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First record of *Thraulus* (*Thraulus*) *bellus* Eaton, 1881 outside Europe (Ephemeroptera, Leptophlebiidae, Choroterpinae)

Majida El Alami[1], Laurent Vuataz[2,3], Kaoutar Belahcen[1], Nard Bennas[1], Michel Sartori[2,3]

1 Laboratory of Ecology, Systematics and Conservation of Biodiversity, URL-CNRST N° 18, FS, Abdelmalek Essaadi University, B.P.2121, Tetouan 93002, Morocco
2 State Museum of Natural Sciences (Naturéum), Department of Zoology, Palais de Rumine, Place Riponne 6, CH-1005, Lausanne, Switzerland
3 University of Lausanne (UNIL), Department of Ecology and Evolution, CH-1015 Lausanne, Switzerland

Corresponding author: Michel Sartori (michel.sartori@vd.ch)

Abstract. We present here the first record of *Thraulus* (*Thraulus*) *bellus* Eaton, 1881 outside Europe. Nymphal populations of this species were discovered in a reservoir in the Middle Atlas of Morocco. The genus had previously been reported from this country but without specific identification. Although the mtDNA COI of the Moroccan population presents a divergence of approximately 6% compared to European counterparts, no significant morphological differences were found.

Key words. Morocco, morphology, mtDNA, North Africa

El Alami M, Vuataz L, Belahcen K, Bennas N, Sartori M (2026) First record of *Thraulus* (*Thraulus*) *bellus* Eaton, 1881 outside Europe (Ephemeroptera, Leptophlebiidae, Choroterpinae). Check List 22 (2): 438–447. https://doi.org/10.15560/22.2.438

Introduction

The genus *Thraulus* Eaton, 1881 was established to accommodate *Thraulus bellus* Eaton, 1881 collected near "Cintra", nowadays Sintra, in Portugal. The genus was later reported from all other regions of the world, mainly based on the peculiar gill morphology, with gills II–VII composed of two plates bearing numerous filaments. Subsequent revisions by, for example, Ulmer (1920, 1939), Traver (1960), Peters and Edmunds (1970), Dominguez and Flowers (1989), and Grant and Peters (1993) have considerably narrowed the generic concept of *Thraulus*. According to Grant's (2024) revision of *Thraulus* and additions by Sartori and Salles (2025), the genus is distributed in the Old World, mainly in Palearctic and Oriental realms, with few species in the Afrotropics and Australasia. Sartori and Salles (2025) proposed to split *Thraulus* into two subgenera, *Thraulus* sensu stricto and *Masharikella* Peters, Gilles & Edmunds, 1964. *Masharikella* had been put into strict synonymy with *Thraulus* by Peters and Edmunds (1970) but was reinstalled at a subgeneric rank by Sartori and Salles (2025). Currently, the genus *Thraulus* encompasses 42 species; 27 belong to the subgenus *Thraulus*, 10 to the subgenus *Masharikella*, and five without certain placement in a subgenus. The subgenus *Thraulus* can be found in the Oriental, Australasian (as far as New Guinea), and Palearctic realms, and only two species are known from the Afrotropics, from the islands of Comoros and Madagascar. There are no records of the subgenus from continental Africa. The subgenus *Masharikella* is mentioned from Afrotropical, Oriental and Australasian realms, but is absent from Palearctic.

In the Western Palearctic, only two species are known: *Thraulus thraker* Jacob, 1988 described from some adults caught in Bulgaria (nymphs unknown), and *Thraulus bellus*, described from Portugal and later found in Spain, France, Italy, and Germany (Bauernfeind and Soldán 2012).

The first mention of this genus in Morocco was based on specimens, identified as *Thraulus* sp., collected at two permanent stations in the Zegzel River, one of Morocco's eastern sub-basins (Maamri et al. 2005; El Alami et al. 2022a).

Our aim here is to report the presence of *Thraulus* (*Thraulus*) *bellus* in Morocco. This is the first record of the species outside Europe.

OPEN ACCESS

Academic editor: Srinivasan Pandiarajan
Received: 18 March 2026
Accepted: 12 April 2026
Published: 5 May 2026

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Study Area

Lake Ouiouane is a small semi-artificial lake situated in Khenifra Province, in the central Middle Atlas Mountains of Morocco, approximately 68 km from the city of Khenifra. Covering an area of 13 ha, it is fed by nearby Oum Er Rbia springs and a small tributary, making it a vital water body in the region's karstic landscape (El Orfi 2023). Nestled within Khenifra National Park, the lake is surrounded by dense forests of cedar (*Cedrus atlantica* (Endl.) G.Manetti ex Carrière) and Holm Oak (*Quercus ilex* L.), contributing to its ecological significance as a habitat for local flora and fauna and as a designated Site of Biological and Ecological Interest (SIBE) with a protection priority level 3 (Chilasse and Dakki 2004; CEIBM 2006). The lake's water levels are modulated by the high-altitude and Mediterranean climate, with annual precipitation ranging from 600 to 1,000 mm, concentrated in wet winters and spring snowmelt (Khalil et al. 2004).

Methods

The material used in this study was collected by the Laboratoire Ecologie, Systématique, Conservation de la Biodiversité, University of Tétouan, Morocco (LESCB) team between 2020 and 2022. Nymphs were collected by kick sampling and preserved in 70–96% ethanol for description and DNA extraction. Nymphs were dissected in Cellosolve (2-ethoxyethanol) or in 10% KOH followed by mounting in Euparal liquid, or the dissected parts were mounted directly in Hoyer's fluid (Alba-Tercedor 1988). Photographs of nymphal habitus were taken using a Canon EOS 6D camera and the Visionary Digital Passport imaging system (formerly available and distributed by Dun Inc., Virginia) and processed with Adobe Photoshop Lightroom and Helicon Focus v. 5.3. Microscopic photographs were taken using an Olympus BX51 microscope coupled with an Olympus SC50 camera; images were enhanced with Olympus Stream Basic v. 2.3.2 stacking software and Adobe Photoshop v. 21.2.2. The distribution map was created using SimpleMappr (Shorthouse 2010).

To complement the morphological investigation, we analyzed pairwise genetic distances and inferred gene trees based on a 658-base pair fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene. The *T. bellus* COI dataset comprised three sequences: two newly generated from fresh specimens (one from Morocco and one from France) and one from a historical paratype specimen (NHMUK010356850) collected in 1880 in Sintra, Portugal (BOLD Systems ProcessID BSNHM115-24). We also included three sequences of the so-called *Thraulus grandis* Gose, 1980 (see Grant 2024 for a discussion on the validity of this species), retrieved from GenBank (accessions MZ820933, MZ820934, and KF563057). These were identified as the closest relatives to *T. bellus* in a preliminary COI tree including all *Thraulus* sequences available in public repositories (data not shown). Two sequences from the subfamily Choroterpinae (HQ563209, *Choroterpes picteti* (Eaton, 1871); MZ820954, *Choroterpes altioculus* Kluge, 1984) were used as outgroups. DNA from the new specimens was extracted using the non-destructive method described in Vuataz et al. (2011). PCR amplification, purification, and sequencing followed the protocol of El Alami et al. (2022b). Forward and reverse reads were assembled and edited in CodonCode Aligner v. 12.0.1 (CodonCode Corporation, Dedham, MA, USA). All sequences were aligned using MAFFT (Katoh et al. 2019) through Jalview v. 2.11.5.1 (Waterhouse et al. 2009) with default settings. The number of parsimony-informative sites was calculated in MEGA v. 10.2.4 (Kumar et al. 2018; Stecher et al. 2020).

Pairwise genetic distances among *T. bellus* sequences were calculated in MEGA using the simple *p*-distance model. A maximum-likelihood (ML) COI tree was reconstructed using IQ-TREE 3, combining best-fit model selection with ModelFinder (Kalyaanamoorthy et al. 2017), tree search, and branch support estimation using the SH-like approximate likelihood ratio test (Guindon et al. 2010) and ultrafast bootstrap (Hoang et al. 2018), each with 1,000 replicates. The resulting tree was visualized and edited in iTOL v. 7.2.1 (Letunic and Bork 2024).

Finally, two complementary single-locus species delimitation methods were applied to the COI dataset: the distance-based ASAP (Assemble Species by Automatic Partitioning; Puillandre et al. 2020) and the tree-based mPTP (multi-rate Poisson Tree Processes; Kapli et al. 2017). The ASAP analysis was performed in ASAPy v. 1.0, downloaded from the iTaxoTools platform (Vences et al. 2021). Genetic distances were calculated from the COI alignment using simple *p*-distances, with all other settings left as default. The optimal partition was selected based on the lowest ASAP score. The mPTP analysis was conducted on the webserver https://mptp.h-its.org/#/tree using the previously generated ML tree as input. The outgroups were specified, while all other parameters were kept at their default values.

Figure 1. *Thraulus bellus* from Lake Ouiouane. Habitus of a male nymph in dorsal view. Scale bar: 1 mm.

Voucher specimens are deposited in the collections of the LESCB and those of the Department of Zoology, State Museum of Natural Sciences (Naturéum), Lausanne, Switzerland (MZL; GBIFCH code).

Results

***Thraulus* (*Thraulus*) *bellus* Eaton, 1881**

Figures 1–5

New records. MOROCCO — Khenifra Province • Middle Atlas**,** Lake Ouiouane; 33°07′56.5″N, 005° 20′38.2″W; 1616 m alt.; 09.VI.2021; K. Belahcen leg.; 1 nymph on slide, GBIFCH01551004; 1 nymph in ethanol, GBIFCH10014058 • same locality; 08.VI.2022; K. Belahcen leg.; 1 nymph on slide, GBIFCH 01144264, GenBank accession PZ163804; 2 nymphs in ethanol, GBIFCH10014059; 7 nymphs in ethanol, LESCB21151110 • same locality; 24.XI.2020; K. Belahcen leg.; 2 nymphs in ethanol, GBIFCH10014057; 1 nymph on slide, LESCB21151120; 5 nymphs in ethanol, LESCB21151121.

FRANCE — Var Department • St Raphaël, Le Grenouillet; 43°26′41″N, 006°51′03″E; 8 m alt.; 03.IV. 2017; A. Wagner leg.; 2 nymphs on slide, GBIFCH00654990; GenBank accession PZ163803; GBIFCH 00654991; 13 nymphs in ethanol, GBIFCH00341289.

ITALY — Piemonte • Alessandria, Acqui Therme, Ponte d'Erro; ca. 44°38′45″N, 008°25′14″E; 160 m alt.; 05.VII.1987; D. Studemann & P. Landolt leg.; 1 nymph (exuvia) on slide, GBIFCH01225870; 15 nymphs in ethanol, GBIFCH01291034.

Identification. Nymph. Body length, male: 5.5–6.0 mm; female: 6.0–6.5 mm.

Colouration. Head. Brownish; greyish brown between ocelli. Antenna: scape light brown, pedicel dark brown, and filament yellow. Compound eye: lower portion black, upper portion brick-reddish brown. Mouth parts: labrum and mandibles medium brown; maxillae and labium light brown. Thorax. Pronotum: medium brown; borders dark brown as in Figure 1. Mesonotum: light brown medially, medium brown laterally. Femur: fore femur greyish brown; mid- and hind femur whitish, distal half washed with greyish brown. Tibia and tarsi: brownish on fore legs; whitish on mid- and hind legs. Abdomen. Terga: evenly dark brown. Sterna: medium brown, darker laterally; nervous ganglia dark brown. Gills: dark grey. Terminal filaments: uniformly medium brown.

Head. Labrum cordiform, ca. 1.90× wider than long (Figure 2A). Ratio labrum width/insertion width ca. 1.20. Labrum width subequal to clypeus width. Medial emargination shallow with a single triangular denticle in middle, bordered by two flat denticles on each side (Figure 2B). Proximal row of setae present, simple. Number of setae on proximal row ca. 40–50. Distal row of setae present, simple. Median part of labrum in ventral view with stout setae in row. Mandibles. Outer margin with a tuft of setae in middle. Left mandible (Figure 2C): incisor with three teeth; kinetodontium with three teeth, longer than incisor; prostheca composed of a thick seta followed by a bunch of long and simple setae. Right mandible (Figure 2D): incisor with three teeth, kinetodontium with two teeth; prostheca composed of a bunch of long and simple setae; nine or 10 setae below mola. Maxillae. Maxillary palp segment II subequal in length to segment I. Maxillary palp segment III ca. 0.70× as long as segment I (Figure 2E). No stout setae on outer margin of segment I. Segment II, inner margin with three or four stout setae. Segment II, outer margin with 4–6 stout and long setae, together with long,

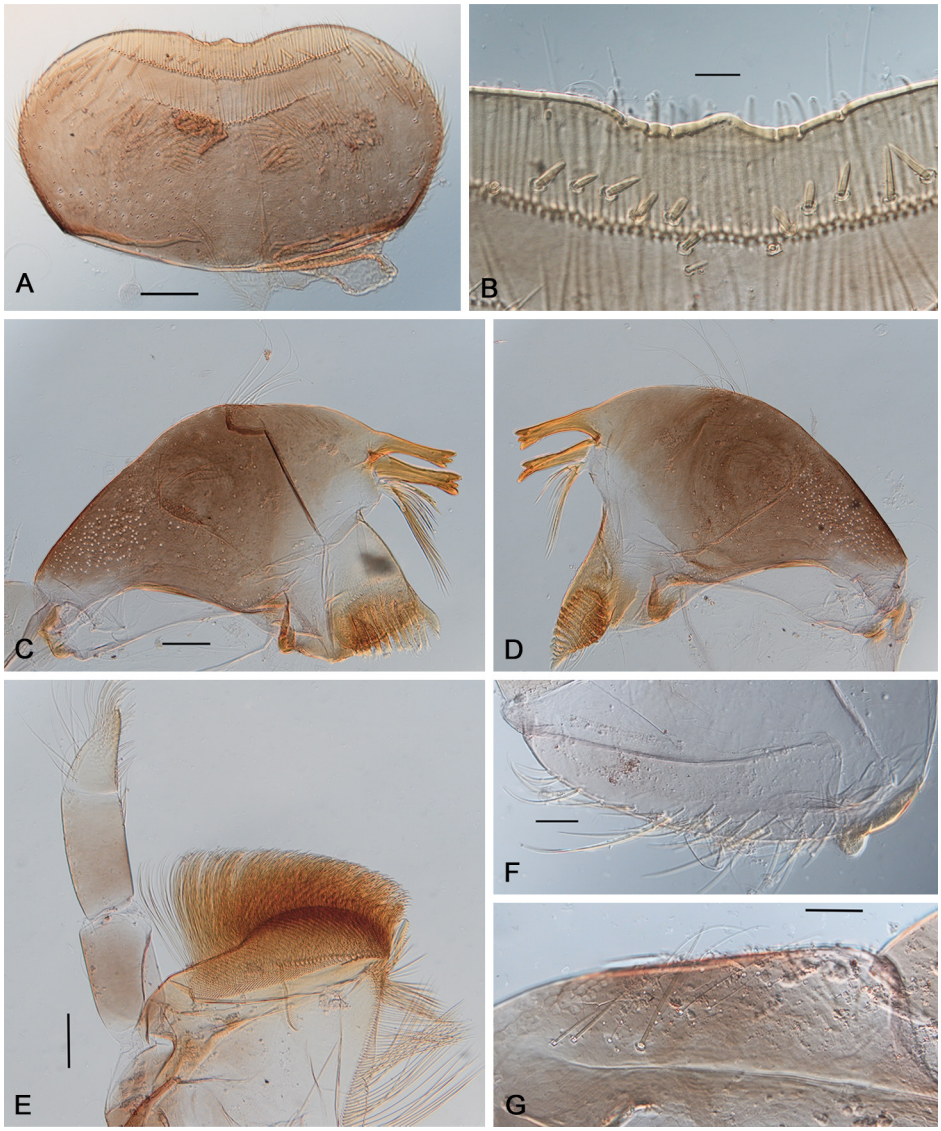

Figure 2. *Thraulus bellus* from Lake Ouiouane. **A.** Labrum. **B.** Labrum emargination. **C.** Left mandible. **D.** Right mandible. **E.** Galea-lacinia and maxillary palp. **F.** Setation of the outer margin of cardo. **G.** Setation on lateral margin of stipes. Scale bars: A, C–E = 100 µm; B = 20 µm; F, G = 50 µm.

hair-like setae. Segment III, inner margin with 6–8 stout setae. Segment III, dorsal surface covered with setae apically. Segment III 1.60–1.70× as long as base width. Posterior margin and submarginal area of cardo with numerous long and stout setae (Figure 2F). Proximolateral margin of stipes with several long and stout, as well as short and stout setae (Figure 2G). Apical-ventral row with 22–26 pectinate setae. Labium. Labial palp segment II 0.80–0.85× as long as segment I. Labial palp segment III 0.85–0.90× as long as segment I, i.e., segments II and III subequal in length (Figure 3A). Segment I, inner margin with 15–20 stout setae. Segment I, outer margin with 25–30 stout setae. Segment II, outer margin with 15–25 stout setae. Segment III, dorsal face with six or seven stout setae. Segment III 3.15–3.30× as long as base width. Lateral margins of submentum with long and simple setae (Figure 3B). Hypopharynx. Superlingua truncate, row of setae on outer margin ending at angle, tip of superlingua with a membranous rounded projection (Figure 3C).

Thorax. Anterolateral margin of pronotum with numerous stout and long setae; anterior margin with few stout setae laterally (Figure 3D). Fore legs femora elongated, ca. 2.65× longer than wide; outer and inner margins and upper surface covered with long, feathered, pointed setae (Figure 3E); tibiae subequal in length to femora; outer margin with sparse, thin, long setae, and inner margin with long, stout, feathered setae. Tarsi 0.45× length of tibiae; outer margin with sparse, long, thin setae, and inner margin with long and pointed entire setae. Middle legs similar to fore legs; femora ca. 2.95× longer than wide; dorsal surface of femora with more numerous, slightly longer, stout, pointed setae; tibiae slightly shorter than femora; tarsi 0.60× length of tibiae. Hind legs with femora 3.3× longer than wide; dorsal surface covered with stout, long, feathered setae more or less in rows. Hind tibiae slightly longer than hind femora and outer margin with both numerous stout, pointed setae, either long entire

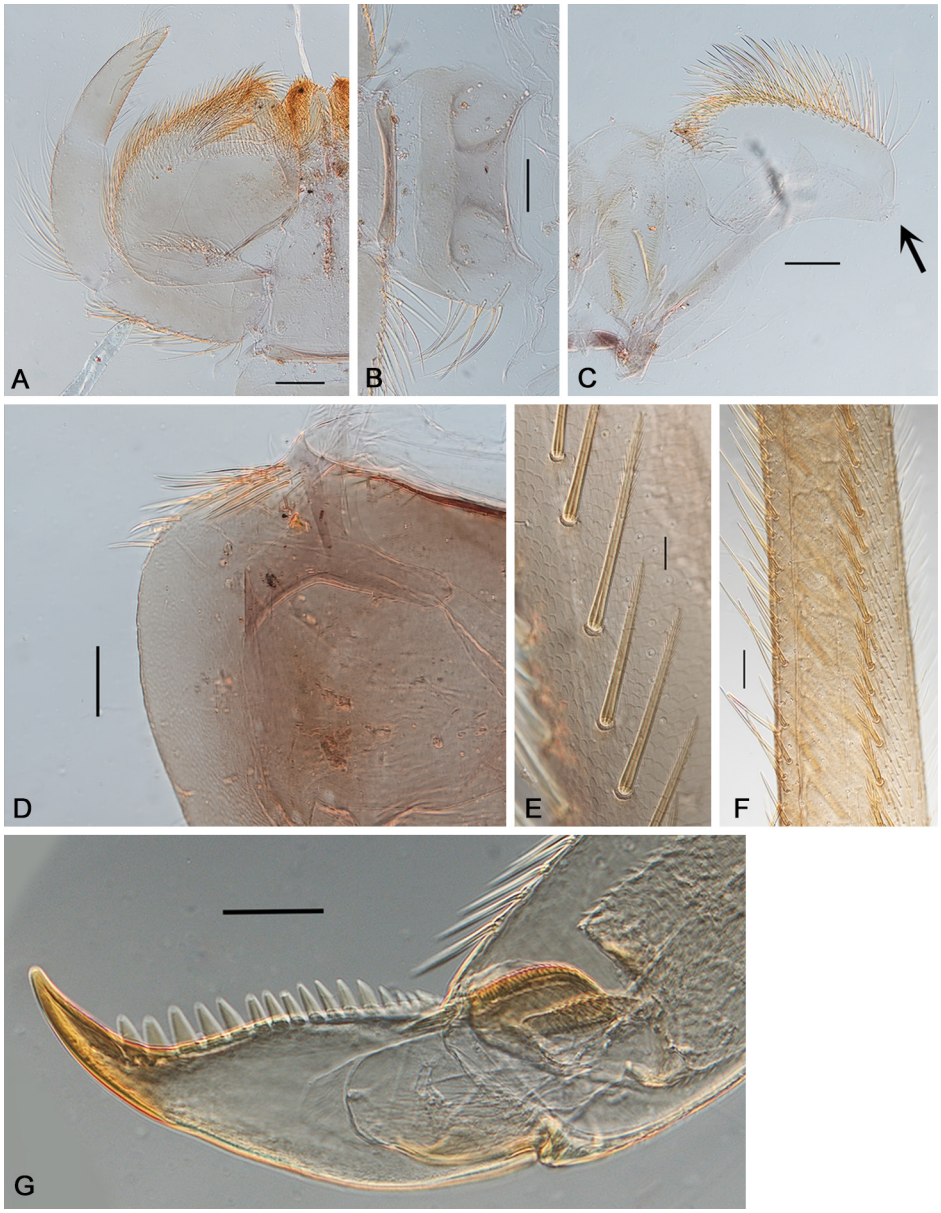

Figure 3. *Thraulus bellus* from Lake Ouiouane. **A.** Labium (half). **B.** Submentum. **C.** Hypopharynx (half) with arrow pointed to membranous rounded projection. **D.** Pronotum (half). **E.** Setae on dorsal face of fore femur. **F.** Setae on dorsal face of hind tibia. **G.** Claw. Scale bars: A–D = 100 µm; E = 20 µm; F, G = 50 µm.

or shorter feathered; inner margin with thin, pointed, entire setae, dorsal face with a row of large, spiculous setae (Figure 3F); tarsi 0.35× length of tibiae; outer margin with a few long, thin setae; inner margin with long, stout, pointed, entire setae. Claws of all legs slightly hooked, with 13–15 denticles slightly increasing in size towards apex (Figure 3G).

Abdomen. Gill I with single, long, bifid lamella, reaching at least abdominal segment VI. Gills II–VII with dorsal and ventral lamellae fringed with numerous filaments, ventral lamella smaller. Posterior margin of tergite V needle-shaped (Figure 4A); that of terga VI–VIII with denticles decreasing in size (Figure 4B–D), and that of tergite IX with long, triangular denticles (Figure 4E). Posterior margin of tergites VI–IX with numerous microdenticles. Posterolateral projections well developed on segments VIII–IX, reduced on segment VII. In male nymphs, protopenis with characteristic tubular penis lobes (Figure 4F).

Molecular analyses. The COI ingroup dataset was 99.8% complete and included 19% parsimony-informative sites. Sequences of *T. bellus* formed a distinct, well-supported clade that was sister to *T. grandis* (Figure 5). Within the *T. bellus* clade, the two European sequences grouped together in a weakly supported subclade, sister to the Moroccan sequence. Pairwise *p*-distances between the Moroccan and the two European *T. bellus* sequences were 5.7% (GBIFCH01144264 and BSNHM115-24) and 6.4% (GBIFCH01144264 and GBIFCH00654990), while the distance between the two European sequences (GBIFCH00654990 and BSNHM115-24) was 5.0%. Both ASAP and mPTP species delimitation

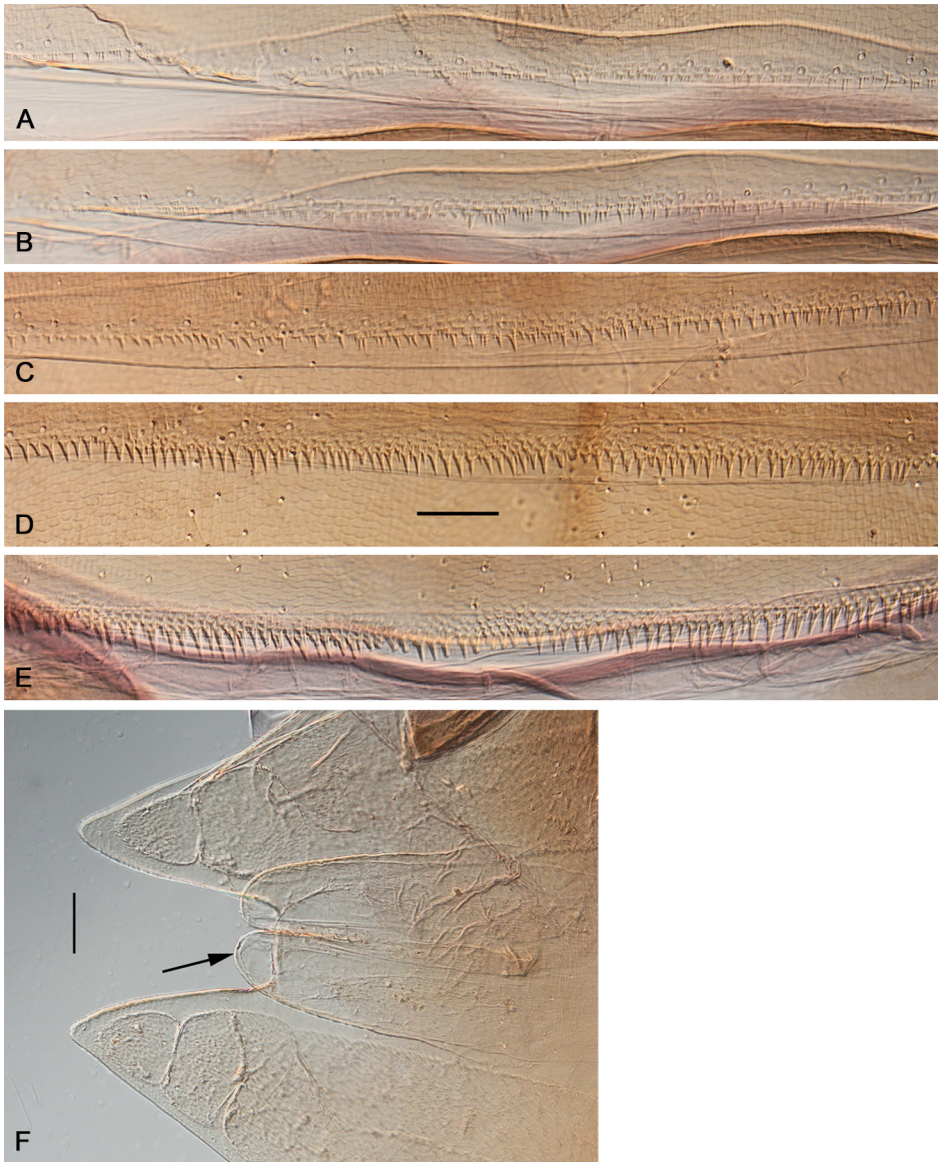

Figure 4. *Thraulus bellus* from Lake Ouiouane. **A.** Posterior margin of tergite V. **B.** Posterior margin of tergite VI. **C.** Posterior margin of tergite VII. **D.** Posterior margin of tergite VIII. **E.** Posterior margin of tergite IX. **F.** Protopenis (arrow pointed to one of the penis lobes). Scale bars: 50 µm.

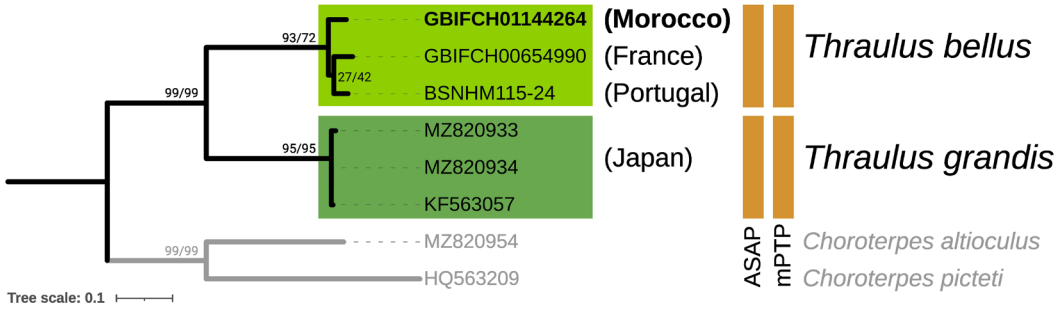

Figure 5. Maximum-likelihood COI tree of *Thraulus bellus* and *T. grandis*. Branch tips labelled with GBIF codes correspond to newly generated sequences, whereas the remaining codes represent sequences retrieved from public repositories (see Materials and Methods). Countries of origin are indicated next to the sequences (or to the clade for Japan), with the Moroccan sequence highlighted in bold. Brown vertical boxes show the species delimitation hypotheses recovered by the ASAP and mPTP analyses, with the corresponding species names indicated alongside. Support values from the SH-like approximate likelihood ratio test and ultrafast bootstrap (SH-aLRT/UFBoot) are indicated at the nodes. The outgroups are shown in grey, with corresponding labels and species names.

methods recovered the same two clades, corresponding to the two morphologically recognized species (Figure 5).

Discussion

The Moroccan nymphal population reported here presents the same morphological characters found in populations of *Thraulus bellus* from France and Italy. The setation and shape of the labrum, the setation of the maxillae, the arrangements of setae on the legs, and the ornamentation of the tergites are similar. The only slight difference is in the shape of the setae on the dorsal surface of the femora, which are more feathered in Moroccan specimens than in their European counterparts. It is unlikely that they belong to a new species or represent the as yet unknown nymph of *Thraulus thraker*. The molecular analyses further support this conclusion, with both ASAP and mPTP species delimitation methods indicating that the Moroccan and European populations are conspecific. The relatively large COI *p*-distances among the three sequences (5.0–6.4%), which might otherwise suggest the presence of cryptic species, are here more likely attributable to the geographic isolation of populations of this uncommon species. Comparable intraspecific COI distances have also been reported in other Leptophlebiidae in a recent European-scale barcoding study (Vuataz et al. in prep.), with mean *p*-distances of 6.3% in *Paraleptophlebia strandii* (Eaton, 1901), 6.7% in *Habroleptoides confusa* Sartori & Jacob, 1986, and 8.3% in *Habroleptoides modesta* (Hagen, 1864). Further integrative taxonomic investigations will be necessary to determine whether cryptic species are present in these cases.

Thraulus bellus is a Western Palearctic element, considered Atlanto-Mediterranean by Jacob (1988). The presence of the genus *Thraulus* in Morocco was first documented by Maamri et al. (2005), who collected nine specimens from two permanent stations along the Zegzel River, a tributary of the Moulouya river system (Maamri et al. 2005; El Alami et al. 2022a). Since then, studies on Moroccan macroinvertebrates have not reported its presence. The species seems absent from other Maghrebian countries, since it has never been reported from Algeria or Tunisia, suggesting that its presence in Morocco likely originates from the Iberian Peninsula.

Nymphs of *T. bellus* inhabit rivers (Gaino and Spano 1975; Maamri et al. 2005), ponds (Tabacchi 1987), and lakes (Verrier 1948; Wendling and Erpelding 1983; present study), but they are not widespread, although locally abundant. Its species' altitudinal range is important, suggesting that the availability of suitable habitats is the major driver. Nevertheless, the Moroccan population reported here is the highest and southernmost record so far (Figure 6).

Recent discoveries in the different regions of Morocco (El Alami et al. 2022b, 2023, 2025; Kaltenbach et al. 2022; Benlasri et al. 2023; El Yaagoubi et al. 2023) seem to indicate that the complete inventory of Moroccan Ephemeroptera is far from complete. Thus, the finding of *T. bellus* in Morocco is an important complement to the mayfly inventory for this country (El Alami et al. 2022a) and adds another species to the biodiversity of North African fauna.

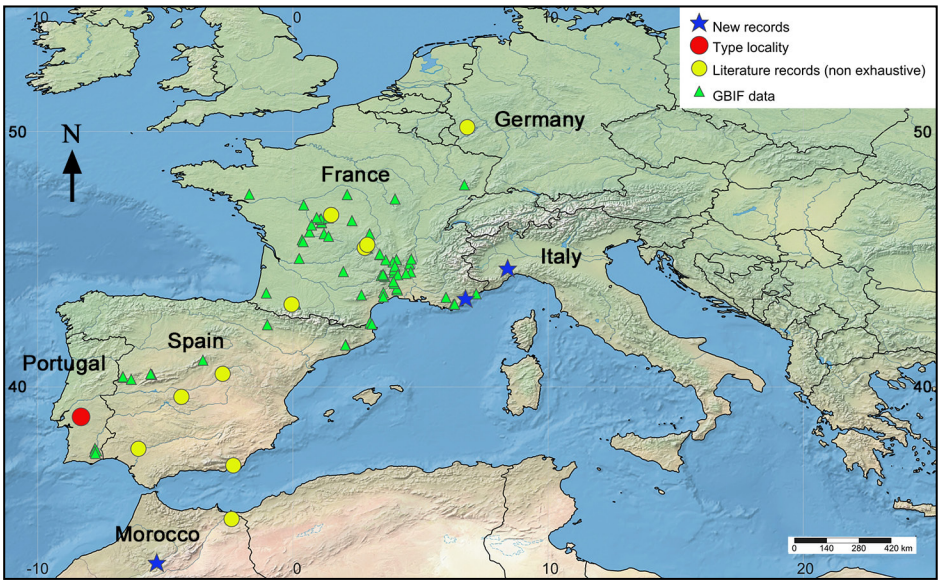

Figure 6. *Thraulus bellus* distribution in the Western Palearctic; data from GBIF (2026).

Acknowledgements

We are indebted to André Wagner (Naturéum), as well as Denise Studemann and Peter Landolt (formerly University of Fribourg) for the gift of comparative material. Our appreciation goes to Céline Stoffel (Naturéum/UNIL) for her dedicated work with the molecular lab. Remarks and corrections by the reviewer, Peter Grant (Southwestern Oklahoma State University), and academic editor, Juliana Rodrigues, greatly improved the quality of the manuscript.

Additional Information

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

Funding

No special funding for this research,

Author contributions

Conceptualization: MEA. Data curation: MS, LV. Formal analysis: LV, MS, MEA. Investigation: MEA, MS, LV. Methodology: MS, LV, KB, NB. Visualization: MS, LV; MEA. Project administration: NB, MEA. Validation: LV. Writing – original draft: MS Writing – review and editing: MEA, LV, MS

Author ORCID iDs

Majida El Alami https://orcid.org/0000-0003-2664-646X
Laurent Vuataz https://orcid.org/0000-0001-9193-8683
Kaoutar Belahcen https://orcid.org/0009-0004-0958-0571
Nard Bennas https://orcid.org/0000-0003-3819-2717
Michel Sartori https://orcid.org/0000-0003-3397-3397

Data availability

All data that support the findings of this study are available in the main text.

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