

Two new *Ptychoptera* Meigen, 1803 (Diptera, Ptychopteridae) from the Western Palaearctic

Libor Dvořák¹, Katarína Fogašová², Jozef Oboňa², Edina Török³, Peter Manko²

¹ *Tři Sekery 21, CZ-35301 Mariánské Lázně, Czech Republic*

² *Department of Ecology, Faculty of Humanities and Natural Sciences, University of Prešov, 17. novembra 1, SK-08116 Prešov, Slovakia*

³ *"Lendület" Landscape and Conservation Ecology Research Group, Institute of Ecology and Botany, Centre for Ecological Research, Alkotmány str. 2-4, Vácrátót, H-2163, Hungary*

Corresponding author: Katarína Fogašová (katarinakanasova2@gmail.com)

Abstract

Ptychoptera xanthopleura Dvořák, Oboňa & Manko, **sp. nov.** from Azerbaijan and Georgia, and *Ptychoptera staryi* Dvořák, Oboňa & Manko, **sp. nov.** from Bulgaria are described. *P. xanthopleura* **sp. nov.** differs from the other member of the *lacustris* group mainly by having almost completely yellow pleurae, and by the shape of the epandrium and gonocoxites. The diagnostics of *P. staryi* **sp. nov.** and *P. incognita* Török, Kolcsár & Keresztes, 2015 based on male genitalia are provided.

Key words: Balkan Peninsula, Caucasus, distributional data, new species, phantom crane flies, Ptychopteridae



Academic editor: Gunnar Kvifte

Received: 11 October 2022

Accepted: 8 May 2023

Published: 6 June 2023

ZooBank: <https://zoobank.org/4B15C8CD-DFF9-4ACE-AD2A-749D3AB5C5AD>

Citation: Dvořák L, Fogašová K, Oboňa J, Török E, Manko P (2023) Two new *Ptychoptera* Meigen, 1803 (Diptera, Ptychopteridae) from the Western Palaearctic. ZooKeys 1166: 91–102. <https://doi.org/10.3897/zookeys.1166.96193>

Copyright: © Libor Dvořák et al.

This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International – CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

Introduction

Ptychopteridae comprises two extant subfamilies: Bittacomorphinae Shiner and Ptychopterinae Alexander. Bittacomorphinae is found in the Nearctic, East Palearctic, and Oriental regions (e.g., Nakamura and Saigusa 2009). Ptychopterinae is widely distributed in the world except for the Australasian Region (Hancock et al. 2006; Fasbender 2017).

The genus *Ptychoptera* Meigen, 1803 comprises more than 90 recent species worldwide (e.g., Kang et al. 2013, 2019, 2022; Fasbender 2014; Zhang and Kang 2021), in Europe one genus occurs, namely *Ptychoptera*, with 18 species (Oosterbroek 2006; Török et al. 2015; Keresztes et al. 2021).

During the last ca. 40 years, eight new *Ptychoptera* were described from the Western Palaearctic region; one from Italy (*P. delmastroi* Zwick & Starý, 2003), four from the Balkans and neighbouring areas (*P. agnes* Krzemiński & Zwick, 1993 from Hungary, *P. incognita* Török, Kolcsár & Keresztes, 2015 from Romania and Bulgaria, and *P. castor* Keresztes & Kappert, 2021 and *P. pollux* Keresztes & Török, 2021 both from the south Balkan area), and three from the Caucasus (*P. peusi* Joost, 1974 from Russian Caucasus, *P. ressl*i Theisinger, 1978 from Iran, and *P. alina* Krzemiński & Zwick, 1993 from Armenia).

The adults live in marshy and moist habitats, near suitable substrates for the larvae as well as quite some distance from the larval habitat (Oosterbroek 2006). The larvae are aquatic to semi-aquatic, living in muddy water, shallow pools in marshes, *Sphagnum* pools, or the margins of streams (e.g., Andersson 1997; Wiberg-Larsen et al. 2021).

Our present study reports the description of two new *Ptychoptera* species, one from the Balkans and one from the Caucasus.

Materials and methods

Taxonomic material

The terminology of male genitalia follows Fasbender (2014) and Kang et al. (2022); the other morphological terminology adopted here follows essentially that of Zitek-Zwyrtek (1971), McAlpine (1981), and Oosterbroek (2006).

All voucher specimens are deposited and accessible in the private collection of the 1st author. Genitalia of *Ptychoptera staryi* sp. nov. and *P. xanthopleura* sp. nov. were macerated in 10% KOH and dehydrated using a series of dehydrating alcoholic solutions (70%, 80%, 96%). After that, parts of genitalia were mounted on permanent slides using Canada balsam as mounting medium.

Photographs of specimens were taken using a Pentax K-50 camera and a reverse-mounted Vivitar 28 mm 1: 2.0 MC lens, Motic SMZ-1 68 stereomicroscope equipped with Canon EOS 1200D camera and EOS utility software, and with Leica M205C stereomicroscope equipped with Leica DFC295 digital camera. Focus stacking was performed using Adobe Photoshop.

Phylogenetic analysis in the case of *P. xanthopleura* sp. nov.

We undertook phylogenetic analyses to understand the relationships between the species in the subgenus *Parapteroptera*. Cladistic analyses of 53 morphological characters on antennae, wing, and male terminalia (Table 1) were selected based on Keresztes et al. (2021) and Fasbender (2014). The list of morphological characters is described in detail by Keresztes et al. (2021).

The morphological data matrix was created and managed with Mesquite 3.5 (Maddison and Maddison 2019) and analysed using Maximum parsimony and Bayesian analysis. For maximum parsimony analysis, we used TNT “Tree Analysis using New Technologies” v. 1.5 (Goloboff and Catalano 2016). A “traditional” search based on 1000 replicates of Wagner trees, through ‘tree bisection reconnection’ (TBR) branch swapping holding 100 trees by the collapsing rule: ‘min. length=0’. Subsequently, we selected the best tree, in terms of species topology and population phylogeographical clades, and resampled with 100 000 replicates using a standard bootstrap procedure. Values at nodes represented absolute frequencies and frequency differences (GC, Group present/Contradicted).

For visualisation of the phylogenetic tree, we used FigTree v. 1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>), and the character state and statistical values visualisation were plotted onto the trees using Adobe Photoshop.

Table 1. Matrix of the 53 morphological data (based on the Keresztes et al. 2021) used in the phylogenetic analyses. For description of characters and character states, see Keresztes et al. (2021). '?' – missing data.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
<i>P. contaminata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>P. agnes</i>	?	1	1	1	?	?	?	1	1	0	0	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	
<i>P. castor</i>	1	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	
<i>P. delmastroi</i>	?	?	?	?	1	0	1	1	0	1	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	
<i>P. handlirschi</i>	1	1	1	1	1	0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	
<i>P. helena</i>	1	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	
<i>P. lacustris</i>	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	
<i>P. longicauda</i>	1	1	1	1	1	0	1	1	0	1	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	
<i>P. paludosa</i>	1	1	1	1	1	0	1	1	0	1	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	
<i>P. pollux</i>	1	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	
<i>P. resseli</i>	?	?	?	?	0	?	?	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	
<i>P. silvicola</i>	1	1	1	1	1	0	1	1	0	1	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0	
<i>P. xanthopleura</i> sp. nov.	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	
	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
<i>P. contaminata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. agnes</i>	0	1	1	0	1	0	1	1	0	0	1	1	0	0	0	1	1	1	1	0	1	1	0	0	1	0	1
<i>P. castor</i>	0	1	1	1	0	0	1	0	1	0	1	0	0	0	1	1	1	1	0	1	1	0	1	0	1	0	1
<i>P. delmastroi</i>	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	1	1	1	1	0	1	1	0	0	1	1	0
<i>P. handlirschi</i>	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	1	1	1	1	0	1	1	0	0	1	1	0
<i>P. helena</i>	0	1	1	1	0	0	1	0	1	0	1	0	0	0	1	1	1	1	0	1	1	0	1	0	1	0	1
<i>P. lacustris</i>	0	1	1	0	0	0	1	0	1	0	1	0	0	1	0	1	1	1	1	0	1	0	1	0	1	0	1
<i>P. longicauda</i>	0	1	1	0	1	0	1	0	0	1	1	1	0	0	0	1	1	1	1	0	1	0	1	0	1	1	0
<i>P. paludosa</i>	0	1	1	0	0	1	1	1	0	0	0	0	1	0	0	1	1	1	1	0	1	1	0	0	1	1	0
<i>P. pollux</i>	1	1	1	1	0	0	1	0	1	0	1	0	0	0	1	1	1	1	0	1	1	0	1	0	1	0	1
<i>P. resseli</i>	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	1	1	0
<i>P. silvicola</i>	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	1	1	1	1	0	1	1	0	0	1	1	0
<i>P. xanthopleura</i> sp. nov.	0	1	1	1	0	0	1	0	1	0	1	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0	1

Taxonomic account

Genus *Ptychoptera* Meigen, 1803

Diagnosis. Medium sized to large (7–15 mm), slender, black lustrous Nematocera, often with lighter markings on thorax and/or abdomen. Antennae, wings, abdomen, and legs long and slender. Ocelli absent; antenna with 15 to 16 segments. Thorax with deep, posteriorly directed transverse suture. Wing with markings, in particular along the crossveins and where veins bifurcate; spurious vein present on either side of crossvein R-M and wing membrane with a distinct fold between veins A_1 and C_uA_2 (Oosterbroek 2006; Fasbender 2014).

***Ptychoptera xanthopleura* Dvořák, Oboňa & Manko, sp. nov.**

<https://zoobank.org/CD413B9C-177D-4A4C-ACB9-3565C502C27B>

Figs 1, 2

Type material. *Holotype*: 1 ♂: AZERBAIJAN, Qum, sidebrook/small tributary of the Ardavacaj (Ardavachay) River + wetland, 845 m a. s. l., 41°28'10.3"N, 46°55'57.2"E, 8.V.2019, leg. J. Oboňa & P. Manko. *Paratypes*: 2 ♂♂: GEORGIA,

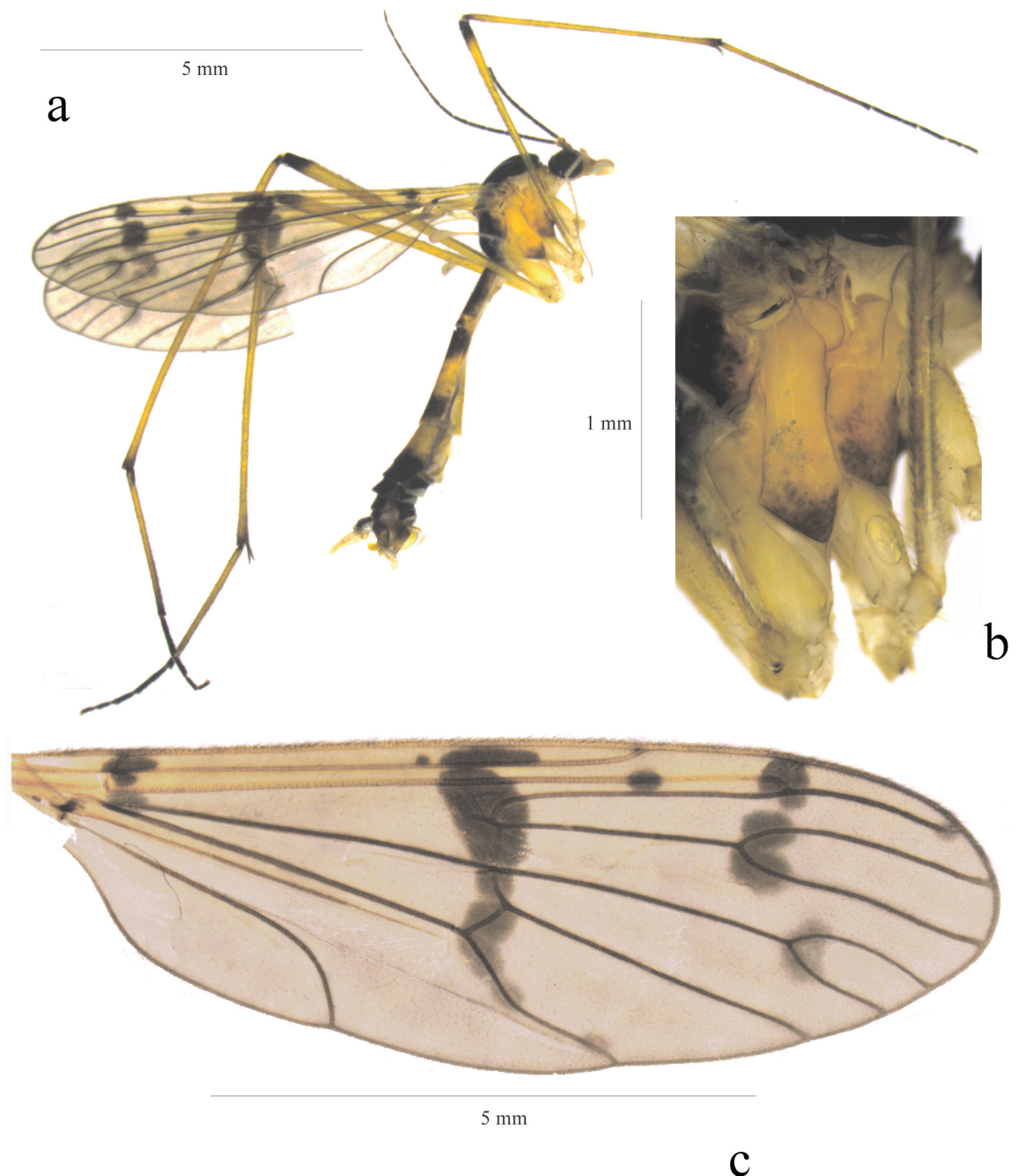


Figure 1. *Ptychoptera xanthopleura* sp. nov. **a** habitus of male, lateral view **b** pleurae, lateral view **c** wing.

border of Imereti and Samtskhe–Javakheti regions, brook and spring, south slope of Zekari pass, 2 050 m a. s. l., 41°49'23"N, 42°51'09"E, 17.VII.2019, leg. G. Vinçon.

Description. Male. Head: Frons, vertex, and occiput black with metallic blue shine, mouthparts including palpi pale yellow, scape and pedicel yellowish orange, antennal flagellomeres a somewhat darker, tending to pale brown.

Thorax: Scutum, paratergite, and mediotergite blackish with metallic blue shine; scutellum, pleurotergite, katepisternum, and katepimeron brownish black with lighter metallic blue shine; other parts yellow. Halteres yellow with light brown knob. Legs yellow except brown extreme apex of femora and tibiae, tarsi somewhat darkened.

Wing length 10 mm (holotype, Fig. 1c). Wing almost hyaline, veins yellowish brown, distinct spots brownish black, forming more or less three stripes, at base of wing at the level of crossvein h, from C to Cu. Middle stripe touching vein C, running through cross-veins up to middle part of vein Cu, isolated spot before end of vein Cu. Isolated spot on around middle of R_1 . Third stripe consist of three large, almost touching spots: at the tip of R_1 and fork of R_{2+3} , one on fork vein R_{4+5} and one on fork vein M_{1+2} . Small spot at the end of vein R_3 .

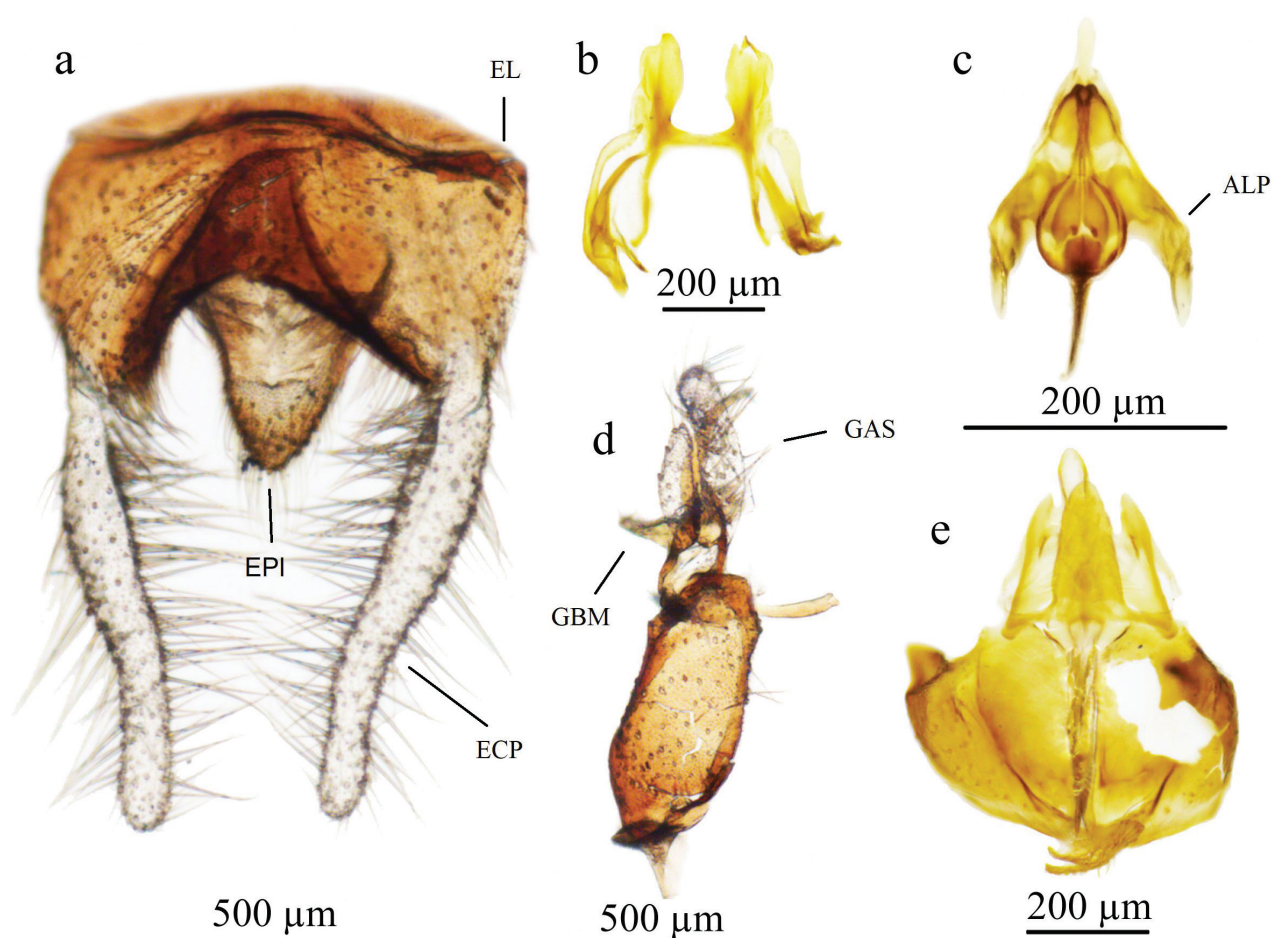


Figure 2. *Ptychoptera xanthopleura* sp. nov. terminalia **a** epandrium **b** paramere **c** aedeagal complex **d** gonostylus **e** hypandrium. Abbreviations: ECP = epandrial clasper, EL = epandrial lobe, EPI = epiproct, GBM = medial lobe of basal lobe of gonostylus, GAS = apical stylus of gonostylus, ALP = lateral ejaculatory process.

Abdomen: Tergum 1 dark shiny brown with yellow apex, sternum 1 yellow. Tergum 2 brown basally and apically, yellow in middle, sternum 2 yellow. Tergum 3 yellow basally, brown apically, sternum 3 yellow. Remaining terga and sterna brown, sternum 4 yellow basally. Auxiliar copulatory organ yellow.

Male genitalia (Fig. 2): Hypopygium almost 2× as wide as long, widest in basal quarter, medially with very deep emargination. Epandrial claspers simple and long (length/width ratio ca. 5.8) and covered by long pale hairs, the longest hair up to 1.75 longer than width of epandrium. Apical stylus of gonostylus robust and rounded apically, secondary lobe long, reaching almost 0.75 of apical stylus length. Media lobe of basal lobe of gonostylus long and sharply pointed (saber-like); anterior lobe of basal lobe of gonostylus bulbous apically with several setae at extreme apex.

Female. The authors have an immature female which was sampled in Lesser Caucasus (Georgia, Kakheti region, Ilto river, above (N of) the Chart'ala village, 790 m a. s. l., 42°8'18"N, 45°7'32"E, 8.VII.2019, leg. P. Manko & G. Vinçon). The characters correspond to the above-described new species. However, its identity cannot be confirmed in this stage of ontogenesis/development and could be solved after collecting more specimens of the genus *Ptychoptera* from the Transcaucasia.

Etymology. The name reflects predominantly yellow pleurae (Fig. 1b), which are unique for the Western Palaearctic species.

Differential diagnosis. According to the presence of auxiliary sexual organ and shining pleurae, *P. xanthopleura* sp. nov. belongs to the subgenus *Parapteroptera* and according to male genitalia and the maximum parsimonious tree based on 53 morphological characters (see Fig. 3 and Table 1), the nearest species is *P. lacustris* and belongs to the highly divergent monophyletic unit, the *lacustris* group, including five species, *P. xanthopleura* sp. nov., *P. lacustris*, *P. castor*, *P. helena*, *P. pollux*.

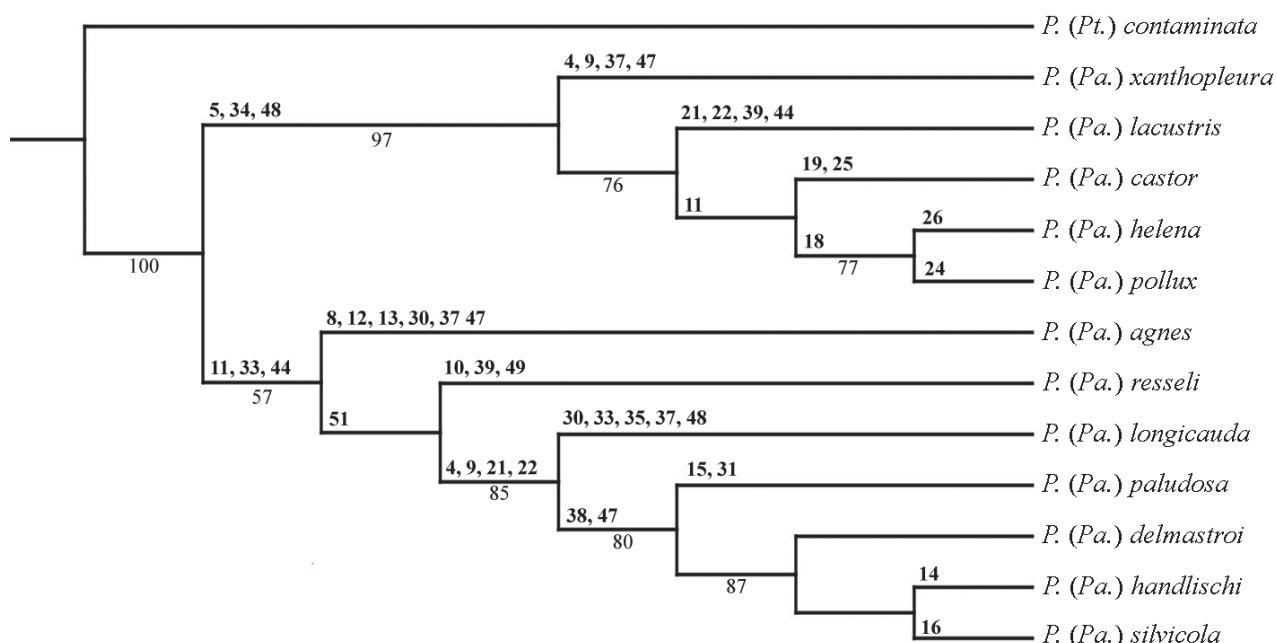


Figure 3. The maximum parsimonious tree based on 53 morphological characters. The characteristics are shown above branches. The parentheses show the maximum parsimony phylogeny bootstrap support value expressed as percentages. Support values under 40 are not shown.

ena, and *P. pollux* (Fig. 3). *Ptychoptera xanthopleura* sp. nov. is close to but differs from the most similar species *P. lacustris* mainly by having an almost completely yellow pleurae, the shape of the hypopygium (epandrial claspers, secondary lobe of gonostylus, and medial lobe of basal lobe of gonostylus).

***Ptychoptera staryi* Dvořák, Oboňa & Manko, sp. nov.**

<https://zoobank.org/21E4C563-97EA-497A-92C6-02A6A8621746>

Figs 4, 5

Type material. Holotype: 1 ♂: BULGARIA, Rhodopes, Yundola, 1 300 m a. s. l., 42°3'47"N, 23°51'17"E, 30.VI.2016, leg. M. Barták et Š. Kubík.

Description. Male. Head: Frons, vertex, and occiput black, mouthparts including palpi pale yellow, scape and pedicel yellowish orange, antennal flagellomeres greyish.

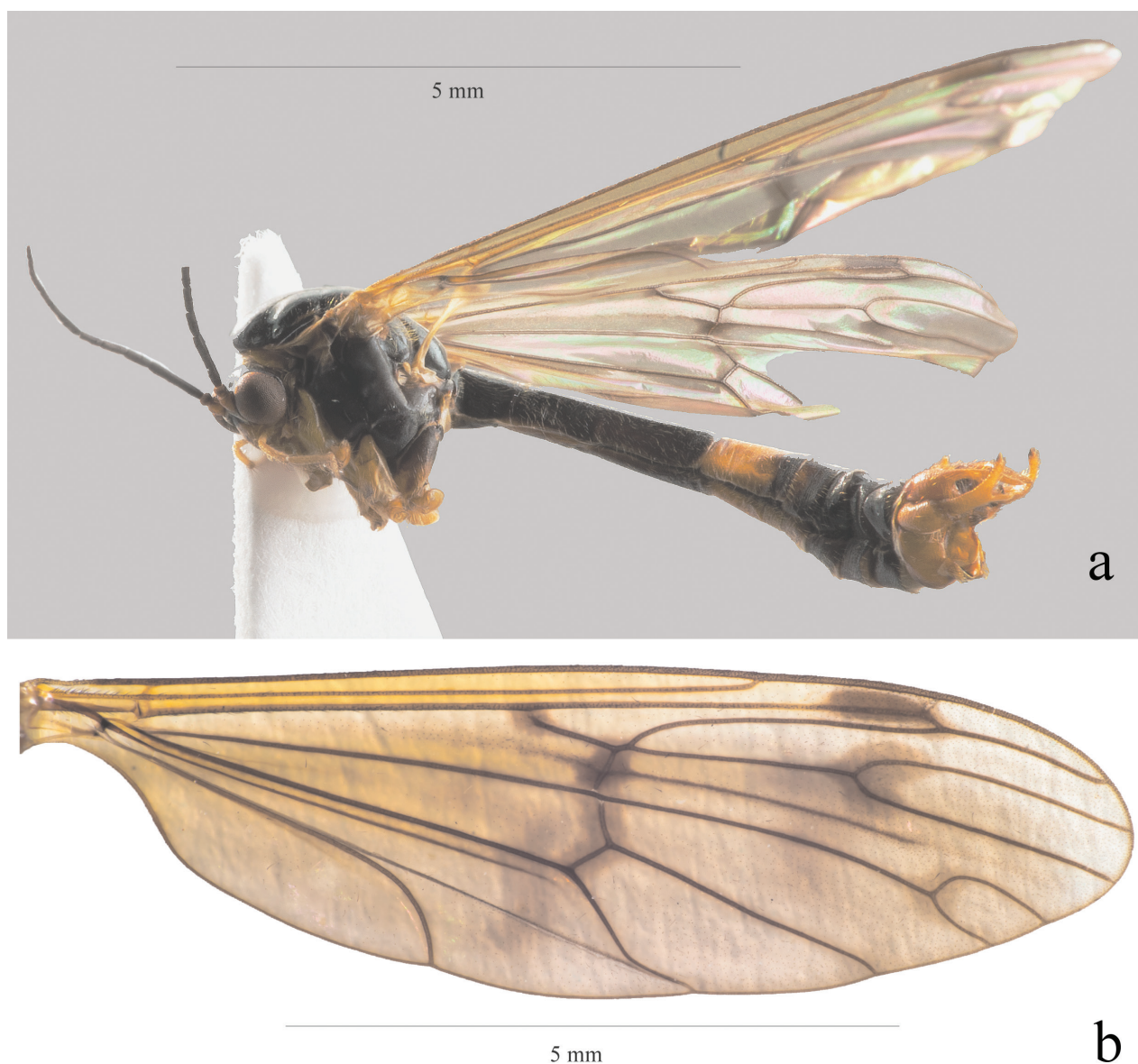


Figure 4. *Ptychoptera staryi* sp. nov. **a** habitus of male, lateral view **b** wing.

Thorax: Predominantly black with silvery pubescent pleurae. Pronotum, epimeron 3 and metanotum 3 yellow. Fore and mid coxae and trochanters yellow, hind coxae brownish black basally, yellow apically, coxae also yellow. Almost all legs are missing. Halteres whitish yellow with a darker knob.

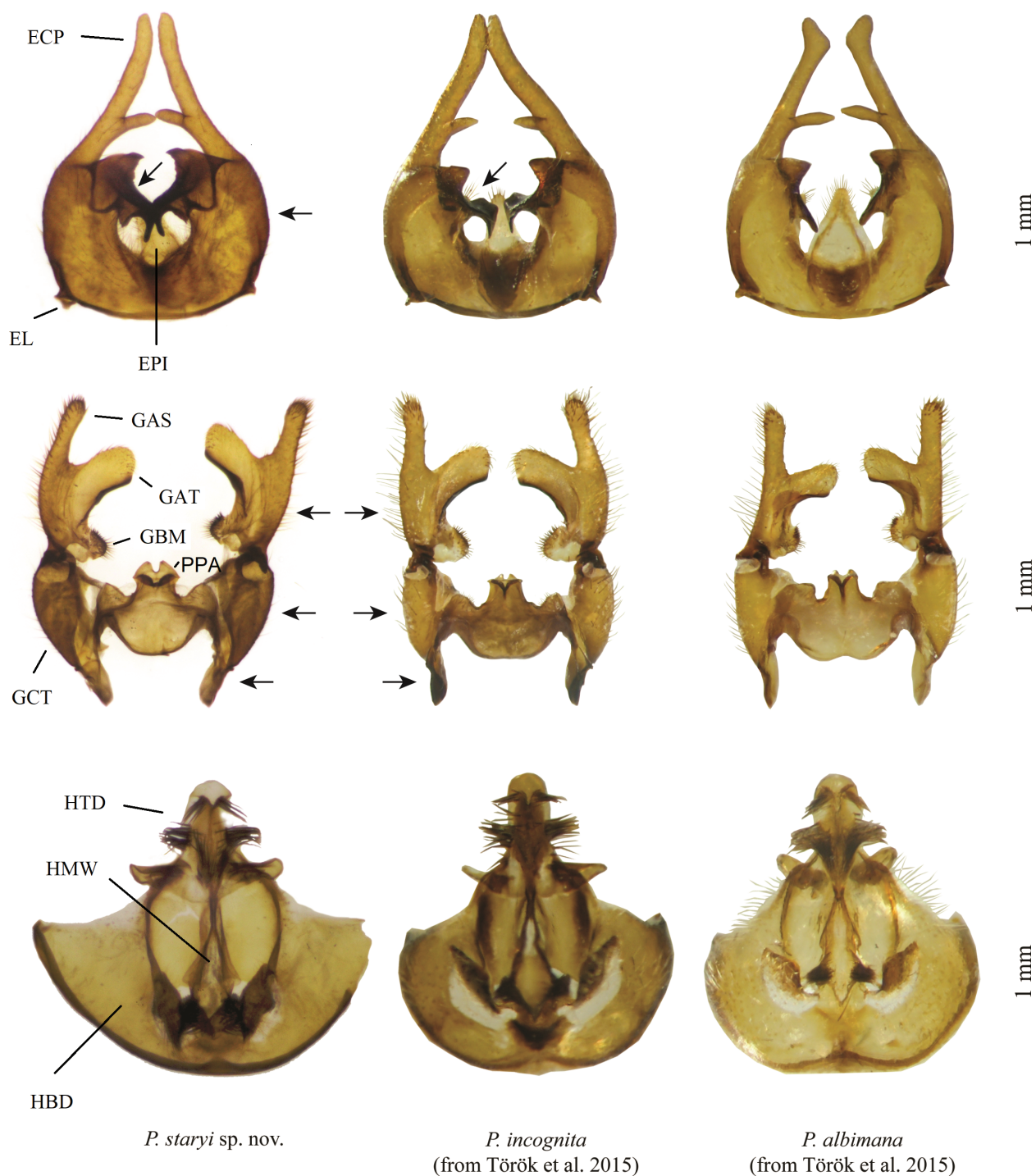


Figure 5. Epandrium, gonocoxite and gonostylus, and hypandrium of *P. staryi* sp. nov., *P. incognita*, and *P. albimana*. Abbreviations: ECP = epandrial clasper, EL = epandrial lobe, EPI = epiproct, GBM = medial lobe of basal lobe of gonostylus, GCT = gonocoxite, GAS = apical stylus of gonostylus, GAT = tertiary lobe of apical stylus of gonostylus, PPA = apical process of paramere, HBD = basal division of hypandrium, HMW = membranous window of terminal division of hypandrium, HTD = terminal division of hypandrium.

Wing length 12 mm (Fig. 4b). Wing with yellowish veins and infuscated spots on fork vein R_{s+R} , all cross-veins, end of R_1 vein up to its fork with R_2 vein, on fork vein R_4+R_5 and on fork vein M_1+M_2 . Legs: femur pale, darker in apical $1/5$, almost black on extreme apex; tibia pale brown in basal $1/2$, darker apically and almost black on extreme apex; tarsomere 1 almost black, tarsomeres 2 and 3 dark brown, tarsomeres 4 and 5 pale brown.

Abdomen: Tergum 1, tergum 2, apical $1/5$ of tergum 3, almost whole tergum 4 except base, and whole terga 5–7 black; sternum 1 black, sternum 2 brown, sternum 5–7 black; the remainder orange yellow.

Male genitalia: similar to *P. incognita*. Epandrial clasper slightly curved outwards with simple obtuse apex; anterior projection of ventromesal lobe sharp, posterior projection bow-shaped backwards; space between both projections is rounded, almost semi-circular. Gonocoxite and gonostylus: apical process of paramere with a U-shaped dark structure with thick edges; paramere base rounded, convex; width to height ratio of dorsal gonocoxal lobe 0.5; dorsal gonocoxal lobe with dense tiny dark hairs. Aedeagus: sides of lateral ejaculatory process distinctly convex, basal projections markedly convergent; transition to lateral ejaculatory process smooth, undulate. Hypandrium: width to length ratio 1.2; apex of hypogynial valves start under basal division of hypandrium. See also differential diagnosis.

Female. Unknown.

Etymology. The name is dedicated to our colleague Jaroslav Starý and his life jubilee. (Jaroslav discovered the holotype of new species in his own material and provided it for the description).

Differential diagnosis. The new species is very similar to *P. incognita* Török, Kolcsár & Keresztes, 2015 (see also Table 2). After comparing the holotype of *P. staryi* sp. nov. with individuals of *P. incognita* (material used in Török et al. 2015: 2 individuals from Bulgaria, 17 individuals from Romania), we found that a diagnosis was possible on the basis of differences in male genitalia (Fig. 5, marked with arrows), namely: (i) shape of the plate on ventral parts of epandrium is of

Table 2. Diagnostics of *P. staryi* sp. nov., *P. incognita*, and *P. albimana* based on male genitalia (see also Fig. 5).

	<i>P. staryi</i> sp. nov.	<i>P. incognita</i>	<i>P. albimana</i>
Epandrium	Shape of the plate on ventral site and the space between projections rounded, almost semi-circular.	Projections of the plate on ventral site in about right angle, space between projections quadrangular.	Projections of the plate on ventral site in obtuse angle, space between projections rounded, more than semicircle.
Gonocoxite and gonostylus	Width to height ratio of dorsal gonocoxal lobe 0.5; dorsal gonocoxal lobe with dense tiny dark hairs. The hairs of margins of gonocoxite and gonostylus much less dense and finer. Chitinisation of the proximo-lateral processes of the gonocoxite not developed, processes light coloured.	Width to height ratio of dorsal gonocoxal lobe 0.6; dorsal gonocoxal lobe with sparse small hairs. The hairs of margins of gonocoxite and gonostylus dense and stronger. Chitinisation of the proximo-lateral processes of the gonocoxite strongly chitinised, dark.	Width to height ratio of dorsal gonocoxal lobe 0.4; dorsal gonocoxal lobe with tiny dark hairs at the top. The hairs of margins of gonocoxite and gonostylus dense and stronger. Chitinisation of the proximo-lateral processes of the gonocoxite not developed, processes pale coloured.
Aedeagus	Sides of lateral ejaculatory process distinctly convex, basal projections markedly convergent; transition to lateral ejaculatory process smooth, undulate.	Sides of lateral ejaculatory process slightly convex, basal projections divergent; transition to lateral ejaculatory process steep, in a right or acute angle to the axis of aedeagus.	Sides of lateral ejaculatory process slightly convex, basal projections almost parallel; transition to lateral ejaculatory process steep, in an obtuse angle to the axis of aedeagus.
Hypandrium	Width and length ratio 1.2; apex of hypogynial valves start under basal division of hypandrium.	Width and length ratio 0.9; apex of hypogynial valves start on bases of basal division of hypandrium.	Width and length ratio 0.9; apex of hypogynial valves start over basal division of hypandrium.

a different shape and orientated at a different angle in *P. staryi*; (ii) chitinisation (sclerotisation) of the proximo-lateral processes of the gonocoxite is not developed and these processes are light coloured in *P. staryi* in contrast to *P. incognita* with strong chitinisation and dark colouration; (iii) the hairs of margins of gonocoxite, gonostylus, and epandrium are much less dense and finer in contrast to *P. incognita* (not visible in Fig. 5).

Acknowledgements

We are grateful to Gilles Vinçon (independent researcher, Grenoble, France) for his help in collecting and for the material he provided us from his own collections and Jaroslav Starý (Olomouc, Czech Republic) for providing us with the specimen for description, which was collected by Miroslav Barták et Štěpán Kubík (both - Czech University of Life Science, Prague, Czech Republic).

Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

Funding

This work of was financially supported by the Grant Agency of University Prešov in Prešov under the contract No. GaPU 1/2022 and by the Slovak Scientific Grant Agency, contract No. VEGA-1/0012/20.

Author contributions

LD is the leading person in preparing the description of both new species. PM took photographs, edited and prepared figures, PM, ET prepared the morphological data matrix for phylogenetic analyses, participated in the description, PM participated in the differential diagnosis, organized and provided funding for sampling trips to the Caucasus, LD, ET, PM, JO, KF contributed substantially to the writing of the manuscript and its revisions.

Author ORCIDs

Libor Dvořák  <https://orcid.org/0000-0002-4712-3679>

Katarína Fogašová  <https://orcid.org/0009-0003-9604-1885>

Jozef Oboňa  <https://orcid.org/0000-0002-1185-658X>

Edina Török  <https://orcid.org/0000-0001-5982-7078>

Peter Manko  <https://orcid.org/0000-0003-1862-9117>

Data availability

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

References

Andersson HU (1997) Diptera Ptychopteridae, phantom crane flies. The Aquatic Insects of North Europe 2: 193–207.

- Fasbender A (2014) Phylogeny and diversity of the phantom crane flies (Diptera: Ptychopteridae). Graduate Theses and Dissertations, Paper 14133, Iowa State University, Ames, Iowa, USA, 868 pp.
- Fasbender A (2017) Ptychopteridae (Phantom Crane Flies or Fold-wing Crane Flies). In: Kirk-Spriggs AH, Sinclair BJ (Eds) Manual of Afrotropical Diptera. Volume 2. Nematocercous Diptera and lower Brachycera. Suricata 5. South African National Biodiversity Institute, Pretoria, 653–657.
- Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32(3): 221–238. <https://doi.org/10.1111/cla.12160>
- Hancock EG, Marcos-García MA, Rotheray GE (2006) Ptychopteridae – A family of flies (Diptera) new to the Neotropical Region and description of a new species. *Zootaxa* 68(1351): 61–68.
- Joost W (1974) *Ptychoptera peusi* n. sp. – eine neue Faltenmücke (Dipt., Ptychopteridae) aus dem oberen Baksangebiet (UdSSR, Zentralkaukasus). *Entomologisches Nachrichtenblatt* (Vienna, Austria) 18: 173–178.
- Kang ZH, Yao G, Yang D (2013) Five new species of *Ptychoptera* Meigen with a key to species from China (Diptera: Ptychopteridae). *Zootaxa* 3682(4): 541–555. <https://doi.org/10.11646/zootaxa.3682.4.5>
- Kang ZH, Xue ZX, Zhang X (2019) New species and record of *Ptychoptera* Meigen, 1803 (Diptera: Ptychopteridae) from China. *Zootaxa* 4648(3): 455–4723. <https://doi.org/10.11646/zootaxa.4648.3.3>
- Kang Z, Gao G, Zhang X, Yang D, Wang J (2022) Three new fold-winged crane flies of the genus *Ptychoptera* Meigen, 1803 (Diptera, Ptychopteridae) from southern China. *ZooKeys* 1122: 159–172. <https://doi.org/10.3897/zookeys.1122.86483>
- Keresztes L, Kappert J, Henning M, Török E (2021) Helen's twins in the Balkans: Discovery of two new *Parapteroptera* Tonnoir, 1919 species closely related to *P. helena* Peus, 1958, with systematic revision of the “*lacustris*” group (Diptera, Ptychopteridae). *ZooKeys* 1071: 63–81. <https://doi.org/10.3897/zookeys.1071.58598>
- Krzeminski W, Zwick P (1993) New and little known Ptychopteridae (Diptera) from the Palaearctic Region. *Aquatic Insects* 15(2): 65–87. <https://doi.org/10.1080/01650429309361504>
- Maddison WP, Maddison DR (2019) Mesquite: a modular system for evolutionary analysis. Version 3.61. <http://www.mesquiteproject.org> [Accessed 10 Oct 2022]
- McAlpine JF (1981) Morphology and terminology – adults. In: McAlpine JF, Peterson BV, Shewell JF, Teskey HJ, Vockeroth JR, Wood DM (Eds) Manual of Nearctic Diptera 1. Monograph No. 27, Research Branch, Agriculture Canada, Ottawa, 674 pp.
- Nakamura TA, Saigusa TO (2009) Taxonomic study of the family Ptychopteridae of Japan (Diptera). *Zoosymposia* 3(1): 273–303. <https://doi.org/10.11646/zoosymposia.3.1.23>
- Oosterbroek P (2006) The European Families of the Diptera: Identification, Diagnosis, Biology. KNNV Publishing, Utrecht, 205 pp. https://doi.org/10.1163/9789004278066_013
- Theischinger G (1978) *Ptychoptera ressi* sp. n., eine neue Faltenmücke aus Iran (Diptera: Ptychopteridae). *Naturkundliches Jahrbuch der Stadt Linz* 23 (1977): 29–34.
- Török E, Kolcsár L-P, Dénes A-L, Keresztes L (2015) Morphologies tells more than molecules in the case of the European widespread *Ptychoptera albimana* (Fabricius, 1787) (Diptera, Ptychopteridae). *North-Western Journal of Zoology* 11(2): 304–315.
- Wiberg-Larsen P, Hansen SB, Rinne A, Viitanen E, Kroch PH (2021) Key to Ptychopteridae (Diptera) larvae of Northern Europe, with notes on distribution and biology. *Zootaxa* 5039(2): 179–200. <https://doi.org/10.11646/zootaxa.5039.2.2>

- Zhang X, Kang ZH (2021) Two new species of the genus *Ptychoptera* Meigen, 1803 (Diptera, Ptychopteridae) from Yunnan, China with remarks on the distribution of Chinese species. ZooKeys 1070: 73–86. <https://doi.org/10.3897/zookeys.1070.58859>
- Zitek-Zwyrtek K (1971) Czechoslovak species of the family Ptychopteridae (Diptera). Acta Entomologica Bohemoslovaca 68: 416–426.
- Zwick P, Starý J (2003) *Ptychoptera delmastroi* sp. n. (Diptera: Ptychopteridae) from Italy. Aquatic Insects 25(3): 241–246. <https://doi.org/10.1076/aqin.25.3.241.15262>