





111

https://doi.org/10.11646/zootaxa.5496.1.6 http://zoobank.org/urn:lsid:zoobank.org:pub:B6EF5CA8-D3E0-4450-A1E0-23E39171F2BB

# The identity of *Psilochironomus* Sublette, 1966 (Chironomidae, Chironominae, Pseudochironomini)

TROND ANDERSEN<sup>1</sup>, ANNUI MALLA SANZ-LAPARRA<sup>1</sup> & WOJCIECH GIŁKA<sup>2,\*</sup>

<sup>1</sup>University of Bergen, University Museum of Bergen, Department of Natural History; P.O. Box 7800, NO-5020 Bergen, Norway. it rond.andersen@uib.no; 
bttps://orcid.org/0000-0003-2201-1870

■ annui.parra@uib.no; ● https://orcid.org/0000-0003-0580-6890

<sup>2</sup>University of Gdańsk, Faculty of Biology, Department of Invertebrate Zoology and Parasitology, Laboratory of Systematic Zoology; Wita Stwosza 59, 80-308 Gdańsk, Poland.

solution wojciech.gilka@ug.edu.pl; https://orcid.org/0000-0002-8403-5432 \*Corresponding author

# Abstract

*Chironomus fumeus* Walley *in* Curran, 1934 was described based on a single male from British Guyana. When reviewing the type specimens of Chironomidae (Diptera) in the American Museum of Natural History, Sublette erected the monotypic genus *Psilochironomus* Sublette, 1966 based on the species. Subsequently, Sæther included the genus when he suggested the new tribe Pseudochironomini Sæther, 1977. However, the type specimen's hypopygium has been missing since before Sublette's examination; thus, Spies & Reiss in 1996 considered both *C. fumeus* and *Psilochironomus* to be *nomina dubia*. Below we redescribe *C. fumeus* based on four males collected by E.J. Fittkau in Pará State in northern Brazil and give an emended diagnosis for *Psilochironomus*. An updated key to the genera of Pseudochironomini is included.

Key words: Diptera, taxonomy, redescription, Brazil, Guyana, key

## Introduction

When reviewing the type specimens of Chironomidae (Diptera) in the American Museum of Natural History, Sublette (1966) erected the monotypic genus *Psilochironomus* based on the original description and remaining parts of the holotype of *Chironomus fumeus* Walley *in* Curran, 1934. Sublette (1966: 19) stated that the new genus "is most closely related to *Megacentron* Freeman but may be distinguished from that and related genera by the genitalia lacking superior and inferior appendages". Subsequently, Sæther (1977: 154) suggested the new tribe Pseudochironomus Malloch, 1915, *Psilochironomus* Sublette, 1966, and *Riethia* Kieffer, 1917. These interpretations were made in spite of the fact that the holotype specimen of *C. fumeus* was missing a decently preserved wing, both antennae, all tarsi, and the hypopygium (Sublette 1966: 20). Thus, the only remaining evidence of the genital structure in *C. fumeus* has been Walley's description: "Hypopygium blackish; hypopygial arms moderately stout; median dorsal process broadly triangular terminating in a short spinose tip" accompanied by a simple drawing showing the outline of tergite IX and the gonocoxite and gonostylus (Walley *in* Curran 1934: 307, fig. 18).

In their catalog of Neotropical Chironomidae, Spies & Reiss (1996)—who had not seen the holotype specimen of *C. fumeus*—considered the available evidence as insufficient for reliable interpretation of *C. fumeus* Walley, thus treated this name and *Psilochironomus* Sublette as nomina dubia. However, Martin Spies (SNSB-ZSM in Munich, Germany) has since examined the holotype (from the AMNH in New York City) and detected its probable taxonomic connection to material in the ZSM collection.

The type specimen of *C. fumeus* was collected at the New York Zoological Society's Tropical Research Station at Kartabo in British Guiana in March 1924. The station is situated in the Bartica District at the junction of the Cuiuni and Mazaruni rivers.

Accepted by B. Rossaro: 8 Jul. 2024; published: 16 Aug. 2024

In the collection at the ZSM in Munich, there are four apparently conspecific males collected along the Rio Paru de Oeste in Pará State in northern Brazil by E.J. Fittkau in April 1962. Three of these males were collected at the mission station for the Tiriyó people near the headwaters of the western Paru River. In the present article we redescribe *C. fumeus* based on the specimens from Brazil, in comparison with what is known from the holotype, and give an emended diagnosis of the genus *Psilochironomus*. In addition, an updated key to the males of the Pseudochironomini genera is presented.

#### Material and methods

The holotype of *C. fumeus* belongs to the American Museum of Natural History, New York City (AMNH); at the time of this writing, it is on loan to M. Spies (pers. comm.). The specimen's preserved parts were on a pin, but have been slide mounted by M. Spies, who has kindly sent us several results from his examinations.

The four specimens in the Zoologische Staatssammlung in Münich (ZSM) were initially slide mounted in Canada Balsam without any prior maceration, but the hypopygia of two of them have since been cleared in KOH and remounted (M. Spies pers. comm.).

Morphological terminology follows Sæther (1980). Measurements are given as ranges, followed by the mean when four specimens were measured. Colouration is based on the slide mounted specimens.

#### **Systematics**

Family: Chironomidae Newman, 1834 Subfamily: Chironominae Newman, 1834 Tribe: Pseudochironomini Sæther, 1977

#### Genus: Psilochironomus Sublette, 1966

*Psilochironomus* Sublette, 1966: 19. Type species: *Chironomus fumeus* Walley *in* Curran, 1934: 307, fig. 18.

#### Emended generic diagnosis. Adult male.

*Body size and colouration*. Medium sized species with wing length about 2.6 mm. Body dark brown, wing with wide dark band in middle 1/3.

Antenna. With 13 flagellomeres, fully plumed. AR about 2.60.

*Head.* Frontal tubercles absent. Temporal setae consisting of inseparably intergrading verticals and postorbitals, briefly bi- to tri-serial near transition of eye to its dorsomedial extension. Eye bare; dorsomedial eye extension nearly parallel-sided, about 2 times as wide as high, with 5–6 facets per diagonal; interocular distance in frontal view about 1.5 times the apical width of the extension. Clypeus with numerous setae. Palp 5-segmented, second palpomere rounded connected subproximally to ventrolateral surface of third palpomere at an angle of up to 90°. Third palpomere slightly swollen proximally and equipped with cluster of 8–12 strong, spine-like setae proximomedially; apparently without sensilla clavata subapically.

*Thorax.* Scutum not overreaching antepronotum; scutal tubercle absent. Antepronotum broad, collar-like, with halves meeting in the middle at anterior margin of scutum; with few ventrolateral setae. Acrostichals numerous, arising from small pale spots, short, decumbent, paired or interspersed, occurring from near antepronotum to mid scutum. Dorsocentrals and prealars in single row. Supraalar 1. Scutellars in single to partly double row. Alveoli of other thoracic setae not surrounded by circles lighter in color than adjacent surfaces.

*Wing.* Membrane without setae, with fine punctuation. Anal lobe well developed. Costa not or only slightly extended, ending proximal to wing apex.  $R_{2+3}$  running and ending close to  $R_1$ . FCu slightly distal to RM. Brachiolum with 1 seta; R with several setae,  $R_1$  and  $R_{4+5}$  without or with few setae. Squama fringed.

*Legs.* Fore tibia with single comb, with central protruding long spur; mid- and hind tibia with two broadly triangular combs, each with protruding spur. Pseudospurs absent. Pulvilli simple, pad-like, not reaching apex of claws.

*Hypopygium.* Tergite IX with several weak setae, laterosternite with few stronger setae. Anal point in dorsal view subtriangular, tapering to rounded apex, in lateral view with apex hooked ventrad. Phallapodeme well developed. Transverse sternapodeme narrow, arched, with low, rounded oral projections. Superior volsella straight with hoked apex, projecting caudally, with microtrichia and seta medially, apically bare. Inferior volsella ovate, with microtrichia and strong marginal and dorsal setae. Pars ventralis, median volsella and pseudovolsella absent. Gonostylus stout with bluntly rounded apex.

## Psilochironomus fumeus (Walley in Curran, 1934)

(Figs 1–3)

**Material examined.** Three adult males, BRAZIL, Pará State, Rio Paru do Oeste, Mission Tiriyó, 2°13'54"N 55°57'39"W, 26.03–21.04.1962, leg. E.J. Fittkau (A361-3, A361-6, A361-10) (ZSM); one adult male, Brazil, Pará State, Rio Paru do Oeste, Maloca Apico, 20.04.1962, leg. E.J. Fittkau (A 366-1) (ZSM) (Fig. 1).

**Redescription.** Adult male (n = 1-4)

*Body size and proportions.* Total length 5.79–6.16, 5.98 mm. Wing length 2.62–2.68, 2.64 mm. Total length / wing length 2.16–2.28, 2.22. Wing length / length of profemur 1.97–2.06, 2.00.

*Colouration.* Head, thorax and abdomen dark brown, legs with femur and tibia brown, tarsi slightly lighter brown. Wing with broad, dark band in median 1/3.

Antenna. AR 2.53–2.71, 2.60. Terminal flagellomere 1112–1148, 1129 μm long.

*Head.* Temporal setae 25–28, partly bi- to tri-serial near transition of eye to its dorsomedial extension. Eye extension nearly parallel-sided, about twice as wide as high, with 5–6 facets per diagonal (Fig. 2B). Clypeus with 48–59 setae. Tentorium 442–480  $\mu$ m long, 100–108  $\mu$ m wide. Stipes 296  $\mu$ m long, 20  $\mu$ m wide. Palpomere lengths / median width (in  $\mu$ m): 68–80 / 51–60, 80–92 / 60–64, 288–294 / 64–72, 296–320 / 52–56, 360–408 / 35–36. Second palpomere rounded, connect to ventrolateral surface subproximally on third palpomere at an angle of up to 90° (Figs 2C, D). Third palpomere slightly swollen proximally, equipped with cluster of 8–12 strong, spine-like setae proximomedially, 62–71  $\mu$ m long. Third to fifth palpomeres with rows of comparatively short, erect setae mesally; third palpomere apparently lacking sensilla clavata subapically.

*Thorax.* Antepronotum broad, collar-like, with 6–7 ventrolateral setae. Acrostichals short, decumbent, arising from small, pale spots, apparently 25–30 in partly double row occurring from near antepronotum to mid scutum; dorsocentrals 8–11 in single row; prealars 4–7, supraalar 1. Scutellum with 16–21 setae in single to partly double row.

*Wing* (Fig. 2A). VR 1.04–1.10, 1.07. Costa not or only barely extended. Brachiolum with 1 seta; R with 20–26, 22 setae;  $R_1$  with 0–4, 1 seta;  $R_{4+5}$  with 1–2 seta apically; other veins bare. Squama with 9–16, 12 setae.



**FIGURE 1.** The four slides of male *Psilochironomus fumeus* (Walley *in* Curran, 1934) from Pára State, Brazil, housed in the Zoologische Staatssammlung in München (ZSM).



**FIGURE 2.** *Psilochironomus fumeus* (Walley *in* Curran, 1934), male. A—Wing; B—Eye extension; C—Palp; D—Connection between second and third palpomere; E—Spur on fore tibia; F—Spur on mid tibia.

	<b>p</b> <sub>1</sub>	p <sub>2</sub>	p <sub>3</sub>
fe	1298–1339, 1324	1421–1524, 1457	1401–1483, 1442
ti	1730–1792, 1756	1607–1710, 1648	1916–1936, 1921
ta <sub>1</sub>	1524–1607	721–762, 747	803-845, 824
ta <sub>2</sub>	515-556	330–371, 350	391–433, 412
ta <sub>3</sub>	494–515	278–299, 288	309–330, 324
ta <sub>4</sub>	453–474	155–175, 164	144–165, 159
ta <sub>5</sub>	227–247	82–103, 88	82–113, 93
LR	0.871-0.905	0.443-0.463, 0.454	0.426-0.430, 0.429
BV	2.644-2.744	4.279–4.357, 4.324	4.102–4.489, 4.240
SV	1.949-2.014	4.054-4.257, 4.159	4.025–4.150, 4.081
BR	1.52–1.84	1.67–1.86, 1.73	1.92–2.31, 2.12

TABLE 1. Lengths (in µm) and proportions of legs of *Psilochironomus fumeus* (Walley in Curran, 1934), male.



**FIGURE 3.** *Psilochironomus fumeus* (Walley *in* Curran, 1934), male. A—Hypopygium, dorsal view; B—Hypopygium with tergite IX and anal point removed, dorsal view; C—Anal point, gonocoxite and gonostylus, lateral view; D—Gonocoxite, gonostylus and inferior volsella, ventral view; E—Superior volsella, dorsal view; F—Inferior volsella, dorsal view.

*Legs.* Spur of fore tibia (Fig, 2E) 69–73, 71  $\mu$ m long; spurs of mid tibia (Fig. 2F) 65–73  $\mu$ m and 72–83  $\mu$ m long; spurs of hind tibia 73–77  $\mu$ m and 83–90  $\mu$ m long. Width at apex of fore tibia 76–83, 80  $\mu$ m; of mid tibia 90–105  $\mu$ m; of hind tibia 92–107  $\mu$ m. Lengths and proportions of legs as in Table 1.

*Hypopygium* (Fig. 3A–F). Tergite IX with about 20 weak setae; laterosternite IX with 6 setae. In dorsal view anal point broadly subtriangular with rounded apex, 78  $\mu$ m long, 75  $\mu$ m wide at base; in lateral view with apex hooked ventrad. Phallapodeme 159  $\mu$ m long. Transverse sternapodeme narrow, arched, with low, rounded oral projections, 102  $\mu$ m long. Gonocoxite 268  $\mu$ m long. Superior volsella straight, projecting caudally, 100  $\mu$ m long, 28  $\mu$ m wide medially, with microtrichia and about 12 setae medially, apical part bare, 25  $\mu$ m long, tapering, with hooked apex. Inferior volsella ovate, 124  $\mu$ m long, 62  $\mu$ m wide medially, with microtrichia and about 18 strong marginal and dorsal setae. Gonostylus stout with bluntly rounded apex, 212  $\mu$ m long. HR 1.34. HV 2.91.

## Discussion

The holotype of *C. fumeus* was collected in at Kartabo, Bartica District in British Guiana on March 6, 1924. The original description is rather short and mostly concerned with the colour of the species (Curran 1934: 307): "MALE.– Length, 4 mm. Fuscous; wings each with a broad median fascia. Basal segment of antenna deep brown, shining; second segment dirty brownish-white; remaining segments and antennal plume brownish. Remainder of head and entire thorax dark brown with traces of grayish pruinescence when viewed obliquely, most conspicuous on the postnotum. Halteres fuscous. Entire femora and tibiae of all legs brown; middle and hind tibiae somewhat thickened and densely covered with rather short blackish subappressed hairs; femora with sparse, longer and suberect brownish hairs. Wings smoky, the veins brownish, the median third of the wing with a distinct fuscous band. Abdomen brownish black with the incisures ash-gray pollinose. Hypopygium blackish; hypopygial arms moderately stout; median dorsal process broadly triangular terminating in a short spinose tip." In addition, the outline of tergite IX, gonocoxite, and gonostylus are illustrated (Curran 1934: fig. 18).

As the specimens from Brazil are all slide mounted it is difficult to compare in detail the colour of the Brazilian specimens with the holotype. However, they are all rather dark brown and the colour of the wing seems to be as described in Curran (1934).

When erecting the genus *Psilochironomus* Sublette (1966: 19–20) states that: "*Psilochironomus* gen. nov. is most closely related to *Megacentron* Freeman but may be distinguished from that and related genera by the genitalia lacking superior and inferior appendages". He also re-describes *C. fumeus* in some detail: "Postocular bristles in two rows, long, erect. Eyes with a parallel sided extension which is about six facets wide. Frontal tubercles absent. Palpi with the first segment globular, the second articulated with the first at almost right angles and with a small lobe projecting medially; proportions, 5:35:25:20. Antennae missing.

Prothorax broad and collar-like, distinctly notched apically but with halves contiguous.

Dorsomedial bristles not discernible; thorax rubbed. Dorsolateral bristle alveoli in one row, small. Scutellar bristles rubbed, so not discernible.

All tarsi missing; fore tibia with a heavy spur arising from a comb. Ratio of length of spur to apical diameter of tibia, 5:10. Middle tibia broken off above spurs; hind tibia with two spurs, the inner slightly longer than the outer; combs of hind tibia broadly triangular, fused or at least contiguous anteriorly and occupying more than half the circumference of the tibia.

One wing missing, the other wing membrane badly crumpled; membrane dark, with a broad bluish-black facia across the middle of the wing. Costa slightly produced, f-Cu distal to r-m, other venation obscured. Squama fully fringed. Wing length, 2.66 mm.

The genital capsule was mounted, since it was illustrated by Walley, but the slide could not be located by Dr. Wygodzynsky."

The specimens from Brazil seem to be of the same size as the holotype of *C. fumeus*. According to Sublette (1966) the wing length of the holotype is 2.66 mm, while the wing length of the Brazilian specimens range from 2.62 to 2.68 mm. Also, in other characters the specimens from Brazil seem to fit the re-description by Sublette (1966).

When studying the holotype of *C. fumeus* M. Spies (in litt.) added several other counts and measurements: "Palpomere lengths/widths (in  $\mu$ m): 60/43, 50/75, 260/75, 262/50 and 350/30. Second palpomere (Pm2) with its distal end connected to a proximal subterminal area of Pm3, i.e. Pm3 with proximal extension beyond joint to Pm2

(Fig. 2C, D). In slide mount aspects (subject to rotation due to compression), the Pm2 attachment site is either proximoventral or proximolateral on Pm3. Proximomedian surface of Pm3 with cluster of approximately 10–12 stiff and thickened setae, 65  $\mu$ m long, 3.5  $\mu$ m wide. Thorax with acrostichals present about 20 in an unorderly, rarely clearly double row running from near antepronotum to about middle of dorsocentrals rows, Ac setae up to about 35  $\mu$ m long, often more or less decumbent, arising in small, light-coloured patches; Ac base patches irregularly interspersed with about as many even smaller (?rudiment) patches without setal alveoli. Dorsocentrals 9 in unevenly interrupted row; prealars 4–5, supraalar 1. Scutellum with 13 setae in a single row. Lengths of thoracic setae other than Ac not measurable on holotype".

When compared to previous descriptions of *C. fumeus*, the Brazilian specimens have somewhat longer palpomeres and apparently more acrostichals. We regard these differences as individual variation and conclude that the Brazilian specimens are conspecific with *C. fumeus*. Based on the present redescription, *C. fumeus* Walley in Curran, 1934 must now be regarded as a valid species and thus *Psilochironomus* Sublette, 1966 is no longer regarded as a *nomen dubium*. Among the Pseudochironomini, *Psilochironomus* is easily recognized on the wide dark band across the wing, the unique connection between second and third palpomere, and by having only superior and inferior volsellae.

The males of tribe Pseudochironomini Sæther, 1977 are characterized by having fore tibia with a slender, long, spurred comb and mid- and hind tibiae with two tall, triangular combs, each bearing a long spur. Although the combs on mid- and hind tibiae are rather wide in *Psilochironomus*, the genus fits these criteria. In other genera belonging to the tribe the males have, in addition to superior and inferior volsella, also either a median volsella or pseudovolsella and in *Pseudochironomus* the males have large pars ventralis. *Psilochironomus* has both superior and inferior volsella, but is lacking median volsella, pseudovolsella and pars ventralis. It is thus the first genus in the tribe to have only two volsellae.

So far, 11 genera of Pseudochironomini have been described, including 7 extant and 4 extinct ones. Apart from *Madachironomus* Andersen, 2016 that is endemic to Madagascar (Andersen 2016), the remaining 6 extant genera, *Aedokritus, Manoa, Megacentron, Riethia, Pseudochironomus*, and *Psilochironomus*, all occur in the Neotropical region. In addition, 4 extinct genera are described: *Eomicromimus* Giłka, Zakrzewska *et* Andersen, 2023 and *Eoriethia* Giłka, Zakrzewska *et* Andersen, 2023 both from Baltic amber, as well as *Mesoacentron* Giłka, Zakrzewska, Lukashevich *et* Cranston, 2022 (Taimyr amber), and *Palaeocentron* Giłka, Zakrzewska, Lukashevich *et* Cranston, 2022 (Burmese amber)—the oldest known representative of the tribe and the subfamily Chironominae (Giłka *et al.* 2022, Zakrzewska *et al.* 2023).

#### Key to genera of Pseudochironomini, males

1.	Extant species
-	Extinct species
2.	With median volsella or pseudovolsella in addition to superior and inferior volsella
-	With only superior and inferior volsella, lacking median volsella or pseudovolsella. Neotropical Psilochironomus Sublette
3.	With pars ventralis. Neotropical, Holarctic
-	Without pars ventralis or, if present, represented by 2 triangular lobes basally fused to gonocoxite
4.	Anal point and median volsella absent, pseudovolsella presen
-	Anal point and median volsella present, pseudovolsella absent
5.	Superior volsella with short digitiform ventral lobe, or lobe absent; inferior without flattened, apically fringed setae and/or
	scales. Neotropical, Afrotropical, Oriental
-	Superior volsella without ventral lobe; inferior volsella often with flattened, apically fringed setae and/or scales. Australasian,
	Neotropical
6.	Wing with dark bands or spots. Neotropical Aedokritus Roback
-	Wings without dark bands or spots, at most with dark shades along veins
7.	Anal point narrow, spatulate or parallel-sided; stem of median volsella directed caudally, single-lobed, evenly covered with
	relatively short and sparse setiform lamellae. Australasian, Neotropical
-	Anal point stout, with broadly rounded apex; stem of median volsella directed medially, apex split, bearing two strong bunches
	of setiform lamellae. Madagascar Madachironomus Andersen
8.	Antenna with 14 flagellomeres. Mid- to Late Cretaceous
-	Antenna with 13 flagellomeres. Cenozoic
9.	Pseudovolsella and pars ventralis absent; anteromedian lobe of inferior absent; anal point stout, with spike-shaped prolongation;
	hind leg tibia with strong thorn-like bristles. Mid-Cretaceous Burmese amber (~100 Mya)

-	Pseudovolsella and pars ventralis present; anteromedian lobe of inferior volsella present; anal point slender, without spike-
	shaped prolongation; hind leg tibia without thorn-like bristles. Late Cretaceous Taimyr amber (~84 Mya)
10.	Anal point well-developed, with peculiar, paired structure subapically; anteromedian lobe of inferior volsella absent. Eocene
	Baltic amber (~40 Mya) Giłka, Zakrzewska et Andersen
-	Anal point absent; anteromedian lobe of inferior volsella present, strong. Eocene Baltic amber (~40 Mya)

#### Acknowledgements

We are greatly indebted to Martin Spies, (SNSB-ZSM, Munich) for lending us the material, for all help and information on the type specimen of *Chironomus fumeus* Walley *in* Curran, 1934 and on the material studied, and for comments on parts of a manuscript draft.

#### References

- Andersen, T. (2016) Madachironomus, a new genus of the tribe Pseudochironomini (Diptera: Chironomidae, Chironominae) from Madagascar. CHIRONOMUS, Journal of Chironomidae Research, 29, 15–26. https://doi.org/10.5324/cjcr.v0i29.2113
- Curran, C.H. (1934) The Diptera of Kartabo, Bartica District, British Guiana, with descriptions of new species from other British Guiana localities. *Bulletin of the American Museum of Natural History*, 66 (3), 287–532.
- Giłka, W., Zakrzewska, M., Lukashevich, E.D., Vorontsov, D.D., Soszyńska-Maj, A., Skibińska, K. & Cranston, P.S. (2022) Wanted, tracked down and identified: Mesozoic non-biting midges of the subfamily Chironominae (Chironomidae, Diptera). Zoological Journal of the Linnean Society, 194, 874–892. https://doi.org/10.1093/zoolinnean/zlab020
- Sæther, O.A. (1977) Female genitalia in Chironomidae and other Nematocera: morphology, phylogenies, keys. *Bulletin of the Fisheries Research Board of Canada*, 197, 1–209.
- Sæther, O.A. (1980) Glossary of Chironomid morphology terminology (Diptera: Chironomidae). *Entomologica scandinavica*, Supplement 14, 1–51.
- Spies, M. & Reiss, F. (1996) Catalog and bibliography of Neotropical and Mexican Chironomidae (Insecta, Diptera). *Spixiana*, Supplement 22, 61–119.
- Sublette, J.E. (1966) Type Specimens of Chironomidae (Diptera) in the American Museum of Natural History. *Journal of the Kansas Entomological Society*, 39 (1), 1–32. [https://www.jstor.org/stable/25083484]
- Zakrzewska, M., Andersen, T. & Giłka, W. (2023) Mimes of the past: Eocene midges of the tribe Pseudochironomini (Chironomidae, Diptera) reveal their peculiarities. *PLoS ONE*, 18 (12), e0295841, 1–22. https://doi.org/10.1371/journal.pone.0295841