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MORPHOLOGY AND PHYLOGENETIC POSITION OF TWO MICROPHALLOID TREMATODE SPECIES, PARASITES OF THE VESPER BAT *PIPISTRELLUS KUHLII* IN THE LOWER VOLGA REGION OF RUSSIA

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Two species of microphalloid trematodes, *Parabascus oppositus* and *Lecithodendrium* cf. *skrjabini*, were found in the Vesper bat, *Pipistrellus kuhlii*, caught in the Astrakhan Oblast', Lower Volga region, Russia. A morphological revision of a paratype of *P. oppositus*, as well as a study of the specimens collected during this survey indicate this species to be devoid of a cirrus-sac. Instead, the species has a convoluted seminal vesicle, a tubular pars prostatica surrounded by an extensive field of prostatic cells, and a short ejaculatory duct. These structures lie freely in the parenchyma. The genital pore is submedian and is situated at the level of the ventral sucker. The body length of *Lecithodendrium* cf. *skjabini* differs from that of *L. skjabini* sensu stricto. A phylogenetic analysis using 28S rDNA unites *P. oppositus* together with *G. amphoraeformis* and *Gyrabascus* sp. in the *Gyrabascus* spp. clade (Pleurogenidae). On this basis, *P. oppositus* has been included into the genus *Gyrabascus,* thus correcting its previous diagnosis. *Lecithodendrium* cf. *skjabini* is clustered with other members of the genus *Lecithodendrium*. The monophyly of the Lecithoodendriidae is confirmed. Our results support the integration of this family together with Microphallidae, Phaneropsolidae, and Stomylotrematidae into a large clade. In the present study, we show the paraphyly of the family Pleurogenidae and the monophyly of the Pleurogenidae + Collyriclidae group.

Keywords: Trematoda, *Parabascus oppositus*, *Lecithodendrium skrjabini*, phylogenetics, taxonomy
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Bats are an extraordinary group of mammals. Their prominent feature is the ability to fly. Bats are also unique among mammals as they possess a diverse assemblage of host-specific helminths (Khotenovsky, 1972).

Fourteen species of bats are now recorded in the Lower Volga region of Russia in southeastern Europe (Zavialov, 2009; Smirnov et al., 2018). Some of these species have recently appeared in the region as a result of habitat expansion to the north. Kuhl's pipistrelle *Pipistrellus kuhlii* (Kuhl 1817) appeared in this region in the 20th century, as recent as the 1960s (Strelkov et al., 1985), apparently originating from the southeastern Transcaucasus (Strelkov, Ilyin, 1990). Limited data exists on the helminth fauna of bats inhabiting the Lower Volga region (Dubinin, 1952; Kurochkin, Kurochkina, 1962; Ivanov et al., 2012), and no information is available on helminths infecting Kuhl's pipistrelle.

During the parasitological investigation of Kuhl's pipistrelle in this region two trematode species were observed, *Parabascus oppositus* Zdzitowiecki 1969 and *Lecithodendrium* cf. *skrjabini* Mazaberidse 1963. *Parabascus oppositus* was originally described from the serotine bat, *Eptesicus serotinus* (Schreder 1774), captured near Warsaw (Zdzitowiecki, 1969). According to Zdzitowiecki (1969), the first specimens of this species were found in the common bent-wing bat *Miniopterus schreibersi* Kuhl 1817 from the former Czhechoslovakia by Mituch (1965), who mistakenly identified them as *P. semisquamosum* Braun 1900. Otherwise, no other records exist for this species. Khotenovsky (1985) synonymized *P. oppositus* with *Parabascus lepidotus* Looss 1907, but in his work there are no appropriate explanations for this synonymization. Sharpilo et al. (1989) did not include *P. oppositus* in the list of *P. lepidotus* synonyms. Niewiadomska and Pojmańska (2018) considered *P. oppositus* and *P. lepidotus* as a separate species. Morphological and molecular phylogenetic investigation of the *P. oppositus* specimens collected for this study, as well as the re-examination of the paratype, facilitates the revision the genus affiliation of this species, resulting in the transfer to the genus *Gyrabascus* Macy 1935.

Lecithodendrium skrjabini was described from Nathusius' pipistrelle, *Pipistrellus nathusii* (Keyserling et Blasius 1839), captured in the Caucasius in western Georgia (Matsaberidze, 1963). Two more records exist for this species, in addition to the first description (Matsaberidze, Khotenovsky, 1967; Kirillov et al., 2012). The specimens collected during this investigation are assigned to *L. skrjabini*, however some doubts remain and are discussed below.

This paper provides the description, drawings, and results of molecular phylogenetic analysis of *Gyrabascus oppositus* comb. n. and *Lecithodendrium* cf. *skrjabini*.

MATERIALS AND METHODS

Specimen collection

Trematodes were collected from six Kuhl's pipistrelles specimens; five captured on the 18th September, 2014 and one on the 29th May, 2018 in the Kalinino village (46°20′ N, 48°52′ E), Astrakhan Oblast, Russia (Lower Volga region). Adult worms were collected for morphological study and relaxed in freshwater at room temperature, fixed in 70% ethanol, and subsequently stained with acetocarmine. All measurements were made in micrometers unless otherwise indicated. Mean values are provided in parentheses. Specimens for genetic analysis were fixed in 96% ethanol and stored at +4°C.

Paratype examination

Zdzitowiecki (1969) has described *P. oppositus* based on holotype and several paratypes. Holotype deposit location remains unknown (according to personal communication by Dr. R. Salamatin). A set of horizontal optical sections of body region between the intestinal bifurcation and the testes of *P. oppositus* paratype were studied from photographs. The paratype is deposited in the Natural History Museum, London (Parasites & Vectors Division, Department of Life Sciences, cat. # 1992.12.3.25) (Natural History Museum, 2014). Photos were kindly provided by Dr. Rodney Bray.

DNA extraction, amplification, sequencing, and phylogenetic analysis

To obtain LSU sequences, DNA was isolated from one *G. oppositus* specimen and one *Lecithodendrium* cf. *skrjabini* specimen using Chelex-100 and Proteinase K. The D1-D3 regions of 28S rDNA (up to 1,200 bp) were amplified with primer pairs 28Sy/28Sz (Hillis, Dixon, 1991) for *Lecithodendrium* cf. *skrjabini* and LSU5/1500R (Tkach et al., 2003) for *G. oppositus*. Amplicons were purified using a Cleanup mini Purification Kit (Eurogene) and sequenced on the ABI-Prism 3500xl using the same primers.

Newly generated sequences were deposited in GenBank (www.ncbi.nlm.nih.gov) as follows: *G. oppositus* – MK575195; *Lecithodendrium* cf. *skrjabini* – MK575196. The sequences were mounted in general alignment with 61 species (Tkach et al., 2000, 2001, 2003; Olson et al., 2003; Al-Kandari et al., 2011; Galaktionov et al., 2012; Lord et al., 2012; Heneberg, Literák, 2013; Boyce et al., 2014; Presswell et al., 2014; Kanarek et al., 2014, 2015, 2017; Kudlai et al., 2015, 2016; Hernandez-Orts et al., 2016; Bell et al., 2018; Galaktionov, Blasco-Costa, 2018) (Table 1). First, sequences were automatically aligned using the Muscle algorithm (Edgar, 2004) as implemented in SeaView 4.0 (Gouy et al., 2010), and then the alignment was adjusted manually. The final length of alignment was 1267 bp. The phylogenetic analysis was performed using the Maximum Likelihood method as implemented in the PhyML program (Guindon, Gascuel, 2003), with the GTR + G + I model, as suggested by the Modeltest program (Posada, Crandall, 1998). The stability of clades was assessed using a non-parametric bootstrap with 1,000 pseudoreplicates. Bayesian analysis was performed using MrBayes 3.2.6 at the CIPRES Science Gateway (Miller et al., 2010). Trees were run as two separate chains (default heating parameters) for 15 million generations, by which time they had ceased converging: the final average standard deviation of the split frequencies was less than 0.01. The quality of chains was estimated using built-in MrBayes tools and using the Tracer 1.6 package (Rambaut et al., 2014). Based on the estimates by Tracer, the first 7,000 generations were discarded for burn-in.

RESULTS

Systematics

Family **Pleurogenidae** Looss 1899

Genus ***Gyrabascus*** Macy 1935

Gyrabascus oppositus (Zdzitowiecki 1969) comb. n. (fig. 1)

Syns: *Parabascus oppositus* Zdzitowiecki 1969, *Parabascus semisquamosum* (Braun 1900) sensu Mituch 1965, *Parabascus lepidotus* Looss 1907 sensu Khotenovsky 1985 pro parte.

Host: *Pipistrellus kuhlii* (Kuhl 1817) (Chiroptera: Vespertilionidae).

Locality: Kalinino village, Astrakhan Oblast of Russia (46°20′ N, 48°52′ E).

Date of collection: 18 September, 2014 and 29 May, 2018.

Site of infection: intestine.

Prevalence and intensity: in 5 of 6, 5–10 ind.

Specimens deposited: mounts № 14277, 14278 in the Museum of Helminthological Collections at the Centre of Parasitology of the A.N. Severtsov Institute

Table 1. List of species, incorporated into molecular analysis

Species	Host species	Geographical region	GenBank accession number	Reference
Collyriclidae				
Collyriclum faba (Bremser in Schmalz 1831)	*Saxicola rubetra* (Linnaeus 1758) (Aves; Muscicapidae)	OrlickéZáhoří, Chech Republic	JQ231122	Heneberg, Literák, 2013
Lecithodendriidae				
Lecithodendrium linstowi Dollfus 1931	*Nyctalus noctula* (Schreber 1774) (Mammalia; Vespertilionidae)	Sumy Region, Ukraine	AF151919	Tkach et al., 2000
Lecithodendrium sp.	*Bithynia tentaculata* (Linnaeus 1758) (Gastropoda; Bithyniidae)	Curonian lagoon, Lithuania	KJ126726	Kudlai et al., 2015
Lecithodendrium spathulatum (Ozaki 1929)	*Pipistrellus pipistrellus* (Schreber 1774) (Mammalia; Vespertilionidae)	England	JF784193	Lord et al., 2012
Ophiosacculus mehelyi (Mödlinger 1930)	*Eptesicus serotinus* (Schreber 1774) (Mammalia; Vespertilionidae)	Ukraine	AF480167	Tkach V.V., direct submission
Paralecithodendrium chilostomum Mehlis 1931	*N. noctula*	Sumy Region, Ukraine	AF151920	Tkach et al., 2000
Paralecithodendrium hurkovaae Dubois 1960	*Myotis daubentoni* (Kuhl 1817) (Mammalia; Vespertilionidae)	Kiev Region, Ukraine	AF151922	Tkach et al., 2000
Paralecithodendrium longiforme (Bhalerao 1926)	*M. daubentoni*	Kiev Region, Ukraine	AF151921	Tkach et al., 2000
Paralecithodendrium parvouterus (Bhalerao 1926)	*Miniopterus schreibersi* (Kuhl 1817) (Mammalia; Miniopteridae)	Rubielos de Mora, Spain	AY220617	Tkach et al., 2003
Paralecithodendrium sp.	*P. pipistrellus*	England	JF784196	Lord et al., 2012
Pycnoporus heteroporus (Dujardin 1845)	*Pipistrellus kuhli* (Kuhl 1817) (Mammalia; Vespertilionidae)	Kherson Region, Ukraine	AF151918	Tkach et al., 2000
Pycnoporus megacotyle (Ogata 1939)	*P. kuhli*	Kherson Region, Ukraine	AF151917	Tkach et al., 2000
Microphallidae				
Floridatrema heardi Kinsella et Deblock 1994	*Oryzomys palustris* (Harlan 1837) (Mammalia; Cricetidae)	Florida, USA	AY220632	Tkach et al., 2003
Levinseniella sp.	*Somateria mollissima* (Linnaeus 1758) (Aves; Anatidae)	Sea of Okhotsk, Skipper Creek, Russia	MG783585	Galaktionov, Blasco-Costa, 2018
Longiductotrema tethepae Kudlai, Cribb et Cutmore 2016	*Gymnothorax pseudothyrsoideus* (Bleeker 1852) (Actinopterygii; Muraenidae)	Lizard Island, Queensland, Australia	KX712085	Kudlai et al., 2016
Maritrema arenaria Hadley et Castle 1940	Barnacle	United Kingdom	AY220629	Tkach et al., 2003

Table 1. (Contd.)

Species	Host species	Geographical region	GenBank accession number	Reference
Maritrema brevisacciferum Shimazu et Pearson 1991	*Posticobia brazieri* (Smith 1882) (Gastropoda; Hydrobiidae)	Moggil Creek, Australia	KT355819	Kudlai et al., 2015
Maritrema corai Hernández-Orts, Pinacho-Pinacho, García-Varela et Kostadinova 2016	*Eudocimus albus* (Linnaeus 1758) (Aves; Threskiornithidae)	Mexico	KT880222	Hernandez-Orts et al., 2016
Maritrema deblocki Presswell, Blasco-Costa et Kostadinova 2014	*Anas platyrhynchos* Linnaeus 1758 (Aves; Anatidae)	New Zealand	KJ144173	Presswell et al., 2014
Maritrema eroliae Yamaguti 1939	*Clypeomorus bifasciatus* (Sowerby II 1855) (Gastropoda; Cerithiidae)	Kuwait	JF826247	Al-Kandari et al., 2011 [as *Maritrema* cf. *eroliae*]
Maritrema novaezealandense Martorelli, Fredensborg, Mouritsen et Poulin 2004	*Zeacumantus subcarinatus* (Sowerby II 1855) (Gastropoda; Batillariidae)	New Zealand	KJ144178	Presswell et al., 2014
Maritrema oocysta Lebour 1907	*Peringia ulvae* (Pennant 1777) (=*Hydrobia ulvae* (Pennant 1777) (Gastropoda; Hydrobiidae)	United Kingdom	AY220630	Tkach et al., 2003
Maritrema poulini Presswell, Blasco-Costa et Kostadinova 2014	*Paracorophium excavatum* (Thomson 1884) (Malacostraca; Corophiidae)	New Zealand	KJ144177	Presswell et al., 2014
Maritrema prosthometra Deblock et Heard 1969	*O. palustris*	USA	AY220631	Tkach et al., 2003
Maritrema subdolum Jägerskiöld 1909	*P. ulvae*	Kandalaksha Bay, White Sea, Russia	HM584135	Galaktionov et al., 2012
Microphallus abortivus Deblock 1974	*P. ulvae*	United Kingdom	AY220626	Tkach et al., 2003
Microphallus basodactylophallus (Bridgman 1969)	*O. palustris*	USA	AY220628	Tkach et al., 2003
Microphallus calidris Belopolskaia et Ryjikov 1963	*Littorina sitkana* Philippi 1846 (Gastropoda; Littorinidae)	Kunashir, KurilIslands, Russia	HM584125	Galaktionov et al., 2012
Microphallus fusiformis Reimer 1963	*P. ulvae*	United Kingdom	AY220633	Tkach et al., 2003 [as Microphallidae gen. sp.]
Microphallus minutus Johnston 1948	*P. brazieri*	Queensland, Churchbank Weir, Australia	KT355823	Kudlai et al., 2015
Microphallus ochotensis Galaktionov et Blasco-Costa 2018	*Falsicingula kurilensis* (Pilsbry 1905) (Gastropoda; Falsicingulidae)	Sea of Okhotsk, Skipper Creek, Russia	MG783589	Galaktionov, Blasco-Costa, 2018
Microphallus piriformes Galaktionov 1983	*Littorina saxatilis* (Olivi 1792) (Gastropoda; Littorinidae)	Vaygach Island, SE Barents Sea, Russia	HM584123	Galaktionov et al., 2012

Table 1. (Contd.)

Species	Host species	Geographical region	GenBank accession number	Reference
Microphallus pseudopygmaeus Galaktionov 2009	*L. saxatilis*	Kandalaksha Bay, White Sea, Russia	HM584127	Galaktionov et al., 2012
Microphallus pygmaeus (Levinsen 1881)	*L. saxatilis*	Kandalaksha Bay, White Sea, Russia	HM584134	Galaktionov et al., 2012
Microphallus similis (Jägerskiöld 1900)	*Larus schistisagus* Stejneger 1884 (Aves; Laridae)	Impoveem, Sea of Okhotsk, Russia	HM584138	Galaktionov et al., 2012
Microphallus triangulatus Galaktionov 1984	*Somateria mollissima v-nigrum* Bonaparte 1855 (Aves; Anatidae)	Yamskaya Bay, Sea of Okhotsk, Russia	HM584139	Galaktionov et al., 2012
Microphallus sp.	*Littorina natica* Reid 1996 (Gastropoda; Littorinidae)	Bering Sea, Chukotka, Russia	HM584129	Galaktionov et al., 2012
Microtrema barusi Sitko 2013	*Prunella modularis* (Linnaeus 1758) (Aves; Prunellidae)	Czech Republic	KJ700421	Kanarek et al., 2014
Pachypsolidae				
Pachypsolus irroratus (Rudolphi 1819)	*Lepidochelyso livacea* (Eschscholtz 1829) (Reptilia; Cheloniidae)	Oaxaca, Mexico	AY222274	Olson et al., 2003
Phaneropsolidae				
Phaneropsolus praomidis Baer 1971	*Rhabdomys* sp. (Mammalia; Muridae)	Malawi	KJ700422	Kanarek et al., 2015
Phaneropsolus sp.	*Terpsiphone paradise* (Linnaeus 1758) (Aves; Monarchidae)	Guangxi Province, China	KY982862	Kanarek et al., 2017
Pleurogenidae				
Brandesia turgida (Brandes 1888)	*Pelophylax lessonae* (Camerano 1882) (=*Rana lessonae* Camerano 1882) (Amphibia; Ranidae)	Near Lesniki, Kiev Region, Ukraine	AY220622	Tkach et al., 2003
Candidotrema loossi (Africa 1930)	*Pelophylax ridibundus* (Pallas 1771) (=*Rana ridibunda* Pallas 1771) (Amphibia; Ranidae)	Vilkovo, Kiliya, Ukraine	AY220621	Tkach et al., 2003
Cortrema magnicaudata (Bykhovskaya-Pavlovskaya 1950)	*Hirundo rustica* Linnaeus 1758 (Aves; Hirundinidae)	Near Záhlinice, Czech Republic	KJ700420	Kanarek et al., 2014
Gyrabascus amphoraephormis (Mödlinger 1930)	*M. daubentoni*	Kiev, Ukraine	AY220620	Tkach et al., (2003) [as *Allassogonoporus amphoraeformis* (Mödlinger 1930)]
Gyrabascus sp.	*Dromiciops bozinovici* D'Elía, Hurtado et D'Anatro 2016 (Mammalia; Microbiotheriidae)	Chile	KY921598	Bell et al., 2018

Table 1. (Contd.)

Species	Host species	Geographical region	GenBank accession number	Reference
Langeronia macrocirra Caballero et Bravo 1949	*Lithobates berlandieri* (Baird 1859) (=*Rana berlandieri* Baird1859) (Amphibia; Ranidae)	Guatemala	AY220624	Tkach et al., 2003 [as *Loxogenes macrocirra* (Caballero et Bravo 1949)]
Leyogonimus polyoon (Linstow 1887)	*Fulica atra* Linnaeus 1758 (Aves; Rallidae)	Poland	KY752116	Kanarek et al., 2017
Macyella massanae (Vaucher 1968)	*Erithacus rubecula* (Linnaeus 1758) (Aves; Muscicapidae)	Near Zahlinice, Czech Republic	KP682451	Kanarek et al., 2015 [as *Collyricloides massanae* Vaucher 1968]
Macyella postgonoporus Neiland 1951	*Dendrocopus major* (Linnaeus 1758) (Aves; Picidae)	Czech Republic	KY752115	Kanarek et al., 2017
Parabascus duboisi Hurková 1961	*M. daubentoni*	Kiev, Ukraine	AY220618	Tkach et al., 2003
Parabascus joannae (Zdzitowiecki 1967)	*M. daubentoni*	Kiev, Ukraine	AY220619	Tkach et al., 2003
Parabascus semisquamosus (Braun 1900)	*P. kuhli*	Kherson Region, Ukraine	AF151923	Tkach et al., 2000
Pleurogenes claviger (Rudolphi 1819)	*Rana temporaria* Linnaeus 1758 (Amphibia; Ranidae)	Kiev Region, Ukraine	AF151925	Tkach et al., 2000
Pleurogenoides medians (Olsson 1876)	*P. lessonae*	Ukraine	AF433670	Tkach et al., 2001
Prosotocus confusus (Looss 1894)	*P. lessonae*	Kiev Region, Ukraine	AY220623	Tkach et al., 2003
Prosthogonimidae				
Prosthogonimus cuneatus (Rudolphi 1809)	*Sturnus vulgaris* Linnaeus 1758 (Aves; Sturnidae)	Nezhin, Chernigiv Region, Ukraine	AY220634	Tkach et al., 2003
Prosthogonimus ovatus (Rudolphi 1803)	*Pica pica* (Linnaeus 1758) (Aves; Corvidae)	Chernigiv region, Ukraine	AF151928	Tkach et al., 2000
Prosthogonimus rarus Braun 1901	*Anas querquedula* (Linnaeus 1758) (Aves; Anatidae)	Golopristansky district, Kherson Region, Ukraine	AY116869	Tkach et al., 2003 [as *Schis-togonimus rarus* (Braun 1901)]
Stomylotrematidae				
Stomylotrema vicarium Braun 1901	*Sclerurus mexicanus* Sclater 1857 (Aves; Furnariidae)	Tocache, Peru	KY982863	Kanarek et al., 2017
Outgroup				
Plagiorchioidea				
Plagiorchiidae				
Plagiorchis elegans (Rudolphi 1802)	*Apodemus sylvaticus* (Linnaeus 1758) (Mammalia; Muridae)	United Kingdom	JX522535	Boyce et al., 2014

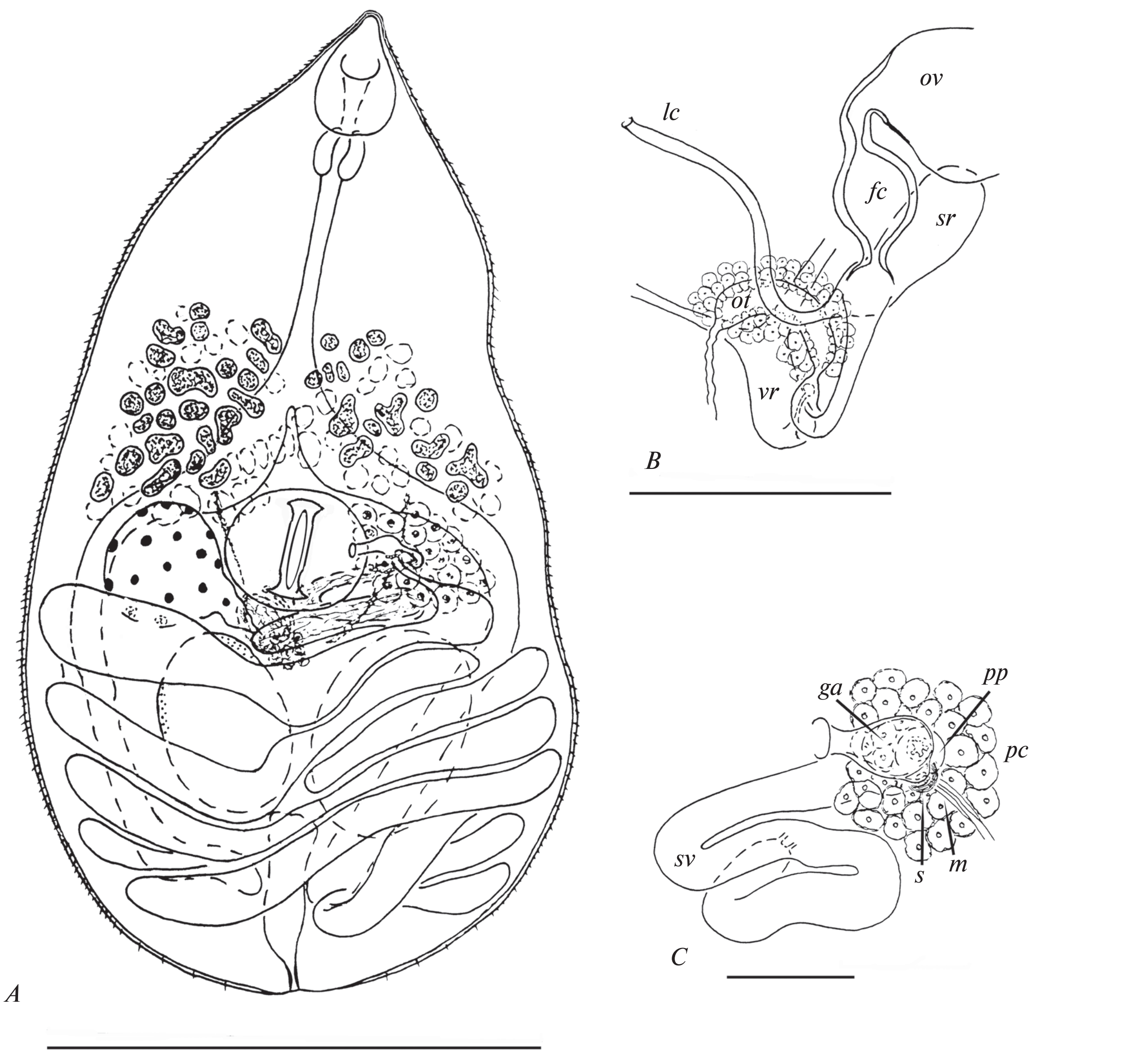

Fig. 1. *Gyrabascus oppositus*: *A* – whole specimen, ventral view; *B* – ovarian complex, dorsal view; *C* – terminal genitalia, ventral view; *fc* – fertilization chamber, *ga* – common genital atrium, *lc* – Laurer's, canal, *m* – metraterm, *ot* – ootype with Mehlis' gland, *ov* – ovary, *pc* – prostatic cells, *pp* – pars prostatica, *s* – sphincter, *sr* – seminal receptacle, *sv* – seminal vesicle, *vr* – vitelline reservoir. Scale bars (mm): *A* – 0.4; *B*, *C* – 0.05.

of Ecology and Evolution (IPEE RAS) in Moscow, Russia.

Description (based on 15 adult specimens). Body pyriform with conical anterior extremity and rounded posterior end; length 0.62–1.01 (0.80) mm, maximum width 0.33–0.44 (0.40) mm at level of testes, rare of ventral sucker. Body length to width ratio 1.44–2.57 : 1 (2.02 : 1); body width to length ratio 1 : 0.39–0.69 (1 : 0.51). Forebody 290–491 (390) which represents 38.9–69.4 (50.7)% of body length. Tegument spinose. Oral sucker drop-shaped with elongated antero-dorsal lobe, 89–108 (97) × 57–70 (64). Mouth opening subterminal. Prepharynx usually not observed. Pharynx 38–51 (43) × 38–51 (45). Oral sucker to pharynx width ratio 1.25–1.67 : 1 (1.44 : 1). Oesophagus 120–215 (163); intestinal bifurcation in posterior third of forebody. Intestinal branches ending blindly far behind testes. Ventral sucker transverse-oval and recessed into body, 82–108 (95) × 108–133 (123). Oral sucker to ventral sucker width ratio 0.50–0.55 : 1 (0.53 : 1). Two testes, round to oval, entire, opposite, in anterior half of hindbody; sinistral 95–152 (122) × 76–138 (122), dextral 90–139 (125) × × 76–138 (110). Cirrus sac absent. Seminal vesicle tubular, convoluted, free in parenchyma. Pars prostatica tubular, surrounded by extensive field of prostatic cells. Ejaculatory duct short, opening into tubular common genital atrium. Genital pore submedian, at level of ventral sucker, on opposite side to ovary. Ovary round to oval, entire, sinistral or dextral, at level of ventral sucker; 82–114 (98) × 95–152 (115). Proximal part of oviduct forms vesicular fertilization chamber.

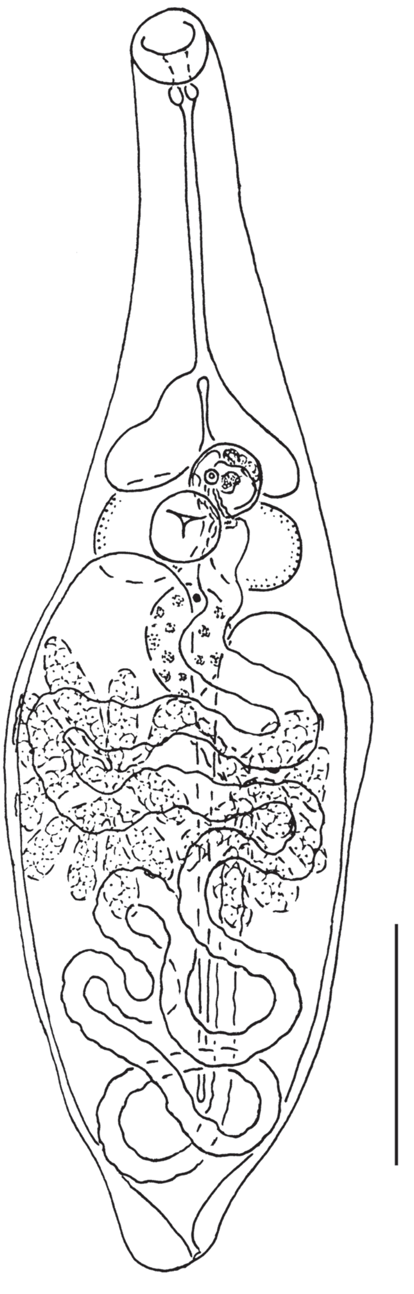

Fig. 2. *Lecithodendrium* cf. *skrjabini*, whole view. Scale bar 0.2 mm.

Seminal receptacle canalicular. Laurer's canal opens on dorsal side of body in ventral sucker region. Ootype with Mehlis' gland and vitelline reservoir median, between ventral sucker and testes. Vitellarium follicular in posterior half of forebody but overlaps with ventral sucker to some extent; follicles in two sublateral fields confluent dorsally. Uterus with transversal loops fills almost all space in hindbody. Metraterm with somewhat thickened walls, terminating with sphincter, and opening into common genital atrium ventral to male pore. Eggs numerous, oval, operculate, 24–26 (26) × × 13–16 (13). Excretory pore terminal; vesicle I-shaped and usually reaches posterior edge of testes.

R e m a r k s. Our specimens are consistent with the prominent morphological features of *P. oppositus,* as described by Zdzitowiecki (1969), specifically the body size and shape, configuration of the inner organs, ratio of the suckers, and eggs size. In Zdzitowiecki's (1969) paper, no data exists on morphology of the male terminal genitalia, however drawing of *P. oppositus* made by Mituch (1965) (named as *P. semisquamosum* by this author) does not indicate that the seminal vesicle is enclosed into the cirrus-sac.

Only the tubular pars prostatica with a field of prostate cells were visible on photos of the paratype terminal genitalia, while the wall of the cirris-sac separating this part of the male duct from the parenchyma is absent. Thus, the paratype of *P. opposites* obviously does not have a cirrus-sac.

Family ***Lecithodendriidae*** Looss 1902

Genus ***Lecithodendrium*** Lühe 1896

Lecithodendrium* cf. *skjabini Mazaberidse 1963 (fig. 2)

Host: *Pipistrellus kuhlii* (Kuhl 1817) (Chiroptera: Vespertilionidae).

Locality: Kalinino village, Astrakhan Oblast of Russia (46°20′ N, 48°52′ E).

Date of collection: 29 May, 2018.

Site of infection: intestine.

Prevalence and intensity: in 1 of 6, 22 ind.

Specimens deposited: mounts № 14279, 14280 in the Museum of Helminthological Collections at the Centre of Parasitology of the A.N. Severtsov Institute of Ecology and Evolution (IPEE RAS), in Moscow, Russia.

D e s c r i p t i o n (based on 11 adult specimens). Body fusiform; length 1.04–1.33 (1.18) mm, maximum width 0.30–0.40 (0.38) mm at mid-level of body. Body length to width ratio 2.56–3.61 : 1 (3.17 : 1); body width to length ratio 1 : 0.28–0.39 (1 : 0.32). Forebody 390–516 (440), which represents 32.3–40.2.4 (37.4)% of body length. Tegument unarmed. Oral sucker rounded, 60–76 (67) × 57–79 (68). Mouth opening subterminal. Prepharynx absent, pharynx 19–28 (23) × 25–32 (27). Oral sucker to pharynx width ratio 2.00–3.00 : 1 (2.60 : 1). Oesophagus 222–294 (251), intestinal bifurcation in forebody. Intestinal branches end near anterior edge of testes. Ventral sucker spherical to subsperical, 63–82 (75) × 63–82 (70). Oral sucker to ventral sucker width ratio 0.77–1.10 : 1 (0.98 : 1). Testes two, entire, round to oval, opposite, at level of ventral sucker; sinistral 82–127 (114) × 82–120 (104), dextral 95–133 (124) × 95–133 (110). Pseudocirrus-sac elongate-oval, 125 × 62–76 (70), with convoluted seminal vesicle, lies transversely to ventral surface of body and communicates with short thick-walled common genital atrium. Genital pore median or slightly sinistro-submedian, near anterior edge of ventral sucker. Ovary elongate-oval, entire, median, or slightly sinistro-median or dextro-submedian; post-testicular; contiguous with testes or separated, 95–133 (113) × 76–120 (97). Seminal receptacle canalicular. Laurer's canal opens on dorsal side of body, at level of posterior edge of ovary or distinctly posterior to ovary. Ootype with Mehlis' gland and vitelline reservoir near postero-sinistral margin of ovary or at level of posterior half ovary. Vitellarium follicular; elongated follicles in two dorsal clusters, 7–9 in each. Clusters postovarian but partly overlapped by ovarian area. Uterus fills almost all space in hindbody. Metraterm of similar length to pseudocirrus-sac, running over posterior surface of pseudocirrus-sac, and opening into common genital atrium. Eggs numerous, oval, operculate, 19–22 (20) × 10–13 (10). Excretory pore terminal; vesicle V-shaped and reaches to testes.

Remarks. Previous descriptions of *L. skrjabini* were deficient. Matsaberidze (1963) and Matsaberidze and Khotenovsky (1967) presented a description based on deformed specimens with compressed forebodies (Matsaberidze, 1963; Matsaberidze, Khotenovsky 1967). Kirillov et al. (2012) described specimens with a stretched forebody, as indicted by the equatorial position of the ventral sucker. Also, in the paper of Matsaberidze and Khotenovsky (1967) there is confusion with the drawing of *L. skrjabini*, which is replaced with the drawing of *L. linstowi* Dollfus 1931. The actual drawing of *L. skrjabini* is depicted in figure 1.

Comparison of the descriptions published by Matsaberidze (1963), Matsaberidze and Khotenovsky (1967) and Kirillov et al. (2012) enable the reconstruction of the body shape of relaxed *L. skrjabini* adults: it is fusiform, while the ventral sucker occupies the pre-equatorial position. The samples within this study are similar to *L. skrjabini* in terms of body shape, internal organ position, sucker size and ratio, the vitellarium morphology, and egg size. However, these trematodes differ from *L. skrjabini* in terms of body length and forebody and oesophagus lenght. This study presents specimens lengths of 1.04–1.33 mm, and the maximum length of *L. skrjabini* is 0.89 mm (Matsaberidze, Khotenovsky 1967). However, the publications of Matsaberidze (1963), and Matsaberidze and Khotenovsky (1967) take measurements from worms with compressed forebodies. At the same time, the adults in this study are evidently larger than the individuals collected by Kirillov et al. (2012). It is put forward that this difference is due to the phenomenon of host-induced morphological variability.

Molecular phylogenetic analysis

In both the ML and BI analysis, *G. oppositus* appears as a member of the well-supported *Gyrabascus* spp. clade that is also includes *G. amphoraeformis* (Mödlinger 1930) and *Gyrabascus* sp. (fig. 3). However, the phylogenetic relationships among representatives within the *Gyrabascus* spp. clade are poorly resolved. In turn, the *Gyrabascus* spp. clade is situated within the major Pleurogenidae + Collyriclidae clade. The Pleurogenidae + Collyriclidae clade appears to be monophyletic, with statistically significant support. Within the Pleurogenidae + Collyriclidae clade, the *Gyrabascus* spp. appears a sister clade to the group, containing representatives of the genera *Cortrema* Tang 1951, *Leyogonimus* Ginetsinskaya 1948 and *Macyella* Neiland 1951, but support of this sister connection is weak.

Lecithodendrium cf. *skrjabini* together with congeneric species form the *Lecithodendrium* spp. clade, which is strongly supported by BI analysis and moderately supported by ML analysis. Inside this clade, *Lecithodendrium* cf. *skrjabini* appears as a weakly supported sister taxon to *L. linstowi*. The *Lecithodendrium* cf. *skrjabini* + *L. linstowi* group is combined with the *Lecithodendrium* sp. into a well-supported monophyletic clade. In turn, the *Lecithodendrium* cf. *skrjabini* + + *L. linstowi* + *Lecithodendrium* sp. clade is strongly supported by BI analysis and moderately supported by ML analysis sister group to *Lecithodendrium spathulatum* (Ozaki 1929). The *Lecithodendrium* spp. clade appears as a member of the family Lecithodendriidae (fig. 3). The family Lecithodendriidae is closely related to Stomylotrematidae, however, this is weakly supported in both ML and BI analyses. The Lecithodendriidae + + Stomylotrematidae group is clustered with the Phaneropsolidae, strongly supported by BI analysis and moderately supported by ML analysis. The Lecithodendriidae + Stomylotrematidae + Phaneropsolidae clade is a sister group to the family Microphallidae, this is also strongly supported by BI analysis and moderately supported by ML analysis.

Meanwhile, the major clade of trematodes containing the Lecithodendriidae, Stomylotrematidae, Phaneropsolidae and Microphallidae appears as a low-supported sister group to the Pleurogenidae + + Collyriclidae clade (fig. 3). In turn, the [(Lecithodendriidae +Stomylotrematidae + Phaneropsolidae) + + Microphallidae] + (Pleurogenidae + Collyriclidae) clade is nested within the well-supported monophyletic group of microphalloids, that also includes the Prosthogonimidae. The Pachypsolidae occupies a basal position to all of the aforementioned taxa.

DISCUSSION

The genus *Parabascus* Looss 1907 combines pleurogenids with a well-developed cirrus sac, a submedian genital pore which lies behind the anterior edge of the ventral sucker, a V-shaped excretory vesicle, and several other morphological characters (Khotenovsky, 1985; Lotz, Font, 2008a; Kanarek et al., 2014). However, *P. oppositus* does not have consistent morphological features characteristic to this genus. The morphology of the male terminal genitalia and other features of *P. oppositus*, excluding the genital pore position, corre-

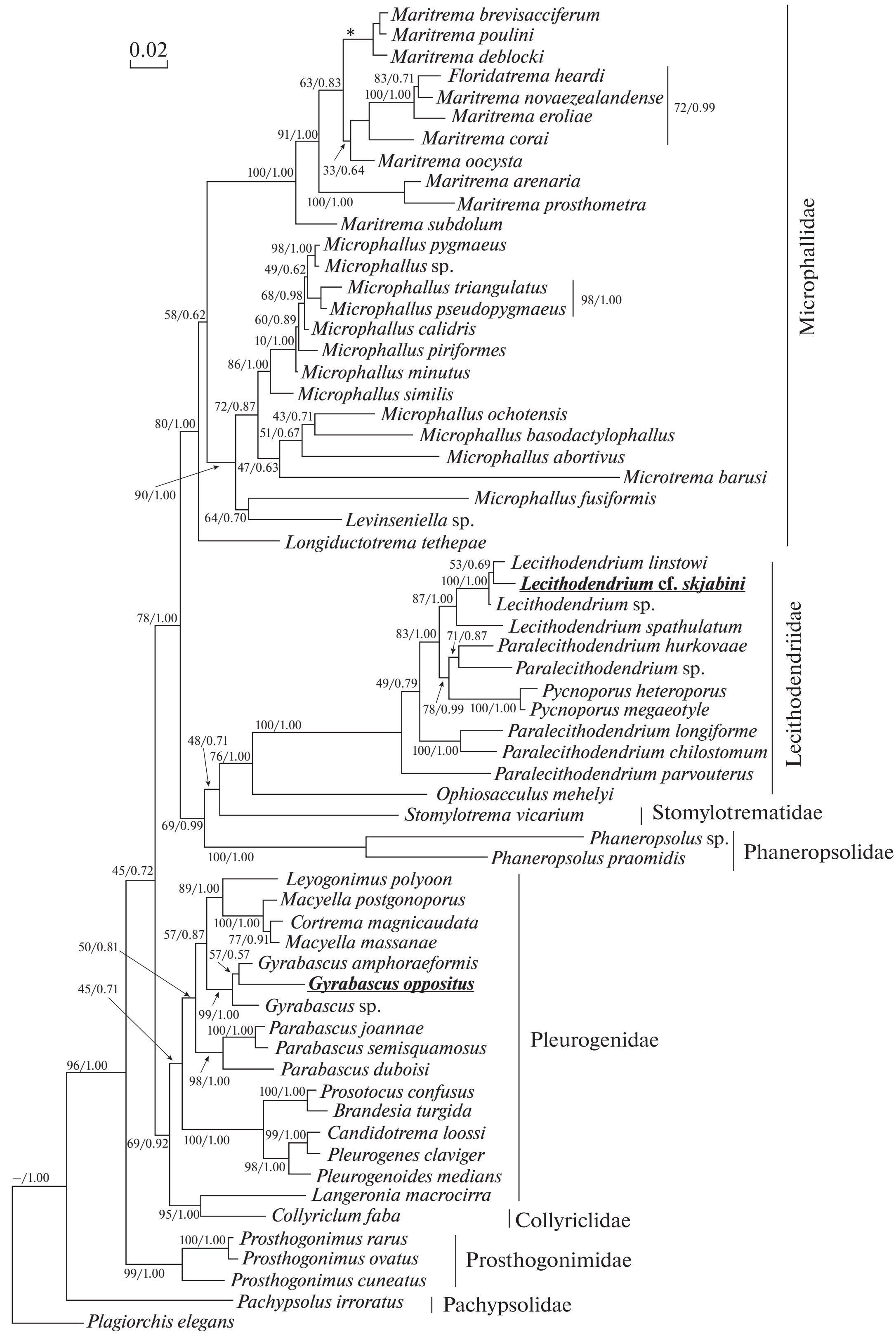

Fig. 3. Phylogenetic position of *Gyrabascus oppositus* and *Lecithodendrium* cf *skrjanbini* based on the analysis of 28S rDNA partial sequences using ML and BI algorithms. Nodal support: ML/BI. The clade which is absent in ML, but present in BI noted with asterisk. Newly obtained sequences are shown in bold. *Plagiorchis elegans* is designated as outgroup taxa.

spond to those for the genus *Gyrabascus* (= *Allassogonoporus* Olivier 1938) (compare with Olivier, 1938; Macy, 1940; Podvyaznaya, 1996; Lotz, Font, 2008). Six well-known representatives of this genus have a marginally located genital pore (Olivier, 1938; Macy, 1940; Dubois, 1956; Khotenovsky, 1974; Tkach, Bray, 2001; Brugni, Flores, 2007; Lotz, Font, 2008; Bell et al., 2018). However, for some specimens of *G. amphoraeformis* (=*Allassogonoporus amphoraeformis*), the sinistro-lateral position of genital pore was described to be located at the midpoint between the edge of the ventral sucker and the sinistral margin of the body (Sharpilo, Iskova, 1989 – fig. 67, g). Molecular genetic data supports the belonging of *G. oppositus* to the genus *Gyrabascus*, which requires an amendment of the diagnosis for this genus.

Genus *Gyrabascus* Macy 1935 emend

Diagnosis (based on Lotz, Font (2008) with changes). Body broadly oval, nearly as wide as long. Oral sucker terminal to subterminal. Ventral sucker equatorial or preequatorial. Prepharynx very short. Testes in middle third of body. Cirrus-sac absent. Seminal vesicle lies transversely or irregularly coiled. Genital pore marginal or submedian, sinistral or dextral, locates in region of ventral sucker, opposite to ovary, not anterior to vitellarium. Ovary entire to lobed, extends anterior to testes. Uterus comprised of overlapping coils that fill posterior half of body. Eggs small, numerous. Vitellarium follicular, in forebody, sometimes reaches into ventral sucker region. In bats and rodents; North America and Eurasia. Type species *G. brevigastus* Macy 1935.

Integration of the *Gyrabascus* spp. into the family Pleurogenidae (fig. 3) can be verified through phylogenetic reconstructions from other authors (Tkach et al., 2002, 2003; Kanarek et al., 2014, 2015, 2017; Bell et al., 2018). However, in phylogram, presented in this article, the family appears to be paraphyletic, because *Langeronia macrocirra* Caballero et Bravo 1949 (Pleurogenidae) forms a highly supported sister relationship with *Collyriclum faba* (Bremser in Schmalz 1831) (Collyriclidae). Earlier, the sister relationship between *C. faba* and *L. macrocirra* was demonstrated by Heneberg and Literák (2013). The combination of *C. faba* with pleurogenid trematodes is supported by the morphological data on cercariae. Cercaria of *C. faba*, has four pairs of penetration glands and a bilobed virgula in the posterior half of the oral sucker, similar to the larvae of other pleurogenids (Heneberg et al., 2015).

The results of Kanarek et al. (2014, 2015, 2017) and Bell et al. (2018) indicate a close relationship between the genera *Gyrabascus* and *Cortrema*. According to our own data, there is no direct phylogenetic relationship between these taxa, as the only species of the genus *Cortrema* that has been sequenced, *Cortrema magnicaudata* (Bykhovskaya-Pavlovskaya 1950), is clustered with two members of the genus *Macyella*: *Macyella massanae* (Vaucher 1968) and *Macyella postgonoporus* Neiland 1951. Furthermore, *M. massanae* was closer to *C. magnicaudata* than to congeneric species (fig. 3). It should be noted that previous to reassigning *M. massanae* to the genus *Macyella,* based on the phylogenetic data of Kanarek et al. (2017), it was considered to be member of the genus *Collyricloides* Vaucher 1968. Consequently, a sister group to the *Gyrabascus* spp. clade cannot be clearly supported based on our own phylogenetic data.

The presented molecular phylogenetic data clearly demonstrates the monophyly of the genus *Lecithodendrium* and the family *Lecithodendriidae* as a whole. The data also clearly indicate the close relationships Lecithodendriidae with the families Phaneropsolidae and Stomylotrematidae, which supports the results of a recent study by Bell et al. (2018). In the study by Bell et al. (2018), the relationship of the Phaneropsolidae + + Stomylotrematidae + Lecithodendriidae clade with the Pleurogenidae, Prosthogonimidae, and Microphallidae was unclear. According to the results of our phylogenetic analysis, the Phaneropsolidae + Stomylotrematidae + Lecithodendriidae clade has a common ancestor with microphallid trematodes. However, the relationships between the Prostogonimidae and the Pleurogenidae + Collyriclidae and Microphallidae + + (Phaneropsolidae + Stomylotrematidae + Lecithodendriidae) clades were poorly resolved.

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МОРФОЛОГИЯ И ФИЛОГЕНЕТИЧЕСКОЕ ПОЛОЖЕНИЕ ДВУХ ВИДОВ МИКРОФАЛЛОИДНЫХ ТРЕМАТОД – ПАРАЗИТОВ ГЛАДКОНОСОЙ ЛЕТУЧЕЙ МЫШИ (*PIPISTRELLUS KUHLII*) В НИЖНЕВОЛЖСКОМ РЕГИОНЕ РОССИИ

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У нетопырей Куля *Pipistrellus kuhlii*, отловленных на территории Астраханской области (нижнее Поволжье), обнаружено два вида микрофаллоидных трематод – *Parabascus oppositus* и *Lecithodendrium* cf. s*krjabini*. Морфологическое изучение собранных экземпляров и паратипа *P. oppositus* показало, что данный вид лишен бурсы цирруса и имеет, свободно лежащие в паренхиме, извитой семенной пузырек, трубчатую простатическую часть, окруженную обширным полем простатических клеток, и короткий семяизвергательный канал. Половая пора у этого вида расположена на уровне брюшной присоски, субмедианно. *Lecithodendrium* cf. *skjabini* отличается от *L. skjabini* s. str. по длине тела. Филогенетический анализ, выполненный с использованием частичных последовательностей 28S рДНК, объединяет *P. oppositus* вместе с *G. amphoraeformis* и *Gyrabascus* sp. в кладу *Gyrabascus* spp. (Pleurogernidae). На основании полученных результатов, *P. oppositus* перемещен в род *Gyrabascus,* а диагноз последнего скорректирован. Анализ поддерживает кластеризацию *Lecithodendrium* cf. *skjabini* с другими членами рода *Lecithodendrium*. Полученные результаты демонстрируют монофилию Lecithodendriidae и свидетельствуют о принадлежности данного семейства к крупной кладе трематод, содержащей Microphallidae, Phaneropsolidae и Stomylotrematidae. Выявлена парафилия семейства Pleurogenidae и монофилия группы Pleurogenidae + Collyriclidae.

Ключевые слова: Trematoda, *Parabascus oppositus*, *Lecithodendrium skrjabini*, филогения, таксономия