Morphological and molecular identification of an echinostomatid digenean *Pegosomum asperum* ex *Ardea alba* (Aves: Pelecaniformes: Ardeidae) from the Volga River delta

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ABSTRACT: *Pegosomum* is a genus of aberrant echinostomatid digeneans that parasitize ardeid birds as adults in the biliary system. Phylogenetic relationships of this genus are not entirely clear. Two specimens of *Pegosomum* were collected from the Great egret *Ardea alba* in the Volga River delta (Russia), and identified based on morphological characteristics as *P. asperum*. Morphological identification of these specimens was confirmed by phylogenetic analysis based on markers of nuclear (*28S* rRNA gene, ITS2 region) and mitochondrial (*nad1* and *cox1*) genes. It is the first comprehensive molecular and morphological evidence of the occurrence of this species in Eastern Europe. The results of our phylogenetic analyses show that *Pegosomum* spp. share the most recent common ancestor with the type species of the genus *Petasiger*, *P. exaeretus*, and morphologically undescribed cercariae *Petasiger* sp. 1 of Laidemitt *et al*. (2019) from *Radix natalensis* (Krauss, 1848), Kenya. The genus *Petasiger* appears to be a non-monophyletic taxon, and its revision is necessary.
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KEY WORDS: Trematoda, Echinostomatidae**,** *Petasiger,* herons, phylogeny.

Морфологическая и молекулярная идентификация вида эхиностоматидных дигеней *Pegosomum asperum* из *Ardea alba* (Aves: Pelecaniformes: Ardeidae) дельты Волги

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РЕЗЮМЕ: *Pegosomum* — род аберрантных эхиностоматидных трематод, паразитирующих на фазе мариты в желчевыводящей системе цапель. Филогенетические связи этого рода не до конца ясны. Два экземпляра *Pegosomum* были обнаружены нами у большой белой цапли *Ardea alba*, добытой в дельте Волги, и идентифицированы по морфологическим признакам как *P. asperum*. Видовая принадлежность паразита была подтверждена результатами филогенетическим анализа, выполненного на основе маркеров ядерной (*28S рРНК* ген, ITS2 регион) и митохондриальной (*nad1* и *cox1*

гены) ДНК. Это первое сообщение о регистрации *P. asperum* в Восточной Европе, подкрепленное комплексном молекулярных и морфологических доказательств. Филогенетический анализ показал, что *Pegosomum* spp. имеет наиболее позднего общего предка с типовым видом рода *Petasiger* (*P. exaeretus*) и обнаруженной в Кении морфологически неописанной церкарией *Petasiger* sp. of Laidemitt *et al*. (2019) из *Radix natalensis*. Род *Petasiger*, по-видимому, не является монофилетическим, что указывает на необходимость его ревизии.

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КЛЮЧЕВЫЕ СЛОВА: Trematoda, Echinostomatidae, *Petasiger*, цапли, филогения.

Introduction

Pegosomum Ratz, 1903 is a genus of aberrant echinostomatid digeneans parasitising herons (Ardeidae) *a*s adults in the biliary system. Their striking morphological character is the absence of the oral sucker (Skrjabin, Bashkirova, 1956; Kostadinova, 2005*)*. Two representatives of this genus have been recorded in Europe, *P. saginatum* (Ratz, 1898) and *P. asperum* (Wright, 1879) (=*P. spiniferum* Ratz, 1903) (Iskova, 1985; Heneberg, Sitko, 2017).

Pegosomum asperum has a rich taxonomic history. This species was originally described as *Distomum* (*Echinostoma*) *asperum* based on specimens collected from the American bittern *Botaurus lentiginosus* (Rackett, 1813) from Canada (Wright, 1879). Ratz (1903) transferred it to *Pegosomum.* Aleksandrova (1976) proposed to consider *P. asperum* as a senior synonym of *P. spiniferum* (=*P. skrjabini* Schachtachtinskaja, 1949), which was originally described from the Eurasian bittern *Botaurus stellaris* (Linnaeus, 1758) from Hungary (Ratz, 1903). According to an almost universally accepted opinion of Bychovskaya-Pavlovskaya (1955), *P. spiniferum* is a senior synonym of *P. skrjabini. Pegosomum skrjabini* was originally described from the herons of Azerbaijan (Schachtachtinskaya, 1949). Iskova (1985) disagreed with the proposal to synonymise *P. spiniferum* with *P. asperum*. According to this author, the conclusions of Aleksandrova (1976) were actually based not on the study of type specimens of *P. asperum* but on the comparison of individuals mentioned under this name by other authors. Unar *et al*. (2011) considered *P. asperum* and *P. spiniferum* as two distinct species. At the same time, Heneberg and Sitko (2017) agreed with Aleksandrova (1976) regarding the synonymy of *P. asperum* and *P. spiniferum*. These authors analysed one nuclear (ITS2) and two mitochondrial (*cox1*, *nad1*) loci of *P. asperum* and *P. saginatum* from Central Europe and confirmed the validity of the taxonomic separation of these two species (Heneberg, Sitko, 2017).

In systems of the Echinostomatidae based on morphology, *Pegosomum* is traditionally allocated to the subfamily Pegosominae Odhner, 1910 (e.g. Skrjabin, Bashkirova, 1956; Yamaguti, 1971; Kostadinova, 2005). According to Feizullaev *et al*. (1990), *Pegosomum* is phylogenetically close to *Chaunocephalus* Dietz, 1910. Recent results of the phylogenetic analysis of echinostomatids based on *28S* rRNA gene sequences do not support the conclusions of these authors and reveal a close affinity of *Pegosomum* spp. (*P. asperum and P. saginatum*) with the type species of *Petasiger* Dietz, 1909, *P. exaeretus* Dietz, 1909 (Le *et al*., 2022, 2024). However, the *28S* rRNA gene sequences of *Pegosomum* spp. available in GenBank NCBI (KY945919 and KY945918) are unsupported by morphological description, which casts some doubt on the reliability of the identification of the genotyped specimens. A close relationship between *P. saginatum* and *P. exaeretus* is also shown by the ITS marker (López-Hernández *et al*., 2023), but in this case the reliability of *P. saginatum* identification is unquestionable.

During parasitological investigation of the Great egret *Ardea alba* Linnaeus, 1758 (Ardeidae) in the Volga River delta, we found digenean specimen morphologically identified as *P. asperum.* Here, we described the morphological characteristics of this species and reconstructed its phylogeny based on nuclear (*28S rRNA* gene, ITS2 region) and mitochondrial (*nad1* and *cox1* genes) DNA markers.

Table 1. List of primers used for amplification and sequencing.
Таблица 1. Список использованных праймеров.

DNA region	Primer	Sequence 5′→3′	Direction	Reference
28S rRNA gene	ZX1aF	ACCCGCTGAATTTAAGCATAT	forward, external	Palm *et al*. (2009)
	1500R	GCTATCCTGAGGGAAACTTCG	reverse, external	Snyder, Tkach (2001)
ITS2 region	3S	GTACCGGTGGATCACGTGGCTAGTG	forward, external	Morgan, Blair (1995)
	ITS2.2	CCTGGTTAGTTTCTTTTCCTCCGC	reverse, external	Cribb *et al*. (1998)
cox1 gene	JB3	TTTTTTGGGCATCCTGAGGTTTAT	forward, external	Bowles *et al.* (1992)
	JB4.5	TAAAGAAAGAACATAATGAAAATG	reverse, external	Bowles *et al*. (1992)
nad1 gene	NDJ11 (JB11)	AGATTCGTAAGGGGCCTAATA	forward, external	Kostadinova *et al.* (2003)
	NDJ2a	CTTCAGCCTCAGCATAAT	reverse, external	Morgan, Blair, (1998)

Material and Methods

SAMPLING AND MORPHOLOGICAL STUDY. One intact and one severely damaged adult specimen of *P. asperum* were collected from the bile duct of the Great egret taken near Kalinino Village, Astrakhan Region, Russia (46°20′9″ N; 48°53′29″ E), in September 2017. The intact specimen was initially relaxed in fresh water and fixed with 70% ethanol, then transferred to 96% ethanol and subsequently used as a hologenophore; the damaged specimen was immediately fixed in 96% ethanol. A small fragment of the body was extracted from the hologenophore using needles and subsequently used for the molecular genetic analysis. The hologenophore was stained with acetocarmine, dehydrated in a graded series of ethanol, cleared with dimethyl phthalate, and finally mounted in Canada balsam. The anterior body end of the damaged specimen was dissected with a razor blade along the sagittal and parasagittal planes in order to make a thick histological section. This section was stained and mounted in Canada balsam according to the procedure described above. All the measurements are given in micrometres. The drawings were made using the camera lucida.

MOLECULAR DATA AND PHYLOGENETIC ANALYSES. Total DNA was isolated from a body fragment of the hologenophore of *P. asperum* using a QIAamp DNA Mini Kit (QIAGEN, Germany). The fragments of nuclear and mitochondrial DNA were amplified using BIO-RAD T100 Thermal Cycler (USA).

Polymerase chain reaction (PCR) with specific primers amplified partial sequences of the *28S* rRNA gene and complete sequences of the ITS2 region of nuclear DNA, as well as partial sequences of the *cox1* and *nad1* genes of mitochondrial DNA (Table 1). PCR were performed in a total volume of 25 µl using the Encyclo Plus PCR kit (Eurogene, Russia) according to the manufacturer's instructions.

The following protocol was used to amplify partial *28S* rRNA gene sequences: initial denaturation at 95 ºC (5 min); 40 cycles of 30 s at 95 ºC; 30 s at 55 ºC; 2 min at 72 ºC; and 7 min at 72 ºC for the final extension. In addition, we amplified ITS2 locus of nuclear DNA and *cox1* gene of mitochondrial DNA.

To amplify the complete sequences of the ITS2 region according to the following protocol: cycle 1 was 95 °C for 3 min, 45 °C for 2 min and 72 °C for 150 s; this was followed by 4 shorter cycles, 95 °C for 45 s, 50 °C for 45 s and 72 °C for 90 s, then further 30 cycles of 95 °C for 20 s, 52 °C for 20 s and 72 °C for 90 s and 5 min at 72 °C for the final extension.

The following protocol was used to amplify partial *cox1* gene sequences: initial denaturation at 95 °C for 5 min, then 95 °C for 20 s, 55 °C for 30 s, 72 °C for 30 s extension for 35 cycles, and 5 min at 72 °C for the final extension.

PCR cycling parameters for amplification partial sequences *nad1* gene sequence included denaturation at 95 °C for 5 min, then 94 °C for 30 s, 48 °C for 20 s, 72 °C for 45 s extension for 35 cycles, and 4 min at 72 °C for the final extension.

The amplicons were purified using Cleanup S-Cap (Eurogene, Russia) and sequenced directly using PCR primers. In addition, we used internal primers to sequence *28S rRNA* gene. All amplicons were sequenced at the Beagle Company (St. Petersburg, Russia). Sequences from both forward and reverse

primers were assembled using Chromas Pro v. 1.7.4 (Technelysium Pty Ltd, Australia).

For the phylogenetic reconstruction based on the *28S* rRNA gene, the ITS2 region, *cox1* and *nad1* genes dataset, the newly obtained sequences were aligned with those of 76 echinostomatid species for 28S-tree, 7 species for *cox1*-tree, 31 species for ITS2-tree and 24 species for *nad1*-tree (Table S1). The final alignment length of the sequence was 1044 bp for the *28S rRNA* gene, 378 bp for the ITS2 region, 397 bp for the *cox1* gene and 402 bp for the *nad1* gene. Alignments were accomplished using the Muscle algorithm (Edgar, 2004) as implemented in SeaView Version 4.0 (Gouy *et al.*, 2010), after which the alignment was adjusted manually. Bayesian algorithm was performed in MrBayes 3.2.7a (Ronquist *et al.*, 2012) with the GTR+G+I model for *28S rRNA* and *nad1* alignments, also TPM2uf+G model for *cox1* and ITS2 alignments. The evolutionary model was estimated as suggested by jModeltest 2.1.7 (Darriba *et al.*, 2012). In the analysis, 15 000 000 generations of the Markov chain Monte Carlo posterior third were simulated; the selection was performed with a frequency of every 100 generations.

The phylogenetic 28S-tree was rooted to *Caballerotrema* sp. (Echinostomatoidea, Caballerotrematidae) based on the findings of Tkach *et al*. (2016) (Table S1). For the ITS2, *nad1* and *cox1* trees, *Echinostoma revolutum* (Fröhlich, 1802) (Echinostomatoidea, Echinostomatidae) was used as an outgroup following the conclusions of Le *et al.* (2022) (Table S1). Estimates of evolutionary divergence (p-distances) were made with MEGA 11.0.13 software (Tamura *et al*., 2021).

Results

TAXONOMY

Family Echinostomatidae Looss, 1899
Genus *Pegosomum* Ratz, 1903
Pegosomum asperum (Wright, 1879)
Figs 1–3.

FINAL HOST: the Great egret *Ardea alba* Linnaeus, 1758 (Ardeidae).

SITE OF INFECTION: bile duct.

LOCALITY: Vicinity of Kalinino Village, Astrakhan Region, Russia.

ACCESSIONS SEQUENCES IN GENBANK: *28S rRNA* gene, PP388212; ITS2 region, PP388213; *cox1* gene, PP388214; *nad1* gene, PP400928.

DESCRIPTION (based on whole mount hologenophore and histological section of anterior end of paragenophore): Body lanceolate; length 9375, maximal width 3700 at about midlevel. Body surface covered with small spikes. Oral sucker absent. Mouth opening almost terminal. Head collar weakly developed, with 27 spines in two rows. Dorsal spines 35–49, lateral spines 155–165 long. Ventral sucker oval 750 × 875. Forebody 46.4% of body length. Prepharynx 50 long. Pharynx pyriform 400 × 260. Oesophagus 3250 long. Intestinal bifurcation in posterior quarter of forebody. Caeca terminate blindly close to posterior extremity. Testes two, slightly indented, in second half of body, median, almost tandem, separated; anterior testis, transversely-oval, 1000 × 2480, posterior testis subtriangular, 1250 × 2510. Post-testicular region 5.3%. Cirrus sac median, reaching posteriorly to anterior third of ventral sucker, 550 × 475. Cirrus everted, club-shaped, 1000 × 500. Genital pore just posterior to intestinal bifurcation. Ovary entire, pyriform, 765 × 600, dextro-submedian, between anterior testis and posterior end of ventral sucker; distance between ovary and posterior margin of ventral sucker 0.53% of body length. Mehlis' gland large, sinistral to ovary. Uterus pre-testicular; Proximal part of uterus acts as uterine seminal receptacle. Eggs numerous, 98 × 75. Vitellarium follicular; follicles in two lateral fields, reaching from middle pharynx to posterior end of body, confluent only anteriorly to cirrus sac. Excretory vesicle not observed.

PHYLOGENETIC STUDY. Bayesian Inference analysis based on *28S* rRNA gene sequences produced a tree in which the newly genotyped specimen of *P. asperum* clustered with a conspecific specimen whose molecular data were deposited in GenBank NCBI under the number KY945919 (Fig. 4). The sequences of these specimens were very similar (p-distance 0.1%). This group of *P. asperum* specimens was pooled together with *Petasiger* sp.1 of Laidemitt *et al.* (2019) and *P. saginatum* into one moderately supported clade, in which the latter species occupied the basal position. The clade of *Pegosomum* spp. and *Petasiger* sp. of Laidemitt *et al*. (2019) appeared as a strongly supported sister to *P. exaeretus*. The clade containing all the mentioned digeneans formed polytomy with a strongly supported *Petasiger phalacrocoracis* (Yamaguti, 1939) + *Petasiger* sp.2 of Laidemitt *et al*. (2019) clade, *Petasiger radiatus* (Dujardin, 1845) and some unidentified *Petasiger* spp. In turn, the large polytomic clade considered was nested within an even larger group of the echinostomatid digeneans designated by Izrailskaia *et al*. (2021) as Group 1.

The results of the analysis for three other genetic markers (ITS2 region, *nad1* and *cox1* genes) also showed both a high similarity of the corresponding sequences of our *P. asperum* specimen with those of conspecific specimens available in GenBank NCBI and the clustering of all these specimens into one clade (Figs 5–7). The p-distances between the sequences of our sample and those of *P. asperum* available in GenBank NCBI had the following values: 0.18–0.55% (ITS2 region), 0.50–1.24% (*nad1* gene), 0–0.60% (*cox1* gene).

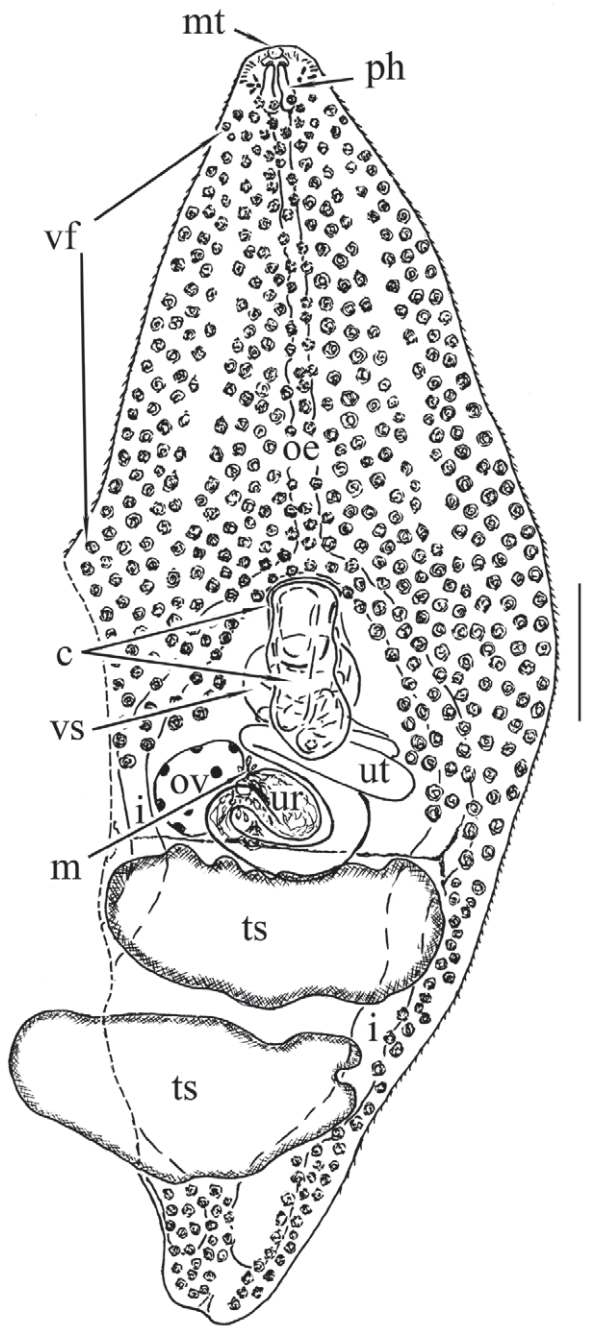

Fig. 1. Hologenophore of *Pegosomum asperum* ex *Arcella alba* from Volga River delta, Russia, whole ventral view. Abbreviations: c — cirrus sac with everted cirrus; i — caeca; m — Mehlis' gland; mt — mouth opening; oe — oesophagus; ov — ovary; ph — pharynx; ts — testes; ur — uterine seminal reciptacle; ut — uterine loops; vs — ventral sucker; vf — vitelline follicles. Scale bar: 1000 μm.

Рис. 1. Гологенофор *Pegosomum asperum* из *Arcella alba*, дельта Волги, Россия, вентрально. Обозначения: c — сумка цирруса с вывернутым циррусам; i — кишечные ветви; m — железа Мелиса; mt — ротовое отверстие; oe — пищевод; ov — яичник; ph — глотка; ts — семенники; ur — маточный семяприемник; ut — петли матки; vs — брюшная присоска; vf — желточные фолликулы. Масштабная линейка: 1000 μm.

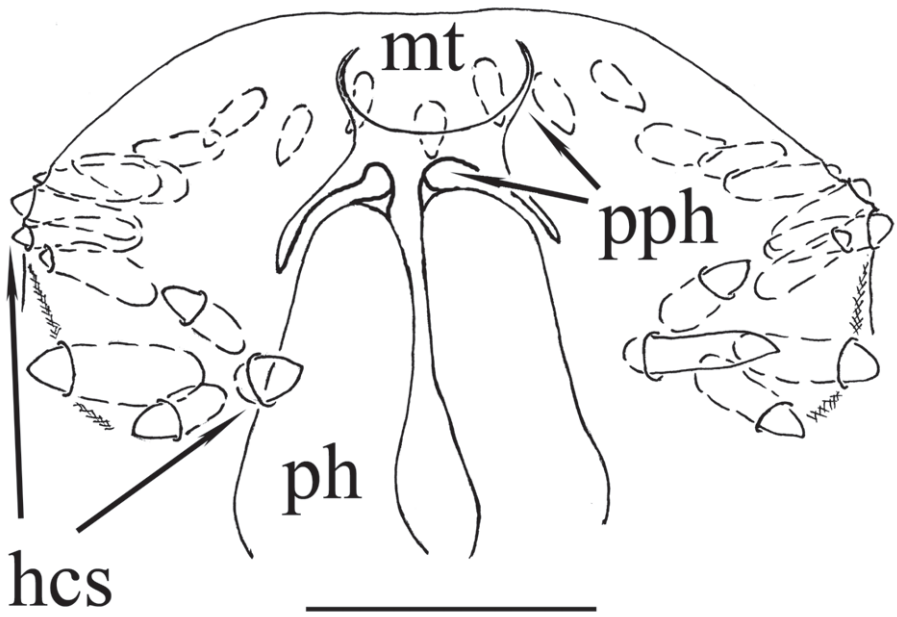

Fig. 2. Anterior end of hologenophore of *Pegosomum asperum*, ventral view.
Abbreviations: hcs — collar *spines;* mt — mouth opening; ph — pharynx; pph — prepharynx. Scale bar: 200 μm.
Рис. 2. Передний конец гологенофора *Pegosomum asperum*, вентрально.
Обозначения: hcs — шипы адорального диска*;* mt — ротовое отверстие; ph — глотка; pph — префаринкс. Масштабная линейка: 200 мкм.

In ITS2-tree, *P. asperum* appeared as a moderately supported sister to *P. exaeretus*. In turn, the *P. asperum* + *P. exaeretus* clade had a strongly supported sister relationship with *P. saginatum* (Fig. 5). However, the phylogenetic position of the clade represented by *Pegosomum* spp. and *P. exaeretus* was poorly resolved on this tree.

In *nad1*-tree, *P. asperum* appeared as a strongly supported sister to the equally strongly supported *P. saginatum* + *Petasiger* sp.1 of Laidemitt *et al*. (2019) clade (Fig. 6). The clade containing all these digeneans was nested into the large clade that also included *Neopetasiger* spp., *Petasiger* spp., *Isthmiophora hortensis* (Asada, 1926) and *Isthmiophora melis* of Kostadinova *et al.* (2003) (probably conspecific to *Petasiger radiatus* (Dujardin, 1845), see Nugaraitė *et al.*, 2017). Overall, however, this large clade was poorly resolved internally.

In *cox1*-tree, *P. asperum* was a poorly supported sister to *P. saginatum*. In turn, the clade of these species formed polytomy with other members of Group 1 (Fig. 7).

Discussion

Morphological features of our specimens, namely, vitelline follicles filling almost the enter forebody and a large cirrus (diameter > 447) unambiguously indicate that they belong to *P. asperum* (Heneberg, Sitko, 2017). Several authors have described a poorly developed oral sucker in this species (Wright, 1879; Ratz, 1903; Sitko, 2012; Heneberg, Sitko, 2017), but Odhner (1910), having examined histological sections of *P. spiniferum* (=*P. asperum*), concluded that the oral sucker was absent. Our results support this conclusion of Odhner (Fig. 3). Molecular data on several genetic markers of our specimen indicate its conspecificity with the specimens of *P. asperum* whose sequences are available in GenBank NCBI. In addition, our data also confirm that the *28S rRNA* gene sequence from GenBank NCBI (KY945919), assigned to *P. asperum* without a morphological confirmation, does indeed belong to this species.

Thus, our study provides the first comprehensive molecular and morphological evidence of the presence in the Volga River delta region (and in Eastern Europe in general) of a *Pegosomum* isolate conspecific with *P. asperum* from Central Europe. Previously, only morphologically confirmed reports on the occurrence of *P. asperum*

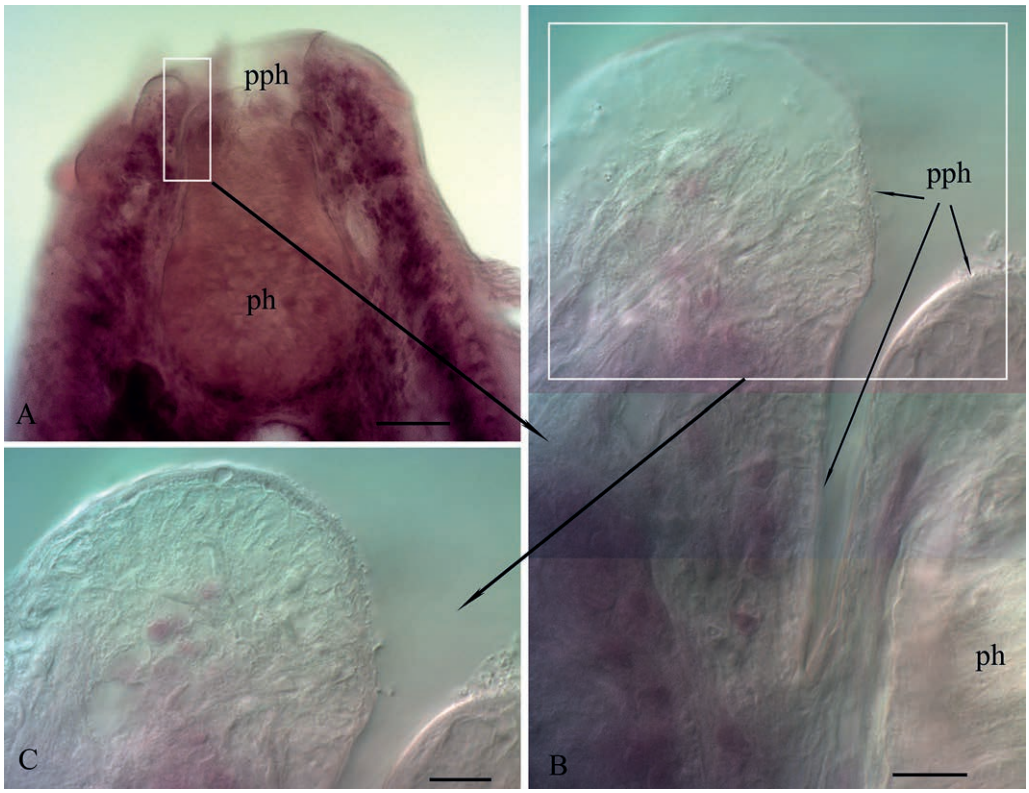

Fig. 3. Microphotographs of thick sagittal section of anterior end of paragenophore of *Pegosomum asperum*. A — pharynx and prepharynx; B — prepharynx within the fragment outlined by white frame in Part A; B — prepharynx within the fragment outlined by white frame in Part B.
Abbreviations: ph — pharynx; pph — prepharynx. Scale bars: A — 100 μm; B–D — 10 μm.
Рис. 3. Микрофотографии толстого сагиттального среза переднего конца парагенофора *Pegosomum asperum*. A — фаринкс и префаринкс;. B — префаринкс в пределах фрагмента, очерченного белой рамкой на рисунке 3A; C — префаринкс в пределах фрагмента, очерченного белой рамкой на рисунке 3B.
Обозначения: ph — фаринкс; pph — префаринкс. Масштабные линейки: A — 100 мкм; B–C — 10 мкм.

(as *P. spiniferum*) in the Volga River delta were published (Dubinin, Dubinina, 1940; Ivanov *et al*., 2012). However, the validity of synonymisation of *P. asperum* with *P. spiniferum* must be verified using molecular data on *P. asperum* isolate from Canada (type locality of this species).

Molecular data on the Echinostomatidae obtained in the last decade have contributed to progress in addressing the taxonomic problems of this digenean group (e.g. Stanevičiūtė *et al*., 2015; Tkach *et al*., 2016; Laidemitt *et al*., 2019; Izrailskaia *et al*., 2021; Pantoja *et al*., 2021; Le *et al*. 2022, 2024; López-Hernández *et al*., 2023; Valadão *et al*., 2023). The results of our predecessors indicate the differentiation of the echinostomatids into two large clades, respectively Group 1 and Group 2 (Stanevičiūtė *et al*., 2015; Tkach *et al*., 2016; Laidemitt *et al*., 2019; Izrailskaia *et al*., 2021; Le *et al*., 2022, 2024). Our data support this conclusion. To date, these clades have no definite taxonomic status. We leave this question open until molecular data are available for as many echinostomatids as possible.

The results of our phylogenetic analyses support the findings of Le *et al*. (2022, 2024) and López-Hernández *et al*. (2023) that *Pegosomum* spp. share the most recent common ancestor with the type species of the genus *Petasiger*, *P. exaeretus*. The descendants of this ancestor also include *Petasiger* sp.1 of Laidemitt *et al*. (2019), known from morphologically undescribed cercariae from *Radix natalensis* (Krauss, 1848), Kenya. Morphological evidence for the clustering of *P. exaeretus* with *Pegosomum* spp.

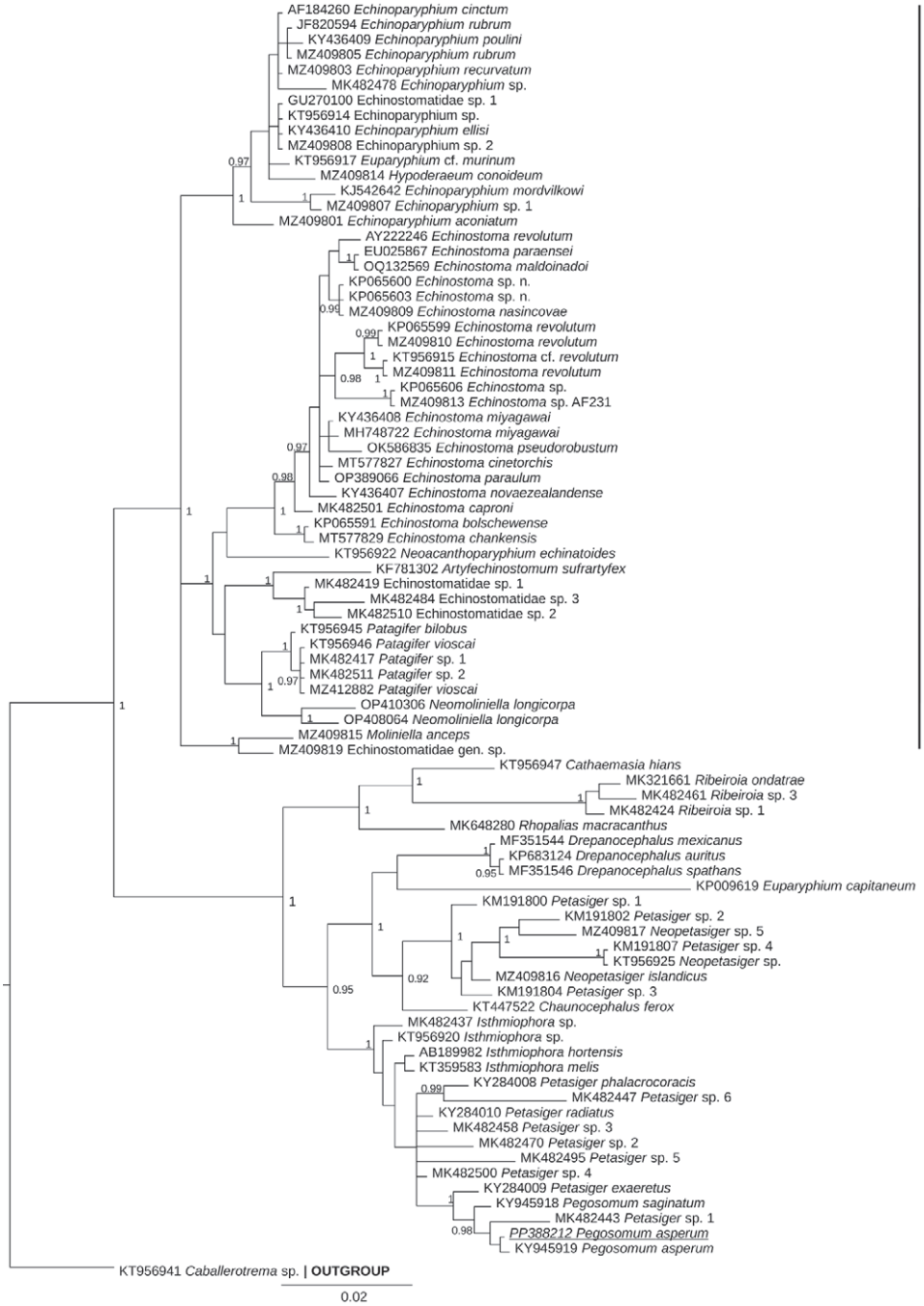

Fig. 4. Phylogenetic relationships of *Pegosomum asperum* based on Bayesian inference analysis of sequences of *28S rRNA* gene. Values of posterior probability supports lower than 0.9 are not shown. Newly obtained sequences are underlined.

Рис. 4. Филогенетические связи *Pegosomum asperum*, реконструированные в ходе Байесовского анализа последовательностей гена *28S рРНК*. Поддержки апостериорных вероятностей ниже 0.9 не указаны. Новые последовательности выделены подчеркиванием.

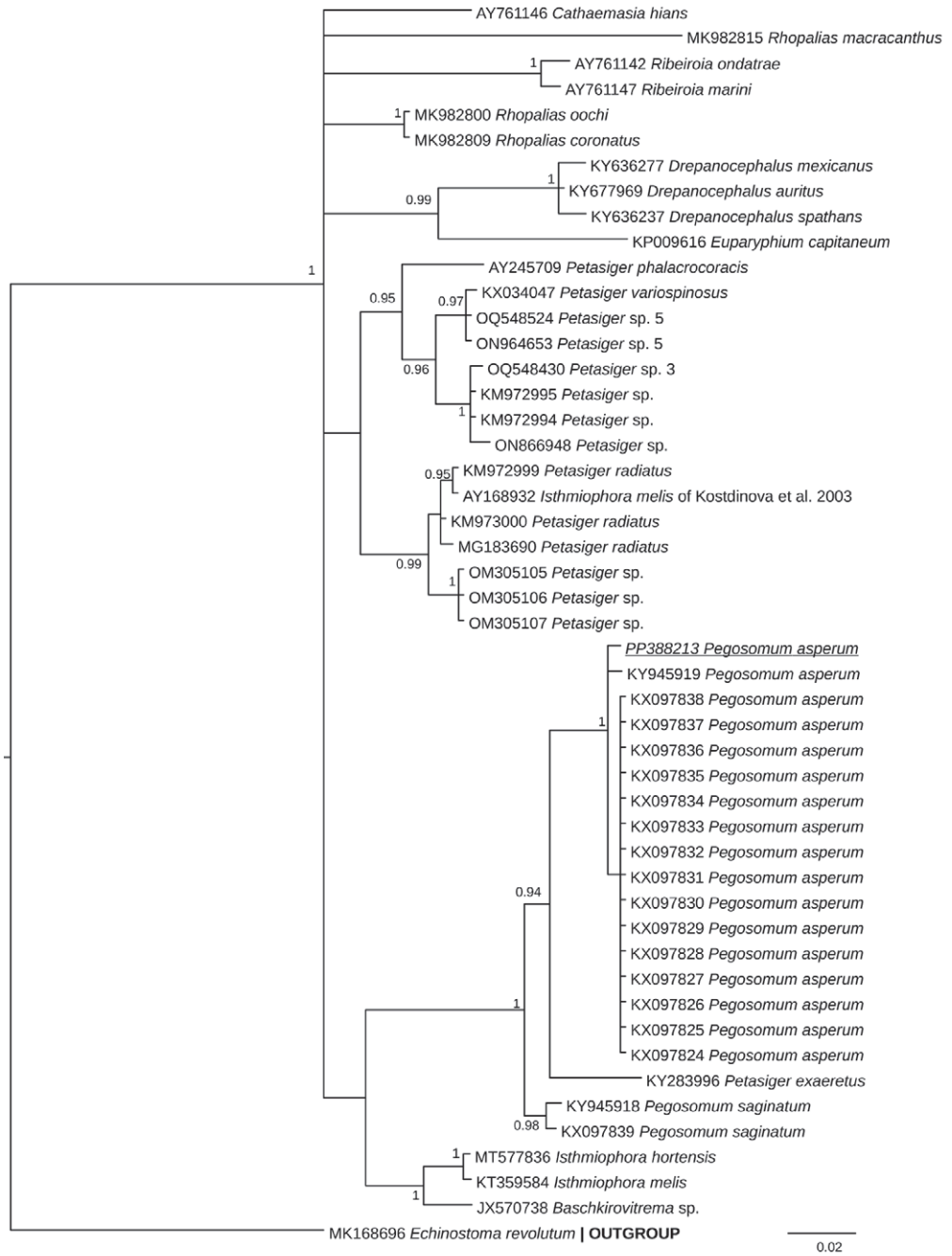

Fig. 5. Phylogenetic relationships of *Pegosomum asperum* based on Bayesian inference analysis of sequences of ITS2 region. Values of posterior probability supports lower than 0.9 are not shown. Newly obtained sequences are underlined.

Рис. 5. Филогенетические связи *Pegosomum asperum*, реконструированные в ходе Байесовского анализа последовательностей ITS2 региона. Поддержки апостериорных вероятностей ниже 0,9 не указаны. Новые последовательности выделены подчеркиванием.

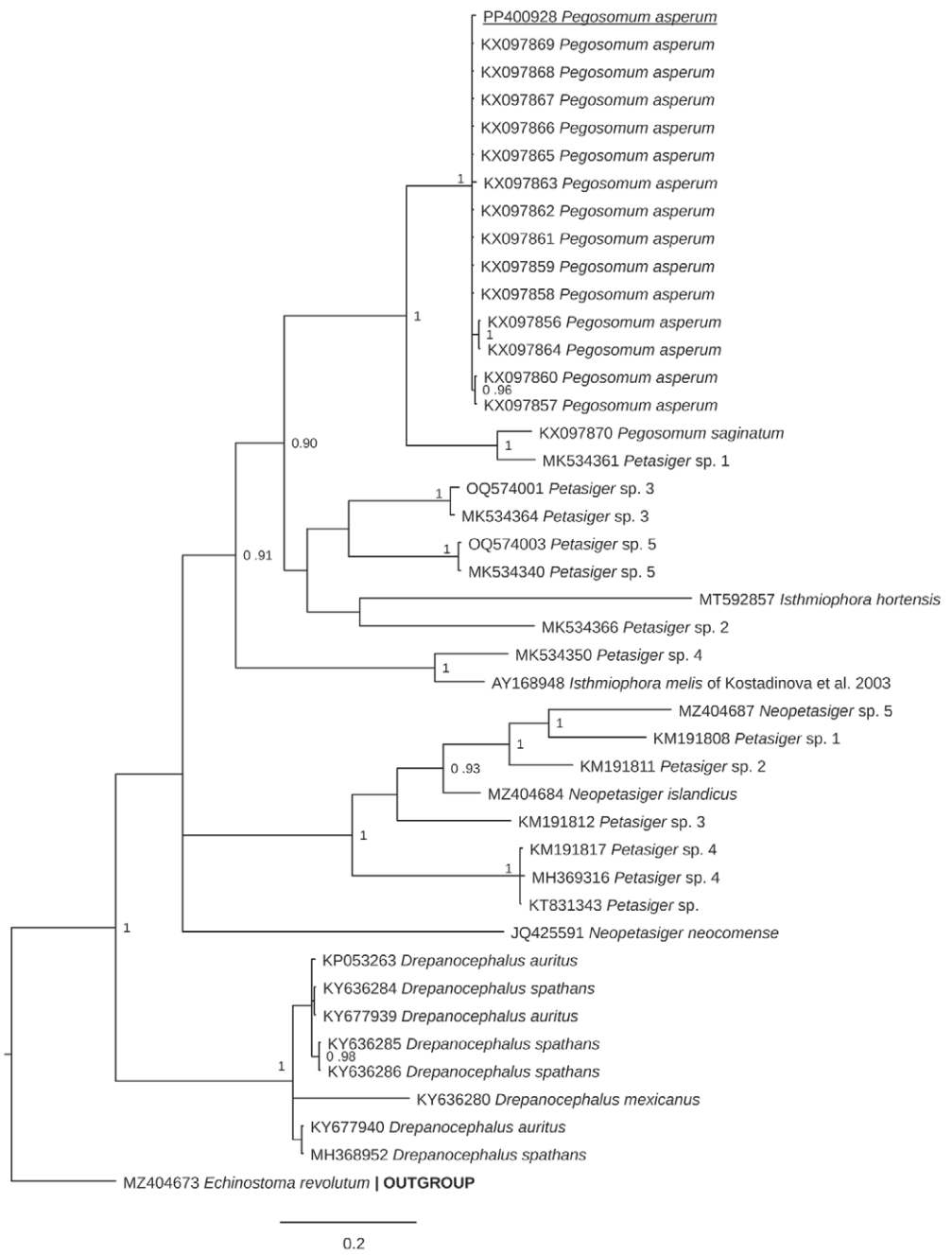

Fig. 6. Phylogenetic relationships of *Pegosomum asperum* based on Bayesian inference analysis of sequences of *nad1* gene. Values of posterior probability supports lower than 0.9 are not shown. Newly obtained sequences are underlined.

Рис. 6. Филогенетические связи *Pegosomum asperum*, реконструированные в ходе Байесовского анализа последовательностей гена *nad1*. Поддержки апостериорных вероятностей ниже 0,9 не указаны. Новые последовательности выделены подчеркиванием.

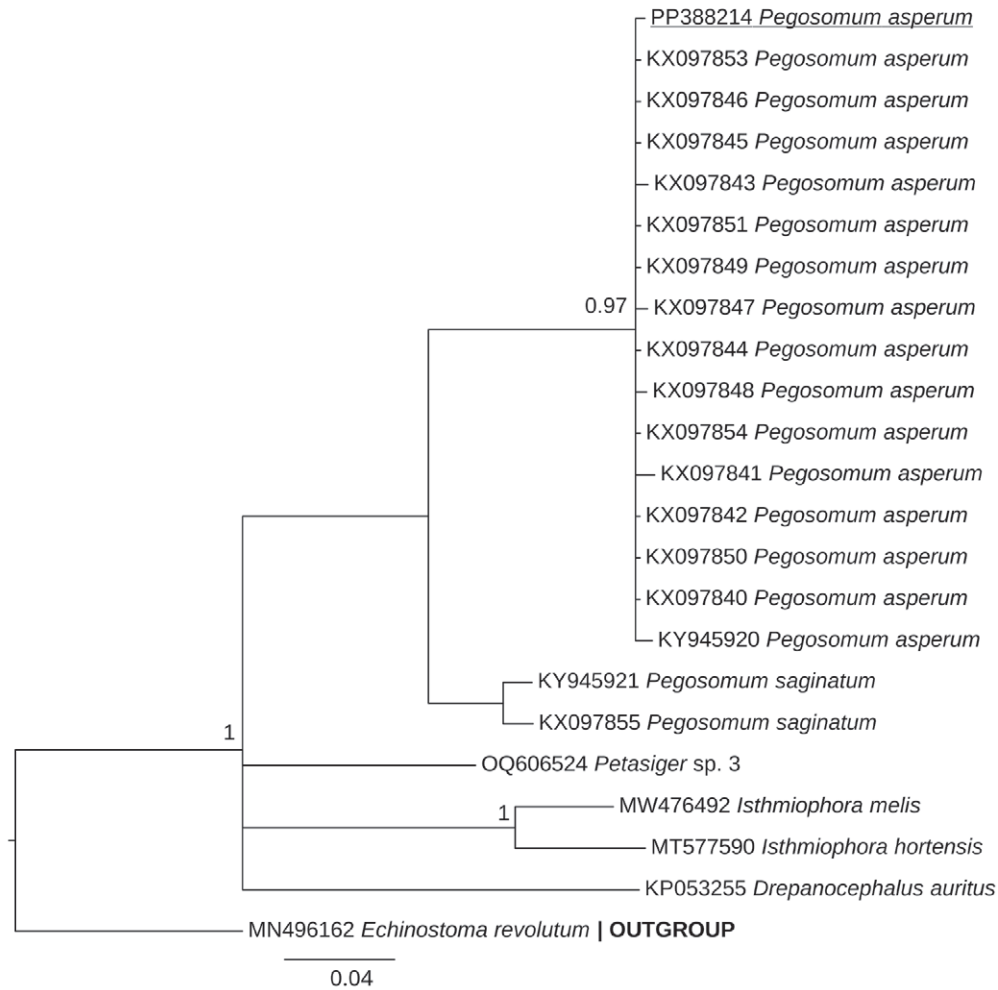

Fig. 7. Phylogenetic relationships of *Pegosomum asperum* based on Bayesian inference analysis of sequences of *cox1* gene. Values of posterior probability supports lower than 0.9 are not shown. Newly obtained sequences are underlined.

Рис. 7. Филогенетические связи *Pegosomum asperum*, реконструированные в ходе Байесовского анализа последовательностей гена *cox1*. Поддержки апостериорных вероятностей ниже 0,9 не указаны. Новые последовательности выделены подчеркиванием.

is not obvious, the only similarity being in body shape and the presence of a massive pharynx (at least as compared to *P. asperum*) (Dietz, 1910; Schachtachtinskaya, 1949; Bychovskaya-Pavlovskaya, 1955; Našincová *et al*., 1994). Unfortunately, only one other marker besides the *28S* rRNA gene is available for *P. exaeretus* and for *Petasiger* sp.1 of Laidemitt *et al*. (2019), namely, the ITS2 region for the former and the *nad1* gene for the latter. The poor resolution of the phylogenetic relationships of the clades represented by *Pegosomum* spp., *P. exaeretus* and/or *Petasiger* sp.1 of Laidemitt *et al*. (2019) with other *Petasiger* spp. does not allow us to draw a definite taxonomic conclusion about the genera *Pegosomum* and *Petasiger*. So far, two taxonomic solutions seem equally probable: (i) retention of the genus *Petasiger* for *P. exaeretus* and erection of separate genera for other *Petasiger* spp. lineages, or (ii) the abolition of the genus *Petasiger* and the transfer of the species of this taxon to the genus *Pegosomum*.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

Supplementary data. The following materials are available online.

Table S1. List of species, incorporated into phylogenetic analysis based on partial sequences of the *28S* rRNA, *cox1* and *nad1* genes, and ITS2 region.

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