A new nematode, *Pongobius hugoti* gen. et sp. n. from the orangutan *Pongo abelii* (Primates: Hominidae)

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Summary

Light and scanning electron microscopical examination and molecular analysis of pinworm samples collected from the Sumatran orangutan (*Pongo abelii*) from Sumatra (Indonesia) revealed the presence of a new taxon, *Pongobius hugoti* gen. et sp. n. (Oxyuridae: Enterobiinae). The monotypic genus *Pongobius* is characterised by the presence of a triangular mouth, three rounded teeth and three chisel-like inner teeth in the buccal cavity, an oesophagus with a long pharyngeal part, corpus posteriorly slightly enlarged and continuing as a pyriform bulb, isthmus absent. These features differentiate *P. hugoti* from all members of the subfamily Enterobiinae. The male has a long caudal appendix (> 50% of total tail length). Molecular analysis of the new taxon is presented for more precise identification.

Key words: *Pongobius hugoti* gen. et sp. n.; Nematoda; *Pongo abelii*; orangutan; Sumatra; morphometric and molecular analyses

Introduction

The Sumatran orangutan, *Pongo abelii* Lesson, 1827, is distributed in Sumatra NW of Lake Toba (Wilson & Reeder, 2005). From the critically-endangered great apes of the genus *Pongo* Lacépède, 1799, three pinworm species have been reported: *Enterobius buckleyi* Sandosham, 1950; *E. foecundus* (Linstow, 1879) and *E. simiae* (Mac Callum, 1921) according to Inglis (1961), Yamashita (1963) and Hugot (1999). Skrjabin *et al.* (1960) noted in this host the species *E. anthropopitheci* (Geddoelst, 1916); however, it is restricted to chimpanzees *Pan troglodytes* (Blumenbach, 1775) and *P. paniscus* Schwartz, 1929 as stated by Hugot (1993) and Hasegawa *et al.* (2005). Close

examination of pinworms collected from orangutans from Sumatra led to the conclusion that they represent a new species and a new genus of the subfamily Enterobiinae Hugot, Gardner *et* Morand, 1996. Herein we describe and differentiate the new taxon, discovered following a long term project “Parasites and Natural Antiparasitics in Orangutan” conducted in Indonesia since 1999.

Material and Methods

The locality of investigation, the village Bukit Lawang (former Rehabilitation Center for Orangutans) is on the Southwest border of Gunung Leuser National Park (Northern Sumatra, Indonesia) (03°32.983' N, 098°06.908' E) at an altitude of 1061 ft. Temperatures range between 21°C and 28°C with humidity between 80 % and 100 %. Annual rainfall is 2,000 – 3,200 mm. The majority of orangutans in this area live in a semi-wild population. From the fresh faeces of two adult female orang-utans, several worms were collected in 2002 and immediately fixed in 40 % ethanol. For light microscopical examination, the nematodes were cleared gradually in glycerin and examined under a light microscope equipped with differential interference contrast (DIC), digital image analysis system (Micro Image 4.0 for Windows), and a drawing attachment was used for morphometric analysis. Parasites used for scanning electron microscopy (SEM) were washed several times in 0.6 % saline, fixed with hot 4 % formaldehyde solution and stored at room temperature. Prior to analysis, they were dehydrated through an ethanol series, dried in a CPD 030 critical point drying apparatus (Bal-tec) using liquid CO₂, mounted on aluminium stubs with double-sided adhesive discs, coated with gold in a SCD 040 sputter coating unit (Balzers) and examined in a VEGA scan-

ning electron microscope operating at 20 kV. Genomic DNA was extracted from ethanol-preserved tissues. DNA using the DNeasy Tissue Kit (QIAGEN). The partial 18S rDNA was amplified using the Mastercycler ep gradient S (Eppendorf) in a finale volume 30µl PCR reaction. Each amplification reaction contained 1X buffer, 1.5mM MgCl₂, 200 µM dNTPs, 0.5 unit of *Taq* polymerase (Fermentas) and 0.5 µM of each primer – Nem 18SF and Nem 18SR designed by Floyd *et al.* (2005). PCR was carried out with the following steps: an initial denaturation at 94 °C for 5 minutes, 35 cycles of 94 °C for 30 seconds, 54 °C for 30 seconds and 72 °C for 1 minute and final extension at 72 °C for 10 minutes. PCR products were separated on 1.5 % agarose gel. PCR products were purified by Wizard® SV Gel and PCR Clean-Up System (Promega) and sent for sequencing to Macrogen, Inc. (Korea) (for details see www.macrogen.com). Sequences were analysed using Sequencher software (Gene Codes Corporation).

Results

Nematoda

Oxyuridae Cobbold, 1864

Enterobiinae Hugot, Gardner et Morand, 1996

Pongobius n. gen.

Diagnosis: Oxyuridae, Enterobiinae. Body fusiform, medium sized. Mouth opening triangular, surrounded by three lips (wider than long). Lips distinctly separate from the head cuticular vesicle. Two nearby hemispherical papillae situated near base of dorsal lip. Each subventral lip bears a hemispherical papilla near ventral rim, and other papilla near lateral rim of lip, with conspicuous amphid opening. Mouth cavity contains three large teeth identical in form and shape. Dental apparatus complex is characterized by three inner chisel-like teeth. Oesophagus with long pharyngeal part, corpus posteriorly slightly enlarged and continuing in pyriform bulb with bulbar apparatus, opening

Plate I. *Pongobius hugoti* sp. n. from *Pongo abelii*

1. Cephalic end of female; 2. Vulva region - lateral view; 3. Tail end of female - ventrolateral view; 4. Cephalic end of male; 5. Cephalic end of male - apical view, reconstructed from SEM micrographs; 6. Male - total lateral view; 7. Posterior extremity of male - lateral view; 8. spicule - lateral view

(Scale-bars: 1, 2, 4 = 200 µm; 3, 6 = 500 µm; 5 = 20 µm; 7 = 50 µm; 8 = 100 µm)

Plate II. *Pongobius hugoti* sp. n. from *Pongo abelii*, scanning electron micrographs

1. Cephalic end of female, apical view; 2. Cephalic end, lateroventral view; 3. Lateroventral lip, apical view (arrow: rugose circumoral zone); 4. Anus - detail, ventral view; 5. Tail of female, total view; 6. Egg, total view; 7. Egg - detail of subpolar plug; 8. Male, lateral view; 9. Detail of tail of male, lateral view (arrow: tail appendix)

(Scale-bars: 1, 4, 9 = 100 μ m; 2, 6 = 20 μ m; 3 = 25 μ m; 5 = 1000 μ m; 7 = 10 μ m; 8 = 500 μ m)

into intestine through small valves. Isthmus absent. Excretory pore postbulbar.

Male: Lateral alae with single crest; four pairs of caudal papillae, first and fourth pedunculate and support the bursa; and second and third pairs sessile, flanking slit-like opening of cloaca. Tubes of the phasmids begin at base of peduncles of fourth pair of caudal papillae. Each papilla of

second pair is surrounded by ornamentation, which encircles third pair of genital papillae. Tail appendix present. Single spicule present, with wide manubrium.

Female: Lateral alae with double crest, suddenly widening from bulb base. Vulva pre-equatorial, followed by muscular vagina and uterine tube divided into two parts by cellular wall, forming diaphragm; no spermatheca observed.

Eggs numerous, with three longitudinal thickenings; operculum subterminal, has a coarsely granulated texture, an irregular elliptical shape; and extends about one-quarter of total length of eggs. Tail long. (Plate I, II, III).

Pongobius hugoti sp. n.

Description: General. Medium sized, whitish nematodes. Cuticle with clear transverse striations; cephalic vesicle present and well developed with transverse markings. Lateral alae present. Mouth triangular, surrounded by three lips; cuticular circle ornamented by slightly rugose structure present in its base. Dorsal lip with two hemispherical papillae; two subventral lips each with two cephalic papillae, one of them with amphideal pore (Plate I/5, II/1, 2). Papillae separated from lip surface by fine incision. In buccal cavity, dental apparatus present, corresponding to respective lips, and consists of three wide and obtuse teeth apposed to lips and three inner chisel-like teeth protruding into buccal cavity (Plate II/2). Oesophagus with distinct muscular pharynx, corpus continuing to bulb, isthmus totally absent.

Female (10 specimens; measurements of holotype in parentheses; 9 paratypes, range and mean $\pm$ S.D.). Lateral alae with double crest, suddenly widening from bulb base (Plate III). Length of body 6.21 – 9.33; 8.32 ± 0.99 (9.19) mm; maximum width 466 – 750; 650 ± 97.45 (777); width at bulb 343 – 467; 411 ± 63.77 (515); at vulva 499 – 750;

645 ± 87.13 (739) μ m; at anus 215 – 312; 272 ± 42.39 (354); cephalic vesicle length 94 – 142; 116 ± 16.75 (110); cephalic vesicle width 104 – 196; 169 ± 27.33 (179). Total oesophagus length 509 – 598; 556 ± 30.13 (594); pharynx length 127 – 158; 142 ± 10.96 (132); width 58 – 82; 70 ± 8.04 (70); corpus length 139 – 200; 176 ± 21.76 (157); corpus width 62 – 107; 82 ± 14.25 (89); bulb length 194 – 278; 241 ± 39.61 (308); bulb width 138 – 304; 233 ± 62.84 (314). Nerve ring 170 – 260; 206 ± 36.84 (237); excretory pore 772 – 1045; 941 ± 91.42 (941), vulva 1497 – 2554; 2022 ± 276.59 (2085) from anterior extremity. Oviduct directed posteriorly, vagina very muscular, 184 – 492; 353 ± 96.32 (442) long, and 68 – 158; 121 ± 24.75 (132) wide. Vagina uterina divided into 2 portions by thick cellular wall (diaphragm) (Plate I/2). Distance between vulva and diaphragm longer than diaphragm and uterine opening. Amphidelphic. Tail long, conical, with pointed apex, 1251 – 1969; 1638 ± 275.29 (2087) (Plate I/3, II/4, 5).

Eggs ($n = 35$) ellipsoidal, with flattened side, 41 – 50; 45 ± 2.50 (44 – 46) long and 19 – 26; 23 ± 2.40 (22 – 23) wide, having three longitudinal thickenings (Plate II/6, 7; III/6, 7, 8). Ratios: Total body length/total oesophagus length 10.96 – 16.60; 14.96 ± 1.63 (15.48); total oesophagus length / pharynx length 3.44 – 4.60; 3.92 ± 0.48 (4.50); total body length / tail length 4.41 – 5.75; 5.07 ± 0.45 (4.41); total body length / vulva distance from anterior extremity 3.49 –

Plate III. *Pongobius hugoti* sp. n. from *Pongo abelii*, lateral alae and eggs

1. SEM – at level of oesophagus end, transition from narrower to wider part of lateral ala; 2. Beginning of ala, transverse section;
 3. Shaping of two crests of ala before their enlargement;
 4. Lateral ala with double crest, middle part of body; 5. Lateral ala, caudal part of body; 6. Transverse section of egg; 7. Longitudinal section of egg;
 8. Longitudinal section of egg, egg pole with granular structure
- (Scale-bars: 1 = 100 μ m; 3, 4, 5 = 25 μ m; 2, 6, 7, 8 = 20 μ m)

5.15; 4.26 ± 0.50 (4.39).

Male (1 specimen; allotype)

Lateral alae with single crest beginning halfway between anterior extremity and nerve ring, and ending before caudal bursa (Plate II/8). Oesophagus ending in pyriform bulb; isthmus absent (Plate I/6). Length of body 2.69 mm, maximum width 239; width at bulb 167, width at excretory pore 226; at cloaca 49. Cephalic vesicle length 126, width 98. Total length of oesophagus 367, pharynx length 97,

width 32; length of corpus 156, width 31; bulb length 103, width 92. Nerve ring 116, excretory pore 722 from anterior extremity. Four pairs of caudal papillae present, first and fourth pairs pedunculate, second and third pairs sessile, flanking cloacal aperture (Plate I/7, II/9). Phasmidial tubes begin near origin of peduncles of fourth pair, rooted into long and fine conical tail, 104 long; tip of tail 80 long. One spicule present, well sclerotized, 104 long, with proximal manubrium 10 wide. Spicule width in middle part 7, distal

Plate IV. The females oesophagus form in genera and subgenera of the Enterobiinae. Not to same scale.

1. *Enterobius* (*E. vermicularis* L., 1758) - according to Skrjabin and Schulz 1928, in Skrjabin *et al.* (1960); 2. *Colobenterobius* (*C. guerezae* Hugot, 1987) - according to Hugot (1987); 3. *Xeroxyuris* (*X. parallela* Linstow, 1908) - according to Hugot (1995); 4. *Trypanoxyuris* (*T. trypanoxyuris* Vevers, 1923) - according to Hugot (1985); 5. *Hapaloxyuris* (*H. goeldii* Inglis et Gosgrove, 1965) - according to Hugot (1984b); 6. *Oxyuronema* (*O. atelophora* Kreis, 1932) - according to Hasegawa *et al.* (2004); 7. *Buckleyenterobius* (*B. atelis* Cameron, 1929) - according to Hasegawa *et al.* (2004); 8. *Rodentoxyuris* (*R. sciuri* Cameron, 1932) - according to Hugot (1984a); 9. *Pongobius* gen. n. (*P. hugoti* sp. n. - original); 10. *Lemuricola* (*L. microcebi* Hugot, Morand et Gardner, 1995) according to Hugot *et al.* (1995); 11. *Protenterobius* (*P. nycticebi* Baylis, 1928) - according to Inglis (1961); 12. *Madoxyuris* (*M. daubentoniae* Petter, Chabaud, Delavenay et Brygoo, 1972) - according to Petter *et al.* (1972); 13. *Inglisoxuris* (*I. inglisi* Chabaud, Petter et Golvan, 1961) - according to Chabaud *et al.* (1961)

part in form of small hook (in lateral view), with sharp point 4 long (Plate I/8). Ratios: Total body length/total oesophagus length 7.23; total oesophagus length/pharynx length 3.78; total body length/tail length 25.77; total oesophagus length/spicule length 3.51.

Molecular analyses

Six individuals were used for molecular analysis. The fragment of 18S rDNA, 910 bp length, was amplified. The fragment of 782 bp was readable after sequencing and used for our study. No intraspecific nucleotide variability was observed among the individuals studied. The significant alignment was produced in BLAST (<http://www.ncbi.nlm.nih.gov>) with 100 sequences of different nematode species including representatives of the Rhigonematida, Ascaridida, Rhabditida and Spirurida. The similarity between the sequence of *P. hugoti* sp. n. and other nematode sequences included in alignment ranged between 83 % and 88 % with the proportion of gaps ranging from 3 % to 5 %. Distance trees using neighbour joining and fast minimum evolution methods produced by BLAST did not resolve the phylogenetic position of the sequenced pinworm. The sequence of *P. hugoti* sp. n. was deposited in GenBank database (<http://www.ncbi.nlm.nih.gov>), accession number EU022678.

Type – host: *Pongo abelii* (Primates: Hominidae)

Site of infection: Intestine (discharged in faeces)

Type locality: North Sumatra, Bukit Lawang (03°32.983' N, 098°06.908' E)

Number of specimens studied: measured 11 (one male, ten females); SEM 5 (one male, four females); molecular analyses 6 females.

Type material: Holotype, allotype and paratypes in the helminthological collection of the Institute of Parasitology, ASCR, in České Budějovice (Cat. No. N-882) and 5 specimens in the Department of Parasitology, Gadjah Mada University, Yogyakarta, Indonesia.

Etymology: The generic name *Pongobius* relates to generic name of the host (the great ape *Pongo*), with the suffix *bius* which is the same as the name of the type genus (*Enterobius*). The species is named for the distinguished French helminthologist Dr. J. P. Hugot, who contributed greatly to the knowledge of systematics and taxonomy in oxyurids parasitising primates and other mammals.

Discussion

Pinworms represent the parasite group occurring in most families and genera of the order Primates. The subfamily Enterobiinae includes 47 species of pinworms parasitising primates, and three species parasitising rodents (see Quentin & Tenora, 1975; Hugot, 1984a, b, 1995, 1999; Hugot *et al.*, 1996; Sorci *et al.*, 1997; Hugot & Baylac 2007). Recently Hasegawa *et al.* (2002, 2003) described two new species of pinworms from monkeys.

A cladistic analysis made by Hugot (1999) confirmed the monophyly of the subfamily, and also the monophyly of three main genera (or groups of genera and related subgenera). We accept, according to Hugot *et al.* (1996), Hugot (1999), Hasegawa *et al.* (2004), and Hugot and Baylac

(2007), the following generic or subgeneric units: 1. *Enterobius* Leach, 1853; 2. *Colobenterobius* Quentin, Beter-ton et Krishasamy, 1979; 3. *Xeroxyuris* Hugot, 1995; 4. *Madoxyuris* Chabaud, Brygoo et Petter, 1959; 5. *Rodentoxuris* Quentin et Tenora, 1974; 6. *Lemuricola* Chabaud et Petter, 1959 (syn. *Biguetius* Chabaud, Brygoo et Petter, 1965); 7. *Protenterobius* Inglis, 1961; 8. *Trypanoxyuris* Vevers, 1923 (syn. *Lobatorobius* Skrjabin et Schikhobalova, 1959); 9. *Hapaloxuris* Inglis et Cosgrove, 1965; 10. *Oxyuronema* Kreis, 1932 (syn. *Paraoxyuronema* Artigas, 1936 pro parte, sensu Hugot *et al.* 1996); 11. *Buckleyenterobius* Sandosham, 1950 (syn. *Odontorobius* Skrjabin et Schikhobalova, 1951; *Paraoxyuronema* Artigas, 1936 pro parte, sensu Hugot *et al.* 1996). The monotypic genus *Inglisoxuris* Chabaud, Petter et Golvan, 1961 was previously classified as a subgenus of *Lemuricola*. According to Hugot *et al.* (1996), the species *I. inglisi* does not share the characters of the subfamily Enterobiinae, and until its precise classification it should be referred to this species as an Oxyuridae *sensu lato*.

The general morphology of *Pongobius hugoti* sp. n. from *Pongo abelii* clearly indicates that the species belongs to the Enterobiinae. It differs from all species of the subfamily in having a long pharynx and an oesophagus without an isthmus (Plate IV). We believe, like Hasegawa *et al.* (2004), that the characteristic form of the oesophagus in both sexes is a significant systematic trait. The male of *P. hugoti* sp. n. has a long caudal appendix, similar to that in *Lemuricola*; species of other genera - *Protenterobius*, *Trypanoxyuris*, *Hapaloxuris*, *Oxyuronema*, *Buckleyenterobius*, *Rodentoxuris* and *Inglisoxuris* – have a markedly shorter caudal appendix (< 50% of total tail length). Species of *Enterobius* and *Colobenterobius* have no tail or caudal appendix, *Madoxyuris* and *Xeroxyuris* also lack a caudal appendix (see Quentin & Tenora, 1975; Quentin *et al.*, 1979; Hugot, 1984a, b, 1985, 1987, 1995; Hugot & Tourte-Schaeffer, 1985). *P. hugoti* sp. n. differs from species of *Lemuricola* in a relatively shorter posterior part with phasmids slightly posterior to the juxta-cloacal papillae, similar to *Protenterobius* (see Hugot & Baylac, 2007). The cephalic and buccal characters of the Enterobiinae are of species and generic significance (Tenora *et al.*, 1981; Hugot *et al.*, 1996). In the presence of three obtuse buccal teeth, and three well-developed inner chisel-like teeth *P. hugoti* sp. n. differs distinctly from all genera (and subgenera) of the Enterobiinae (survey in Hugot *et al.*, 1996; Hasegawa *et al.*, 2004). The general morphology of our parasites indicates they are closely related to species of *Lemuricola* and *Protenterobius*, but its specific morphology (mainly the form of the oesophagus, head and teeth structures) differentiates it from all primate pinworms (Enterobiinae). Therefore, a new genus and species are proposed for the nematode. The molecular analysis of the new taxon was investigated for more precise identification. As mentioned above, the following nominal taxa were found in the orangutan: *E. buckleyi*, *E. foecundus*, and *E. simiae*, all having a short but obvious oesophageal isthmus. The first two species differ from the new species by the

absence of the tail appendix. *E. simiae* was correctly considered as a *species inquirenda* by Sandosham (1950). Inglis (1961) preferred to consider this species, and probably also *E. foecundus*, as *nomina dubia*. According to the original description by Sandosham (1950), *E. buckleyi*, parasitising the Bornean orangutan *Pongo pygmaeus* (Linnaeus, 1760), differs from *Pongobius hugoti* sp. n. by the longer oesophagus (male 570, female 900-990), spicule length (122) with rounded distal tip, larger eggs (56x26), and location of vulva nearer the middle of the body (ratio body length/vulva distance of anterior extremity = 1 : 1.70 – 1.78).

Due to the relatively high differences between the partial 18S rDNA sequences of *P. hugoti* sp. n. compared to other nematode species available in GenBank, we propose that this marker could be applied for molecular identification of *P. hugoti* sp. n. However, analyses of closely related species from the genera *Lemuricola* or *Protenterobius* should be performed to estimate the level of interspecific variability. Moreover, we suggest the need for broader phylogenetic analyses of a range of nematode species to solve the phylogenetic position of *Pongobius hugoti* sp. n. For further molecular analyses, we also propose to analyse the mitochondrial cytochrome *c* oxidase subunit 1 (CO1) gene and nuclear internal transcribed spacer 2 rDNA (ITS2) region of *Pongobius hugoti* sp. n. The analyses of those genes were recently applied for the molecular identification of *Enterobius vermicularis* and the phylogenetic analyses of pinworms in humans and chimpanzees (Nakano *et al.*, 2006).

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References

CHABAUD, A. G., PETTER, A. J., GOLVAN, Y. (1961): Les nematodes parasites de lémuriens Malgaches III. Collection récoltée par M. et Mme Francis Petter. *Ann. Parasit. Hum. Comp.*, 36: 113 – 126
 FLOYD, R. M., ROGERS, A. D., LAMBSHEAD, J. D., SMITH, C. (2005): Nematode-specific PCR primers for the 18S small subunit rRNA gene. *Mol. Ecol. Notes*, 5: 611 – 612
 HASEGAWA, H., MATSUO, K., ONUMA, M. (2003): *Enterobius (Colobenterobius) serratus* sp. nov. (Nematoda: Oxyuridae) from the Proboscis Monkey, *Nasalis larvatus* (Wurmb, 1787) (Primates: Cercopithecidae: Colobinae), in Sarawak, Borneo, Malaysia. *Comp. Parasitol.*, 70: 128 – 131

HASEGAWA, H., MURATA, K., ASAKAWA, M. (2002): *Enterobius (Colobenterobius) pygathrichus* sp.n. (Nematoda: Oxyuridae) Collected from a Golden Monkey *Pygathrix roxellana* (Milne-Edwards, 1870) (Primates: Cercopithecidae: Colobinae). *Comp. Parasitol.*, 69: 62 – 65
 HASEGAWA, H., IKEDA, Y., DIAZ-AQUINO, D.J.J., FUKUI, D. (2004): Redescription of two pinworms from the black-handed spider monkey, *Ateles geoffroyi*, with reestablishment of *Oxyuronema* and *Buckleyenterobius* (Nematoda: Oxyuroidea). *Comp. Parasitol.*, 71: 166 – 174
 HASEGAWA, H., IKEDA, Y., FUJISAKI, A., MOSCOVICE, L.R., PETRZELKOVA, K. J., KAUR, T., HUFFMAN, M.A. (2005): Morphology of chimpanzee pinworms, *Enterobius (Enterobius) anthropopitheci* (Geddoelst, 1916) (Nematoda: Oxyuridae), collected from Chimpanzees, *Pan troglodytes*, on Rubondo Island, Tanzania. *J. Parasitol.*, 91: 1314 – 1317
 HUGOT, J.P. (1984a): Sur le genre *Trypanoxyuris* (Oxyuridae, Nematoda): I. Parasites de Sciuridés: sous-genre *Rodentoxyuris*. *B. Mus. Natl. Hist. Nat., Série A, Zoologie*, 6: 711 – 720
 HUGOT, J. P. (1984b): Sur le genre *Trypanoxyuris* (Oxyuridae, Nematoda) II. Sous-genre *Hapaloxxyuris* parasites de Primates Callitrichidae. *B. Mus. Natl. Hist. Nat., Série A, Zoologie*, 6: 1007 – 1019
 HUGOT, J. P. (1985): Sur le genre *Trypanoxyuris* (Oxyuridae, Nematoda) III. Sous-genre *Trypanoxyuris* parasite de primates Cebidae et Atelidae. *B. Mus. Natl. Hist. Nat., Série A, Zoologie*, 7: 131 – 155
 HUGOT, J. P. (1987): Sur le genre *Enterobius* (Oxyuridae, Nematoda): s.g. *Colobenterobius* I. Parasites de Primates Colobinae en region éthiopienne. *B. Mus. Natl. Hist. Nat., Série A, Zoologie*, 9: 341 – 352
 HUGOT, J. P. (1993): Redescription of *Enterobius anthropopitheci* (Geddoelst, 1916) (Nematoda, Oxyuroidea), a parasite of chimpanzees. *Syst. Parasit.*, 26: 201 – 207
 HUGOT, J. P. (1995): Redescription of *Xeroxyuris parallela* (Linstow, 1908) n. gen., n. cb., parasite of *Xerus inauris*. *Parasite*, 2: 1 – 7
 HUGOT, J. P. (1999): Primates and their pinworm parasites: Cameron hypothesis revisited. *Syst. Biol.*, 48: 523 – 546
 HUGOT, J. P., BAYLAC, M. (2007): Shape patterns of genital papillae in pinworms (Enterobiinae, Oxyurida, Nematoda) parasite of primates: A landmark analysis. *Inf. Gen. Evol.*, 7: 168 – 179
 HUGOT, J. P., TOURTE-SCHAFFER, C. (1985): Etude morphologique des deux oxyures parasites de l'Homme: *Enterobius vermicularis* et *E. gregorii*. *Ann. Parasit. Hum. Comp.*, 60: 57 – 64
 HUGOT, J. P., GARDNER, S. L., MORAND, S. (1996): The Enterobiinae subfam. nov. (Nematoda, Oxyurida) pinworm parasites of primates and rodents. *Int. J. Parasitol.*, 26: 147 – 159
 HUGOT, J. P., MORAND, S., GARDNER, S. L. (1995): Morphology and morphometric of three oxyurids parasitic in primates with a description of *Lemuricola microcebi* n.sp. *Int. J. Parasitol.*, 25: 1065 – 1075
 INGLIS, W. G. (1961): The oxyurids parasites (Nematoda)

of primates. *P. Zool. Soc. Lond.*, 136: 103 – 122

NAKANO, T., OKAMOTO, M., IKEDA, Y., HASEGAWA, H. (2006): Mitochondrial cytochrome *c* oxidase subunit 1 gene and nuclear rDNA regions of *Enterobius vermicularis* parasitic in captive chimpanzees with special reference to its relationship with pinworms in humans. *Paras. Res.*, 100: 51 – 57

PETTER, A. J., CHABAUD, A. G., DELAVENAY, R., BRYGOO, E. R. (1972): Une nouvelle espèce de Nématode du genre *Lemuricola*, parasite de *Daubentonia madagascariensis* Gmelin, et considérations sur le genre *Lemuricola*. *Ann. Parasit. Hum. Comp.*, 47: 391 – 398

QUENTIN, J. C., TENORA, F. (1975): Morphologie et position systématique de *Lemuricola* (*Rodentoxyuris*) *sciuri* (Cameron, 1933) nov. comb., nov. subg., et *Syphacia* (*Syphatineria*) *funambuli* Johnson, 1967. Oxyures (Nematoda) parasites de Rongeurs Sciurides. *B. Mus. Natl. Hist. Nat., Serie A, Zoologie*, 178: 1525 – 1535

QUENTIN, J. C., BETTERTON, C., KRISHNASAMY, M. (1979): Oxyures nouveaux ou peu connus, parasites de Primates, de Rongeurs et de Dermoptères en Malaisie. Création du sous-genre *Colobenterobius* n. subg. *B. Mus. Natl. Hist.*

Nat., Serie A, Zoologie, 1: 1031 – 1050

SANDOSHAM, A. A. (1950): On *Enterobius vermicularis* (Linnaeus, 1758) and some related species from primates and rodents. *J. Helminthol.*, 24: 171 – 204

SKRJABIN, K. I., SCHIKHOBALOVA, N. P., LAGODOVSKAYA, E. A. (1960): Oxyurids of animals and man. *Principles of Nematodology*, Vol. 8, Publ. House AN SSSR, Moscow, 557 pp. (In Russian)

SORCI, G., MORAND, S., HUGOT, J. P. (1997): Host parasites coevolution: comparative evidence for covariation of life history traits in primates and oxyurid parasites. *P. Zool. Soc. Lond.*, 264: 285 – 289

TENORA, F., BARUŠ, V., WIGER, R., RYŠAVÝ, B. (1981): Scanning electron microscopic studies on nematode species of the genera *Passalurus*, *Enterobius* and *Lemuricola* (Oxyurida). *Acta U. Agr. Fac. Agron.*, 29: 327 – 339

WILSON, D. E., REEDER, D. A. (2005): Mammals species of the world. A taxonomic and geographic reference. Vol.1. The Johns Hopkins University Press, Baltimore, 743 pp.

YAMASHITA, J. (1963): Ecological relationships between parasites and Primates. I. Helminth parasites and primates. *Primates*, 4: 1 – 35

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