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Review

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Revised classification of the subfamily Leishmaniinae (Trypanosomatidae)

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Abstract: In the present study, we critically revised the recently proposed classification of the subfamily Leishmaniinae Maslov et Lukeš in Jirků et al., 2012. Agreeing with erection of the genus *Zelonia* Shaw, Camargo et Teixeira in Espinosa et al., 2017 and the subgenus *Mundinia* Shaw, Camargo et Teixeira in Espinosa et al., 2017 within the genus *Leishmania* Ross, 1908, we argue that other changes are not well justified. We propose to: (i) raise *Paraleishmania* Cupolillo, Medina-Acosta, Noyes, Momen et Grimaldi, 2000 to generic rank; (ii) create a new genus *Borovskyia* gen. n. to accommodate the former *Leptomonas barvae* Maslov et Lukeš, 2010 as its type and only species; (iii) leave the subfamily Leishmaniinae as originally defined, but establish two infrafamilies within it: Leishmaniatae infrafam. n. and Crithidiatae infrafam. n.

Keywords: taxonomy, new genera, new infrafamilies, *Paraleishmania*, *Borovskyia*, Leishmaniatae, Crithidiatae

The family Trypanosomatidae Doflein, 1901 unites uniflagellate parasitic protists of the class Kinetoplastea Honigberg, 1963. This group is intensively studied because of their peculiar molecular and biochemical features (Stuart and Panigrahi 2002, Martinez-Calvillo et al. 2010, Opperdoes et al. 2016, Záhonová et al. 2016). In addition, some trypanosomatids are of medical or economic importance as they cause diseases of humans, domestic animals and cultured plants (Lumsden and Evans 1976). These flagellates are traditionally divided into monoxenous (with one host in the life cycle) and dixenous (shuttling between two hosts) species. These are non-taxonomical groups, since dixeny has independently evolved at least three times during evolution of trypanosomatids, giving rise to the genera *Trypanosoma* Gruby, 1843, *Leishmania* Ross, 1908 and *Phytomonas* Donovan, 1909 (reviewed in Lukeš et al. 2014).

For a long time, classification of trypanosomatids was based on (i) host specificity, (ii) life cycle and (iii) morphology (Baker 1963, Wallace 1966, Vickerman 1976). Use of molecular methods revealed the artificial nature of the old system and caused its substantial revision with expansion in the number of supra-specific taxa. Moreover, the molecular phylogenetic approach allowed uniting genera into higher level taxa, i.e. subfamilies (d'Avila-Levy et al. 2015, Votýpka et al. 2015). The first delineated subfamily was Leishmaniinae Maslov et Lukeš in Jirků et al., 2012, which combined the dixenous genus *Leishmania* with the monoxenous genera *Leptomonas* Kent, 1880 and *Crithidia* Léger, 1902 (see Jirků et al. 2012). The Leishmaniinae is a species-rich group that explored a wide range of hosts including dipterans, heteropterans, hymenopterans and vertebrates (Maslov et al. 2013).

Recently, a revision of the taxonomy and the nomenclature of the subfamily Leishmaniinae with a focus on the genera *Leishmania* and *Endotrypanum* Mesnil et Brimont, 1908 has been put forward (Espinosa et al. 2017). The authors made the following major taxonomic changes: (i) erection of the new subgenus *Mundinia* Shaw, Camargo et Teixeira in Espinosa et al., 2017 within the genus *Leishmania* to include *L. enriettii* Muniz et Medina, 1948 and *L. martiniquensis* Desbois, Pratlong, Quist et Dedet, 2014; (ii) establishing of the new genus *Porcisia* Shaw, Camargo et Teixeira in Espinosa et al., 2017 comprising former *Leishmania hertigi* Herrer, 1971 and *L. deanei* Lainson et Shaw, 1977; (iii) transfer of *Leishmania colombiensis* Kreutzer, Corredor, Grimaldi, Grogl, Rowton, Young, Morales, McMahon-Pratt, Guzman et Tesh, 1991, *L. equatoriensis* Grimaldi, Kreutzer, Hashiguchi, Gomez, Mimory et Tesh, 1992 and *L. herreri* Zeledon, Ponce et Murillo, 1979 to the genus *Endotrypanum*; (iv) erection of the genus *Zelonia* Shaw, Camargo et Teixeira in Espinosa et al., 2017 to accommodate former *Leptomonas costaricensis* Yurchen-

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ko, Lukeš, Jirků, Zeledon et Maslov, 2006; (v) restriction of the subfamily Leishmaniinae to the clade encompassing the genera *Leishmania*, *Porcisia*, *Endotrypanum*, *Zelonia* and *Novymonas* Kostygov et Yurchenko, 2016. Modifications of the entangled taxonomy of these parasites were long overdue. However, in our view, the proposed scheme is not ideal. We fully recognise the rationale of establishing the taxa *Zelonia* and *Mundinia*. However, we do not consider other changes to be well justified. Our argumentation is explained in detail below.

LEISHMANIINAE

In the latest revision the subfamily Leishmaniinae was contracted to dixenous *Leishmania*-related species along with *Zelonia* and *Novymonas* (see Espinosa et al. 2017). The main argument for such an act was high support of this group on phylogenetic trees. However, the subfamily Leishmaniinae *sensu* Maslov et Lukeš, 2012 is also a strongly supported clade (Maslov et al. 2010, Jirků et al. 2012, Kostygov et al. 2014, Schwarz et al. 2015). As a matter of fact, a clade with high support corresponds to a natural taxon but has no relation to a particular rank. In our opinion, the proposed change is not warranted and results in confusion with two alternatively defined taxa bearing the same name – Leishmaniinae *sensu* Maslov et Lukeš, 2012 and Leishmaniinae *sensu* Shaw, Camargo et Teixeira, 2017. In addition, the expelled genera *Crithidia*, *Leptomonas* and *Lotmaria* Evans et Schwarz, 2014 become an orphan group. Of note, this group contains a number of model species which have been widely used as proxies for the monoxenous ancestors of *Leishmania*, the relation to which is lost upon the redefinition of the Leishmaniinae (see Maslov et al. 2013, Kraeva et al. 2015, Flegontov et al. 2016, Opperdoes et al. 2016).

The subfamily Leishmaniinae *sensu* Maslov et Lukeš, 2012 represents one of the highest-level clades within the family Trypanosomatidae and, thus, corresponds to the subfamily rank. The revised Leishmaniinae *sensu* Shaw, Camargo et Teixeira, 2017 is a subdivision of the subdivision, and therefore should be regarded as a taxon of a lower rank.

To solve this issue, we propose the following: (i) leave the subfamily Leishmaniinae as originally defined; (ii) create two subordinate taxa in the rank of infrafamilies. The first infrafamily, Leishmaniatae, is a substitution for Leishmaniinae *sensu* Shaw, Camargo et Teixeira 2017; the second one, Crithidiatae, unites the genera *Crithidia*, *Leptomonas* and *Lotmaria* (Fig. 1). The rank 'infrafamily' is non-canonical and therefore no tradition exists for the formation of its ending. We selected *-atae* because it is harmonious and distinct enough from terminations of other ranks.

The only unresolved issue with such a system would be the nomenclature of *Leptomonas barvae* Maslov et Lukeš, 2010. It was assigned to the genus *Leptomonas* based on morphology and monoxenous life cycle. Nevertheless, it is phylogenetically distant from other *Leptomonas* spp. and has no close relatives in any other described genera (Maslov et al. 2010, Espinosa et al. 2017). Instead, it falls within the infrafamily Leishmaniatae and is sister to all other members of this group (Votýpka et al. 2012, Kostygov et al. 2014). We propose to erect a new genus, *Borovskyia*, to accommodate this species (Fig. 1). Several recently analysed environmental isolates from the Neotropics (Kozminsky et al. 2015) apparently belong to this genus as well (see Taxonomical section for details). The name honours Petr Borovsky (1863–1932), a Russian surgeon and bacteriologist, who first correctly characterised the causative agent of Oriental sore (cutaneous leishmaniasis) and ascribed it to Protozoa in 1898 (Borovsky 1898). This happened a few years earlier than William Boog Leishman, Charles Donovan and Ronald Ross did the same for *Leishmania donovani* (Laveran et Mesnil, 1903) and visceral leishmaniasis. Borovsky's priority was not internationally recognised until much later, because his observation was published in the low-circulation Russian Military-Medical Journal (Hoare 1938).

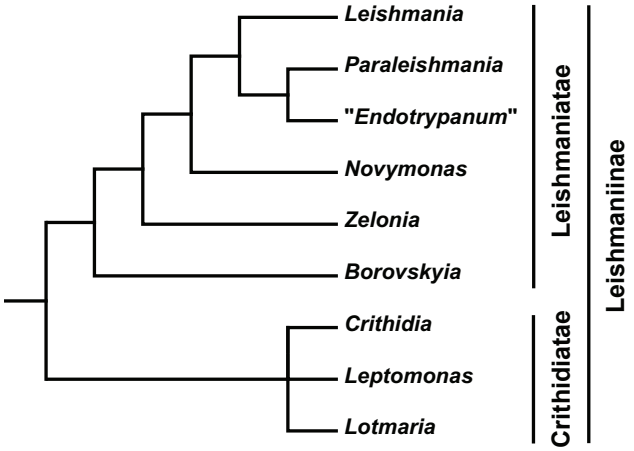

Fig. 1. Schematic phylogenetic tree of the subfamily Leishmaniinae summarised from previously published works. The uncertain status of the genus *Endotrypanum* is symbolised by the quotation marks.

ENDOTRYPANUM

The genus *Endotrypanum* was originally described to accommodate a novel trypanosomatid, *E. schaudinni* Mesnil et Brimont, 1908, residing in erythrocytes of two-toed sloth *Choloepus didactylus* (Linnaeus) (Mesnil and Brimont 1908). The second species in this genus, *E. monterogeii* Shaw, 1969, was described over 60 years later from *Choloepus* sp. (Shaw 1969). The main diagnostic trait for the genus *Endotrypanum* was its ability to infect erythrocytes of sloths (Mesnil and Brimont 1908, Darling 1914). Parasites were thought to be transmitted by phlebotomine sand flies (Shaw 1964, Christensen and Herrer 1976).

Subsequently, several laboratory strains were isolated from sloths or from the supposed insect vectors. Some of them were assigned to *E. schaudinni* and *E. monterogeii*, while others were described as *Leishmania* spp. (summarised in Espinosa et al. 2017). Importantly, all these flagellates differ from the parasites originally described under the name *Endotrypanum* in several key aspects. Firstly and most significantly, these strains were never shown to

infect erythrocytes in experimental infections. Secondly, they are morphologically distinct from the forms observed in sloth's blood (Shaw 1964, Franco and Grimaldi 1999).

The issue of these strains' identity was debated before (Cupolillo et al. 2000), but has not been satisfactorily resolved to date. We recognise that all the laboratory cultures currently assigned to *Endotrypanum* constitute a natural taxon. However, we cast doubt that it should be called *Endotrypanum.* We believe that transferring *L. colombiensis*, *L. equatoriensis* and *L. herreri* to the genus *Endotrypanum* without confirming their relationship to the intra-erythrocytic parasites was incorrect. This trait cannot be ignored. For the moment, it is the only link between the taxonomic name *Endotrypanum* and a particular group of trypanosomatids.

We prefer to leave the composition of this genus in the state proposed by Espinosa et al. (2017) and provisionally include all five species, since there is no direct evidence in favour or against such classification. For the reasons explained above, we also propose to refer *Endotrypanum* as a *nomen dubium* until its taxonomical status is clarified.

PARALEISHMANIA

The taxon names *Euleishmania* Cupolillo, Medina-Acosta, Noyes, Momen et Grimaldi, 2000 and *Paraleishmania* Cupolillo, Medina-Acosta, Noyes, Momen et Grimaldi, 2000 were proposed to designate two clades (sections) within the *Leishmania*/*Endotrypanum* group (Cupolillo et al. 2000). These names have been considered informal and disregarded in the recent classification (Espinosa et al. 2017). Nevertheless, in accordance with the International Code of Zoological Nomenclature (ICZN) article 10.4 'Availability of names for divisions of genera', both names are available and should be considered as subgeneric, i.e. names of genus-group taxa. As judged by the ICZN article 43.1 'Statement of the principle of coordination applied to genus-group names', the names *Euleishmania* and *Paraleishmania* were simultaneously established for all genus-group ranks (supergenus, genus, subgenus, etc.), while being used only for one of them. It means that these two names may compete with other names proposed for the genus-group taxa.

Since in the original publication proposing the names *Euleishmania* and *Paraleishmania* (see Cupolillo et al. 2000) type species were not designated, according to the ICZN article 69.1 'Type species by subsequent designation' the first author who subsequently designates one of the originally included species validly designates the type species of the nominal genus-group taxon, and no later designation is valid. As the first authors dealing with this problem, we fix here *Leishmania donovani* as the type species for *Euleishmania*. Given that *Euleishmania* contains the same type species as *Leishmania*, it falls into the synonymy with the latter regardless of the rank (genus, subgenus etc.). Consequently, the name *Euleishmania* is not valid and should not be used.

Concerning *Paraleishmania*, by the right of the first revisers, we fix *L. hertigi* as the type species. Since *Porcisia* has the same type species, and this name was proposed later, according to the ICZN article 23.1 'Statement of the principle of priority' it should be considered an objective junior synonym of *Paraleishmania* and therefore invalid. The fact that the names were proposed for taxa of different ranks and with different composition is not essential, since according to the ICZN articles 42.3 'Application of genus-group names', 43.1 'Statement of the principle of coordination applied to genus-group names', and 44 'Genus group: nominotypical taxa', all taxa within a genus group having the same type species must bear the same name. Then, in our system the name *Paraleishmania* is a substitute for the generic name *Porcisia*. The taxon *Paraleishmania* as defined by Cupolliloet al. (2000) may be regarded as a supergenus.

TAXONOMICAL SUMMARY

Taxonomical changes are underlined; included species are not listed for *Crithidia*, *Leishmania*, *Leptomonas* and *Lotmaria*.

Class **Kinetoplastea** Honigberg, 1963
Subclass **Metakinetoplastina** Vickerman, 2004
Order **Trypanosomatida** Kent, 1880
Family **Trypanosomatidae** Doflein, 1901
Subfamily **Leishmaniinae** Maslov et Lukeš in Jirků et al., 2012

Infrafamily **Leishmaniatae** Maslov et Lukeš in Jirků et al., 2012 **infrafam. n.**

ZooBank number for infrafamily:
urn:lsid:zoobank.org:act:5BCFBF2E-280C-44C5-8C93-E02AAEA0A86B

Remarks. The authorship of the nominotypical infrafamily is given is accordance with ICZN article 37 'Family group: nominotypical taxa'.

Genus ***Leishmania*** Ross, 1908, syn. *Euleishmania*

Type species: *Leishmania donovani* (Laveran et Mesnil, 1903).

Genus ***Paraleishmania*** Cupolillo, Medina-Acosta, Noyes, Momen et Grimaldi, 2000

Type species: *Paraleishmania hertigi* (Herrer, 1971), syns. *Leishmania hertigi*, *Porcisia hertigi.*

Additional species: *P. deanei* (Lainson et Shaw, 1977).

Genus ***Endotrypanum*** Mesnil et Brimont, 1908, *nomen dubium*

Type species: *Endotrypanum schaudinni* Mesnil et Brimont, 1908.

Additional species: *E. monterogeii* Shaw, 1969, *E. colombiensis* (Kreutzer, Corredor, Grimaldi, Grogl, Rowton, Young, Morales, McMahon-Pratt, Guzman et Tesh, 1991), *E. equatoriensis* (Grimaldi, Kreutzer, Hashiguchi, Gomez, Mimory et Tesh, 1992) and *E. herreri* (Zeledon, Ponce et Murillo, 1979).

Remarks. Affiliation of the type species *E. schaudinni* with the subfamily Leishmaniinae is questionable.

Genus ***Zelonia*** Shaw, Camargo et Teixeira in Espinosa et al., 2017

Type species: *Zelonia costaricensis* (Yurchenko, Lukeš, Jirků, Zeledon et Maslov, 2006).

Additional species: *Z. australiensis* Barratt, Kaufer et Ellis, 2017.

Genus ***Novymonas*** Kostygov et Yurchenko, 2015

Type and only species: *Novymonas esmeraldas* Votýpka, Kostygov, Maslov et Lukeš, 2015.

Genus ***Borovskyia*** **gen. n.**

ZooBank number for genus:
urn:lsid:zoobank.org:act:4CC529D2-FD9F-4F83-BA01-6924F16853E

Type and only species: *Borovskyia barvae* comb. n. (Maslov et Lukeš, 2010), syn. *Leptomonas barvae.*

Remarks. Based on the sequences of SL RNA (KP717771, KP717772, KP717882, KP717883, KP717885, KP717893, and KR056278), the environmental samples of Typing Units 94, 102, 143, 144 and 160 also belong to the genus *Borovskyia*.

Infrafamily **Crithidiatae infrafam. n.**

ZooBank number for infrafamily:
urn:lsid:zoobank.org:act:BA61A592-5C28-48A8-861F-0031F7D890EF

Genus ***Crithidia*** Léger, 1902

Type species: *Crithidia fasciculata* Léger, 1902.

Genus ***Leptomonas*** Kent, 1880

Type species: *Leptomonas buetschlii* Kent, 1880.

Genus ***Lotmaria*** Evans et Schwarz, 2014

Type species: *Lotmaria passim* Schwarz, 2014.

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REFERENCES

d'Avila-Levy C.M., Boucinha C., Kostygov A., Santos H.L., Morelli K.A., Grybchuk-Ieremenko A., Duval L., Votýpka J., Yurchenko V., Grellier P., Lukeš J. 2015: Exploring the environmental diversity of kinetoplastid flagellates in the high-throughput DNA sequencing era. Mem. Inst. Oswaldo Cruz 110: 956–965.

Baker J.R. 1963: Speculations on the evolution of the family Trypanosomatidae Doflein, 1901. Exp. Parasitol. 13: 219–233.

Borovsky P.F. 1898: [On sart sore]. Rus. Mil. Med. J. 11: 925. (In Russian.)

Christensen H.A., Herrer A. 1976: Neotropical sand flies (Diptera: Psychodidae), invertebrate hosts of *Endotrypanum schaudinni* (Kinetoplastida: Trypanosomatidae). J. Med. Entomol. 13: 299–303.

Cupolillo E., Medina-Acosta E., Noyes H., Momen H., Grimaldi G. Jr. 2000: A revised classification for *Leishmania* and *Endotrypanum*. Parasitol. Today 16: 142–144.

Darling S.T. 1914: The *Endotrypanum* of Hoffman's sloth. J. Med. Res. 31: 195–204 191.

Espinosa O.A., Serrano M.G., Camargo E.P., Teixeira M.M., Shaw J.J. 2017: An appraisal of the taxonomy and nomenclature of trypanosomatids presently classified as *Leishmania* and *Endotrypanum*. Parasitology: (in press). DOI: https://doi.org/10.1017/S0031182016002092

Flegontov P., Butenko A., Firsov S., Kraeva N., Eliáš M., Field M.C., Filatov D., Flegontova O., Gerasimov E.S., Hlaváčová J., Ishemgulova A., Jackson A.P., Kelly S., Kostygov A., Logacheva M.D., Maslov D.A., Opperdoes F.R., O'Reilly A., Sádlová J., Ševčíková T., Venkatesh D., Vlček Č., Volf P., Votýpka J., Záhonová K., Yurchenko V., Lukeš J. 2016: Genome of *Leptomonas pyrrhocoris*: a high-quality reference for monoxenous trypanosomatids and new insights into evolution of *Leishmania*. Sci. Rep. 6: 23704.

Franco A.M., Grimaldi G. Jr. 1999: Characterization of *Endotrypanum* (Kinetoplastida: Trypanosomatidae), a unique parasite infecting the neotropical tree sloths (Edentata). Mem. Inst. Oswaldo Cruz 94: 261–268.

Hoare C.A. 1938: Early discoveries regarding the parasite of Oriental sore (with an English translation of the memoir by P. F. Borovsky: "On Sart sore." 1898). Trans. R. Soc. Trop. Med. Hyg. 32: 67–92.

Jirků M., Yurchenko V.Y., Lukeš J., Maslov D.A. 2012: New species of insect trypanosomatids from Costa Rica and the proposal for a new subfamily within the Trypanosomatidae. J. Eukaryot. Microbiol. 59: 537–547.

Kostygov A.Y., Grybchuk-Ieremenko A., Malysheva M.N., Frolov A.O., Yurchenko V. 2014: Molecular revision of the genus *Wallaceina*. Protist 165: 594–604.

Kozminsky E., Kraeva N., Ishemgulova A., Dobáková E., Lukeš J., Kment P., Yurchenko V., Votýpka J., Maslov D.A. 2015: Host-specificity of monoxenous trypanosomatids: statistical analysis of the distribution and transmission patterns of the parasites from Neotropical Heteroptera. Protist 166: 551–568.

Kraeva N., Butenko A., Hlaváčová J., Kostygov A., Myškova J., Grybchuk D., Leštinová T., Votýpka J., Volf P., Opperdoes F., Flegontov P., Lukeš J., Yurchenko V. 2015: *Leptomonas seymouri*: adaptations to the dixenous life cycle analyzed by genome sequencing, transcriptome profiling and co-infection with *Leishmania donovani* PLOS Pathog. 11: e1005127.

Lukeš J., Skalický T., Týč J., Votýpka J., Yurchenko V. 2014: Evolution of parasitism in kinetoplastid flagellates. Mol. Biochem. Parasitol. 195: 115–122.

Lumsden W.H.R., Evans D.A. 1976: Biology of Kinetoplastida. Academic Press, London, 563 pp.

Martinez-Calvillo S., Vizuet-de-Rueda J.C., Florencio-Martinez L.E., Manning-Cela R.G., Figueroa-Angulo E.E. 2010: Gene expression in trypanosomatid parasites. J. Biomed. Biotechnol. 2010: 525241.

Maslov D.A., Votýpka J., Yurchenko V., Lukeš J. 2013: Diversity and phylogeny of insect trypanosomatids: all that is hidden shall be revealed. Trends Parasitol. 29: 43–52.

Maslov D.A., Yurchenko V.Y., Jirků M., Lukeš J. 2010: Two new species of trypanosomatid parasites isolated from Heteroptera in Costa Rica. J. Eukaryot. Microbiol. 57: 177–188.

Mesnil F., Brimont E. 1908: Sur un hématozoaire nouveau (*Endotrypanum* n. gen.) d'un édenté de la Guyane C.R. Séances Soc. Biol. Ses. Fil. 65: 581–583.

Opperdoes F.R., Butenko A., Flegontov P., Yurchenko V., Lukeš J. 2016: Comparative metabolism of free-living *Bodo saltans* and parasitic trypanosomatids. J. Eukaryot. Microbiol. 63: 657–678.

Schwarz R.S., Bauchan G.R., Murphy C.A., Ravoet J., de Graaf D.C., Evans J.D. 2015: Characterization of two species of Trypanosomatidae from the honey bee *Apis mellifera*: *Crithidia mellificae* Langridge and McGhee, and *Lotmaria passim* n. gen., n. sp. J. Eukaryot. Microbiol. 62: 567–583.

Shaw J.J. 1964: A possible vector of *Endotrypanum schaudinni* of the sloth *Choloepus hoffmanni*, in Panama. Nature 201: 417–418.

Shaw J.J. 1969: The Haemoflagellates of Sloths. H. K. Lewis, London, 132 pp.

Stuart K., Panigrahi A.K. 2002: RNA editing: complexity and complications. Mol. Microbiol. 45: 591–596.

Vickerman K. 1976: Comparative cell biology of the kinetoplastid flagellates. In: K. Vickerman and T.M. Preston (Eds.), Biology of Kinetoplastida. Academic Press, London, pp. 35–130.

Votýpka J., d'Avila-Levy C.M., Grellier P., Maslov D.A., Lukeš J., Yurchenko V. 2015: New approaches to systematics of Trypanosomatidae: criteria for taxonomic (re)description. Trends Parasitol. 31: 460–469.

Votýpka J., Klepetková H., Yurchenko V.Y., Horák A., Lukeš J., Maslov D.A. 2012: Cosmopolitan distribution of a trypanosomatid *Leptomonas pyrrhocoris*. Protist 163: 616–631.

Wallace F.G. 1966: The trypanosomatid parasites of insects and arachnids. Exp. Parasitol. 18: 124–193.

Záhonová K., Kostygov A., Ševčíková T., Yurchenko V., Eliáš M. 2016: An unprecedented non-canonical nuclear genetic code with all three termination codons reassigned as sense codons. Curr. Biol. 26: 2364–2369.

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