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ORIGINAL ARTICLE

Morphological and molecular insights into the invasive strawberry aphid *Chaetosiphon fragaefolii* – a critical pest and virus vector new to Poland

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Abstract

The present research reports the first record in Poland of the alien invasive and quarantine species *Chaetosiphon* (*Pentatrichopus*) *fragaefolii* (Cockerell, 1901) – the strawberry aphid. Native to North America, it is a critical pest and viral vector associated with strawberry crops. This study provides valuable insights into the genetic and morphological characteristics of the strawberry aphid. By integrating morphological and molecular analyses, the taxonomic resolution has been improved and deepened the understanding of this economically important species, particularly its genetic diversity, distribution, and potential invasion routes. For the first time, scanning electron microscopy (SEM) analyses were performed to elucidate the general morphology, chaetotaxy, and sensilla of the antennae and mouthparts of this species, providing a better understanding in the context of its natural and chemical control.

Keywords: alien species, aphids, *Fragaria*, sensilla, virus vectors

Introduction

Invasive alien species constitute serious challenges to quarantine measures, threaten economically important crops, and are harmful to native ecosystems (Hurley *et al.* 2016; Panzavolta *et al.* 2021). Their global introduction has accelerated due to climate change and the intensification of international trade (Kim *et al.* 2024).

Insects are the most common of the vectors, and among these, aphids account for the transmission of 50% of insect-vectored viruses (Nault 1997; Ng and Perry 2004). Aphids are among the most important plant pests worldwide, particularly due to their global distribution and the more than 200 species known to act as plant virus vectors (Eastop 1983; Hull 2002; Nault 1997). They are highly adapted for their role as vectors. Their piercing-sucking mouthparts facilitate the delivery of virions into plant cells without causing irrevocable damage. Through asexual reproduction, aphid populations can increase at extraordinarily high rates, thereby potentiating disease epidemics and enhancing both short- and long-distance virus transmission (Ng and Perry 2004; Alford 2012; Blackman and Eastop 2006; Brault *et al.* 2010; Guerrieri and Digilio 2008).

The genus *Chaetosiphon* contains 18 species in three subgenera: *Chaetosiphon*, *Chaitomyzus* and the most economically important *Pentatrichopus* (Remaudière and Remaudière 1997; Blackman and Eastop 2006). Unlike other genera in the tribe Macrosiphini, species of this genus are characterized by their yellowish-white to dark-green apterous and alate viviparous females, with the latter additionally distinguished

by a large black dorsal abdominal patch. The dorsum of apterous viviparous females is densely covered with small warts on abdominal segments, tuberculate bases, or protuberances of setae. The head of apterae has well-developed frontal tubercles, antennae have secondary rhinaria, and the first segment of the tarsi have 5-5-5 setae (Blackman 2010). The economically important species of *Pentatrichopus* can be easily recognized among other *Chaetosiphon* by the presence of siphunculi without setae (Heie 1994). Members of *Chaetosiphon* are widely distributed in the Northern Hemisphere. They predominantly live without host alternation, and are associated with Rosaceae of the *Rosa-Fragaria-Potentilla* group (Blackman 2010). One species, the strawberry aphid *Chaetosiphon fragaefolii* (Cockerell 1901), which is native to North America, is considered an important alien species in Europe and pest of cultivated strawberries worldwide. *Chaetosiphon fragaefolii* transmits at least four viruses, most notably *Cytorhabdovirus*, also known as strawberry crinkle virus (SCV), one of the most dangerous viruses affecting strawberry (Alford 1976; Krczal 1979; Alford 2007; Wieczorek *et al.* 2019; Rondon *et al.* 2022; EPPO 2025).

The strawberry aphid *Chaetosiphon fragaefolii* was described in Arizona, USA in 1901 (Cockerell 1901) and since then has been reported from several localities. Besides Arizona, this serious strawberry pest has been reported in California, Florida, Illinois, Michigan, Minnesota, South Carolina, and Washington (USA), Argentina, Australia, Canada, Chile, Japan, northern Mexico, New Zealand and South Africa (Hottes and Frison 1931; Miyazaki 1971; Blackman and Eastop 2000; Rondon and Cantliffe 2004; Cédola and Greco 2010; Lavandero *et al.* 2012). Since the very first reports of its presence in the UK (Theobald 1912) and France (Balachowsky 1933), in Europe, strawberry aphid has been recorded in Austria, Belgium, Bulgaria, Croatia, the Czech Republic, Hungary, Germany, Ireland, Italy (including Sicily), Latvia, North Macedonia, the Netherlands, and Norway (caught in a suction trap in Akerhus according to Heie (1994), but according to Krokene *et al.* (2021), it has been reported only once and is now considered absent), Portugal (including the Azores and Madeira), Romania, Serbia, Slovenia, Spain (including the Canary Islands), Sweden and Switzerland (Krczal 1982; Ilharco 1973, 1984; Karl *et al.* 1978; Tashev 1985; Milenković 1993; Nieto Nafría 1976; Nieto Nafría *et al.* 1984; Heie 1994; Holman 2009; Coeur d'acier *et al.* 2010; EPPO 2025). With this background, the territory of Poland seemed to have remained free of this alien pest species. Voluminous research (including alien species reports) has been conducted in the southern and western parts of the country (e.g., Osiadacz and Wieczorek 2006; Osiadacz and Wojciechowski 2008; Wieczorek 2011; Wojciechowski *et al.* 2011; Trela and Herczek 2014; Starowicz *et al.* 2015; Kaszyca *et al.* 2018; Kanturski *et al.* 2017, 2018a; Kaszyca-Taszakowska and Depa 2019; Wieczorek and Chłond 2019; Wieczorek *et al.* 2024), as well as in Slovakia, where the species is still absent (Wojciechowski *et al.* 2016).

In 2020, representatives of *Chaetosiphon fragaefolii* were discovered in southern Poland for the first time, and since then have been observed on commercially grown strawberry (*Fragaria* x *ananassa*). This study had two primary objectives. First, it aimed to monitor and identify the strawberry aphid associated with strawberry crops in Poland through comprehensive morphological and molecular analyses. For the first time, scanning electron microscopy (SEM) research was conducted to elucidate the gross morphology and sensilla of this species. For molecular identification, genetic divergences within and between species were assessed using the mitochondrial cytochrome c oxidase subunit I (COI) gene, which is a reliable marker for aphid species identification. Second, there was an attempt to predict the potential invasion routes of the strawberry aphid. To achieve this, a TCS network analysis of haplotypes was performed, alongside the construction of a neighbor-joining (NJ) tree based on genetic distance data.

Materials and Methods

Materials

The first colony of several apterous viviparous females and alatoid nymphs of the species *Chaetosiphon fragaefolii* was discovered on July 13, 2020 in Branice, Opole Voivodeship (Southern Poland) (50°03,05'N; 17°47,09'E) on *Fragaria* x *ananasa* var. Toscana (Fig. 1). The observations were continued successively in 2021 and 2022 in Branice and in subsequent years in other localities in the Opole and Silesian regions. Aphids for morphological study were preserved in 80% ethanol and in 99.6% ethanol to undergo molecular analysis.

Molecular protocol

Genomic DNA was extracted from individual samples collected from the colony using the DNeasy Blood & Tissue kit (Qiagen, Dusseldorf, Germany) following a modification of the protocols. A 513 COI bp of the cytochrome oxidase I gene (COI) was amplified using the following set of primers: LepF 5'-ATTCAACCAATCATAAAGATATTGG-3' and LepR 5'-TAAACTTCTGGATGTCCAAAAAATCA-3'.

Polymerase chain reaction (PCR) was performed using AccuPower PCR Premix (Bioneer, Daejeon, Republic of Korea) in 20 µl reaction volumes. The amplification protocol consisted of an initial denaturation at 94°C for 3 minutes, followed by 35 cycles at 94°C for 30 s, an annealing temperature of 45.2°C for 30 seconds, extension at 72°C for 1 minute, and the final extension step at 72°C for 5 minutes. PCR products were checked in 1.5% agarose gel, purified, and sequenced at Bionics, Inc. (Seoul, Republic of Korea).

Molecular data analysis

A total of 23 COI sequences of *Chaetosiphon* spp. were analyzed, including three sequences generated in this study and 20 sequences retrieved from GenBank (Supplementary Table 1). *Phylloxera coccinea* (GenBank accession number: MG403377) was used as the outgroup. The sequences generated in this study have been deposited in GenBank (accession numbers PV013678 to PV013680) and are detailed in Supplementary Table 1. Raw sequences were assembled and edited using SeqMan Pro v7.1.0 (DNASTAR, Inc., Madison, Wisconsin, USA). Sequence alignment and neighbor-joining (NJ) tree analyses were performed using MEGA 7 (Kumar *et al.* 2016) under the Kimura-2-Parameter (K2P) model. Haplotype data were generated using DnaSP v6.12.03 (Rozas *et al.* 2017) to identify unique haplotypes. A haplotype network was constructed to infer population-level gene genealogies and visualize haplotype relationships using the statistical parsimony approach implemented in TCS v1.2.1 (Clement *et al.* 2000) and PopART (Leigh and Bryant 2015).

Scanning electron microscopy

Dehydration of the ethanol preserved samples was provided by ethanol series of 80, 90, 96% and two changes of absolute ethanol for 10 minutes each. From absolute alcohol the samples were transferred to pure chloroform and stored at room temperature for 24 h. Dehydrated and cleaned specimens were dried using the Leica EM CPD 300 auto critical point dryer (Leica Microsystems, Vienna, Austria). Dry samples were mounted on aluminum stubs with double-sided adhesive carbon tape and sputter-coated with a 30 nm layer of gold in a Quorum 150 T ES Plus sputter coater (Quorum Technologies Ltd., Laughton, East Sussex, UK). The specimens were imaged with the Hitachi SU8010 field emission scanning electron microscope (FESEM; Hitachi High-Technologies Corporation, Tokyo, Japan) at 10 kV accelerating voltage with a secondary electron detector (ESD) in the SEM laboratory of the Institute of Biology, Biotechnology and Environmental Protection, University of Silesia in Katowice (Katowice, Poland).

Results

Morphological identification

Apterous viviparous females of the strawberry aphid *Chaetosiphon fragaefolii* collected on *Fragaria* x *ananassa* in Poland were translucent greenish-yellow with yellowish-brown appendages (antennae and legs) (Fig. 1). In mounted specimens, according to Blackman and Eastop (2006), the aphids differ from other species found on *Fragaria* by the following characteristics:

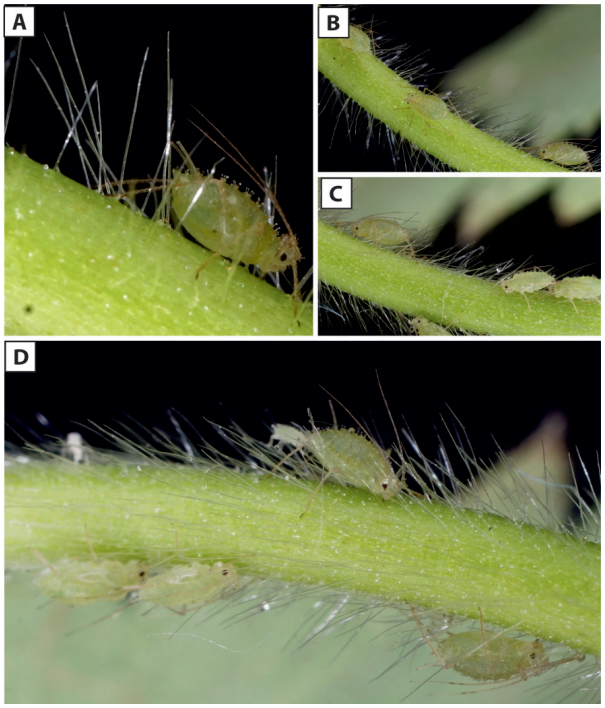

Fig. 1. *Chaetosiphon fragaefolii* apterous viviparous females in life: A – habitus and color, B–C – apterous viviparous females and nymphs of *C. fragaefolii* on the petiole of Fragaria × ananassa, D – apterous viviparous female giving birth to first instar nymph

Processus terminalis much longer than the basal part of the sixth antennal segment (characteristic distinguishing it from *Eriosoma* sp. and *Smynthurodes betae*),

Dorsal body with at least some long, thick hairs, with capitate apices, and arising from tuberculate bases (characteristic distinguishing it from species of the genera: *Abstrusomyzus*, *Acyrthosiphon*, *Amphorophora*, *Aphis*, *Aulacorthum*, *Brachycaudus*, *Dysaphis*, *Ericaphis*, *Hyalomyzus*, *Macrosiphum*, *Myzaphis*, *Neomyzus*, *Rhodobium*, *Rhopalosiphoninus* and *Sitobion*) (Fig. 2, Figs. S1, S2),

First antennal segment without a finger-like process on the inner side (characteristic distinguishing it from species of the genus *Matsumuraja*) (Fig. 2A),

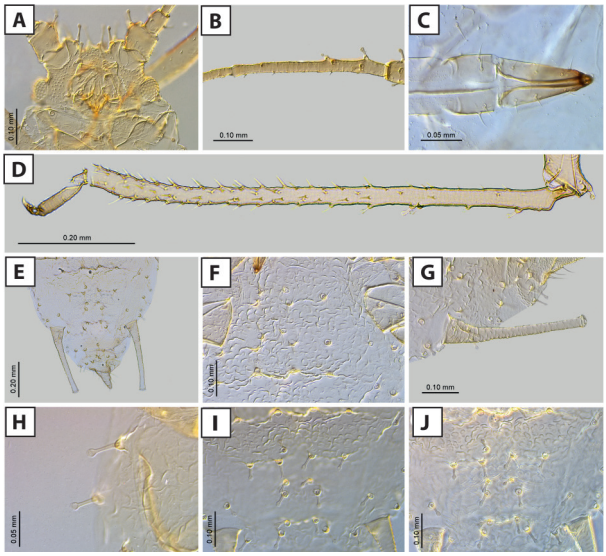

Fig. 2. *Chaetosiphon fragaefolii* apterous viviparous female main morphological characteristics: A – head and antennal tubercles chaetotaxy, B – antennal segment III, C – ultimate rostral segment, D – hind tibia, E – abdomen, F – dorsal abdominal microsculpture, G – siphunculus, H – dorsal abdominal setae shape, I – dorsal chaetotaxy DIC, J – dorsal chaetotaxy (phase contrast)

At least four long capitate setae (two spinal and two marginal) on each abdominal tergite I-V (characteristic distinguishing it from *Chaetosiphon minor*) (Fig. 2H–J),

Pale dorsal abdomen (characteristic distinguishing it from *Chaetosiphon jacobi*) (Fig. 2E).

Molecular confirmation and analysis

Genetic divergence

Genetic divergences among all species included in this study are presented in Table 1. Except for one species (*Chaetosiphon tetrarhodum*), which has only one sequence, a total of 231 comparison pairs for one species (*Ch. fragaefolii*) were analyzed within the species. The average intraspecific genetic divergence (GD) for *Ch. fragaefolii* was 0.1%, with a maximum intraspecific divergence of 0.8%. Interspecific GD was calculated using 22 pairwise comparisons. The minimum interspecific GD was 7.8%, observed between *Ch. tetrarhodum* and *Ch. fragaefolii*, while the maximum interspecific GD was also 7.8% (average: 7.8%) between the same species pair.

Neighbor-joining tree analysis

Species identification was conducted using phylogenetic analysis with neighbor-joining (NJ) tree construction, a heuristic approach based on genetic distance. The analysis revealed that *Chaetosiphon fragaefolii* and *Ch. tetrarhodum* grouped into two distinct clades, designated as clade A and clade B, respectively (Fig. 3A). In clade A, individuals of *Ch. fragaefolii* from Ontario and New Brunswick, Canada, were the first to branch out. Subsequently, populations from Poland, the Czech Republic, and other regions of Canada (Alberta, British Columbia, Manitoba, and Nova Scotia) formed a single cohesive subclade within clade A, supported by high bootstrap values (BS = 100%).

Haplotype analysis

The TCS network analysis identified three haplotypes from the 24 COI sequences analyzed (Fig. 3B). Details of haplotype distribution across all individuals are provided in Supplementary Table 1. Among the 23 sequences of *Chaetosiphon fragaefolii* and *C. tetrarhodum*, three distinct haplotypes (Hap_1–Hap_3) were detected. Hap_1 and Hap_2, representing 22 sequences, were associated with *Ch. fragaefolii*. Hap_1 was observed in populations from Poland, the Czech Republic, and Canada (Alberta, British Columbia, Manitoba, Nova Scotia). Hap_2 was identified exclusively in samples from Canada (New Brunswick, Ontario). In contrast, Hap_3, representing two sequences, was attributed to *Ch. tetrarhodum*.

SEM morphology and sensilla of apterous viviparous females of *Chaetosiphon fragaefolii*

General morphology

Apterous viviparous females of *C. fragaefolii* are oval with a characteristic dorsal side of the body covered with numerous well-visible tuberculate setal bases and sculptured cuticle (Fig. 4A). The prothorax is well separated from the head and from the rest of the thorax,

Table 1. Genetic divergences within all species included in this study

(1) Intraspecific genetic divergence				
Species	comparison pairs (CP)	intraspecific genetic divergence		
		maximum	minimum	average
Chaetosiphon fragaefolii	231	0.8	0.0	0.1
(2) Interspecific genetic divergence				
Species	*Chaetosiphon tetrarhodum*			
Chaetosiphon fragaefolii	CP = 22, Ave. 7.8 (Min.7.8–Max.7.8)			

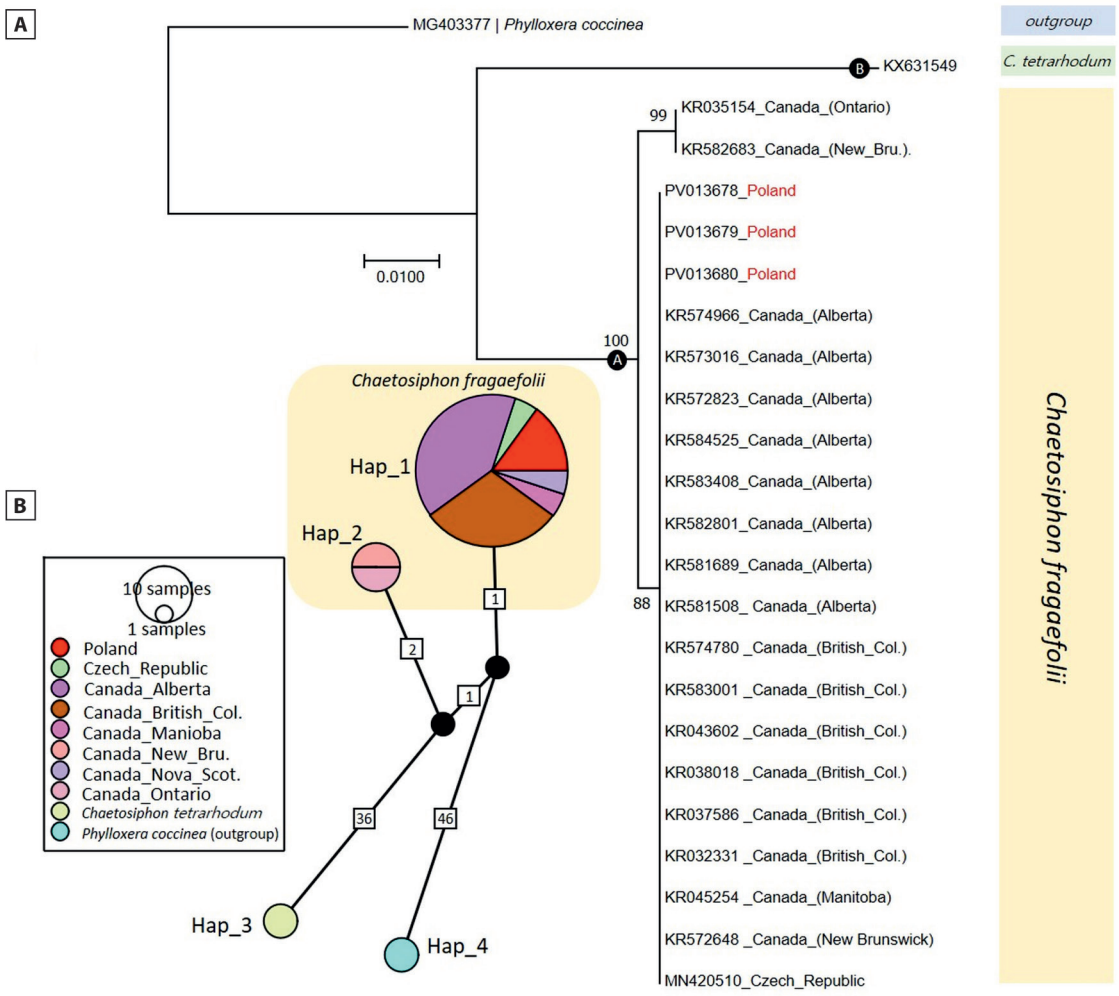

Fig. 3. Molecular data analysis of *Chaetosiphon* species of the 24 COI sequences: A – neighbor-joining tree analysis. The species name and distribution information for each individual, B – TCS networks of 4 haplotypes, with pie sizes proportional to haplotype frequency. The number in the box indicates the number of mutations

which is visible from the dorsal and lateral sides of the body (Fig. 4A, B). The mesothorax can be distinguished from other parts by two transverse wrinkles, but the metathorax is fused with abdominal tergites (Fig. 4A, B). Evident and characteristic sculpture can also be found on both sides of the abdomen in particular. Also, long, thick, capitate setae are visible on the dorsal side of the head, thorax, and abdomen (Fig. 4B). The ventral side of the body is covered with fine, pointed setae, and the cuticle sculpture is different from the dorsal one in the form of scales (head and thorax) and regular denticles (abdomen) (Fig. 4C). The head of apterous viviparous females is characterized by very well-visible sculpture in the form of robust denticles on the dorsal and ventral sides as well as long, thick, capitate trichoid sensilla on narrow-tuberculate bases (Fig. 5A–C). The compound eyes are semispherical with very well-developed, rounded ommatidia and well-defined triommatidia on an ocular tubercle (Fig. 5D, E). Siphunculi are long, tubular, slightly curved, and slightly wider at the bases (Fig. 5F, G). The surface of siphunculi is wrinkled, with well-visible, wide denticles with five to seven minute scales at the wide end (Fig. 5H). The siphunculi flange is well-developed, rounded and slightly rolled up outside (Fig. 5I). Abdominal segment VIII is separated from the rest of the abdominal segments. The cauda is triangular from the dorsal view and finger-like from the lateral side (Fig. 5J, K). The genital plate is well-developed and rectangular in shape, with anterior and posterior setae (Fig. 5L).

Antennal sensilla

The antennae bear the majority of known sensilla in aphids. All segments of both antennae bear type I trichoid sensilla, which in the case of *Ch. fragaefolii* are robust and short, with large, protuberant sockets, thick stems, and large, bulbous apices (Fig. 6). On the pedicel, two kinds of sensilla may be found besides trichoid sensilla – a campaniform sensillum on the dorsal apical part and a rhinariolum on the ventral side (Fig. 6A). The rhinariolum in *Ch. fragaefolii* occurs

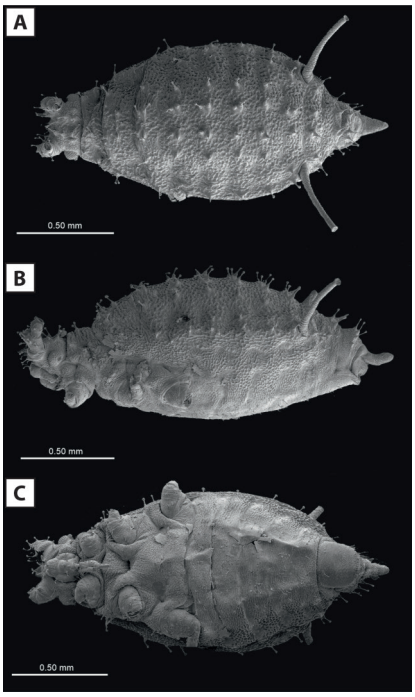

Fig. 4. Scanning electron microscopy (SEM) of apterous viviparous female of *Chaetosiphon fragaefolii*: A – dorsal side, B – lateral side, C – ventral side

as a small opening in the cuticle about 1.2–1.5 µm in diameter, with a slightly raised edge. The main sensillum peg of the rhinariolum is not visible and probably lies inside the cavity (Fig. 6B). Type I trichoid sensilla are most numerous on the antennal flagellum, especially on antennal segment III. Almost all type I trichoid sensilla arise from the segments' cuticle at an angle of about 40–50°, and are of different lengths, about 0.20–0.50 µm. All antennal type I trichoid sensilla are robust, with large protruding sockets that are trapezoid in shape and longer than they are wide. The main sensillum has a thick, smooth stem and a large, bulbous apical part (Fig. 6D), but in some cases the apex is narrow and capitate (Fig. 6E). On antennal segment V near the apical part, a large, multiporous placoid sensillum (primary rhinarium) can be found (Fig. 6E). The large, multiporous placoid sensillum is rounded, 10–13 µm in diameter and surrounded by a robust cuticular collar with 16–20 single or branched projections each about 2–4 µm long (Fig. 6F, G). The sensillum membrane is covered with numerus circular micropores 16–20 per µm^2 in the form of small depressions (Fig. 6H). At the distal end of the basal part of antenna VI a circular nest of sensilla (also

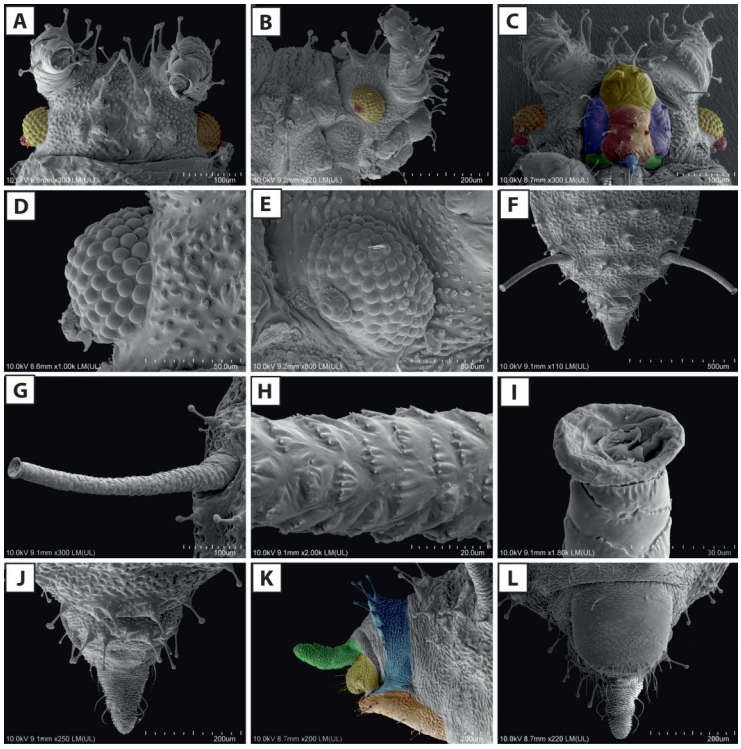

Fig. 5. SEM of apterous viviparous female of *Chaetosiphon fragaefolii* morphological characters: A – dorsal side of the head with rounded compound eyes (yellow) and triommatidia on ocular tubercles (orange), B – lateral side of the head with rounded compound eyes (yellow) and triommatidia on ocular tubercles (orange), C – ventral side of the head with rounded compound eyes (yellow), triommatidia on ocular tubercles (orange) and mouthparts: postclypeus (yellow), anteclypeus (orange), mandibular lamina (violet), maxillary lamina (green), labrum (blue), D – structure of dorsal side of the compound eye and triommatidium, E – structure of dorsal side of the compound eye and triommatidium, F – dorsal side of abdomen, G – siphunculus, H – structure of siphunculus cuticle, I – siphunculus flange, J – dorsal side of end of abdomen and cauda, K – lateral side of abdomen showing perianal structures: abdominal segment VIII (blue), cauda (green), anal plate (yellow) and genital plate (orange), L – ventral side of end of abdomen showing genital plate and cauda

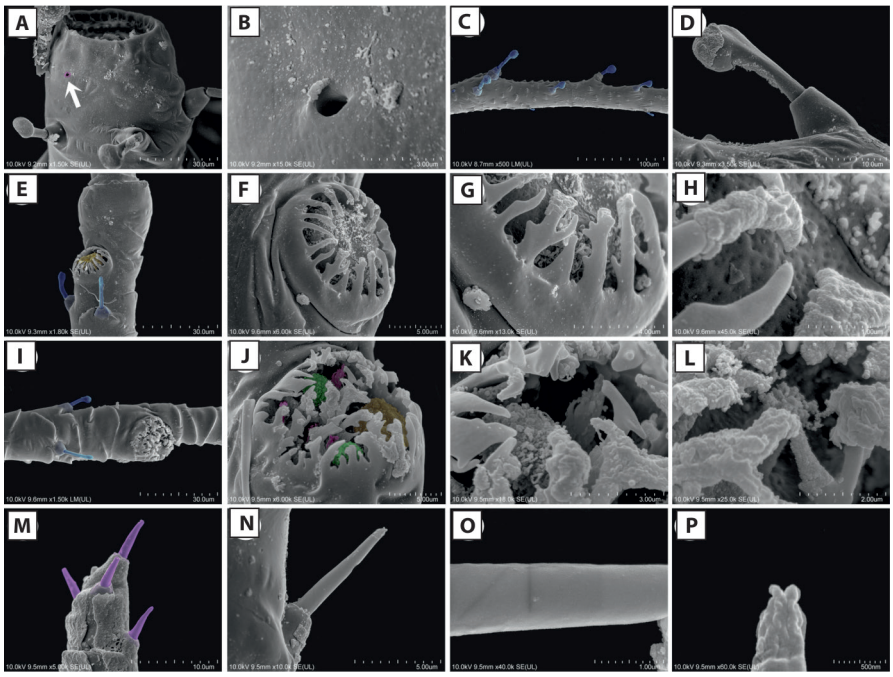

Fig. 6. SEM of antennal sensilla of apterous viviparous females of *Chaetosiphon fragaefolii*: A – pedicel with type I trichoid sensilla and rhinariolum (pink) indicated by arrow, B – ultrastructure of opening of rhinariolum without visible sensillum peg, C – type I trichoid sensilla (blue) on antennal segment III, D – structure of type I trichoid sensillum, E – apical part of antennal segment III with large multiporous placoid sensillum (yellow) and type I trichoid sensilla (blue), F – structure of the large multiporous placoid sensillum (primary rhinarium), G – ultrastructure of sclerotic collar and projections of the large multiporous placoid sensillum on antennal segment V, H – ultrastructure of the porous membrane of the large multiporous sensillum, I – apical part of the base of antennal segment VI showing type I trichoid sensilla and tightly adjoining sensilla (primary rhinaria), J – primary rhinaria on antennal segment VI: large multiporous placoid sensillum (yellow) – major rhinarium, small multiporous placoid sensilla (green) and four sunken coeloconic sensilla (pink) – accessory rhinaria, K – ultrastructure of sunken coeloconic sensillum with long projections, L – ultrastructure of sunken coeloconic sensillum with short projections, M – apical part of terminal process of antennal segment VI with type II trichoid sensilla (violet), N – type II trichoid sensillum structure, O – ultrastructure of the type II trichoid sensillum stem, P – ultrastructure of the type II trichoid sensillum apex

primary rhinaria) can be found besides trichoid sensilla (Fig. 6I). Deeper analysis revealed four kinds of sensilla: one large, multiporous placoid sensillum (major rhinarium), about 5.0–5.5 µm in diameter, two small multiporous placoid sensilla about 2.5 µm in diameter in polar positions, and four sunken coeloconic sensilla – two with short (type I) and two with long (type II) projections. Small, multiporous placoid sensilla and sunken coeloconic sensilla are accessory rhinaria. The sensilla on antennal segment VI are rather small and delicate, lying very close together and moreover are surrounded by a well-developed and expanding cuticular collar with numerous projections (Fig. 6J–L). On the very apical part of the antennal VI terminal process (also along the terminal process), short, thick type II trichoid sensilla can be found (Fig. 6M). Each sensillum is about 5–6 µm long and arises from a trapezoid socket which is much more delicate than those of type I sensilla (Fig. 6N). The type II trichoid sensilla are straight and tubular with smooth stems and a ruffled apical part (Fig. 6O, P).

Mouthparts sensilla

Mouthparts of *Ch. fragaefolii* are characterized by numerous sensilla, but they are not highly varied. Accessory mouthparts on the head are covered with trichoid sensilla which are similar to those of the rest of the dorsal side of the body (Fig. 5C). The labial segments are mostly sclerotized (except the first segment, which is membranous) and covered mostly with trichoid sensilla. Additionally, the cuticle of labial segment II is covered with numerous well-developed denticles (Fig. 7A, D). Ultimate rostral segments (URS or IV+V) bear three kinds of sensilla: type II basiconic sensilla on the proximal part, trichoid sensilla (accessory setae) along the segment up to the distal part, and type III sensilla on the very apical part (Fig. 7B, C, J). Type I trichoid sensilla on labial segments II and III are rather short, arising from protruding sockets, and are smooth and pointed (Fig. 7E, F). Type II basiconic sensilla are short, pointed and rather poorly visible, with rounded sockets (Fig. 7G, H). Type III basiconic sensilla are very short, arising from small cavities,

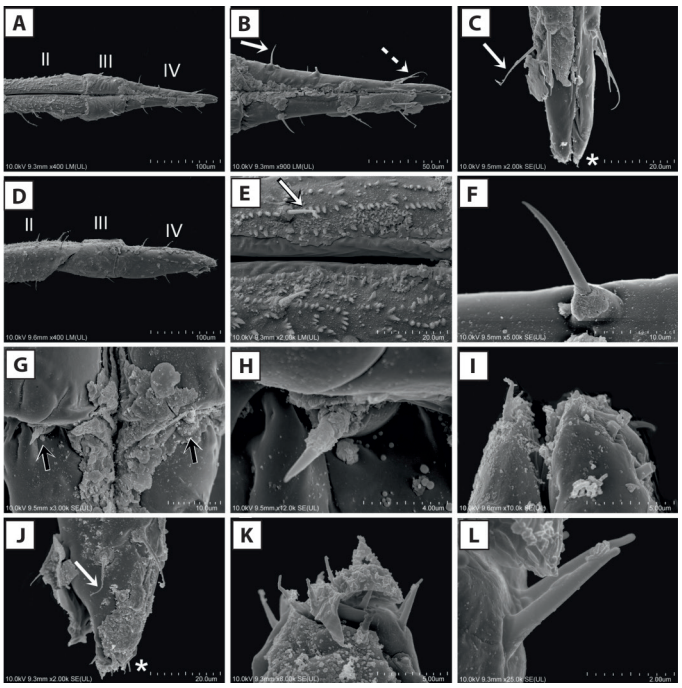

Fig. 7. SEM of *Chaetosiphon fragaefolii* mouthparts sensilla: A – ventral side of labium showing part of labial segment II (II), labial segment III (III) and the ultimate rostral segment – labial segment IV (IV), B – ultimate rostral segment with trichoid sensilla on the distal part – primary setae (dotted arrow) and on the proximal and middle part – accessory setae (solid arrow), C – distal part of the last labial segment with trichoid setae – primary setae (arrow) and almost invisible basiconic sensilla (asterisk), D – lateral side of labium showing part of labial segment II (II), labial segment III (III) and the ultimate rostral segment – labial segment IV (IV), E – labial segment II cuticle with numerous denticles and trichoid sensilla (arrow), F – structure of trichoid sensillum on labial segment II and III, G – ventral proximal part of the ultimate rostral segment with type II basiconic sensilla (black arrows), H – ultrastructure of the type II basiconic sensillum, I – ventral apical part of the ultimate rostral segment with broken type III basiconic sensilla, J – lateral apical part of ultimate rostral segment with trichoid sensilla – primary setae (arrow) and type III basiconic sensilla (asterisk), K – type III basiconic sensilla on the very apical part of the ultimate rostral segment, L – ultrastructure of type III basiconic sensillum

are tapering and with narrow but rounded apices (Fig. 7I, K, L).

Dorsal abdominal cuticle and sensilla

The dorsal abdomen of *Ch. fragaefolii* is very interesting with respect to the cuticle and trichoid sensilla, which arise from evident tuberculate bases. The dorsal abdominal cuticle is characterized by microsculpture in the form of numerous dense cavities, holes and depressions (Fig. 8A). The extensive microsculpture is more clearly visible when observed from the lateral side, where bulbous trichoid sensilla are also visible in groups, arising from large sockets on cuticular protuberances (Fig. 8B). The cuticular microsculpture appears to have a spatial structure, and at first can be seen as irregular, but upon closer examination the shapes of cavities and depressions are quite schematic, rounded or semicircular and occur singly or in groups of two or three (Fig. 8C–E). On the very lateral side, around the spiracles, the cuticular microsculpture is even more regular, in the form of somewhat oval depressions (Fig. 8F), and the spiracle openings are partially surrounded by semicircular nodules (Fig. 8G). The area of the cauda is densely covered with well-developed denticles in transverse groups of five to ten (Fig. 8H). The dorsal side of the body of *Ch. fragaefolii* is covered with numerous regularly arranged type I trichoid sensilla, which are very characteristic and unique due to their enlarged and bulbous apical ends (Fig. 9). In general, dorsal type I trichoid sensilla are large, protuberant sockets, in almost all cases longer than wider, and the main part of the sensillum is a robust, thick, stiff stem with an enlarged, bulbous apical part. On the head, the sensilla are 45–55 µm long, arranged symmetrically in 6–7 pairs (Fig. 9A). The free area between the sensillum stem and the socket collar is very clearly visible (Fig. 9B, C) and the stem is smooth (Fig. 9D). The apical part is almost ideally spherical, 9–11 µm in diameter, and its surface bears quite unusual minute, wart-like protuberances, which in the case of head trichoid sensilla are rather sparse (Fig. 9E). Abdominal trichoid sensilla are shorter in the marginal area than in the spinal area (Fig. 9F). The marginal trichoid sensilla are about 55–65 µm long; of this, the socket is about 20 µm long and the main sensillum is about 35–45 µm long. Marginal trichoid sensilla are characterized by

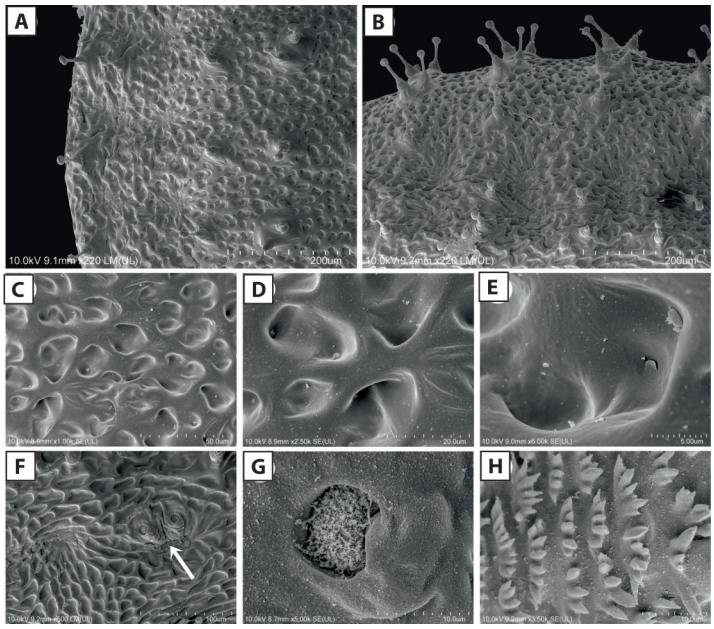

Fig. 8. SEM of *Chaetosiphon fragaefolii* abdominal cuticle: A – fragment of dorsal abdomen showing evident sculpture of the cuticle, B – fragment of lateral abdomen showing evident sculpture and spinal setae on setae in groups on tuberculate bases, C – structure of the microsculpture in the form of somewhat deep cavities, D–E – ultrastructure of the abdominal microsculpture, F – lateral side of abdomen with more regular microsculpture and visible spiracles, G – ultrastructure of the spiracle opening plugged with secretions, H – microsculpture in the form of denticles of the dorsal side of cauda

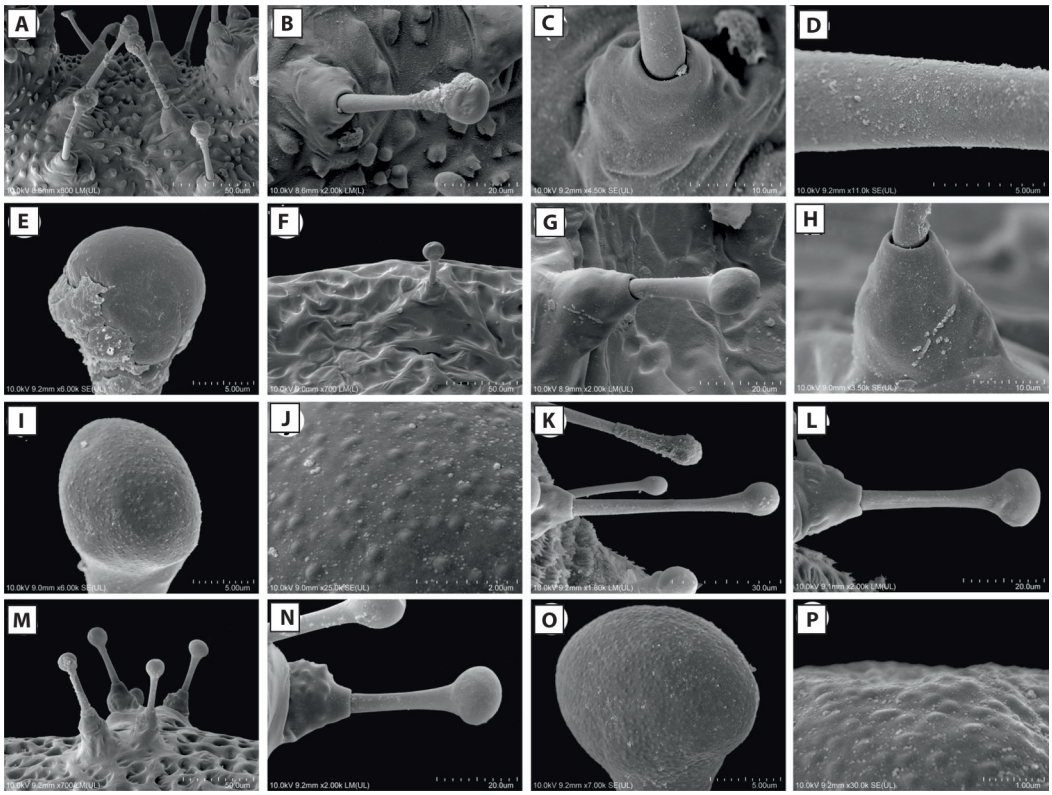

Fig. 9. SEM of *Chaetosiphon fragaefolii* body trichoid sensilla: A – dorsal side of head between antennal tubercles showing cuticular microsculpture and trichoid sensilla, B – structure of the trichoid sensillum showing the tuberculate socket, thick stem and capitate apex, C – ultrastructure of the socket of the trichoid sensillum, D – ultrastructure of the stem of the sensillum showing its smooth surface, E – ultrastructure of the bulbous capitate apex with some wart-like protuberances, F – marginal part of thorax showing shorter trichoid sensilla, G – ultrastructure of the thoracic sensillum with short, expanding stem and bulbous apex, H – ultrastructure of the long socket of the sensillum, I – ultrastructure of the bulbous apex of the sensillum showing numerous wart-like protuberances on the surface, J – surface of the sensillum apex, K–N trichoid sensilla on abdomen showing different lengths, O–P – ultrastructure of the bulbous apex of abdominal trichoid sensilla with the most numerous and densely occurring wart-like protuberances

a thick stem, which is often wider in the apical part than at the base (Fig. 9G, H). The bulbous apical part of the marginal trichoid sensilla is about 11–15 μm in diameter, and its surface bears many more wart-like protuberances than the cephalic trichoid sensilla (Fig. 9I) – about four to six per 1 μm^2 (1–2 in trichoid sensilla on the head) (Fig. 9J).

Discussion

This study provides valuable insights into the genetic and morphological characteristics of the strawberry aphid, *Chaetosiphon fragaefolii*, a critical pest and viral vector associated with strawberry crops. By integrating morphological and molecular analyses, taxonomic resolution and understanding of this economically important species, particularly its genetic diversity, distribution, and potential invasion routes have been enhanced.

Chaetosiphon fragaefolii apterous viviparous females have been examined using SEM for the first time, and the general morphology follows the Macrosiphini scheme, shown in many publications. On the other hand, the chaetotaxy of the strawberry aphid is similar to that of the previously analyzed, e.g., *Pleotrichophorus glandulosus*, due to the characteristic long, thick and capitate setae (Barjadze *et al.* 2022). Capitate setae of different shapes at the apices have also been observed in other Macrosiphini species like *Rhinariaphis tuberculata*, *Eucarazzia elegans* or *Klimaszewskia salviae* (Kanturski and Stekolshchikov 2018). Apices of setae of *Ch. fragaefolii* are visibly larger, more rounded and characterized by unusual, minute, wart-like protuberances, so far not observed in other species. Also, the dorsal surface seems to be quite unique for the representatives of *Ch. fragaefolii* in which the cuticle microsculpture is very complicated, in the form of numerous dense cavities, holes and depressions. In many Macrosiphini species which have been examined using SEM the dorsal cuticle was smooth like in e.g., *Macrosiphoniella davazhamci* (Kanturski and Barjadze 2018) or *M. sunschine* (Jensen *et al.* 2020), somewhat smooth to wrinkled like in *R. tuberculata*, *E. elegans*, *K. salviae* (Kanturski and Stekolshchikov 2018) or evidently wrinkled with regular sculpture like in *Acyrthosiphon pisum* (Kanturski *et al.* 2020 or *Macromyzus diplazius* (Lee *et al.* 2024). By examining the characteristics of the cuticle sculpture, it can be seen that individuals of *Ch. fragaefolii* are most similar to *Myzaphis rosarum*, in which a very similar sculpture has been observed, but in the form of regular, oval and similar in size depressions (Kanturski *et al.* 2018b).

In Macrosphini, the antennal sensilla characteristics of different species which have been analyzed and described using SEM, showed that close adherence of primary rhinaria to each other on the last antennal segment is a general scheme in the tribe. The primary rhinaria of *Ch. fragaefolii* are characterized by the same layout pattern in which particular sensilla form a somewhat rounded group. Within this group the major rhinarium (big multiporous placoid sensillum) lies on one side, whereas the accessory rhinaria (two small multiparous placoid sensilla and sunken coeloconic sensilla) lie on the other side of this group. Therefore, the small placoid sensilla are always closer to the major one and the sunken coeloconic sensilla can lie between them or at their sides. This general scheme of arrangement has also been observed in other genera like in *Myzaphis* (Kanturski *et al.* 2018), *A. pisum* (Kanturski *et al.* 2020), *U. remaudierei* (Kanturski *et al.* 2025) and *M. davazhamci*. Even similar in general scheme, small differences can be observed e.g., in *M. sunschine*, in which the accessory rhinaria formed a somewhat independent group on the side of the major rhinarium, with the small placoid sensilla evidently over and under the big multiparous placoid sensillum (Jensen *et al.* 2020). A similar arrangement model can also be observed in *Pleotrichophorus* (Barjadze *et al.* 2022). On the other hand, in *R. tuberculata* and *M. diplazius* the small multiparous placoid sensilla lie close to each other at the side of the major rhinarium and are surrounded by the group of sunken coeloconic sensilla (Kanturski and Stekolshchikov 2018; Lee *et al.* 2024).

According to previous information on the range, and new records of *Ch. fragaefolii* in various continents, the area of Poland stayed free from the occurrence of this alien species despite very thorough aphidological works (including alien species reports) in the southern and western parts of the country (Osiadacz and Wieczorek 2006; Osiadacz and Wojciechowski 2008; Wieczorek 2011; Wojciechowski *et al.* 2011; Trela and Herczek 2014; Starowicz *et al.* 2015; Kaszyca *et al.* 2018; Kanturski *et al.* 2017, 2018; Kaszyca-Taszakowska and Depa 2019; Wieczorek and Chłond 2019; Wieczorek *et al.* 2024). As the village Branice is located in the very southern part of Poland near the Polish-Czech border, it is natural that *C. fragaefolii* is spreading from south to north. We are not able to indicate the precise time of the occurrence and record of strawberry aphid in the Czech Republic, as the first mention of the species comes from Holman (2009), in which its presence in the Czech Republic was based on the collection of materials of Jaroslav Holman, unfortunately without more data.

The NJ tree analysis further supports the distinction between the two species (*C. fragaefolii* and *C. tetrarhodum*), with *C. fragaefolii* individuals clustering into a single, well-supported clade (BS = 100%). Geographic clustering within the clade reveals that Polish and Czech populations share haplotypes with

Canadian populations, particularly from Alberta, British Columbia, Manitoba, and Nova Scotia. This finding suggests a potential transcontinental link, likely mediated by anthropogenic activities such as trade and the international movement of strawberry plants. The presence of identical haplotypes (Hap_1) across these geographically disparate regions highlights the role of clonal reproduction in aphid populations and underscores the need for stringent phytosanitary measures to prevent further spread.

Genetic divergence analyses revealed a clear distinction between *Chaetosiphon fragaefolii* and *C. tetrarhodum*, with minimal intraspecific variation within *C. fragaefolii* (maximum 0.8%) and consistently high interspecific divergence exceeding 7.8%. These results underscore the reliability of neighbor-joining tree analysis for resolving closely related aphid species and support the suitability of the COI marker for species identification and phylogenetic inference, consistent with previous findings (Foottit *et al.* 2008). Aphid studies have shown that conspecific individuals typically exhibit low pairwise divergence (mean 0.05%, range 0.00–1.00%), whereas congeneric species display significantly higher divergence (mean 5.84%, range 0.00–14.04%), reinforcing the effectiveness of COI-based species delimitation (Lee *et al.* 2011). The genetic homogeneity observed within *C. fragaefolii* populations suggests limited genetic variability, which might be attributed to recent population expansions or founder effects associated with its invasive spread.

The haplotype network analysis corroborates the phylogenetic findings, identifying three distinct haplotypes among the analyzed sequences. Hap_1, shared by European and Canadian populations, represents the most widespread haplotype, while Hap_2 appears restricted to Canadian populations (New Brunswick and Ontario). Hap_3, corresponding to *C. tetrarhodum*, is unique to this species, reinforcing its genetic distinction. The limited number of haplotypes detected in this study aligns with previous observations in other aphid taxa, where clonal reproduction and limited dispersal contribute to low haplotype diversity (Simon *et al.* 2002). However, further sampling and broader geographic coverage are necessary to capture the full extent of genetic diversity within these species.

These findings provide significant insights into the invasion biology of *C. fragaefolii*. Haplotype analysis revealed three distinct haplotypes (Hap_1–Hap_3), with Hap_1 observed in populations from Poland, the Czech Republic, and multiple regions of Canada, suggesting a likely North American origin of Polish populations. This is further supported by the exclusive detection of Hap_2 in Canadian populations, indicating that European populations may have been introduced from a subset of North American populations. Such introductions may have been facilitated by the global strawberry trade, as strawberries are hosts for *C. fragaefolii*. The genetic uniformity observed among invasive populations may reflect the founder effect, wherein a small number of individuals establish a new population, leading to reduced genetic variability. This phenomenon has been documented in other invasive aphid species and highlights the critical role of human-mediated dispersal in shaping aphid population structure and dynamics (Muirhead *et al.* 2008).

In conclusion, this study advances our understanding of *C. fragaefolii* biology, highlighting its genetic homogeneity, geographic distribution, and potential invasion routes. These findings underscore the importance of international collaboration and comprehensive monitoring programs to mitigate the spread of this economically significant pest. Future research should focus on expanding geographic and host plant sampling to better elucidate the evolutionary history and ecological adaptability of *C. fragaefolii*. Additionally, investigating its role as a viral vector and assessing its impact on strawberry production will provide critical insights for integrated pest management strategies.

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ORIGINAL ARTICLE

Morphological and molecular insights into the invasive strawberry aphid *Chaetosiphon fragaefolii* – a critical pest and virus vector new to Poland

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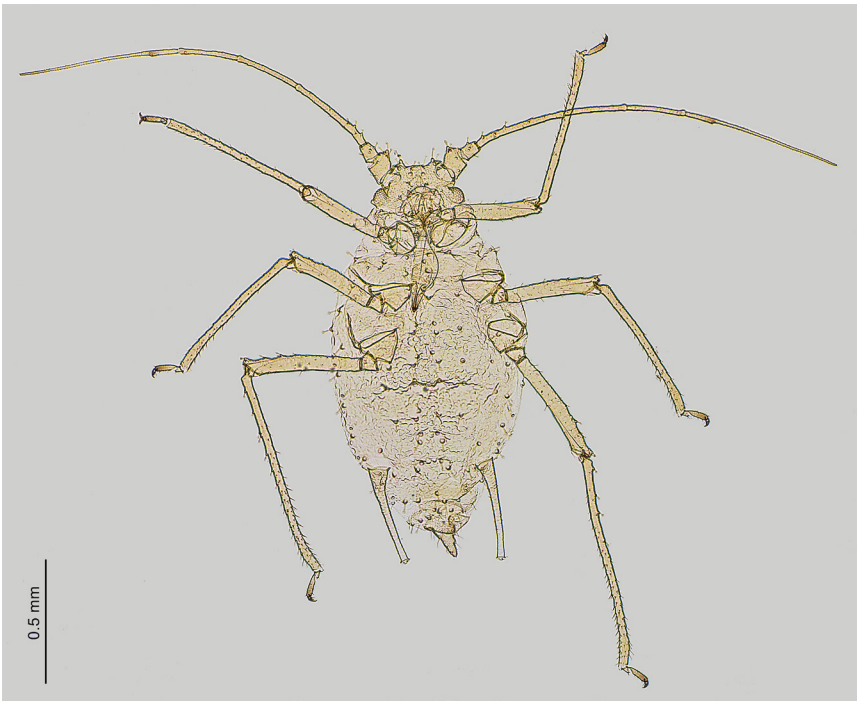
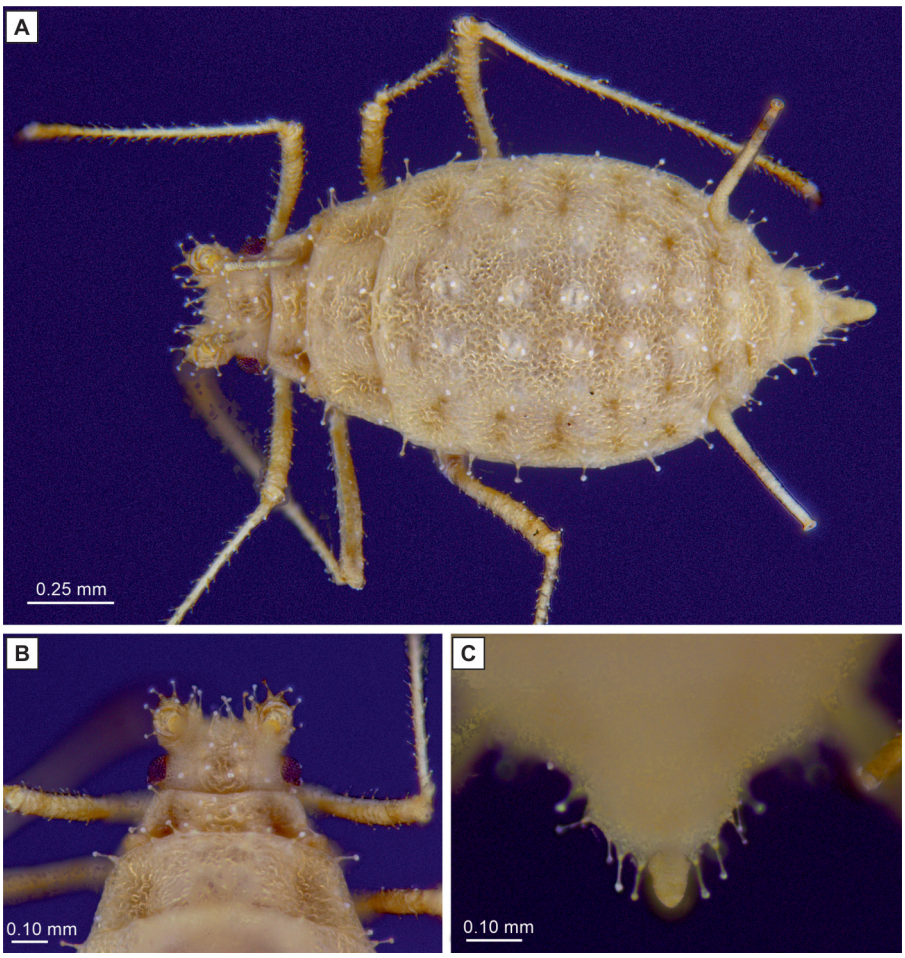
SUPPLEMENTARY MATERIAL

The authors are fully responsible for both the content and the formal aspects of the supplementary material. No editorial adjustments were made.



Supplementary Fig. S1. Apterous viviparous female of *Chaetosiphon fragaefolii* on a mounted slide



Supplementary Fig. S2. Dorsal side of body of *Chaetosiphon fragaefolii* in life: A – general view of the habitat showing microsculpture, and capitate setae on tuberculate bases, B – dorsal side of head and thorax, C – setae on end of abdomen

Supplementary Table 1. Summary of information of four haplotypes from the two *Chaetosiphon* species and one outgroup used in the present analyses

No.	Species	Location	Acc. No.	Haplotype	Ref.
01	*Chaetosiphon fragaefolii*	Czech Republic	MN420510	Hap_1	Fránová *et al.* (2019)
02	*Chaetosiphon fragaefolii*	Canada, Alberta	KR574966	Hap_1	Hebert *et al.* (2016)
03	*Chaetosiphon fragaefolii*	Canada, Alberta	KR573016	Hap_1	Hebert *et al.* (2016)
04	*Chaetosiphon fragaefolii*	Canada, Alberta	KR572823	Hap_1	Hebert *et al.* (2016)
05	*Chaetosiphon fragaefolii*	Canada, Alberta	KR584525	Hap_1	Hebert *et al.* (2016)
06	*Chaetosiphon fragaefolii*	Canada, Alberta	KR583408	Hap_1	Hebert *et al.* (2016)
07	*Chaetosiphon fragaefolii*	Canada, Alberta	KR582801	Hap_1	Hebert *et al.* (2016)
08	*Chaetosiphon fragaefolii*	Canada, Alberta	KR581689	Hap_1	Hebert *et al.* (2016)
09	*Chaetosiphon fragaefolii*	Canada, Alberta	KR581508	Hap_1	Hebert *et al.* (2016)
10	*Chaetosiphon fragaefolii*	Canada, British Columbia	KR574780	Hap_1	Hebert *et al.* (2016)
11	*Chaetosiphon fragaefolii*	Canada, British Columbia	KR583001	Hap_1	Hebert *et al.* (2016)
12	*Chaetosiphon fragaefolii*	Canada, British Columbia	KR043602	Hap_1	Gwiazdowski *et al.* (2015)
13	*Chaetosiphon fragaefolii*	Canada, British Columbia	KR038018	Hap_1	Gwiazdowski *et al.* (2015)
14	*Chaetosiphon fragaefolii*	Canada, British Columbia	KR037586	Hap_1	Gwiazdowski *et al.* (2015)
15	*Chaetosiphon fragaefolii*	Canada, British Columbia	KR032331	Hap_1	Gwiazdowski *et al.* (2015)
16	*Chaetosiphon fragaefolii*	Canada, Manitoba	KR045254	Hap_1	Gwiazdowski *et al.* (2015)
17	*Chaetosiphon fragaefolii*	Canada, Nova Scotia	KR572648	Hap_1	Hebert *et al.* (2016)
18	*Chaetosiphon fragaefolii*	Poland	PV013678	Hap_1	this study
19	*Chaetosiphon fragaefolii*	Poland	PV013679	Hap_1	this study
20	*Chaetosiphon fragaefolii*	Poland	PV013680	Hap_1	this study
21	*Chaetosiphon fragaefolii*	Canada, New Brunswick	KR582683	Hap_2	Hebert *et al.* (2016)
22	*Chaetosiphon fragaefolii*	Canada, Ontario	KR035154	Hap_2	Gwiazdowski *et al.* (2015)
23	*Chaetosiphon tetrarhodum*		KX631549	Hap_3	Choi *et al.* (2018)
24	*Phylloxera coccinea* (outgroup)		MG403377	Hap_4	Unpublished