



<http://dx.doi.org/10.11646/zootaxa.3873.4.3>

<http://zoobank.org/urn:lsid:zoobank.org:pub:7FCB1765-9A81-4BA7-9633-F896B2B808BA>

Phylogenetic relationships and taxonomic revision of *Paranoplocephala* Lühe, 1910 sensu lato (Cestoda, Cyclophyllidea, Anoplocephalidae)

VOITTO HAUKISALMI¹, LOTTA M. HARDMAN², ERIC P. HOBERG³ & HEIKKI HENTTONEN⁴

¹Finnish Museum of Natural History Luomus, P. Rautatiekatu 13, 00014 University of Helsinki, Finland.

E-mail: voitto.haukisalmi@helsinki.fi

²Murkelsvängen 6, 10650 Ekenäs, Finland. E-mail: lotta.hardman@gmail.com

³US National Parasite Collection, USDA, Agricultural Research Service, BARC East 1180, Beltsville, Maryland, USA 20705.

E-mail: eric.hoberg@ars.usda.gov

⁴Finnish Forest Research Institute, Vantaa Unit, Jokiniemenkuja 1, 01370 Vantaa, Finland. E-mail: heikki.henttonen@metla.fi

Abstract

An extensive phylogenetic analysis and genus-level taxonomic revision of *Paranoplocephala* Lühe, 1910-like cestodes (Cyclophyllidea, Anoplocephalidae) are presented. The phylogenetic analysis is based on DNA sequences of two partial mitochondrial genes, i.e. cytochrome c oxidase subunit 1 (*cox1*) and NADH dehydrogenase subunit 1 (*nad1*), and includes 51 cestode isolates. The revision concerns all 34 *Paranoplocephala*-like species considered valid, of which 21 species could be included in the molecular phylogenetic analysis. Based on the phylogenetic relationships and main morphological features, with emphasis on the structure of the scolex, suckers and neck, length of the vagina (relative to the cirrus sac) and distribution of testes, 12 new genera are proposed for cestodes traditionally assigned to *Paranoplocephala* s. l. This results in 23 new combinations. The new genera are: *Gulyaevia* n. g., *Chionocestus* n. g., *Microticola* n. g., *Beringitaenia* n. g., *Arctoceustus* n. g., *Rauschoides* n. g., *Eurotaenia* n. g., *Douthittia* n. g., *Lemminia* n. g., *Tenoraia* n. g., *Rodentocestus* n. g. and *Cookiella* n. g. In addition, *Paranoplocephala* (s. s.) and *Parandrya* Gulyaev & Chechulin, 1996 are redescribed; the latter genus is considered valid, although it has been earlier synonymized with *Paranoplocephala*. A new species (*Beringitaenia nanushukensis* n. sp.) from *Microtus miurus* is described. Based on the DNA sequence data, several additional lineages probably representing independent species are identified, but not described as new taxa because of lack of good-quality specimens or absence of reliable morphological differences. The study also presents the first evidence for the phylogenetic position of the monotypic genus *Gallegoides* Tenora & Mas-Coma, 1978 based on DNA sequence data. A key for the *Paranoplocephala*-like genera is presented. The patterns of diversity and zoogeography of cestodes representing the “arvicoline clade” (72 species) are complex, involving mechanisms of dispersal, geographic colonization and host switching linking faunas across Eurasia and North America.

Key words: *Gulyaevia* n. g., *Chionocestus* n. g., *Microticola* n. g., *Beringitaenia nanushukensis* n. g., n. sp., *Arctoceustus* n. g., *Rauschoides* n. g., *Eurotaenia* n. g., *Douthittia* n. g., *Lemminia* n. g., *Tenoraia* n. g., *Rodentocestus* n. g., *Cookiella* n. g., *Parandrya*, *Gallegoides*, cytochrome c oxidase subunit 1 (*cox1*), NADH dehydrogenase subunit 1 (*nad1*), rodents, Arvicolinae

Introduction

In terms of species diversity, the anoplocephalid cestodes, particularly the genus *Paranoplocephala* Lühe, 1910 s. l., comprise the dominant helminth group of rodents at higher latitudes in the northern hemisphere. Phylogenetic analyses (Wickström *et al.* 2005, Haukisalmi *et al.* 2008, 2009a) based on nuclear (28S rDNA, ITS1) and mitochondrial (*cox1*) sequences show that *Paranoplocephala* spp. belong to the diverse “arvicoline clade” of cestodes along with *Anoplocephaloides* Baer, 1923 s. s., *Microcephaloides* Haukisalmi, Hardman, Hardman, Rausch & Henttonen, 2008 and *Diandrya composita* Darrach, 1930, most of them from arvicoline rodents (voles and lemmings). *Paranoplocephala* s. s. [i.e. *Paranoplocephala omphalodes* (Hermann, 1783) and related species] forms an exclusive monophyletic group, but otherwise the phylogenetic structure within *Paranoplocephala* s. l.

for their invaluable efforts under harsh field conditions, especially acknowledging contributions by S. O. MacDonald, A. M. Runck, A. V. A. Koehler, K. E. Galbreath, A. Tsvetkova and N. E. Dokuchaev. For other materials, we acknowledge the help of the following collaborators and local experts: J. D. Boone, C. J. Conroy, V. Fedorov, C. Feliu, P. Foronda, K. Fregda, A. Gubányi, E. Kallio, A. Kenney, C. Krebs, J. Laakkonen, J. Margaletič, A. Markotič, G. Muruyeva, J. Niemimaa, K. Norrdahl, J. L. Patton, S. Shulunov, O. Vapalahti and N. Yoccoz. V.H. has been supported by NSF PBI award Nos. 0818696 and 0818823. We further recognize and acknowledge the foundations for our current understanding of diversity among arvicoline tapeworms that emanated from the seminal studies of Robert L. Rausch and Virginia R. Rausch who in many ways set the stage for taxonomic explorations of hosts and parasites across the expanse of Beringia. Boyko B. Georgiev and an anonymous reviewer are thanked for detailed and constructive comments on the manuscript.

References

- Babero, B.B. & Cattan, P.E. (1975) Helminthofauna de Chile: III. Parásitos del roedor degú, *Octodon degus* Molina, 1782, con la descripción de tres nuevas especies. *Boletín Chileno de Parasitología*, 30, 68–76.
- Baer, J.G. (1923) Considérations sur le genre *Anoplocephala*. *Bulletin de la Société Neuchâtoise des Sciences Naturelles*, 48, 1–16.
- Baer, J.G. (1924) Contribution à la Faune helminthologique sud-africaine. Note préliminaire. *Annales de Parasitologie humaine et comparée*, 2, 239–247.
- Baer, J.G. (1927) Monographie des cestodes de la famille des Anoplocephalidae. *Bulletin Biologique de la France et de la Belgique*, 10 (Supplement), 1–241.
- Beveridge, I., Shamsi, S., Hu, M., Chilton, N.B. & Gasser, R.B. (2007) Genetic variation in the mitochondrial cytochrome c oxidase subunit I within *Progamotaenia festiva* (Cestoda: Anoplocephalidae) from macropodid marsupials. *Parasitology*, 134, 1465–1476.
<http://dx.doi.org/10.1017/s0031182007002752>
- Blanchard, R. (1891) Notices helminthologiques (deuxième série). *Mémoires de la Société Zoologique de France*, 4, 420–466.
- Braun, M. (1894) Vermes, Part I, Cestodes. In: Bronn, H.G. (Ed.), *Klassen un Ordnungen des Thierreichs*. H. G. Bronn, Leipzig, pp. 927–1731.
- Brunhoff, C., Galbreath, K.E., Fedorov, V.B., Cook, J.A. & Jaarola, M. (2003) Holarctic phylogeography of the root vole (*Microtus oeconomus*): implications for late Quaternary biogeography of high latitudes. *Molecular Ecology*, 12, 957–968.
<http://dx.doi.org/10.1046/j.1365-294x.2003.01796.x>
- Caira, J.N., Jensen, K. & Barbeau, E. (2012) Global Cestode Database. World Wide Web electronic publication. Available from: <http://tapewormdb.uconn.edu/> (accessed 5 September 2014)
- Chechulin, A.I. & Gulyaev, V.D. (1998) *Paranoplocephala longivaginata* sp. n. (Cyclophyllidea: Anoplocephalidae) - novaya cestoda ot gryzunov Vostochnoi Sibiri. *Parazitologiya*, 32, 352–356.
- Cholodkovsky, N. (1913) Cestodes nouveaux ou peu connus. Deuxième Série. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences, St.-Petersbourg*, 18, 221–232.
- Conroy, C.J. & Cook, J.A. (1999) MtDNA evidence for repeated pulses of speciation within arvicoline and murid rodents. *Journal of Mammalian Evolution*, 6, 221–245.
- Conroy, C.J. & Cook, J.A. (2000) Molecular systematics of a Holarctic rodent (*Microtus*: Muridae). *Journal of Mammalogy*, 81, 344–359.
- Cook, J.A., Hoberg, E.P., Koehler, A., Henttonen, H., Wickström, L., Haukisalmi, V., Galbreath, K., Chernyavski, F., Dokuchaev, N., Lahzuhtkin, A., MacDonald, S.O., Hope, A., Waltari, E., Runck, A., Veitch, A., Popko, R., Jenkins, E., Kutz, S. & Eckerlin, R. (2005) Beringia: Intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. *Mammal Study*, 30, S33–S44.
- Darrah, J.R. (1930) A new anoplocephalid cestode from the woodchuck, *Marmota flaviventris*. *Transactions of the American Microscopical Society*, 49, 252–257.
<http://dx.doi.org/10.2307/3222351>
- Douthitt, H. (1915) Studies on the cestode family Anoplocephalidae. *Illinois Biological Monographs*, 1, 1–96.
- Drummond, A.J., Ashton, B., Cheung, M., Heled, J., Kearse, M., Moir, R., Stones-Havas, S., Thierer, T. & Wilson, A.C. (2010) Geneious Pro 5.3.6. Available from: <http://www.geneious.com/> (accessed 5 September 2014)
- Fair, J.M., Schmidt, G.D. & Wertheim, G. (1990) New species of *Andrya* and *Paranoplocephala* from voles and mole-rats in Israel and Syria. *Journal of Parasitology*, 76, 641–644.
<http://dx.doi.org/10.2307/3282975>
- Fedorov, V.B. & Stenseth, N.C. (2001) Glacial survival of the Norwegian lemming (*Lemmus lemmus*) in Scandinavia: inference from mitochondrial DNA variation. *Proceedings of the Royal Society of London, Series B (Biological Sciences)*, 268, 809–814.
<http://dx.doi.org/10.1098/rspb.2001.1584>

- Frölich, J.A. (1802) Beiträge zur Naturgeschichte der Eingeweidewürmer. *Der Naturforscher*, 29, 5–96.
- Galbreath, K.E. & Cook, J.A. (2004) Genetic consequences of Pleistocene glaciations for the tundra vole (*Microtus oeconomus*) in Beringia. *Molecular Ecology*, 13, 135–148.
<http://dx.doi.org/10.1046/j.1365-294x.2004.02026.x>
- Galbreath, K.E. & Hoberg, E.P. (2012) Return to Beringia: parasites reveal cryptic biogeographic history of North American pikas. *Proceedings of the Royal Society B*, 279, 371–378.
<http://dx.doi.org/10.1098/rspb.2011.0482>
- Galli-Valerio, B. (1905) Einige Parasiten von *Arvicola nivalis*. *Zoologischer Anzeiger*, 28, 519–522.
- Genov, T. & Georgiev, B.B. (1988) Review of the species of the genus *Anoplocephaloides* Baer, 1923 emend Rausch, 1976 (Cestoda: Anoplocephalidae) parasitizing rodents in Bulgaria, with an analysis of the taxonomic structure of the genus. *Parasitologica Hungarica*, 21, 31–52.
- Genov, T., Georgiev, B.B. & Biserkov, V.Y. (1984) *Anoplocephaloides rauschi* sp. n. (Cestoda: Anoplocephalidae), a parasite of *Microtus nivalis* Mart. (Rodentia) in Bulgaria. *Comptes rendus de l'Académie bulgare des Sciences*, 37, 795–798.
- Genov, T., Vasileva, G.P. & Georgiev, B.B. (1996) *Paranoplocephala aquatica* n. sp. (Cestoda, Anoplocephalidae) from *Arvicola terrestris* and *Ondatra zibethica* (Rodentia), with redescription and comments on related species. *Systematic Parasitology*, 34, 135–152.
<http://dx.doi.org/10.1007/bf00009687>
- Gubányi, A. & Murai, É. (2002) New anoplocephalid parasites (Cestoda: Anoplocephalidae, *Paranoplocephala*) from the Fertő-Hanság National Park. In: Mahunka, S. (Ed.), *The fauna of the Fertő-Hanság National Park*. Hungarian Natural History Museum, Budapest, pp. 111–120.
- Gubányi, A., Murai, É., Hajdú, É., Dudich, A., Mtskási, I. & Mészáros, F. (2002) On the parasite fauna of mammals from the Fertő-Hanság National Park and its surroundings (Cestoda, Trematoda, Nematoda, Acanthocephala, Siphonaptera). In: Mahunka, S. (Ed.), *The fauna of the Fertő-Hanság National Park*. Hungarian Natural History Museum, Budapest, pp. 99–110.
- Gubányi, A., Tenora, F. & Murai, É. (1998) *Paranoplocephala genovi* sp. n. (Cestoda, Anoplocephalidae) from the muskrat (*Ondatra zibethica* L.). *Parasitologica Hungarica*, 31, 33–38.
- Gulyaev, V.D. (1996) O taksonomicheskoi samostoyatel'nosti *Anoplocephaloides* spp. (Cestoda: Anoplocephalidae) s serijnym cheredovaniem polovyh atriumov. *Parazitologiya*, 30, 263–269.
- Gulyaev, V.D. & Chechulin, A.I. (1996) *Parandrya feodorovi* gen. n., sp. n. - novaya cestoda (Cyclophyllidea: Anoplocephalidae) ot polevok Sibiri. *Parazitologiya*, 30, 132–140.
- Gulyaev, V.D. & Krivopalov, A.V. (2003) Novyj vid cestody *Paranoplocephala gubanovi* sp. n. (Cyclophyllidea: Anoplocephalidae) ot lesnogo lemminga *Myopus schisticolor* Vostochnoj Sibiri. *Parazitologiya*, 37, 488–495.
- Gurlt, E.F. (1831) *Lehrbuch der pathologischen Anatomie der Haus-Säugethiere. Erste Theil*. G. Reimer, Berlin, 399 pp.
- Hansen, M. (1947) Three anoplocephalid cestodes from the prairie meadow vole, with description of *Andrya microti* n. sp. *Transactions of the American Microscopical Society*, 66, 279–282.
<http://dx.doi.org/10.2307/3223395>
- Haukisalmi, V. (2008) Review of *Anoplocephaloides* species from African rodents, with the proposal of *Afrobaeria* n. g. (Cestoda: Anoplocephalidae). *Helminthologia*, 45, 57–63.
<http://dx.doi.org/10.2478/s11687-008-0011-6>
- Haukisalmi, V. (2009) A taxonomic revision of the genus *Anoplocephaloides* Baer, 1923 sensu Rausch (1976), with the description of four new genera (Cestoda: Anoplocephalidae). *Zootaxa*, 2057, 1–31.
- Haukisalmi, V. (2013) *Afrojoyeuxia* gen. n. and *Hunkeleriella* gen. n., two new genera of cestodes (Cyclophyllidea: Anoplocephalidae) from African rodents. *Folia Parasitologica*, 60, 475–481.
<http://dx.doi.org/10.14411/fp.2013.051>
- Haukisalmi, V. & Eckerlin, R.P. (2009) A new anoplocephalid cestode from the southern bog lemming *Synaptomys cooperi*. *Journal of Parasitology*, 95, 690–694.
<http://dx.doi.org/10.1645/ge-1717.1>
- Haukisalmi, V., Hardman, L.M., Foronda, P., Feliu, C. & Henttonen, H. (2010a) Systematic relationships of *Mosgovoyia* Spasskii, 1951 (Cestoda: Anoplocephalidae) and related genera inferred from mitochondrial and nuclear sequence data. *Systematic Parasitology*, 77, 71–79.
<http://dx.doi.org/10.1007/s11230-010-9264-9>
- Haukisalmi, V., Hardman, L.M., Hardman, M., Laakkonen, J., Niemimaa, J. & Henttonen, H. (2007a) Morphological and molecular characterisation of *Paranoplocephala buryatiensis* n. sp. and *P. longivaginata* Chechulin & Gulyaev, 1998 (Cestoda: Anoplocephalidae) in voles of the genus *Clethrionomys*. *Systematic Parasitology*, 66, 55–71.
<http://dx.doi.org/10.1007/s11230-006-9059-1>
- Haukisalmi, V., Hardman, L.M., Hardman, M., Rausch, R.L. & Henttonen, H. (2008) Molecular systematics of the Holarctic *Anoplocephaloides variabilis* (Douthitt, 1915) complex, with the proposal of *Microcephaloides* n. g. (Cestoda: Anoplocephalidae). *Systematic Parasitology*, 70, 15–26.
<http://dx.doi.org/10.1007/s11230-008-9129-7>
- Haukisalmi, V., Hardman, L.M. & Henttonen, H. (2010b) Taxonomic review of cestodes of the genus *Catenotaenia* Janicki, 1904 in Eurasia and molecular phylogeny of the Catenotaeniidae (Cyclophyllidea). *Zootaxa*, 2489, 1–33.

- Haukisalmi, V., Hardman, L.M., Henttonen, H., Laakkonen, J., Niemimaa, J., Hardman, M. & Gubányi, A. (2009a) Molecular systematics and morphometrics of *Anoplocephaloides dentata* (Cestoda, Anoplocephalidae) and related species in voles and lemmings. *Zoologica Scripta*, 38, 199–220.
<http://dx.doi.org/10.1111/j.1463-6409.2008.00363.x>
- Haukisalmi, V., Hardman, L.M., Niemimaa, J. & Henttonen, H. (2007b) Taxonomy and genetic divergence of *Paranoplocephala kalelai* (Tenora, Haukisalmi & Henttonen, 1985) (Cestoda: Anoplocephalidae) in the grey-sided vole *Myodes rufocanus* in northern Fennoscandia. *Acta Parasitologica*, 52, 335–341.
<http://dx.doi.org/10.2478/s11686-007-0043-y>
- Haukisalmi, V. & Henttonen, H. (2000) Description and morphometric variability of *Paranoplocephala serrata* n. sp. (Cestoda: Anoplocephalidae) in collared lemmings (*Dicrostonyx* spp., Arvicolinae) from Arctic Siberia and North America. *Systematic Parasitology*, 45, 219–231.
<http://dx.doi.org/10.1023/a:1006244331243>
- Haukisalmi, V. & Henttonen, H. (2001) Biogeography of helminth parasitism in *Lemmus* Link (Arvicolinae), with the description of *Paranoplocephala fellmani* n. sp. (Cestoda: Anoplocephalidae) from the Norwegian lemming *L. lemmus* (Linnaeus). *Systematic Parasitology*, 49, 7–22.
<http://dx.doi.org/10.1023/a:1010778504559>
- Haukisalmi, V. & Henttonen, H. (2003) What is *Paranoplocephala macrocephala* (Douthitt, 1915) (Cestoda: Anoplocephalidae)? *Systematic Parasitology*, 54, 53–69.
<http://dx.doi.org/10.1023/a:1022141809571>
- Haukisalmi, V. & Henttonen, H. (2005) Description of *Paranoplocephala yoccozi* n. sp. (Cestoda: Anoplocephalidae) from the snow vole *Chionomys nivalis* in France, with a review of anoplocephalid cestodes of snow voles in Europe. *Parasite*, 12, 203–211.
<http://dx.doi.org/10.1051/parasite/2005123203>
- Haukisalmi, V. & Henttonen, H. (2007) A taxonomic revision of the *Paranoplocephala primordialis* (Douthitt) complex (Cestoda: Anoplocephalidae) in voles and squirrels. *Zootaxa*, 1548, 51–68.
- Haukisalmi, V., Henttonen, H. & Hardman, L.M. (2006) Taxonomy and diversity of *Paranoplocephala* spp. (Cestoda: Anoplocephalidae) in voles and lemmings of Beringia, with a description of three new species. *Biological Journal of the Linnean Society*, 89, 277–299.
<http://dx.doi.org/10.1111/j.1095-8312.2006.00672.x>
- Haukisalmi, V., Henttonen, H., Hardman, L.M., Hardman, M., Laakkonen, J., Murueva, G., Niemimaa, J., Shulunov, S. & Vapalahti, O. (2009b) Review of tapeworms of rodents in the Republic of Buryatia, with emphasis on anoplocephalid cestodes. *ZooKeys*, 8, 1–18.
<http://dx.doi.org/10.3897/zookeys.8.58>
- Haukisalmi, V., Henttonen, H., Niemimaa, J. & Rausch, R.L. (2002) Description of *Paranoplocephala etholeni* n. sp. (Cestoda: Anoplocephalidae) in the meadow vole *Microtus pennsylvanicus*, with a synopsis of *Paranoplocephala* s.l. in Holarctic rodents. *Parasite*, 9, 305–314.
<http://dx.doi.org/10.1051/parasite/2002094305>
- Haukisalmi, V. & Wickström, L.M. (2005) Morphological characterisation of *Andrya* Railliet, 1893, *Neandrya* n. g. and *Paranoplocephala* Lühe, 1910 (Cestoda: Anoplocephalidae) in rodents and lagomorphs. *Systematic Parasitology*, 62, 209–219.
<http://dx.doi.org/10.1007/s11230-005-5499-2>
- Haukisalmi, V., Wickström, L.M., Hantula, J. & Henttonen, H. (2001) Taxonomy, genetic differentiation and Holarctic biogeography of *Paranoplocephala* spp. (Cestoda: Anoplocephalidae) in collared lemmings (*Dicrostonyx*; Arvicolinae). *Biological Journal of the Linnean Society*, 74, 171–196.
<http://dx.doi.org/10.1111/j.1095-8312.2001.tb01385.x>
- Haukisalmi, V., Wickström, L.M., Henttonen, H., Hantula, J. & Gubányi, A. (2004) Molecular and morphological evidence for multiple species within *Paranoplocephala omphalodes* (Cestoda, Anoplocephalidae) in *Microtus* voles (Arvicolinae). *Zoologica Scripta*, 33, 277–290.
<http://dx.doi.org/10.1111/j.0300-3256.2004.00148.x>
- Hermann, J. (1783) Helminthologische Bemerkungen. *Der Naturforscher*, 19, 31–59.
- Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. *Nature*, 405, 907–913.
- Hewitt, G.M. (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, 58, 247–276.
<http://dx.doi.org/10.1111/j.1095-8312.1996.tb01434.x>
- Hoberg, E.P. & Brooks, D.R. (2008) A macroevolutionary mosaic: Episodic host-switching, geographic colonization, and diversification in complex host-parasite systems. *Journal of Biogeography*, 35, 1533–1550.
<http://dx.doi.org/10.1111/j.1365-2699.2008.01951.x>
- Hoberg, E.P. & Brooks, D.R. (2010) Beyond vicariance: Integrating taxon pulses, ecological fitting and oscillation in historical biogeography and evolution. In: Morand, S. & Krasnov, B. (Eds.), *The Geography of Host-Parasite Interactions*. Oxford University Press, Oxford, pp. 7–20.
- Hoberg, E.P. & Brooks, D.R. (2013) Episodic processes, invasion, and faunal mosaics in evolutionary and ecological time. In:

- Rohde, K. (Ed.), *The Balance of Nature and Human Impact*. Cambridge University Press, Cambridge, pp. 199–213.
- Hoberg, E.P., Galbreath, K.E., Cook, J.A., Kutz, S.J. & Polley, L. (2012) Northern host-parasite assemblages: History and biogeography on the borderlands of episodic climate and environmental transition. *In*: Rollinson, D. & Hays, S.I. (Eds.), *Advances in Parasitology*, 79, pp. 1–97.
- Hoberg, E.P., Kutz, S.J., Cook, J.A., Galaktionov, K., Haukismäki, V., Henttonen, H., Laaksonen, S., Makarikov, A. & Marcogliese, D.J. (2013) Parasites in terrestrial, freshwater and marine systems. *In*: Møller, H. (Ed.), *Arctic Biodiversity Assessment-Status and Trends in Arctic Biodiversity*. Conservation of Arctic Flora and Fauna, Arctic Council, pp. 476–505.
- Hoberg, E.P., Kutz, S.J., Galbreath, K.E. & Cook, J.A. (2003) Arctic biodiversity: from discovery to faunal baselines - revealing the history of a dynamic ecosystem. *Journal of Parasitology*, 89 (Supplement), S84–S95.
- Hope, A.G., Takebayashi, N., Galbreath, K.E., Talbot, S.L. & Cook, J.A. (2013) Temporal, spatial and ecological dynamics of speciation among amphi-Beringian small mammals. *Journal of Biogeography*, 40, 415–429.
<http://dx.doi.org/10.1111/jbi.12056>
- Hu, M., Gasser, R.B., Chilton, N.B. & Beveridge, I. (2005) Genetic variation in the mitochondrial cytochrome *c* oxidase subunit 1 within three species of *Progamotaenia* (Cestoda: Anoplocephalidae) from macropodid marsupials. *Parasitology*, 130, 117–129.
<http://dx.doi.org/10.1017/s0031182004006377>
- Huelsenbeck, J.P., Ronquist, F., Nielsen, R. & Bollback, J.P. (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. *Science*, 294 (5550), 2310–2314.
- Hunkeler, P. (1972) Les Cestodes parasites des petits mammifères (Rongeurs et Insectivores) de Côte-d'Ivoire et de Haute-Volta (note préliminaire). *Bulletin de la Société neuchâteloise des Sciences naturelles*, 95, 121–132.
- Hunkeler, P. (1973) Les Cestodes parasites des petits mammifères (Rongeurs et Insectivores) de Côte-d'Ivoire et de Haute-Volta. *Revue Suisse de Zoologie*, 80, 809–930.
- Jaarola, M., Martinková, N., Gündüz, I., Brunhoff, C., Zima, J., Nadachowski, A., Amori, G., Bulatova, N.S., Chondropoulos, B., Fragedakis-Tsolis, S., González-Esteban, J., López-Fuster, M.J., Kandaurov, A.S., Kefelioglu, H., da Luz Mathias, M., Villate, I. & Searle, J.B. (2005) Molecular phylogeny of the speciose vole genus *Microtus* (Arvicolinae, Rodentia) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 33, 647–663.
<http://dx.doi.org/10.1016/j.ympev.2004.07.015>
- Janicki, C. (1904) Zur Kenntnis einiger Säugetiercestoden. *Zoologischer Anzeiger*, 27, 770–782.
- Joyeux, C. (1923) Recherches sur la faune helminthologique Africaine. *Archives de l'Institut Pasteur de Tunis*, 12, 119–167.
- Kirshenblat, Y.D. (1938) *Zakonomernosti dinamiki parazitofauni myschevidnyh gryzunov*. Izdanie Leninskogo Gosudarstvennogo Universiteta, Leningrad, U.S.S.R., 92 pp.
- Kirshenblat, Y.D. (1941) Novyj lentochnyj cherv' iz Zakavkazskikh polevok. *Coobscheniya Akademii Nauk Gruzinskoi SSR*, 2, 273–276.
- Krabbe, G. (1879) Lentochnye (Cestodes). *In*: Fedchenko, A.P. (Ed.), *Puteshestvie v' Turkestan' (Reise in Turkestan)*. Gesellschaft der Freunde der Naturwissenschaften in Moskau, Moskau, pp. 1–23.
- Linstow, O. (1901) *Taenia horrida*, *Tetrabothrium macrocephalum* und *Heterakis distans*. *Archiv für Naturgeschichte*, 67, 1–10.
- Linstow, O.F.B.v. (1904) Neue Helminthen. *Centralblatt für Bakteriologie und Parasitenkunde (I abt. Origin.)*, 37, 678–683.
- Littlewood, D.T.J., Waeschenbach, A. & Nikolov, P.N. (2008) In search of mitochondrial markers for resolving the phylogeny of cyclophyllidean tapeworms (Platyhelminthes, Cestoda) - a test study with Davaineidae. *Acta Parasitologica*, 53, 133–144.
<http://dx.doi.org/10.2478/s11686-008-0029-4>
- Lühe, M. (1910) *Die Süßwasserfauna Deutschlands. Heft 18: Parasitische Plattwürmer. II. Cestoden*. Gustav Fischer Verlag, Jena, 153 pp.
- Makarikov, A.A., Galbreath, K.E. & Hoberg, E.P. (2013) Parasite diversity at the Holarctic nexus: Species of *Arostrilepis* (Eucestoda: Hymenolepididae) in voles and lemmings (Cricetidae: Arvicolinae) from greater Beringia. *Zootaxa*, 3608 (6), 401–439.
<http://dx.doi.org/10.11646/zootaxa.3608.6.1>
- Mas-Coma, S. & Tenora, F. (1997) Proposal of *Arostrilepis* n. gen. (Cestoda: Hymenolepididae). *Research and Reviews in Parasitology*, 57, 93–101.
- Meggitt, F.J. (1927) Report on a collection of Cestoda, mainly from Egypt. Part I. Families Anoplocephalidae, Davaineidae. *Parasitology*, 19, 314–327.
<http://dx.doi.org/10.1017/s0031182000005746>
- Mobedi, I. & Ghadirian, E. (1977) *Schizorchis arfaai* sp. n. (Cestoda: Anoplocephalidae) from the wood-mouse, *Apodemus sylvaticus*, in caspian area of Iran. *Journal of Helminthology*, 51, 63–67.
<http://dx.doi.org/10.1017/s0022149x00007252>
- Moniez, R. (1880) Études sur les cestodes. *Bulletin Scientifique de Département du Nord, 2me Série*, 3, 240–246.
- Moniez, R. (1891) Notes sur les helminthes. *Revue Biologique du Nord de la France*, 4, 65–79.
- Murai, É., Tenora, F. & Rocamora, J.M. (1980) *Paranoplocephala mascomai* sp. n. (Cestoda: Anoplocephalidae) a parasite of *Microtus cabrerai* (Rodentia) in Spain. *Parasitologica Hungarica*, 13, 35–37.

- Nakao, M., Lavikainen, A., Iwaki, T., Haukisalmi, V., Konyaev, S., Oku, Y., Okamoto, M. & Ito, A. (2013) Molecular phylogeny of the genus *Taenia* (Cestoda: Taeniidae): Proposals for the resurrection of *Hydatigera* Lamarck, 1816 and the creation of a new genus *Versteria*. *International Journal for Parasitology*, 43, 427–437.
- Nieberding, C., Morand, S., Libois, R. & Michaux, J.R. (2004) A parasite reveals cryptic phylogeographic history of its host. *Proceedings of the Royal Society of London Series B Biological Sciences*, 271, 2559–2568.
<http://dx.doi.org/10.1098/rspb.2004.2930>
- Parra, B.E. (1952) *Paranoplocephala threlkeldi*, a new species of tapeworm (Cestoda: Anoplocephalidae) from *Lagidium peruanum*. *Journal of the Tennessee Academy of Science*, 27, 205.
- Posada, D. (2008) jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution*, 25, 1253–1256.
<http://dx.doi.org/10.1093/molbev/msn083>
- Quentin, J.-C. (1979) Anatomie et taxonomie d'*Aprostotandrya gundi* (Joyeux, 1923), cestode parasite du rongeur *Ctenodactylus gundi* (Rothman). *Bulletin du Museum National d'Histoire Naturelle Section A Zoologie Biologie et Ecologie Animales*, 1, 251–256.
- Railliet, A. (1893) *Traité de zoologie médicale et agricole. Fasc. I*. Asselin & Houzeau, Paris, 1303 pp.
- Rausch, R. (1946) *Paranoplocephala troeschi*, new species of cestode from the meadow vole, *Microtus p. pennsylvanicus* Ord. *Transactions of the American Microscopical Society*, 65, 354–356.
<http://dx.doi.org/10.2307/3223549>
- Rausch, R. (1947) *Andrya sciuri* n. sp., a cestode from the northern flying squirrel. *Journal of Parasitology*, 33, 316–318.
<http://dx.doi.org/10.2307/3273359>
- Rausch, R. (1948) Notes on cestodes of the genus *Andrya* Railliet, 1883, with the description of *A. ondatrae* n. sp. (Cestoda: Anoplocephalidae). *Transactions of the American Microscopical Society*, 67, 187–191.
<http://dx.doi.org/10.2307/3223500>
- Rausch, R. (1952a) Helminths from the round-tailed muskrat, *Neofiber alleni nigrescens* Howell, with descriptions of two new species. *Journal of Parasitology*, 38, 151–155.
<http://dx.doi.org/10.2307/3273835>
- Rausch, R. (1952b) Studies on the helminth fauna of Alaska. XI. Helminth parasites of microtine rodents - taxonomic considerations. *Journal of Parasitology*, 38, 415–444.
<http://dx.doi.org/10.2307/3273922>
- Rausch, R. (1954) Studies on the helminth fauna of Alaska. XXII *Paranoplocephala wigginsii* n. sp., a cestode from an Arctic ground squirrel. *Transactions of the American Microscopical Society*, 73, 380–383.
<http://dx.doi.org/10.2307/3223582>
- Rausch, R.L. (1976) The genera *Paranoplocephala* Lühe, 1910 and *Anoplocephaloides* Baer, 1923 (Cestoda: Anoplocephalidae), with particular reference to species in rodents. *Annales de Parasitologie Humaine et Comparée*, 51, 513–562.
- Repenning, C.A. (2001) Beringian climate during intercontinental dispersal: a mouse eye view. *Quaternary Science Reviews*, 20, 25–40.
- Repenning, C.A., Fejfar, O. & Heinrich, W.D. (1990) Arvicolid rodent biochronology of the Northern Hemisphere. In: Fejfar, O. & Heinrich, W.D. (Eds.), *International symposium on evolution, phylogeny, and biostratigraphy of Arvicolids (Rodentia, Mammalia)*. Pfeil-Verlag, Prague, pp. 385–418.
- Riehm, G. (1881) Studien an Cestoden. *Zeitschrift für die Gesamten Naturwissenschaften*, 54, 545–610.
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
<http://dx.doi.org/10.1093/bioinformatics/btg180>
- Ryzhikov, K.M., Gvozdev, E.V., Tokobaev, M.M., Shaldybin, L.S., Macaberidze, G.V., Merkusheva, I.V., Nadtochii, E.V., Hohlova, I.G. & Sharpilo, L.D. (1978) *Opredelitel' gelmintov gryzunov fauny SSSR. Cestody i trematody*. Nauka, Moskva, 231 pp.
- Sato, H., Kamiya, H., Tenora, F. & Kamiya, M. (1993) *Anoplocephaloides dentatoides* sp. n. from the gray-backed vole, *Clethrionomys rufocanus bedfordiae*, in Hokkaido, Japan. *Journal of the Helminthological Society of Washington*, 60, 105–110.
- Sawada, I. & Kugi, G. (1979) Studies on the helminth fauna of Kyushu Part 5. Cestode parasites of wild mammals and birds from Ôita prefecture. *Annotationes Zoologicae Japonensis*, 52, 133–141.
- Schad, G.A. (1954) Helminth parasites of mice in northeastern Quebec and the coast of Labrador. *Canadian Journal of Zoology*, 32, 215–224.
<http://dx.doi.org/10.1139/z54-021>
- Setti, E. (1892) Elminti dell' Eritrea e delle regioni limitrofe. *Atti della Società Ligustica di Scienze Naturali e Geografiche*, 4, 10–13.
- Spasskii, A.A. (1950) Novyi vid paranoplocefaly ot surkov Tyan'-Shanya. *Trudy Gel'mintologicheskoi Laboratorii, Akademiya Nauk SSSR*, 3, 119–124.
- Spasskii, A.A. (1951) *Anoplocephalate tapeworms of domestic and wild animals (English translation)*. The Academy of Sciences of the USSR, Moscow, 783 pp.
- Stewart, J. & Lister, A. (2001) Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology and Evolution*,

- Tenora, F., Gubányi, A. & Murai, É. (1999) *Paranoplocephala maseri* n. sp. (Cestoda, Anoplocephalidae), a parasite of sagebrush voles *Lemmys curtatus* (Rodentia) in the USA. *Systematic Parasitology*, 42, 153–158.
<http://dx.doi.org/10.1023/a:1006077930526>
- Tenora, F., Haukisalmi, V. & Henttonen, H. (1985a) *Andrya kalelai* sp. n. and (?) *Anoplocephaloides* sp., Cestoda, Anoplocephalidae, parasites of *Clethrionomys*-rodents in Finland. *Annales Zoologici Fennici*, 22, 411–416.
- Tenora, F. & Mas-Coma, S. (1978) Records of *Gallegoides arfaai* (Mobedi & Ghadirian, 1977) n. comb. (Cestoda: Anoplocephalidae) in *Apodemus sylvaticus* L. from western Europe. Proposition of *Gallegoides* nov. gen. *Säugetierkundliche Mitteilungen*, 26, 222–226.
- Tenora, F. & Murai, É. (1980) The genera *Anoplocephaloides* and *Paranoplocephala* (Cestoda) parasites of Rodentia in Europe. *Acta Zoologica Academiae Scientiarum Hungaricae*, 26, 263–284.
- Tenora, F., Murai, E. & Vaucher, C. (1984) On Anoplocephalidae (Cestoda), parasitizing Rodentia and Lagomorpha in Europe. *Parasitologica Hungarica*, 17, 51–57.
- Tenora, F., Murai, É. & Vaucher, C. (1985b) On some *Paranoplocephala* species (Cestoda: Anoplocephalidae) parasitizing rodents (Rodentia) in Europe. *Parasitologica Hungarica*, 18, 29–48.
- Tenora, F., Murai, É. & Vaucher, C. (1986) On *Andrya* Railliet, 1893 and *Paranoplocephala* Lühe, 1910 (Cestoda, Monieziinae). *Parasitologica Hungarica*, 19, 43–75.
- Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acid Research*, 24, 4876–4882.
- Triant, D.A. & DeWoody, J.A. (2007) The occurrence, detection and avoidance of mitochondrial DNA translocations in mammalian systematics and phylogeography. *Journal of Mammalogy*, 88 (4), 908–920.
<http://dx.doi.org/10.1644/06-mamm-a-204r1.1>
- Waltari, E., Hoberg, E.P., Lessa, E.P. & Cook, J.A. (2007) Eastward ho: phylogeographic perspectives on colonization of hosts and parasites across the Beringian nexus. *Journal of Biogeography*, 34, 561–574.
<http://dx.doi.org/10.1111/j.1365-2699.2007.01705.x>
- Wickström, L.M., Hantula, J., Haukisalmi, V. & Henttonen, H. (2001) Genetic and morphometric variation in the Holarctic helminth parasite *Andrya arctica* (Cestoda, Anoplocephalidae) in relation to the divergence of its lemming hosts (*Dicrostonyx* spp.). *Zoological Journal of the Linnean Society*, 131, 443–457.
- Wickström, L.M., Haukisalmi, V., Varis, S., Hantula, J., Fedorov, V.B. & Henttonen, H. (2003) Phylogeography of the circumpolar *Paranoplocephala arctica* species complex (Cestoda: Anoplocephalidae) parasitizing collared lemmings (*Dicrostonyx* spp.). *Molecular Ecology*, 12, 3359–3371.
<http://dx.doi.org/10.1111/j.1096-3642.2001.tb01321.x>
- Wickström, L.M., Haukisalmi, V., Varis, S., Hantula, J. & Henttonen, H. (2005) Molecular phylogeny and systematics of anoplocephaline cestodes in rodents and lagomorphs. *Systematic Parasitology*, 62, 83–99.
<http://dx.doi.org/10.1007/s11230-005-5488-5>
- Voge, M. (1946) A new anoplocephalid cestode, *Andrya neotomae*, from the wood rat *Neotoma fuscipes*. *Journal of Parasitology*, 32, 36–39.
- Voge, M. (1948) A new anoplocephalid cestode, *Paranoplocephala kirbyi*, from *Microtus californicus californicus*. *Transactions of the American Microscopical Society*, 67, 299–303.
<http://dx.doi.org/10.2307/3223198>
- Yamaguti, S. (1942) *Studies on the helminth fauna of Japan. Part 42. Cestodes of mammals, II*. Published by the author, Kyoto, 18 pp.
- Yun, L., Tang, Z.X., Lin, Y.G., Hong, L.X., Yang, W.C. & Liu, G.C. (2004) A study on superfamily Anoplocephaloidea (Cestode) of grassland glires from Ximong, Inner Mongolia, China (Cestoidea, Cyclophyllidea). *Acta Zootaxonomica Sinica*, 29, 248–254.
- Zeder, J.G.H. (1803) *Anleitung zur Naturgeschichte der Eingeweidewürmer. Für Aerzte, Thieraerzte und Naturforscher*. Komptoir der Zeitung, Bamberg, 432 pp.