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First records of the order Schizomida from tropical hothouses in Denmark: *Stenochrus portoricensis* and a new species of *Bamazomus* (Schizomida: Hubbardiidae)

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Abstract. Anthropogenic transport of plants, food, and other materials has been a route of dispersal for many arthropods and some tropical species have inadvertently been introduced to European hothouses where they have established reproducing populations. This study reports the first records of the introduction of the arachnid order Schizomida to Danish hothouses: namely *Stenochrus portoricensis* as well as a new species of *Bamazomus* (Schizomida: Hubbardiidae). The latter, *Bamazomus serendipitus* **sp. n.** is described. Possible origins of introductions for both species are addressed, based on comparison of newly generated and publicly available DNA barcodes, history of introduction of plants, and for *B. serendipitus* **sp. n.** also morphological similarity to other *Bamazomus* species. *Stenochrus portoricensis* has likely been introduced from Costa Rica and *B. serendipitus* **sp. n.** is suggested to originate from Southeast Asia.

Keywords: COI, short-tailed whipscorpions, species introduction, taxonomy

Zusammenfassung. Erstnachweise der Ordnung Schizomida aus tropischen Gewächshäusern in Dänemark: Stenochrus portoricensis und eine neue Art von Bamazomus (Schizomida: Hubbardiidae). Anthropogener Transport von Pflanzen, Nahrungsmitteln und anderen Materialien ist für viele Arthropoden ein Verbreitungsweg und manch tropische Art wurden unbeabsichtigt in europäische Gewächshäuser eingeschleppt, wo sie reproduzierende Populationen bilden konnte. Diese Studie präsentiert den ersten Nachweis einer Verschleppung der Spinnentierordnung Schizomida in dänische Gewächshäuser anhand der Art Stenochrus portoricensis wie auch einer neuen Art der Gattung Bamazomus (Schizomida: Hubbardiidae). Die letztere, Bamazomus serendipitus sp. n., wird neu beschrieben. Mögliche Einschleppungswege für beide Wege werden anhand von öffentlich verfügbaren DNA Barcodes, Herkunftsgeschichte der Pflanzen wie auch morphologischen Ähnlichkeiten von B. serendipitus sp. n. zu anderen Bamazomus-Arten diskutiert. Stenochrus portoricensis wurde wahrscheinlich aus Costa Rica eingeschleppt und B. serendipitus sp. n. stammt vermutlich aus Südostasien.

Presently, humans transport immense quantities of food, building materials, plants, etc. across the globe. Alongside, hidden in, e.g., soil, ballast water, plants, timber, and food, many species are inadvertently transported outside their native distributions. These stowaway occurrences have led to expanded distributions of some species (Inward 2020, Roll et al. 2007). Hothouses of botanical- and zoological gardens contain plants imported from all over the world, and in hothouses in temperate regions where artificial tropical climates are maintained, with regulated temperature and humidity, occasionally tropical and subtropical exotic species survive and reproduce (e.g. Oszust et al. 2020, Vierbergen 2008). At least from the perspective of the introduced species, these hothouses could be regarded as "tropical islands" (Kolicka et al. 2015). In accordance with this notion, species such as the ant Strumigenys rogeri Emery, 1890 and Stenochrus portoricensis Chamberlin, 1922, which have been successfully introduced to many new areas both intra- and intercontinentally (Monjaraz-Ruedas et al. 2022, Wetterer 2012), have also been found in hothouses and other horticultural buildings in temperate regions (Armas & Rehfeldt 2015, Christophoryová et al. 2013, Korenko et al. 2009, Lauterbach et al. 2020, Noordijk & Heijerman 2022, Schär et al. 2017, Wetterer 2012, Zawierucha et al. 2013). In European hothouses species of various arthropod orders from around the world have been recorded, including woodlice (Isopoda) (Cifuentes et al. 2022, Noël et al. 2014), earwigs (Dermaptera) (Matzke & Kocarek 2015), ants (Hymenoptera: Formicidae) (Schär et al. 2017, Vierbergen 2008), mites (Acari) (Oszust et al. 2020), spiders (Araneae) (Hänggi

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et al. 2021, Pfliegler 2014, Šestáková et al. 2017), and shorttailed whipscorpions (Schizomida) (e.g. Christophoryová et al. 2013, Armas & Rehfeldt 2015, Korenko et al. 2009, Lauterbach et al. 2020, Zawierucha et al. 2013). Additionally, synanthropic faunas of European hothouses have been the source of discovery of multiple undescribed arthropod species and provided specimens used for their description, e.g. the earwig Euborellia arcanum Matzke & Kocarek, 2015, the short-tailed whipscorpions Zomus bagnalli (Jackson, 1908) and Bucinozomus hortuspalmarum Armas & Rehfeldt, 2015, and the newly described diplurid spider, Masteria boggildi Lissner, 2023 (Lissner & Craig 2023). Evidently, studying the tropical faunas of hothouses in Europe could potentially lead to further discovery of undescribed species, and could help increase our understanding of poorly investigated taxonomic groups and/or regions.

While investigating the introduced ant fauna of Randers Regnskov Tropical Zoo (RRTZ; in Randers, Denmark) in February 2022, which was previously examined for ants by Schär et al. (2017), the first author (SBBC) found a juvenile short-tailed whipscorpion, which was the first recording of an introduction of the order Schizomida into hothouses in Denmark. Further faunistic investigations of RRTZ and Odense Zoo (OZ) led to the discovery of seemingly reproducing populations of two species of short-tailed whipscorpions, which we identified as Stenochrus portoricensis (in RRTZ and OZ) and an undescribed species in the Old World genus Bamazomus Harvey, 1992 (only present in RRTZ). The aim of this study is to report the first observation of the order Schizomida from hothouses in Denmark and to describe the species Bamazomus serendipitus sp. n. The present study also discusses possible origins of the introduction of Bamazomus serendipitus sp. n. and Stenochrus portoricensis on the basis of comparisons of DNA sequences of the mitochondrial cytochrome oxidase subunit I (COI) gene to sequences available in the NCBI GenBank and the history of major plant introductions to RRTZ. For B. serendipitus sp. n. this is additionally based

on morphological similarity to other Bamazomus spp. in the literature

Materials and methods

Apart from the first caught specimen, the 41 specimens studied in this paper were collected in RRTZ (*B. serendipitus* **sp. n.**, 19 specimens and *S. portoricensis*, 15 specimens) during 5 visits between 19. Dec. 2022 and 3. Apr. 2023 and OZ (*S. portoricensis*, 7 specimens) during 2 visits, 7. Dec. 2023 and 20. Dec. 2023. Specimens were found by turning stones and pieces of wood, brushing aside leaf litter and observing the soil surface, and shaking leaf litter in plastic trays. Type specimens have been deposited in the collection of the Natural History Museum of Denmark (NHMD). Remaining specimens have been deposited in either NHMD or JL's personal collection. Specimens from both collections can be accessed through contact with NHMD. Specimens in JL's personal collection will be transferred to NHMD's collection.

Photos of selected features were taken using a Leica M165 C stereomicroscope or Leica DME microscope fitted with Leica MC 190 HD digital camera connected to a computer with Leica Application Suite software v. 4.12.0 and Zerene Stacker software v. 1.04. Line drawings were made digitally on top of photos using the vector graphics editor Inkscape v. 1.2.2.

Nomenclature of the female genitalia follows Reddell & Cokendolpher (1995), with additions of nomenclature for the chitinized arch from Moreno-González et al. (2014). Flagellar setae position nomenclature follows Moreno-González et al. (2014) and Monjaraz-Ruedas et al. (2016). The nomenclature for cheliceral and opisthosomal setation follows Villarreal et al. (2016). The pedipalpal setae nomenclature follows Monjaraz-Ruedas et al. (2017).

Abbreviations

Dl1: Dorsolateral 1; refers to the first dorsolateral setae pair of the opisthosoma

Dl2: Dorsolateral 2; refers to both the second dorsolateral opisthosomal and flagellar setae pair

Dl3: Dorsolateral 3; refers to the third dorsolateral flagellar setae pair

Dm: Dorsomedian; refers to dorsomedian setae pairs on the opisthosoma

Dm1: Dorsomedian 1; refers to seta on flagellum

Dm4: Dorsomedian 4; refers to seta on flagellum

Fe1: Femur ectal 1 Fe5: Femur ectal 5

Fed3: Femur ectal dorsal 3

Fev1: Femur ectal ventral 1

Fev2: Femur ectal ventral 2

Fmv1: Femur mesal ventral 1

Fmv2: Femur mesal ventral 2

Fmv3: Femur mesal ventral 3

Fmv4: Femur mesal ventral 4

JL: Jørgen Lissner

NHMD: Natural History Museum of Denmark

OZ: Odense Zoo Pm: Patella mesal

Pme1: Patella medial ectal 1 Pmm3: Patella medial mesal 3

RRTZ: Randers Regnskov Tropical Zoo

SBBC: Sean Birk Bek Craig

Ter: Tibia external row

Tir: Tibia internal row

Tm: Tibia medial

Tmr: Tibia medial row

Vl1: Ventrolateral 1; refers to setae on both opisthosoma and flagellum

Vl1A: Occasionally an additional opisthosomal setae pair is present and Vl1 is split to two pairs, Vl1A being the most lateral pair of the two

Vl1B: Occasionally an additional opisthosomal setae pair is present and Vl1 is split to two pairs, Vl1B being the most median pair of the two

Vl2: Ventrolateral 2; refers to setae on both opisthosoma and flagellum

Vm1: Ventromedian 1; refers to setae on both opisthosoma and flagellum

Vm2: Ventromedian 2; refers to setae on both opisthosoma and flagellum

Vm4: Ventromedian 4; refers to seta on flagellum Vm5: Ventromedian 5; refers to setae on flagellum

Laboratory work and DNA barcoding

DNA was extracted in laboratories at the Department of Biology, Aarhus University. We performed DNA extractions on 1-3 legs of each of six specimens (three of Bamazomus serendipitus sp. n. and three of Stenochrus portoricensis). DNA extractions were carried out using the E.Z.N.A.® Tissue DNA Kit (Omega Bio-tek, Cat. no. D3396-01) according to the manufacturer's protocol and eluted in a final volume of 70 µl. One PCR reaction was set up for each of the 6 specimens using the standard forward primer LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-'3) and reverse primer HCO2198 (5'-TAAACTTCAGGGTGAC-CAAAAAATCA-'3) (Folmer et al. 1994). Each PCR was set up in 25 µl total volume containing 1 µl template DNA, 10 μl HotStarTaq Master Mix (Qiagen), 11 μl ddH2O, 1 μl of each primer (10 μM), and 1 μl bovine serum albumin (BSA) (20 mg/ml). Thermocycling parameters were: 95°C for 15 min, 40 cycles of 94°C for 30 s, 40°C for 30 s, 72°C for 1.5 min, and a final elongation of 72°C for 7 min. Fragment sizes were verified on 2% agarose gel stained with GelRedTM and sent to be purified and commercially Sanger-sequenced in both forward and reverse direction by Macrogen Europe (Cambridge, UK). Resulting sequence chromatograms were assembled and manually inspected and quality checked using Geneious (v.10.2.6) (Kearse et al. 2012).

Phylogenetic analysis and tree construction

A dataset of COI-sequences was compiled from NCBI Gen-Bank and all bioinformatic treatments of the dataset were conducted in MEGA11 (Tamura et al. 2021). The dataset was compiled from sequences available on NCBI GenBank belonging to the taxon *Bamazomus* (NCBI:txid483292), the distantly related taxon *Baalrog magico* (Monjaraz-Ruedas & Francke, 2018) (NCBI:txid2572815), and the following taxa which were included in a phylogeny in Abrams et al. (2019) to represent genera closely related to *Bamazomus*, *Apozomus watsoni* Harvey, 1992 (NCBI:txid2584186) and *Draculoides bramstokeri* Harvey and Humphreys, 1995 (NCBI:txid483297). Duplicate sequences were removed from

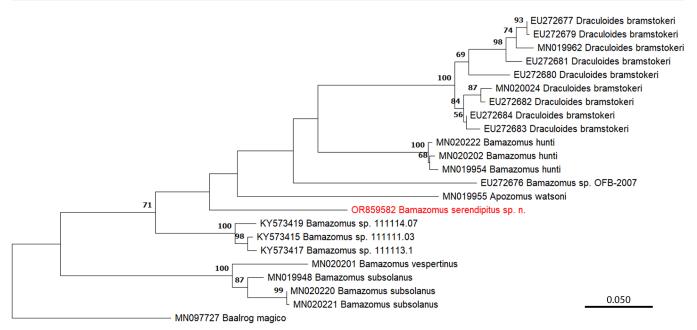


Fig. 1: Phylogenetic tree of *Bamazomus serendipitus* **sp. n.** (in red) and *Apozomus watsoni* Harvey, 1992 (NCBI:txid2584186), *Draculoides bramstokeri* Harvey & Humphreys, 1995 (NCBI:txid483297), *Bamazomus* ssp. (NCBI:txid483292) with COI-sequences available on GenBank, and *Baalrog magico* (Monjaraz-Ruedas & Francke, 2018) (NCBI:txid2572815) as the outgroup. The shown tree is the one with highest log likelihood (–2577.71). Bold numbers refer to bootstrap support values (1000 bootstraps). The tree is drawn to scale and the horizontal length of the branches relate to the length measured as number of substitutions per site, with scale bar as %

the final dataset (Tab. 1), and the remaining sequences were aligned with a B. serendipitus sp. n. sequence generated in this study using the MUSCLE algorithm (Edgar 2004) with default settings. Only one B. serendipitus sp. n. sequence was included in the dataset because all three sequences generated in this study were identical. Model selection was performed in MEGA11 (Tamura et al. 2021) with default settings. A phylogenetic tree was constructed in MEGA11 (Tamura et al. 2021). The *B. serendipitus* **sp. n.** sequence and the sequences collected from GenBank are named with a two letter and six number reference code (GenBank accession codes, see Tab. 1) followed by their species name (the names of the sequences not identified to species are followed by a number or letter and number sequence, which is part of their current name on NCBI) (Fig. 1). The phylogeny was inferred by Maximum Likelihood using the bootstrap method set to 1000 replications and the General Time Reversible model (Nei & Kumar 2000) as the substitution model, with invariant sites ([+/], 30.33% sites). 23 nucleotide sequences were included in the analysis and 488 positions were included in the final dataset, after eliminating all positions with less than 95% site coverage. The analysis was conducted in MEGA11 (Tamura et al. 2021). The tree was rooted on Baalrog magico.

Additionally, a Tamura-Nei (Tamura & Nei 1993) corrected pairwise distance estimation was performed in MEGA11 (Tamura et al. 2021) on the dataset, estimating variance using the bootstrap method with 1000 replications. The substitution model was set to the Tamura-Nei model (Tamura & Nei 1993), and the missing data treatment to partial deletion with site coverage cutoff at 95%, resulting in a total of 488 positions included in the final dataset. The settings were otherwise set to default.

The *S. portoricensis* barcode generated in this study was compared in query coverage and percent identity to available sequences in GenBank using BLAST (Zhang et al. 2000).

Nomenclature

This paper and the nomenclatural act it contains has been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:D6350B2D-BDF7-4C64-963A-B1992CD91BEE

Results

DNA barcodes

Sequencing of all three specimens of *Bamazomus serendipitus* **sp. n.** were successful yielding congruent sequences of 658 bp. One of the three specimens of *Stenochus portoricensis* successfully yielded a sequence of 658 bp. Barcodes and information on vouchered specimens have been deposited in The Barcode of Life Data System (BOLD, www.boldsystems.org) (Ratnasingham & Hebert 2007) and uploaded to GenBank (See Tab. 1 for accession numbers).

Phylogenetics

With the maximum likelihood tree, we found high bootstrap support for a clade of *Draculoides bramstokeri*, a clade of *Bamazomus hunti* Harvey, 2001, one clade consisting of three specimens identified as *Bamazomus* sp. which are from the country of Vanuatu (from now on referred to as the Vanuatu group), a clade including *B. subsolanus* Harvey, 2001 and *B. vespertinus* Harvey, 2001, and a clade of *B. subsolanus* (Fig. 1). We also found bootstrap support for a clade including both *D. bramstokeri*, *B. hunti*, *Bamazomus* sp. OFB-2007, *Apozomus watsoni*, *B. serendipitus* sp. n., and the Vanuatu group. *Bamazomus serendipitus* sp. n. was recovered sister to a clade with *D. bramstokeri*, *Bamazomus* sp. OFB-2007, *B. hunti*, and *A. watsoni* without significant bootstrap, the Vanuatu group respectively sister to the previous clade (Fig. 1). Although the Vanuatu group was not recovered sister to *B. serendipi*

Tab. 1: List of genus and species names or operational taxonomic units (OTU), NCBI GenBank accession numbers, NCBI taxonomy ID, and references of COI-sequences used in this study, incl. newly generated sequences. Sequences included in the dataset used for the phylogenetic analyses of *B. serendipitus* **sp. n.** are marked with ^ in the GenBank accession code column

Genus	Species/OTU	NCBI Taxonomy ID	GenBank accession code	References
Apozomus	watsoni	NCBI:txid2584186	MN019955 ^	Abrams et al. (2019)
Baalrog	magico	NCBI:txid2572815	MN097727 ^	Monjaraz-Ruedas et al. (2019)
Bamazomus	hunti	NCBI:txid2584187	MN019954 ^	Abrams et al. (2019)
Bamazomus	hunti	NCBI:txid2584187	MN020202 ^	Abrams et al. (2019)
Bamazomus	hunti	NCBI:txid2584187	MN020222 ^	Abrams et al. (2019)
Bamazomus	serendipitus sp. n.		OR859582 ^	Present study
Bamazomus	serendipitus sp. n.		OR859583	Present study
Bamazomus	serendipitus sp. n.		OR859584	Present study
Bamazomus	sp. 111111.03	NCBI:txid1953473	KY573415 ^	Clouse et al. (2017)
Bamazomus	sp. 111113.1	NCBI:txid1953475	KY573417 ^	Clouse et al. (2017)
Bamazomus	sp. 111114.07	NCBI:txid1953477	KY573419 ^	Clouse et al. (2017)
Bamazomus	sp. OFB-2007	NCBI:txid483293	EU272676 ^	Harvey et al. (2008)
Bamazomus	subsolanus	NCBI:txid2584188	MN019948 ^	Abrams et al. (2019)
Bamazomus	subsolanus	NCBI:txid2584188	MN020220 ^	Abrams et al. (2019)
Bamazomus	subsolanus	NCBI:txid2584188	MN020221 ^	Abrams et al. (2019)
Bamazomus	vespertinus	NCBI:txid2584189	MN020201 ^	Abrams et al. (2019)
Draculoides	bramstokeri	NCBI:txid483297	EU272677 ^	Harvey et al. (2008)
Draculoides	bramstokeri	NCBI:txid483297	EU272679 ^	Harvey et al. (2008)
Draculoides	bramstokeri	NCBI:txid483297	EU272680 ^	Harvey et al. (2008)
Draculoides	bramstokeri	NCBI:txid483297	EU272681 ^	Harvey et al. (2008)
Draculoides	bramstokeri	NCBI:txid483297	EU272682 ^	Harvey et al. (2008)
Draculoides	bramstokeri	NCBI:txid483297	EU272683 ^	Harvey et al. (2008)
Draculoides	bramstokeri	NCBI:txid483297	EU272684 ^	Harvey et al. (2008)
Draculoides	bramstokeri	NCBI:txid483297	MN019962 ^	Abrams et al. (2019)
Draculoides	bramstokeri	NCBI:txid483297	MN020024 ^	Abrams et al. (2019)
Stenochrus	portoricensis	NCBI:txid61974	JX280413	Zawierucha et al. (2013)
Stenochrus	portoricensis	NCBI:txid61974	KY573390	Clouse et al. (2017)
Stenochrus	portoricensis	NCBI:txid61974	KY573408	Clouse et al. (2017)
Stenochrus	portoricensis	NCBI:txid61974	OR859581	Present study

tus sp. n. in the maximum likelihood tree, the Vanuatu clade presented the shortest genetic distance to B. serendipitus sp. n., with a minimum and maximum genetic distance of 15.6±2.5% and 16.9±2.7% respectively. This is less than the distance between B. serendipitus sp. n. and the next closest taxon which in this dataset is Apozomus watsoni with a genetic distance to B. serendipitus sp. n. of 19.0±2.8%. The distance between B. serendipitus sp. n. and D. bramstokeri varies from 19.7±3.0% to 23.7±3.6% and overlap with the distance between B. serendipitus sp. n. and all species included, apart from the Vanuatu group, A. watsoni and B. vespertinus, the latter with a divergence from B. serendipitus sp. n. of 25.2±3.6%. All pairwise genetic distances and their respective variances are available in Tab. S1.

We compared the barcode of a specimen from the RRTZ population of *S. portoricensis* with the *S. portoricensis* sequences available on GenBank. Three specimens on GenBank had COI-sequences that both had 100% query coverage and were completely identical to our sequence, two of the barcodes (GenBank: KY573390 & KY573408) were from specimens collected in USA, and one barcode from a specimen collected from a hothouse in Poland (GenBank: JX280413) (Tab. 1) and published in Zawierucha et al. (2013). Two additional barcodes had more than 90% query coverage and 100% similarity to our sequence, both from specimens collected in Po-

land (GenBank: JX280414.1 and JX280415.1). Five barcodes have a query coverage of 100% and has between 99–99.99% similarity with the specimen from RRTZ, all from specimens collected in USA (GenBank: KY573404; KY573406; KY573407; KY573410; KY573411).

Taxonomy

Bamazomus Harvey, 1992 (Hubbardiidae)

Bamazomus serendipitus Craig sp. n. (Figs 1-9, Tabs 1-3) (urn:lsid:zoobank.org:act:4E0BE9DA-E77A-4FAE-AB43-35E852230D46)

Material examined listed in Tab. 2.

Etymology

The specific epithet is a Latinisation of the English word 'serendipitous', the adjective form of the word 'serendipity', and should be treated as a noun. The name, 'serendipitus', refers to the serendipitous circumstances surrounding the discovery of the species, including the inadvertent introduction of the species from its native origin, which is as of yet undetermined, to a tropical hothouse in Denmark.

Diagnosis

The new species is assigned to the genus *Bamazomus*, based on the following characters: (1) mesal spur on pedipalpal

Tab. 2: List of *Bamazomus serendipitus* **sp. n.** material examined in this study. All specimens are from the hothouses of Randers Regnskov Tropical Zoo, DENMARK, 2 m a.s.l., collected by JL and SBBC. The holotype and paratype, and a juvenile specimen are deposited in the NHMD collection, the rest of the specimens are deposited in JL's personal collection.

•	•	•		
Africa Dome (56.4569°N, 1	Coll.#			
1 juvenile	26. Feb. 2022	NHMD-223344		
Holotype ♀, paratype ♂	19. Dec. 2022	NHMD-223368		
2 juveniles	19. Dec. 2022	JL13635		
2 juveniles	28. Dec. 2022	JL13648		
1 juvenile	17. Jan. 2023	JL13667		
19, 4 juveniles	03. Apr. 2023	JL13689		
Asia Dome (56.4566°N, 10.0331°E)				
1 juvenile	19. Dec. 2022	JL13630		
1 ♂	28. Dec. 2022	JL13644		
1 \vec{o} , 1 \vec{v} , 2 juveniles	03. Apr. 2023	JL13690		
South America Dome (56.4570°N, 10.0316°E)				
1 juvenile	28. Dec. 2022	JL13657		

trochanter, (2) presence of an accessory tooth on the movable cheliceral finger, (3) female genitalia with numerous spermathecal lobes, and (4) male flagellum dorsoventrally flattened.

The female can be distinguished from other *Bamazomus* ssp. by the combination of the shape of the chitinized arch, 5



Fig. 2: *Bamazomus serendipitus* **sp. n.**, female in vivo from a hothouse in Randers Regnskov Tropical Zoo, Demark

pairs of long spermathecal lobes (some lobes might be basally bifurcated), and a long and distally distinctly bifurcated gonopod. The gonopod is very similar to that of *Bamazomus siamensis* (Hansen, 1905) (illustrated in Cokendolpher & Reddell (1986)) which differs by having very short spermathecal lobes. The male *B. serendipitus* **sp. n.** can be distinguished from

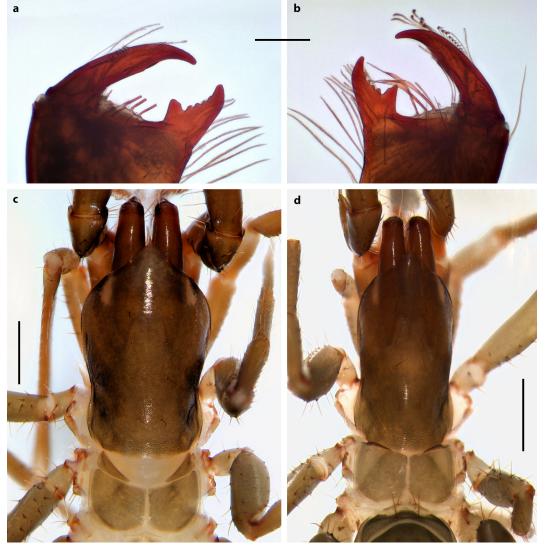


Fig. 3: Bamazomus serendipitus **sp. n. a.** female chelicera in prolateral view; **b.** male chelicera in retrolateral view; **c.** female propeltidium; **d.** male propeltidium. Scale bar a-b = 0.2 mm; c-d = 0.5 mm



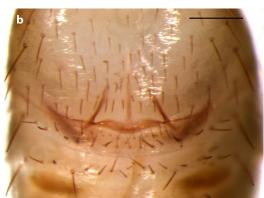


Fig. 4: Bamazomus serendipitus **sp. n.**, genital area in ventral view. **a.** female; **b.** male. Scale bar 0.2 mm

other species of *Bamazomus* by the shape and setal pattern of the flagellum. *Bamazomus siamensis* is very similar but has a longer and more acutely pointed dorsal process on segment XII, and a more elongate flagellum, posteriorly with lateral lobes as long as the central lobe – in *B. serendipitus* **sp. n.** the lateral lobes are shorter and less acute than the central lobe. *Bamazomus pileti* (Brignoli, 1974) (\$\Perp\$ unknown) is also very similar but can be distinguished by the flagellar setational pattern and having a more elongated flagellum.

Description

Female (Holotype: Coll. NHMD-223368)

Colour (live female: Fig. 2). General colour pattern light yellow brown. Chelicerae are reddish brown. Pedipalp dark reddish brown; dorsally on trochanter and dorsoproximal on femur slight bluish grey. Leg I femur dorsally bluish grey and otherwise mostly reddish or lacking pigment; terminal to femur reddish brown. Femur II, and III mostly unpigmented prolaterally, blueish grey-green dorsally and retrolaterally. Leg II and III terminal of femur mostly unpigmented. Leg IV femur bluish grey; terminal to femur mostly yellow brown, similar to posterior tergites; metatarsus and telotarsus reddish to unpigmented. Peltidial plates light yellow brown; propeltidium gradually increasingly reddish anteriorly, probably due to the colour of the pedipalps and chelicerae. Tergites brownish green and yellow brown, the posterior tergites more yellow and the anterior tergites with a more greenish tinge, the colour changing gradually between the posterior and anterior tergites. Flagellum is similar in colour to posterior tergites. Prosoma (Fig. 3c). Propeltidium with 11 setae arranged

Prosoma (Fig. 3c). Propeltidium with 11 setae arranged 2:1:2:2:2:2, the first pair of dorsosubmedian setae longer than the following pairs; the anterior margin of propeltidium produced to a sharp downward point between chelicerae; eyespots present, suboval to half circular. Mesopeltidium is widely separated. Metapeltidium is clearly divided. Anterior sternum subtriangular, longer than wide; anterior margin

straight, anterior corners rounded; posteriorly pointed, reaching slightly posterior to the hind margin of coxa of leg II; with 19 setae, including 2 sternapophysial setae. Posterior sternum elongate triangular, with 7 setae.

Opisthosoma. Tergite I–VIII with a pair of Dm setae each; tergite I with 2 pairs of microsetae anteriorly, positioned diagonally with anterior pair closer together than the posterior pair, and tergite II anteriorly with 3 pairs of microsetae in a column; tergite IV with an additional single seta in the left Dl1 position; tergite V-VII with a pair of Dl1 setae positioned approximately the same distance from Dm setae as the two Dm setae are from each other; tergite VII with an additional single seta lateral to left Dl1; tergite VIII with pairs of Dl1 and Dl2 setae, the Dl1 closer to Dm setae than the two Dm setae are from each other. Tergite IX with pairs of Dl1 and Dl2 setae, and additionally with a pair of setae in between Dl1 and Dl2; the Dl2 setae longer than the other setae. Tergite X with a pair of Dl2 setae. Tergite XI with one pair of setae, placed more median than D12 on tergite X, and therefore assumed positioned as Dl1 setae. Tergite XII with pairs of Dm and Dl2 setae. The chaetotaxy formula of tergite I-XII, is 2+4 (microsetae diagonal):2+6 (microsetae in column):2:3:4:4:5:6:6:2:2:4. Sternite II (Fig. 4a), the genital plate, with the chitinized arch visible through the genital plate without dissection; with many scattered setae of various sizes; with 2 large lateral setae, on level with the posterior branch of the chitinized arch. Sternite III is very slim, with 2 rows of setae; posterolateral with 2 pairs of large setae. Sternite IV-VIII with 2 transversal rows of setae, very irregular on sternite IV, less on sternite V-VII; sternite IV-VII with 2 pairs of large posterolateral setae; sternite VIII with an anterior row of 8 setae and a posterior row consisting of setae pair Vm1, Vm2, Vl1B, Vl1A and Vl2. Sternite IX with setae pairs Vm1, Vm2, Vl1, Vl2; additionally with a pair of small setae between Vm2 and Vl1, the one on the right side placed anterior to the rest of the setae. Sternite X-XI with setae pairs

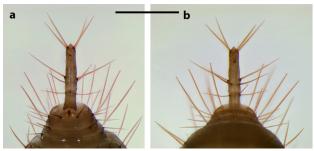




Fig. 5: Bamazomus serendipitus sp. n. a-b. female flagellum. a. dorsal view; b. ventral view; c. male pedipalp in retrolateral view

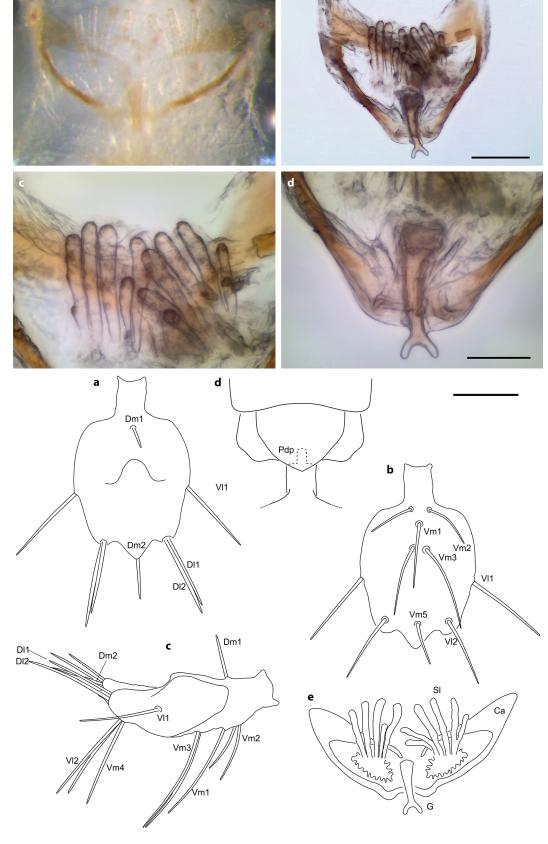


Fig. 6: Bamazomus serendipitus sp. n., female spermathecal lobes, chitinized arch and gonopod. a. shown in its natural shape before removal from cuticle; b. shown in a slightly distorted state caused by slide preparation; c. spermathecal lobes; appearing closer to each other than they are in their natural position due to slight distortion; d. gonopod. Scale bar upper images 0.1 mm, lower images 0.05 mm

Fig. 7: Line drawings of Bamazomus serendipitus sp. n. a-c. male flagellum. a. dorsal view; b. ventral view; c. Lateral view; d. posterodorsal process (Pdp) on segment XII; e. female, chitinized arch (Ca) with spermathecal lobes (SI) and gonopod (G). Scale bar a-d 0.2 mm, e 0.1 mm

Vm1, Vm2, Vl1, and Vl2; setae Vm1, Vm2 and Vl1 all distally bifurcated; Vl2 setae smaller than the other setae. Sternite XII with setae pairs Vm2, Vl1B, Vl1A, and Vl2, and a pair of thin hyaline setae between pairs Vm2 and Vl1B; setae Vm2, and Vl1B apically bifurcated. The most lateral dorsal, Dl2,

and ventral setae, V12, on the opisthosomal segment XII are positioned very closely adjacent to each other. Sternite V–VII each with 2 apodemes, which are chitinized and distinctly darker than surrounding sternite, and more than 2 times wider than long.



Fig. 8: Bamazomus serendipitus **sp. n.**, male in vivo from a hothouse in Randers Regnskov Tropical Zoo, Demark

Female flagellum with 3 flagellomeres, i.e. 2 annuli, flagellomere I longer than flagellomere II, and the terminal flagellomere about 4.8 times as long as flagellomere II (measured dorsally) (Fig. 5a-b).

Female genitalia (Figs 4a, 6, 7e). Spermatheca with 5 pairs of long spermathecal lobes, which are anteriorly directed; the lateral lobe on one side is basally bifurcated in the holotype; the single lobe can vary in length and in the holotype one of the median pairs of lobes are shorter than the rest; the lobes have external pores. The chitinized arch is hastate shaped sensu Monjaraz-Ruedas et al. (2019); the posterior branch is broadly U-like and the branches slim until they reach the internal angle; the anterior arch forms two large subtriangular plates, with the lateral tips reaching distinctly anterior to the internal angle, and is anteromedially divided, with the median tips turned posteriorly, creating a resemblance to a deep V-like anteromedian notch; the lateral tips well projected and sharp; the internal angle rounded. The gonopod is long and distinctly bifurcated distally.

Pedipalps. Trochanter strongly produced distally to a blunt tip, i.e. with an apical process; ventral margin with stout setae; mesal spur situated subdistally, on length with the ventral most part of the trochanter-femur joint; trochanter mesally with 4 setae in a diagonal row, the most distal seta positioned on the distal side of the mesal spur, and a 5th mesal seta is situated adjacent to the trochanter-femur joint. Femur dorsally with strong setae, and dorsoanterior with some weaker setae, otherwise with setae Fmv1, Fmv2, Fmv3, Fmv4, Fev1, Fev2, Fe1, Fe5, and Fed3 present; Fmv1, Fmv2, and Fmv3 situated closely adjacent to each other. Patella with 3 Pe setae, with

some smaller setae more lateral to these; Pm with 3 setae; with Pme1 and Pmm3. Tibia with 5 setae in Ter; 2 setae in the Tm group, one small and one large; Tmr with 5 setae and Tir with 5 setae; Tir reaches further anterior and posterior to Tmr. Pm, Tmr, and Tir with setae that are white and plumose the terminal half. Tarsus with 2 spurs ventrodistally.

Chelicera (Fig. 3a). Fixed finger with 2 large teeth, distally and proximally, and 4 smaller median teeth in between, the proximal large tooth with a small and very blunt lateral tooth on the distal side. The movable finger is rounded on the tip and distally curved; with a very blunt and broad median accessory tooth, with the tip proximally continuing almost straight into the ventral margin of the movable finger, about 1/3 of the movable finger's length from the tip, adjacent to the middle of serrula; serrula with 19 hyaline teeth; with a round distal guard tooth; lamella present, approximately half the length of the serrula, immediately distal to the accessory tooth. Setae group G1 with 3 spatulate setae, with the terminal 1/3 pedunculate, with short pilosity, and the proximal 1/3 stout. G2 with 5 setae. G3 with 5 setae. G4 with 4 setae. G5A with 11 setae, with short pilosity apically. G5B with 10 setae, becoming gradually shorter apically, apart from 2 proximal setae, which are much shorter; setae with short pilosity apically for most of their length. G6 with 1 smooth seta; the seta is about 0.6 times the length of the movable finger. G7 with 4 setae. Setal group formula: 3:5:5:4:11:10:1:4.

Legs. Telotarsus I with 6 segments; femur IV 2.96 times as long as wide.

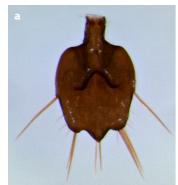
Measurements of dimensions listed in Tab. 3.

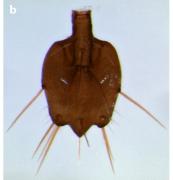
Male (Paratype: Coll. NHMD-223368)

Colour (live male: Fig. 8). Generally lighter than the female. Leg IV patella and tibia bluish grey, metatarsus and telotarsus mostly unpigmented. Flagellum reddish brown.

Prosoma. Propeltidium with 11–13 setae (n = 3; Paratype with 13 setae) arranged 2:1:2:2:2:2(:2), the first pair of dorsosubmedian setae longer than the following pairs. Anterior sternum with 17 setae, including 2 sternapophysial setae.

Opisthosoma (Fig. 7d). Tergite I–VIII with a pair of Dm setae each; tergite I with 2 pairs of microsetae anteriorly, positioned diagonally with anterior pair closer together than the posterior pair, and tergite II anteriorly with 3 pairs of microsetae in a column, with the middle pair more widely separated than anterior and posterior; tergite VII-VIII each sometimes with an additional single setae (left Dl1 present on tergite VIII on the paratype); tergite VIII with a pair of Dl2 setae. Tergite IX same as female, though sometimes an additional





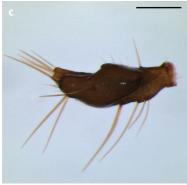


Fig. 9: Bamazomus serendipitus sp. n., male flagellum. a. dorsal view; b. ventral view; c. lateral view. Scale bar 0.2 mm

Tab. 3: Measurements of body length and various body parts of holotype and paratype. The body length is measured from the tip of the propeltidial apophysis to the posterior margin of the last opisthosomal segment (excl. flagellum)

Dimensions (mm)	holotype ♀	paratype ♂
Body length	5.60	4.29
Propeltidial length/width	1.78/1.05	1.37/0.79
Chelicera	1.15	0.89
Flagellum length (\mathfrak{P}) and length/width (\mathfrak{F})	0.45	0.58/0.36
Pedipalp: trochanter	0.82	0.67
Pedipalp: femur	0.81	0.63
Pedipalp: patella	0.84	0.61
Pedipalp: tibia	0.76	0.61
Pedipalp: tarsus	0.37	0.30
Pedipalp: claw	0.17	0.14
Pedipalp total length (excl. claw)	3.60	2.82
Leg I: coxa	0.88	0.80
Leg I: trochanter	0.46	0.53
Leg I: femur	1.94	1.73
Leg I: patella	2.52	2.23
Leg I: tibia	1.90	1.74
Leg I: basitarsus	0.48	0.50
Leg I: telotarsus	0.69	0.75
Leg I: total length	8.00	7.49
Leg IV: trochanter	0.38	0.44
Leg IV: femur	1.83	1.49
Leg IV: patella	0.86	0.70
Leg IV: tibia	1.32	1.04
Leg IV: basitarsus	1.17	0.93
Leg IV: telotarsus	0.67	0.64
Leg IV: total length (excl. claws)	6.23	5.24

single seta is present. Tergite X and XI with pairs of Dl1 and Dl2 setae; tergite XI with an additional single submedian seta on the left or right side (present on the right side on the paratype). Tergite XII with pairs of Dm and Dl2 setae, the Dm setae are stout and bent. The chaetotaxy formula of tergite I-XII is 2+4 (microsetae diagonal):2+6 (microsetae in column):2:2:2:2:2-3:4-5:6-7:4:5:4. Tergite XII with a curvilinear triangular posterodorsal process. Sternite IX with setae Vm1, Vm2, Vl1, and Vl2; setae Vm1, Vm2, and Vl1 with bifurcated setae.

Male flagellum (Figs 7a-d, 9) is dorsoventrally flattened; the general shape is subrectangular; trilobed, with the median lobe triangular in shape and longer than the lateral lobes which are more rounded; in the centre, with a semi-circular ridge rounding anteriorly when viewed dorsally, approximately mirroring the shape of the median lobe; with a longitudinal lanceolate structure between the semi-circular ridge anteriorly and the median lobe posteriorly, laterally framed by convex longitudinal furrows. Setae pairs D12 and D13 positioned dorsoposteriorly on the lateral lobes, so closely adjacent that their bases are touching each other; Dm4 placed on the tip of the median triangular lobe; 7 smaller setae positioned posteroventrolaterally, and 3 small setae situated laterally on the plateau and slope to the lower posterior half of flagellum. Seta Vm1 is positioned immediately posterior to



Fig. 10: Habitat of *Bamazomus serendipitus* **sp. n.** Specimens were found in leaf litter and under stones and pieces of wood on the forest floor of a tropical hothouse in Randers Regnskov Tropical Zoo, Denmark

Vm2; setae Vm2 are situated approximately in line with the anterior margin of the flagellum, where it is sharply constricted to the stalk; Seta Vm1 is positioned immediately posterior to Vm2; setae Vm2 are situated approximately in line with the anterior margin of the flagellum, where it is sharply constricted to the stalk; Vm3 are situated in line with the posterior margin of the anteroventral depressions; Vm5 is situated between, or even slightly anterior to, Vl2; setae Vl1 is situated on the lateral edge of flagellum, between Vm3 and Vm5; Dm1 is positioned at level of the sharp constriction of flagellum to stalk. The flagellum (stalk included) is 1.59 times longer than wide.

Pedipalp (Fig. 5c). No obvious sexual dimorphism present; setation similar to female, apart from Pe seemingly with 2 setae and Tir with 6 setae.

Chelicera (Fig. 3b). G2 with 6 setae. The serrula on the movable finger with 21 hyaline teeth.

Legs. Femur IV 2.83 times as long as wide.

Description otherwise similar to the female.

Measurements of dimensions listed in Tab. 3.

Variation

Body length of female (4,98-5.60, n=3) and male (4.29-5.09, n=4). Number of propeltidial setae was found to vary between 11–13 in the male. The number of setae on both tergites and sternites was found to vary due to a presence of single and pairs of supernumerary setae.

Remarks

Newly moulted specimens appear very green, as was one

Tab. 4: List of *Stenochrus portoricensis* Chamberlin, 1922 material examined in this study. Specimens are from the hothouses of Randers Regnskov Tropical Zoo, DENMARK, 2 m a.s.l., and the hothouse Oceanium at Odense Zoo, DENMARK, 9 m a.s.l., and collected by JL and SBBC. All specimens are deposited in JL's personal collection

Asia Dome (56.4566°N, 10.0331°E) Coll. #				
1 9	08. Feb. 2023	JL13895		
1♀	03. Apr. 2023	JL13704		
South America Dome (56.4570°N, 10.0316°E)				
2 99	28. Dec. 2022	JL13654		
6 ♀♀, 2 juveniles	08. Feb. 2023	JL13669		
3 ♀♀	03. Apr. 2023	JL13693		
Oceanium OZ (55.3773°N, 10.3719°E)				
1 ♂, 3 ♀	07. Dec. 2023	JL13911		
3 99	20. Dec. 2023	JL13947		

presumably newly moulted juvenile specimen (JL13667). Juvenile *B. serendipitus* **sp. n.** specimens were separated from juveniles of *S. portoricensis*, the only sympatric short-tailed whipscorpion in RRTZ, by the divided metapeltidium, and propeltidium with 3 apical setae and more than 2 pairs of dorsosubmedian setae. The posterior branch of the chitinized arch was more widely opened and U-shaped before dissection (Fig. 7a), suggesting that the chitinized arch has been distorted during slide preparation. In some females tergite X and XI is only pigmented medially, and tergite XII and flagellum are mostly unpigmented. The barcodes of the female and male (JL13690) were identical, confirming their conspecificity.

Distribution

Only known distribution is the hothouses of RRTZ in Randers, Denmark. The native distribution is yet unknown. The geographic origin of the species is likely Southeast Asia, and possibly Thailand (see Discussion below).

Natural history

The specimens were found under stones and pieces of wood, in leaf litter, and on the soil, when removing leaf litter (Habitat: Fig. 10). They were mostly found on and in relatively dry soil and leaf litter in the Africa-dome and semi wet soil and leaf litter in the Asia-dome. Specimens were found in all



Fig. 11: Stenochrus portoricensis Chamberlin, 1922, female in vivo from a hothouse in Randers Regnskov Tropical Zoo, Demark

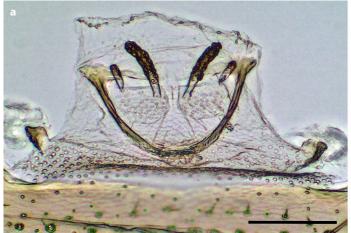
three hothouse domes of RRTZ, in two of which it was found to be sympatric with *Stenochrus portoricensis*. When disturbed, one juvenile suddenly exhibited an odour resembling vinegar, which likely resulted from excreting acetic acid (Villarreal & García 2012).

Stenochrus portoricensis Chamberlin, 1922

(Figs 11, 12, Tab. 4)

Material examined listed in Tab. 4.

We report here the first records of *Stenochrus portoricensis* Chamberlin, 1922 from Denmark. The species identity was confirmed both morphologically, incl. the shape of the female genitalia (Fig. 12) and male flagellum, and molecularly, by comparing a COI-barcode with sequences on GenBank. Specimens belonging to this species were found in both RRTZ and OZ. In RRTZ the species was found in two of three domes, the South America dome and the Asia dome. No specimens were found in the Africa dome, despite it be-



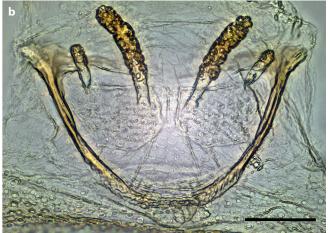


Fig. 12: Stenochrus portoricensis Chamberlin, 1922, female spermatheca. a. 100x; b. 400x. Scale bar a. 0.1 mm; b. 0.05 mm

ing closely connected to the Asia dome, in which *S. portoricensis* lives in sympatry with *Bamazomus serendipitus* **sp. n.** In OZ specimens of *S. portoricensis* were found in multiple areas within the hothouse Oceanium, one of which was a rare male (see Discussion). Specimens were found under leaf litter, stones, and pieces of wood, on semi wet soil.

Discussion

This study reports the first records of short-tailed whipscorpions (Schizomida) from hothouses in Denmark. During faunistic investigations in RRTZ and OZ, two species of short-tailed whipscorpions were discovered. Adults and juveniles of both species were found in multiple hothouse domes in RRTZ during multiple visits, indicating that both species have reproducing populations in the hothouses. The two species were found in sympatry in RRTZ in two out of three domes (South American and Asian) and in the third (African) dome, only B. serendipitus sp. n. was observed. However, in the domes where S. portoricensis was found, this species was seemingly more abundant. This could reflect a higher abundance of this species, as seen compared to other species (Teruel 2017), which could be a result of the facultative parthenogenetic reproduction of S. portoricensis (Rowland & Reddell 1977). However, it is also possible that *B. serendipitus* **sp. n.** is more difficult to find, due to undetermined behavioural circumstances, despite S. portoricensis being a markedly smaller species. In OZ only S. portoricensis was found.

Origin of the Danish S. portoricensis

No males of *S. portoricensis* were found in RRTZ, which is congruent with other studies finding populations of this species to likely consist of parthenogenetic females (Monjaraz-Ruedas et al. 2022, Rowland & Reddell 1977). However, we did find a single male specimen in OZ, which is atypical for populations outside nuclear Central America (Rowland & Reddell 1977).

Stenochrus portoricensis is widely distributed in Central America and the Caribbean, and has populations in South America. Most of the populations likely stem from human introductions (Monjaraz-Ruedas et al. 2022). It is therefore not easy to pinpoint where an introduction of the species to Europe might have originated. We have however attempted to pinpoint a possible origin of introduction of the Danish populations of *S. portoricensis* based on the history of plant introductions to the hothouses in RRTZ and OZ, and a phylogenetic comparison. The first indications of an origin of *S. portoricensis* in Europe is provided by the phylogenetic analyses by Monjaraz-Ruedas et al. (2022), which showed that Polish specimens of *S. portoricensis* published by Zawierucha et al. (2013) were closely related to specimens from Yucatán, Mexico, and Jamaica.

According to Sergio Pacinotti, plant curator at RRTZ, the plants in the exhibits of RRTZ have various origins, from private donations to larger importations from e.g. Costa Rica (pers. comm.). The history of plant introductions to RRTZ is outlined in detail in Lissner & Craig (2023), with a focus on plant introductions from Central America. Lissner & Craig (2023) suggest that Aguas Zarcas, Costa Rica is the most likely origin of the population of *Masteria boggildi* which has been introduced to RRTZ. It is plausible that *S. portoricensis* in RRTZ have been transported alongside *M. boggildi*. This is

further supported by the presence of *S. portoricensis* in Oceanium, since Oceanium has been supplied with plants from the same horticulture (Tropical Zoo Plants) in Costa Rica as RRTZ (Jesper Pedersen, Gardener at Odense Zoo, pers. comm.).

RRTZ also received a large donation of plants from Aarhus Botanical Gardens hothouse in 2014, when they renovated their Palm House (Sergio Pacinotti, pers. comm.) and the RRTZ population of *S. portoricensis* could therefore have originated in Aarhus Botanical Gardens. We did, however, survey the hothouses of Aarhus Botanical Garden for short-tailed whipscorpions, but found neither optimal habitat nor any specimens. We have investigated various hothouses in Denmark for short-tailed whipscorpions, and only found short-tailed whipscorpions in RRTZ and OZ, suggesting that there is only a limited introduction of short-tailed whipscorpions in Denmark.

We additionally investigated the possible origin of the RRTZ population of S. portoricensis phylogenetically. Since the specimen from RRTZ were identical to both specimens from Poland and the USA it is not possible based on the COI-barcodes to ascertain whether the population of S. portoricensis in RRTZ and the population in Poland reported in Zawierucha et al. (2013) are the result of a single or two separate transatlantic introductions. It does, however, show that the RRTZ population, like the Polish population, is nested in the Subclade 1 found by Monjaraz-Ruedas et al. (2022). Subclade 1 was proposed by Monjaraz-Ruedas et al. (2022) to be the subclade that has most often been anthropogenically dispersed. Because the population in RRTZ is part of Subclade 1, it could have been derived from any population of Subclade 1. Most introduced populations both in Europe, Central- and South America have not been sequenced and could potentially stem from Subclade 2, however, because Subclade 1 has been shown to be most often dispersed by human activities, it suggests that it is at least likely that many introduced populations of S. portoricensis would be derived from this subclade. Even though this does not serve particularly well to elucidate the origin of the introduction of the RRTZ population, it does not disagree with the possibility of the Danish populations of S. portoricensis having been introduced alongside M. boggildi which has likely been introduced from Aguas Zarcas, Costa Rica (Lissner & Craig 2023). This is plausible because S. portoricensis is also known from Costa Rica (Villarreal et al. 2023) and this population is not unlikely to belong to Subclade 1.

Origin of B. serendipitus sp. n.

Some tropical species that have been described from specimens found in European hothouses, such as *Zomus bagnallii*, have been found in the wild since the initial description of the species, indicating Southeast Asia, Cook Islands, Fiji, Mauritius (Rodriguez), or the Seychelles as its native origin (Reddell & Cokendolpher 1995, Harvey 2003). However, the native origin of other species remains elusive, such as the case of *Euborellia arcanum* (Matzke & Kocarek 2015). This is also the case of *Bamazomus serendipitus* **sp. n.**, which is as of yet only known from its type locality in hothouses of RRTZ in Randers, Denmark. The genus *Bamazomus* is an Old World genus, so it is unlikely that *B. serendipitus* **sp. n.** has been introduced alongside the sympatric *S. portoricensis*.

The genus *Bamazomus* is very widespread, and species assigned to the genus occur in Madagascar and the Seychelles, Southeast Asia, and Oceania (World Schizomida Catalog 2022). Including Australian specimens of *Bamazomus*, Abrams et al. (2019) did however find the genus paraphyletic and suggested that various species have possibly been misplaced in the genus. The morphologically most similar species to *Bamazomus serendipitus* **sp. n.** are *B. siamensis*, e.g. in the shape of the male flagellum and female gonopod, which has been found in Thailand, China (Hong Kong), Japan and U.S.A. (Hawaii), and *B. pileti*, e.g. in the shape of the male flagellum, which is known from Malaysia (World Schizomida Catalog 2022). Based on this, it is plausible that *B. serendipitus* **sp. n.** originates somewhere in Southeast Asia.

The clade with the shortest genetic distance to *B. serendip*itus sp. n. was the Vanuatu group, which suggests that B. serendipitus sp. n. is only remotely related to the included Australian species and amongst the sequences available on GenBank is closest to the Vanuatu group (Tab. S1). The genetic distance between B. serendipitus sp. n. and the Vanuatu group is, however, relatively large and suggest that even though it could possibly be found congeneric in future taxonomic revisions of the Bamazomus genus it does not represent a species closely related to *B. serendipitus* **sp. n.** There was no bootstrap support for resolving higher phylogenetic relations of the sequences included in the phylogenetic analysis in this study, apart from separating the clade of B. subsolanus and B. vespertinus from the clade including all other species included in the analysis, excluding the outgroup, Baalrog magico. Therefore, future analyses, including more genetic markers and genetic data on supposed closely related Southeast Asian species such as B. siamensis and B. pileti, are needed to properly understand the evolutionary origin and relationships of B. serendipitus sp. n., which could also help resolve the paraphyletic genus Bamazomus. Despite not resolving the relationship of B. serendipitus sp. n. to other species and genera, the results are plausibly congruent with the morphological similarity of B. serendipitus sp. n. with B. pileti and B. siamensis, suggesting a Southeast Asian origin.

In RRTZ B. serendipitus sp. n. is most prevalent in the African and Asian domes, which opened in 1996 and were supplied with plants through NordFyns Gartneri, and horticultures in Belgium (which is now closed) and the Netherlands (Fachjan and Nieuwkoop) which have imported many plants from Asia (Lars Bo Kjeldstrøm, owner of Tropical Zoo Plants, pers. comm.). The company Fachjan did not start importing plants from Asia before around 2002, according to Fred Janssen, Director of Fachjan (pers. comm.), and therefore this company should be ruled out as the path of introduction of B. serendipitus sp. n. The company Nieuwkoop did import plants from Asia prior to 1996, specifically from Thailand (Jan Breedijk, Key account manager at Nieuwkoop Europe B.V., pers. comm.). It is therefore likely that the origin of B. serendipitus sp. n. is Thailand, if the species has been introduced along plants supplied by Nieuwkoop. However, if this is not the case, then according to Lars Bo Kjeldstrøm, Thailand is one of the major exporters of Asian trees and other plants to European horticultures, and therefore still a plausible origin of B. serendipitus sp. n., but he also mentions China, Indonesia, and Malaysia as likely candidates.

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