PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

Series 4, Volume 64, No. 12, pp. 347–359, 8 figs.

March 29, 2018

Range Extension for the Elusive New England Medicinal Leech, *Macrobdella sestertia* Whitman, 1886 (Hirudinida: Macrobdellidae), in South Carolina, U.S.A., with Notes on Morphology, Coloration, and Biology

William J. Poly

Aquatic Biodiversity Research Institute, 11205 Schroeder Road, Saint Marys, OH 45885, USA; Department of Ichthyology, California Academy of Sciences, 55 Music Concourse Drive, Golden Gate Park, San Francisco, CA 94118, USA. E-email: wpoly@calacademy.org

Two species of the leech genus Macrobdella (North American medicinal leeches), M. decora (Say, 1824) and M. ditetra Moore, 1953, have been reported from South Carolina. Collections made in 2008 revealed the presence of a third species, Macrobdella sestertia Whitman, 1886, in the state. The species had been collected rarely in the northeastern United States, with only seven specimens collected during the 20th century and the original type specimen(s) lost. The recent South Carolina collections add three locality records and nine specimens, and two other specimens that had been collected in 1984 and 2002 were found in museum collections, resulting in a total of five locations and eleven specimens. This report of *M. sestertia* in South Carolina is a significant southward extension of its distribution (approximately 1,360 km), which formerly included only Massachusetts, Maine, and New Hampshire, and is also the largest sample ever reported for the species. Life colors of *M. sestertia* are shown for the first time. Morphological variations were observed for copulatory gland pore number and for annuli arrangement. Evidence is presented for predation on fish eggs in New Hampshire by M. sestertia and M. decora. At one location on Sleepy Creek, M. sestertia harbored another leech, Placobdella nuchalis Sawyer and Shelley, 1976 (Glossiphoniidae), which is a new association. Three new county records of M. ditetra in South Carolina also are included.

KEYWORDS: Annelida, Hirudinea, leeches, South Carolina, morphological variation

Currently, there are four valid species of North American medicinal leeches recognized in the genus *Macrobdella*: *M. decora* (Say, 1824), *M. sestertia* Whitman, 1886, *M. ditetra* Moore, 1953, and *M. diplotertia* Meyer, 1975 (Say 1824; Whitman 1886; Moore 1953; Meyer 1975; Smith 1977). All of the species are sanguivorous (or presumed to be), feeding on vertebrates (mainly frogs) and at least *M. decora* and *M. diplotertia* are predators of embryos and juveniles of amphibians (Cory and Manion 1953; Cargo 1960; Schalk et al. 2002; Trauth and Neal 2004; Connior and Trauth 2010). Two species, *M. decora* and *M. sestertia*, are known or presumed to attack and feed on the blood of humans, and *M. decora* has been used in medical practice since the 1800s (Smith 1843, 1845). Sawyer (1973) discussed cases of leech attacks on swimmers in several South Carolina lakes and indicated that *M. decora* was the species involved in the attacks at Lake Jemiki (Oconee Co., SC) in the late 1960s and early 1970s. Smith (1977) documented leech attacks on swimmers at a lake in Massachusetts where *M. sestertia* was collected. The nervous systems of both *M. decora* and *M. sestertia* have been studied in relation to their swimming (Weeks 1982).

Macrobdella decora has a wide distribution in eastern and central North America from north-

ern Mexico to southern Canada (Klemm 1982); however, only a single locality has been reported in South Carolina (Sawyer and Pass 1972). Macrobdella ditetra occurs in coastal states from Virginia to Louisiana and inland to Arkansas (Moore 1953; Sawyer and Shelley 1976; Klemm 1982), and has been collected at seven locations on the coastal plain of South Carolina (Sawyer and Shelley 1976). Macrobdella diplotertia has been found in Missouri, Kansas, and Arkansas (Meyer 1975; Klemm et al. 1979; Turbeville and Briggler 2003). Macrobdella sestertia occurs in Massachusetts, Maine, and New Hampshire (Whitman 1886; Smith 1977; Smith and Hanlon 1997; Phillips et al. 2016), with reports from Louisiana (Klemm 1972; Davies 1991) being erroneous (Smith 1977). Phillips et al. (2016) reported a new state record for M. sestertia in New Hampshire, listing the collection site as "Suncoop Pond," a misspelling of "Suncook Pond," which is itself an unofficial, local name for Northwood Lake (the correct name that appears on maps; see Bailey 1938; Hoover 1938; Warfel and Fuller 1938). Seven species of leeches were reported from the middle to lower Savannah River (Patrick et al. 1967). Since the comprehensive review of leeches of the Carolinas by Sawyer and Shelley (1976), additional information on leeches in South Carolina has been published by Sawyer (1979), Klemm (1995), Moser et al. (2005), Light et al. (2005), Moser et al. (2011), and Phillips et al. (2016). In 2008, specimens of M. sestertia were collected from several Savannah River basin streams in South Carolina, which is a significant extension of the known range of this rarely-collected species. In addition, an association between M. sestertia and Placobdella nuchalis was observed for the first time.

MATERIALS AND METHODS

Leeches were collected by hand and with dipnets from streams in South Carolina in 2008 and 2011 (Poly 2011). Some leeches were brought from the field alive, and activity, swimming, and feeding were observed in captivity before preservation. Leeches were narcotized by slow addition of 70% ethanol to water in their containers, then were preserved in 70% ethanol. Photos were taken of some *M. sestertia* while alive in an aquarium and of two immediately after preservation. Others were fixed in 70% ethanol in the field without narcotization; however, these had been killed by summer heat and were relaxed prior to preservation. One M. ditetra was allowed to attach to several frogs to feed while in captivity. Additional leeches were borrowed from museum collections. Leech identifications were made using morphological characteristics given in original descriptions and subsequent works (Whitman 1886; Moore 1959; Sawyer and Shelley 1976; Klemm 1982; Davies 1991; Govedich et al. 2010). Annuli designations follow Sawyer (1986a). Leech specimens were deposited in the California Academy of Sciences, Invertebrate Zoology collection (CASIZ), San Francisco, California, USA, and the Charleston Museum (ChM), Charleston, South Carolina, USA. Comparative material was borrowed from ChM, the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts, USA and the North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA (NCSM; ChM specimens are now housed at NCSM) (see Appendix 1).

RESULTS AND DISCUSSION

A total of 10 specimens of *Macrobdella* spp. were collected in South Carolina from four locations in 2008 and 2011. Eight leeches collected in 2008 had the following characteristics that identify them as *Macrobdella sestertia*: 1) male and female gonopores separated by two and one-half annuli, lying on annulus 33 and between annuli 35 and 36, respectively, 2) a total of 24 copulatory gland pores arranged in four rows of six on annuli 42–44, 3) median longitudinal row of 20 pale orange spots along a diffuse mid-dorsal stripe with marginal rows of 20 quadrangular black blotches, and 4) body pigmentation olive green dorsally, orange to reddish-orange with scattered black blotches ventrally (the number and position of the blotches were variable among specimens Figs. 1, 2). Total lengths of the eight leeches were 39.7, 47.8, 48.1, 53.7, 62.4, 69.1, 79.3, and 93.7 mm; one additional specimen (ninth specimen) from Turkey Creek was considered to be M. sestertia; however, it escaped after capture. The copulatory gland pores are inconspicuous and lying hidden between annuli in smaller leeches, becoming more exposed as the glands develop. The three largest leeches had noticeable gland development that appeared white, contrasting with the orange coloration on the ventral side of the body. All M. sestertia had dark pigment on the postero-ventral and ventro-lateral margins of the caudal sucker (= acetabulum) (Figs. 1, 2), with the pigment being more extensive in larger leeches. Later, an unidentified leech collected in 1984 was found in ChM and was identified as M. sestertia (ChM IO6, 69.3

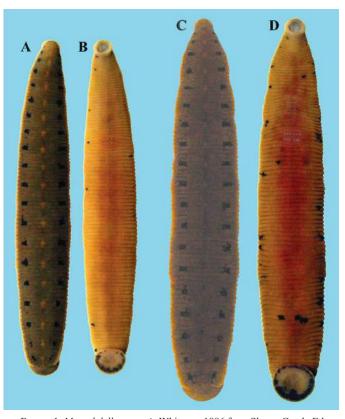


FIGURE 1. *Macrobdella sestertia* Whitman, 1886 from Sleepy Creek, Edgefield Co., South Carolina (dorsal (A, C) and ventral (B, D) views; CASIZ 224101 (69.1 mm TL [A, B]; 79.3 mm TL [C, D]). These two specimens were photographed immediately after preservation in 70% ethanol, and the pigments began to fade rapidly.

mm TL); an additional leech collected in 2002 was found in NCSM (as *M. decora*) and was reidentified as *M. sestertia* (NCSM 29791). Both of these collections were from Turkey Creek in Edgefield Co. (Fig. 3, Appendix 1). One *M. sestertia* possessed unusual overlapping annuli (Fig. 4, ChM IO7, 47.8 mm TL), and this condition does not appear to have been reported for any species of *Macrobdella*. The type specimens of *M. sestertia* could not be located, and the only localities mentioned in the original description were on page 382 as "Found in the neighbourhood of Cambridge; geographical limits unknown." and in the legend for Fig. 57 on page 414 as "obtained from Charles River, Watertown, Mass." (Whitman 1886).

In addition to collections of *M. sestertia*, one specimen of *M. ditetra* (44.1 mm TL) was collected from Willow Creek, Florence Co., SC in 2011. This specimen has male and female gonopores separated by two annuli and possesses a total of 8 copulatory gland pores arranged in two rows of four. Its pigmentation was gray/brown dorsally with one wide median dusky stripe, two narrow longitudinal stripes medially, two longitudinal rows of closely-spaced dark blotches medial to the two narrow stripes, and rusty-orange brown (in life) with scattered dark blotches ventrally and was consistent with what has been reported for *M. ditetra* and with museum specimens examined (Fig. 5; see Sawyer and Shelley 1976). Collections of *M. ditetra* from Florence, Hampton-Allendale, and Colleton counties represent new county records for the species in South



FIGURE 2. *Macrobdella sestertia* Whitman, 1886 from Sleepy Creek, Edgefield Co., South Carolina (CASIZ 224101). Specimens were photographed alive on 1 August 2008.

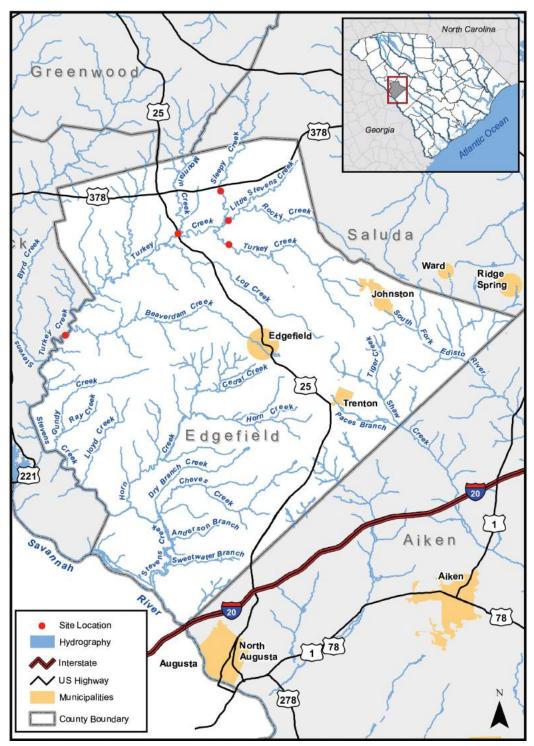


FIGURE 3. Distribution of Macrobdella sestertia Whitman, 1886 in Edgefield Co., South Carolina, USA.



FIGURE 4. Unusual overlapping annuli (annuli 48-49) observed on one specimen of Macrobdella sestertia (ChM IO7).



FIGURE 5. *Macrobdella ditetra* Moore, 1953 from Willow Creek, Florence Co., South Carolina (dorsal (A) and ventral (B) views; CASIZ 224103).

Carolina (Appendix 1). Between the time of collection on 10 August 2011 and the date of preservation on 2 September 2011, the *M. ditetra* specimen was allowed to attach to and feed on two green tree frogs, *Hyla cinerea* (Schneider, 1799) (14 and 26 August), and on one southern leopard frog, *Lithobates sphenocephalus* (Cope, 1886) (21 August; Fig. 6). In each case, the leech attached to one of the rear legs of the frogs and was allowed to feed for 30 minutes to nearly two hours before it was removed and the frog hosts were released.

Coloration and pigmentation of M. decora, M. diplotertia, and M. sestertia are similar, with M. ditetra differing most from these three species. The coloration and pigmentation of South Carolina specimens of *M. sestertia* appear to be the same as those described by Whitman (1886). In fact, M. decora and M. sestertia appear to be nearly identical in their coloration and pigmentation as noted by Smith (1977). Ventral pigmentation of the caudal sucker of M. sestertia was not mentioned by Whitman (1886) or subsequent authors but is documented herein for the specimens from South Carolina; it agrees closely with Sawyer's (1972) description for M. decora and that shown for M. diplotertia in McCallum et al. (2008). Pigments were faded on many of the museum specimens, thus, comparisons of pigment differences, particularly on the caudal suckers, could not be made using this material. The two preserved specimens in Fig. 1 were photographed immediately after preservation in 70% ethanol, and the orange-red color on the ventral surface began to fade rapidly (compare with that shown in photographs of live specimens [Fig 2]).

None of the *M. sestertia* or *M. ditetra* collected in South Carolina exhibited any variations in copulatory gland pore number or position. However, specimens of *M. decora* and *M. sestertia* from Maine displayed variations in pore count. One *M. decora* (MCZ 84111, larger specimen of two) was missing one anterior gland and pore, and one *M. sestertia* (MCZ 56624) had three additional pores associated with the two anterior and lateral copulatory glands. Copulatory gland pore number and pattern is one of the primary morphological characteristics used to separate species of *Macrobdella*. Variation in number and arrangement of copulatory gland pores has been noted for *Macrobdella decora* in Ontario, Georgia, South Carolina, and Maine (Moore 1922; Sawyer and Pass 1972; this study), *M. ditetra* in Louisiana (Moore 1953), and *M. sestertia* in Maine (this study). No variation in copulatory gland pore count or arrangement has been found in *M. diplotertia* (Turbeville and Briggler 2003). Most of the reported variants would not cause confusion in determining the species identity; however, one *M. decora* from Georgia had a pore count and pattern typical of *M. ditetra* (Sawyer and Pass 1972).

The unusual overlapping annuli observed on one specimen of *M. sestertia* in this study have not been mentioned for *Macrobdella* spp. by previous authors, but they have been observed occasionally in other genera and species of leeches (e.g., Blanchard 1893, 1894; Roy T. Sawyer, pers. comm.). A recent study of the *Macrobdella* spp. preserved at the National Museum of Natural History did not report any overlapping annuli (or variations in copulatory pores) (Phillips et al. 2016); however, the authors might have overlooked such variations because many museum specimens are contracted and curled due to preservation.

Macrobdella sestertia captured in Sleepy Creek on 31 July 2008 had a smaller species of leech associated with them. The smaller leeches detached during transport; therefore, detailed information on numbers occurring on each *M. sestertia* could not be obtained; however, it appeared that the largest *M. sestertia* had harbored most or all of the leeches. The nine smaller leeches were identified as *Placobdella nuchalis* and based on their sizes represent one adult (engorged with blood) and its offspring (Fig. 7, Appendix 1). The nuchal constriction remained on most of the juveniles after preservation, but the adult specimen contracted enough to obliterate the constriction and alter its morphology. *Placobdella nuchalis* was reported previously from two coastal plain counties in South Carolina (Sawyer and Shelley 1976), and the authors noted that records of *P. montifera* from the Savannah River in Patrick et al. (1967) possibly represented *P. nuchalis*. The specimens reported herein further support the statement of Sawyer and Shelley (1976). The only host reported for *P. nuchalis* was the bluegill, *Lepomis macrochirus* Rafinesque, 1819, collected in North Carolina (Shelley and Braswell 1981).

All of the streams from which *M. sestertia* were collected are in the upper portion of the Stevens/Turkey creek basin (Savannah River drainage) in northern Edgefield County. The streams had rocky bottoms with clear, shallow water, and the streams were under drought conditions when the collections were made. Leeches were found by moving or disturbing cobble-sized rocks. The leeches were agile swimmers, using undulations of the body for locomotion and were very active when disturbed. The coastal plain stream where *M. ditetra* was collected had clay and sand substrates with coarse organic debris.

It is unclear whether *M. sestertia* is a native species in South Carolina or is an accidental or intentional introduction. In 1797 in South Carolina, Dr. David Ramsay, "proposed . . . the practicability of introducing the leeches of this country into the practice of physic and surgery." (Waring 1964:124), and in the early- and mid-1800s, advertisements for the sale of leeches appeared in several Charleston, SC newspapers, although many of the leeches were European imports (Hagy 1991). Both the European medicinal leech, *Hirudo medicinalis* Linné, 1758, and the North American medicinal leech, *M. decora*, were used in medicine in the U.S. (Smith 1843, 1845). A letter dated March 26, 1877 from E.M.

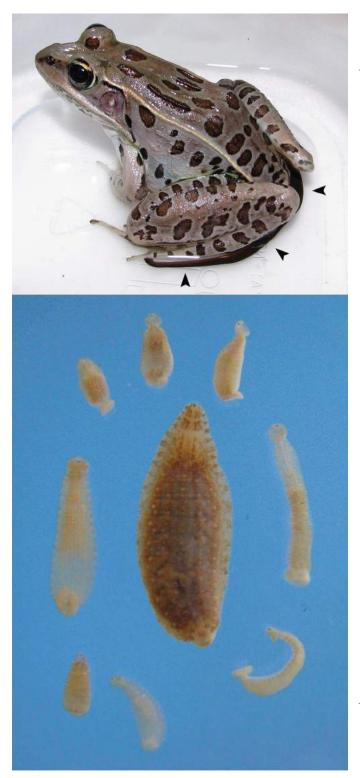


FIGURE 6. *Macrobdella ditetra* Moore, 1953 (CASIZ 224103) feeding on *Lithobates sphenocephalus* (Cope, 1886); arrows point to the leech.

Seabrook of Sumter, SC requests that two leeches be shipped to him from an unspecified source Mikell (Ephraim Seabrook Papers, South Caroliniana Library, University of South Carolina). Therefore, historical records indicate the use of and distribution of leeches in the eastern United States and in South Carolina. It is possible that specimens of M. sestertia were transported from New England, then were released or escaped. Sawyer (1973) presented information suggesting that M. decora in Lake Jemiki, South Carolina could have been introduced through discarded fishing bait. The records of M. ditetra from Colleton, Florence, and Hampton-Allendale counties, SC expands the distribution within the state (Sawyer and Shelley 1976).

The first report of *M. sestertia* from New Hampshire was by Phillips et al. (2016) based on a collection from 1938 by Reeve Maclaren Bailey (1911–2011; see Stewart and Smith 2000) and James A. Oliver. Although unknown to Phillips et al. (2016), Bailey's original field notes are available at the Fish Division, University of Michigan Museum of Zoology (UMMZ) and listed the fishes captured, amphibians seen or heard, and a note about large leeches consuming eggs

FIGURE 7. *Placobdella nuchalis* Sawyer & Shelley, 1976 from Sleepy Creek, Edgefield Co., South Carolina (dorsal view; CASIZ 224102); one engorged adult and eight juveniles.

une 3, 193 Watershed marringe Suncor Pond along north Stream or Lak 2747 wood No.M76-40. Coll No. County Rochi RIO Quad & No. uncook Color Water Dan Turbidity C amore eet a. Water_69 _Temp: Dist. from Sl 2 Depth Depth of Wate Collected By en Orig. Pre Weathe Shelter Cove for the Remarks: nd mer off and mil 2 en and dianegard the base N. H. FISH COLLECTION BLANK Abundance Specie Remarks R+ notemponey C. R 3. Exce my Traturus v. n * Rana catego

FIGURE 8. Field notes for *Macrobdella* collections at Northwood Lake (aka Suncook Pond), Rockingham Co., New Hampshire on 3 June 1938 by Reeve M. Bailey and James A. Oliver. Courtesy of Fish Division, University of Michigan Museum of Zoology (UMMZ).

(Fig. 8; also see Bailey 1938). Under remarks for the smallmouth bass (*Micropterus dolomieu*), the notes read: "No yearlings taken. One abandoned nest with eggs seen. Several large leeches eating eggs." The only leech specimens known to have been preserved by Bailey and Oliver from North-

wood Lake (aka "Suncook Pond") on 3 June 1938 are USNM 1405211 (n = 3 M. sestertia) and USNM 50162 (n = 1 M. decora) (Phillips et al. 2016). This appears to be the first known case of predation on fish eggs by the genus *Macrobdella* and isn't surprising considering that *Macrobdella* spp. prey on amphibian eggs/embryos and young and that other leeches are known to consume fish eggs (Richardson 1948; Light et al. 2005). The presence of American bullfrog, *Lithobates catesbeianus* (Shaw, 1802), and eastern newt, *Notophthalmus viridescens* (Rafinesque, 1820), in Northwood Lake was included in R.M. Bailey's field notes and by Oliver and [J.R.] Bailey (1939). McCallum et al. (2008) noted a mimetic relationship between *N. viridescens* and *M. diplotertia*, and the same likely applies to *M. decora* and *M. sestertia*, which all have similar coloration.

This study documents the first reported occurrence of *Placobdella nuchalis* being attached to another leech, *M. sestertia*. Other leech associations have been reported for *Placobdella ornata* (as "*Clepsine ornata*, Var. b, *stellata*") on *Macrobdella decora* in Connecticut (Verrill 1874; Moore 1952), for *P. picta* on *M. diplotertia* in Arkansas (Turbeville and Briggler 2003; Connior and Trauth 2010), and for other genera and species of leeches (Sawyer 1986b). The nature of these associations of *Placobdella* spp. with *Macrobdella* spp. is unknown but may be worthy of further investigation.

ACKNOWLEDGMENTS

The author thanks Roy T. Sawyer for sharing his expertise and ideas on taxonomy of the genus *Macrobdella*, for supplying the Blanchard references about anomalous annuli, and for giving help-ful comments about the manuscript. Doug W. Nelson (Fish Division, University of Michigan Museum of Zoology) kindly provided copies of Reeve M. Bailey's field notes from 1938. Museum staff at CAS, ChM, MCZ, and NCSM loaned or cataloged specimens. South Carolina Department of Natural Resources (SCDNR) Stream Team members assisted with collecting, and Holly Gillam (SCDNR) produced the Edgefield County map. Library staff at CAS provided some of the references. Lastly, my appreciation to Douglas Smith for his helpful comments.

References

- BAILEY, R.M. 1938. The fishes of the Merrimack watershed. Pages 149–185 *in* E.E. Hoover, *Biological Survey of the Merrimack Watershed*. Survey Report No. 3. New Hampshire Fish and Game Department, Concord, New Hampshire. 238 pp., 3 maps.
- BLANCHARD, R. 1893. Courtes notices sur les Hirudinées, IX. Variations de la constitution du somite. Bulletin de la Société Zoologique de France 18:30–35.
- BLANCHARD, R. 1894. Hirudinées de l'Italie continentale et insulaire. *Bollettino dei musei di zoologia ed anatomia comparata della R. Università di Torino* 9(no. 192):1–84.
- CARGO, D.G. 1960. Predation of eggs of the spotted salamander, *Ambystoma maculatum*, by the leech, *Macrobdella decora. Chesapeake Science* 1(2):119–120.
- CONNIOR, M.B., AND S.E. TRAUTH. 2010. Seasonal activity of the Ozark Highlands Leech, *Macrobdella diplotertia*, (Annelida: Hirudinea) in North-central Arkansas. *Journal of the Arkansas Academy of Science* 64(art. 16):77–79.
- CORY, L., AND J.J. MANION. 1953. Predation on eggs of the woodfrog, *Rana sylvatica*, by leeches. *Copeia* 1953(1):66.
- DAVIES, R.W. 1991. Annelida: leeches, polychaetes, and acanthobdellids. Pages 437–479 in J.H. Thorp and A.P. Covich, eds., *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, Inc., San Diego, California, USA. xii + 911 pp.
- GOVEDICH, F.R., B.A. BAIN, W.E. MOSER, S.R. GELDER, R.W. DAVIES, AND R.O. BRINKHURST. 2010. Annelida (Clitellata): Oligochaeta, Branchiobdellida, Hirudinida, and Acanthobdellida. Pages 385–436 in J.H. Thorp and A.P. Covich, eds., *Ecology and Classification of North American Freshwater Invertebrates* (3rd ed.). Academic Press / Elsevier, London, UK,, Burlington, Massachusetts and San Diego, California,

USA. i–xiv + 1–1021 pp.

- HAGY, J.W. 1991. Mosquitoes, leeches and medicine in Charleston, South Carolina (1670–1861). *Blood Coagulation & Fibrinolysis* 2(1):65–68.
- HOOVER, E.E. 1938. Stocking policy for the streams and lakes of the Merrimack watershed. Pages 8–117 in E.E. Hoover, *Biological Survey of the Merrimack Watershed*. Survey Report No. 3. New Hampshire Fish and Game Department, Concord, New Hampshire. 238 pp., 3 maps.
- KLEMM, D.J. 1972. Freshwater leeches (Annelida:Hirudinea) of North America. Biota of Freshwater Ecosystems, Identification Manual No. 8. Water Pollution Control Research Series 18050 ELDO5/72. U.S. Environmental Protection Agency, Washington, D.C., USA. viii + 53 + [1] pp.
- KLEMM, D.J. 1982. Leeches (Annelida: Hirudinea) of North America. U.S. Environmental Protection Agency, Environmental Monitoring and Support Laboratory, Cincinnati, Ohio. EPA-600/3-82-025. xvii + 177 pp.
- KLEMM, D.J. 1995. Identification Guide to the Freshwater Leeches (Annelida: Hirudinea) of Florida and other Southern States. Florida Department of Environmental Protection, Tallahassee, Florida, USA. v + 82 pp.
- KLEMM, D.J., D.G. HUGGINS, AND M.J. WETZEL. 1979. Kansas leeches (Annelida: Hirudinea) with notes on distribution and ecology. *Technical Publication, State Biological Survey, Kansas* 8:38–46.
- LIGHT, J.E., A.C. FIUMERA, AND B.A. PORTER. 2005. Egg-feeding in the freshwater piscicolid leech *Cystobranchus virginicus* (Annelida, Hirudinea). *Invertebrate Biology* 124(1):50–56.
- MCCALLUM, M.L., S. BEHARRY, AND S.E. TRAUTH. 2008. A complex mimetic relationship between the Central Newt and Ozark Highlands Leech. *Southeastern Naturalist* 7(1):173–179.
- MEYER, M.C. 1975. A new leech, *Macrobdella diplotertia* sp. n. (Hirudinea: Hirudinidae), from Missouri. *Proceedings of the Helminthological Society of Washington* 42(2):82–85.
- MOORE, J.P. 1922. The freshwater leeches (Hirudinea) of southern Canada. *Canadian Field-naturalist* 36(1): 6–11, (2):37–39.
- MOORE, J.P. 1952. Professor A.E. Verrill's fresh-water leeches a tribute and a critique. *Notulae Naturae* of the Academy of Natural Sciences of Philadelphia 245:1–15.
- MOORE, J.P. 1953. Three undescribed North American leeches (Hirudinea). *Notulae Naturae of the Academy* of Natural Sciences of Philadelphia 250:1–13.
- MOORE, J.P. 1959. Hirudinea (chapter 23). Pages 542–557 in W.T. Edmondson, ed., Fresh Water Biology (2nd ed.). John Wiley & Sons, Inc., New York and London. xxi + 1248 pp.
- MOSER, W.E., R.W. VAN DEVENDER, AND D.J. KLEMM. 2005. Life history and distribution of the leech Oligobdella biannulata (Moore, 1900) (Euhirudinea: Glossiphoniidae). Comparative Parasitology 72(1):17–21.
- MOSER, W.E., D.J. KLEMM, A.J. PHILLIPS, S.E. TRAUTH, R.G. NEAL, J.W. STANLEY, M.B. CONNIOR, AND J.E. FLOTEMERSCH. 2011. Distribution of the genus *Philobdella* (Macrobdellidae: Hirudinida), including new locality records from Arkansas and Oklahoma. *Comparative Parasitology* 78(2):387–391.
- OLIVER, J.A., AND J.R. BAILEY. 1939. Amphibians and reptiles of New Hampshire exclusive of marine forms. Pages 195–217 in H.E. Warfel, *Biological Survey of the Connecticut Watershed. Survey Report No. 4*. New Hampshire Fish and Game Department, Concord, New Hampshire. 256 pp., 3 maps.
- PATRICK, R., J. CAIRNS, JR. AND S.S. ROBACK. 1966 [1967]. An ecosystematic study of the fauna and flora of the Savannah River. *Proceedings of the Academy of Natural Sciences of Philadelphia* 118(5):109–407.
- PHILLIPS, A.J., R. SALAS-MONTIEL, AND A. OCEGUERA-FIGUEROA. 2016. Distribution of the New England Medicinal Leech, *Macrobdella sestertia* Whitman, 1886 and redeterminations of specimens of *Macrobdella* (Annelida: Clitellata: Macrobdellidae) at the National Museum of Natural History, Smithsonian Institution. *Proceedings of the Biological Society of Washington* 129(1):103–113.
- POLY, W.J. 2011. First record of the leech, Macrobdella sestertia (Annelida: Hirudinida), in South Carolina. Pages 142–145 in Statewide Research — Freshwater Fisheries Annual Progress Report (2011, F–63), Division of Wildlife and Freshwater Fisheries, South Carolina Department of Natural Resources. ix + 159 pp.
- RICHARDSON, L.R. 1948. *Piscicola punctata* (Verrill) feeding on the eggs of *Leucosomus corporalis* (Mitchill). *Canadian Field-Naturalist* 62(4):121–222.
- SAWYER, R.T. 1972. North American freshwater leeches, exclusive of the Piscicolidae, with a key to all species. *Illinois Biological Monographs* 46. [5] + 1–154 + [1] pp.

- SAWYER, R.T. 1973. Bloodsucking freshwater leeches: observations on control. *Journal of Economic Entomology* 66(2):537.
- SAWYER, R.T. 1979. Leeches of special concern from South Carolina. Pages 100–102 in D.M. Forsythe and W.B. Ezell, Jr., eds., *Proceedings of the First South Carolina Endangered Species Symposium*. November 11–12, 1976, Charleston, South Carolina. 201 pp.
- SAWYER, R.T. 1986a. Leech Biology and Behaviour. Vol. 1, Anatomy, Physiology, and Behaviour. Clarendon Press, Oxford. i–xiv + 1–417 pp.
- SAWYER, R.T. 1986b. *Leech Biology and Behaviour*. Vol. 2, *Feeding Biology, Ecology, and Systematics*. Clarendon Press, Oxford. i–xiv + 420–793 pp.
- SAWYER, R.T., AND K.A. PASS. 1972. The occurrence of *Macrobdella decora* (Say, 1824) (Annelida: Hirudinea) in the Appalachian Mountains of Georgia and South Carolina. *Journal of the Elisha Mitchell Scientific Society* 88(1):34–35.
- SAWYER, R.T., AND R.M. SHELLEY. 1976. New records and species of leeches (Annelida: Hirudinea) from North and South Carolina. *Journal of Natural History* 10(1):65–97.
- SAY, T. 1824. Appendix. Part I.— Natural History. 1. Zoology. Pages 253–378 + pls. 14–15 in W.H. Keating, Narrative of an Expedition to the Source of St. Peter's River, Lake Winnepeek, Lake of the Woods, &c., &c. Performed in the Year 1823, by Order of the Hon. J. C. Calhoun, Secretary of War, under the Command of Stephen H. Long, Major U. S. T. E. Compiled from the Notes of Major Long, Messrs. Say, Keating, and Colhoun. Volume II. H.C. Carey & I. Lea, Philadelphia, Pennsylvania. i–vi + 5–459 pp., + pls. 6–15.
- SCHALK, G., M.R. FORBES, AND P.J. WEATHERHEAD. 2002. Developmental plasticity and growth rates of green frog (*Rana clamitans*) embryos and tadpoles in relation to a leech (*Macrobdella decora*) predator. *Copeia* 2002(2):445–449.
- SHELLEY, R.M., AND A.L. BRASWELL. 1981. Host record for the leech *Placobdella nuchalis* Sawyer and Shelley (Rhynchobdella: Glossiphoniidae). *Journal of Parasitology* 67(5):748.
- SMITH, D.B. 1843. Hirudo. Pages 369–372 in G.B. Wood and F. Bache, *The Dispensatory of the United States of America*, 5th Edition. Grigg & Elliot, Philadelphia, Pennsylvania, USA. i–x + 1–1368 pp.
- SMITH, D.B. 1845. Hirudo. Pages 369–372 in G.B. Wood and F. Bache, *The Dispensatory of the United States of America*, 6th Edition. Grigg and Elliot, Philadelphia, Pennsylvania, USA. x + [2] + 1368 pp.
- SMITH, D.G. 1977. The rediscovery of Macrobdella sestertia Whitman (Hirudinea: Hirudinidae). Journal of Parasitology 63(4):759–760.
- SMITH, D.G., AND S. HANLON. 1997. Macrobdella sestertia (Hirudinea: Hirudinidae) in Maine and a key to the hirudiniform leeches of Maine. Northeastern Naturalist 4(4):231–236.
- STEWART, M.M., AND G.R. SMITH. 2000. Historical perspective: Reeve Maclaren Bailey. Copeia 2000(4): 1118–1124.
- TRAUTH, S.E., AND R.G. NEAL. 2004. Geographic range expansion and feeding response by the leech Macrobdella diplotertia (Annelida: Hirudinea) to wood frog and spotted salamander egg masses. Journal of the Arkansas Academy of Science 58:139–141.
- TURBEVILLE, J.M., AND J.T. BRIGGLER. 2003. The occurrence of *Macrobdella diplotertia* (Annelida: Hirudinea) in the Ozark Highlands of Arkansas and preliminary observations on its feeding habits. *Journal of Freshwater Ecology* 18(1):155–159.
- VERRILL, A.E. 1874. Synopsis of the North American fresh-water leeches. Pages 666–689 in *Report of the Commissioner of Freshwater Fisheries for 1872–73, Part 2*. Government Printing Office, Washington, DC, USA. [637]–709 pp. + 3 plates.
- WARFEL, H.E. AND J.L. FULLER. 1938. Notes on the lakes of the Merrimack watershed. Pages 118–135 in E.E. Hoover, *Biological survey of the Merrimack Watershed. Survey Report No. 3*. New Hampshire Fish and Game Department, Concord, New Hampshire, USA. 238 pp., 3 maps.
- WARING, J.I. 1964. *A History of Medicine in South Carolina, 1670–1825*. The South Carolina Medical Association. Printed by The R.L. Bryan Co., Columbia, South Carolina, USA. i–xviii + 1–407 pp.
- WEEKS, J.C. 1982. Segmental specialization of a leech swim-initiating interneuron, cell 205. The Journal of Neuroscience 2(7):972–985.
- WHITMAN, C.O. 1886. The leeches of Japan. Part I. The ten-eyed leeches, or the Hirudinidae. *Quarterly Journal of Microscopical Science* (New Series, No. 103) 26(part 3):317–416, pls. 17–21.

359

APPENDIX 1. MATERIAL EXAMINED

Macrobdella decora

MASSACHUSETTS: MCZ 56596 (formerly in University of Massachusetts, Amherst collection as UMA AN.404), n = 2, Rutland Brook, Barre, Worcester Co., 8 August 1988, A. Richmond, S. Jackson; **MAINE**: MCZ 84111, n = 2, Proctor Pond, Albany, Crooked/Presumpscot river system, Oxford Co., 44°14′36″N, 70°47′56″W, 15 July 1992, EMAP Program, U.S. EPA; **SOUTH CAROLINA:** Upper Lake Jemiki [also spelled Jemike] (Notes: the lower [downstream] and smaller of the two ponds is where swimmers were attacked by leeches according to the current landowner, Donald Payne and his two sons. Years ago, the lakes were drained and dried, which apparently eradicated the leech population [in conversation with W.J. Poly, 2011]), approx. 6 km WNW of Walhalla at end of Lake Jemiki Road (WA-3), Oconee Co. (no voucher specimens; Sawyer and Pass [1972]).

Macrobdella ditetra

SOUTH CAROLINA: MCZ 53008, n = 1, Coosawhatchie River, US 321, Hampton-Allendale Co. line, 29 December 1982, F. Rohde; MCZ 53009, n = 2, Ashepoo River, US 17, Colleton Co., 30 December 1982, F. Rohde; CASIZ 224103, n = 1, Willow Creek, approx. 11 km SE of Florence, downstream of Flowers Road (SSR 726), Florence Co., 34.11604°N / -79.67809°W, 10 August 2011, W.J. Poly, K.M. Kubach, M.T. Cribb, A.R. Gelder, J. Johnston, S. Mycko.

Macrobdella sestertia

MASSACHUSETTS: Essex Co.: MCZ 56398 (formerly UMA AN.207), n = 2, Lake Chebacco, along shore at public beach, Hamilton, 25 June 1976 (cited in Smith, 1977); Barnstable Co.: MCZ 56412 (formerly in UMA), n = 1, Herring River, 0.5 mi. S US 6, North Harwich Village, 21 May 1977 (cited in Smith and Hanlon, 1997); MAINE: MCZ 56624 (formerly UMA AN.431), n = 1, Mill Brook Pond, Sebec Lake, at end of logging road, Pisquataquis Co., 12 July 1993, EMAP personnel (cited in Smith and Hanlon, 1997); SOUTH CAR-**OLINA:** ChM IO6 / NCSM 28341, n = 1, Turkey Creek, approx. 10 km NNW of Edgefield, at US Route 25 crossing [Station 61-PSC-84], Edgefield Co., 33.89012°N / -82.02378°W, 13 April 1984, P.S. Coleman & J.F. McKinney; NCSM 29791, n = 1, Turkey Creek, ca. 12.6 air mi. [20.3 km] W of Edgefield, ca. 200 m below Key Road (SSR 68 / SSR 227), Edgefield / McCormick co. line, 33.79473°N / -82.14547°W, 15 May 2002, W.C. Starnes et al; no voucher (escaped after capture), n = 1, Turkey Creek, approx. 10 km NNW of Edgefield, upstream of Elmwood Road (SSR 100), Edgefield Co., 33.88178°N / -81.96879°W, 29 July 2008, W.J. Poly, K.M. Kubach, C.A. Marion, M.T. Cribb, A.R. Gelder, A. Sayer, G. Satterfield, C. Guinn; CASIZ 224100, n = 3, Little Stevens Creek, approx. 13 km N of Edgefield, Edgefield Co., 33.90094°N / -81.96870°W, 29 July 2008, W.J. Poly, K.M. Kubach, C.A. Marion, M.T. Cribb, A.R. Gelder, A. Sayer, G. Satterfield, C. Guinn; ChM IO7 / NCSM 28342, n = 1, Sleepy Creek, upstream of Sleepy Creek Road (SSR 62) and downstream of US Route 378, Edgefield Co., 33.92844°N / -81.97770°W, 29 July 2008, W.J. Poly, K.M. Kubach, C.A. Marion, M.T. Cribb, A.R. Gelder, A. Sayer, G. Satterfield, C. Guinn; CASIZ 224101, n = 4, Sleepy Creek, upstream of Sleepy Creek Road (SSR 62) and downstream of US Route 378, Edgefield Co., 33.92844°N / -81.97770°W, 31 July 2008, W.J. Poly.

Placobdella nuchalis

SOUTH CAROLINA: CASIZ 224102, n = 9, Sleepy Creek, upstream of Sleepy Creek Road (SSR 62) and downstream of US Route 378, Edgefield Co., 33.92844°N / -81.97770°W, 31 July 2008, W.J. Poly [attached to *M. sestertia*].