MD, VA
<i>Stygobromus leensis</i> Holsinger, 1978	VA
<i>Stygobromus obrutus</i> Holsinger, 1978	VA
<i>Stygobromus phreaticus</i> Holsinger, 1978	VA
<i>Stygobromus pseudospinosus</i> Holsinger, 1978	VA
<i>Stygobromus stegerorum</i> Holsinger, 1978	VA

Holsinger, J. R. 1978. Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae). Part II: Species of the eastern United States. *Smithsonian Contributions to Zoology* 266: 1–144.

<i>Stygobromus hubbardi</i> Holsinger, 2009	VA
<i>Stygobromus mausi</i> Holsinger, 2009	VA
<i>Stygobromus sextarius</i> Holsinger, 2009	DC, MD, VA

Holsinger, J. R. 2009. Three new species of the subterranean amphipod genus *Stygobromus* (Crangonyctidae) from the District of Columbia, Maryland, and Virginia. Pp. 261–276 *In* S. M. Roble & J. C. Mitchell (eds.), *A Lifetime of Contributions to Myriapodology and the Natural History of Virginia: A Festschrift in Honor of Richard L. Hoffman's 80th Birthday*. Virginia Museum of Natural History Special Publication No. 16, Martinsville, VA.

<i>Stygobromus foliatus</i> Holsinger, 2011	MD, VA
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Holsinger, J. R., L. M. Ansell, & J. Shafer. 2011. Four new species of the subterranean amphipod genus *Stygobromus* (Amphipoda: Crangonyctidae) from shallow groundwater habitats on the Coastal Plain and eastern margin of the Piedmont in Maryland and Virginia, USA. *Zootaxa* 2972: 1–21.

Other taxa of note from nearby states

Gyrinophilus subterraneus Besharse and Holsinger, 1977 WV West Virginia Spring Salamander
Besharse, J. C., & J. R. Holsinger. 1977. *Gyrinophilus subterraneus*, a new troglobitic salamander from southern West Virginia. *Copeia* 1977: 624–634.

Caecidotea franzi (Holsinger and Steeves, 1971) KY, MD, PA, WV Cave isopod
(Described as *Asellus franzi* Holsinger and Steeves, 1971)
Holsinger, J. R., & H. R. Steeves, III. 1971. A new species of subterranean isopod crustacean (Asellidae) from the central Appalachians, with remarks on the distribution of other isopods of the region. *Proceedings of the Biological Society of Washington* 84: 189–200.

Caecidotea scypha (Steeves and Holsinger, 1968) TN, WV Cave isopod
(Described as *Asellus scyphus* Steeves and Holsinger, 1968)
Steeves, H. R., III, & J. R. Holsinger. 1968. Biology of three new troglobitic asellids from Tennessee. *American Midland Naturalist* 80: 75–83.

Gammarus cohabitatus Holsinger and Shafer, 2008 PA Amphipod
Holsinger, J. R., J. Shafer, D. W. Fong, & D. C. Culver. 2008. *Gammarus cohabitatus*, a new species of subterranean amphipod crustacean (Gammaridae) from groundwater habitats in central Pennsylvania, USA. *Subterranean Biology* 6: 31–41.

Table 2. North American genera and species described in honor of John R. Holsinger.

Genus patronyms

Holsingerius Barnard and Karaman, 1982 TX Genus of subterranean amphipods (Family Hadziidae)

Contains 2 described species: *Holsingerius samacos* (Holsinger, 1980) and *H. smaragdinus* Holsinger, 1992

Barnard, J. L., & G. S. Karaman. 1982. Classificatory revisions in gammaridean Amphipoda (Crustacea), Part 2. Proceedings of the Biological Society of Washington 95: 167–187.

Holsingeria Hershler, 1989 VA Monotypic genus of aquatic cave snail (Family Hydrobiidae)

Hershler, R. 1989. *Holsingeria unthinksensis*, a new genus and species of aquatic cavesnail from eastern North America. Malacological Review 22: 93–100.

Species patronyms

Sphalloplana holsingeri Kenk, 1977 VA Groundwater planarian

Kenk, R. 1977. Freshwater triclads (Turbellaria) of North America, IX: The genus *Sphalloplana*. Smithsonian Contributions to Zoology, Number 246. Smithsonian Institution Press, Washington, DC. 38 pp.

Fontigens holsingeri Hubricht 1976 WV Aquatic snail

(now regarded as a junior synonym of *Fontigens tartarea* Hubricht, 1963)

Hubricht, L. 1976. The genus *Fontigens* from Appalachian caves (Hydrobiidae: Mesogastropoda). The Nautilus 90: 86–88.

Caecidotea holsingeri (Steeves, 1963) MD, VA, WV Cave isopod

(Described as *Asellus holsingeri* Steeves, 1963)

Steeves, H. R., III. 1963. Two new troglobitic asellids from West Virginia. American Midland Naturalist 70: 462–465.

Stygobromus holsingeri Ward, 1977 CO Amphipod

Ward, J. V. 1977. First records of subterranean amphipods from Colorado with descriptions of three new species of *Stygobromus* (Crangonyctidae). Transactions of the American Microscopical Society 96: 452–466.

Apochthonius holsingeri Muchmore, 1967 VA Cave pseudoscorpion

Muchmore, W. B. 1967. New cave pseudoscorpions of the genus *Apochthonius* (Arachnida: Chelonethida). Ohio Journal of Science 67: 89–95.

Hesperocheles holsingeri Muchmore, 1964 IN Cave pseudoscorpion

Muchmore, W. B. 1994. Some pseudoscorpions (Arachnida: Pseudoscorpionida) from caves in Ohio and Indiana, U.S.A. Transactions of the American Microscopical Society 113: 316–324.

Mundochthonius holsingeri Benedict and Malcolm, 1974 VA Cave pseudoscorpion

Benedict, E. M., & D. R. Malcolm. 1974. A new cavernicolous species of *Mundochthonius* from the eastern United States (Pseudoscorpionida: Chthoniidae). Journal of Arachnology 2: 1–4.

Cicurina holsingeri Gertsch, 1992 TX Cave spider

Gertsch, W. J. 1992. Distribution patterns and speciation in North American cave spiders with a list of the troglobites and revision of the cicurinas of the subgenus *Cicurella*. Texas Memorial Museum, Speleological Monograph 3: 75–122.

Nesticus holsingeri Gertsch, 1984 VA Cave spider

Gertsch, W. J. 1984. The spider family Nesticidae (Araneae) in North America, Central America, and the West Indies. Texas Memorial Museum Bulletin 31: 1–91.

Pseudotremia johnholsingeri Shear 2011 VA Cave milliped

Shear, W. A. 2011. Cave millipeds of the United States. X. New species and records of the genus *Pseudotremia* Cope. 2. Species from Virginia, USA (Diplopoda, Chordeumatida, Cleidogonidae). Zootaxa 3109: 1–38.

Pseudanophthalmus holsingeri Barr, 1965 VA Cave beetle

Barr, T. C., Jr. 1965. The *Pseudanophthalmus* of the Appalachian Valley (Coleoptera: Carabidae). American Midland Naturalist 73: 41–72.

**Publications of John R. Holsinger
relevant to Virginia and nearby
states, plus selected other papers**

(* = Not included in Holsinger bibliography compiled by Culver [2018]).

Holsinger, J. R. 1963. Annotated checklist of the macroscopic troglobites of Virginia, with notes on their geographic distribution. *Bulletin of the National Speleological Society* 24: 23–36.

Holsinger, J. R. 1964a. The gray myotis (*Myotis grisescens*) in Virginia. *Journal of Mammalogy* 45: 151–152.

Holsinger, J. R. 1964b. The biology of Virginia caves. Pp. 57–74 *In* H. H. Douglas (ed.), *Caves of Virginia*. Virginia Cave Survey, Falls Church, VA.

Holsinger, J. R. 1965a. Redescriptions of two poorly known species of cavernicolous rhagidiid mites (Acarina: Trombidiformes) from Virginia and Kentucky. *Acarologia* 7: 654–662.

Holsinger, J. R. 1965b. Free living mites (Acarina) in caves of the eastern United States. *Bulletin of the National Speleological Society* 27: 47–64.

Holsinger, J. R. 1966. A preliminary study on the effects of organic pollution of Banners Corner Cave, Virginia. *International Journal of Speleology* 2: 75–89.

Holsinger, J. R. 1967a. Systematics, speciation, and distribution of the subterranean amphipod genus *Stygonectes* (Gammaridae). *Bulletin of the United States National Museum* 259: 1–176.

Holsinger, J. R. 1967b. New data on the range of the troglotic trichoniscid isopod *Caucasonethes henroti*. *Journal of the Tennessee Academy of Science* 42: 15.

Steeves, H. R., III, & J. R. Holsinger. 1968. Biology of three new species of troglotic asellids from Tennessee. *American Midland Naturalist* 76: 100–124.

Holsinger, J. R. 1969. Biogeography of the freshwater amphipod crustaceans (Gammaridae) of the central and southern Appalachians. Pp. 19–50 *In* P. C. Holt (ed.), *The Distributional History of the Biota of the Southern Appalachians, Part I: Invertebrates*. Research Division Monograph 1, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Culver, D. C., & J. R. Holsinger. 1969. Preliminary observation on sex ratios in the subterranean amphipod genus *Stygonectes* (Gammaridae). *American Midland Naturalist* 82: 631–633.

Holsinger, J. R., & D. C. Culver. 1970. Morphological variation in *Gammarus minus* Say (Amphipoda, Gammaridae) with emphasis on subterranean forms. *Postilla* 146: 1–24.

Holsinger, J. R., & S. B. Peck. 1971. The invertebrate cave fauna of Georgia. *Bulletin of the National Speleological Society* 33: 23–44.

Barr, T. C., Jr., & J. R. Holsinger. 1971. Biogeography of troglobites. *Bulletin of the National Speleological Society* 33: 115–118.

Holsinger, J. R., & H. R. Steeves, III. 1971. A new species of subterranean isopod crustacean (Asellidae) from the central Appalachians, with remarks on the distribution of other isopods of the region. *Proceedings of the Biological Society of Washington* 84: 189–200.

Holsinger, J. R. 1972. The freshwater amphipod crustaceans (Gammaridae) of North America. *Biota of Freshwater Ecosystems, Identification Manual* 5. U.S. Environmental Protection Agency, Washington, DC. 89 pp.

Holsinger, J. R., & T. E. Bowman. 1974. A new troglotic isopod of the genus *Lirceus* (Asellidae) from southwestern Virginia, with notes on its ecology and additional cave records for the genus in the Appalachians. *International Journal of Speleology* 5: 261–271.

Culver, D. C., J. R. Holsinger, & R. A. Baroody. 1974. Toward a predictive cave biogeography: The Greenbrier Valley as a case study. *Evolution* 27: 689–695.

Holsinger, J. R. 1974. Systematics of the subterranean amphipod genus *Stygobromus* (Gammaridae), Part I: Species of the western United States. *Smithsonian Contributions to Zoology* 160: 1–63.

Holsinger, J. R. 1975. Descriptions of Virginia caves. *Virginia Division of Mineral Resources Bulletin* 85: 1–450.

Estes, J.A., & J. R. Holsinger. 1976. A second troglotic species of the genus *Lirceus* (Isopoda, Asellidae) from southwestern Virginia. *Proceedings of the Biological Society of Washington* 89: 481–490.

- Holsinger, J. R. 1976. The cave fauna of Pennsylvania. Pp. 72–87 *In* W. B. White (ed.), *Geology and Biology of Pennsylvania Caves*. Pennsylvania Geological Survey (4th series), General Geology Report 66. Harrisburg, PA.
- Holsinger, J. R., R. A. Baroody, & D. C. Culver. 1976. The invertebrate cave fauna of West Virginia. *West Virginia Speleological Survey Bulletin* 7: 1–82.
- Holsinger, J. R., & G. W. Dickson. 1977. Burrowing as a means of survival in the troglobitic amphipod crustacean *Crangonyx antennatus* Packard (Crangonyctidae). *Hydrobiologia* 54: 196–199.
- Besharse, J. C., & J. R. Holsinger. 1977. *Gyrinophilus subterraneus*, a new troglobitic salamander from southern West Virginia. *Copeia* 1977: 624–634.
- Holsinger, J. R. 1977. A review of the systematics of the Holarctic amphipod family Crangonyctidae. *Crustaceana Supplement* 4: 244–281.
- Holsinger, J. R. 1978. Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae), Part II: Species of the eastern United States. *Smithsonian Contributions to Zoology* 266: 1–144.
- Dickson, G. W., G. W. Patton, J. R. Holsinger, & J. Aise. 1979. Genetic variation in cave-dwelling and deep-sea organisms, with emphasis on *Crangonyx antennatus* (Crustacea: Amphipoda) in Virginia. *Brimleyana* 2: 119–130.
- *Holsinger, J. R. 1979a. Freshwater and terrestrial isopod crustaceans (Order Isopoda). Pp. 130–148 *In* D. W. Linzey (ed.), *Proceedings of the Symposium on Endangered and Threatened Plants and Animals of Virginia*. Center for Environmental Studies, Virginia Polytechnic Institute and State University, Blacksburg, VA.
- *Holsinger, J. R. 1979b. Freshwater amphipod crustaceans (Order Amphipoda). Pp. 149–169 *In* D. W. Linzey (ed.), *Proceedings of the Symposium on Endangered and Threatened Plants and Animals of Virginia*. Center for Environmental Studies, Virginia Polytechnic Institute and State University, Blacksburg, VA.
- *Holsinger, J. R. 1979c. Subterranean freshwater planarians (Order Seriata). Pp. 187–191 *In* D. W. Linzey (ed.), *Proceedings of the Symposium on Endangered and Threatened Plants and Animals of Virginia*. Center for Environmental Studies, Virginia Polytechnic Institute and State University, Blacksburg, VA.
- Holsinger, J. R., & G. Longley. 1980. The subterranean amphipod crustacean fauna of an artesian well in Texas. *Smithsonian Contributions to Zoology* 308: 1–62.
- Collins, T. L., & J. R. Holsinger. 1981. Population ecology of the troglobitic isopod crustacean *Antrolana lira* Bowman (Cirolanidae). *Proceedings of the 8th International Congress of Speleology*, Bowling Green, Kentucky 1: 129–132.
- Hubbard, D. A., Jr., & J. R. Holsinger. 1981. Karst development in Rye Cove, Virginia. *Proceedings of the 8th International Congress of Speleology*, Bowling Green, Kentucky 2: 515–517.
- Dickson, G. W., & J. R. Holsinger. 1981. Variation among populations of the troglobitic amphipod crustacean *Crangonyx antennatus* Packard (Crangonyctidae) living in different habitats, III: Population dynamics and stability. *International Journal of Speleology* 11: 33–48.
- Holsinger, J. R. 1982. A preliminary report on the cave fauna of Burnsville Cove, Virginia. *Bulletin of the National Speleological Society* 44: 98–101.
- Estes, J. A., & J. R. Holsinger. 1982. A comparison of the structure of two populations of the troglobitic isopod crustacean *Lirceus usdagalum* (Asellidae). *Polskie Archiwum Hydrobiologii* 29: 453–461.
- Barr, T. C., Jr., & J. R. Holsinger. 1985. Speciation in cave faunas. *Annual Review of Ecology and Systematics* 16: 313–337.
- Lewis, J. J., & J. R. Holsinger. 1985. *Caecidotea phreatica*, a new phreatobitic isopod crustacean (Asellidae) from southeastern Virginia. *Proceedings of the Biological Society of Washington* 98: 1004–1011.
- Holsinger, J. R. 1986. Zoogeographic patterns of North American subterranean amphipod crustaceans. Pp. 85–106 *In* R. H. Gore & K. L. Heck (eds.), *Crustacean Biogeography, Crustacean Issues* 4. Balkema, Rotterdam, The Netherlands.
- Holsinger, J. R. 1988. Troglobites: The evolution of cave-dwelling organisms. *American Scientist* 76: 146–153.

- Holsinger, J. R., & D. C. Culver. 1988. The invertebrate cave fauna of Virginia and a part of eastern Tennessee: Zoogeography and ecology. *Brimleyana* 14: 1–162.
- Godfrey, R. B., J. R. Holsinger, & K. A. Carson. 1988. A comparison of the morphology of calceoli in the freshwater amphipods *Crangonyx richmondensis* s. lat. (Crangonyctidae) and *Gammarus minus* (Gammaridae). *Crustaceana Supplement* 13: 115–121.
- Hershler, R., & J. R. Holsinger. 1990. Zoogeography of North American hydrobiid cavesnails. *Stylogia* 5: 5–16.
- Hershler, R., J. R. Holsinger, & L. Hubricht. 1990. Systematics of the North American hydrobiid genus *Fontigens* (Prosobranchia: Hydrobiidae). *Smithsonian Contributions to Zoology* 509: 1–49.
- Botosaneanu, L., & J. R. Holsinger. 1991. Some aspects concerning colonization of the subterranean realm – especially of subterranean waters: A response to Rouch & Danielopol. *Stylogia* 6: 11–39.
- Holsinger, J. R. 1991a. What can vicariance biogeographic models tell us about the distributional history of subterranean amphipods? *Hydrobiologia* 223: 43–45.
- *Holsinger, J. R. 1991b. Freshwater amphipods. Class Malacostraca: Order Amphipoda Subphylum Crustacea. Pp. 180–186 *In* K. Terwilliger (coordinator), Virginia's Endangered Species: Proceedings of a Symposium. McDonald and Woodward Publishing Co., Blacksburg, VA.
- *Holsinger, J. R. 1991c. Freshwater isopods. Class Malacostraca: Order Isopoda Subphylum Crustacea. Pp. 186–189 *In* K. Terwilliger (coordinator), Virginia's Endangered Species: Proceedings of a Symposium. McDonald and Woodward Publishing Co., Blacksburg, VA.
- Holsinger, J. R. 1992. Four new species of subterranean amphipod crustaceans (Artesiidae, Hadziidae, Sebiidae) from Texas, with comments on their phylogenetic and biogeographic relationships. *Texas Memorial Museum Speleological Monographs* 3: 1–22.
- Culver, D. C., W. K. Jones, & J. R. Holsinger. 1992. Biological and hydrological investigation of The Cedars, Lee County, Virginia, an ecologically significant and threatened karst area. *Proceedings of the 1st International Conference on Ground Water Ecology*, 281–290.
- Culver, D. C., & J. R. Holsinger. 1992. How many species of troglobites are there? *Bulletin of the National Speleological Society* 54: 79–80.
- Holsinger, J. R. 1993a. Biogeographic patterns of North American subterranean amphipods in the genus *Stygobromus* (Crangonyctidae). *Proceedings of the XI International Congress of Speleology*, Beijing, China, 118–120.
- Holsinger, J. R. 1993b. Biodiversity of subterranean amphipod crustaceans: global patterns and zoogeographic implications. *Journal of Natural History* 27: 821–835.
- Holsinger, J. R. 1994a. Pattern and process in the biogeography of subterranean amphipod crustaceans. *Hydrobiologia* 287: 131–145.
- Holsinger, J. R. 1994b. Subterranean amphipods. Pp. 147–163 *In* C. Juberthie & V. Decu (eds.), *Encyclopaedia Biospeologica*, Tome I., Société de Biospéologie, Moulis, France and Bucarest, Romania.
- Holsinger, J. R., D. A. Hubbard, Jr., & T. E. Bowman. 1994. Biogeographic and ecological implications of newly discovered populations of the stygobiont isopod crustacean *Antrolana lira* Bowman (Cirolanidae). *Journal of Natural History* 28: 1047–1058.
- Holsinger, J. R. 2000. Ecological derivation, colonization, and speciation. Pp. 399–415 *In* H. Wilkens, D. C. Culver, & W. F. Humphreys (eds.), *Subterranean Ecosystems*. Elsevier, Amsterdam, The Netherlands.
- Koenemann, S., & J. R. Holsinger. 2000. Phylogenetic reconstruction of the subterranean amphipod genus *Bactrurus* (Crangonyctidae), comparing molecular and morphological data. *Polskie Archiwum Hydrobiologii* 47: 401–412.
- Koenemann, S., & J. R. Holsinger. 2001. Systematics of the North American subterranean amphipod genus *Bactrurus* (Crangonyctidae). *Beaufortia* 51: 1–56.
- Wang, D., & J. R. Holsinger. 2001. Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae) in western North America, with emphasis on species of the *hubbsi* group. *Amphipacifica* 3: 39–146.

- Zhang, J., & J. R. Holsinger. 2003. Systematics of the freshwater amphipod genus *Crangonyx* (Crangonyctidae) in North America. Virginia Museum of Natural History Memoir 6: 1–274.
- Holsinger, J. R. 2005. Vicariance and dispersalist biogeography. Pp. 591–599 *In* D. C. Culver & W. B. White (eds.), *Encyclopedia of Caves*. Elsevier Academic Press, Amsterdam, The Netherlands.
- Graening, G. O., M. E. Slay, & J. R. Holsinger. 2005. Annotated checklist of the Amphipoda of Arkansas with emphasis on groundwater habitats. *Proceedings of the Arkansas Academy of Science* 59: 80–87.
- Graening, G. O., J. R. Holsinger, D. B. Fenolio, E. A. Bergey, & C. C. Vaughn. 2006. Annotated checklist of the Amphipoda of Oklahoma, with emphasis on groundwater habitats. *Proceedings of the Oklahoma Academy of Science* 86: 65–74.
- Holsinger, J. R., J. Shafer, D. W. Fong, & D. C. Culver. 2008. *Gammarus cohabitatus*, a new species of subterranean amphipod crustacean (Gammaridae) from groundwater habitats in central Pennsylvania, USA. *Subterranean Biology* 6: 31–41.
- Holsinger, J. R., J. Shafer, & G. Schulte. 2009. Development and application of a database for the subterranean amphipod crustacean genera *Stygobromus* and *Bactrurus*. *Proceedings of the 15th International Congress of Speleology, Kerrville, Texas* 3: 1286–1289.
- Holsinger, J. R. 2009. Three new species of the subterranean amphipod crustacean genus *Stygobromus* (Crangonyctidae) from the District of Columbia, Maryland, and Virginia. Pp. 261–276 *In* S. M. Roble & J. C. Mitchell (eds.), *A Lifetime of Contributions to Myriapodology and the Natural History of Virginia: A Festschrift in Honor of Richard L. Hoffman's 80th Birthday*. Virginia Museum of Natural History Special Publication No. 16, Martinsville, VA.
- Culver, D. C., J. R. Holsinger, M. C. Christman, & T. Papan. 2010. Morphological differences among eyeless amphipods in the genus *Stygobromus* dwelling in different subterranean habitats. *Journal of Crustacean Biology* 30: 68–74.
- Niemiller, M. L., M. S. Osbourn, D. B. Fenolio, T. K. Pauley, B. T. Miller, & J. R. Holsinger. 2010. Conservation status and habitat use of the West Virginia Spring Salamander (*Gyrinophilus subterraneus*) and Spring Salamander (*G. porphyriticus*) in General Davis Cave, Greenbrier Co., West Virginia. *Herpetological Conservation and Biology* 5: 32–43.
- Holsinger, J. R., L. M. Ansell, & J. Shafer. 2011. Four new species of the subterranean amphipod genus *Stygobromus* (Amphipoda: Crangonyctidae) from shallow groundwater habitats on the Coastal Plain and eastern margin of the Piedmont in Maryland and Virginia, USA. *Zootaxa* 2972: 1–21.
- Culver, D. C., J. R. Holsinger, & D. J. Feller. 2012. The fauna of seepage springs and other shallow subterranean habitats in the mid-Atlantic Piedmont and Coastal Plain. *Northeastern Naturalist Monograph* 19: 1–42.
- Holsinger, J. R. 2012. Vicariance and dispersalist biogeography. Pp. 849–858 *In* W. B. White & D. C. Culver (eds.), *Encyclopedia of Caves*. Academic Press, Amsterdam, The Netherlands.
- Holsinger, J. R. 2013. A brief history of biospeleology in Virginia. *Banisteria* 42: 3–8.
- Holsinger, J. R., D. C. Culver, D. A. Hubbard, Jr., W. D. Orndorff, & C. S. Hobson. 2013. The invertebrate cave fauna of Virginia. *Banisteria* 42: 9–56.
- Holsinger, J. R., & L. Ansell. 2014. A new species of the subterranean amphipod genus *Stygobromus* (Amphipoda: Crangonyctidae) from two caves and a seep in western Maryland, USA with additional records of undescribed species from groundwater habitats in central Maryland. *Zootaxa* 3768: 386–394.

Unpublished reports

*Holsinger, J. R. 1980. Annotated list of significant caves and karst areas in Virginia. Unpublished report for the Virginia Cave Commission. 55 pp. plus appendix.

*Holsinger, J. R. 1985. Annotated list of significant caves and karst areas in Virginia. Unpublished report for the Virginia Cave Board. 251 pp.