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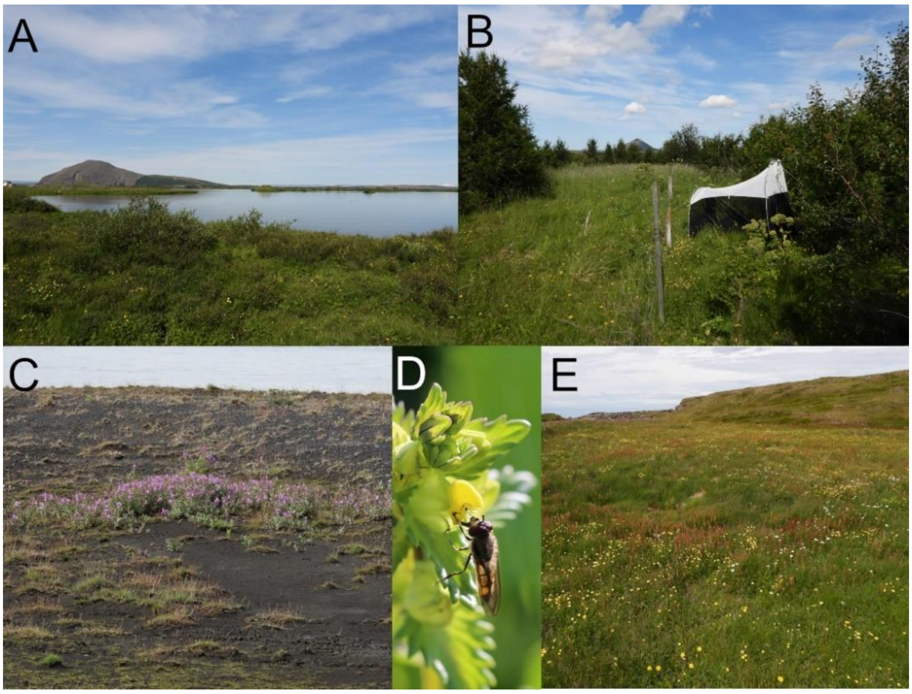

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Iceland, a mere remote island or a hoverfly (Diptera, Syrphidae) hotspot for endemism? A case study of *Platycheirus islandicus* Ringdahl, 1930 and *P. manicatus* Meigen, 1822

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Abstract. During a short expedition in 2021 several individuals of *Platycheirus* Meigen, 1822 were collected, both as dry material and in alcohol. Among this material we found a single *Platycheirus* species of the *manicatus* subgroup and another species belonging to the *peltatus* subgroup. The molecular and morphological data suggest the presence of *Platycheirus islandicus* Ringdahl, 1930 as a non-migratory endemic species for Iceland and *Platycheirus manicatus* Meigen, 1822 as a migratory species with regular influx from mainland Europe. The DNA barcodes as well as morphological characters are given for both species. A discussion about colonisation, and related topics like the nunatak and *tabula rasa* hypotheses, and migration theory on the endemism in Iceland is given.

Keywords. molecular data, melanism, nunatak, *tabula rasa*, migration

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Introduction

Iceland is a remote island situated in the Northern part of the Atlantic Ocean, about 300 km east of Greenland and 1000 km west of Norway. The average height is about 500 m above sea level with high peaks reaching just over 2000 m a.s.l. and a broad shoreline lying below 200 m a.s.l. A large proportion of the landmass is covered by glaciers, and there are abundant rivers and lakes, which occupy just under 20% total landmass. The vegetation cover consists of very sparse (60%) to continuous cover (25%). The continuously covered area consists of dry-land vegetation with predominantly flower rich heath (15%); wetland vegetation, with wet meadows, peat bogs and reedbeds (10%) and remnant birch forest (1%). Arable land, which in some cases is entirely barren, covers about 25% of the island's surface including planted pine forests. Soil erosion is one of the main environmental problems, partly due to the grazing of sheep throughout the island. Only about 2% of the total landmass consists of urban areas and roads. The flora consists of a small number of vascular plants with only birch (*Betula pubescens* Ehrh.), rowan (*Sorbus aucuparia* L.) and willow (*Salix phylicifolia* L.) as native trees. About 1100 years ago, at the time of the first settlement, birch forest covered about 25-40% of the total surface. Since the 1990s planting of trees to restore the birch forests has started, increasing the forest cover to 1.5%. In more recent times coniferous trees (*Larix sibirica* Ledeb., *Picea sitchensis* (Bong.) Carrère and *Pinus contorta* Douglas ex Loudon) have been introduced and now occupy about 0.5% (Horrebow 1758; Nielsen *et al*. 1954; Gíslason & Ólafsson 1989; Anonymous 2001; Denk *et al*. 2011; Eysteinsson & Halldórsson 2017).

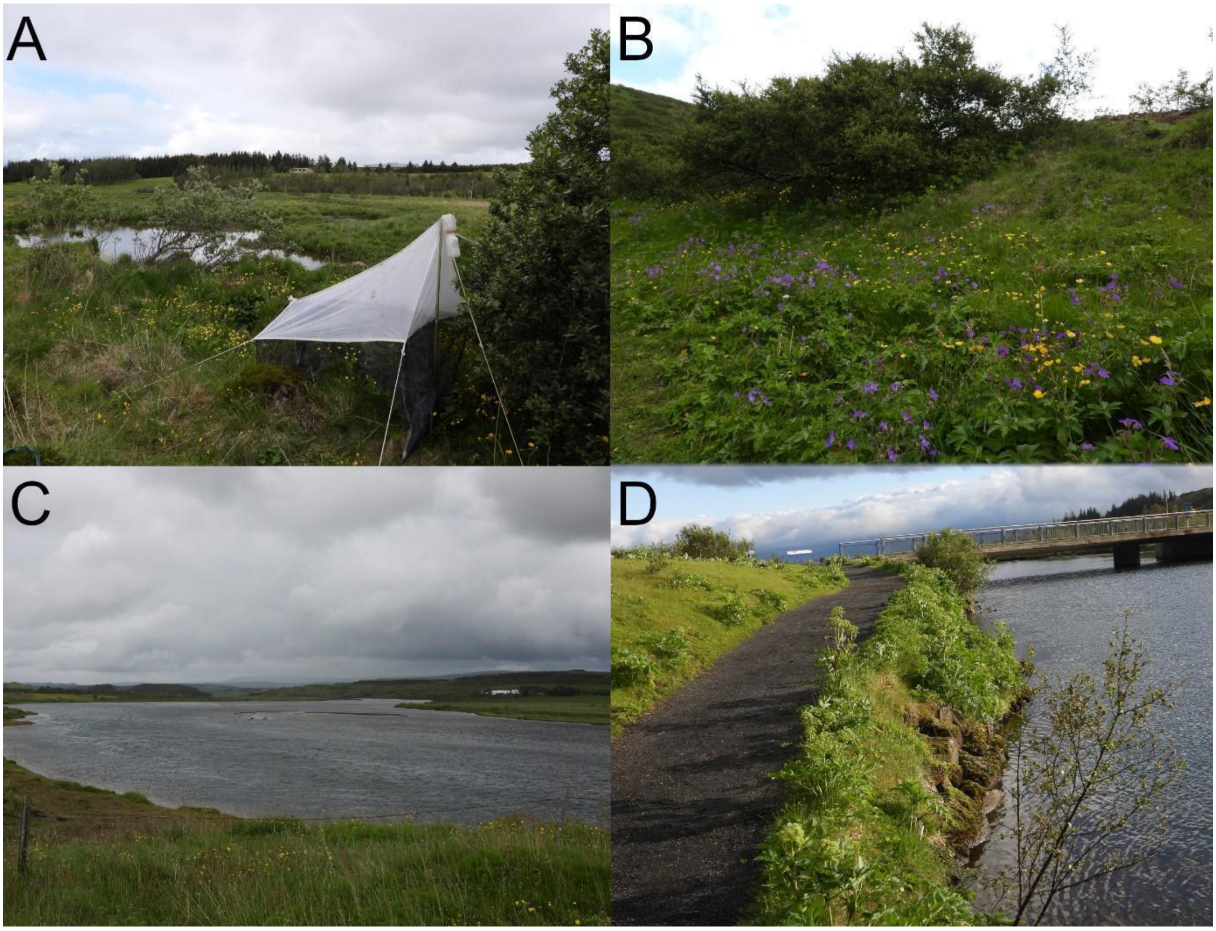

Figure 1. Habitat and malaistrap localities in Iceland. **A**. Malaise trap at Gardðabær, Vífilsstaðavatn. **B**. Habitat at laval field, Gardðabær, Grímssetur. **C**. Habitat near Reykholt, along river Tungufljót. **D**. Habitat at Þingvellir at 20.00 hours.

The known insect fauna consists of more than 1250 recorded species, of which Diptera is the most diverse group with almost 375 reported species. The entomofauna has been extensively studied by Danish and Swedish researchers (Ringdahl 1930; Lindroth 1931; Fristrup 1943; Nielsen *et al*. 1954; Gíslason & Ólafsson 1989) and by Icelandic researchers since its independence (Gíslason & Ólafsson 1989; Ólafsson 1991). A total of 30 species of hoverflies (Diptera, Syrphidae) are recorded from the country (Ólafsson 1991 and unpublished data) and several of them show migratory behaviour (Jeekel & Overbeek 1968; Aubert & Goeldlin de Tiefenau 1981; Gatter & Schmid 1990; Speight 1996; Wotton *et al*. 2019).

Only one species, *Eupeodes nigroventris* (Fluke, 1933), has a strict Nearctic origin, while the rest are Palaearctic in origin or have a Holarctic distribution. Despite the remoteness, vulcanic and glaciation history, only a few hoverfly (sub)species have been described from Iceland (Ringdahl 1930; Lindroth 1931). One of these taxa, namely *Platycheirus islandicus* Ringdahl, 1930, was for long time regarded as a synonym of *Platycheirus peltatus* Meigen, 1822, but it was validated as a species by van Steenis & Goeldlin (1998). The other *Platycheirus* species reported from Iceland is *P. manicatus* Meigen, 1822 (Lambeck 1968).

Figure 2. Habitat and Malaise trap localities in Iceland. **A**. Malaise trap at Laugarvatn, Gultulág. **B**. Habitat at Laugarvatn, Gultulág. **C**. Malaise trap at Laugarvatn, rivervalley. **D**. Malaise trap at Borgarnes, Myrar.

The species of the genus *Platycheirus* Lepeletier & Serville, 1828 are predominantly arctic and alpine in distribution and can be found in most biogeographical regions (e.g. Thompson 1972; Vockeroth 1990; Bartsch *et al*. 2009; Nielsen 2016; Young *et al*. 2016; van Steenis *et al*. 2019). *Platycheirus* is a member of the Bacchini, subfamily Syrphinae (Mengual 2020) and its species are characterised by a slender, parallel-sided abdominal shape and by the modifications of the legs in the males, especially the pro- and mesoleg with setae, pile patches, presence of cavae or enlargements of the tibia and tarsomeres. The two species studied in the present work belong to the *Platycheirus albimanus* species group *sensu* Vockeroth (1990) and further defined by Young *et al*. (2016): *P. islandicus* is a member of the *peltatus* subgroup and *P. manicatus* belongs to the *manicatus* subgroup. Both species are compared with similar species and a diagnosis is given.

The discussion focuses on several aspects to underline the species status of *P. islandicus* as an endemic taxon from Iceland and *P. manicatus* as a European migratory species reaching Iceland probably since the early 1960s. Important aspects in this discussion are melanism, the nunatak or *tabula rasa* hypotheses on the theory of colonisation and the migrating behaviour of Syrphidae. Before the work of van Steenis & Goeldlin (1998) *Platycheirus islandicus* was considered as a melanistic form of *P. peltatus* based on the colder and wetter climate on Iceland fitting in with the theory on melanism (e.g. Ringdahl 1930; Lambeck 1968). The nunatak and *tabula rasa* hypotheses are two different theories about the re-colonisation of arctic areas after the Ice-Ages. In short, the nunatak hypothesis states that ice-free areas occurred in the arctic regions where faunal elements survived. The *tabula rasa* hypothesis is based on the recolonisation of arctic areas through ice masses on which faunal elements drifted off (Holder *et al*. 1999; Brochmann *et al*. 2003).

Material and Methods

Sampling

A collecting trip during 2021 covered most of the Icelandic natural habitats. The starting point was the Reykjavik area including Þingvellir and Laugarvatn. Further North-West, through Myrar close to Borgarnes, the Snæfellsness Peninsula was reached. Road 1 was followed in the eastern direction visiting Mývatn and Ásbyrgi. In the South-West Höfn and Skaftafell were visited before reaching Laugarvatn and ending on the Reykjanes Peninsula. A short description of the habitat of the localities visited during the 2021 collecting trip are given below.

Reykjavik: In the SE border of Reykjavik, in the city district of Gardðabær, two days were spent hand netting Syrphidae. Along a rivulet flowing to the Vífilsstaðavatn a Malaise trap (Fig. 1A) was in place for 17 days. Hand netting was done on an old lava field with flower-rich meadows and low growing shrubs (Fig. 1B), birch and coniferous trees.

Þingvellir and *Laugarvatn*: During the 3 days stay in the Þingvellir area the weather was cold and rainy with a cloud cover of almost 100%. Along the river Tungufljót (Fig. 1C) only one Syrphidae specimen was collected, namely *Platycheirus manicatus*. At the Þingvellir site on the evening of the 14th the sky opened up and temperature rose from 6 to 12 degrees Celsius and in full sunshine several species of Syrphidae could be collected (Fig. 1D). In the nearby village of Laugarvatn Malaise traps were in place for 14 days, one (Fig. 2A) in a flower-rich mixed coniferous-birch forest (Fig. 2B) on the south-slope of a low mountain and the other in a peat march with low growing birch and willow trees along a river (Fig. 2C) in an otherwise almost barren terrain.

Borgarnes, Myrar: In the wetland area Myrar NW from Borgarnes a Malaise trap was mounted for 4 days (Fig. 2D). The trap was placed in a *Carex* spp. bog along a rivulet close to the mainstream running east-west through agricultural pastures.

Snæfellsness: On the Snæfellsness peninsula only few Syrphidae have been collected due to the cold weather.

Myvatn: In the Myvatn area (Fig. 3A) one day was spent hand netting Syrphidae (Fig. 3D) and a Malaise trap (Fig. 3B) was active for 5 days. The habitat of collecting consisted of herb rich wet shrubland with willows and some birch trees.

Ásbyrgi to *Nypskatla*: The area between Ásbyrgi and Nypskatla in the North was visited on two days when the weather was sunny and temperatures rose above 20 degrees Celsius. Collecting took place on *Geranium* spp on a further barren sandbank (Fig. 3C) and in herb-rich meadows along the sea-coast (Fig. 3E).

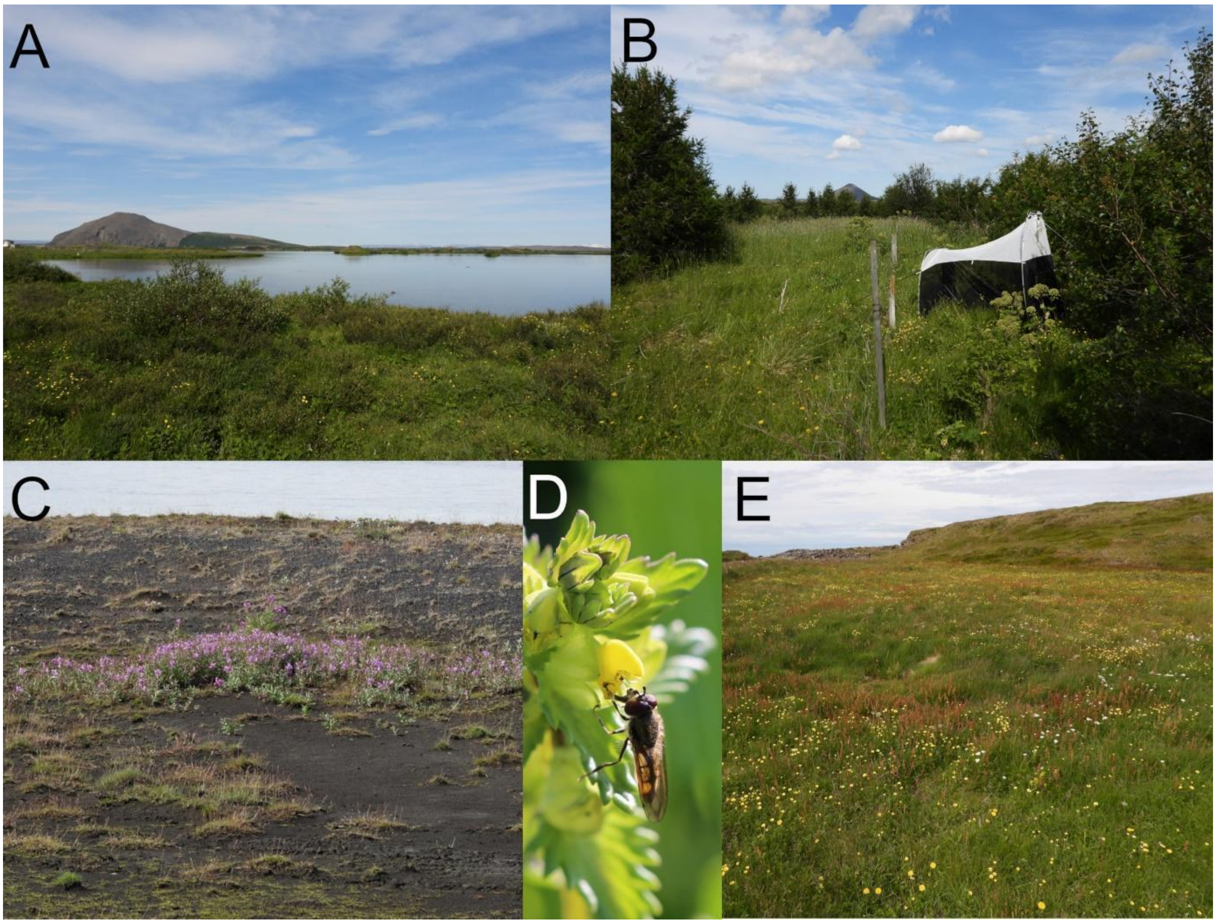

Figure 3. Adult *Platycheirus* species, habitat and malaistrap localities in Iceland. **A**. Habitat at Reykjalið, Neslandatangi, Myvatn surroundings. **B**. Malaise trap at Myvatn, Hamarshólar. **C**. Habitat at Þverá, Brunná. **D**. *Platycheirus manicatus* ♂ feeding on *Rhinanthus minor* L. at Vogahraun, camping. **E**. Habitat at Nypskatla, farmhouses.

Höfn and *Skaftafell*: In the south-east of Iceland two days were spent hand netting Syrphidae. One along the coast at Höfn with abundant flowering herbs and some small trees (Fig. 4A, 4B). The other locality was in the herb-rich mountain birch forest at Skaftafell (Fig. 4C).

Grindavik and *Krýsuvík*: The last two days were spent on the Reykjanes peninsula and collecting took place near Grindavik and Krýsuvík in mountain herb rich meadows (Fig. 4D).

The *Platycheirus* specimens were collected by hand-net and Malaise traps in Iceland in a period between the 15th and 31st of July 2021. During this period on several days the weather was too cloudy and cold and no Syrphidae could be collected, however during sunny spells, temperatures only rising to 12 degrees Celsius and as late as 20:00 hours Syrphidae started to fly around and visit flowers. Several of the hand collected specimens and all Malaise-trap material were killed and preserved in 96% ethanol. These specimens were used for molecular analysis. Additional material from several institutions, listed below, has been studied as well: IINH - Icelandic Institute of Natural History, Gardðabær, Iceland; JSB - private collection of Jeroen van Steenis, Baarn, The Netherlands; MZLU - Lund zoological museum, Lund, Sweden; NBC - Naturalis Biodiversity Center, Leiden, The Netherlands; NHRS - National history museum, Stockholm, Sweden; ZFMK - Museum Koenig, Bonn, Germany; ZMUN - Zoology Collection, Natural History Museum, University of Oslo, Norway.

Plant names are from the world flora online (WFO 2023).

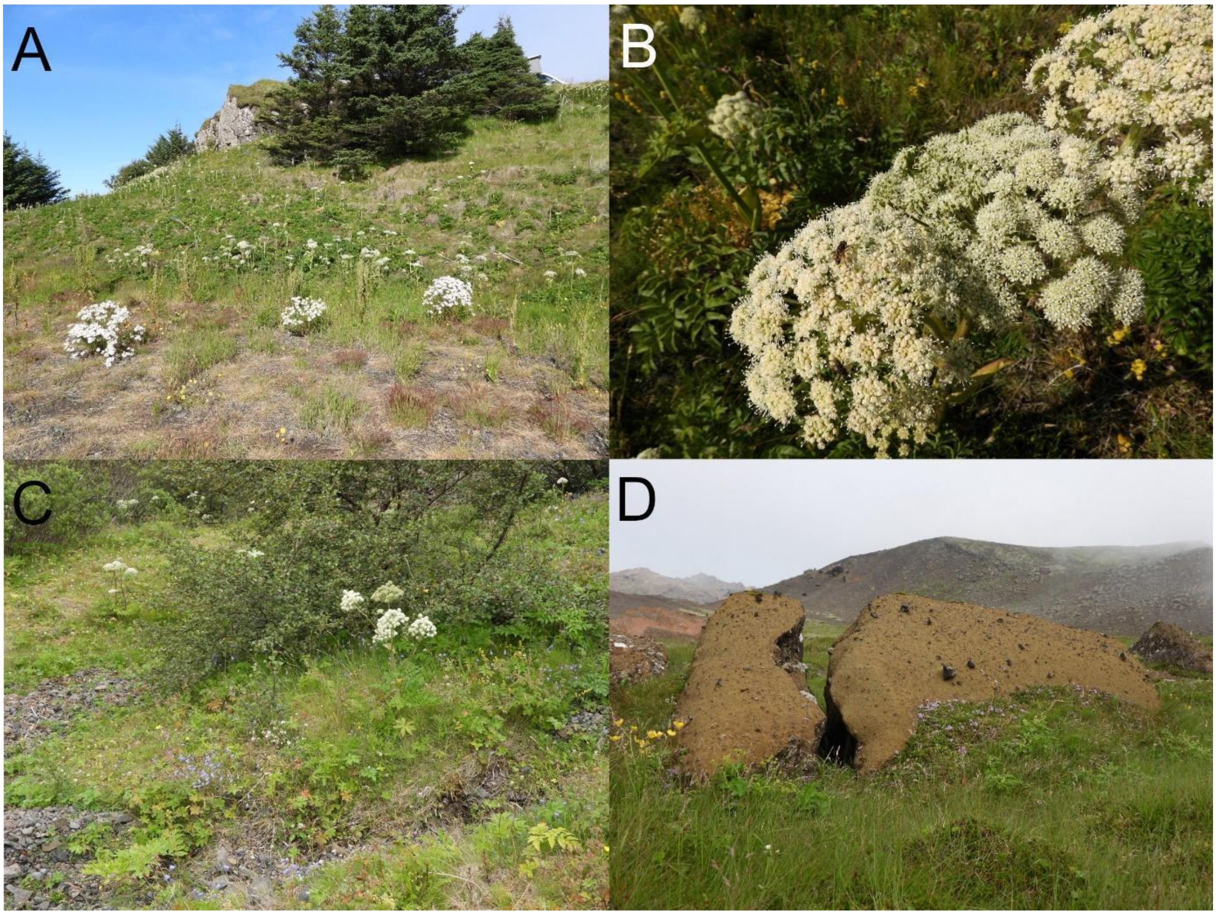

Figure 4. Habitat and flowering plants in Iceland. **A**. Habitat at Höfn, camping. **B**. Flowering foodplants at Höfn, camping. **C**. Habitat at Skaftafell, Skerhólsmýri. **D**. Habitat at Krýsuvík, Seltún.

Morphology and photography

The terminology used is based on van Steenis *et al*. (2023). The photos of the *Platycheirus* specimens were made with a Canon EOS 6D DSLR camera and a Canon MP-E 1–5 x macro lens equipped with a Yongnuo YN14EX macro ring lite flash. Several photos of each specimen were taken and stacked together with Zerene Stacker 1.04 and further edited with the image manipulation program GIMP 2.8.22.

DNA sequencing

For the selected *Platycheirus* specimens, the 5′-end of the mitochondrial cytochrome oxidase *c* subunit I (COI) gene was sequenced. One leg was used for DNA extraction and the rest of the individual was kept for morphological comparison and properly labelled as DNA voucher. DNA was extracted following standard protocols of the commercially available DNeasy Blood & Tissue Kit (QIAgen®). The COI barcode region was amplified and sequenced using the forward primer LCO1-1490 and the reverse primer COI-Dipt-2183R (Mengual *et al*.

2022). PCR amplification, purification, sequencing protocols, and editing were carried out as described in Rozo-Lopez & Mengual (2015) and Mengual *et al*. (2022). GenBank accession numbers are listed for each sequenced specimen in the excel sheet (supplement 1).

Figure 5. COI gene distance-based Neighbor-Joining tree of *Platycheirus*.

Molecular analysis

The selected public sequences (with more than 500 bp and without contaminants) of all species of the *peltatus* and *manicatus* subgroups available at BOLD were downloaded (https://www.boldsystems.org/index.php; accessed on 15 October 2022). Together with the newly obtained sequences, an alignment of the COI sequences without gaps or stop codons using Geneious ver. 7.1.3 (Biomatters Ltd) was produced.

A distance-based Neighbor-Joining (NJ) analysis, using the Jukes-Cantor Model, was conducted as implemented in the software Geneious ver. 7.1.3. The two sequences of *Pyrophaena granditarsa* (Forster, 1771) were constrained as the root for the tree. Bootstrap support values (BS) were calculated directly from Geneious using 1000 replicates. The NJ tree (Fig. 5) was drawn with the aid of FigTree ver. 1.3.1 (Rambaut 2018) and Adobe® Illustrator CS 5.1.

Results

***Platycheirus islandicus* Ringdahl, 1930**
Figs. 6A, 7A, 7B, 8B, 8C, 9B, 9C, 10A, 10B.

Platychirus peltatus var. *islandicus* Ringdahl, 1930: 173.

Differential diagnosis.
Male: Face (Fig. 8C) black, pile on face and all structures on the dorsal part of the head mixed black and white as in *Platycheirus peltatus*, face entirely white pilose in *P. nearcticus* Vockeroth, 1990; thorax with mixed white and black pile as in *P. peltatus*, in *P. nearcticus* and sometimes also in *P. peltatus* entirely white pilose, on scutum sometimes entirely black; posterior anepisternum with long mixed white and black posteriorly directed pile with wrinkled apex covering most of the pile on the anepimeron, in *P. peltatus* and *P. nearcticus* entirely white pilose; anepimeron with long, dense, mixed black and white dorsally directed pile, in *P. peltatus* and *P. nearcticus* entirely white pilose; basal wing cells almost entirely microtrichose, at most a very small spot on extreme base of cell bm bare, in *P. peltatus* and *P. nearcticus* bare areas much more extended, at least basal 10% of cell bm bare of microtrichia; protibia (Figs 10A, 10B) with wider apex and black margin of postero-apical corner, in *P. peltatus* (Figs 10C, 10D) and *P. nearcticus* less wide and with yellow margin throughout; basitarsus of protarsus (Fig. 10A) wider, with postero-lateral margin straight and the apical margin weakly skewed anteriorly, in *P. peltatus* (Fig. 10C) posterior margin straight to slightly concave, in *P. nearcticus* strongly concave; second tarsomere of protarsus wide (Fig. 10A), only slightly narrower than basitarsus and clearly wider than the third tarsomere, in *P. peltatus* (Fig. 10C) less wide, only slightly wider than third tarsomere and in *P. nearcticus* much less wide, almost as wide as third tarsomere; abdomen (Figs 6A, 7A) black with grey-brownish markings on terga II–IV, in *P. peltatus* (Figs 6C, 7C) and *P. nearcticus* with large orange-yellow maculae on terga II–IV; pile on postero-lateral corner of tergum II predominantly black, in *P. peltatus* and *P. nearcticus* almost entirely yellow; sterna slightly dull, predominantly greyish pruinose, in *P. peltatus* and *P. nearcticus* shiny, almost entirely bare.

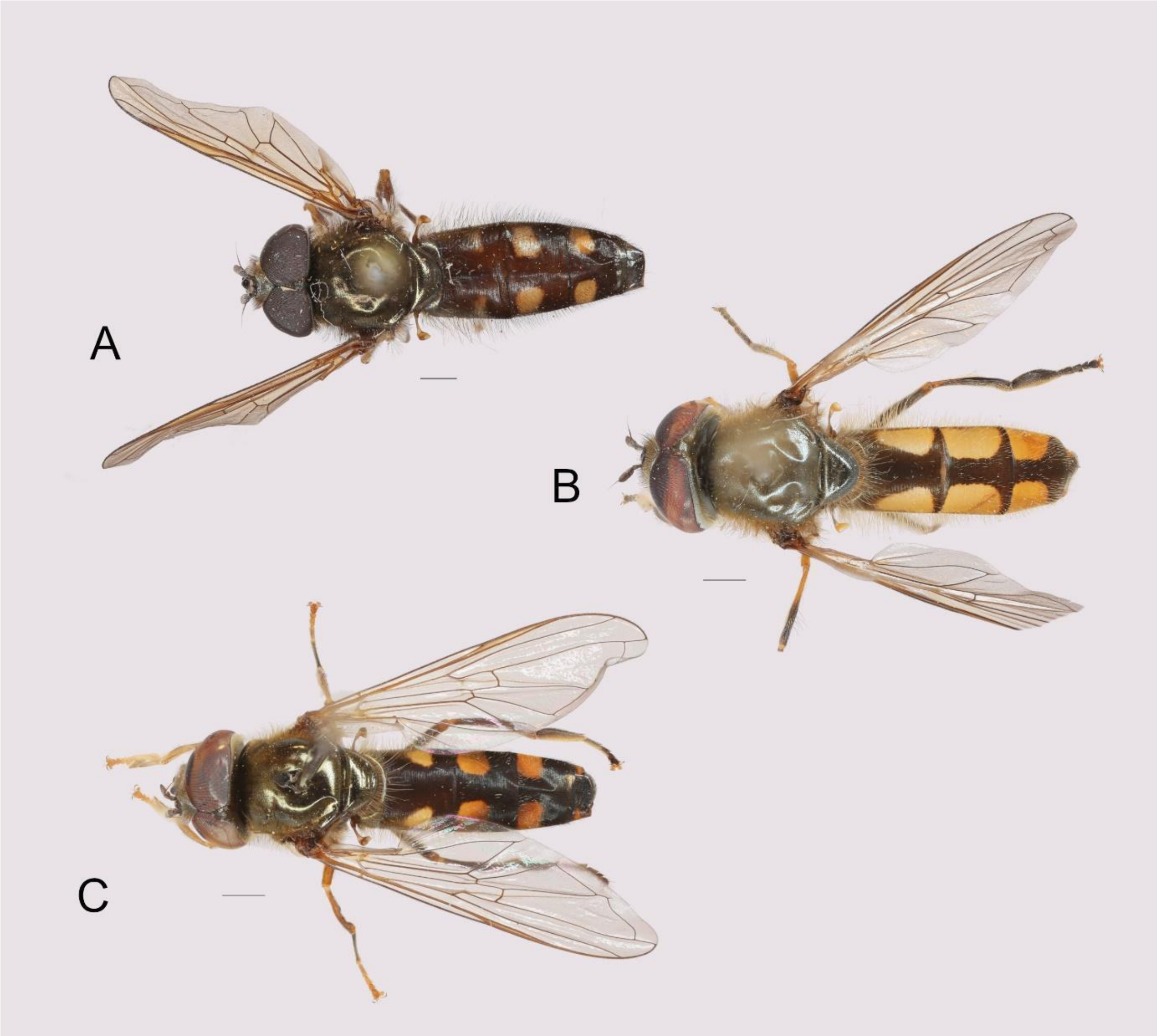

Figure 6. Habitus of *Platycheirus* species, dorsal view. **A**. *P. islandicus* ♂, Skaftafell, Iceland. **B**. *P. manicatus* ♂, ID No 2021-00.084, Iceland. **C**. *P. peltatus* ♂, Doorn, The Netherlands. Scale 1,0 mm.

Female: Frons (Fig. 8B) with extensive brownish-yellow pruinosity, medio-lateral pruinose maculae trapezoid shaped and ill defined, with additional pruinosity on anterior part of the frons, especially well developed laterally, in *P. nearcticus* and *P. peltatus* (Fig. 8F) pruinosity more greyish-yellow clearly defined and with anterior part widely non-pruinose); thorax mixed yellow and black pilose (Fig. 7B), at least postero-medially with two large black pile patches, in *P. nearcticus* and *P. peltatus* (Fig. 7F) entirely whitish-yellow pilose; scutellum and its posterior margin extensively black pilose, in *P. nearcticus* and *P. peltatus* entirely whitish-yellow pilose; legs predominantly black (Fig. 7B), at most basal half of pro- and mesofemur yellow and narrow apex and base of femora and tibia yellow; at most basal 1–2 tarsomeres of pro- and mesotarsus yellow, in *P. nearcticus* and *P. peltatus* pro- and mesofemur and tibia predominantly yellow (Fig. 7F); abdomen predominantly black (Fig. 9C) or with vague orange-brownish spots (Fig. 9B), in *P. peltatus* (Fig. 9E) and *P. nearcticus* with large orange-yellow maculae on terga II–V; long pile on lateral margin predominantly white, with extensive long black pile in postero-lateral corner of tergum II and shorter black pile along postero-lateral margin of terga III and IV, in *P. peltatus* and *P. nearcticus* long pile almost entirely white; sterna III and IV dull, greyish pruinose, in *P. peltatus* and *P. nearcticus* shiny and bare.

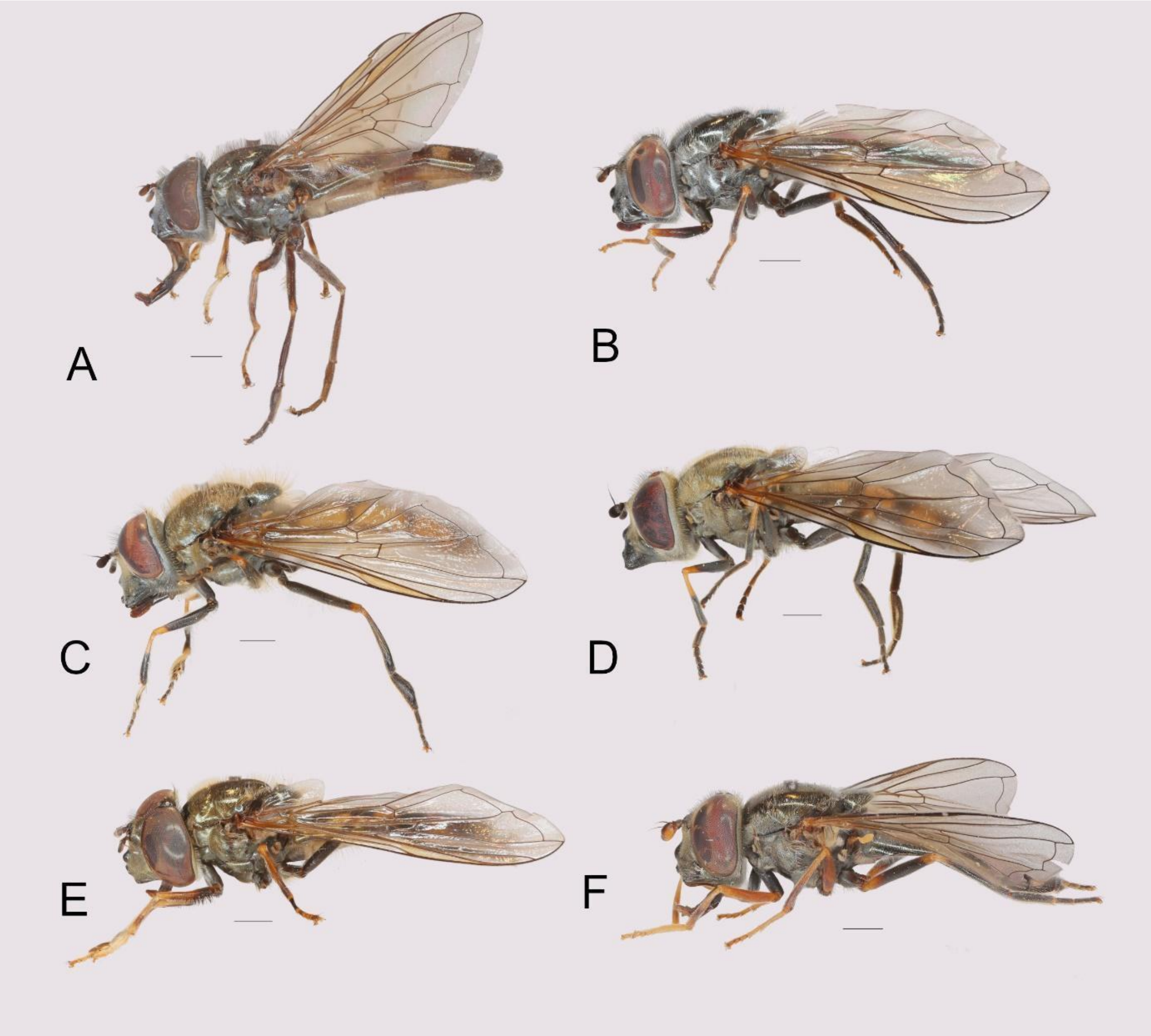

Figure 7. Habitus of *Platycheirus* species, lateral view. **A**. *P. islandicus* ♂, Skaftafell, Iceland. **B**. *P. islandicus* ♀, ID No 2021-00.121, Iceland. **C**. *P. manicatus* ♂, ID No 2021-00.084, Iceland. **D**. *P. manicatus* ♀, ID No 2021.00-199, Iceland. **E**. *P. peltatus* ♂, Doorn, The Netherlands. **F**. *P. peltatus* ♀, Storfors, Sweden. Scale 1,0 mm.

Type material studied: Lectotype ♂ and Paralectotypes (9 ♂♂, 4 ♀♀) have been studied by the first author (van Steenis & Goeldlin, 1998). Type locality: **Iceland**: Húsadalur and Hamraskógar. The whereabouts of this material is not sure as it was not found in Gothenburg where it was supposed to be (pers. comm. C. Jonsson and T. Nielsen).

Additional material studied: All listed in supplement 1. Only known from Iceland and distributed as seen in Fig. 11A.

Biology. Mostly connected to forested areas within *Betula* forest with a lush undergrowth of low and high herbs. Also found feeding on flowers of *Epilobium latifolium* L. on a further barren sandbank. Other flowers visited: *Angelica archangelica* L., *Geranium sylvaticum* L., *Ranunculus acris* L. and *R. reptans* L. Distributed over the entire island. The flight period is from the 27th of May to the 1st of August.

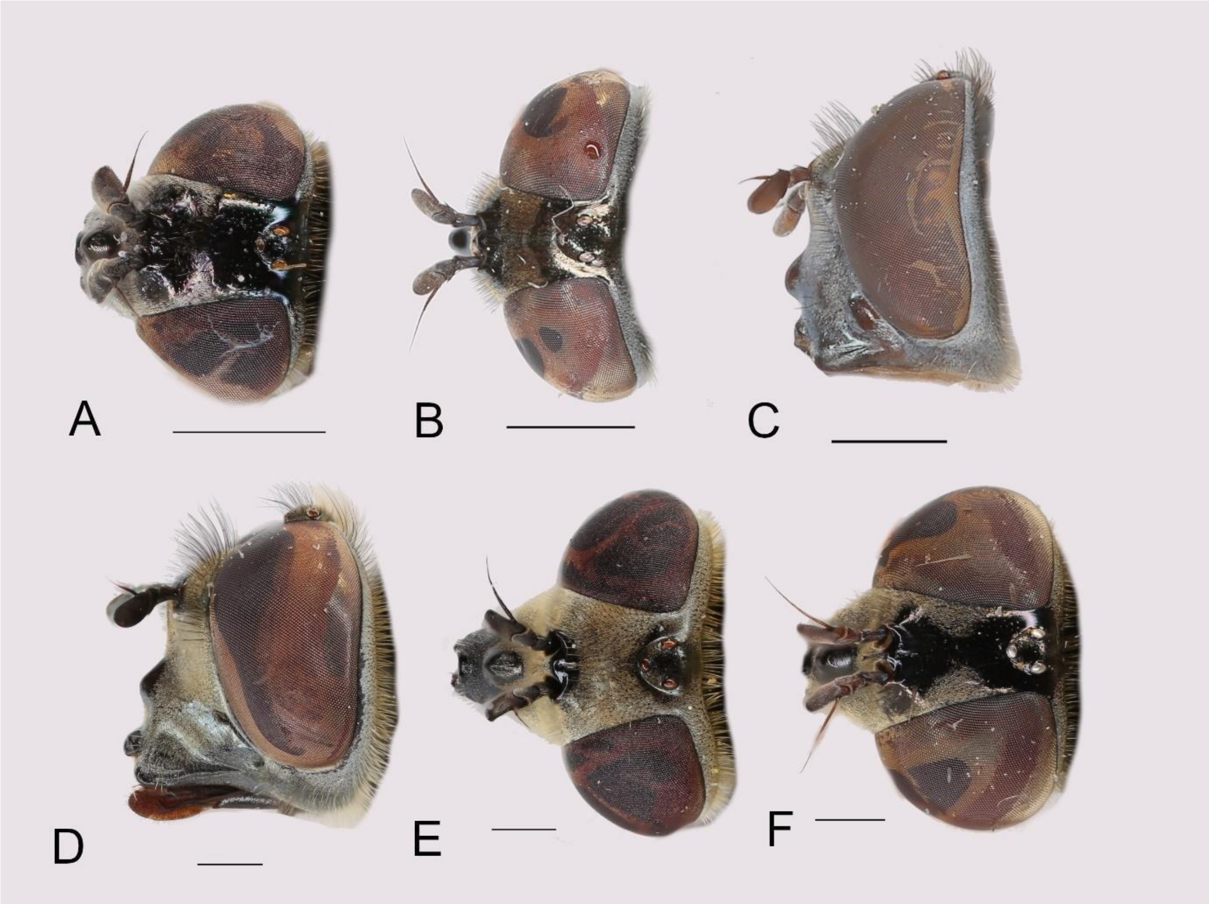

Figure 8. Heads of *Platycheirus* species; A, B, E, F dorsal view; C, D lateral view. **A**. *P. albimanus* ♀, ID No 2021-00.112, Iceland. **B**. *P. islandicus* ♀, ID No 2021-00.121, Iceland. **C**. *P. islandicus* ♂, Skaftafell, Iceland. **D**. *P. manicatus* ♂, ID No 2021-00.084, Iceland. **E**. *P. manicatus* ♀, ID No 2021.00-199, Iceland. **F**. *P. peltatus* ♀, Storfors, Sweden. Scale 1,0 mm.

Remarks. The DNA analysis clustered all the sequences of *Platycheirus islandicus* together, but among a larger cluster with other *Platycheirus* species. Nevertheless, the characters given in the diagnosis are clear enough to separate *Platycheirus islandicus* from *P. peltatus*. The variability of some characters turned out to be larger than stated in van Steenis & Goeldlin (1998), like the length and colour of the pile on the thorax and the shape of the metabasitarsomere.

The melanistic appearance will immediately separate this species from *P. manicatus* besides the differences in the shape of the face, the pruinosity on the thorax and the characters of the legs. The females with entirely black abdomen are similar to females of *Platycheirus albimanus* (Fabricius, 1781) and can be separated from this species by the somewhat larger size, *P. albimanus* smaller (Fig. 9A); the clypeal tubercle which is almost at level of the facial tubercle, in *P. albimanus* facial tubercle slightly more produced; frons with very large trapezoid-shaped pruinose maculae and also anterior part of frons extensively pruinose, in *P. albimanus* frons with very small, triangular shaped medio-lateral pruinose macula (Fig. 8A); scutum with mixed white and black pile, in *P. albimanus* entirely white pilose; scutellum with mixed black and white pile and length of pile along posterior margin much longer than length of subscutellar pile fringe, in *P. albimanus* entirely white pilose and marginal pile only very slightly longer than length of subscutellar pile fringe; femora almost entirely black, occasionally pro- and mesofemur apical 1/3 brown-yellow, in *P. albimanus* pro- and mesofemur predominantly brown-yellow.

Molecular data. Eight specimens of *P. islandicus* (GenBank accession numbers OP898506, OP898517, OP898519, OP898520, OP898523, OP898524, OP898525, and OP898526) were successfully sequenced. These eight COI sequences are very similar to one another (p-distance = 0.0–0.27%). In the NJ tree (Fig. 5) all specimens identified as *P. islandicus* clustered together, but embedded in a cluster that contains other species of the *peltatus* subgroup.

Except for *Platycheirus parmatus* (Rondani, 1857) and *P. ferrumitarsis* van Steenis *et al*. 2019, all other members of the *peltatus* subgroup were resolved in a large cluster, and within this large cluster only five species present all their individuals grouped together: *P. jaerensis* Nielsen, 1971 and *P. nearcticus* are resolved each in independent clusters; and all sequences of *P. inversus* Ide, 1926, *P. peltatoides* Curran, 1923 and *P. islandicus* cluster independently within a large group that lacks resolution for the rest of the taxa, namely specimens identified as *P. nielseni* Vockeroth, 1990, *P. peltatus*, *P. naso* (Walker, 1849), *P. amplus* (Curran, 1927) and *P. octavus* Vockeroth, 1990.

Platycheirus species of the *peltatus* subgroup show little interspecific difference in their COI sequences. The p-distance found between *P. jaerensis*, the most distinct taxon of this cluster, and any other member of the large group referring species of the *peltatus* subgroup (except *P. parmatus* and *P. ferrumitarsis*) is 1.39–2.83%, while all other species in the large cluster of the *peltatus* subgroup (including *P. nearcticus*) show interspecific p-distance below 2.0%.

***Platycheirus manicatus* Meigen, 1822**
Figs 6B, 7C, 7D, 8D, 8E, 9D, 10E, 10F

Diagnosis. Easy to distinguish in Iceland based on the extensively pruinose head and thorax (Figs 6B, 7C, 7D, 8D, 8E, 9D) and the large orange-yellow maculae on the abdomen (Figs 6B, 7C, 7D, 9D). In the male, the shape of the protibia and protarsus and the pilosity of the profemur (Figs 10E, 10F) are unmistakable.

Type material: No type material has been studied.
Additional material studied: Material from the following countries has been studied (supplement 1): Austria, Denmark, France, Germany, Iceland, Montenegro, the Netherlands, Norway, Sweden and Switzerland. The distribution on Iceland is shown in Fig. 11B.

Biology: On Iceland *Platycheirus manicatus* is a widespread species occurring in a wide range of biotopes, from rather barren seashores, to *Betula* forests and mountainous meadows. Mostly restricted to the South-West coast with two recent records from the North-East (Fig. 11). Found less frequently in the *Betula* forests than *Platycheirus islandicus*. *Platycheirus manicatus* has been found visiting flowers of *Hieracium* spp., *Plantago maritima* L., *Ranunculus acris*, *R. reptans*, *Rhinanthus minor* L., and *Stellaria media* (L.) Vill. The flight period in Iceland is from the 29th May to the 13th of September.

Remarks. The specimens of *Platycheirus manicatus* from Iceland are as brightly coloured as those from mainland Europe and they are also equal in size. The DNA barcodes are identical too and the specimens of the Icelandic and mainland European subpopulations are considered conspecific.

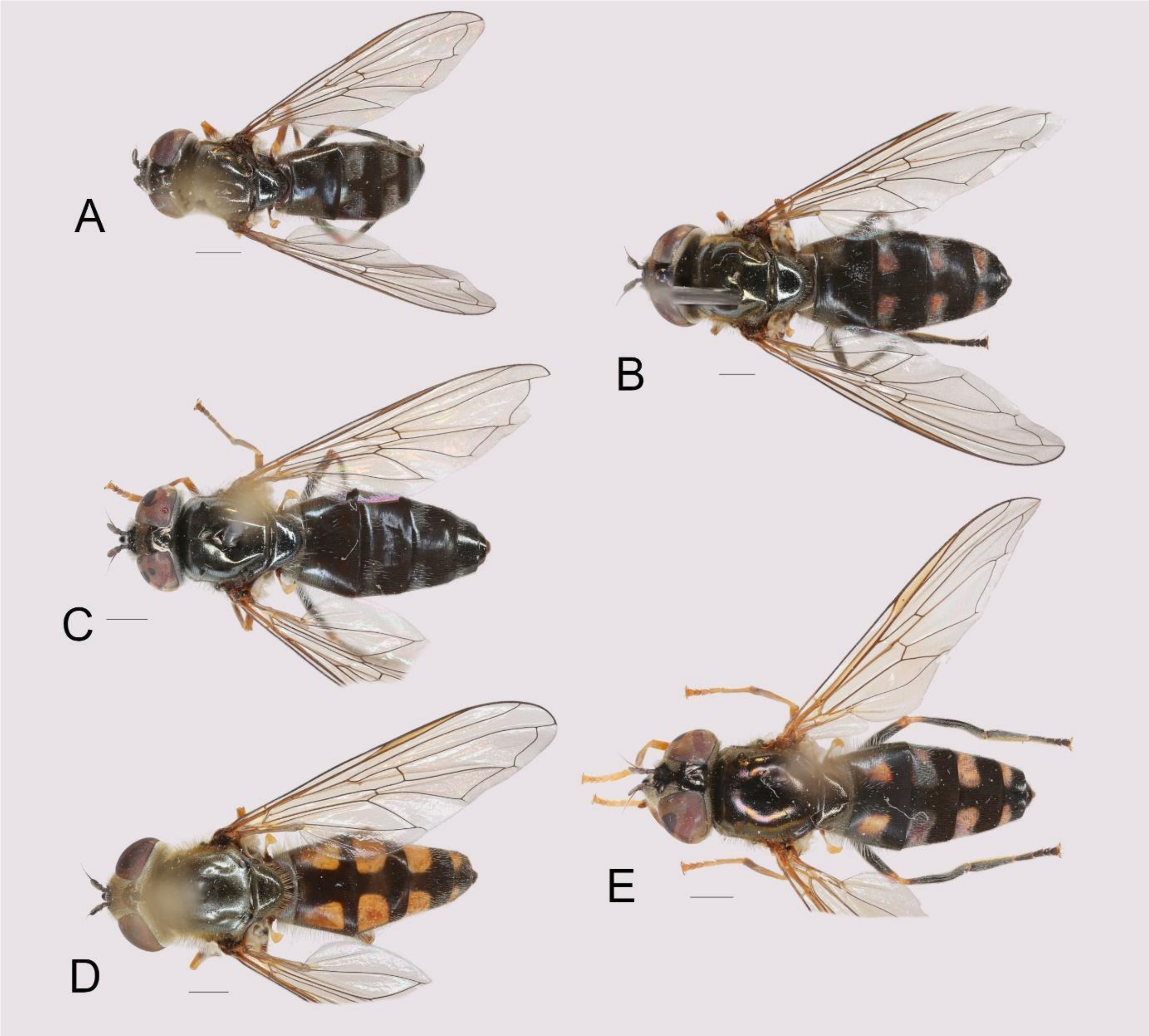

Figure 9. Habitus of *Platycheirus* species, dorsal view. **A**. *P. albimanus* ♀, ID No 2021-00.112, Iceland. **B**. *P. islandicus* ♀, ID No 2021-00.121, Iceland. **C**. *P. islandicus* ♀, ID No 2021-00.132, Iceland. **D**. *P. manicatus* ♀, ID No 2021.00-199, Iceland. **E**. *P. peltatus* ♀, Storfors, Sweden. Scale 1,0 mm.

Molecular data. Three specimens of *P. manicatus* collected on Iceland (GenBank accession numbers OP898511, OP898514, and OP898518) were successfully sequenced. These three COI sequences are very similar to one another (p-distance = 0–0.11%) and also quite similar to other barcode sequences from Palaearctic specimens identified as *P. manicatus* (0.11–1.15%). This intraspecific variability between Icelandic *P. manicatus* and other Palaearctic individuals lies in the range seen for the whole species (maximum p-distance: 1.25%; between DRYAS11256-15 [Russia] and AMTPD4491-16 [Germany]). In the NJ tree (Fig. 5), all specimens identified as *P. manicatus* clustered together.

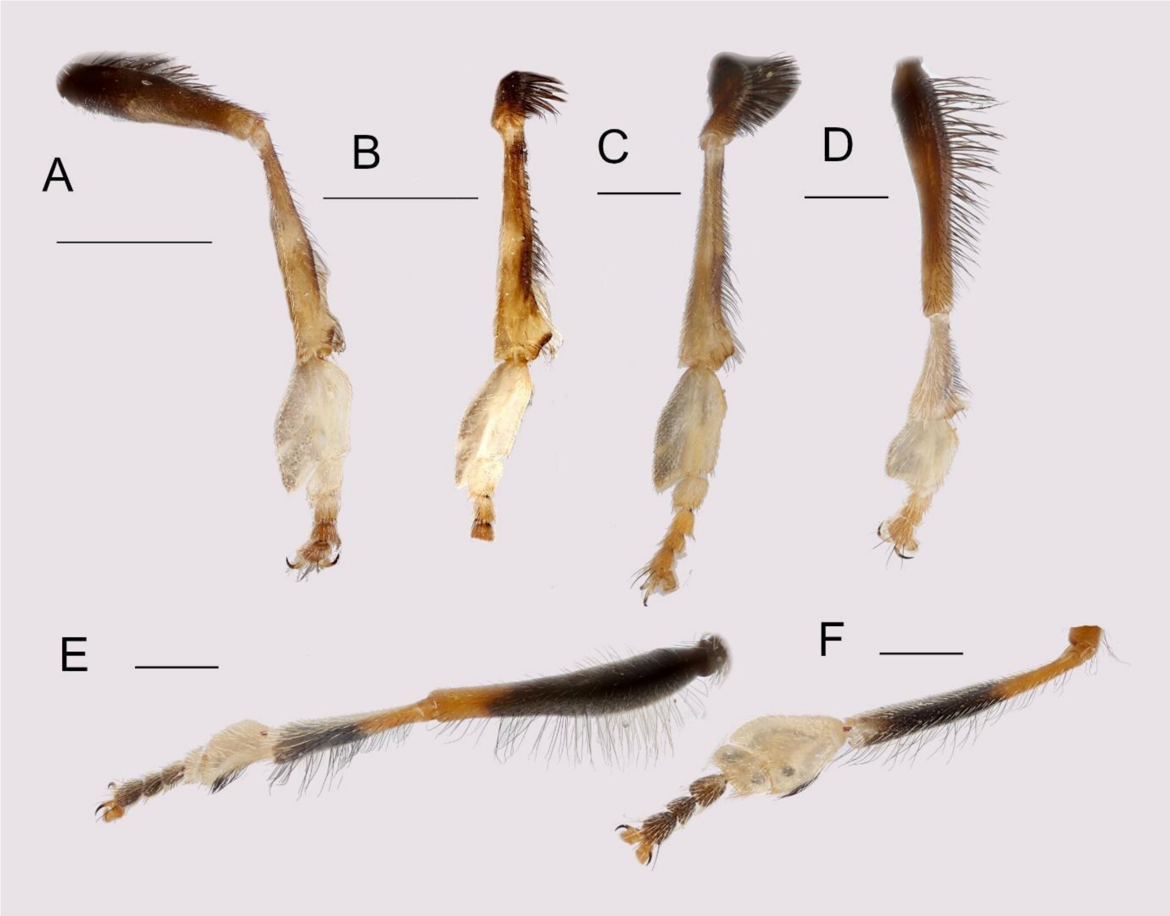

Figure 10. Proleg of *Platycheirus* species, dorsal view. **A**. tarsus, *P. islandicus* ♂. Skaftafell, Iceland. **B**. tibia, *P. islandicus* ♂. Skaftafell, Iceland. **C**. tibia and tarsus, *P. peltatus* ♂, Doorn, The Netherlands. **D**. femur, *P. peltatus* ♂, Doorn, The Netherlands. **E**. femur and tibia, *P. manicatus* ♂, ID No 2021-00.084, Iceland. **F**. tarsus, *P. manicatus* ♂, ID No 2021-00.084, Iceland. Scale 1,0 mm.

Discussion

Melanism occurs frequently in Syrphidae, most often in relatively small and infertile females (Doesburg 1964) or intersex specimens (van Steenis *et al*. 2019), who also tend to be smaller than normally developed conspecific specimens. In other animal groups there is also a tendency in arctic species to be larger than their sibling species occurring in a more temperate climate, known as the Bergman's rule (Salewski & Watt 2016), although colour tends to be brighter for the arctic individuals. Another interesting phenomenon is that species from the Atlantic Islands and the tropical rainforest tend to be darker (Goldenberg *et al*. 2022). These phenomena are considered as either the Bergman's or the Gloger's rule, but they can also be explained as phenotypic plasticity (Bradshaw 1965; Ottenheim *et al*. 1996; Shelomi 2012; Salewski & Watt 2016; Delhey 2019). Many more theories exist, from the *thermal melanism hypothesis* to the *fire-driven camouflage coloration hypothesis*, with conflicting outcomes concerning the formation of darker and larger specimens under certain circumstances (Clusella-Trullas & Nielsen 2020; Delhey *et al*. 2020; Goldenberg *et al*. 2022).

Colour dependence on pupal temperature is known for many genera of Syrphinae (e.g., *Episyrphus* Matsumura, 1917; *Eupeodes* Osten-Sacken, 1877; *Sphaerophoria* Lepeletier & Serville, 1828), as well as for some Eristalini (Dušek & Láska 1974; Heal 1982; Holloway 1993; Wright & Skevington 2013; Young *et al*. 2016) leading to darker individuals under colder conditions. The hypotheses behind melanism are however multifactorial and at least five mechanisms play a role in it, namely a colder climate, a wetter climate, higher UVB radiation, higher fire frequency and higher desiccation risk; all giving rise to darker specimens (Clusella-Trullas & Nielsen 2020). A darker and also larger body in ectotherms enables a better thermoregulation in a colder climate (Goldenberg *et al*. 2022).

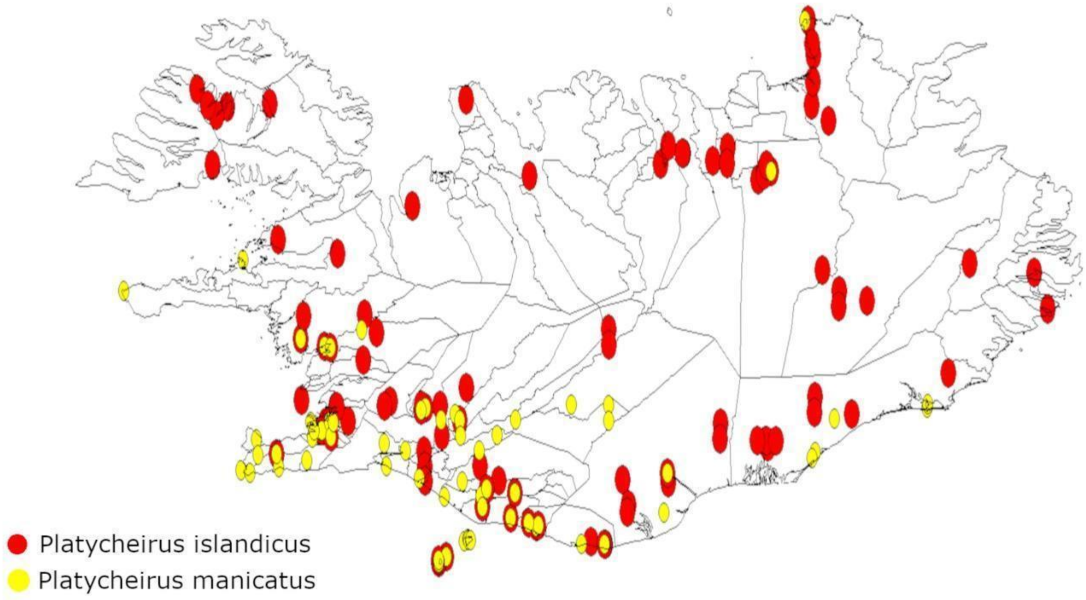

Figure 11. Distribution map of *Platycheirus islandicus* and *P. manicatus* on Iceland.

Specimens of *Platycheirus islandicus* are larger than the mainland specimens of *P. peltatus*, and many *P. islandicus* specimens have weakly developed orange-brown to dark-yellow spots, a phenomenon seen in other arctic and island endemic hoverfly species (Frey 1945; Knutson 1971; Wakeham-Dawson *et al*. 2004). Many of the Syrphinae on Iceland consist of dark coloured specimens, such as *Eupeodes lundbecki* (Soot-Ryen, 1946); *Melanostoma mellinum* (Linnaeus, 1758); *Parasyrphus tarsatus* (Zetterstedt, 1838) and *Syrphus torvus* Osten Sacken, 1875 (Lambeck 1968). Most of these species are Holarctic in distribution and the occurrence of dark coloured individuals in the Nearctic region has been reported (Vockeroth 1992; Young *et al*. 2016). In the genus *Platycheirus* there is one exception, *P. manicatus*, whose Icelandic individuals are almost as brightly coloured as those from mainland Europe. Dark coloured Icelandic specimens identified as *Platycheirus islandicus* might be just a dark variation of *P. peltatus* caused by phenotypic plasticity, like it is found in *Eristalis* Latreille, 1804 (Ottenheim *et al*. 1996; Ottenheim *et al*. 1998; Holloway 1993); or they might indeed belong to different species. We believe that *Platycheirus islandicus* represents a valid taxon separated from *P. peltatus*. as seen in the differential diagnosis and the discussion on the molecular data and that given below.

Iceland is an island created by volcanic activity along the Mid-Atlantic Ridge, a divergence zone between the Eurasian and North-American sub continental plates (Harðarson *et al*. 2008; Heezen *et al*. 2012). There is evidence that land bridges have existed from the Faroe Islands over Iceland to Greenland circa 55 and 9 Mya (McKenna 1975; Gradstein *et al*. 1994; Denk *et al*. 2011) and colonisation of Iceland occurred over these land bridges. Iceland has been covered in ice several times and during the latest Weichselian Ice Age a nearly entirely closed ice sheet was present (Brochmann *et al*. 2003; Geirsdóttir *et al*. 2009; Ingólfsson *et al*. 2010). The current fauna of Iceland consists of species that survived during the Last Glacial Maximum or of species that recolonised Iceland since circa 10.000 years BP.

The pre- Ice Age fauna, as based on fossils from the tertiary, was similar to the Nearctic fauna (Grímsson *et al*. 2007). The current fauna, however, is much more similar to that of the Palaearctic region (Böcher 2001) indicating the recolonization after the latest Ice Age. The establishment of the current fauna is based on the nunatak or the *tabula rasa* hypotheses (Fernald 1925; Lindroth 1931; Buckland & Dugmore 1991; Holder *et al*. 1999; Brochmann *et al*. 2003). The *tabula rasa* theory, now accepted as the most likely (Buckland & Panagiotakopulu 2010; Panagiotakopulu 2014; Vickers & Buckland 2015; Gíslason & Pálson 2020), builds on the idea of a rapid warming and subsequent melting of the ice sheet causing an influx of ice sheet transported debris, and thus flora and fauna, with the Atlantic currents, moving the melting ice from Scotland and especially SW Norway to the northern parts of Iceland (Buckland *et al*. 1986; Buckland & Dugmore 1991; Panagiotakopulu 2014). In that framework, a *Platycheirus* species might have colonised Iceland and speciated over 10.000 years into *P. islandicus*.

The occurrence of *Eupeodes nigriventris* Fluke, 1933 (not *E. rufipunctatus* Curran, 1925, see Evenhuis & Pape 2022), a species described from Greenland and only known from the Nearctic region, might be explained by the nunatak hypothesis: a taxon that survived during the ice-age(s) on land masses or mountains not covered by the ice-sheet, i.e. Nunataks. The influx of melanistic Nearctic specimens into Iceland like *Parasyrphus tarsatus*, *Pyrophaena granditarsa* (Foster, 1771) and *Syrphus torvus* could maintain a constant gene flow not causing speciation like in *Platycheirus islandicus*. These previously mentioned species show phenotypic plasticity while the Palaearctic fauna elements like *Platycheirus islandicus* have colonised Iceland once through the *tabula rasa* hypothesis.

The migration of species of Syrphidae is well documented (Shannon 1916, 1926; Heydemann 1967; Nielsen 1967; Jeekel & Overbeek 1968; Aubert *et al*. 1976; Gatter & Schmid 1990; Menz *et al*. 2019; Wotton *et al*. 2019). Migration of Syrphidae has been recorded both during spring and autumn and includes species from the subfamily Syrphinae like *Episyrphus balteatus* (De Geer, 1776); *Eupeodes corollae* (Fabricius, 1794); *Platycheirus albimanus*; *P. manicatus*; *P. scutatus* (Megen, 1822); *Scaeva selenitica* (Meigen, 1822); *Sphaerophoria scripta* (Linnaeus, 1758); *Syrphus ribesii* (Linnaeus, 1758) and *Syrphus torvus*, as well as from the tribe Eristalini, such as *Eristalis arbustorum* (Linnaeus, 1758); *E. tenax* (Linnaeus, 1758) and *Helophilus pendulus* (Linnaeus, 1758) (e.g. Nielsen 1968; Aubert *et al*. 1976; Gatter & Schmid 1990; Speight 1996; Menz *et al*. 2019; Fisler & Marcacci 2023; Hlaváček *et al*. 2022). Some species migrate distances of up to 160 km in 6 to 10 hours (Aubert & Goeldlin 1981) making long distance migrations a likely scenario. However, investigating an invasion of migrating insects on the Faroe Islands Jensen (2001) found that, during the same period, almost the same species of Lepidoptera were observed on both the Faroe Islands and on Iceland but no migrating Syrphidae were recorded on Iceland. Long distance migration of Syrphidae over land and sea has been found in recent studies (Hu *et al*. 2016; Gao *et al*. 2020; Clem *et al*. 2022; Hawkes *et al*. 2022). Species of the *Platycheirus peltatus* subgroup are known for their hill-topping behaviour, while they are seldom recorded as migratory species (Aubert *et al*. 1976; Gatter & Schmid 1990; Young *et al*. 2016). The establishment of *Platycheirus manicatus* seems to be of recent origin as it is not mentioned by the early researchers (Ringdahl 1930; Lindroth 1931) and firstly recorded by Lambeck (1968) from South-West Iceland. Since then, *Platycheirus manicatus* has spread over the country and is present now along the entire south coast, with two additional records from the North-East (Fig. 11).

Only three hoverfly (sub)species have been reported as endemic to Iceland, namely *Platycheirus islandicus* Ringdahl, 1930; *Pyrophaena granditarsa* var. *lindrothi* Ringdahl, 1930 and *Syrphus ribesii* var. *interruptus* Ringdahl, 1930 (Ringdahl 1930; Lambeck 1968; van Steenis & Goeldlin 1998). In other Diptera families also a very few endemic (sub)species are known, most of which are melanistic compared to their widespread nominate species: two species of Sciaridae and four subspecies in the families Agromyzidae, Muscidae and Mycetophilidae respectively (Nielsen *et al*. 1954). In birds, however, several endemic subspecies are known, e.g. Merlin, Rock Ptarmigan, Black tailed Godwit, Raven, Eurasian Wren, Redpoll, Redwing and Purple Sandpiper (Holder *et al*. 1999; Alves *et al*. 2010; Barisas *et al*. 2015). In the light of the long-distance migratory behaviour of several of these bird species flying non-stop distances of up to 10.000 km in 7 days (Battley *et al*. 2012; Conklin *et al*. 2017) and the relatively short migration distances in Diptera (Aubert & Goeldlin 1981), it is likely that more Icelandic Diptera species would classify as endemic (sub)species.

The occurrence in Iceland of a melanistic form of *Platycheirus peltatus* (those specimens here identified as *P. islandicus*) but a normal-coloured form of *P. manicatus* is unlikely in our opinion, and we already discussed the hypothesis that the Icelandic *P. islandicus* is a taxon separate from the mainland *P. peltatus*. The pairwise distances of the COI gene sequences between these two taxa is rather small, which may indicate a recent loss of the gene flow between them (among other causes). These facts make the survival *in situ* of an Icelandic taxon during the ice age as part of the nunatak hypothesis unlikely. While *Platycheirus peltatus* and *P. manicatus* both are elements of the Palaearctic fauna only, post-glacial immigration to Iceland (*tabula rasa* hypothesis) is thus more likely to have occurred. Migration is documented in *Platycheirus manicatus* while *P. peltatus* seems to be a non-migrant taxon. Based on the COI gene sequences and the morphological evidence we conclude that the Icelandic specimens belong to a different taxon, namely *Platycheirus islandicus*, and that this species is a post-glacial coloniser of Iceland through the *tabula rasa* hypothesis. On the other hand, *Platycheirus manicatus* is a recent coloniser of Iceland by its migratory activity and the similarity in the COI gene indicating a continuing gene flow between the European mainland and the Icelandic population.

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