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Evolution and phylogeny of the family Issidae (Hemiptera: Auchenorrhyncha): African and American branches

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RESEARCH ARTICLE

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ABSTRACT

Chimetopon camerunensis Schmidt, 1910 from Equatorial Africa along with *Oronoqua orellana* Gnezdilov et Bartlett, 2020 and *Sarnus rhomboidalis* Fennah, 1965 from South America are included in the molecular analysis of the family Issidae for the first time. DNA of *Ch. camerunensis* was extracted from an old dry specimen collected more than 50 years ago. Based on our analysis, the tribe Chimetopini Gnezdilov, 2017 is nested within the subfamily Hysteropterinae, showing close relationships to North African and southern European genera *Falcidius* Stål, 1866 and *Numidius* Gnezdilov, Guglielmino et D'Urso, 2003. Additionally, we confirm the monophyly of the tribe Thioniini Melichar, 1906 and its position as a sister group to the tribe Issini Spinola, 1839 within the subfamily Issinae Spinola, 1839.

KEYWORDS

Chimetopini, multilocus phylogeny, evolutionary scenario, Thioniini, wing morphology

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INTRODUCTION

The family Issidae or issid planthoppers, comprises over 1000 species and almost 220 genera worldwide, with the Mediterranean and Oriental regions showing particularly rich documented faunas (Gnezdilov 2013a, 2016a, Gnezdilov et al. 2014, Bourgoin 2023). The taxonomy of Issidae was predominantly shaped in the 20th century by the contributions of Melichar (1906) and Fennah (1954) since Spinola's establishment of the family in the early 19th century (Spinola 1839). Recently, a comprehensive effort has been undertaken to revise the phylogeny of the Issidae, leading to the erection of new tribes and the establishment of a phylogenetic framework (Gnezdilov 2003, 2013a, 2016a, 2017a, 2018a, 2019, Gnezdilov et al. 2020, 2022, Wang et al. 2016).

The evolutionary history of Issidae has been a subject of debate, leading to the proposal of two distinct scenarios. Gnezdilov (2016a, 2016b) and Gnezdilov et al. (2020, 2022) hypothesized an Eocene origin in southeastern Asia, with subsequent dispersal to the New World, Western Palaearctic, tropical Africa, and Australia, supporting the division of the family into two subfamilies Issinae and Hysteropterinae. In contrast, Wang et al. (2016) and Bourgoin et al. (2018) suggested a New World origin in the early Cretaceous, leading to potential Gondwanan vicariance and resulting in the subdivision of Issidae into three subfamilies Thioniinae, Issinae, and Hemisphaeriinae.

Our study focuses on two primary objectives. First, we explore the taxonomic position of the tribe Chimetopini Gnezdilov, 2017, consisting of several issid genera found in tropical Africa, which have not been previously included in molecular analyses due to the lack of freshly collected specimens. Second, we investigate the composition of the tribe Thioniini Melichar, 1906, by analyzing two additional genera and species from the Neotropics. Specifically, we examine *Oronoqua orellana* Gnezdilov et Bartlett, 2020, a canopy-dwelling taxon with well-developed wings, and *Sarnus rhomboidalis* Fennah, 1965, a taxon with coleopterous (shortened) forewings and rudimentary hind wings, commonly found in semiarid open communities (Gnezdilov 2017b). According to Elgueta and Campodónico (2018), *S. rhomboidalis* Fennah, 1965 is a junior synonym of *S. decipiens* (Spinola, 1852), however, we leave this nomenclatorial question open.

As a result of our study, we shed light on the relationships of the genus *Chimetopon* Schmidt, 1910 (type genus of the tribe Chimetopini) within the family Issidae. Additionally, we confirm the monophyly of the tribe Thioniini, considered recently by Bucher et al. (2023), and confirm its taxonomic position within the subfamily Issinae, as previously suggested by Gnezdilov et al. (2020, 2022, 2023).

MATERIALS AND METHODS

Taxon sampling

Our taxon sampling combines newly generated data *for Chimetopon camerunensis*, *Oronoqua orellana*, and *Sarnus rhomboidalis* (labels listed below) with all issid and 14 outgroup taxa available from a previous analysis (Gnezdilov et al. 2022). A total of 99 taxa representing most issid tribes and subtribes were included in the dataset (Suppl. Table 1).

Chimetopon camerunensis Schmidt, 1910
Material studied – 1 ♀, Cameroon, Metoui, 5.XI.1970, "Test Cacao" (Muséum nationale d'Histoire naturelle, Paris, France).

Oronoqua orellana Gnezdilov et Bartlett, 2020
Material studied – 1♀, paratype, Ecuador: "1023 Ecuador Orellana/Erwin Transect/Onkone Gare Camp/Reserva Etnica Waorani"//"00399 25.70S 076 279 10.80W/10.X.94 T.L. Erwin et al./Fogging terre firme forest" (Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia).

Sarnus rhomboidalis Fennah, 1965
Material studied – 1♂, 1♀, Chile, Parque National La Campana, 60 km NW Santiago, W71°08′ S32°59′, 17.XII.2013, A.F. Emeljanov leg. (Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia).

DNA extraction, amplification, and sequencing

Total genomic DNA was isolated from the thoracic musculature of the specimens. Homogenization was performed using the mill Tissue Lyser LT (Qiagen, Hilden, Germany) according to the original protocol for animal and human tissues. Genomic DNA was extracted using the phenol-chloroform method. Stock solutions were prepared in line with the protocol suggested by Green and Sambrook (2017). The initial stage was incubation in the lysis buffer (500 uL) with proteinase K (5 uL of a 100 μg mL^{-1} stock) at 37 °C overnight. In the second stage, we added an equal volume of tris-saturated phenol (pH 8.0) and selected the upper phase; this procedure was repeated twice. Then we added an equal volume of chloroform and transferred the upper phase into a sterile tube. Ethanol precipitation was performed first using isopropanol with supersaturated ammonium acetate solution. We added 70% ethanol twice at the final stage. DNA was dissolved in 40 uL TE-buffer and stored at −20 °C.

NGS libraries were prepared using the NEBNext Ultra II DNA Library Prep Kit for Illumina (New England Biolabs, Beijing, China). The resulting PCR products were purified and concentrated using AMPure XP beads (Beckman Coulter, Beverly, MA, USA). The concentration of samples was measured using a Qubit 4 fluorometer (Thermo Fisher Scientific, Waltham, MA, USA), while the final quality control of the libraries was implemented using the Bioanalyzer 2100 instrument and the DNA High Sensitivity Kit (Agilent, Boulder, CO, USA).

Sequencing was performed on an Illumina HiSeq 4000 system, resulting in raw pair-end reads of 75 bp. DNA quality was checked with a Qubit 4 fluorometer, and the final distribution of lengths of the libraries' adapter content checking was conducted using Bioanalyzer 2100 (Agilent, Boulder, CO, USA). DNA extraction, library preparation, and sequencing were performed in the Core Sequencing Centre of Kurchatov Centre for Genome Research, Russia.

Mitochonfrial genome assembly, annotation

The quality of raw reads was evaluated using FastQC ver. 0.11.9 (Andrews 2010). Reads were cleaned from Illumina adapters, and overrepresented sequences and low-quality reads (<Q20) were cleaned using the Trimmomatic v0.39 (Bolger et al. 2014). De novo assemblies were conducted with Spades 3.14.1 (Prjibelski et al. 2020) using default settings and IDBA_UD

(Peng et al. 2012) using an initial k-mer size of 21, an iteration size of 10 and a maximum k-mer size of 91. Received contigs were identified using BLAST search implemented in the Geneious Prime 2019.2.1 (Biomatters Ltd., Auckland, New Zealand, https://www.geneious.com, accessed on 26 November 2021). Contigs were annotated using the MITOS web server (Bernt et al. 2013) with the default settings. Annotated contigs were manually combined to build longer sequences. Available data on five fragments, COI-5' (681 bp), COI-3' (572 bp), CytB (603 bp), 12S rRNA (354 bp), 16S rRNA (509 bp) (Suppl. Table 1), were added to the dataset of Gnezdilov et al. (2022).

Alignment and phylogenetic analysis

Gene fragments were aligned using MAFFT v. 7.450 (Katoh & Standley 2013) under G-INS-i algorithm and were concatenated using Sequence Matrix 1.7.8 (Vaidya et al. 2011). The resulting matrix of nine gene fragments and 6062 aligned sites was analyzed in RAxML-NG 1.2.0 (Kozlov et al. 2019), IQ-Tree 2.2.2.6 (Minh et al. 2020), and MrBayes 3.2.7 (Ronquist et al. 2012). The dataset was partitioned by gene fragments and by codon position in the case of protein coding genes with GTR+G+I model applied for each partition.

The Bayesian and RAxML analyses were performed on the CIPRES Science Gateway V. 3.3 (Miller et al. 2010). MrBayes was set to two independent runs with 12 chains each, 0.1 temperature setting, 50 million generations, sampling every 1000 generations and burn-in at 25%. The RAxML-NG and IQ-Tree searches were performed with 10000 Felsenstein and ultrafast bootstrap iterations, respectively. The resulting topologies were visualized using FigTree 1.4.4 (Rambaut 2008). Nodes that exhibited IQ-Tree ultrafast bootstrap values (UFB) greater than 0.95, Bayesian posterior probability (PP) higher than 0.90, and RAxML bootstrap (BS) values exceeding 80 were considered strongly supported. Nodes with UFB values between 0.95 and 0.85, PP values ranging from 0.80 to 0.90, or BS values between 70 and 80 were considered moderately supported.

RESULTS AND DISCUSSION

We performed Bayesian, IQ-Tree, and RAxML analyses on our dataset, yielding nearly identical topologies. For further discussion, we selected the Bayesian tree (Fig. 1), which includes support values obtained from IQ-Tree and RAxML indicated above each branch.

Our data support the monophyly of the family Issidae Spinola, 1839 and its basal split into two clades corresponding to the subfamilies Issinae Spinola, 1839 and Hysteropterinae Melichar, 1906 sensu Gnezdilov et al. (2020, 2022). Within the subfamily Issinae, the tribes Issini Spinola, 1839, Thioniini Melichar, 1906, Sarimini Wang, Zhang et Bourgoin, 2016, Hemisphaeriini Melichar, 1906, Parahiraciini Cheng et Yang, 1991, and Kodaianellini Wang, Zhang et Bourgoin, 2016 are recovered as monophyletic units with high support, confirming our previous results (Fig. 1).

Our study supports the result that the tribe Thioniini, which includes species of 12 genera from North, Central, and South America, is not sister to the remaining issids as suggested by Wang et al. (2016). Instead, it is sister to Issini+ Kodaianellini within the subfamily Issinae. Our study also reveals a clear geographic pattern among the main issid clades. Specifically, the tribe Thioniini is exclusively New World taxon closely related to the Palaearctic tribe Issini.

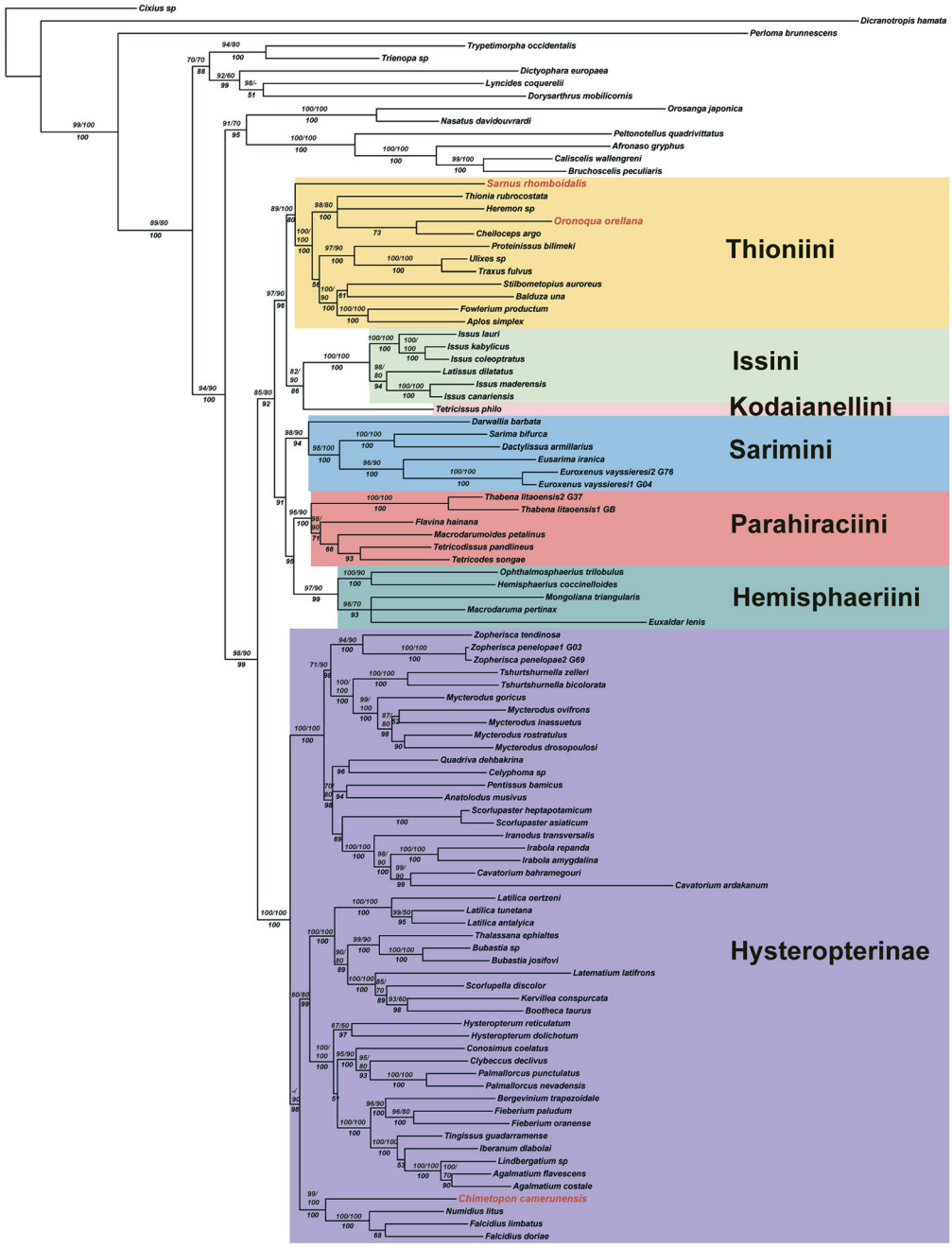

Fig. 1. The 50% majority-rule consensus tree obtained from the Bayesian analysis. Posterior probabilities are shown below each clade. Supporting values from the IQ-Tree and RAxML analyses are indicated above each branch, before and after the slash, respectively.

The tribe Thioniini includes taxa with well-developed fore and hind wings e.g., the genera *Thionia* Stål, 1859, *Oronoqua* Fennah, 1947, and *Dracela* Signoret, 1861 as well as taxa, with coleopterous (shortened) forewings and reduced hind wings, including *Traxus* Metcalf, 1923, *Ulixes* Stål, 1861, *Stilbometopius* Gnezdilov et O'Brien, 2006, and *Sarnus* Stål, 1866. In this study, we added two Neotropical representatives, *Sarnus rhomboidalis* Fennah, 1965 and *Oronoqua orellana* Gnezdilov et Bartlett, 2020, to test the monophyly of Thioniini. *S. rhomboidalis* has reduced hind wings, externally resembling species from the Mediterranean genus *Hysteropterum* Amyot et Audinet-Serville, 1843 (Fennah 1965, Gnezdilov 2017b), while *O. orellana* belongs to the subtribe Oronoquina Gnezdilov, 2018 (Gnezdilov 2018b, Gnezdilov & Bartlett 2020) and possesses well-developed fore and hind wings. Despite their different morphologies, both taxa nested within Thioniini (Fig. 1).

Oronoqua orellana nested with taxa possessing 3-lobed hind wings known from Central and South America, including *Heremon* sp. and *Cheiloceps argo* (Fennah, 1949). *Sarnus rhomboidalis* is sister to the rest of Thioniini. Other taxa with shortened forewings and more or less reduced (3-lobed or unilobed, with narrow or rudimentary vannus, or undeveloped) hind wings, *Stilbometopius auroreus* (Uhler, 1876), *Balduza una* (Ball, 1910), *Proteinissus bilimeki* Fowler, 1904, *Ulixes* sp., and *Traxus fulvus* Metcalf, 1923, are separated into two distinct clades, even though the first two species are nested together with taxa possessing well-developed 3-lobed hind wings, viz. *Fowlerium productum* (Van Duzee, 1908) and *Aplos simplex* (Germar, 1830). The resulting tree topology indicates an independent reduction of hind wings in different, not closely related genera and species within Thioniini.

Other groups within the Issinae exhibit different hind wing characteristics, with three-, two- or unilobed hind wings. Thus, Oriental-Australian Sarimini retain the ancestral 3-lobed hind wings, with nearly equal lobes, and a simple second anal (A_2) vein, in contrast to the branched A_2 in Thioniini (Gnezdilov 2012, 2016a). The tribe Issini, sister to Thioniini, is characterized by 2-lobed hind wings, with a strongly reduced anal lobe (Gnezdilov 2017a). However, the closely related Oriental tribe Kodaianellini exhibits 3-lobed hind wings despite a narrowed vannus. The sister groups Parahiraciini and Hemisphaeriini have 2-lobed (with a deep cubital cleft) and unilobed hind wings, respectively. This suggests that the ancestral condition of hind wings in Issinae is similar to that of Sarimini and Eupilisini Gnezdilov, 2020 (still not available for the analysis). This ancestral condition appears to have undergone modification in other tribes of the subfamily, likely influenced by brachypterization and possibly a shift in locomotion from flying in the forest canopy to jumping in low vegetation (Gnezdilov 2016a).

The Hysteropterinae are recovered as a monophyletic group with strong support. The Afrotropical tribe Chimetopini originally erected in the subfamily Issinae (Gnezdilov 2017a) is nested within the Hysteropterinae. Specifically, *Chimetopon camerunensis* Schmidt, 1910 is sister to the genera *Falcidius* Stål, 1866 and *Numidius* Gnezdilov, Guglielmino et d'Urso, 2003 (Clade C sensu Gnezdilov et al. 2020, 2022). These data substantiate the hypothesis that tropical African Issidae may be considered as closely related to the ancestral form of Western Palaearctic Issidae (Gnezdilov 2016a, 2016b).

Chimetopon camerunensis, *Cascaruna grumosa* Gnezdilov, 2017, and *Ikonza angolensis* Gnezdilov, 2016 are characterized by well-developed 3-lobed hind wings (Gnezdilov 2016b, 2017a), while *Numidius litus* Gnezdilov, Guglielmino et D'Urso, 2003 has 2-lobed hind wings with a narrow anal lobe and very weak vannal cleft (Gnezdilov 2016a), and *Falcidius* spp. have undeveloped hind wings (Gnezdilov & Wilson 2008). Furthermore, *Chimetopon*, *Ikonza*

Hesse, 1925, and *Numidius* exhibit a three- or multi-branched radius vein of the fore wing. Additionally, *Ch. camerunensis* and *I. angolensis* share strongly curved ventral aedeagal hooks, which are also found in *Falcidius* spp., as well as in the genera *Lethierium* Dlabola, 1980 and *Granum* Gnezdilov, 2003, distributed in northern Africa and the Apennine and Pyrenean Peninsulas, respectively (Gnezdilov 2003, 2022).

The placement of Chimetopini within Hysteropterinae suggests that the ancestral condition for Hysteropterinae is 3-lobed hind wings. Reduction of hind wings and distinct coleopterization of fore wings observed in most taxa of this subfamily may represent an adaptation to the Mediterranean conditions (Gnezdilov 2013b). However, the unfused Pcu and $A_{1.1}$ along with the simple A_2 of hind wings of *Ch. camerunensis* and other Chimetopini suggest a close relationship to the ancestral condition of Issidae, particularly with Oriental taxa. This may provide further evidence supporting the hypothesis of the dispersal of the family Issidae from the Oriental region to the Mediterranean and tropical Africa (Gnezdilov 2016a, Gnezdilov et al. 2022).

Contrary to the proposed basal split of the Issidae between New World (Thioniini) and Old-World taxa suggested by Wang et al. (2016) and Bourgoin et al. (2018), our data favor an Oriental origin of the family, with subsequent dispersal into the Palearctic, tropical Africa, and the New World (Gnezdilov 2016a, 2016b, Gnezdilov et al. 2022). Our findings also highlight distinctive geographic patterns among the tribes and groups of genera, demonstrating the independent reduction of hind wings in Issinae and Hysteropterinae. Further research on Australian taxa is needed to test the hypothesized dispersal of Sarimini from the Oriental region to Australia (Gnezdilov 2013a, 2016a, Gnezdilov & Fletcher 2010).

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SUPPLEMENTARY MATERIAL

Supplementary data to this article can be found online at https://doi.org/10.1556/1777.2024.12966.

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