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ORIGINAL PAPER

Phylogenetic position of the family Orientocreadiidae within the superfamily Plagiorchioidea (Trematoda) based on partial 28S rDNA sequence

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Abstract Trematodes of the family Orientocreadiidae are mostly parasites of freshwater fishes. Here, the phylogenetic position of this family is inferred based on the partial 28S rDNA sequence from a representative of the genus *Orientocreadium* s. str.–*O. pseudobagri* Yamaguti, 1934. Sequences were analysed by maximum likelihood and Bayesian inference algorithms. Both approaches placed the Orientocreadiidae within a clade corresponding to the superfamily Plagiorchioidea and supported the family Leptophallidae as a sister taxon.

Keywords *Orientocreadium* · Orientocreadiidae · Leptophallidae · Plagiorchioidea · Trematoda · Phylogeny · 28S rDNA

Introduction

Adult orientocreadiid trematodes typically inhabit the intestine of freshwater Eurasian and African siluriform and perciform fishes, but some species parasitise Indian terrestrial reptiles (Beverley-Burton 1962; Yamaguti 1971; Hafeezullah 1989). The systematic position of this group of parasites has repeatedly been discussed in the literature (e.g. Tubangui 1931; Yamaguti 1958; Skrjabin and Koval 1963; Fischthal and Kuntz 1963; Sirikantayakul 1985). According to the current point of view (Jones and Bray 2008), these trematodes belong to the separate family Orientocreadiidae Yamaguti 1958 within the superfamily Plagiorchioidea. This opinion has developed based on Fischthal and Kuntz (1963) taxonomic analysis of adult orientocreadiids and data on the morphology of *Orientocreadium batrachoides* Tubangui, 1931 and *Orientocreadium pseudobagri* Yamaguti, 1934 cercariae (Tang and Lin 1973; Besprozvannykh 1984). According to Jones and Bray (2008), the Orientocreadiidae is a monogeneric family with the following list of invalidated generic taxa that are congeneric with its type-genus—*Orientocreadium* Tabangui, 1931, *Ganada* Chatterji, 1933, *Neoganada* Dayal, 1938, *Nizamia* Dayal, 1938, *Ganadotrema* Dayal, 1949, *Macrotrema* Gupta, 1951 nec Regan, 1912 and *Paratormopsolus* Bychowsky et Dubinina 1954. A total of 28 nominal species of orientocreadiids have been described (Yamaguti 1971; Agrawal and Sharma 1990; Shimazu 1990; Kim and Rim 1995; Besprozvannykh et al. 2009; Nigam et al. 2015); however, the validity of many of them is questionable (Hafeezullah 1989). Sequences of 28 rDNA have been used successfully as a data source for phylogenetic reconstruction within the superfamily Plagiorchioidea (Tkach et al. 1999, 2000a, b, 2001a, b; Pérez-Ponce de León et al. 2011; Hernández-Mena et al. 2016). In this paper, we investigate the phylogenetic position of the Orientocreadiidae inferred from the same fragment of DNA from one of the representatives of the genus *Orientocreadium* s. str.–*O. pseudobagri*.

Materials and methods

Specimens of *O. pseudobagri* (Fig. 1) were recovered from the intestine of *Perccottus glenii* (Dybowski, 1877) (Actinopterygii, Odontobutidae), caught in July 2010 in the water body with the working name “Ozero 1”, Primorsky Kray, Russia (Sokolov 2013). Trematodes were fixed in

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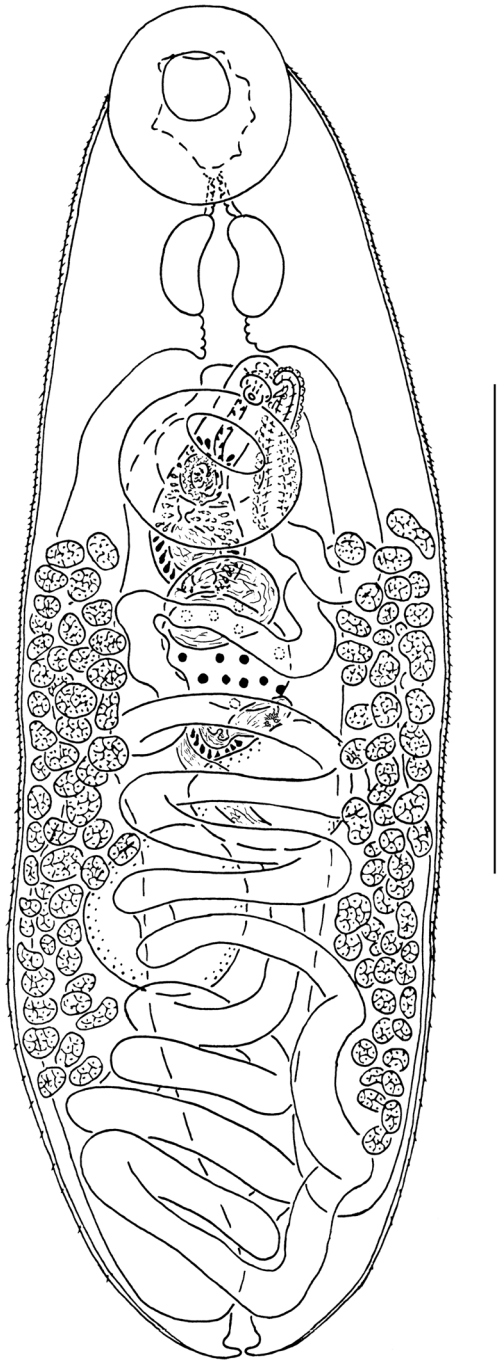


Fig. 1 *Orientocreadium pseudobagri* from *Perccottus glenii*, Primorsky Kray, Russia. Scale bar 0.4 mm

70% ethanol and stained with acetocarmine. Some specimens were fixed in 96% ethanol for further molecular analysis. Trematode species were identified with the aid of the publications of Yamaguti (1934), Shimazu (1990, 2014), Kim and Rim (1995), Besprozvannykh et al. (2009) and Shimazu et al. (2011).

In order to obtain 28 rDNA sequence, total DNA was isolated with a ZymoBead Genomic DNA Kit (http://www.zymoresearch.com). Only single trematode specimens were used for each DNA extraction. The DNA fragment of about 1200 bp localised at the 5′ end of 28 rDNA was amplified using the BIO-RAD C1000 Thermal Cycler. PCR were performed in a total volume of 20 μl (11.5 μl) H_20, 2.5 μl Taq buffer, 2 μl dNTP at concentration 10 pM, 0.5 μl of each primer at concentration 10 pM, 1 μl of Taq polymerase ("Syntol") and 1 μl of DNA template.

Trematode-specific forward primer LSU-5 (5′-TAG GTC GAC CCG CTG AAY TTA AGC A-3′) and reverse primer 1500R (5′-GCT ATC CTG AGG GAA ACT TCG-3′) were used. Genbank numbers of sequences used in analysis are provided in the Table 1. Thermal cycle parameters were as follows: initial denaturation at 95 °C (3 min); 35 cycles of 20 s at 95 °C; 20 s at 56 °C; 120 s at 72 °C; 5 min at 72 °C for final extension. Amplicons were purified using Cleanup mini Purification Kit (Eurogene). All amplicons were sequenced directly using the equipment of the Research Park of Saint-Petersburg State University (Centre for Molecular and Cell Technologies). Sequences from both forward and reverse primers were assembled using Chromas Pro 1.7.4.

Obtained sequences were included in the general alignment (Table 1). In total, 133 sequences (in addition to the newly obtained one) were used for alignment. First, sequences were automatically aligned using Muscle algorithm (Edgar 2004), as implemented in SeaView 4.0 (Gouy et al. 2010), followed by manual alignment verification. The phylogenetic analysis was performed using the maximum likelihood method (ML) with GTR + G + I model. In total, about 1100 sites were selected for the analysis. The ML phylogenetic tree was obtained using RaxML program (Stamatakis 2006) at CIPRES Science Gateway (www.phylo.org) (Miller et al. 2010). The stability of clades was assessed using a non-parametric bootstrap with 1000 pseudoreplicates. All model parameters were estimated from the data. Bayesian inference analysis (BI) was performed using MrBayes 3.1.2, GTR model with gamma correction for inter-site rate variation (8 categories) and the covarion model. Trees were run as two separate chains (default heating parameters) for 15 million generations at which point they had ceased converging. The quality of chains was estimated using built-in MrBayes tools and additionally using Tracer 1.6 (Rambaut et al. 2014). Based on the estimates by Tracer, 50,000 generations were discarded for burn-in (relative burn-in parameter was switched off).

Results

The general topology of the trees constructed by ML and BI was almost coincided (Fig. 2). Incongruent branches are labelled with an asterisk (*). In most of the cases, the mismatches of branching in ML and BI are caused by settings of BI analysis (because all trees with tripartitions were excluded).

Table 1 List of species, incorporated into molecular analysis: systematic affiliation by Olson et al. (2003) with additions (Overstreet and Curran 2005; Choudhury et al. 2007; Bray 2008; Bray and Cribb 2012; Heneberg and Literák 2013; Kanarek et al. 2014; Besprozvannykh et al. 2015a; Shedko et al. 2015; Bray et al. 2016; Littlewood et al. 2015; Hernández-Mena et al. 2016; Martínez-Salazar et al. 2016)

Species	Host species	Geographical region	GenBank accession number	Authority
Allocreadioidea				
Allocreadiidae				
Allocreadium isoporum	*Alburnus alburnus* (Actinopterigii: Cyprinidae)	Lake Oster, Karelia, Russia	GU462126	Petkevičiūtė et al. (2010)
Auriculostoma astyanace	*Astyanax fasciatus* (Actinopterigii: Characidae)	Rio Sapoa, Guanacaste, Costa Rica	KF631422	Razo-Mendivil et al. (2014a)
Bunodera luciopercae	*Perca fluviatilis* (Actinopterigii: Percidae)	River Tvertsa, Tver Oblast, Russia	GU462124	Petkevičiūtė et al. (2010)
Crepidostomum nemachilus	*Barbatula toni* (Actinopterigii: Nemacheilidae)	Water bodies of Russian Far East	FR821409	Atopkin and Shedko (2014)
Creptotrematina aguirrepeguenoi	*Astyanax mexicanus* (Actinopterigii: Characidae)	Filipinas, Veracruz, Mexico	KF631421	Razo-Mendivil et al. (2014a)
Margotrema bravoae	*Allotoca dugesii* (Actinopterigii: Goodeidae)	Mexico	KT833278	Pérez-Ponce de León et al. (2016)
Megalogonia ictaluri	*Ictalurus punctatus* (Actinopterigii: Ictaluridae)	Pearl River, Mississippi, USA	EF032694	Curran et al. (2006)
Paracreptotrema heterandria	*Heterandria bimaculata* (Actinopterigii: Poeciliidae)	Agua Bendita, Xico, Veracuz, Mexico	KF697697	Razo-Mendivil et al. (2014b)
Pseudoparacreptotrema macroacetabulata	*Profundulus punctatus* (Actinopterygii: Profundulidae)	Rio Primavera, Guatemala	KT833316	Pérez-Ponce de León et al. (2016)
Wallinia chavarriae	*Astyanax aeneus* (Actinopterygii: Characidae)	Rio Animas, Guanacaste, Costa Rica	HQ833703	Curran et al. (2011)
Gorgoderoidea				
Dicrocoeliidae				
Brachylecithum glareoli	*Myodes glareolus* (Mammalia: Cricetidae)	Lower Silesia, Poland	KU212203	Hildebrand et al. (2016)
Dicrocoelium dendriticum	*Marmota bobak* (Mammalia: Sciuridae)	Kharkiv Region, Ukraine	AF151939	Tkach et al. (2000a)
Eurytrema pancreaticum	*Bos indicus* (Mammalia: Bovinae)	India	KC602456	Tandon et al. (direct submission)
Lutztrema attenuatum	*Turdus merula* (Aves: Turdidae)	Czech Republic	KT387688	Hildebrand et al. (unpublished)
Lyperosomum colluriomis	*Sylvia atricapilla* (Aves: Sylviidae)	Central Moravia, Czech Republic	KU212193	Hildebrand et al. (2016)
Encyclometridae				
Encyclometra colubrimurarum	*Natrix natrix* (Reptilia: Colubridae)	Kiev Region, Ukraine	AF184254	Tkach et al. (2000b)
Gorgoderidae				
Anaporrhutum sp.	*Chiloscyllium punctatum* (Elasmobranchii: Hemiscyllidae)	Moreton Bay, Queensland, Australia	KF013184	Cutmore et al. (2013)
Degeneria halosauri	*Halosauropsis macrochir* (Actinopterigii: Halosauridae)	NE Atlantic Ocean	AY222257	Olson et al. (2003)
Gorgodera cygnoides	*Pelophylax ridibundus* (Amphibia: Ranidae)	Kokaljane, near Sofia, Bulgaria	AY222264	Olson et al. (2003)
Nagmia floridensis	*Dasyatis sabina* (Elasmobranchii: Dasyatidae)	Ocean Springs, Mississippi, USA	EF032691	Curran et al. (2006)
Plesiochorus sp.	*Caretta caretta* (Reptilia: Cheloniidae)	Atlantic coast of Virginia, USA	KF013180	Cutmore et al. (2013)
Phyllodistomum folium	*Sphaerium corneum* (Bivalvia: Sphaeriidae)	River Hegga, Norway	KJ729551	Petkevičiūtė et al. (2015)
Pseudophyllodistonum johnstoni	*Macrobranchium australiense* (Malacostraca: Palaemonidae)	Warrill Creek, Queensland, Australia	KF013177	Cutmore et al. (2013)
Staphylorchis cymatodes	*Sphyrna lewini* (Elasmobranchii: Sphyrnidae)	St. Helena Island, Moreton Bay, Australia	HM486319	Cutmore et al. (2010)
Xystretrum solidum		Conch Key, Florida, USA	KF013188	Cutmore et al. (2013)

Table 1 (continued)

Species	Host species	Geographical region	GenBank accession number	Authority
	Sphoeroides testudineus (Actinopterygii: Tetraodontidae)			
Paragonimidae				
Paragonimus heterotremus	*Indochinamon manipurense* (Malacostraca: Potamidae)	India	KF781294	Tandon and Athokpam (direct submission)
Troglotrematidae				
Nanophyetus salminicola	*Oncorhynchus mykiss* (Actinopterygii: Salmonidae)	Alsea hatchery, Benton Country, Oregon, USA	AY116873	Olson et al. (2003)
Nephrotrema truncatum	*Neomys anomalus* (Mammalia: Soricidae)	Carpathian Mountains, Zakarpatska Region, Ukraine	AF151936	Tkach et al. (2000a)
Skrjabinophyetus neomidis	*Neomys anomalus* (Mammalia: Soricidae)	Zakarpatska Region, Ukraine	AF184252	Tkach et al. (2000b)
Haploporoidea				
Atractotrematidae				
Atractotrema sigani	*Siganus lineatus* (Actinopterygii: Siganidae)	Lizard Island, Coral Sea, Australia	AY222267	Olson et al. (2003)
Isorchis anomalus	*Chanos chanos* (Actinopterygii: Chanidae)	Learmonth, Western Australia	KU873018	Andres et al. (2016)
Pseudomegasolena ishigakiense	*Scarus rivulatus* (Actinopterygii: Scaridae)	Heron Island, Coral Sea, Australia	AY222266	Olson et al. (2003)
Haploporidae				
Dicrogaster contracta	*Liza aurata* (Actinopterygii: Mugilidae)	Santa Pola, Spain	FJ211261	Blasco-Costa et al. (2009)
Forticulcita gibsoni	*Mugil cephalus* (Actinopterygii: Mugilidae)	Santa Pola, Spain	FJ211239	Blasco-Costa et al. (2009)
Haplodena nasonis	*Naso unicornis* (Actinopterygii: Acanthuridae)	Lizard Island, Coral Sea, Australia	AY222265	Olson et al. (2003)
Haploporus benedeni	*Liza ramado* (Actinopterygii: Mugilidae)	Santa Pola, Spain	FJ211237	Blasco-Costa et al. (2009)
Lecithobotrys putrescens	*Liza saliens* (Actinopterygii: Mugilidae)	Ebro Delta, Spain	FJ211236	Blasco-Costa et al. (2009)
Parasaccocoelium mugili	*Liza haematocheila* (Actinopterygii: Mugilidae)	–	HF548472	Besprozvannykh et al. (unpublished)
Ragaia lizae	*Liza saliens* (Actinopterygii: Mugilidae)	Ebro Delta, Spain	FJ211235	Blasco-Costa et al. (2009)
Saccocoelioides olmecae	*Dorminator maculatus* (Actinopterygii: Eleotridae)	Boca del Río, Veracruz, Mexico	KU061136	Andrade-Gómez et al. (2017)
Skrjabinolecithum spasskii	*Liza haematocheila* (Actinopterygii: Mugilidae)	Kievka River, Primorsky Kray, Russia	HE806370	Besprozvannykh et al. (2015b)
Lecithodendrioidea				
Allassogonoporidae				
Allassogonoporus amphoraephormus	*Myotis daubentoni* (Mammalia: Vespertilionidae)	Kiev, Ukraine	AY220620	Tkach et al. (2003)
Lecithodendriidae				
Lecithodendrium linstowi	*Myotis daubentoni* (Mammalia: Vespertilionidae)	Kiev Region, Ukraine	AF151919	Tkach et al. (2000a)
Ophiosacculus mehelyi	*Eptesicus serotinus* (Mammalia: Vespertilionidae)	Ukraine	AF480167	Tkach (direct submission)
Paralecithodendrium chilostomum	*Viviparus viviparous* (Gastropoda: Viviparidae)	Dnieper River, Kiev, Ukraine	KJ126725	Kudlai et al. (2015)
Paralecithodendrium parvouterus	*Miniopterus schreibersi* (Mammalia: Miniopteridae)	Rubielos de Mora, Spain	AY220617	Tkach et al. (2003)
Pycnoporus heteroporus	*Pipistrellus kuhli* (Mammalia: Vespertilionidae)	Kherson Region, Ukraine	AF151918	Tkach et al. (2000a)

Table 1 (continued)

Species	Host species	Geographical region	GenBank accession number	Authority
Pleurogenidae				
Brandesia turgida	*Pelophylax lessonae* (Amphibia: Ranidae)	Near Lesniki, Kiev Region, Ukraine	AY220622	Tkach et al. (2003)
Collyricloides massanae	*Erithacus rubecula* (Aves: Muscicapidae)	Near Zahlinice, Czech Republic	KP682451	Kanarek et al. (2015)
Cortrema magnicaudata	*Hirundo rustica* (Aves: Hirundinidae)	Near Záhlinice, Czech Republic	KJ700420	Kanarek et al. (2014)
Loxogenes macrocirra	*Pelophylax berlandieri* (Amphibia: Ranidae)	Guatemala	AY220624	Tkach et al. (2003)
Parabascus joannae	*Myotis daubentoni* (Mammalia: Vespertilionidae)	Kiev, Ukraine	AY220619	Tkach et al. (2003)
Pleurogenoides medians	*Pelophylax lessonae* (Amphibia: Ranidae	Ukraine	AF433670	Tkach et al. (2001b)
Pleurogenes claviger	*Rana temporaria* (Amphibia: Ranidae)	Kiev Region, Ukraine	AF151925	Tkach et al. (2000a)
Prosotocus confusus	*Pelophylax lessonae* (Amphibia: Ranidae)	Kiev Region, Ukraine	AY220623	Tkach et al. (2003)
Lepocreadioidea				
Lepidapedidae				
Bulbocirrus aulostomi	*Aulostomus chinensis* (Actynopterigii: Aulostomidae)	Heron Island, Coral Sea, Australia	FJ788470	Bray et al. (2009)
Intusatrium robustum	*Bodianus perditio* (Actynopterigii: Labridae)	New Caledonia	FJ788481	Bray et al. (2009)
Myzoxenus insolens	*Notolabrus tetricus* (Actynopterigii: Labridae)	Tasmania	FJ788486	Bray et al. (2009)
Microphalloidea				
Collyriclidae				
Collyriclum faba	*Saxicola rubetra* (Aves: Muscicapidae)	Orlické Záhoří, Chech Republic	JQ231122	Heneberg and Literák (2013)
Eucotylidae				
Tanaisia fedtschenkoi	*Anas platyrhynchus* (Aves: Anatidae)	Kherson Region, Ukraine	AY116870	Olson et al. (2003)
Tamerlania zarudnyi	*Corvus monedula* (Aves:Corvidae)	Chernigiv Region, Ukraine	AF184248	Tkach et al. (2000b)
Paratanaisia bragai	*Helmeted guinea* (Aves: Numididae)	Brazil	JX231099	Unwin et al. (2013)
Faustulidae				
Bacciger lesteri	*Selenotoca multifasciata* (Actynopterygii: Scatophagidae)	Moreton Bay, Brisbane, Australia	AY222269	Olson et al. (2003)
Microphallidae				
Candidotrema loossi	*Pelophylax ridibundus* (Amphibia: Ranidae)	Vilkovo, Kiliya, Ukraine	AY220621	Tkach et al. (2003)
Floridatrema heardi	*Oryzomys palustris* (Mammalia: Cricetidae)	Florida, USA	AY220632	Tkach et al. (2003)
Microphallus triangulatus	*Somateria mollissima v-nigrum* (Aves: Anatidae)	Yamskaya Bay, Sea of Okhotsk, Russia	HM584139	Galactionov et al. (2012)
Maritrema subdolum	*Peringia ulvae* (Gastropoda: Hydrobiidae)	Kandalaksha Bay, White Sea, Russia	HM584135	Galactionov et al. (2012)
Pachypsolidae				
Pachypsolus irroratus	*Lepidochelys olivacea* (Reptilia: Cheloniidae)	Oaxaca, Mexico	AY222274	Olson et al. (2003)
Prosthogonimidae				
Prosthogonimus cuneatus	*Sturnus vulgaris* (Aves: Sturnidae)	Nezhin, Chernigiv Region, Ukraine	AY220634	Tkach et al. (2003)
Shistogonimus rarus	*Anas querquedula* (Aves: Anatidae)	Golopristansky district, Kherson Region, Ukraine	AY116869	Tkach et al. (2003)

Table 1 (continued)

Species	Host species	Geographical region	GenBank accession number	Authority
Renicolidae				
Nephromonorcha varitestis	*Pelecanus erythrorhynchos* (Aves: Pelecanidae)	North Dakota, USA	KP710187	Patitucci et al. (2015)
Renicola sp.	*Numenius arquata* (Aves: Scolopacidae)	Kherson Region, Ukraine	AY116871	Olson et al. (2003)
Zoogonidae				
Deretrema nahaense	*Thalassosoma lunare* (Actinopterygii: Labridae)	Lizard Island, Coral Sea, Australia	AY222273	Olson et al. (2003)
Lepidophyllum steenstrupi	*Anarhichus lupus* (Actinopterygii: Anarchichadidae)	North Sea	AY157175	Lockyer et al. (2003)
Plectognathotrema kamegaii	*Pseudomonacanthus peroni* (Actinopterygii: Manacanthidae)	Ningaloo Reef, Australia	KM505035	Cutmore et al. (2014)
Zoogonoides viviparus	*Callionymus lyra* (Actinopterygii: Callionymidae)	North Sea, UK	AY222271	Olson et al. (2003)
Monorchioidea				
Lissorchiidae				
Asymphylodora perccotti	*Perccottus glenii* (Actinopterygii: Odontobutidae)	Bolshaya Ussurska River Basin, Russia	FR822730	Besprozvannykh et al. (2012)
Lissorchis kritskyi	*Minytrema melanops* (Actinopterygii: Catostomidae)	Pascagoula River, Mississippi, USA	EF032689	Curran et al. (2006)
Monorchiidae				
Ancylocoelium typicum	*Trachurus trachurus* (Actinopterygii: Carangidae)	North Sea, UK	AY222254	Olson et al. (2003)
Helicometroides longicollis	*Diagramma labiosum* (Actinopterygii: Haemulidae)	Heron Island, Coral Sea, Australia	KJ658287	Searle et al. (2014)
Diplomonorchis leiostomi	*Leiostomus xanthurus* (Actinopterygii: Sciaenidae)	Gulf of Mexico, Ocean Springs, Mississippi, USA	AY222252	Olson et al. (2003)
Lasiotocus arrhichostoma	*Diagramma labiosum* (Actinopterygii: Haemulidae)	Heron Island, Coral Sea, Australia	KJ658289	Searle et al. (2014)
Lasiotocus lizae	*Liza longimanus*(Actinopterygii: Mugilidae)	Cat Ba Island, Tonkin Bay, Vietnam	LN831724	Atopkin et al. (2017)
Proctotrema addisoni	*Diagramma labiosum* (Actinopterygii: Haemulidae)	Heron Island, Coral Sea, Australia	KJ658291	Searle et al. (2014)
Provitellus turrum	*Pseudocaranx dentex* (Actinopterygii: Carangidae)	Heron Island, Coral Sea, Australia	AY222253	Olson et al. (2003)
Plagiorchioidea				
Alloglossidiidae				
Alloglossidium floridense	*Noturus leptacanthus* (Actinopterygii: Ictaluridae)	Spring, feeding into the Santa Fe River, Florida	KC812276	Kasl et al. (2014)
Magnivitellinum simplex	*Astyanax aeneus* (Actinopterygii: Characidae)	Metzabok Lake, Chiapas, Mexico	KU535683	Hernández-Mena et al. (2016)
Auridistomidae				
Auridistomum chelydrae	*Chelydra serpentine* (Reptilia: Chelydridae)	Jackson Country, Mississippi, USA	AY116872	Olson et al. (2003)
Brachycoeliidae				
Mesocoelium sp.	*Bufo marinus* (Amphibia: Bufonidae)	Brisbane, Queensland, Australia	AY222277	Olson et al. (2003)
Cephalogonimidae				
Cephalogonimus retusus	*Pelophylax ridibundus* (Amphibia: Ranidae)	Kokaljane, near Sofia, Bulgaria	AY222276	Olson et al. (2003)
Choanocotylidae				
Choanocotyle nematoides	*Emydura macquarii* (Reptilia: Chelidae)	New South Wales	EU196360	Tkach and Snyder (2007)
Glypthelminthidae				
Glypthelmins facioi	*Rana* sp. (Amphibia: Ranidae)	Guanacaste, Costa Rica	AY875675	Razo-Mendivil et al. (2006)

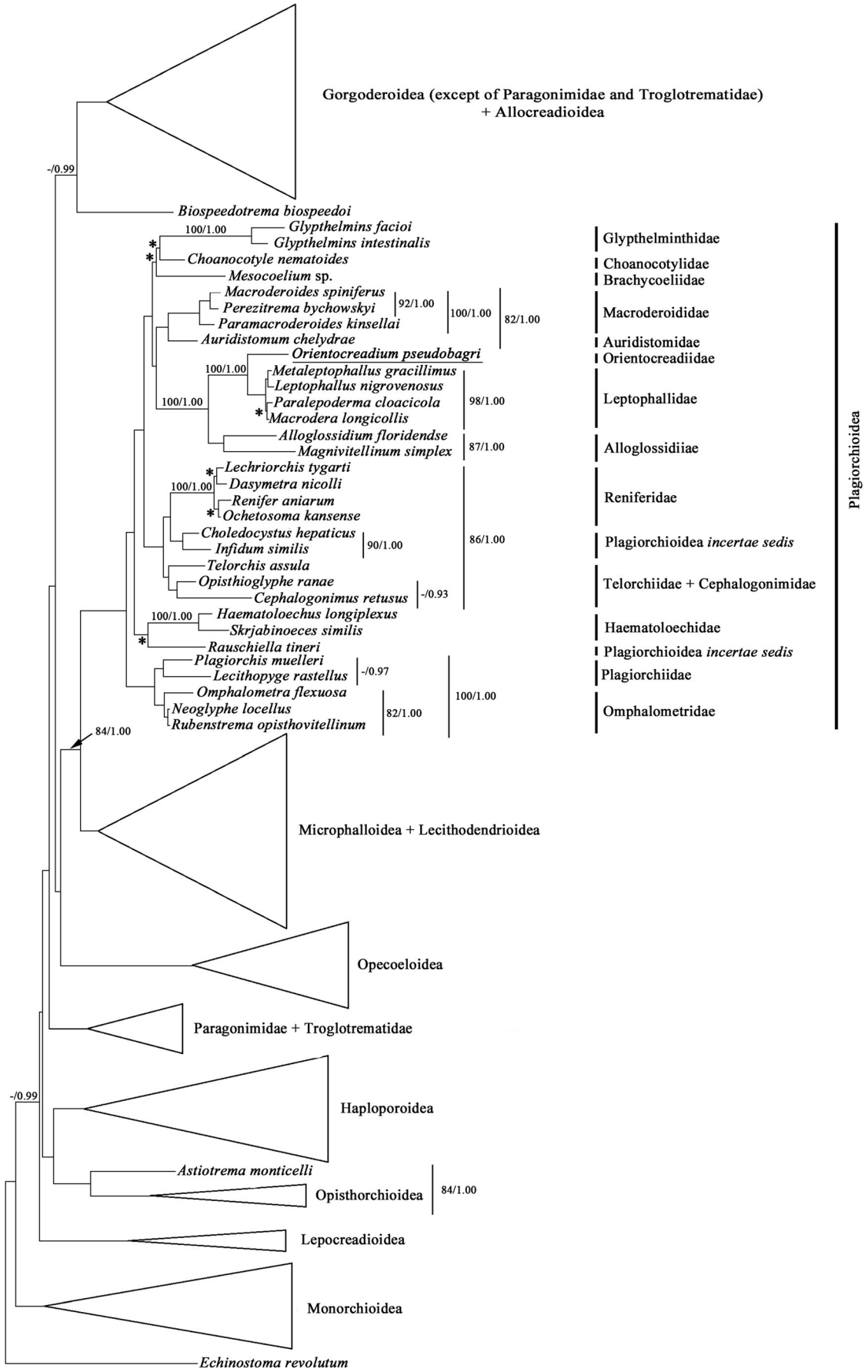
Table 1 (continued)

Species	Host species	Geographical region	GenBank accession number	Authority
Glypthelmins intestinalis	*Rana luteiventris* (Amphibia: Ranidae)	Glacier National Park, Montana, USA	AY875673	Razo-Mendivil et al. (2006)
Haematoloechidae				
Haematoloechus longiplexus	*Pelophylax temporaria* (Amphibia: Ranidae)	Gage Country, Nebraska, USA	AF387801	Snyder and Tkach (2001)
Skrjabinoeces similis	*Pelophylax ridibundus* (Amphibia: Ranidae)	Kokaljane, near Sofia, Bulgaria	AY222279	Olson et al. (2003)
Leptophallidae				
Leptophallus nigrovenosus	*Natrix natrix* (Reptilia: Colubridae)	Kiev Region, Ukraine	AF151914	Tkach et al. (1999)
Macrodera longicollis	*Natrix natrix* (Reptilia: Colubridae)	Kiev and Odessa Regions, Ukraine	AF151913	Tkach et al. (1999)
Metaleptophallus gracillimus	*Natrix natrix* (Reptilia: Colubridae)	Kiev Region, Ukraine	AF151912	Tkach et al. (1999)
Paralepoderma cloacicola	*Natrix natrix* (Reptilia: Colubridae)	Kiev Region, Ukraine	AF151910	Tkach et al. (1999)
Macroderoididae				
Macroderoides spiniferus	*Lepisosteus osseus* (Actinopterygii: Lepisosteidae)	USA	AF433674	Tkach et al. (2001b)
Paramacroderoides kinsellai	*Lepisosteus oculatus* (Actinopterygii: Lepisosteidae)	Oxbow lake, Mississippi, USA	HM137664	Tkach et al. (2010)
Perezitrema bychowskyi	*Atractosteus tropicus* (Actinopterygii: Lepisosteidae)	San Pedro, Pantanos de Centla, Tabasco, Mexico	KU535686	Hernández-Mena et al. (2016)
Omphalometridae				
Neoglyphe locellus	*Sorex araneus* (Mammalia: *Soricidae*)	Odessa Region, Ukraine	AF300330	Tkach et al. (2001a)
Omphalometra flexuosa	*Planorbis planorbis* (Gastropoda: Planorbidae)	Kosewo Górne, Poland	AF300333	Tkach et al. (2001a)
Rubenstrema opisthovitellinum	*Sorex araneus* (Mammalia: *Soricidae*)	Odessa Region, Ukraine	AF300332	Tkach et al. (2001a)
Orientocreadiidae				
Orientocreadium pseudobagri	*Perccottus glenii* (Actinopterygii: Odontobutidae)	Primorsky Kray, Russia	MF611697	This study
Plagiorchiidae				
Lecithopyge rastellus	*Rana temporaria* (Amphibia: Ranidae)	Kiev Region, Ukraine	AF151932	Tkach et al. (2000a)
Plagiorchis neomidis	*Lymnaea stagnalis* (Gastropoda: Lymnaeidae)	Danube River near Gabčíkovo, Czech Republic	KJ533397	Zikmundová et al. (2014)
Reniferidae				
Dasymetra nicolli	*Nerodia rhombifer* (Reptilia: Colubridae)	USA	AF433672	Tkach et al. (2001b)
Lechriorchis tygarti	*Lithobates sylvaticus* (Amphibia: Ranidae)	North Dakota, USA	JF820602	Pulis et al. (2011)
Ochetosoma kansense	*Drymarchon corais*(Reptilia: Colubridae)	USA	AF433671	Tkach et al. (2001b)
Renifer aniarum	*Natrix natrix* (Reptilia: Colubridae)	Calabria, Italy	HQ665460	Santoro et al. (2011)
Telorchiidae				
Opisthioglyphe ranae	*Rana arvalis* (Amphibia: Ranidae)	Ivano-Frankivsk Region, Ukraine	AF151929	Tkach et al. (2000a)
Telorchis assula	*Natrix natrix* (Reptilia: Colubridae)	Kiev Region, Ukraine	AF151915	Tkach et al. (2000a)
Plagiorchioidea *incertae sedis*				
Choledocystus hepaticus	*Rhinella marina* (Amphibia: Bufonidae)	San Pedro las Playas, Guerrero, México	HM137617	Razo-Mendivil and Pérez-Ponce de León (2011)
Infidum similis	*Leptophis diplotropis* (Reptilia: Colubridae)	El Podrio, Acapulco, Guerrero, México	KU726885	Martínez-Salazar et al. (2016)

Table 1 (continued)

Species	Host species	Geographical region	GenBank accession number	Authority
Rauschiella tineri	*Leptodactylus melanonotus* (Amphibia: Leptodactylidae)	San Pedro las Playas, Guerrero, México	HM137620	Razo-Mendivil and Pérez-Ponce de León (2011)
Opecoeloidea				
Opecoelidae				
Allopodocotyle epinepheli	*Epinephelus cyanopodus* (Actinopterygii: Serranidae)	New Caledonia	KU320598	Bray et al. (2016)
Anomalotrema koiae	*Sebastes viviparous* (Actinopterygii: Sebastidae)	Shetland Islands	KU320595	Bray et al. (2016)
Cainocreadium lintoni	*Epinephelus morio* (Actinopterygii: Serranidae)	Caribbean Sea	KJ001208	Andres et al. (2014)
Hamacreadium mutabile	*Lutianus fulviflamma* (Actinopterygii: Lutjanidae)	New Caledonia	KU320601	Bray et al. (2016)
Helicometra boseli	*Sargocentron spiniferum* (Actinopterygii: Holocentridae)	New Caledonia	KU320600	Bray et al. (2016)
Macvicaria macassarensis	*Lethrinus miniatus* (Actinopterygii: Lethrinidae)	Heron Island, Coral Sea, Australia	AY222208	Olson et al. (2003)
Neolebouria lanceolata	*Polymixia lowei* (Actinopterygii: Polymixiidae)	Gulf of Mexico	KJ001210	Andres et al. (2014)
Opecoeloides fimbriatus	*Micropogonias undulates* (Actinopterygii: Sciaenidae)	Gulf of Mexico	KJ001211	Andres et al. (2014)
Opistholebes amplicoelus	*Tetractenos hamiltoni* (Actynopterygii: Tetraodontidae)	Stradbroke Island, Australia	AY222210	Olson et al. (2003)
Pacificreadium serrani	*Plectropomus leopardus* (Actinopterygii: Serranidae)	New Caledonia	KU320602	Bray et al. (2016)
Pseudopycnadena tendu	*Pseudobalistes fuscus* (Actinopterygii: Balistidae)	New Caledonia	FJ788506	Bray et al. (2009)
Urorchis goro	*Rhinogobius kurodai* (Actinopterygii: Gobiidae)	Metoba River Nagano, Japan	LC149880	Shimazu (2016)
Opisthorchioidea				
Opisthorchiidae				
Opisthorchis viverrini	*Mesocricetus auratus* (Mammalia: Cricetidae)	Thailand	HM004188	Thaenkham et al. (unpublished)
Heterophyidae				
Cryptocotyle lingua	*Littorina littorea* (Gastropoda: Littorinidae)	Isle of Sylt, North Sea, Germany	AY222228	Olson et al. (2003)
Superfamily and family indet.				
Astiotrema monticelli	*Natrix natrix* (Reptilia: Colubridae)	Kiev Region, Ukraine	AF184253	Tkach et al. (2000b)
Biospeedotrema biospeedoi	*Thermichthys hollisi* (Actinopterygii: Bythitidae)	South East Pacific Rise	KF733986	Bray et al. (2014)
Outgroup				
Echinostomatoidea				
Echinostomatidae				
Echinostoma revolutum	*Lymnaea stagnalis* (Gastropoda: Lymnaeidae)	Pond Hluboký u Hamru, Czech Republic	KP065598	Georgieva et al. (2014)

Phylograms from both ML and BI placed the Orientocreadiidae (=*O. pseudobagri*) within a major clade corresponding to the superfamily Plagiorchioidea (see Table 1) with the family Leptophallidae supported as the sister taxon (Fig. 2). In turn, the clade of Orientocreadiidae + Leptophallidae has a strongly supported sister relationship with the clade of the Alloglossidiidae. The monophyletic clade uniting orientocreadiids, leptophallids and alloglossidiids grouped into a large weakly supported clade containing members of the families Brachycoeliidae, Choanocotylidae, Glypthelminthidae, Auridistomidae and Macroderoididae. In all cases, the Auridistomidae and Macroderoididae appeared sister groups, as did the Brachycoeliidae and Choanocotylidae + Glypthelminthidae (with strong and weak support,


Gorgoderoidea (except of Paragonimidae and Troglotrematidae)
+ Allocreadioidea
-/0.99
Biospeedotrema biospeedoi
100/1.00
Glypthelmins facioi
Glypthelmins intestinalis
Choanocotyle nematoides
Mesocoelium sp.
Macroderoides spiniferus
Perezitrema bychowskyi
92/1.00
Paramacroderoides kinsellai
100/1.00
82/1.00
Auridistomum chelydrae
Orientocreadium pseudobagri
100/1.00
Metaleptophallus gracillimus
Leptophallus nigrovenosus
100/1.00
Paralepoderma cloacicola
98/1.00
Macrodera longicollis
Alloglossidium floridense
Magnivitellinum simplex
87/1.00
Lechriorchis tygarti
100/1.00
Dasymetra nicolli
Renifer aniarum
Ochetosoma kansense
Choledocystus hepaticus
Infidum similis
90/1.00
86/1.00
Telorchis assula
Opisthioglyphe ranae
Cephalogonimus retusus
-/0.93
100/1.00
Haematoloechus longiplexus
Skrjabinoeces similis
Rauschiella tineri
Plagiorchis muelleri
Lecithopyge rastellus
-/0.97
Omphalometra flexuosa
Neoglyphe locellus
82/1.00
100/1.00
Rubenstrema opisthovitellinum
84/1.00
Microphalloidea + Lecithodendrioidea
Opecoeloidea
Paragonimidae + Troglotrematidae
-/0.99
Haploporoidea
Astiotrema monticelli
Opisthorchioidea
84/1.00
Lepocreadioidea
Monorchioidea
Echinostoma revolutum
Glypthelminthidae
Choanocotylidae
Brachycoeliidae
Macroderoididae
Auridistomidae
Orientocreadiidae
Leptophallidae
Alloglossidiiae
Reniferidae
Plagiorchioidea incertae sedis
Telorchiidae + Cephalogonimidae
Haematoloechidae
Plagiorchioidea incertae sedis
Plagiorchiidae
Omphalometridae
Plagiorchioidea

◀ **Fig. 2** Bayesian tree of the Orientocreadiidae based on the analysis of 28S rDNA partial sequences. Nodal numbers are indicated: bootstrap value to the left from slash mark and Bayesian statistics to the right; only significant values are shown (above 80% for bootstrap value and 0.9 for BI). Sequence of *Echinostoma revolutum* is used as outgroup

respectively). BI analysis revealed that the group of Auridistomidae + Macroderoididae is aggregated with the Alloglossidiidae + (Orientocreadiidae + Leptophallidae) clade, while the Brachycoeliidae + (Choanocotylidae + Glypthelminthidae) clade occupied a sister position to all the former mentioned trematodes. In ML analysis, Auridistomidae + Macroderoididae appear as a weakly supported sister clade to that formed by the brachycoeliids, choanocotylids and glypthelminthids.

Other plagiorchioid trematodes analysed in the phylogenetic reconstruction are the Haematoloechidae, Omphalometridae, Plagiorchiidae, Telorchiidae, Cephalogonimidae, Reniferidae and the genera *Choledocystus* Pereira et Cuocolo, 1941, *Infidum* Travassos, 1916, and *Rauschiella* Babero, 1951 (as Plagiorchioidea *incertae sedis* by Hernández-Mena et al. (2016) and Martínez-Salazar et al. (2016)) are basal taxa to orientocreadiids. The families Haematoloechidae, Omphalometridae, Plagiorchiidae, Reniferidae and the clade of *Choledocystus* + *Infidum* are resolved inside it as well-supported monophyletic groups. In the same time, intergeneric relationships of the telorchiids and cephalogonimids were poorly resolved with the exception of node *Cephalogonimus retusus* (Dujardin, 1845)/*Opisthioglyphe ranae* (Frölich, 1791) in BI analysis. Position of the genus *Rauschiella* on phylograms that are produced by different methods is unstable.

Discussion

Our molecular data reveal a close phylogenetic relationship between orientocreadiids and both alloglossidiids and leptophallids, which justifies the placement of the Orientocreadiidae in the Plagiorchioidea. Previously, Hernández-Mena et al. (2016) showed molecular evidence of phylogenetic affinity between alloglossidiids and leptophallids. Analysis of the sequences obtained in the present study demonstrated a closer relationship between leptophallids with orientocreadiids than with the alloglossidiids. Dayal (1938) was the first to notice that orientocreadiids (at that time attributable to the genera *Ganada*, *Neoganada* and *Nizamia*) are morphologically close to leptophallids. An indisputable synapomorphy of the Orientocreadiidae + Leptophallidae clade is the presence of an external seminal vesicle. The external seminal vesicle in both families is unipartite, tubular or saccular, without associated gland cells (Tkach et al. 1999; Shimazu 2014). Within the Plagiorchioidea, this organ is characteristic only of representatives of the said clade (Bray 2008). In general, this structure is not unique to plagiorchioids and appears with varying frequency in other superfamilies of trematodes, in particular, in the Opecoeloidea and Lepocreadioidea. The most significant morphological difference between adult leptophallids and orientocreadiids is the presence of a canalicular seminal receptacle in the Leptophallidae. In orientocreadiids, there is a uterine seminal receptacle (Bray 2008).

Leptophallid and orientocreadiid trematodes are parasites of different groups of vertebrates. Adult leptophallids are parasites of the intestine or lungs of snakes (Tkach 2008) and orientocreadiids mainly parasitise the intestine of the ray-finned fishes (Actinopterygii). Only two species of the family have been described from terrestrial lizards (Hafeezullah 1989), one of which—*Orientocreadium ottoi* Agrawal, 1966—is considered by some authors as conspecific with *O. batrachoides*, a parasite of the catfishes (Pandey 1970; Hafeezullah 1989).

The first intermediate hosts of the trematode groups in question are pulmonate snails—Lymnaeidae for orientocreadiids (Tang and Lin 1973; Besprozvannykh 1984; Sirikantayakul 1985; Besprozvannykh et al. 2009), and Lymnaeidae or Planorbidae for leptophallids (Grabda-Kazubska 1963; Dobrovol ski 1969). Xiphidiocercariae of orientocreadiids and leptophallids are similar in general morphology. These larvae have a relatively large bodies (about 0.3 mm in length), anterior organs with a stylet of an "open type" (the small bulb is not covered), and a relatively long prepharynxes (Tkach et al. 1999; Besprozvannykh et al. 2009). The excretory bladder in orientocreadiid and many leptophallid cercariae is Y-shaped, thick-walled, with the terminal mouths of the main collecting ducts (Tkach et al. 1999; Besprozvannykh et al. 2009). Only in representatives of the genus *Macrodera* Lühe, 1899 do the main collecting ducts open into the arms subterminally (Tkach et al. 1999). The protonephridial formula is 2[(3 + 3 + 3) + (3 + 3 + 3)] = 36 in all known cercariae in both families. Cercariae of leptophallids, however, have 4 or 8 pairs of non-differentiated penetration glands (Tkach et al. 1999), whereas only 3 or 5 pairs of penetration glands have been reported for orientocreadiid cercariae (Tang and Lin 1973; Besprozvannykh et al. 2009).

General topology of orientocreadiid cercarial sensillae demonstrates great similarities with other plagiorchioid trematodes including leptophallids (Besprozvannykh et al. 2009). The presence of numerous sensillae on the anterior end of *O. pseudobagri* cercariae (well expressed "C"-circles and groups of "St"), as well as AID row (equal to StD_3 group in Besprozvannykh et al. 2009) and two S-circles ($9S_1$ and $5S_2$ according to Besprozvannykh et al. 2009), is consistant with the plagiorchioid type of the chaetotaxy. Nevertheless, the main character, which approximates *O. pseudobagri* cercaria with other species of plagiorchioid trematodes, is the presence of 2 UD ("U" in Besprozvannykh et al. 2009) sensillae on tail tegument.

Miracidia of representatives of the genus *Orientocreadium* are very similar to those at other plagiorchioid species including leptophallids. They have the same epithelial formula (3 + 3) and related glandular apparatus—two large penetration glands situated immediately posterior to the terebratorium (Tang and Lin 1973). Unfortunately, nothing is known about organisation of the excretory system and germinative primordium in orietocreadiid miracidia. In addition, even less is known about sporocysts of leptophallids and orientocreadiids other that they have an elongated body with a thick wall. In all studied species, the birth pore is situated terminally (Dobrovol ski 1969; Tang and Lin 1973; Besprozvannykh et al. 2009).

No morphological synapomorphy is apparent for the clade of Alloglossidiidae + (Orientocreadiidae + Leptophallidae). External phylogenetic connections of this group with other plagiorchioid trematodes cannot yet be adequately identified.

In general, only the Telorchiidae among the nine families of the Plagiorchioidea (represented in our study by more than one species) has not been demonstrated to be monophyletic. The Telorchiidae is represented here by members of two subfamilies—Telorchiinae (*Telorchis assula* (Dujardin, 1845)) and Opisthioglyphinae (*Opisthioglyphe ranae* (Frölich, 1791)) (see Font and Lotz 2008). The association of these taxa into one family is supported by data on the cercarial chaetotaxy (Grabda-Kazubska and Lis 1993) and the results of the molecular study by Tkach et al. (2000a). However, the molecular data of a number of subsequent authors testify to the paraphyly of the Telorchiidae (Olson et al. 2003; Bray et al. 2005; Pérez-Ponce de León et al. 2011; Martínez-Salazar et al. 2016).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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