Phylogenomic placement and revision of *Iranattus* Prószyński, 1992 jumping spiders (Salticidae, Plexippini, Plexippina)

Kiran Marathe¹,²*, Rishikesh Tripathi³*, Ambalaparambil V. Sudhikumar³, Wayne P. Maddison⁴*

1 Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, V6T 1Z4, Canada
2 National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK Campus, Bengaluru, 560065, India
3 Centre for Animal Taxonomy and Ecology, Department of Zoology, Christ College, Irinjalakuda, Kerala, 680 125, India
4 Departments of Zoology and Botany and Beaty Biodiversity Museum, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, V6T 1Z4, Canada

https://zoobank.org/4488FFD3-5621-439E-9253-058E974EB0B3

Corresponding author: Kiran Marathe (marathe12@gmail.com)

Abstract

The jumping spider genus *Iranattus* Prószyński, 1992, distributed from Africa to southwestern Asia, has been placed within the Harmochirina because of their male palp structures and elongated third legs. Here, we present phylogenomic evidence that it belongs instead to the subtribe Plexippina, further supported by the presence of two coupling pockets in the female epigyne. In this study, we redescribe *I. principalis* (Wesołowska, 2000) and *I. rectangularis* Prószyński, 1992. Additionally, the female of *I. rectangularis*, the type species of the genus, is described for the first time, and we report its range extension east to India.

Key Words

Afrotropics, Araneae, biodiversity research, classification, deserts, Harmochirina, Indomalaya, phylogenomics, systematics, taxonomy, xeric scrublands

Introduction

When Prószyński (1992) originally described the jumping spider genus *Iranattus* Prószyński, 1992, based on a single male specimen from Iran, he characterized it by features such as a simple tegulum (bulbus) and embolus, unusual cymbial apophysis, and an extraordinarily long pair of legs (which his text erroneously states are the fourth pair, but which in fact are the third, as in his figures 35–36). These traits led Maddison (2015) to place it within the Harmochirina, some of which have very long third legs (e.g., *Neaetha* Simon, 1885), and some of which (e.g., *Pellenes limbatus* Kulczyński, 1895) have an apophysis on the male cymbium very similar to that of *Iranattus*. A relationship with Harmochirines was suggested by Wesołowska (2000), who, when describing *Monomotapa* Wesołowska, 2000 (later synonymized with *Iranattus*; Prószyński 2017), commented on its similarity in body and leg lengths with the harmochirines *Neaetha* Simon, 1885, and *Pellolessertia* Strand, 1929.

Subsequent studies and new material now give the opportunity to reconsider the phylogenetic placement of *Iranattus*, currently composed of two species (World Spider Catalog 2024). Females were unknown until Wesołowska and Russell-Smith’s (2022) recent redescriptions of the African *I. principalis* (Wesołowska, 2000), known from Côte d’Ivoire, Nigeria, and Zimbabwe (Wesołowska 2000; Wesołowska and Russell-Smith 2011, 2022). We have recently collected *I. rectangularis* Prószyński, 1992,
Materials and methods

Materials examined

The specimens of *I. rectangularis* were recently collected from the Desert National Park, Rajasthan, India. They are currently housed in the collection of the Centre for Animal Taxonomy and Ecology (CATE), Christ College, Kerala, with plans for eventual transfer to the Research Collections at the National Centre for Biological Sciences (NCBS), Bengaluru, Karnataka, India (http://collections.ncbs.res.in), for permanent deposition. NRC-AA-#### represent NCBS voucher codes of *I. rectangularis* used for taxonomic work, where #### represents a four-digit number.

The *I. principalis* specimens used in this study were in vials in a large jar of poorly labeled salticid specimens in the Natural History Museum, London (NHMUK). All the vials in the jar contained, typically, African salticids. Their labels bore only codes of the form “PNB ####”, where #### is a two- or three-digit number. We interpret these to likely be Lamotte’s collection from Parc Nacional Banco (hence, “PNB”), Côte d’Ivoire, from which Wanless (1985) cites similar code labels under *Sonotia lightfooti* Peckham & Peckham, 1903, e.g., PNB 179, PNB 146. Some specimens are identified by voucher codes of the form DDKM21,####, where #### is a three-digit number.

Morphology

We examined and photographed ethanol-preserved specimens using an Olympus OM-D E-M10 II camera mounted on an Olympus SZX12 or a Leica DMC4500 camera attached to a Leica M205 C stereoscope. We used a drawing tube attached to a Nikon ME600L compound microscope to prepare illustrations of *I. principalis*. We used clove oil for clear viewing of epigyne after digesting the internal epigynal soft tissues with pancreatin. We stacked photographs using Helicon Focus 7.6.6 Pro. We prepared the drawings of *I. rectangularis* specimens by digitally tracing the photographs.

Descriptions of color patterns are based on ethanol-preserved specimens. Carapace length is measured from the base of the anterior median eyes to the posterior margin of the carapace medially, while abdomen length is measured from the anterior to the end of the anal tubercle. All measurements are in millimeters. Leg measurements are represented as follows: total length (femur, patella, tibia, metatarsus, and tarsus). Abbreviations used here are as follows: CO, copulatory opening; ECP, epigynal coupling pocket; PME, posterior median eye; PLE, posterior lateral eye; RTA, retrolateral tibial apophysis.

Taxon sampling for phylogenomic analysis

To test the phylogenetic placement of *Iranattus*, molecular data was gathered for *I. rectangularis* and added to Marathe et al.’s (2024) UCE phylogenomic dataset, which included 15 plexippines, two harmochirines, and one salticine. Because *Iranattus*’s former placement in the Harmochirina was based in part on some *Pellenes* having a similar cymbial apophysis, one such *Pellenes* (*Pellenes limbatus*) was added to the dataset to give the harmochirines the best chance to capture *Iranattus* in the phylogenetic analysis. An extra outgroup taxon, *Chrysilla volupe* (Karsch, 1879), was also added. The total set of 21 species used in the phylogenomic analysis, with their taxonomic authority indicated, is listed in Table 1.

Ultraconserved element (UCE) data

Molecular data was gathered for UCE loci using target enrichment sequencing methods (Faircloth 2017), using the RTA_v2 proberset (Zhang et al. 2023), and following the protocols of Marathe et al. (2024).

Raw demultiplexed reads were processed with PHYLUCE v. 1.6 (Faircloth 2016), quality control and adapter removal were performed with Illumiprocessor wrapper (Faircloth 2013), and assemblies were created with SPAdes v. 3.14.1 (Nurk et al. 2013) using options at default settings. The UCE loci were recovered using RTA_v2 proberset (Zhang et al. 2023). The recovered loci were aligned with MAFFT using L-INS-i option (Katoh and Standley 2013). The aligned UCE loci were then trimmed with Gblocks (Castresana 2000; Talavera and Castresana 2007) using −b1 0.5, −b2 0.7, −b3 8, −b4 8, −b5 0.4 settings and re-aligned with MAFFT using L-INS-i option within Mesquite v. 3.81 (Maddison and Maddison 2023b). As in the analysis of Maddison et al. (2020), suspected paralogous loci were deleted based on branch lengths in RAxML (Stamatakis 2014) inferred gene trees. Loci represented in fewer than 10 taxa total were deleted.

Phylogenetic analysis

Maximum-likelihood phylogenetic and bootstrap analyses were performed with IQ-TREE v. 2.2.0 (Nguyen et al. 2015) using the Zephyr v. 3.31 package (Maddison and Maddison 2023a) in Mesquite v. 3.81 (Maddison and Maddison 2023b) on the concatenated, unpartitioned UCE dataset with 20 taxa. For the phylogenetic tree inference, the option -m TEST (standard model selection followed by tree inference, edge-linked partition model,
no partition-specific rates) was used with 10 search replicates. For the bootstrap analysis, a single IQ-TREE search was used for each of the 1000 search replicates.

**Data availability**

The raw sequence reads obtained from UCE capture are stored within the Sequence Read Archive (BioProject: https://www.ncbi.nlm.nih.gov/bioproject/1101580), and their accession numbers are listed in Table 1. The UCE loci matrices from SPAdes assemblies, pre-Gblocks, and the concatenated matrices used for phylogenetic and bootstrap analysis, along with trees, are available on the Dryad data repository (https://doi.org/10.5061/dryad.ht76hdrpz).

### Results

**Phylogenetic results**

Table 2 lists the sequence data recovered from the 21 taxa. 3398 UCE loci were initially recovered. Of these, 3140 remained after removing those represented in fewer than 10 taxa, and 3104 remained after removing those suspected to include paralogies on branch lengths. These were concatenated into the final matrix, whose aligned length is 2779616 base pairs, in which each taxon had on average ~2.2 million base pairs of sequence data (min. 985191, max. 2462121).

The phylogenetic results are shown in Fig. 1. The reciprocal monophyly of the subtribes Plexippina and Harmochirina is recovered distantly from the subtribe Harmochirina and placed as the sister lineage to *Evarcha sensu lato* within the subtribe Plexippina.

### Table 1. Specimens used in phylogenomic analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Voucher</th>
<th>Sex</th>
<th>Locality</th>
<th>Lat, long</th>
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<td>♂</td>
<td>Singapore</td>
<td>1.355–7, 103.774–5</td>
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<td>Baryphas ahenus Simon, 1902</td>
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<td>Bionator maculatus (Keyserling, 1883)</td>
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**Figure 1.** The IQ-TREE-based maximum-likelihood tree, represented here, is the best of 10 replicates, inferred from a concatenated dataset of 3104 UCE loci. The numbers at the nodes are the percentage recovery of the clade based on 500 bootstrap replicates. *Iranattus rectangularis* is recovered distantly from the subtribe Harmochirina and placed as the sister lineage to *Evarcha sensu lato* within the subtribe Plexippina.
is consistent with previous molecular phylogenetic studies with both Sanger sequencing and UCEs (Maddison and Hedin 2003; Maddison et al. 2008; Bodner and Maddison 2012; Marathe et al. 2024). The phylogenetic structure within Plexippina is largely consistent with Marathe et al. (2024) and has generally high bootstrap values.

Iranattus is nestled well within Plexippina, placed as a sister lineage to Evarcha Simon, 1902 sensu lato (see Fig. 1). The harmochirine included in the analysis with a similar cymbial apophysis, Pellenes limbatus, is placed as expected within the harmochirines. Thus, the similarities between Iranattus and harmochirines noted by Weśolowska (2000) and Maddison (2015) are convergences.

The placement of Iranattus in the Plexippina is also supported by the form of the epigyne. Wesołowska and Russell-Smith, 2022). We therefore recognize Iranattus as a member of the subtribe Plexippina.

**Taxonomic results**

**Family Salticidae Blackwall, 1841**

**Tribe Plexippini Simon, 1901**

**Subtribe Plexippina Simon, 1901**

**Iranattus Prószyński, 1992**

Figs 2–41


**Type species.** Iranattus rectangularis Prószyński, 1992.

**Species included.** Iranattus principalis (Wesołowska, 2000); Iranattus rectangularis Prószyński, 1992.

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Table 2. Specifics of molecular data used for this phylogenomic analysis. Molecular data was generated based on the RTA_v2 probeset. “SRA” is the Sequence Read Archive accession number available through NCBI; “Reads pass QC” is the number of reads after the removal of adapter contamination and low-quality bases using Illumiprocessor; “Total UCE loci” is the total number of UCE loci recovered with RTA_v2 probeset; “After paralogy filter” is the number of UCE loci after deletion of suspected paralogous loci based on branch length ratios; “In at least 10 taxa” is the number of UCE loci in at least 10 or more taxa after branch length criteria; “Filtered UCE sequence length” is the concatenated sequence length of filtered UCE loci; “Total loci” is the number of UCE loci represented among all taxa.

<table>
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<th>Species</th>
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<th>In at least 10 taxa</th>
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<th>Filtered UCE sequence length</th>
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Average: 2843
Minimum: 2256
Maximum: 3092
Total loci: 3398

SRA: the Sequence Read Archive accession number available through NCBI; Reads pass QC: the number of reads after the removal of adapter contamination and low-quality bases using Illumiprocessor; Total UCE loci: the total number of UCE loci recovered with RTA_v2 probeset; After paralogy filter: the number of UCE loci after deletion of suspected paralogous loci based on branch length ratios; In at least 10 taxa: the number of UCE loci in at least 10 or more taxa after branch length criteria; Filtered UCE sequence length: the concatenated sequence length of filtered UCE loci; Total loci: the number of UCE loci represented among all taxa.
Diagnosis. The remarkably long third legs of *Iranattus* (Figs 15, 18, 30, 32) and scoop-shaped cymbial apophysis (Fig. 4) differentiate it from all other plexipinnies. The very robust carapace, bulging outward at the PLE and bearing the PLEs on tubercles, is unusual but shared also with *Afrobeata* Caporiacco, 1941, and *Vailimia* Kammerer, 2006. *Vailimia* especially might be confused with *Iranattus*, as they share erect hairs on the carapace (see Figs 34, 38, 41) and a compact crouch stance, but, besides the cymbial apophysis and long third legs, *Iranattus* also has a shorter embolus lacking membrane (membrane-accompanied long embolus in *Vailimia*), a short RTA (long and curved in *Vailimia*), and two distinct deep conical ECPs (absent in *Vailimia*). From *Afrobeata*, *Iranattus* differs in having longer third legs, a cymbial apophysis (lacking in *Afrobeata*), a shorter embolus (longer in *Afrobeata*), a simple short RTA (bifurcated in *Afrobeata*), shorter copulatory ducts (long in *Afrobeata*), and deep conical ECPs (shallow in *Afrobeata*). Some other plexipinnies have cymbial apophyses (*Plexippoides* Prószyński, 1984; *Epeus* Peckham & Peckham, 1886; and *Erasinus* Simon, 1899), but their apophyses are different in shape—in *Iranattus*, a long, broad blade with a rounded tip, concave in front so as to form a scoop; in *Plexippoides*, sharply pointed, for example.

*Iranattus principalis* (Wesołowska, 2000)

Figs 2–19

*Iranattus principalis* Prószyński, 2017: 36, 14K, 17F (transferred from *Monomotapa*).

Materials examined. In NHMUK, lacking complete labels. These are likely from Parc Nacional Banco, Côte d’Ivoire (see “Materials examined” for explanation).
2♀♀ (PNB21) • 1♂ 1♀ (PNB146) • 3♀♀ (PNB156) • 2♀♀ (PNB159) • 2♂♂ (PNB167) • 2♀♀ (PNB181) • 1♂ 1♀ (PNB192) • 2♂♂ 2♀♀ (PNB203).

**Diagnosis.** Larger than *I. rectangularis*, with an almost ovoid tegulum with a less prominent shoulder, RTA slightly bent near the tip (Figs 10, 11), and a multi-chambered spermatheca sandwiched between copulatory ducts dorsally and the epigynal plate ventrally.

**Description.** ♀ (DDKM21.089). Measurements: Carapace 2.2 long, 2.1 wide. Abdomen length 1.7; width 1.4. Leg measurements: I–11.2 (3.4, 2.2, 2.4, 1.8, 1.3); II–10 (2.8, 2, 2.4, 1.5, 1.2); III–16.6 (6.3, 2.9, 3.2, 2.5, 1.7); IV–10.1 (3.7, 1.6, 1.7, 1.8, 1.3). Leg formula III-IV-II-I. **Carapace** wider than abdomen. Ocular area shaped like an isosceles trapezoid, narrow at the anterior eye row and wide at the PLEs. PLEs on tubercles. Thoracic area slopes acutely downward behind ocular area. Ocular area anteriorly golden yellow, and remaining carapace dark brown. Lateral sides posteriorly and back sparsely covered with pale hairs. **Clypeus** narrow, yellowish-brown sparsely covered with hairs. **Chelicerae** vertical, narrow, yellowish brown. **Pulps** (Figs 2–5, 8–11): Embolus medium-long, starting at 7 o’clock. RTA stout, short with blunt tip. Cymbium extends retrolaterally to form scoop-shaped apophysis. Tegulum prolaterally rounder; retrolaterally slightly angular at distal and proximal edges. **Legs:** III femur distinctly long. Femur golden yellow, distal segments yellowish-brown. **Abdomen** narrow, ovoid. Golden yellow with less prominent transverse pale bands. Spinnerets yellowish.

♀ (DDKM21.090). Measurements: Carapace 5.1 long, 5.1 wide. Abdomen length 6.4; width 4.8. Leg measurements: I–11.7 (3.8, 1.8, 2.7, 2.1, 1.3); II–11.6 (3.3, 2.8, 2.4, 1.8, 1.3); III–19.7 (6.9, 3.3, 4.7, 3.1, 1.8); IV–11.4 (2.9, 2.1, 2.3, 2.6, 1.5). Leg formula III-I-II-IV. **Carapace** shape similar to male, width about same as abdomen. Brown, sparsely covered with pale hairs. **Clypeus** similar to male. **Chelicerae** similar to male. **Legs** similar to male. **Abdomen** ovoid, bulky, yellowish, covered with brown hairs, and more posteriorly.

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Spinnerets yellowish. **Epigyne** (Figs 6, 7, 12, 13): Medially located copulatory opening flanked by conical-shaped ECP.

**Natural history.** Wesołowska and Russell-Smith (2022) report *Iranattus principalis* as collected from the branches of savannah shrubs. G. Azarkina (pers. comm.) has seen material of this species from canopy fogging in tropical savannas in Cameroon (2♀ 8.40°N, 12.80°E) and Côte d’Ivoire (1♀ 8.40°N, 12.80°E; 2♂ 2♀ 8°44’N, 3°49’W) in the Musée royal de l’Afrique centrale, collected from the trees *Cola laurifolia*, *Combretum fragrans*, *Anogeissus leiocarpus*, and *Crossopteryx febrifuga*.

**Distribution.** Côte d’Ivoire, Nigeria, Zimbabwe, and Cameroon.

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**Iranattus rectangularis** Prószyński, 1992

Figs 20–41


**Materials examined.** 1 ♂, 1 ♀, & 4 juveniles. From INDIA: RAJASTHAN: Jaisalmer: Thar Desert: Desert National Park, Myajlar area, 26.28°N, 70.40°E, 275 m elev., 20 Aug 2022, leg. R. Tripathi.

**Diagnosis.** Smaller than *I. principalis*, with a bright orange face and erect hairs on the carapace, an angular tegulum with a prominent shoulder, a simple RTA, and a simple spermatheca with copulatory ducts ventrally.

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Description. ♂ (NRC-AA-7708). Measurements: Carapace 1.46 long, 1.26 wide. Abdomen length 1.32, width 0.86. Leg measurements: Leg I 2.04 [0.69, 0.33, 0.48, 0.32, 0.22], leg II 1.88 [0.67, 0.33, 0.44, 0.28, 0.16], leg III 3.56 [1.52, 0.55, 0.72, 0.43, 0.34], leg IV 1.94 [0.70, 0.31, 0.34, 0.38, 0.24]. Leg formula: III–I–IV–II. Carapace wider than abdomen. Ocular area shaped like an isosceles trapezoid, narrow at the anterior eye row and wide at the PLEs. PLEs on tubercles. Thoracic area slopes acutely downward behind ocular area. Ocular area from base of front eyes to PMEs orange, covered with black hairs, posterior with pale hairs. Pale erect hairs on ocular area. Pale hair patch beneath PMEs. Black hair band starts anteriorly, encircles carapace at ocular area edge. White band along lateral edge, narrow front, broadens posteriorly and behind. Clypeus narrow. Orange, covered with pale hairs, more densely near integument edge. Chelicerae vertical, narrow, yellowish brown. Palp (Figs 20, 21, 24–27): Embolus medium-long, starting at 9 o’clock, somewhat thick. RTA stout, short with blunt tip. Cymbium extends retrolaterally to form scoop-shaped apophysis. Tegulum prolaterally rounder; retrolaterally angular at distal and proximal edges. Legs: III femur distinctly long relative to others. Femur yellowish, distal segments yellowish.

Figures 30–33. Iranattus rectangularis habitus. 30. Male, dorsal view (NRC-AA-7708); 31. Ditto, lateral view (NRC-AA-7708); 32. Female, dorsal view (NRC-AA-7709); 33. Ditto, lateral (NRC-AA-7709). Scale bars: 1 mm. Arrows in Figs 30 and 32 point to the elongated third legs.

♀ (NRC-AA-7709). Measurements: Carapace 1.91 long, 1.56 wide. Abdomen length 1.83, width 1.27. Leg measurements: Leg I 2.67 [0.95, 0.53, 0.56, 0.36, 0.27], leg II 2.41 [0.85, 0.47, 0.50, 0.32, 0.27], leg III 4.30 [1.78, 0.70, 0.92, 0.50, 0.40], leg IV 2.44 [0.87, 0.40, 0.42, 0.44, 0.31]. Leg formula III–I–IV–II. *Carapace* shape similar to male. Ocular area orange anteriorly, white hairs sparsely posteriorly. Pale erect hairs on ocular area. Thoracic slope covered with black hairs. Lateral sides covered with pale hairs, almost merging behind. *Clypeus* similar as in male. *Chelicerae* similar to male. *Legs* similar to male. *Abdomen* shape comparable to male, but with a ‘kite’-shaped black color pattern between posterior edge and median. *Epigyne* (Figs 22, 23, 28–29): Medially located copulatory opening flanked by conical-shaped ECP.

**Natural history.** *Iranattus rectangularis* was collected from the branches of non-native *Vachellia tortilis* alongside artificial water canals in the Desert National Park, a xeric and desert ecosystem located in Rajasthan, India (Figs 42, 43). The mosaic of orange, black, and grey body coloration helps them blend in with the branches, making them inconspicuous, except that in the field, the orangish faces of males (Fig. 34) sometimes stood out.

**Distribution.** Iran, India (Rajasthan).
Figures 42, 43. Iranattus rectangularis habitat. 42. Vachellia tortilis woodland; 43. Aerial views of the landscape of the Desert National Park, Rajasthan, India.

Discussion. *Iranattus rectangularis* is reported for the first time east of Iran, in western India. This seemingly ‘disjunct’ distributional pattern is quite possibly due to a lack of collecting between the sites and mirrors that of *Stenaelurillus marusiki* Logunov, 2001 (Salticidae: Aelurollina), where the type locality of *S. marusiki* is Iran. However, it has been reported much farther southeast in Maharashtra, India (Marathe et al. 2022). With the transfer of *Iranattus* to Plexippina, the subtribe now contains 35 genera, and the number of plexippines in India stands at 47 species and 18 genera.

Acknowledgements

Collection of *I. rectangularis* was facilitated by the Bustard Recovery Programme of the Wildlife Institute of India (WII), funded by the National Compensatory Afforestation Fund Management and Planning Authority, Government of India, and supplemented by an additional grant from the Rajasthan State Pollution Control Board. RT and AVS thank Rev. Fr. Jolly Andrews, CMI of Christ College (Irinjalakuda), for facilities and NCBS research collections. RT acknowledges the support of Dr. Sutirtha Dutta, Dr. Manju Siliwal, and Mr. Ashish Kumar Jangid from WII, as well as the Rajasthan State Forest Department, for the collecting permit. Special thanks to Sohan Lal Genwa and Amrat Genwa for their assistance during field activities. RT thanks Anshuman Pati and Jason D. Gerard for habitat photographs. RT acknowledges CSIR-UGC for fellowship. KM thanks Dr. Krishnamgeeh Kunte, NCBS, for providing the lab space and supplies. KM and WPM thank Carol Ritland and Allyson Miscampbell of the Genetic Data Centre at the University of British Columbia for assistance with lab facilities. We thank J. Beccaloni (NHMUK) for the loan of *I. principalis* specimens. We thank Galina Azarkina for providing information on additional material of *I. principalis* she examined. We thank Dmitry Logunov, Galina Azarkina, and Tamás Szűts for their time reviewing the manuscript and providing valuable comments. Funding to WPM was provided by an NSERC Canada Discovery Grant.

References


