Journal of Helminthology

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Two new marine species of *Rhinebothrium* (Cestoda: Rhinebothriidea) from stingrays from the Persian Gulf and Gulf of Oman

S. Omrani[1], K. Golzarianpour[2], M. Malek[1,3], M. Golestaninasab[4] and Marjan Seiedy[1]

[1]School of Biology and Center of Excellence in Phylogeny of Living Organisms, College of Sciences, University of Tehran, Tehran, Iran; [2]Department of Biology, Faculty of Sciences and Engineering, Gonbad Kavous University, Golestan, Iran; [3]Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada and [4]Department of Biology, Faculty of Sciences, Semnan University, Semnan, Iran

Research Paper

Cite this article: Omrani S, Golzarianpour K, Malek M, Golestaninasab M and Seiedy M (2025). Two new marine species of *Rhinebothrium* (Cestoda: Rhinebothriidea) from stingrays from the Persian Gulf and Gulf of Oman. *Journal of Helminthology*, **99**, e18, 1–14
https://doi.org/10.1017/S0022149X24000701.

Received: 27 July 2024
Revised: 22 September 2024
Accepted: 03 October 2024

Keywords:
Dasyatidae; *Maculabatis randalli*; *Maculabatis arabica*; *Rhinebothrium gossi* sp. nov; *Rhinebothrium palmeri* sp. nov

Corresponding author:
M. Malek;
Email: mmalek1@ualberta.ca, memalek@ut.ac.ir

Abstract

The genus *Rhinebothrium* (Cestoda: Rhinebothriidea) comprises tapeworm species parasitizing elasmobranch hosts, particularly batoids. Despite numerous recent findings regarding the ecological importance of marine fish parasites throughout the world, the biodiversity of cestodes inhabiting fishes of the Persian Gulf and the Gulf of Oman remains understudied. Here, two new species of *Rhinebothrium* from stingrays from the Persian Gulf and Gulf of Oman are described: *Rhinebothrium gossi* sp. nov. and *Rhinebothrium palmeri* sp. nov. from *Maculabatis arabica* and *Maculabatis randalli*, respectively. However, each new cestode species is found with a lower frequency in the other host species, too. These new species were already subjected to a molecular analysis and the revealed genetic distinctiveness requires detailed morphological examinations at the species level. A combination of morphomeristic characteristics including body size, scolex features, proglottid morphology, and reproductive structures distinguish the new species from the other congeners. Although these new species are morphologically similar, however, they differ from each other in the number of testes (6–8 and 8–14), and bothridial loculi (50 and 42 in *R. gossi* sp. nov. and *R. palmeri* sp. nov., respectively). These findings contribute to our understanding of marine cestode diversity and underscore the importance of further research in this ecologically significant region.

Introduction

Cestodes of the family Rhinebothriidae Euzet, 1953 are specifically known to parasitise batoids. Among them, the genus *Rhinebothrium* Linton, 1890 stands out as the most diverse taxon, with 58 valid species (Global Cestode Database 2024; Golzarianpour et al. 2020a; Menoret & Ivanov 2023; Trevisan & Caira 2020) from approximately 50 host species (Global Cestode Database 2024; Menoret & Ivanov 2023; Trevisan & Caira 2020).

Although more than 40 batoid species have been recorded in the Persian Gulf and the Gulf of Oman (Jabado et al. 2017), only four *Rhinebothrium* species have been described so far, namely *R. persicum* Golestaninasab & Malek, 2016, and *R. kruppi* Golestaninasab & Malek, 2016 from *Glaucostegus granulatus*; *R. atabaki* Golzarianpour, Malek, Golestaninasab, Sarafrazi & Kochmann, 2020 from *Maculabatis randalli*; *R. klimpeli* Golzarianpour, Malek, Golestaninasab, Sarafrazi & Kochmann, 2020 from *Pateobatis fai* and *Brevitrygon walga* (Global Cestode Database 2024; Golzarianpour et al. 2020b).

Although the Rhinebothriidea Healy, Caira, Jensen, Webster and Littlewood, 2009 have been primarily recognised as oioxenous parasites (Caira & Jensen 2017), it has been recently shown that at least some species are not strictly host-specific, e.g., *R. atabaki* parasitises seven host species (Golestaninasab 2014; Golzarianpour et al. 2020a). Although marine *Rhinebothrium* species typically parasitise one or occasionally two host species (Healy 2006), freshwater lineages often parasitise various host species (Laudet et al. 2011). Challenges arise when metastenoxenous species infect hosts that are neither sympatric nor congeneric (Mantovani 2018). Healy (2006) suggests that our current understanding of host specificity among rhinebothriid species is based on limited sampling and misidentification of hosts and parasites, emphasising the need for additional evidence to evaluate host specificity accurately.

In our previous study for describing two other species, it was verified that there are also two new sister taxa of *Rhinebothrium* with a very close genetic distance and remarkable morphological similarities. Therefore, by examining more specimens and employing a meticulous morphomeristic approach, we aim to describe these new sister species of *Rhinebothrium.* For a higher certainty, the host specificity patterns were also studied by examining numerous host species from different geographical locations (a total of 102 individuals including seven different species from four different stations) for these two sister parasite species. Furthermore, a relevant comment on the host specificity is presented in the conclusion.

Material and methods

Host specimen collection

Host specimens were collected as bycatch with the cooperation of local fishermen along the northern coastlines of the Persian Gulf and the Gulf of Oman. Sampling localities are presented in Figure 1. Those specimens that were alive were returned to the sea. The specific localities were as follows: from the Persian Gulf, off Bushehr (28° 52’45.6"N 50°43’09.7"E) in March 2011 and August 2017, off Hormuz Island (27°02’52.9"N 56°31’49.1"E) in July 2017, off Bandar Abbas (27°06’41.9"N 56°13’32.6"E) in July 2017, and from the Gulf of Oman, off Djod, Zarabad (25°26’59.4"N 59°30’27.4"E) in June 2010, April 2011, August 2014, January 2016, March and June 2017. A total of 102 individuals representing seven batoid species were examined, comprising *Brevitrygon walga* (N = 3), *Glaucostegus granulatus* (N = 23), *Glaucostegus halavi* (N = 1), *Pastinachus sephen* (N = 21), *Rhynchobatus laevis* (N = 1), *Maculabatis arabica* (N = 11), and *Maculabatis randalli* (N = 42) (Table 1). Each specimen was designated a unique MM number for consistent identification purposes.

The spiral intestine of each host specimen was excised and longitudinally opened. A section of the intestine was initially fixed in 4% seawater-buffered formalin, and after two weeks transferred to 70% ethanol for morphological examination, the remaining portion was preserved in 96% ethanol for any relevant study in future. The taxonomic classification of batoids adheres to the guidelines outlined by Last et al. (2016). Moreover, the hosts’ identity was molecularly analysed in our previous study (Golzarianpour et al. 2020b); the details are provided in Table 2.

Parasite specimen preparation

Specimens underwent preparation as whole mounts and for scanning electron microscopy (SEM) following the protocols outlined by Healy (2006) and Golzarianpour et al. (2020a), respectively. Prepared whole mounts were subjected to measurement and examination using Leica Application Suite V.3 software installed on a Leica DM500 microscope (Buffalo Grove, Illinois, USA) equipped with a Leica ICC50 HD built-in camera. Measurements of all genitalia were conducted on the terminal proglottid, except in cases where specimens exhibited a terminal proglottid with atrophied testes and expanded vas deferens, wherein the testes were measured on the mature subterminal proglottid. The parasites identity was molecularly analysed in our previous study (Golzarianpour et al. 2020a) and the respective details are provided in Table 2. All measurements were performed using Digimizer software *v.* 6.4.0 (MedCalc Software Ltd., Belgium). The scolex and remaining proglottids of each specimen included in the molecular analysis were mounted as a voucher and subjected to measurement. Measurement data are presented as range followed by a parenthesis including the mean and standard error. All measurements are in µm

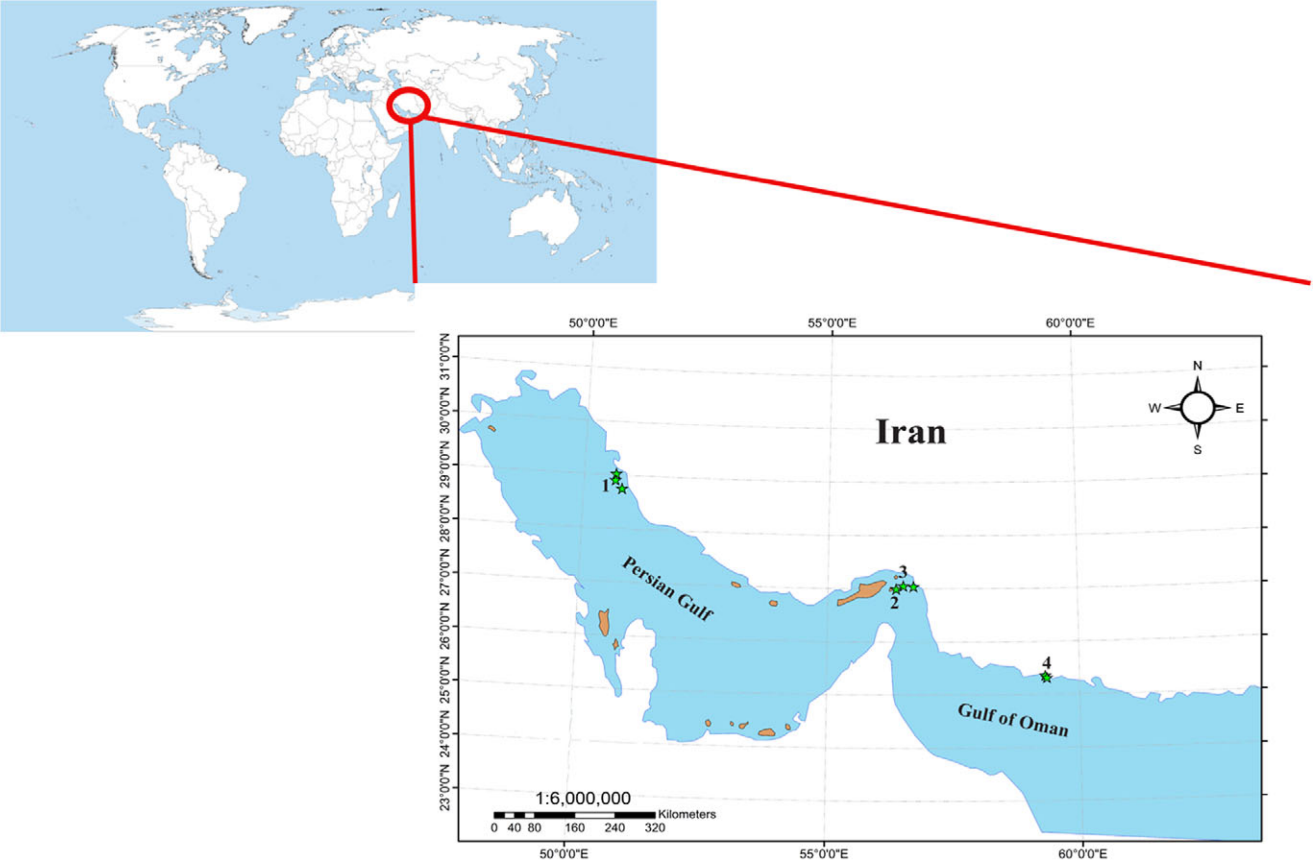

Figure 1. Sampling localities: 1: Off Bushehr; 2: Off Hormuz Island; 3: Off Bandar Abbas; 4: Off Djod, Zarabad.

Table 1. Summary of the examined hosts and the sampling localities

Host species	Number	Sampling localities			
		Off Bushehr	Off Hormuz Island	Off Bandar Abbas	Off Djod, Zarabad
Brevitrygon walga	3		✓		
Glaucostegus granulatus	23				✓
Glaucostegus halavi	1				✓
Pastinachus sephen	21	✓	✓		✓
Rhynchobatus laevis	1		✓		
Maculabatis arabica	11			✓	✓
Maculabatis randalli	42	✓	✓	✓	✓

Table 2. Details of the molecularly analysed host and parasite specimens (Golzarianpour et al., 2020a; Golzarianpour et al., 2020b)

Parasite species	DNA voucher code	Gene bank acc. no.	Host species	*ND2* gene bank acc. no.	MM code	References
Rhinebothrium goosi[a] sp. nov.	MM1613P1	SSU: PQ642762 LSU: PQ642732 *COI*: PQ641614	*Maculabatis arabica*	MN602003	MM1613	Present study
	MM1547P3	SSU: MT033095 LSU: MT032162	*Maculabatis arabica*	PQ661798	MM1547	Golzarianpour et al. 2020a
	MM1470P1	SSU: MT033096 LSU: MT032161 *COI*: MT153860	*Maculabatis randalli*	PQ661799	MM1470	Golzarianpour et al. 2020a
	MM1531P2	*COI*: PQ641616 LSU PQ642731	*Maculabatis randalli*	PQ661800	MM1531	Present study
Rhinebothrium palmeri[b] sp. nov.	MM1441P3	LSU: PQ642733	*Maculabatis arabica*	MN602004	MM1441	Present study
	MM1617P3	LSU: PQ642734 *COI*: MT153864	*Maculabatis randalli*	PQ661801	MM1617	Golzarianpour et al. 2020a
	MM1496P1	LSU: PQ642774	*Maculabatis randalli*	MN602006	MM1496	Golzarianpour et al. 2020a
	MM1557P	SSU: MT033105 LSU: MT032171	*Maculabatis randalli*	PQ661802	MM1557	Golzarianpour et al. 2020a
	MM1618P2	LSU: MT032172	*Maculabatis randalli*	PQ661803	MM1618	Golzarianpour et al. 2020a
	MM1553P1	*COI*: PQ641615 LSU: PQ642735	*Maculabatis randalli*	MN602007	MM1553	Present study
	MM1531P4	LSU: PQ642736	*Maculabatis randalli*	PQ661804	MM1531	Present study

Abbreviations: *COI*, cytochrome c oxidase subunit I; LSU, large subunit ribosomal RNA gene; *ND2*, NADH dehydrogenase subunit 2 gene; SSU, small subunit ribosomal RNA gene.

[a] *Rhinebothrium* cf. *oligotesticulare* as mentioned in Golzarianpour et al. 2020a.

[b] *Rhinebothrium* sp. A as mentioned in Golzarianpour et al. 2020a.

unless stated otherwise; number of specimens measured as N and total number of measurements as n.

Line drawings were generated utilizing a line tube attached to Richert Biovar Microscope and optimised in Adobe Illustrator CC 2022. Scanning electron micrographs were captured using a field emission SEM (4160102HIT, Hitachi, Tokyo, Japan). Microthrix terminology follows the conventions outlined by Chervy (2009). The corrections provided by Coleman et al. (2018) on the orthography of specific epithets of species of *Rhinebothrium* were followed throughout this manuscript.

Abbreviations utilised are DW, disk width; INPM, Iranian National Parasitology Museum, Tehran, Iran; MM, Prof. Masoumeh Malek's parasite collection; ZMB, Museum für Naturkunde, Berlin, Germany; ZUTC, Collection of Zoological Museum, University of Tehran, Iran.

Results

Hosts Descriptive Report

Of 11 individuals of *Maculabatis arabica*, three were female and eight were male. Total length, disk width and disk length of hosts were 56–119.4 cm (86.2 ± 23.3 cm), 17–47 cm (32.6 ± 12.1 cm), and 15.5–46 cm (29.8 ± 11.9 cm), respectively.

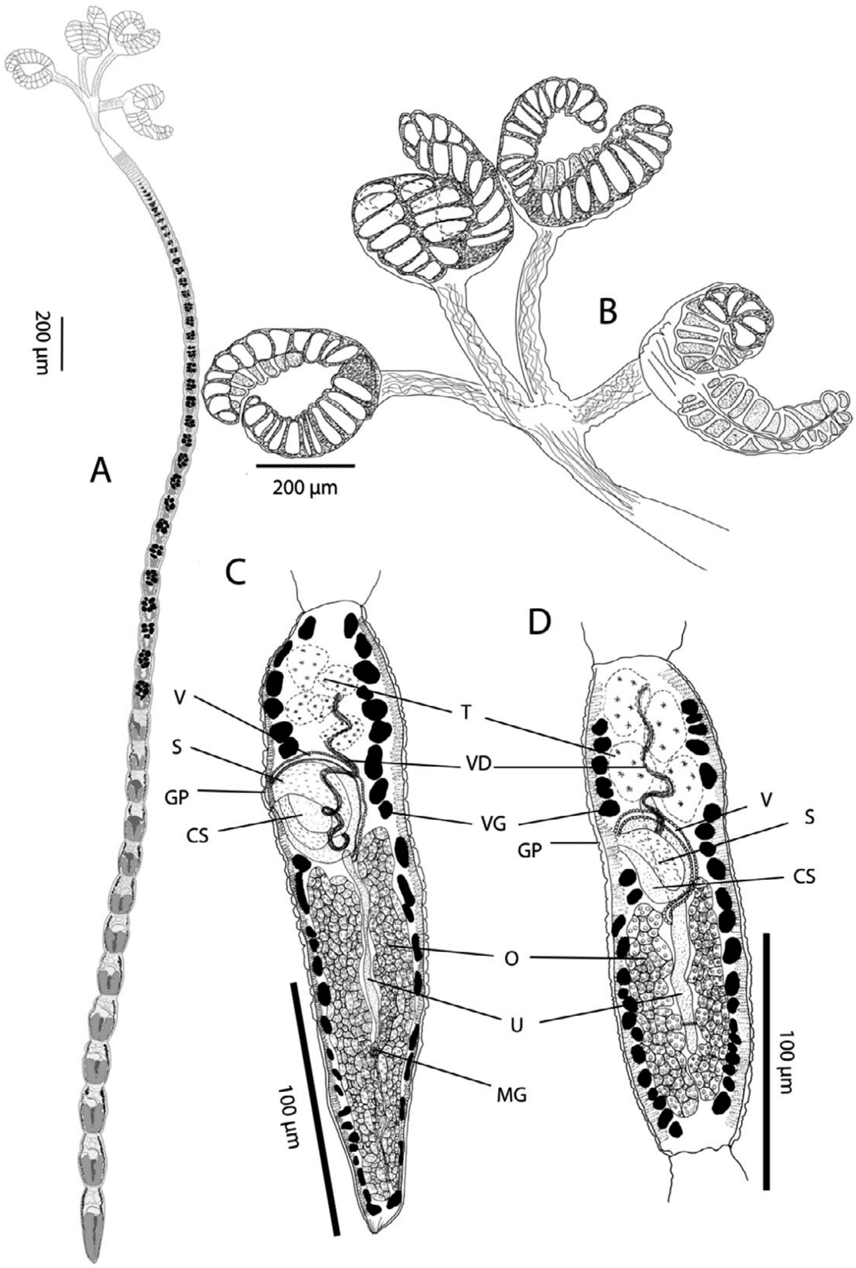

Figure 2. Line drawing of *Rhinebothrium gossi* sp. nov. from it's host stingray *Maculabatis arabica*: A and B, the holotype (ZUTC Platy. 1900, slide MM1441F4); C and D, paratype (ZUTC Platy. 1904, slide MM1547F8). A, Whole worm; B, scolex; C, the terminal proglottid; D, a mature proglottid.

Of 42 individuals of *Maculabatis randalli*, 23 were female and 19 were male. Total length, disk width and disk length of hosts were 64.4–128.2 cm (99.7 ± 17.9 cm), 19.2–45.3 cm (32.9 ± 6.5 cm), and 15.8–41.4 cm (27.5 ± 5.8 cm), respectively.

Description of Parasites

***Rhinebothrium gossi* sp. nov.** (Figs 2-3)

Zoobank code. http://zoobank.org/urn:lsid:zoobank.org:act:B3418FFD-BE0C-47D9-9C27-85BE3068B686

Diagnosis (Figs. 2–3). The distinctive features of *Rhinebothrium gossi* sp. nov. are the euapolytic reproductive strategy; bearing a single loculus at the posteriormost end of the bothridia, 50 loculi in each bothridium, loculi absent at the bothridia hinge; six to eight testes limited to the anterior field of the genital pore; position of the genital pore in the anterior region of the mature proglottids; vitelline glands interrupted at the level of genital pore, not interrupted neither at the aporal level of genital pore nor by the ovary; cirrus sac containing coiled armed cirrus.

Description (Figs. 2A–B, 3A–B). Based on whole mounts of 10 mature worms, four scoleces prepared for SEM, four strobila of SEM vouchers, and three molecular vouchers. Rhinebothriidae: worms euapolytic, slightly craspedote proglottids; total length 7.2–12.4 mm (9.1 ± 0.7 mm; N = 10), maximum width 0.2–1.2 mm (0.7 ± 0.1 mm; N = 10) at the level of scolex, with 33–145 (65.3 ± 16.6; N = 10) proglottids. Scolex consists of scolex proper with four stalked bothridia, stalklet and myzorhynchus lacking. Bothridia 237.7–464.8 (320.2 ± 19.8; N = 10; n = 15) long by

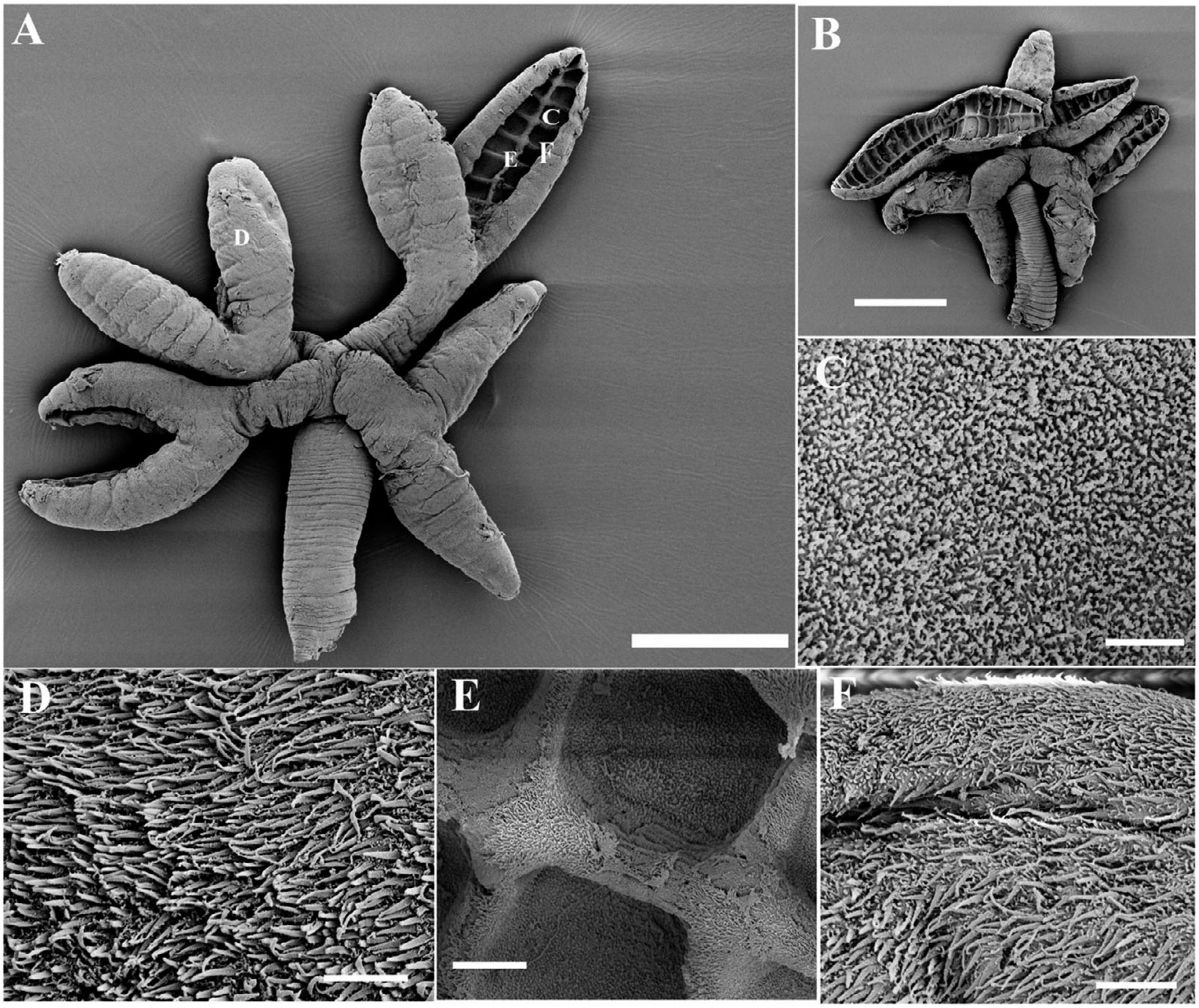

Figure 3. SEM of *Rhinebothrium gossi* sp. nov. from it's host stingray *Maculabatis arabica.* A (MM1531P2S2 voucher) and B (MM1547P1S2 voucher), Scolex; C, The middle region of loculi on the adhesive distal surface of bothridium; D, Non-adhesive proximal surface of bothridium; E, Transverse and longitudinal septa on the adhesive surface; F, Bothridium rim on the non-adhesive surface. Scale: A = 200 μm; B = 300 μm; F, D, C = 3 μm, and E = 9 μm. Note: both vouchers were molecularly assigned to the given species.

129.2–293.5 (143.4 ± 15.3; N = 10; n = 13) wide, no loculi at the hinge site, anterior and posterior halves of bothridia almost equal in size (Fig. 2B), each divided by 11 pairs of transverse septa and a single conspicuous medial longitudinal septum into two columns of transversely orientated loculi, with a single loculus at the tip of each half of bothridium, in total 50 loculi (N = 14; n = 43) per bothridium, widest in the middle of each bothridium, marginal loculi lacking; posteriormost loculus single 18.1–44.4 (32.6 ± 2.5; N = 10) in length and 39.7–65.6 (52.4 ± 3; N = 10) in width. Stalk 89.5–449.2 (194.9 ± 19.6; N = 10; n = 21) long by 38.1–156.7 (105.5 ± 7.1; N = 10; n = 21) wide, attaching to the middle region of bothridium. Cephalic peduncles vary in constriction state 40.1–221 (90.2 ± 33.5; N = 10) long, shorter than bothridium stalks in most.

Strobila (Figs. 2A). Immature proglottids numerous, 21–137 (53.8 ± 17.5; N = 10), wider than long in the anterior half, 11.8–403.2 (96.9 ± 15.9; N = 18; n = 38) in length, 14.9–241.9 (126.2 ± 7.1; N = 18; n = 38) in width. Fewer mature proglottids 7–16 (11 ± 1.4; N = 10) apparently longer than wide, with a length of 183.1–958.8 (390.8 ± 35.6; N = 18; n = 25), and a width of 116.8–290.8 (175.4 ± 9.9; N = 18; n = 25), usually beginning at the posterior one third, mostly with atrophying testes; terminal proglottid spindle-shaped with atrophied testes, 267.8–958.8 (575.9 ± 78.3; N = 13) long and 140.9–288.5 (201.5 ± 20.6; N = 13) wide. No gravid proglottids observed.

Reproductive system (Figs 2C–D). Genital pores lateral, irregularly alternating, anteriorly positioned at 69–73.3% (70.4% ± 1.4; N = 10) of proglottid length from posterior end; genital atrium conspicuous, non-muscular. Testes 6–8 (6.7 ± 0.3; N = 13) in number, 11.3–46.2 (27.5 ± 1; N = 13; n = 52) long by 11.2–67 (40.1 ± 2.2; N = 13; n = 52) wide, in single field anterior to genital pore, arranged in two columns and oval shaped, gradually atrophying in most mature proglottids; postporal testes lacking. Vas deferens duct coiled, entering cirrus sac from anterior margin; cirrus sac small, oval shaped, reaching the ovarian level, 114.8–193.5 (154.3 ± 8.4; N = 10) long by 28.9–103.6 (65 ± 6.3; N = 10) wide in the terminal proglottid. Cirrus sac crossing proglottid midline. Cirrus coiled, bearing conspicuous spinitriches. Vagina connecting common atrium anterior to cirrus, thick-walled in mature and terminal proglottids, extending anteriorly with relatively even width from genital atrium far from middle line of the proglottid, then bending towards posterior region along the aporal margin of cirrus sac, extending to the ootype, slightly overlapping cirrus sac margins in some, the proximal region of the vagina has a vaginal sphincter. Ovary ∀-shaped, almost symmetrical, lobular, occupied 39.3–59.8% (47.2 ± 3.4; N = 10) of the terminal proglottid, poral lobe 89.6–396.1 (215.6 ± 27.7; N = 15; n = 18) long by 22.5–77.8 (46.4 ± 4.4; N = 15; n = 18) wide, aporal lobe 87.2–400.4 (203.5 ± 25.3; N = 15; n = 18) long by 18.2–61.3 (39.9 ± 2.9; N = 15; n = 18) wide; ovarian isthmus close to posterior apex of the ovary. Mehlis' gland, and seminal receptacle anterior to ovarian isthmus. Vitellaria follicular, follicles with irregular shapes, 3.2–37.5 (15.9 ± 1.4; N = 17; n = 38) long by 3.1–26.1 (12.6 ± 0.9; N = 17; n = 38) wide, occupying two lateral bands in two dorsal and ventral columns, extending from anterior extent of testicular field to posterior margin of proglottid far from the level of ovary, interrupted at the level of genital pore, uninterrupted neither at the aporal level of genital pore nor by the ovary; uterus saccate, obvious at the mature terminal proglottids, extending from the posterior region of the proglottid to the anteriormost margin of the testes field.

SEM (Fig 3). Distal surfaces of anterior and posterior regions of bothridia covered with varying densities of small gladiate spinitriches and acicular or capilliform filitriches; distal surfaces of the middle part of bothridia covered with small gladiate spinitriches and capilliform filitriches. Proximal surfaces of bothridia covered with capilliform filitriches. An obvious rim encircles the bothridium.

Taxonomic summary

Classification. Rhinebothriidea (Order), Rhinebothriidae (Family)

Type materials. Holotype: (ZUTC Platy. 1990), slide MM1441F4; paratypes: seven whole mounts (ZUTC Platy. 1901–1907), one whole mount (INPM.ACC.2023.C.29), slide MM1412F4, one whole mount (ZMB E.7759), slide MM1412F1, one SEM (ZUTC Platy. 1908), and DNA hologenophores (ZUTC Platy. 1912).

Other Material Examined. Three SEM (ZUT Platy. 1909–1911) and two DNA vouchers (ZUT Platy. 1913–1914).

Type host. *Maculabatis arabica* Manjaji-Matsumoto and Last, 2016 (Myliobatiformes: Dasyatidae), MM1441: DW=46.7 cm, female.

Additional host. *Maculabatis randalli* (Last, Manjaji-Matsumoto & Moore, 2012).

Prevalence. 45.5% (five of 11 individuals) in *M. arabica*, 7.1% (three of 42 individuals) in *M. randalli.*

Mean Intensity. 3.4 ± 1.4 in *M. arabica*, 1 in *M. randalli.*

Type locality. Off Djod (25°26'59.4"N 59°30'27.4"E), Zarabad, Gulf of Oman, Iran.

Additional localities. Off Bandar Abbas (27°06'41.9"N 56° 13'32.6"E), Hormuzgan, Persian Gulf, Iran.

Site in host. Spiral intestine.

Etymology. The species is named in honor of Professor Greg Goss, University of Alberta for his invaluable and significant research on fish physiology and toxicology.

Remarks. *Rhinebothrium gossi* sp. nov. was determined by Golzarianpour et al. (2020a) as *Rhinebothrium* cf. *oligotesticulare* (Subramaniam, 1940) and they mentioned that a more detailed consideration on this species is nessessary. By having a single posteriormost loculus (vs. paired loculi at the posterior end of the bothridium) it differentiates from *R. brooksi* Reyda & Marques, 2011, *R. copianullum* Reyda, 2008, *R. corbatai* Menoret & Ivanov, 2011, *R. fulbrighti* Menoret & Ivanov, 2011, *R. ghardaguense* Ramadan, 1984, *R. jaimei* Marques & Reyda, 2015, *R. mistyae* Menoret & Ivanov, 2011, *R. margaritense* Mayes & Brooks, 1981, *R. paratrygoni* Rego & Dias, 1976, *R. rhinobati* Dailey & Carvajal, 1976, *R. setiensis* Euzet, 1955, *R. taeniuri* Ramadan, 1984, *R. tetralobatum* Brooks, 1977, and *R. tumidulum* (Rudolphi, 1819). More details are provided in Table 2. Of the remaining 42 species, it compares with taxa bearing more than four and fewer than 10 testes. By having 6–8 testes, *R. gossi* sp. nov. resembles *R. bunburyense* Coleman, Beveridge & Campbell, 2019, *R. gravidum* Friggens & Duszynski, 2005, *R. maccallumi* Linton, 1924, *R. oligotesticulare* (Subramaniam, 1940), *R. palmeri* sp. nov., *R. ruhnkei* Trevisan & Caira, 2020, *R. urobatidum* Young, 1955, *R. vandiemeni* Coleman, Beveridge & Campbell, 2019, and *R. walga* Shipley & Hornell, 1906. However, it differs in the number of loculi; i.e., 50 in *R. gossi* sp. nov. vs. 34 in *R. bunburyense*, 29–31 in *R. maccallumi*, 34–50 as mentioned by Coleman et al. (2018) or 9–13 pairs of loculi on each half bothridium as mentioned by Subhapradha (1955) in *R. oligotesticulare*, 42 in *R. palmeri* sp. nov., 68–78 in *R. ruhnkei*, 38–42 in *R. urobatidum*, 38 in *R. vandiemeni*, and 20 in *R. walga.*

Although *R. gravidum* have 40–56 loculi, euapolytic *vs.* apolytic strategy, higher number of proglottids (9–21 vs. 33–145), and acraspedote *vs.* slightly craspedote segments distinguish it from *R. gossi* sp. nov. The characteristics of the *R. gossi* sp. nov. are very similar to the *R. oligotesticulare*, but this species has 9–13 pairs of loculi on each half bothridium as mentioned by Subhapradha (1955) or 34–50 as mentioned by Coleman et al. (2018), which is a larger range, whereas in this newly introduced species only 12 pairs of loculi on each half of bothridium was observed. Moreover, the *R. oligotesticulare* was introduced with the total length of the body as 14.5–20 mm (vs. 7.2–12.4 mm in *R. gossi* sp. nov.) and 66 proglottids (vs. 33–145 in *R. gossi* sp. nov.). Furthermore, *R. oligotesticulare* has 4–7 testes and an H or X-shaped ovary while *R. gossi* sp. nov. bears 6–8 testes and an ∀-shaped ovary. *Rhinebothrium oligotesticulare* was reported from *Glaucostegus granulatus* while *R. gossi* sp. nov. was discovered from *Maculabatis arabica.* Accordingly, it is reasonable to conclude that the worm is distinct from *R. oligotesticulare.*

***Rhinebothrium palmeri* sp. nov. (Figs 4–5)**

Zoobank code. http://zoobank.org/urn:lsid:zoobank.org:act:1330CA70-DF04-4751-A9BC-AE9B55B9012B

Diagnosis (Figs 4–5). The distinctive features of *R. palmeri* sp. nov. are the euapolytic reproductive strategy; bearing a single loculus at the posteriormost end of the bothridia, 42 loculi in each bothridium, loculi absent at the bothridia hinge; 8–14 testes in the anterior field of the genital pore; the presence of the genital pore in the anterior region of the mature proglottids; vitelline glands interrupted at the level of genital pore, not interrupted neither at the aporal level of genital pore nor by the ovary; cirrus sac containing coiled armed cirrus.

Description (Figs. 4A–B, 5A–B). Based on whole mounts of 35 mature worms, four scoleces prepared for SEM, four strobila of SEM vouchers, and five molecular vouchers. Rhinebothriidae: Worms euapolytic, slightly craspedote proglottids, total length 5.6–19.6 mm (10.6 ± 0.7 mm; N = 28), maximum width 0.7–1.3 mm (1.0 ± 0.04 mm; N = 35) at the level of scolex, with 40–173 (92.3 ± 7.0; N = 28) proglottids. Scolex consists of scolex proper with four stalked bothridia, stalklet and myzorhynchus lacking. Bothridia 173.8–523.7 (329.2 ± 7.3; N = 35; n = 91) long by 113.4–282.1 (177.7 ± 4.1; N = 35; n = 75) wide; no loculi at the hinge site, anterior and posterior halves of bothridia almost equal in size (Fig. 4B), each divided by 10 pairs of transverse septa and a single conspicuous medial longitudinal septum into two columns of

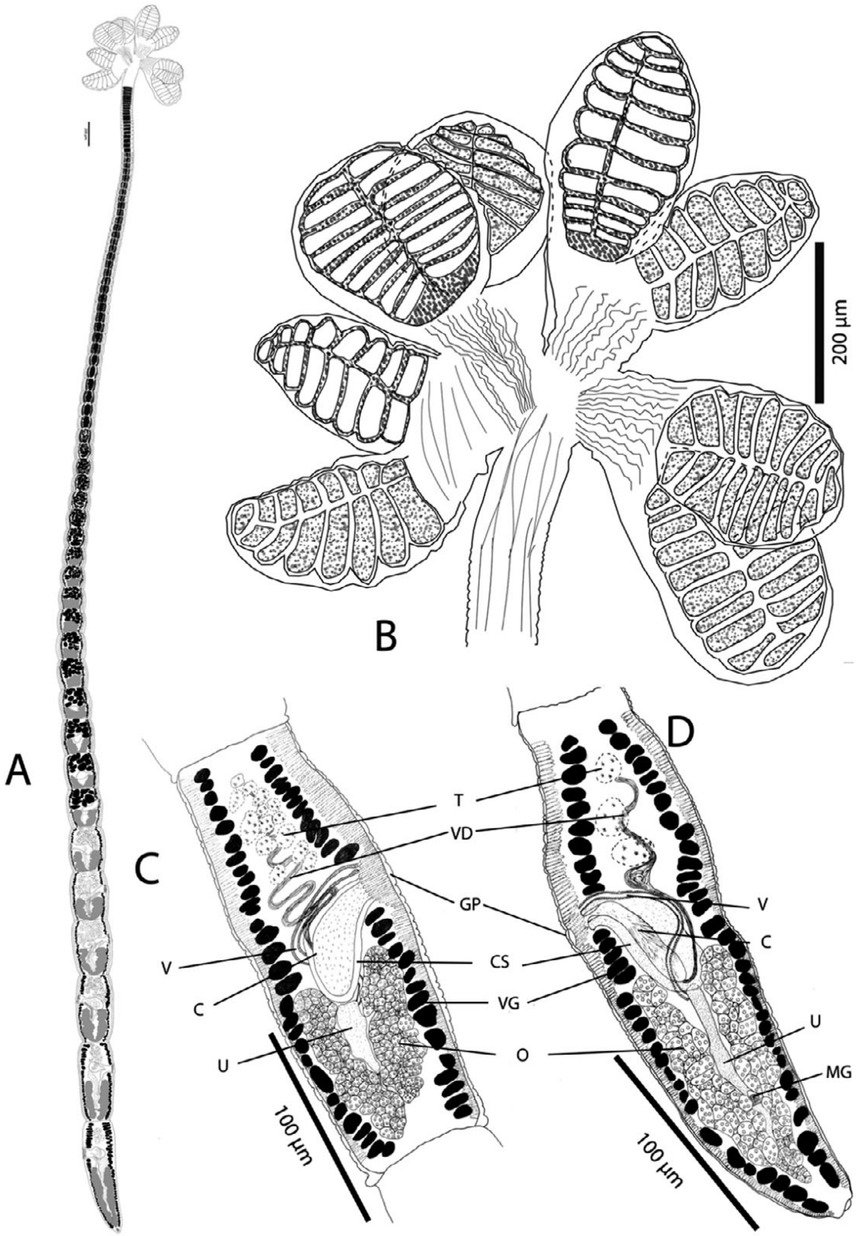

Figure 4. Line drawing of *Rhinebothrium palmeri* sp. nov. from it's host stingray *Maculabatis randalli*: A and B, holotype (ZUTC Platy. 1915, slide MM1486F1); C and D, paratype (ZUTC Platy. 1926, slide MM1485F2). A, whole worm, scale = 200 µm; B, scolex; C, a mature proglottid; D, the terminal proglottid.

transversely orientated loculi, with a single loculus at the tip of each half of bothridium, in total 42 loculi (N = 39; n = 141) per bothridium, widest in the middle of each bothridium, marginal loculi lacking; Posteriormost loculus single 16.8–45.9 µm (32.6 ± 0.8; N = 33; n = 62) in length and 23.9–83.1 (49.9 ± 1.4; N = 33; n = 62) in width. Stalks 96.1–584.8 (241.1 ± 10.5; N = 35; n = 75) long by 63.1–230.9 (115.9 ± 4.3; N = 35; n = 75) wide, attaching to the middle region of bothridium. Cephalic peduncles vary in constriction state 18.6–107.0 (48.5 ± 3.5; N = 34) long, shorter than bothridium stalks in most.

Strobila (Figs. 4A). Immature proglottids numerous, 38–160 (86.1 ± 6.5; N = 35), wider than long in the anterior half, 12.4–435.8 (140.6 ± 7.8; N = 38; n = 137) in length, 49.2–466.5 (168.3 ± 6.4; N = 38; n = 137) in width. Fewer mature proglottids 1–17 (6.2 ± 0.7; N = 35) apparently longer than wide, with a length of 224.1–859.4 (454.9 ± 24.9; N = 45; n = 40), and a width of 83.4–441.1 (222.3 ± 14.0; N = 45; n = 40), usually beginning at the posterior one third, mostly with atrophying testes; terminal proglottid spindle-shaped with atrophied testes, 448.0–1074.1 (732.5 ± 43.9; N = 40) long and 115.9–253.2 (192.6 ± 13.5; N = 40) wide. No gravid proglottids observed.

Reproductive system (Figs 4C–D). Genital pores lateral, irregularly alternating, anteriorly positioned at 53.9%–76.6% (66.3% ± 2.3; N = 26) of proglottid length from posterior end; genital atrium conspicuous, non-muscular. Testes 8–14 (10.3 ± 1.3; N = 35) in number, 11.3–46.2 (28.3 ± 1.1; N = 35; n = 60) long by 11.2–70.2 (39.6 ± 2.1; N = 35; n = 60) wide, in single field anterior to genital pore, in an irregular arrangement and oval shaped, gradually atrophying in most mature proglottids; post-poral testes lacking. Vas deferens duct coiled, entering cirrus sac

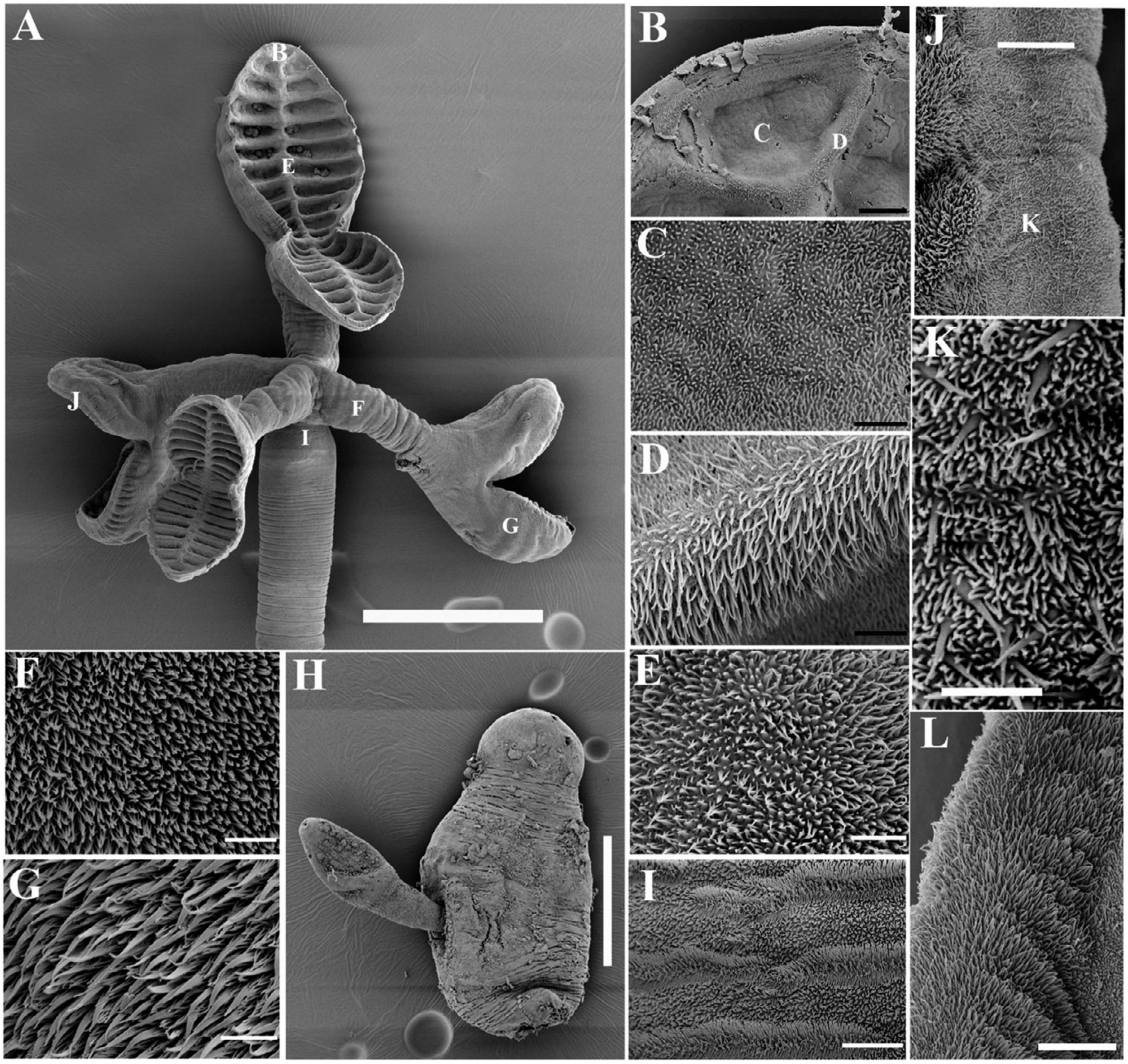

Figure 5. SEM of *Rhinebothrium palmeri* sp. nov. from it's host stingray *Maculabatis randalli* (MM1531S3 voucher). A, Scolex; B, the single loculus at the anterior tip of bothridium; C, the middle region of loculi on the distal adhesive surface of bothridium; E, transverse septum on adhesive surface; F, bothridium stalk; G, non-adhesive proximal surface of bothridium; H, terminal proglottid with the protruding cirrus [detached from MM1413S1 voucher]; I, the short cephalic peduncle; J, the margin of bothridium; K, the margin of bothridium on the non-adhesive surface; L, the margin of bothridium on the adhesive surface; A = 300 µm; B = 10 µm; C, E = 2 µm; F, 3 µm; G = 2 µm; H = 200 µm; I = 9 µm; K = 2 µm; L = 5 µm.

from anterior margin; Cirrus sac small, oval shaped, reaching the ovarian level, 114.8–273.7 (173.3 ± 17.1; N = 28; n = 30) long by 28.9–166.9 (78.6 ± 11.1; N = 28; n = 30) wide in the terminal proglottid. Cirrus sac crossing proglottid midline. Cirrus coiled, bearing conspicuous spinitriches. Vagina connecting common atrium anterior to cirrus, thick-walled in mature and terminal proglottids, extending anteriorly with relatively even width from genital atrium far from middle line of the proglottid, then bending towards posterior region along the aporal margin of cirrus sac, extending to the ootype, slightly overlapping cirrus sac margins in some, the proximal region of the vagina has a vaginal sphincter. Ovary ∀-shaped, almost symmetrical, lobular, occupied 31.9%–53.3% (42.2% ± 2.7; N = 35) of the terminal proglottid, 100.0–581.9 (323.4 ± 27.2; N = 30; n = 36) long by 30.5–101.0 (62.5 ± 5.7; N = 30; n = 36) wide, aporal lobe 119.2–572.3 (316.9 ± 22.1; N = 30; n = 36) long by 20.2–95.9 (55.4 ± 5.2; N = 30; n = 36) wide; ovarian isthmus close to posterior apex of the ovary. Mehlis' gland, and seminal receptacle anterior to ovarian isthmus. Vitellaria follicular, follicles with irregular shapes, 7.7–28.3 (15.5 ± 0.4; N = 40; n = 76) long by 4.2–20.6 (9.1 ± 0.5; N = 40; n = 77) wide, occupying two lateral bands in two dorsal and ventral columns, extending from anterior extent of testicular field to posterior margin of proglottid far from the level of ovary, interrupted at the level of genital pore, uninterrupted at neither the aporal level of genital pore nor by the ovary; uterus saccate, obvious at the mature terminal proglottids, extending from the posterior region of the proglottid to the anteriormost margin of the testes field.

SEM (Fig 5). Distal surfaces of anterior and posterior regions of bothridia covered with varying densities of small gladiate spinitriches and acicular or capilliform filitriches; distal surfaces of the middle part of bothridia covered with small gladiate spinitriches and capilliform filitriches. Proximal surfaces of bothridia covered with capilliform filitriches. An obvious rim encircles the bothridium.

Taxonomic summary

Classification. Rhinebothriidea (Order), Rhinebothriidae (Family)

Type materials. Holotype: (ZUTC Platy. 1915), slide MM1486F1; Paratypes: 32 whole mount (ZUTC Platy. 1916–1947), one whole mount (INPM.ACC.2023.C.30), slide MM1567F4, one whole mounts (ZMB E.7760), slide MM1486F5, one SEM (ZUTC Platy. 1948), and DNA hologenophores (ZUT Platy.1952).

Other Material Examined. Three SEM (ZUT Platy.1949–1951) and four DNA vouchers (ZUT Platy.1953–1956).

Type host. *Maculabatis randalli* (Myliobatiformes: Dasyatidae), MM1486: DW=37.4 cm, Male.

Additional host. *Maculabatis arabica* (Myliobatiformes: Dasyatidae).

Prevalence. 40.5% (17 of 42 individuals) in *M. randalli.* 9.1% (1 of 11 individuals) in *M. arabica.*

Mean Intensity. 2.4 ± 0.3 in *M. randalli* and 2 in *M. arabica.*

Type locality. Off Hormuz Island (27°02’52.9"N 56°31’49.1"E), Persian Gulf, Iran.

Additional localities. Off Djod (25°26’59.4"N 59°30’27.4"E), Zarabad, Gulf of Oman, Iran.

Site in host. Spiral intestine.

Etymology. The species is named in honor of Professor Rich Palmer, University of Alberta, for his many years of contribution towards ecology and evolution of marine invertebrates.

Remarks. This new species was mentioned in Golzarianpour et al. (2020a) as *Rhinebothrium* sp. A. It is also found in *Maculabatis arabica.* It differs from all but seven (i.e., *R. euzeti* Williams, 1958, *R. gravidum*, *R. gossi* sp. nov. (Fig. 6), *R. hawaiiense* Cornford, 1974, *R. ruhnkei*, *R. urobatidium* (Young, 1955), and *R. verticillatum* (Subhaprada, 1955) of 58 species of the genus *Rhinebothrium* because of bearing fewer than 15 testes and more than seven testes. Those marine and freshwater species that possess paired loculi at the posterior end of the bothridium (vs. single in *R. palmeri* sp. nov.) were excluded from the comparison (see Table 2). It has fewer number of loculi than *R. euzeti*, *R. gossi* sp. nov., *R. ruhnkei*, and *R. verticillatum* (42 vs. 78, 50, 68–78, and 48–50, respectively). It has more loculi than *R. hawaiiense* (42 vs. 23–25). It differs from *R. gravidum* and *R. urobatidium* in greater size (5.6–19.6 vs. 1.8–5.3 and 3.1–3.4, respectively), higher number of proglottids (40–173 with average 97 vs. 9–21 and 30–41, respectively), and location of genital pore (53.9–76.6% vs. 50–60% and a genital pore in the posterior half of the mature segments, respectively). Moreover, *R. palmeri* sp. nov. distinguishes from *R. gravidum* by its reproductive strategy (euapolytic vs. apolytic).

Figure 6. Light micrograph of the Holotypes: Left, *Rhinebothrium gossi* sp. nov. from it’s host stingray *Maculabatis arabica* (ZUTC Platy. 1990, slide MM1441F4); Right, *Rhinebothrium palmeri* sp. nov. from it’s host stingray *Maculabatis randalli* (ZUTC Platy. 1915, slide MM1486F1); Scale = 0.5 mm.

Discussion

Both new species described here (Fig. 6) are distinguishable from four other congeneric species previously described from the given region, the type species *R. flexile* and other valid species of *Rhinebothrium* by a combination of a single posteriormost loculus and number of testes along with some other morphological characteristics discussed earlier. A brief report of the main morphomeristic characteristics of these two species and the other related congeners with less than 15 testes has been reported in Table 3. In this table, the species have been sorted based on the state of the posteriormost loculus (being paired instead of single) and the testicular number. Therefore, it provides a proper insight into distinguishing the close species from each other with more ease. Some other species, including *R. setiense* Euzet, 1955 and *R. ghardaguense* also bear paired loculi at the posteriormost part

Table 3. The main morpho-meristic characteristics, hosts, and ecological regions of *Rhinebothrium* species with less than 15 testes, including *Rhinebothrium gossi* sp. nov. and *Rhinebothrium palmeri* sp. nov

Species	Number of posteriormost loculus	Number of testes	Number of loculi	Total length (mm)	Number of proglottids	Position of genital pore (%)	Type of proglottids	Reproduction strategy	Type host	Ecoregion
R. biorchidum	1	2	22–30	1.2–2.5	15–26	Half of proglottid	–	–	*Urobatis jamaicensis*	Jamaica
R. ditesticulum	1	2	48–54	9.6–28.7	160–276	Anterior half	Craspodate	Apolytic	*Urobatis halleri*	Pacific Ocean; California
R. spinicephalum	1	2	32–34	1.7–4.4	36–49	Anterior half	Craspodate	Apolytic	*Dasyatis americana*	Atlantic, North America,
R. urolophi	1	2–4	46	6.9–13	68–135	63–79	Craspodate	Euapolytic	*Urolophus expansus*	Australia
R. fungiforme	1	2–4	34	6.4–14.1	59–119	56–72	–	Euapolytic	*Hemitrygon fluviorum*	Australia
R. chollaensis	1	4	40–49	1.3–5.1	32–84	60	Acraspodate	Apolytic	*Urobatis helleri*	Gulf of California
R. reydai	1	4	34–44	2.2–7.4	26–68	31–49	Acraspodate	Euapolytic	*Styracura schmardae*	Caribbean Sea
R. dasyatidis	1	3–5	42	2.7–5.7	34–46	57–70	–	–	*Dasyatis brevicaudata*	Spencer Gulf
R. kruppi	1	4–5	42–46	1.6–2.4	12–17	61.1–77	Slightly craspodate	Euapolytic	*Glaucostegus granulatus*	Gulf of Oman
R. fluviorum	1	4–5	58–62	1.8–3.5	11–18	58–77	Acraspodate	Euapolytic	*Hemitrygon fluviorum*	Australia
R. ramosi	1	4–5	39–49	1.7–4	12–32	43–59	Acraspodate	Euapolytic	*Hypanus guttatus*	Tropical Atlantic
R. maccallumi	1	3–6	29–31	6–28	66–211	Pre-equatorial	Acraspodate	Euapolytic	*Dasyatis centroura*	Atlantic Ocean
R. bunburyense	1	3–6	34	4.36*	55	57–62	–	–	*Myliobatis tenuicaudatus*	off Bunbury, Western Australia
R. vandiemeni	1	4–6	38	17.7*	304	60–70	–	–	*Himantura australis*	Australia
R. walga	1	4–6	20	–	–	–	–	–	*Brevitrygon walga*	Gulf of Manaar
R. oligotesticulare	1	4–7	36–52	14.5*	66	–	–	–	*Glaucostegus granulatus*	Indian Ocean
R. taeniuri	1	4–8	18–22	5.1–5.7	29–30	Anterior third	Craspodate	–	*Taeniura lymma*	Red Sea
R. gossi sp. nov.	1	6–8	50	7.2–12.4	33–145	69.01–73.3	Slightly craspodate	Euapolytic	*Maculabatis arabica*	Gulf of Oman
R. urobatidum	1	6–12	38–42	3.1–3.4	30–41	Posterior half	Slightly craspodate	–	*Urobatis halleri*	Pacific Ocean; California
R. ruhnkei	1	7–10	68– 78	10.5–15.8	48–78	58–64	Acraspodate	Euapolytic	*Himantura leoparda*	Australia
R. gravidum	1	8–10	40–56	1.8–5.3	9–21	50–60	Acraspodate	Apolytic	*Urobatis halleri*	Gulf of California
R. palmeri sp. nov.	1	8–14	42	5.6–19.6	40–173	53.9–76.6	Craspodate	Euapolytic	*Maculabatis randalli*	Persian Gulf
R. hui	1	12	–	15	40–50	Half of proglottid	–	–	*Dasyatis akajei*	Japan
R. euzeti	1	12	78	5*	–	–	Craspodate	–	*Dasybatis* sp.	Sri Lanka
R. hawaiiense	1	11–13	23–25	2.1*	13	–	Acraspodate	Apolytic	*Dasyatis lata*	Pacific Ocean,
R. verticillatum	1	12–14	48–50	6.8–17.5	53–80	45–58	Slightly craspodate	Euapolytic	*Rhynchobatus laevis*	Indian Ocean
R. rhinobati	2	2	23	1.8–2.8	18–33	Half of proglottid	Acraspodate	Euapolytic	*Rhinobatos planiceps*	Southeastern Pacific

(*Continued*)

Table 3. (*Continued*)

Species	Number of posteriormost loculus	Number of testes	Number of loculi	Total length (mm)	Number of proglottids	Position of genital pore (%)	Type of proglottids	Reproduction strategy	Type host	Ecoregion
R. tetralobatum	2	2	47–69	4.1–19	80–206	18–33	Craspodate	Euapolytic	*Styracura schmardae*	Caribbean Sea
R. fulbrighti	2	2–3	43–53	3.1–18	90–250	69–86	Craspodate	Euapolytic	*Potamotrygon orbignyi*	Amazon River
R. corbatai	2	3–5	71–75	3.3–7.5	96–100	–	Craspodate	Euapolytic	*Potamotrygon motoro*	Neotropial freshwater
R. margaritense	2	3–6	53–55	5.7*	75–100	48–52	Craspodate	Apolytic	*Dasyatis guttata*	Caribbean Sea
R. jaimei	2	6–8	49–55	3.1–6.5	18–33	52–68	Craspodate	Euapolytic	*Potamotrygon orbignyi*	Neotropical freshwater
R. mistyae	2	4–7	75–79	20–59.9	353–974	60–81	Craspodate	Euapolytic	*Potamotrygon motoro*	Neotropial freshwater
R. paratrygoni	2	4–9	63–71	8–80	266–1060	63–84	Very Craspodate	Euapolytic, rarely Apolytic	*Potamotrygon sp.*	Neotropial freshwater
R. copianullum	2	4–12	35–55	10–68	128–880	27–58	Craspodate	Euapolytic	*Paratrygon aiereba*	South American freshwater
R. brooksi	2	7–13	55–65	6–27	53–139	69–86	Very Craspodate	Euapolytic, rarely Apolytic	*Paratrygon aiereba*	Amazon River
R. tumidulum	2	10–12	22	10–15	80–100	–	–	–	*Dasyatis pastinaca*	Atlantic Ocean

-, characteristic not mentioned in the original paper; *, just one specimen reported.

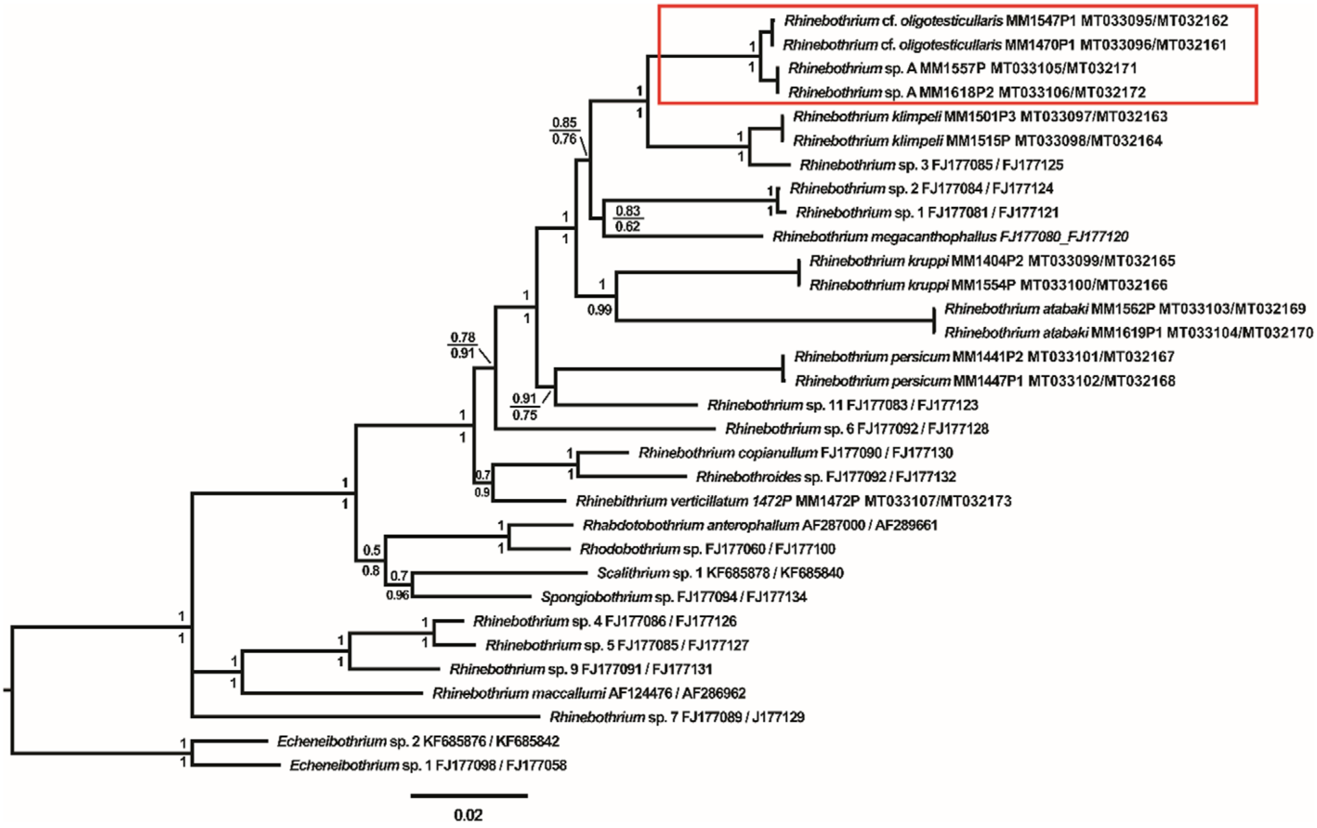

Figure 7. Phylogenetic relationships tree of Rhinebothriidae adapted from Golzarianpour et al. (2020a); Note: the sister relationship is shown in the red rectangle.

of the bothridium, but they were removed from the list because of having higher than 15 testes in their mature proglottids. These two characteristics are reliable to delimit species, whereas other traits show a mosaic inconsistent pattern among the present taxa. Of 38 listed species, 26 taxa have a single loculus at the posteriormost end. Among them, seven species namely *R. urobatidum, R. ruhnkei, R. gravidum, R. gossi* sp. nov., *R. tumidulum, R. euzeti, R. hawaiiense, and R. verticillatum* have such a number of testes, which match with the testicular range of *Rhinebothrium palmeri* sp. nov. The number of loculi of the bothridium, as the third distinctive trait, is robust enough to distinguish this new species from those taxa. The same order of characteristics usage could be applied to *Rhinebothrium gossi* sp. nov. for differentiating it from close species.

In this study, we reported two shared parasite species from two different but genetically close hosts, *Maculabatis arabica* and *M. randalli.* Taxonomic relationships of the hosts were analysed using the *NADH2* marker, with verification through using the reference samples (Figures 7 and 1 in Golzarianpour et al. 2020b). The accession numbers of these host individuals are MN602003 and MN602004 for *M. arabica*; MN602006 and MN602007 for *M. randalli* (the details are mentioned in Table 2). In the current study, the introduced parasites were obtained from the same host individuals which were analysed molecularly in our previous study. Notably, the interspecific mean p-distance between them was as low as 3% in the *NADH2* marker (Table 3 in Golzarianpour et al. 2020b).

On the basis of K2P distance from *NADH2* marker, the average intraspecific and interspecific distance values for elasmobranchs are 0.27%, and 10.81%, respectively (Naylor et al. 2012). Golzarianpour et al. (2020b) have mentioned that the distribution range of *M. arabica* is broader than what was discussed by Manjaji-Matsumoto & Last (2016) and Fernando et al. (2019), and documented the presence of this species in the Persian Gulf. These findings confirm that *M. arabica* and *M. randalli* coexist in the northern regions of the Persian Gulf and the Gulf of Oman, where they have overlapped dispersion. Although there is no geographical barrier between these stingrays in their present distribution, this close relationship could be caused by a recent divergence in the northwest region of the Indian Ocean. As mentioned by Martin et al. (1992) and because of this slight interspecific mean p-distance, the speciation phenomenon may have been occurred in the Persian Gulf during the early Pleistocene, when the level of water in the oceans was changed repeatedly. This could be considered as a geographical barrier in this region which was resulted into a reproductive barrier. They may extend their distribution subsequently and diversify in the Holocene, when the Persian Gulf was connected once again (Jabado et al. 2014).

Although new parasite species presented here (i.e., *Rhinebothrium gossi* sp. nov. and *Rhinebothrium palmeri* sp. nov.) are morphologically differentiable they were found to have only diminutive genetic distance (Table 2 in Golzarianpour et al. 2020a). As it was analysed in our previous study, the minimum genetic distance between *Rhinebothrium gossi* sp. nov. and *Rhinebothrium palmeri* sp. nov. (which were named as *Rhinebothrium* cf. *oligotesticullaris* and *Rhinebothrium* sp. A, respectively) was 0.9% (12–13 bp of 1259), 0.3% (6 bp of 1930), and 11.7% (61–64 bp of 570) for 28s rDNA, 18s rDNA, and *COI* genes, respectively (Golzarianpour et al. 2020a). Additionally, the molecular hologenophore and paragenophores from the aforementioned study were used as a basis for the morphological descriptions

(Golzarianpour et al. 2020a). The accession numbers of these parasites' individuals are MT153860 for *COI*, MT033095-MT033095 for SSU and MT032161-MT032162 for LSU in *Rhinebothrium gossi* sp. nov.; and MT153864 for *COI*, MT033105 for SSU and MT032171-MT032172 for LSU in *Rhinebothrium palmeri* sp. nov. The details are mentioned in Table 2.

This observation highlights a very close relationship between the species, like their host species as illustrated in Figure 1 of Golzarianpour et al. (2020b). In the phylogenetic tree for Rhinebothriidae presented by Golzarianpour et al. (2020a) (Fig. 7), the two sister taxa, *Rhinebothrium* cf. *oligotesticullaris* and *Rhinebothrium* sp. A, are markedly distinct. These were described here as new species: *Rhinebothrium gossi* sp. nov. and *Rhinebothrium palmeri* sp. nov., respectively. Notably, these worms were occasionally found in the same host individual. As previously mentioned, only minor genetic differentiation was observed between their hosts.

Each tapeworm parasitises both hosts in nature; however, the infection rate is unbalanced. *Rhinebothrium gossi* sp. nov. was isolated from eight hosts, 62.5% of which was *Maculabatis arabica*, whereas *Rhinebothrium palmeri* sp. nov. was obtained from 18 hosts, 94.4% of which was *M. randalli.* The overall intensity was 2.6 and 3.4 for *Rhinebothrium gossi* sp. nov. and *Rhinebothrium palmeri* sp. nov., respectively. Both parasite species were found simultaneously in one host *M. randali* (MM1531: 43.5 cm DW, male) from the Gulf of Oman. It can be concluded that *R. gossi* sp. nov. was more frequent in *M. arabica*, but *M. randalli* was mostly infected by *R. palmeri* sp. nov.

This fact that different host species are infected by the same parasite species is contrary to the common belief (Caira & Jensen 2014; Fyler 2009; Mantovani 2018; Pickering 2012). First, it provides more evidence that the genus *Rhinebothrium* may not be an oioxenous worm. Golzarianpour et al. (2020a) well explained about other parasite species in the region. These findings confirm that different patterns of host specificity, including oioxenous, mesostenoxenous, and euryxenous, shape host-parasite association in the genus *Rhinebothrium* at least in the Persian Gulf and the Gulf of Oman. Second, it could be an example of co-speciation in a host-parasite system in which when the host species, namely *M. arabica* and *M. randalli* have been diverged, their parasites also speciated concurrently. This possible scenario can explain the ultimate answer to the way that such hosts are infected by these parasites. To reveal other possibilities or proximate answers, why *Rhinebothrium gossi* sp. nov. and *Rhinebothrium palmeri* sp. nov. have respectively chosen *M. arabica* and *M. radalli* as their main host, we need to have a more comprehensive view of their life cycle and many diverse factors such as the immune system capabilities, physiologic condition of the spiral intestine of different hosts, and foraging behaviors, which cause a parasite to select a special host (Johnson et al. 2019). On the other hand, it is possible that a given host bears different parasite species in different localities because of the environmental conditions, feeding behaviors, and available intermediate hosts (Golzarianpour et al. 2020a; Healy 2006). For example, although *R. leopardensis*, *R. nandoi*, and *R. ruhnkei* were introduced from *Himantura leoparda* in Australian waters (Trevisan & Caira 2020), no Rhinebothriid cestodes have been recorded from this species from the region so far. However, we are aware that more host samples should be investigated.

Considering the great diversity of batoid species in the Indo-Pacific region and the limited parasitological studies in the mentioned areas, describing new species was not far from the mind. According to the present knowledge, of 58 *Rhinebothrium* species found globally, 22 of them have been introduced from water bodies connected to the Indian Ocean (Menoret & Ivanov 2023; Trevisan & Caira 2020). The present study increases this number to 24 and the global number to 60 species. Additional taxonomic works are essential to shed more light on the phylogeny of the genus *Rhinebothrium* in the extended global view.

Acknowledgements. We express our appreciation to people of Djod village for their hospitality. We thank Hussein Salari and local fishermen that provided invaluable assistance during sampling off Djod. We appreciate Skipper Fazel and his anonymous fishers for providing us with his fishing boat to sample the waters of Bushehr.

Funding. This study was financially supported by the National Science Foundation of Iran [grant number: 4030722].

Competing interest declaration. The authors declare none.

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