Zootaxa 3947 (4): 508–526
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3947.4.3
http://zoobank.org/urn:lsid:zoobank.org:pub:2EA27694-0D0E-40D5-A0F1-EC053A622594

Microdrile Oligochaeta in bromeliad pools of a Honduran cloud forest

RÜDIGER M. SCHMELZ[1,2], MERLIJN JOCQUE[3, 4, 5] & RUT COLLADO[2]

[1]*ECT Oekotoxikologie GmbH, Böttgerstr. 2–14, 65439 Flörsheim. E-mail: r.schmelz@ect.de*
[2]*Universidade da Coruña, Fac. Ciencias, Dep. de Bioloxía Animal, Biol. Vexetal y Ecoloxía, Alejandro da Sota, 10; E-15008 A Coruña, Spain*
[3]*Jessica Ware Lab, Rutgers, The State University of New Jersey, 195 University Avenue, Newark, NJ 07102, USA*
[4]*Koninklijk Belgisch Instituut voor Natuurwetenschappen (KBIN), Vautierstraat 29; 1000 Brussels, Belgium*
[5]*Operation Wallacea, Hope House, Old Bolingbroke, Lincolnshire, UK*

Abstract

Phytotelmata, or plant-held water bodies, often house complex aquatic invertebrate communities. Microdrile oligochaetes (Clitellata, Annelida) are known to be part of that community, but specimens are rarely identified to species level. Here we report three species of Enchytraeidae and three species of Naididae from a collection sampled in phytotelms of bromeliads in Cusuco National Park, Honduras. Two species of enchytraeids are new to science. *Bryodrilus hondurensis* **sp. nov.** is distinguished from other members of the genus by the high number of ventral chaetae, up to 11 per bundle. The genus is Holarctic and this is the southernmost record so far of a *Bryodrilus* species. *Hemienchytraeus phytotelmatus* **sp. nov.** is distinguished by a combination of characters, among which the huge spermathecae and seminal vesicles are most conspicuous. The genus is common in tropical and subtropical soils around the world. A third species of enchytraeids in the collection, *Cernosvitoviella atrata* (Bretscher), is redescribed, together with three known species of Naididae, *Pristina jenkinae* (Stephenson), *Pristina osborni* (Walton) and *Pristina terrena* Collado & Schmelz. Presence of ingested debris and humus in the intestine of most specimens suggests that the collected animals live and reproduce in the phytotelms. We provide a list of oligochaete species recorded so far from bromeliad pools in Central and South America.

Key words: Clitellata, Enchytraeidae, Naididae, phytotelmata, Cusuco National Park, new species

Introduction

In the Neotropics, numerous species of bromeliads are able to hold water in their central tube- or funnel-shaped tanks of tightly overlapping leaves and their lateral leaf axils. These compartments, named phytotelmata (Varga 1928), are plant delineated water bodies, typically filled with water and decaying plant matter. They are developed also in other plant taxa, in Asia for example mostly in the carnivorous pitcher plants (*Nepenthes* spp.). Phytotelmata frequently house complex aquatic animal communities, ranging from protozoans to vertebrates (Picado 1913; Frank & Lounibos 1983; Frank *et al*. 2004). These small aquatic habitats have been studied for their specialised fauna and as a brooding site for mosquitoes as vectors of human pathogens. Recently they have received renewed interest due to their potential as model systems to address ecological questions in small but natural ecosystems (Srivastava *et al.* 2004). There are several overviews of the insect fauna in these habitats (e.g. Frank & Lounibos 1983); a more comprehensive overview of inhabitants in pitcher plants was published by Adlassnig *et al.* (2011).

Less information is available on the non-insect fauna in phytotelmata, but see the overview of Crustacea in phytotelmata (Jocque *et al.* 2013). Oligochaetes are often recorded from these habitats (Picado 1913; Laessle 1961; Paoletti *et al.* 1991; Richardson *et al.* 2000; Carrias *et al*. 2001; Ospina-Bautista *et al.* 2004; Jocque *et al.* 2010), but after the seminal monograph of Picado (1913), they were rarely identified to species level. Both megadrile and microdrile oligochaetes have been found. Four earthworm species belonging to two families were recorded in Picado (1913) from bromeliads in Costa Rica, all identified or described by W. Michaelsen (1912). From 1995 on, a more directed search for earthworms in bromeliad tanks revealed the presence of more species (Righi 1995;

 Accepted by B. Sket: 26 Mar. 2015; published: 17 Apr. 2015

accidental finds of epiphytic or terrestrial oligochaetes living in the surrounding litter, moss or bark of the trees, and trapped in the phytotelms. A truly terrestrial enchytraeid, once submerged in water, empties the gut within one or two days and does not ingest new material (Schmelz & Collado 2010). The preserved and whole-mounted Honduras specimens have humus and plant debris often in the anterior regions of the gut (from segment XIV on), which means that the material has been ingested only a short time (less than an hour) before fixation (Schmelz, unpublished observations).

Furthermore, species of *Pristina* and *Cernosvitoviella* are considered to be aquatic oligochaetes, and two species (*P. jenkinae*, *P. osborni*) have been found in bromeliad pools previously, *P. jenkinae* together with the specialist *Aulophorus superterrenus* (Marcus 1943). It might however be that these species live in a thin water film covering the vegetation. A large number of aquatic microcrustaceans in the same location are found thriving in a thin water film on the leaf litter and on vegetation and are occasionally washed in bromeliads (Jocque *et al.* 2013). Although nothing at all is known about enchytraeids in Honduras, extrapolations from other tropical sites suggest that the permanently moist litter and organic soil of these montane cloud forest harbours a species-rich and abundant community of enchytraeids, with *Hemienchytraeus* as one of the dominant genera (Schmelz *et al.* 2013).

The affinity of oligochaetes to bromeliad pools differs greatly among species, and the same species may behave differently in different habitats. At one end of the scale are species that are only sporadically found in the pools and whose natural habitat is elsewhere, litter, soil, decaying wood, freshwater sediment, or soils; an example for the latter is *Dichogaster bolaui* (Michaelsen, 1891) (James & Brown 2006). At the other end of the scale are the true specialists that are mainly found in the pools and which may show adaptations for dispersal among bromeliads. Up to now the only bromeliad specialist among microdrile oligochaetes is the naidid *Aulophorus superterrenus* Michaelsen, 1912 (=*Dero superterrena*), found frequently, almost exclusively and often in high abundance in epiphytic and terrestrial bromeliads in Central and South America (Picado 1913; Marcus 1943; Righi 1984; Christoffersen 2007). Only one record so far is outside this peculiar habitat (Di Persia 1980: fluvial littoral, Argentina). These worms have the special adaptation of actively using frogs as dispersal agents by attaching to their moist skin (Lopez *et al*. 1999, 2005). Marcus (1943) gives a detailed account of the species' anatomy and reproduction.

Among earthworms, many species of *Eutrigaster* are described as specialists from bromeliad pools, however these species are often found in litter or soil as well. Interestingly, the degree of affinity of *Eutrigaster* species to phytotelms is dependant on the geographical region and the habitat: In tropical forests of Central America these species are predominantly found in bromeliad pools, but in pine-oak forests of Costa Rica > 1000 m asl, most of the species are found in the litter (Fragoso *et al.* 1995). Fragoso and Rojas-Fernández (1996) present a series of interesting ecological, historical and phylogenetic hypotheses to explain this peculiar distribution pattern.

Some of the microdile oligochaetes found in the Honduras bromeliad pools seem to have a large geographic distribution. Among the three species of *Pristina* identified here, two (*P. jenkinae*, *P. osborni*) are cosmopolitan. *P. jenkinae* has been recorded from terrestrial habitats in moist forest soils of the Brazilian Amazon (Collado & Schmelz 2000, 2001; Augustsson 2001) and the Mata Atlântica (Römbke *et al.* 2005), where it can be abundant. It seems to be a common inhabitant of moist tropical and subtropical forest soils. The same may apply to *P. terrena*, originally described from tropical forest soil.

Acknowledgments

Thanks to Samuel James and Csaba Csuzdi for help with literature on earthworms described or recorded from bromeliad pools. Tarmo Timm and one anonymous referee made useful suggestions to improve the manuscript. Barbara Richardson kindly forwarded the letter of the late Brenda Healy with details on enchytraeid identification. Thanks also to Willem Stock for assistance with sampling in the field.

References

Adis, J. & Righi, G. (1989) Mass migration and life cycle adaptation - a survival strategy of terrestrial earthworms in Central Amazonian inundation forests. *Amazoniana,* 11, 23–30.

Adlassnig, W., Peroutka, M. & Lendi, T. (2011) Traps of carnivorous pitcher plants as a habitat: composition of the fluid,

biodiversity and mutualistic activities. *Annals of Botany*, 107, 181–194.
http://dx.doi.org/10.1093/aob/mcq238
Augustsson, A. (2001) *On enchytraeids and naidids: Life-history traits and responses to environmental stress.* Doctoral thesis, Department of Animal Ecology, Lund University, Lund, 135 pp. [Sweden, ISBN 97-7105-151-1]
Bell, A.W. (1954) Some enchytraeid worms (Oligochaeta) from East Africa. *Transactions of the American Microscopical Society,* 73, 279–311.
http://dx.doi.org/10.2307/3224072
Bell, A.W. (1962) Enchytraeids (Oligochaeta) from various parts of the world. *Transactions of the American Microscopical Society,* 81, 158–178.
http://dx.doi.org/10.2307/3223675
Botea, F. (1983) Oligochètes souterraines de Cuba. *Résultats des expéditions biospéologiques cubano-roumaines à Cuba,* 4, 19–38.
Bretscher, K. (1903) Beobachtungen über die Oligochaeten der Schweiz, VII. Folge. *Revue Suisse de Zoologie,* 11, 1–21.
Brinkhurst, R.O. (1971) Naididae. *In:* Brinkhurst, R.O. & Jamieson, B.G. (Eds.), *Aquatic Oligochaeta of the World*. Oliver & Boyd, Edinburg, pp. 304–443.
Brinkhurst, R.O. (1985) The generic and subfamilial classification of the Naididae (Annelida: Oligochaeta). *Proceedings of the Biological Society of Washington,* 98, 470–475.
Carrias, J.F., Cussac, M.E. & Corbara, B. (2001) A preliminary study of freshwater protozoa in tank bromeliads. *Journal of Tropical Ecology,* 17, 611–617.
http://dx.doi.org/10.1017/S0266467401001456
Cech, G., Boros, G. & Dózsa-Farkas, K. (2012) Revision of *Bryodrilus glandulosus* (Dózsa-Farkas, 1990) and *Mesenchytraeus kuehnelti* Dózsa-Farkas, 1991 (Oligochaeta: Enchytraeidae) using morphological and molecular data. *Zoologischer Anzeiger,* 251, 253–262.
http://dx.doi.org/10.1016/j.jcz.2011.09.005
Céréghino, R., Leroy, C., Carrias, J.-F., Pelozuelo, L., Segura, C., Bosc, C., Dejean, A., Corbara, B. (2011) Ant-plant mutualisms promote functional diversity in phytotelm communities. *Functional Ecology,* 25, 954–963.
http://dx.doi.org/10.1111/j.1365-2435.2011.01863.x
Černosvitov, L. (1928) Die Oligochaetenfauna der Karpathen. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere. Jena,* 55, 1–28.
Černosvitov, L. (1934) Zur Kenntnis der Enchytraeiden. II. *Zoologischer Anzeiger,* 105, 295–305.
Černosvitov, L. (1938) Mission scientifique de l'Omo. Oligochaeta. *Mémoires du Muséum National d'Histoire Naturelle*, 4, 255–318.
Chalupský, J. (1992) Terrestrial Enchytraeidae (Oligochaeta) and Parergodrilidae (Polychaeta) from Sweden, with description of a new enchytraeid species. *Zoologica Scripta,* 21, 133–150.
http://dx.doi.org/10.1111/j.1463-6409.1992.tb00316.x
Chen, J. & Xie, Z.C. (2006) *Bryodrilus fuscistriatus*, a new enchytraeid species (Oligochaeta: Enchytraeidae) from northeastern China. *Proceedings of the Biological Society of Washington,* 119, 195–201.
http://dx.doi.org/10.2988/0006-324X(2006)119[195:BFANES]2.0.CO;2
Christensen, B. & Dózsa-Farkas, K. (1999) The enchytraeid fauna of the Palearctic tundra (Oligochaeta, Enchytraeidae). *The Royal Danish Academy of Sciences and Letters, Biologiske Skrifter,* 52, 1–37.
Christoffersen, M.L. (2007) A catalogue of aquatic microdrile oligochaetes (Annelida: Clitellata) from South America. *Acta Hydrobiologica Sinica,* 31 (Supplement), 59–86.
Cognetti de Martiis, L. (1927) Lumbricidi dei Carpazi. *Bollettino dei Musei di Zoologia e Anatomia comparata della Reale Università di Genova*, 7, 1–8.
Collado, R. & Schmelz, R.M. (2000) *Pristina silvicola* and *Pristina terrena* spp. nov., two new soil-dwelling species of Naididae (Oligochaeta, Annelida) from the tropical rain forest near Manaus, Brazil, with comments on the genus *Pristinella*. *The Journal of Zoology, London,* 251, 509–516.
http://dx.doi.org/10.1111/j.1469-7998.2000.tb00806.x
Collado, R. & Schmelz, R.M. (2001) Descriptions of three *Pristina* species (Naididae, Clitellata) from Amazonian forest soils, including *P. marcusi* sp. nov. *Hydrobiologia,* 463, 1–11.
http://dx.doi.org/10.1023/A:1013103100981
Collado, R. & Schmelz, R.M. (2002) *Pristina trifida* sp. nov., a new soil-dwelling microannelid (Oligochaeta: Naididae) from Amazonian forest soils, with comments on species recognition in the genus. *Zootaxa,* 118, 1–14.
Csuzdi, C. (2012) Earthworm species, a searchable database. *Opuscula Zoologica, Budapest,* 43, 97–99.
Csuzdi, C. (2014) Replacement names for *Eutrigaster* (*Graffia*) Csuzdi & Zicsi, 1991 and *Dichogaster* (*Malawia*) Csuzdi, 2010 (Oligochaeta, Acanthodrilidae). *Zootaxa,* 3811, 149–150.
http://dx.doi.org/10.11646/zootaxa.3811.1.11
Csuzdi, C. & Pavlicek, T. (2009) New records of earthworms from Guadeloupe with description of a new species (Oligochaeta: Glossoscolecidae, Acanthodrilidae, Megascolecidae and Eudrilidae). *Opuscula Zoologica Budapest,* 40, 9–15.
Di Persia, D.H. (1980) The aquatic Oligochaeta of Argentina: current status of knowledge. *In:* Brinkhurst, R.O. & Cook, D.G. (Eds.), *Aquatic Oligochaete Biology*. Plenum Press, New York, pp. 79–113.

Dózsa-Farkas, K. (1989) Neue Enchytraeiden-Arten (Oligochaeta) aus Ekuador. *Acta Zoologica Hungarica,* 35, 191–203.
Dózsa-Farkas, K., Porco, D. & Boros, G. (2012) Are *Bryodrilus parvus* Nurminen, 1970 and *Bryodrilus librus* (Nielsen and Christensen, 1959) (Annelida: Enchytraeidae) really different species? A revision based on DNA barcodes and morphological data. *Zootaxa,* 3276, 38–50.
Ehrenberg, G.C. (1828) *Symbolae physicae seu icones et descriptiones animalium evertebratorum. Animalia evertebrata. Phytozoa*. Berlin, 293 pp.
Erséus, C. & Grimm, R. (1998) *Pristina proboscidea* and *Pristinella osborni* (Oligochaeta, Naididae) from a freshwater creek near Darwin, Northern Territory, Australia, with descriptions of the genital organs of both species. *The Beagle, records of the museums and art galleries of the Northern Territory,* 14, 149–158.
Feijoo, M.A. & Celis, L.V. (2012) New species of earthworms (Oligochaeta: Glossoscolecidae) in the Amazon region of Colombia. *Zootaxa*, 103–119.
Fragoso, C. & Rojas-Fernández, P. (1996) Earthworms inhabiting bromeliads in Mexican tropical rainforests: ecological and historical determinants. *Journal of Tropical Ecology*, 12, 729–734.
http://dx.doi.org/10.1017/S0266467400009925
Fragoso, C., James, S.W. & Borges, S. (1995) Native earthworms of the north Neotropical region: current status and controversies. *In:* Hendrix, P.F. (Ed.), *Earthworm ecology and biogeography in North America*. Lewis, CRC Press, Boca Raton, FL, pp. 67–115.
Frank, H. & Lounibos, L.P. (Eds.) (1983) *Phytotelmata: Terrestrial hosts for aquatic insect communities*. Plexus Publishing, Medford, NJ, 293 pp.
Frank, J.H., Sreenivasan, S., Benshoff, P.J., Deyrup, M.A., Edwards, G.B., Halbert, S.E., Hamon, A.B., Lowman, M.D., Mockford, E.L., Scheffrahn, R.H., Steck, G.J., Thomas, M.C., Walker, T.J. & Welbourn, W.C. (2004) Invertebrate animals extracted from native *Tillandsia* (Bromeliales : Bromeliaceae) in Sarasota County, Florida. *Florida entomologist*, 87, 176–185.
http://dx.doi.org/10.1653/0015-4040(2004)087[0176:IAEFNT]2.0.CO;2
Harman, W.J. (1982) The aquatic Oligochaeta (Aeolosomatidea, Opistocystidae, Naididae) of Central America. *The Southwestern Naturalist,* 27, 287–298.
http://dx.doi.org/10.2307/3670877
Harman, W.J., Brinkhurst, R.O. & Marchese, M. (1988) A contribution to the taxonomy of the aquatic Oligochaeta (Naididae) of South America. *Canadian Journal of Zoology*, 66, 2233–2242.
http://dx.doi.org/10.1139/z88-331
Healy, B. (1996) Records of Enchytraeidae (Annelida: Oligochaeta) from west Florida, 1. *Mesenchytraeus*, *Cognettia*, *Bryodrilus*, *Hemienchytraeus*, *Henlea* and *Buchholzia*. *Proceedings of the Biological Society of Washington,* 109, 118–137.
James, S.W. (1996) Nine new species of *Dichogaster* (Oligochaeta, Megascolecidae) from Guadeloupe (French West Indies). *Zoologica Scripta,* 25, 21–34.
http://dx.doi.org/10.1111/j.1463-6409.1996.tb00149.x
James, S.W. (2004) Earthworms (Clitellata, Acanthodrilidae) of the mountains of Eastern Jamaica. *Organisms, Diversity & Evolution,* 4, 277–294.
http://dx.doi.org/10.1016/j.ode.2004.04.003
James, S.W. & Brown, G.G. (2006) Earthworm ecology and diversity in Brazil. *In:* Moreira, F.M.S., Siqueira, J.O. & Brussaard, L. (Eds.), *Soil biodiversity in Amazonian and other Brazilian ecosystems*. CABI Publishing, Cambridge, MA, pp. 56–116.
http://dx.doi.org/10.1079/9781845930325.0056
Jocque, M., Kernaham, A., Nobes, A., Williams, C. & Field, R. (2010) How effective are non-destructive sampling methods to assess aquatic invertebrate diversity in bromeliads? *Hydrobiologia,* 649, 293–300.
Jocque, M., Fiers, F., Romero, M. & Martens, K. (2013) Crustacea in phytotelmata: a global overview. *Journal of Crustacean Biology*, 33, 451–460.
http://dx.doi.org/10.1163/1937240X-00002161
Kathman, R.D. (1985) Synonymy of *Pristinella jenkinae* (Oligochaeta: Naididae). *Proceedings of the Biological Society of Washington*, 98, 1022–1027.
Laessle, A.M. (1961) A micro-limnological study of Jamaican bromeliads. *Ecology*, 42, 499–517.
http://dx.doi.org/10.2307/1932236
Lastočkin, D.A. (1924) New and rare Copepoda and Oligochaeta form Central Russia. *Bulletin de l'Institut d'Hydrobiologie de Russe, Leningrad,* 9, 5–6.
Lopez, L.C.S., Filizola, B., Deiss, I. & Rios, R.I. (2005) Phoretic behaviour of bromeliad annelids (*Dero*) and ostracods using frogs and lizards as dispersal vectors. *Hydrobiologia,* 549, 15–22.
http://dx.doi.org/10.1007/s10750-005-1701-4
Lopez, L.C.S., Rodrigues, P.J.F.P. & Rios, R.I. (1999) Frogs and snakes as phoretic dispersal agents of bromeliad ostracods (Limnocytheridae: *Elpidium*) and annelids (Naididae: *Dero*). *Biotropica,* 31, 705–708.
http://dx.doi.org/10.1111/j.1744-7429.1999.tb00421.x
Marcus, E. (1943) Sôbre Naididae do Brasil. *Boletins da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo,* 7, 3–247.

Michaelsen, W. (1912) Über einige zentralamerikanische Oligochäten. *Archiv für Naturgeschichte*, 78A, 112–129.
Nielsen, C.O. & Christensen, B. (1959) The Enchytraeidae. Critical revision and taxonomy of European species (Studies on Enchytraeidae VII). *Natura Jutlandica*, 8–9, 1–160.
Nurminen, M. (1970) Records of Enchytraeidae (Oligochaeta) from the west coast of Greenland. *Annales Zoologici Fennici,* 7, 199–209.
Ospina-Bautista, F., Estévez-Varón, J.V., Betancur, J. & Realpe-Rebolledo, E. (2004) Estructura y composición de la comunidad de macro invertebrados acuáticos asociados a *Tillandsia turneri* Baker (Bromeliaceae) en un bosque alto andino colombiano. *Acta Zoologica Mexicana nueva serie,* 20, 153–166.
Paoletti, M.G., Taylor, R.A.J., Stinner, B.R., Stinner, D.H. & Benzing, D.H. (1991) Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. *Journal of Tropical Ecology,* 7, 373–383.
http://dx.doi.org/10.1017/S0266467400005654
Picado, C. (1913) Les broméliacées épiphytes considerées comme milieu biologique. *Bulletin Scientifique de la France et de la Belgique,* 47, 215–360.
Piguet, E. (1906) *Observations sur les Naididées et revision systématique de quelques espèces de cette famille*. Imprimerie W. Kündig & Fils, Genève, 316 pp. + pls. IX–XI.
Piper, S.R., MacLean, S.F. & Christensen, B. (1982) Enchytraeidae (Oligochaeta) from taiga and tundra habitats of northeastern U.S.S.R. *Canadian Journal of Zoology,* 60, 2594–2609.
http://dx.doi.org/10.1139/z82-334
Richardson, B. (1999) The bromeliad microcosm and the assessment of faunal diversity in a neotropical forest. *Biotropica*, 31, 321–336.
http://dx.doi.org/10.1111/j.1744-7429.1999.tb00144.x
Richardson, B., Rogers, C. & Richardson, M.J. (2000) Nutrients, diversity, and community structure of two phytotelm systems in a lower montane forest, Puerto Rico. *Ecological Entomology,* 25, 348–356.
http://dx.doi.org/10.1046/j.1365-2311.2000.00255.x
Richardson, B.A., Borges, S. & Richardson, M.J. (2006) Differences between epigeic earthworm populations in tank bromeliads from Puerto Rico. *Caribbean Journal of Science,* 42, 380–385.
Righi, G. (1973a) Sobre trés espécies Brasileiras de Enchytraeidae (Oligochaeta). *Boletim de Zoologia e Biologia Marina, São Paulo,* 30, 469–482.
Righi, G. (1973b) On *Pristina minuta* (Oligochaeta, Naididae) from Brazilian Soil and its epizoic *Rhabdostyla pristinis*, sp. n. (Ciliata, Epistylidae). *Zoologischer Anzeiger,* 191, 295–299.
Righi, G. (1984) *Oligochaeta*. *In*: Schaden, R. (Ed.), *Manual de Identificação de Invertebrados Límnicos do Brasil*, 17, pp. 1–48. [CNPq, Conselho Nacional de Desenvolvimiento Científico e Tecnológico, Brasilia]
Righi, G. (1988) Dois novos Microdrili, Oligochaeta, terrestres da Amazônia. *Papéis Avulsos de Zoologia. Museu de Zoologia da Universidade de São Paulo*, 36, 315–321.
Righi, G. (1995) Colombian earthworms. *In:* Van der Hammen, T. & Dos Santos, A.G. (Eds.), *Studies on Tropical Andean Ecosystems / Estudios de Ecosistemas Tropandinos. Vol. 4*. Cramer, Berlin, pp. 485–607.
Righi, G., Ayres, I. & Bittencourt, E. (1976) Glossoscolecidae (Oligochaeta) do Instituto Nacional de Pesquisas da Amazônia. *Acta Amazonica*, 6, 335–367.
Righi, G. & Hamoui, V. (2002) Oligochaeta, Naididae of the West Indies and adjacent regions. *Papéis Avulsos de Zoologia. Museu de Zoologia da Universidade de São Paulo*, 42, 119–167.
Römbke, J., Collado, R. & Schmelz, R.M. (2005) Oligochaetes (Clitellata) of the Mata Atlântica (Parana, Brazil): first results of the SOLOBIOMA project. *Proceedings of the Estonian Academy of Sciences: Biology, Ecology,* 54, 302–309.
Rota, E. (2013) How many lookalikes has *Marionina argentea* (Michaelsen, 1889) (Annelida: Clitellata: Enchytraeidae)? Three new species described from morphological evidence. *Zoologischer Anzeiger,* 252, 123–137.
http://dx.doi.org/10.1016/j.jcz.2012.05.001
Rota, E. & Healy, B. (1999) A taxonomic study of some Swedish Enchytraeidae (Oligochaeta), with descriptions of four new species and notes on the genus *Fridericia*. *Journal of Natural History*, 33, 29–64.
http://dx.doi.org/10.1080/002229399300461
Schenkova, J. & Čermak, V. (2013) Description of *Pristina armata* n. sp (Clitellata: Naididae: Pristininae) from a carnivorous plant (*Nepenthes* sp.) in Borneo, Indonesia. *Zootaxa*, 3686 (5), 587–592.
http://dx.doi.org/10.11646/zootaxa.3686.5.7
Schmelz, R.M. (2003) Taxonomy of *Fridericia* (Oligochaeta, Enchytraeidae). Revision of species with morphological and biochemical methods. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (Neue Folge),* 38, 1–415, figs. 1–73.
Schmelz, R.M. & Collado, R. (2012) An updated checklist of currently accepted species of Enchytraeidae (Oligochaeta). *vTI Agriculture and Forestry Research, Special Issue,* 357, 67–87.
Schmelz, R.M. & Collado, R. (2007) Revision of *Hemienchytraeus stephensoni* (Cognetti, 1927) (Enchytraeidae, Oligochaeta, Annelida). *Folia Facultatis scientiarum naturalium Universitatis Masarykianae Brunensis, Biologia,* 110, 67–85.
Schmelz, R.M. & Collado, R. (2010) A guide to European terrestrial and freshwater species of Enchytraeidae (Oligochaeta). *Soil Organisms*, 82, 1–176.
Schmelz, R.M., Niva, C.C., Römbke, J. & Collado, R. (2013) Diversity of terrestrial Enchytraeidae (Oligochaeta) in Latin

America: Current knowledge and future research potential. *Applied Soil Ecology,* 69, 13–20. http://dx.doi.org/10.1016/j.apsoil.2012.12.012
Schmelz, R.M. & Römbke, J. (2005) Three new species of *Hemienchytraeus* (Enchytraeidae, Oligochaeta) from Amazonian forest soil. *Journal of Natural History,* 39, 2967–2986. http://dx.doi.org/10.1080/00222930500218664
Sherlock, E. & Csuzdi, C. (2013) Two new earthworm species from Belize (Oligochaeta: Acanthodrilidae). *Journal of Natural History,* 47, 1911–1919. http://dx.doi.org/10.1080/00222933.2013.770931
Sherlock, E., Lee, S., McPhee, S., Steer, M., Maes, J.M. & Csuzdi, C. (2011) The first earthworm collections from Nicaragua with description of two new species (Oligochaeta). *Zootaxa*, 2732, 49–58.
Sperber, C. (1948) A taxonomic study of the Naididae. *Zoologiska Bidrag från Uppsala,* 28, 1–296.
Srivastava, D.S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S.P., Miller, T.E., Munguia, P., Romanuk, T., Schneider, D.C. & Trzcinski, M.K. (2004) Are natural microcosms useful model systems for ecology? *Trends in Ecology & Evolution*, 19, 379–384.
Standen, V. (1988) Oligochaetes in fire climax grassland and conifer plantations in Papua New Guinea. *Journal of Tropical Ecology,* 5, 39–48. http://dx.doi.org/10.1017/S0266467400002480
Stephenson, J. (1914) On a collection of Oligochaeta mainly from Northern India. *Records of the Indian Museum of Calcutta,* 10, 321–366.
Stephenson, J. (1924) Oligochaeta of the Siju Cave, Garo Hills, Assam. *Records of the Indian Museum of Calcutta*, 26, 127–137.
Stephenson, J. (1931) Oligochaeta from Burma, Kenya and other parts of the world. *Proceedings of the Zoological Society of London,* 1931, 33–92.
Stout, J.D. (1956) Aquatic Oligochaetes occurring in forest litter. - I. *Transactions of the Royal Society of New Zealand,* 84, 97–102.
Stout, J.D. (1958) Aquatic Oligochaetes occurring in forest litter. - II. *Transactions of the Royal Society of New Zealand,* 85, 289–299.
Timm, T. (2009) A guide to the freshwater Oligochaeta and Polychaeta of Northern and Central Europe. *Lauterbornia,* 66, 1–235.
Ude, H. (1892) Ein neues Enchytraeiden-Genus. *Zoologischer Anzeiger*, 401, 344–345.
Van Haaren, T. & Soors, J. (2013) *Aquatic oligochaetes of The Netherlands and Belgium*. KNNV Publishing, Zeist, 302 pp. [The Netherlands]
Varga, L. (1928) Ein interessanter Biotop der Biocönose von Wasserorganismen. *Biologisches Zentralblatt*, 48, 143–162.
Vejdovský, F. (1879) *Beiträge zur vergleichenden Morphologie der Anneliden. I. Monographie der Enchytraeiden*. Verlag von Friedrich Tempsky, Prag, 61 pp. + 14 pls.
Walton, L.B. (1906) Naididae of Cedar Point, Ohio. *The American Naturalist,* 40, 683–706. http://dx.doi.org/10.1086/278670
Xie, Z.C., Liang, Y.L. & Wang, H.Z. (2000) A taxonomic study of *Bryodrilus* (Enchytraeidae, Oligochaeta) from Changbaishan Mountain, China. *Species Diversity,* 5, 93–101.