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PRACA DOKTORSKA

Rewizja taksonomiczna i pokrewieństwa wśród mszyc z rodzaju *Drepanaphis* Del Guercio (Hemiptera, Aphididae: Drepanosiphinae) w oparciu o analizy morfologiczne i molekularne

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Podziękowania

Składam serdeczne podziękowania

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za cierpliwość i merytoryczne wsparcie na każdym etapie powstawania niniejszej rozprawy. Jestem wdzięczna za dostępność i sprawną komunikację, które pomagały mi realizować kolejne etapy badań i podejmować trafne decyzje naukowe. Dziękuję również za pomoc w organizowaniu i koordynowaniu staży oraz za aktywne poszukiwanie możliwości prowadzenia badań i wspieranie mnie w ich rozwijaniu.

Pani Promotor dr Agnieszce Bugaj-Nawrockiej

za cierpliwość, stałą dostępność i poświęcony czas. Jestem wdzięczna za cenne wskazówki merytoryczne i uważność na szczegóły, które pomogły mi w realizacji pracy doktorskiej. Dziękuję również za wsparcie i dobre słowo w najbardziej wymagających momentach.

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Spis treści

1. Wykaz prac naukowych wchodzących w skład cyklu stanowiącego podstawę rozprawy doktorskiej

Publikacja 1 (P1):

Malik, K., Bugaj-Nawrocka, A., Wieczorek, K. (2023). Distribution of *Drepanaphis acerifoliae* – aphid pest of *Acer* trees – faced with global climate change. *Folia Biologica* (Kraków), 71, 115–130. https://doi.org/10.3409/fb_71-3.12

IF_{2023}: 0,8, MNiSW: 100 pkt

Publikacja 2 (P2):

Malik, K., Bugaj-Nawrocka, A., Wieczorek, K. (2024). Taxonomic revision of the Nearctic genus *Drepanaphis* Del Guercio (Hemiptera: Aphididae: Drepanosiphinae). *Insects*, 15(7), 1–71. https://doi.org/10.3390/insects15070553

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Publikacja 3 (P3):

Malik, K*., Jousselin, E., Clamens, A.-L., Sugimoto, S., Wieczorek, K. (2025). Molecular phylogeny of the *Acer*-feeding aphid subfamily Drepanosiphinae (Insecta: Hemiptera: Aphididae) and the evolution of its endosymbiotic consortia. *Zoological Letters*, 11, 9. https://doi.org/10.1186/s40851-025-00255-2

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Łączna suma IF = 6,3

Łączna suma punktów MNiSW = 340

2. Streszczenie

Drepanaphis Del Guercio, 1909 jest najliczniejszym rodzajem mszyc (Hemiptera, Aphididae) w obrębie podrodziny Drepanosiphinae, obejmującym 18 gatunków i 44 znane morfy. Występuje w Ameryce Północnej, a jeden gatunek *Drepanaphis acerifoliae* także w Europie i Azji. Roślinę żywicielską stanowią drzewa z rodzaju *Acer*, a w przypadku *D. monelli – Aesculus glabra*. Charakterystyczną cechą przedstawicieli tego taksonu są wyrostki na grzbietowej stronie odwłoka, które stanowią unikatową cechę diagnostyczną grupy.

Dotychczas rodzaj *Drepanaphis* był weryfikowany wyłącznie na podstawie cech morfologicznych, bez uwzględnienia pokrewieństw opartych o dane molekularne.

Główne cele pracy obejmowały: określenie zasięgu występowania *D. acerifoliae* i modelowanie jego niszy ekologicznej; rewizję taksonomiczną całego rodzaju z uwzględnieniem analizy biogeograficznej i troficznej; a także przeprowadzenie analizy filogenetycznej z charakterystyką składu endosymbiontów.

Materiał do badań uwzględniał preparaty mikroskopowe mszyc z kolekcji muzealnych oraz świeży materiał pozyskany w trakcie badań terenowych w Stanach Zjednoczonych.

Zastosowano szereg metod badawczych, w tym: mikroskopię świetlną, elektronową mikroskopię skaningową (SEM) oraz sekwencjonowanie materiału genetycznego. Podparto się analizami statystycznymi i szeroko pojętymi analizami bioinformatycznymi.

W toku badań zweryfikowano błędnie zidentyfikowane osobniki siedmiu gatunków i wyznaczono nowy gatunek *Drepanaphis robinsoni* Malik, 2024. Analiza porównawcza samic jajorodnych (amfigonicznych) pozwoliła rozwiązać niejasności taksonomiczne gatunków morfologicznie podobnych. Natomiast analizy molekularne potwierdziły, że rodzaj *Drepanaphis* jest monofiletyczny. W oparciu o specyficzność żywicielską i rozmieszczenie geograficzne wyróżniono trzy grupy troficzne (*grandidentatum*, *saccharum*, *rubrum*), wsparte wynikami analiz molekularnych. Bakterie *Sodalis* zostały stwierdzone u wszystkich badanych przedstawicieli rodzaju *Drepanaphis*; jednocześnie wykazano, że mogą one pełnić rolę drugiego endosymbionta obligatoryjnego.

Uzyskane wyniki znacząco poszerzają zbiór danych molekularnych i mikrobiologicznych dla podrodziny Drepanosiphinae. Sugeruje się, aby przyszłe badania filogenetyczne nad tą grupą uwzględniały m.in. zależności troficzne mszyc obejmujące zarówno roślinę żywicielską, jak i skład endosymbiontów.

3. Summary

Drepanaphis Del Guercio, 1909 is the most numerous aphid (Hemiptera, Aphididae) genus within the subfamily Drepanosiphinae, comprising 18 species and 44 known morphs. It occurs in North America, with one species, *Drepanaphis acerifoliae*, also found in Europe and Asia. Its host plants are trees of the genus *Acer*, and in the case of *D. monelli*, *Aesculus glabra*. A characteristic feature of representatives of this taxon are the dorsal tubercles on the abdomen, which constitute a unique diagnostic characteristic of the group.

Until now, the genus *Drepanaphis* has been verified solely on the basis of morphological characters, without considering relationships based on molecular data.

The main objectives of the work included: determining the distribution range of *D. acerifoliae* and modeling its ecological niche; taxonomic revision of the entire genus, taking into account biogeographic and trophic analyses; and conducting phylogenetic analyses with characterization of the endosymbiont consortia.

The study material included microscopic slides of aphids from museum collections and fresh material obtained during fieldwork in the United States.

A range of research methods was used, including light microscopy, scanning electron microscopy (SEM), and sequencing of genetic material. The study was supported by statistical analyses as well as broadly defined bioinformatic analyses.

During the course of the study, misidentified specimens of seven species were corrected, and a new species, *Drepanaphis robinsoni* Malik, 2024, was described. Comparative analysis of oviparous females resolved taxonomic ambiguities among morphologically similar species. Molecular analyses confirmed that the genus *Drepanaphis* is monophyletic. Based on host specificity and geographic distribution, three trophic groups were distinguished (*grandidentatum*, *saccharum*, *rubrum*), the result supported by molecular data. *Sodalis* bacteria were detected in all representatives of the genus *Drepanaphis*, indicating that they may serve as a second obligate endosymbiont.

The obtained results significantly expand the molecular and microbiological data for the Drepanosiphinae subfamily. It is suggested that future phylogenetic studies of this group should consider, among other things, the trophic relationships of aphids, including both the host plant and the composition of endosymbionts.

4. Wstęp

Kompleksowe analizy morfologiczne i molekularne poszczególnych grup organizmów stanowią podstawę współczesnej taksonomii. Dotyczy to również mszyc – wyspecjalizowanej grupy pluskwiaków, charakteryzującej się wysoką specyficznością pokarmową oraz złożonymi przystosowaniami rozrodczymi.

Drepanosiphinae (Hemiptera, Aphididae) to morfologicznie i biogeograficznie zróżnicowana podrodzina mszyc, obejmująca obecnie 42 gatunki należące do sześciu rodzajów: *Drepanaphis* Del Guercio, 1909 (18 gatunków); *Drepanosiphoniella* Davatchi, Hille Ris Lambers & Remaudière, 1957 (3 gatunki); *Drepanosiphum* Koch, 1855 (9 gatunków); *Megalosiphonaphis* Sugimoto, 2024 (1 gatunek); *Shenahweum* Hottes & Frison, 1931 (1 gatunek) oraz *Yamatocallis* Matsumura, 1917 (10 gatunków) (Favret, 2025, Blackman i Eastop, 2025).

Mszyce z tej podrodziny wykazują wysoką specyficzność pokarmową, związane są przede wszystkim z gatunkami z rodzaju *Acer* (klon), wyjątkowo *Aesculus* (kasztanowiec). Mszyce te żerują na liściach, zazwyczaj nie tworzą kolonii i relacji mutualistycznych z mrówkami. Opisane dotychczas gatunki są jednodomne i holocykliczne, a w ich cyklu życiowym wszystkie (z wyjątkiem *Drepanosiphoniella*) samice pokolenia partenogenetycznego są uskrzydlone (Blackman i Eastop, 2025). Gatunki reprezentujące podrodzinę Drepanosiphinae związane są z odmiennymi obszarami zoogeograficznymi. Rodzaj *Drepanosiphum* ma zasięg holarktyczny (Wieczorek i inni, 2016), podczas gdy *Drepanosiphoniella* występuje głównie w regionie śródziemnomorskim (Wieczorek i inni, 2015). W azjatyckiej części Palearktyki rodzaj *Yamatocallis* notowany jest w Indiach, Chinach, Korei i Japonii (Sugimoto, 2017), natomiast *Megalosiphonaphis* został dotychczas stwierdzony wyłącznie w Japonii (Sugimoto, 2024). Rodzaje *Shenahweum* i *Drepanaphis* mają zasięg nearktyczny (Wieczorek i inni, 2013, 2017).

Istotnym, choć słabo dotąd poznanym aspektem biologii Drepanosiphinae, są ich relacje symbiotyczne. Większość mszyc pozostaje w obligatoryjnej symbiozie z bakterią *Buchnera aphidicola*, dostarczającą aminokwasów egzogennych oraz witamin z grupy B, ograniczonych w diecie roślinnej (Xu i inni, 2021). Badania metagenomiczne wykazały jednak, że w niektórych liniach mszyc relacja ta może obejmować dodatkowe symbionty

bakteryjne, które kompensują utracone funkcje metaboliczne *Buchnera*, prowadząc do powstania złożonych układów symbioz współobligatoryjnych. Zjawisko to stwierdzono również u niektórych przedstawicieli Drepanosiphinae, jednak dotychczasowe badania obejmowały jedynie pojedyncze gatunki i nie uwzględniały najliczniejszego rodzaju *Drepanaphis* (Jousselin i inni, 2016, 2024; Manzano-Marín i inni, 2023).

Dotychczasowe badania poświęcone podrodzinie Drepanosiphinae pozwoliły przeprowadzić rewizję i weryfikację taksonomiczną rodzajów *Shenahweum* (Wieczorek i inni, 2013), *Drepanosiphoniella* (Wieczorek i inni, 2015), *Drepanosiphum* (Wieczorek i inni, 2016), *Yamatocallis* (Sugimoto, 2017) oraz ustalić pokrewieństwa na poziomie rodzajów reprezentujących tę podrodzinę (Wieczorek i inni, 2017). Na tym tle rodzaj *Drepanaphis* pozostaje w szczególności słabo opracowany, a pozycja wielu gatunków pozostaje niejasna.

Historia rodzaju sięga końca XIX wieku i była obarczona licznymi wątpliwościami nomenklatorycznymi, które częściowo uporządkowano dopiero w XX wieku. Pierwszy gatunek zaliczany dziś do wymienionego rodzaju opisano jako *Siphonophora acerifoliae* (Thomas, 1878), podczas gdy w 1909 r. Del Guercio ustanowił rodzaj *Drepanaphis* (równolegle Davis zaproponował nazwę *Phymatosiphum*, później uznaną za młodszy synonim). Pierwsza połowa XX wieku przyniosła opisy kolejnych gatunków reprezentujących rodzaj *Drepanaphis*: Davis (1909) opisał *D. monelli*, umieszczony początkowo przez autora w rodzaju *Phymatosiphum* i przeniesiony następnie do właściwego rodzaju przez Gillette (1910). Granovsky (1931) opisał *D. keshenae*, Miller (1937) opisał *D. sabrinae* podczas gdy Smith (1941), opisał siedem kolejnych taksonów: *D. carolinensis*, *D. kanzensis*, *D. nigricans*, *D. parvus*, *D. rubrum* oraz *D. spicata*. W 1943 roku Smith i Knowlton opisali *D. granovskyi* i *D. utahensis*, jednocześnie uznając *D. rubrum* za synonim *D. parvus*. Następnie Smith opisał *D. tissoti* (1944) i *D. simpsoni* (1959). Ostatni znany gatunek, *D. pallida*, został opisany przez Richardsa w 1969 roku.

Rewizję rodzaju przeprowadzili w 1968 Smith i Dillery. Opisali oni cztery nowe gatunki: *D. choanotricha*, *D. idahoensis*, *D. knowltoni* i *D. saccharini*. Na podstawie szeregu cech morfologicznych, do których należą: kształt i stosunek długości wyrostków na grzbietowej części odwłoka oraz jego pigmentacja, proporcje odpowiednich członów czułka czy kształt syfonów uskrzydlonych samic pokolenia partenogenetycznego oraz

nimf, opracowali klucz do oznaczania wszystkich znanych wówczas morf. Natomiast opisy morf pokolenia obupłciowego w przypadku większości gatunków były nieznane, co nie dawało pełnego wglądu w zróżnicowanie gatunków omawianego rodzaju. Autorzy przedstawili również szczegółowe opisy wyglądu przyżyciowo, w tym cechy barwne, co w przypadku gatunków podobnych morfologicznie i trudnych do pozyskania w terenie, stanowi cenne źródło danych diagnostycznych. Na podstawie przeprowadzonych badań porównawczych 17 znanych taksonów reprezentujących rodzaj *Drepananphis* podzielono na pięć morfologicznie podobnych grup gatunków. Podział ten oparto przede wszystkim na cechach morfologicznych dorosłych samic pokolenia partenogenetycznego, jednak autorzy wyraźnie uwzględniali także cechy nimf, jako element wspierający diagnozę morfo-grup.

Grupa *utahensis* (*D. utahensis*, *D. granovskyi*, *D. simpsoni*) została wyróżniona na podstawie układu szczecinek na głowie u samic partenogenetycznych. Grupa *monelli* (*D. monelli*, *D. keshenae, D. knowltoni, D. spicata*) obejmuje gatunki morfologicznie bardzo podobne, rozdzielane głównie na podstawie odmiennej rośliny żywicielskiej, a u dorosłych uskrzydlonych samic typowe są intensywniejsza pigmentacja i owoszczenie. Grupa *acerifoliae* (*D. acerifoliae*, *D. carolinensis*, *D. sabrinae*) częściowo przypomina grupę *monelli*, ale wyróżnia się proporcjami wyrostków grzbietowych odwłoka, przy czym zwracano uwagę na niejasności dotyczące cech stadiów młodocianych. Grupa *parva* (*D. idahoensis*, *D. saccharini*, *D. parva*) skupia gatunki zbliżone morfologicznie, rozdzielane głównie na podstawie roślin żywicielskich; u dorosłych uskrzydlonych samic występują jaśniejsze odnóża i słabsza pigmentacja odwłoka. Za najbardziej wyspecjalizowaną uznano grupę *nigricans* (*D. nigricans*, *D. tissoti*, *D. choanotricha*), odróżnianą zestawem cech dorosłych samic partenogenetycznych (m.in. proporcjami członów czułka), przy jednoczesnym uwzględnianiu cech morfologicznych nimf. W tym podziale szczególną pozycję zajmuje *D. kanzensis*, trudny do jednoznacznego przypisania, łączący cechy zbliżające do grup *monelli* i *parva*. Mimo to autorzy sklasyfikowali go do grupy *monelli*, uwzględniając również cechy nimf.

Od czasu tej rewizji nie przeprowadzono kompleksowego opracowania *Drepanaphis*, mimo że w kolejnych latach następowały zmiany w statusie taksonomicznym niektórych gatunków, w tym synonimizacje oparte częściowo na nieudokumentowanych przesłankach (Remaudière i Remaudière, 1997). Dodatkowo, w ostatnich dekadach

pojawiły się doniesienia o występowaniu *Drepanaphis acerifoliae* (Rycina 1) poza rodzimym zasięgiem nearktycznym, m.in. w Europie, co wskazuje na potencjał inwazyjny tego gatunku i wymaga pogłębionej analizy jego rozmieszczenia (Lozzia i Binaghi, 1992; Barbagallo i Cocuzza, 2014; Petrović-Obradović i inni, 2021).

Współcześnie, mimo że badania morfologiczne nadal stanowią podstawę analiz porównawczych, obserwuje się intensywny rozwój systematyki i filogenetyki, opartych na danych molekularnych (Deng i inni, 2025). W badaniach nad bioróżnorodnością oraz relacjami pokrewieństwa taksonów coraz powszechniej wykorzystuje się zestawy markerów molekularnych charakteryzujących się zróżnicowanym tempem ewolucji. Markery mitochondrialne, ze względu na stosunkowo szybkie tempo ewolucji, haploidalny charakter dziedziczenia oraz brak rekombinacji, dostarczają informacji użytecznej w rozdzielaniu blisko spokrewnionych linii ewolucyjnych oraz w analizach relacji filogenetycznych na poziomie międzygatunkowym i wewnątrzrodzajowym. Z kolei markery jądrowe, zazwyczaj bardziej konserwatywne, umożliwiają rekonstrukcję głębszych relacji filogenetycznych (Springer i inni, 2001; Chan i inni, 2021; Lee i inni, 2022).

Badania filogenetyczne obejmujące Drepanosiphinae opublikowano w 2017 roku, jednak ze względu na ograniczoną dostępność materiału do badań molekularnych, uwzględniały one jedynie niewielką liczbę taksonów, w tym dwa gatunki reprezentujące rodzaj *Drepanaphis* (Wieczorek i inni, 2017).

Dotychczasowe badania nad rodzajem *Drepanaphis* miały więc charakter fragmentaryczny i ograniczały się niemal wyłącznie do analiz morfologicznych, przeprowadzonych ponad pół wieku temu. Brak aktualnej rewizji taksonomicznej, niepełne opisy morf pokolenia obupłciowego oraz niemal całkowity brak danych molekularnych istotnie ograniczają możliwość weryfikacji obowiązującego ujęcia systematycznego oraz rekonstrukcji relacji filogenetycznych w obrębie rodzaju.

Dodatkowo, przedstawiciele rodzaju *Drepanaphis* nie byli dotychczas analizowani pod kątem składu zespołów endosymbiontów bakteryjnych, co stanowi istotną lukę w wiedzy dotyczącej biologii i ekologii tej grupy mszyc. Współczesna systematyka owadów opiera się na podejściu integracyjnym, łączącym różne źródła danych biologicznych, co jednoznacznie wskazuje na potrzebę ponownego, kompleksowego opracowania rodzaju *Drepanaphis*.

Rycina 1. Postać przyżyciowa uskrzydlonej partenogenetycznej samicy gatunku typowego *Drepanaphis acerifoliae*.

Źródło: V. Charny, na podstawie licencji Creative Commons 3.0.

5. Cele i hipotezy badawcze

Uwzględniając przedstawiony stan badań oraz zidentyfikowane ograniczenia poznawcze, celem niniejszej rozprawy doktorskiej było przeprowadzenie kompleksowej analizy rodzaju *Drepanaphis*, ze szczególnym uwzględnieniem jego zróżnicowania morfologicznego, relacji filogenetycznych oraz wzorców rozmieszczenia i powiązań troficznych.

Wyznaczono następujące cele badawcze:

(1) określenie wzorców rozmieszczenia geograficznego *Drepanaphis acerifoliae* – gatunku typowego rodzaju – w odniesieniu do naturalnego zasięgu roślin żywicielskich, poprzez analizę aktualnego występowania oraz modelowanie potencjalnego rozmieszczenia w warunkach przeszłych, współczesnych i prognozowanych scenariuszy zmian klimatu, w celu oceny jego potencjału inwazyjnego **(P1)**;

(2) przeprowadzenie rewizji taksonomicznej rodzaju *Drepanaphis* w oparciu o krytyczną analizę okazów zdeponowanych w kolekcjach entomologicznych, w tym materiału typowego, obejmującej szczegółową analizę zmienności morfologicznej i morfometrycznej wszystkich dostępnych dorosłych morf, w tym przedstawicieli pokolenia obupłciowego, wraz z aktualizacją danych o rozmieszczeniu gatunków w Ameryce Północnej oraz weryfikacją zasadności podziału rodzaju na morfologiczne grupy gatunków zaproponowane przez Smitha i Dillery'ego (1968) **(P2)**;

(3) rekonstrukcję powiązań filogenetycznych w obrębie rodzaju *Drepanaphis* w oparciu o sekwencje wybranych markerów molekularnych, z uwzględnieniem możliwości identyfikacji i charakterystyki zespołów endosymbiontów bakteryjnych pozyskiwanych równolegle w trakcie analiz molekularnych **(P3)**.

W pracy doktorskiej postawiono następujące hipotezy badawcze:

H1. *Drepanaphis acerifoliae* wykazuje potencjał inwazyjny, przejawiający się możliwością zasiedlania obszarów poza rodzimym zasięgiem nearktycznym, których warunki klimatyczne oraz dostępność roślin żywicielskich są zbliżone do warunków występujących w jego naturalnym obszarze występowania.

H2. Przedstawiciele rodzaju *Drepanaphis* charakteryzują się ograniczoną zmiennością cech morfometrycznych, przy jednoczesnym kluczowym znaczeniu cech

morfologicznych o charakterze jakościowym, a uwzględnienie cech morfologicznych samic jajorodnych i samców dostarcza taksonomicznie użytecznej informacji umożliwiającej weryfikację zasadności podziału rodzaju na morfologiczne grupy gatunków zaproponowane przez Smitha i Dillery'ego (1968).

H3. Rodzaj *Drepanaphis* stanowi klad monofiletyczny, a w jego obrębie możliwe jest wyróżnienie grup gatunków powiązanych z rozmieszczeniem geograficznym oraz specjalizacją względem roślin żywicielskich.

6. Materiały i metody

Materiał do badań obejmował mszyce z rodzaju *Drepanaphis* i uwzględniał zarówno preparaty mikroskopowe z kolekcji muzealnych (siedmiu krajów), jak i świeży materiał pozyskany w trakcie badań terenowych w USA.

W celu pozyskania materiału do badań morfologicznych skontaktowano się z kuratorami światowych kolekcji entomologicznych, których wykaz przedstawiono w Tabeli 1. Materiał sukcesywnie gromadzono od początku roku 2022 do połowy 2023 poprzez osobiste wizytacje w muzeach; w przypadkach, gdy było to niemożliwe, preparaty mikroskopowe były wypożyczane i analizowane w laboratoriach IBBiOŚ Uniwersytetu Śląskiego w Katowicach.

Kluczowy etap pracy rewizyjnej to analiza materiału typowego, który w przypadku mszyc z rodzaju *Drepanaphis* zdeponowany jest w Stanach Zjednoczonych, w kolekcji entomologicznej the Smithsonian National Museum of Natural History (Washington D.C.) oraz the Systematic Entomology Laboratory (Beltsville). Wizytacje w celu weryfikacji dostępnych okazów nastąpiły we wrześniu i październiku 2022.

Równocześnie przeprowadzano badania terenowe na wschodnim wybrzeżu Stanów Zjednoczonych, przy czym materiał gatunków występujących w zachodniej części USA i Europy pozyskano dzięki współpracy międzynarodowej.

Pozostały dostępny materiał typowy został udostępniony przez Muzeum Historii Naturalnej Champaign z Illinois, USA pod koniec 2023 roku. W kolekcji znajduje się seria preparatów okazów typowych między innymi dla gatunku *D. acerifoliae* (allotyp, paratyp, lektotyp i morfotyp) i *D. keshenae*, których nie udało się wcześniej zweryfikować.

Pełną listę gatunków uwzględnionych w badaniach morfologicznych przedstawiono w Tabeli 2.

6.1 Zbiór materiału do badań

6.1.1 Kolekcje muzealne

Tabela 1. Wykaz kolekcji muzealnych, z których pozyskano preparaty mikroskopowe do badań morfologicznych

Kolekcja	Nazwa instytucji	Liczba zweryfikowanych preparatów
DZUS	Uniwersytet Śląski w Katowicach, Polska	**61**
IECA	Centrum Biologiczne Czeskiej Akademii Nauk, Czechy	**53**
INHS Insect Collection	Muzeum Historii Naturalnej Champaign, Illinois, USA	**189**
MNHN	Muzeum Historii Naturalnej, Paryż, Francja	**72**
MZLU	Muzeum Zoologiczne Uniwersytetu w Lund, Szwecja	**35**
MZPW	Muzeum Instytutu Zoologii Polskiej Akademii Nauk, Warszawa, Polska	**20**
NHMUK	Muzeum Historii Naturalnej, Londyn, Wielka Brytania	**150**
USNM	Narodowe Muzeum Stanów Zjednoczonych, Smithsonian Institution, Waszyngton, USA	**59**
ZMUC	Muzeum Historii Naturalnej, Kopenhaga, Dania	**25**
Jensen Andrew	Prywatna kolekcja	**16**
Favret Colin	Prywatna kolekcja	**19**
Suma zweryfikowanych preparatów		**699**

Źródło: opracowanie własne.

Tabela 2. Lista gatunków zweryfikowanych w badaniach morfologicznych

Gatunek	Liczba zweryfikowanych preparatów	Uskrzydlone samice dzieworodne	Samice jajorodne (amfigoniczne)	Samce	Liczba morf
Drepanaphis acerifoliae (Thomas, 1878)	173	412	5	3	**420**
Drepanaphis carolinensis Smith, 1941	39	82	3	3	**88**
Drepanaphis choanotricha Smith & Dillery, 1968	14	29	1	2	**32**
Drepanaphis granovskyi Smith & Knowlton, 1943	14	33	1	1	**35**
Drepanaphis idahoensis Smith & Dillery, 1968	10	14	1	–	**15**
Drepanaphis *kanzensis* Smith, 1941	29	54	4	3	**61**
Drepanaphis keshenae Granovsky, 1931	17	26	2	3	**31**
Drepanaphis knowltoni Smith & Dillery, 1968	23	39	–	2	**41**
Drepanaphis monelli (Davis, 1909)	20	54	3	2	**59**
Drepanaphis nigricans Smith, 1941	25	74	1	–	**75**
Drepanaphis parva Smith, 1941	21	57	–	1	**58**
Drepanaphis robinsoni Malik, 2024	6	13	–	–	**13**
Drepanaphis sabrinae Miller, 1937	44	57	2	–	**59**
Drepanaphis saccharini Smith & Dillery, 1968	16	30	–	–	**30**
Drepanaphis simpsoni Smith, 1959	15	20	3	3	**26**

Drepanaphis spicata Smith, 1941	13	25	1	1	**27**
Drepanaphis tissoti Smith, 1941	8	20	1	–	**21**
Drepanaphis utahensis Smith & Knowlton, 1943	71	83	15	18	**116**
Drepanaphis sp.	141	71	91	49	**213**
Suma	**699**	**1168**	**134**	**91**	**1420**

Źródło: opracowanie własne.

6.1.2 Badania terenowe

Materiał do badań morfologicznych i molekularnych zebrano podczas wyjazdu terenowego do Stanów Zjednoczonych we wrześniu i październiku 2022 roku. Wizytę studyjną celowo zaplanowano jesienią, w celu zgromadzenia morf pokolenia obupłciowego, które występują w tym okresie. Łącznie zebrano 172 osobniki pięciu gatunków, w tym dwa samce *D. carolinensis*, cztery samce *D. kanzensis* oraz młodociane stadia, których nie udało się zweryfikować. Samic jajorodnych nie zebrano. Badania prowadzono w czterech różnych stanach: New Jersey, Maryland, Pensylwania, Północna Karolina i Dystryktu Kolumbii.

Wykaz gatunków zebranych podczas badań terenowych w USA przedstawia Tabela 3.

Tabela 3. Gatunki z rodzaju *Drepanaphis* pozyskane w trakcie badań terenowych w Stanach Zjednoczonych w 2022 roku

Gatunek	**Lokalizacja**	**Liczba osobników**
Drepanaphis acerifoliae (Thomas, 1878)	Karolina Północna, New Jersey, Maryland	**27**
Drepanaphis carolinensis Smith, 1941	Karolina Północna, New Jersey	**23**
Drepanaphis kanzensis Smith, 1941	Karolina Północna, New Jersey	**34**
Drepanaphis robinsoni Malik, 2024	Dystrykt Kolumbii	**1**
Drepanaphis sabrinae Miller, 1937	Karolina Północna	**87**

Źródło: opracowanie własne.

Materiał został odpowiednio zebrany do:

(a) 70% roztworu alkoholu etylowego w celu przeprowadzenia badań morfologicznych;

(b) 99% roztworu alkoholu etylowego w celu przeprowadzenia badań molekularnych.

Materiał zebrany w trakcie badań terenowych został sfotografowany i wstępnie oznaczony przy pomocy klucza Blackman i Eastop, 2025 pod mikroskopem stereoskopowym Nikon DS-Fi2 camera (Nikon Corporation, Tokyo, Japan), a następnie przechowywany w lodówce w temperaturze –8 °C.

6.2 Modelowanie niszy ekologicznej dla *D. acerifoliae*

Dane o występowaniu *Drepanaphis acerifoliae* zebrano z piśmiennictwa, kolekcji muzealnych oraz baz danych – Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) i iNaturalist (https://www.inaturalist.org/). Dodatkowe informacje pozyskano dzięki współpracy z kuratorami muzeów, a część okazów zweryfikowano osobiście. Usunięto rekordy bez lokalizacji oraz punkty położone bliżej niż 10 km. Wszystkie stanowiska zapisano w układzie WGS84. Łącznie uzyskano 90 unikatowych stanowisk w Ameryce Północnej i 22 w Europie. Do modelowania wykorzystano 19 zmiennych bioklimatycznych z portalu WorldClim (https://www.worldclim.org/), dane paleoklimatyczne oraz informacje o typach klimatu za klasyfikacją klimatów Köppena-Geigera i eko-regionach. Modele potencjalnej niszy ekologicznej wykonano w MaxEnt ver. 3.4.1 **(P1)**. Wyniki przedstawiono jako mapy potencjalnego rozmieszczenia gatunku w przeszłości, teraźniejszości i przyszłości, opracowane w QGIS ver. 3.30.1.

6.3 Badania morfologiczne

6.3.1 Przygotowanie preparatów mikroskopowych do analiz morfologicznych

W celu dokładnej weryfikacji taksonomicznej gatunków sporządzono preparaty mikroskopowe zebranych okazów zgodnie z metodyką zawarta w opracowaniu Kanturskiego i Wieczorek (2012). Obserwacje prowadzono pod mikroskopem świetlnym Leica DM 3000 LED, a okazy mszyc zostały sfotografowane przy użyciu kamery Leica

MC 190 HD (Leica Microsystems GmbH, Wetzlar, Germany). Wykonane preparaty zostały zdeponowane w kolekcji entomologicznej Instytutu Biologii, Biotechnologii i Ochrony Środowiska Uniwersytetu Śląskiego w Katowicach (DZUS).

6.3.2 Przygotowanie materiału do obserwacji w elektronowym mikroskopie skaningowym (SEM)

Do obserwacji w elektronowym mikroskopie skaningowym (SEM) wykorzystano osiem osobników *D. acerifoliae*, sześć *D. kanzenis* i sześć *D. sabrinae*. Metoda ta posłużyła do zobrazowania struktur morfologicznych uskrzydlonych samic dzieworodnych, w tym niewidocznych przy użyciu mikroskopu świetlnego do których należą sensilla czy zakończenia wyrostków grzbietowych odwłoka. Osobniki przeznaczone do analizy przechowywano w 70% etanolu. Proces odwadniania przeprowadzono w kolejnych roztworach etanolu o rosnących stężeniach: 20 minut w 80%, 15 minut w 90%, 10 minut w 96% oraz dwukrotnie po 10 minut w etanolu absolutnym. Całość wysuszono w suszarce punktu krytycznego Leica EM CPD300 (Leica Microsystems, Wiedeń, Austria). Próbki umieszczano na aluminiowych podstawkach przy pomocy dwustronnej taśmy węglowej i pokrywano warstwą złota o grubości 30 nm w napylarce Safematic CCU-010 HV (Safematic GmbH, Zizers, Szwajcaria, Echlin, 2009). Tak przygotowane próbki obserwowano w skaningowym mikroskopie elektronowym Hitachi SU8010 (Hitachi High-Technologies Corporation, Tokio, Japonia) przy napięciu 7,0 i 10,0 kV, z wykorzystaniem detektora elektronów wtórnych.

6.3.3 Analizy morfometryczne i morfologiczne

W analizach morfometrycznych zastosowano analizę głównych składowych (PCA) opartą na danych uzyskanych z pomiarów posiadanych okazów mszyc. Punktem wyjścia były zbiory danych (Tabele S1, S2 zawarte w publikacji **P2**) obejmujące zmienne morfometryczne, wskaźniki morfometryczne oraz jakościowe cechy morfologiczne dla uskrzydlonych samic partenogenetycznych (52 cechy), samców (51 cech) oraz samic jajorodnych (46 cech). Zestawy danych (Tabele S3, S4, S5 zawarte w publikacji **P2**) przetestowano za pomocą analizy korelacji wielokrotnej i ostatecznie wybrano zmienne o najniższych wartościach redundancji. Dla 213 uskrzydlonych samic partenogenetycznych, 30 samców i 43 samic jajorodnych (amfigonicznych) wybrano po 24 cechy (w różnych proporcjach zmiennych morfometrycznych, współczynników morfometrycznych i cech morfologicznych) (Tabele S1 i S2 zawarte w publikacji **P2**).

Przed analizą PCA każdą cechę przeliczono na średnią zerową i odchylenie standardowe jednostkowe w zredukowanych zbiorach danych, dzięki czemu wszystkim nadano taką samą wagę. Następnie stworzono nowe, nieskorelowane zmienne (składowe główne), które są kombinacjami liniowymi oryginalnych zmiennych. W toku analizy wybrano tylko te składowe, które wyjaśniają najwięcej wariancji (informacji). Otrzymane wyniki wykorzystano do oceny zróżnicowania morfologicznego badanych morf.

6.4 Wyznaczenie zasięgów występowania gatunków z rodzaju *Drepanaphis*

Dane o występowaniu gatunku pozyskano z literatury naukowej, zbiorów muzealnych, własnych badań terenowych w USA, obserwacji z serwisu iNaturalist oraz z baz różnorodności biologicznej (GBIF). Kuratorzy kolekcji udostępniali informacje i fotografie preparatów, a część okazów została zbadana bezpośrednio podczas wizyty w muzeach. Dla wszystkich stanowisk gatunku określono współrzędne geograficzne (współrzędne w układzie WGS84), a zasięgi roślin żywicielskich wykorzystano z dostępnych cyfrowych map zasięgów roślin w oparciu o opracowanie Conservation Biology Institute (http://databasin.org) **(P2)**. Na tej podstawie utworzono mapy rozmieszczenia gatunków z wykorzystaniem QGIS.

6.5 Badania molekularne

Badania molekularne przeprowadzono w okresie maj 2023 – kwiecień 2024 w laboratoriach IBBiOŚ Uniwersytetu Śląskiego w Katowicach oraz częściowo w Centre de Biologie pour la Gestion des Populations (INRAE) w Montpellier we Francji, we współpracy z dr Emmanuelle Jousselin.

Analizą objęto dziesięć gatunków z rodzaju *Drepanaphis*. Materiał obejmował gatunki pozyskane w trakcie badań terenowych w USA w 2022, do których należą: *D. acerifoliae*, *D. carolinensis*, *D. kanzensis*, *D. robinsoni*, *D. sabrinae*.

Ponadto w badaniach uwzględniono także *D. granovskyi, D. monelli* i *D. utahensis* zebrane w USA w 2023 roku dzięki współpracy z dr Williamem Pittem z Washington State University, USA oraz z dr Andrew Jensenem z California Academy of Sciences, USA.

Dodatkowo wykorzystano osobniki *D. acerifoliae* z Serbii zebrane w 2023 roku we współpracy z dr Oliverą Petrovic-Obradovic z University of Belgrade, Serbia.

Osobnik *D. simpsoni* z 1976 roku został pozyskany z kolekcji MNHN w Paryżu, Francja.

6.5.1 Izolacja DNA, amplifikacja, elektroforeza i sekwencjonowanie materiału genetycznego

Do izolacji DNA zastosowano zestaw DNeasy Blood & Tissue Kit (Qiagen, Niemcy), postępując zgodnie z zaleceniami producenta, z wyjątkiem wydłużenia etapu inkubacji próbek w buforze lizującym do 24 godzin oraz zastosowania końcowej objętości elucji wynoszącej 80 µL.

W analizach wykorzystano dwie grupy markerów molekularnych:

(a) fragmenty genów jądrowych obejmujące fragment o długości 900 pz genu czynnika elongacyjnego 1 alfa (EF1α) oraz fragment o długości 700 pz genu dehydrogenazy 6-fosfoglukonianowej (PGD);
(b) fragmenty genów mitochondrialnych obejmujące gen kodujący podjednostkę 1 oksydazy cytochromowej COI (mtDNA) o długości 700 pz oraz fragmenty o długości 780 pz genu cytochromu b (Cytb).

Zestaw starterów użytych w reakcjach PCR znajduje się w publikacji **(P3)**.

Reakcje PCR przeprowadzono przy użyciu EURx Color OptiTaq PCR Master Mix (25 µL), odpowiednich starterów (po 1 µL) oraz 2 µL izolatu DNA jako matrycy, uzupełniając wodą wolną od nukleaz do finalnej objętości 50 µL. Reakcje PCR przeprowadzano w termocyklerze Biometra TProfessional Basic Gradient. Profil termiczny PCR obejmował: wstępną denaturację w 94°C przez 60 s, następnie 35 cykli: denaturacja w 95°C przez 40 s, hybrydyzacja w 45°C przez 45 s oraz elongacja w 72°C przez 60 s, a na końcu wydłużanie końcowe w 72°C przez 180 s. Rozdział elektroforetyczny produktów mieszaniny poreakcyjnej przeprowadzono w żelu agarozowym (1%) w buforze TBE z dodatkiem SimplySafe (EURx) i analizowano przy użyciu transiluminatora ETX (Vilber Lourmat).

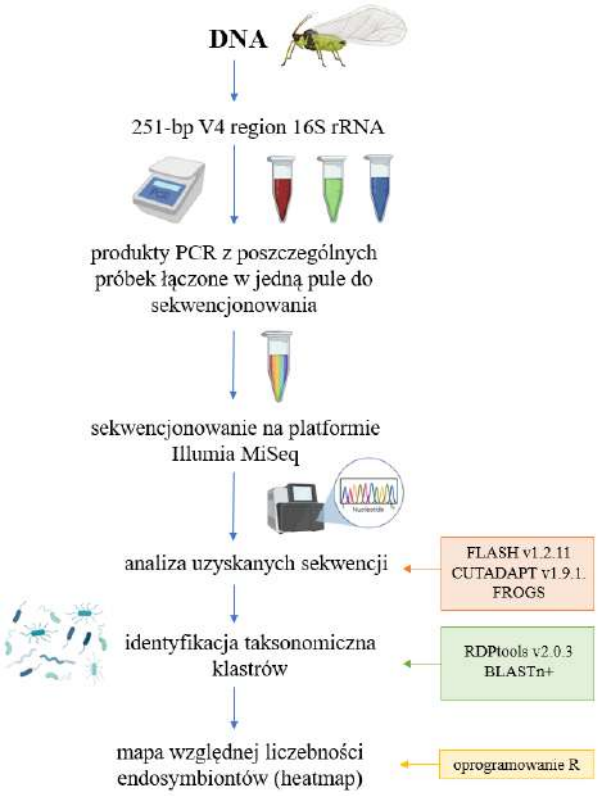
Produkty amplifikacji sekwencjonowano w obu kierunkach w firmie GenoMed (Warszawa, Polska). Uzyskane sekwencje zdeponowano w bazie GenBank. Spośród gatunków, których nie udało się pozyskać podczas badań terenowych, jedynie *Drepanaphis parva* posiadał sekwencję dostępną w GenBank; została ona pobrana z bazy i wykorzystana w analizach.

6.5.2 Analizy filogenetyczne

Otrzymane sekwencje porównano z danymi dostępnymi w bazie GenBank, a następnie wyrównano metodą ClustalW zaimplementowaną w programie MEGA. Analizy filogenetyczne przeprowadzono dwiema metodami: największej wiarygodności (Maximum Likelihood, ML) w programie IQ-TREE oraz rekonstrukcją bayesowską w programie MrBayes. Dla każdego analizowanego zestawu sekwencji dobierano optymalny model ewolucji, obejmujący model substytucji nukleotydów oraz założenia dotyczące zmienności tempa podstawień. Wyniki analiz zaprezentowano w formie kladogramu zwizualizowanego w programie FigTree v1.4.4.

6.5.3 Charakterystyka endosymbiontów

Do analizy bakteryjnych endosymbiontów wykorzystano te same ekstrakty DNA, które posłużyły do analizy filogenetycznej. Zamplifikowano fragment regionu V4 genu 16S rRNA, a produkty PCR zindeksowano i zsekwencjonowano w trybie paired-end na platformie Illumina MiSeq. Każdą próbkę amplifikowano w dwóch replikatach z kontrolami negatywnymi, umieszczając replikaty na osobnych płytkach w celu ograniczenia ryzyka kontaminacji. Produkty PCR oczyszczono, oznaczono ilościowo i połączono we wspólną bibliotekę z próbkami z innych projektów. Otrzymane odczyty poddano standardowej obróbce bioinformatycznej (filtracja jakości, scalanie odczytów, przycinanie starterów, łączenie klastrów o wysokiej identyczności) oraz przypisaniu taksonomicznemu względem bazy Silva. Usunięto rzadkie sekwencje (<0,5% odczytów w próbce) i zachowano klastry obecne w obu replikatach, na podstawie których scharakteryzowano skład endosymbiontów (Rycina 2).



Rycina 2. Schemat procedury analizowania składu endosymbiontów w rodzaju *Drepanaphis*.

Źródło: opracowanie własne. Schemat stworzony z użyciem platformy BioRender (https://app.biorender.com). Prawo do publikacji poświadczone licencją.

7. Omówienie wyników prowadzonych badań

7.1 Publikacja 1: Modelowanie niszy ekologicznej dla *D. acerifoliae*

Malik, K., Bugaj-Nawrocka, A., Wieczorek, K. (2023). Distribution of *Drepanaphis acerifoliae* – aphid pest of *Acer* trees – faced with global climate change. *Folia Biologica* (Kraków), 71, 115–130. https://doi.org/10.3409/fb_71-3.12

IF_{2023}: 0,8

Punkty MNiSW: 100

Publikacja pt. „Distribution of *Drepanaphis acerifoliae* – aphid pest of *Acer* trees – faced with global climate change" poświęcona jest modelowaniu niszy ekologicznej dla gatunku typowego *D. acerifoliae*. Gatunek ten jako jedyny w rodzaju *Drepanaphis* osiągnął wysoki stopień ekspansji nowych terenów obejmujący Europę i Azję, zatem zweryfikowanie **czynników wpływających na jego rozmieszczenie** uznano za kluczowe w kontekście **potencjalnej inwazyjności**.

W badaniu wykorzystano modelowanie niszy ekologicznej oparte na dostępnych danych klimatycznych z przeszłości (ostatni interglacjał; maksimum lodowcowe; środkowy holocen) z uwzględnieniem teraźniejszych danych i prognoz na przyszłość, w celu określenia potencjalnego rozmieszczenia *Drepanaphis acerifoliae*. Model uzyskano z wykorzystaniem zmiennych bioklimatycznych, które odzwierciedlają temperatury i opady w różnych porach roku, przy czym największe znaczenie dla przewidywań miała średnia temperatura najcieplejszego kwartału. Wskazuje to, że rozprzestrzenianie *D. acerifoliae* jest ściśle związane z ciepłymi, umiarkowanymi warunkami klimatycznymi i preferuje klimat umiarkowany wilgotny i kontynentalny.

W przeprowadzonych analizach uwzględniono tereny z odmiennym typem roślinności i zaobserwowano następujące powiązania:

- 69% populacji zasiedla lasy liściaste i mieszane strefy umiarkowanej, 10% lasy iglaste, a pozostałe występują w środowiskach trawiastych, śródziemnomorskich i kserotermicznych.

- Występuje wyraźna zależność ekologiczno-troficzna gatunku od siedlisk leśnych, w których występują gatunki klonów będące kluczowymi roślinami żywicielskimi mszyc z rodzaju *Drepanaphis*.

W badaniach został wyznaczony obszar występowania *D. acerifoliae*: obecny naturalny zasięg obejmuje wschodnią część Ameryki Północnej, od Florydy po Kanadę (Figure 2), co pokrywa się z rozmieszczeniem *Acer saccharinum*, *A. rubrum* i *A. saccharum,* które stanowią rośliny żywicielskie gatunku.

Ponadto przeprowadzono modelowanie niszy ekologicznej dla omawianego gatunku. Uzyskane rezultaty potwierdziły, że:

- Najbardziej odpowiednie siedliska w USA występują w stanach wschodnich i centralnych, natomiast na zachodzie w ograniczonym zakresie (Figure 4).
- W Europie potencjalne nisze gatunku obejmują basen Morza Śródziemnego, zachodnią i środkową Europę (Hiszpanię, Włochy, Francję, Niemcy, Węgry, Bałkany), a także obszary stepowe i lasostepowe Ukrainy, Rosji i Kazachstanu (Figure 5).
- Sprzyjające warunki panują w północnej Afryce oraz w Azji Zachodniej. Modele paleoklimatyczne sugerują, że *D. acerifoliae* w przeszłości zasiedlał północno-wschodnie rejony Ameryki Północnej, migrując na południe w okresie glacjalnym i rozszerzając zasięg w holocenie (Figure 6, 7).

Modele prognozują dalsze przesuwanie się potencjalnych nisz ku północy, a zwłaszcza w Kanadzie (Figure 8) oraz w Europie Środkowej i Północnej (Figure 5).

Dzięki przeprowadzonym analizom wyselekcjonowano także **główne czynniki ekologiczne** wpływające na rozprzestrzenienie *D. acerifoliae*. Należą do nich: temperatura najcieplejszego kwartału, opady zimowe czy średnie opady roczne. Dane te wskazują, że gatunek preferuje stabilne, umiarkowanie wilgotne środowiska leśne, o stosunkowo niskiej zmienności termicznej.

Jest to pierwsza praca, która analizuje przedstawiciela rodzaju *Drepanaphis* poza jego naturalnym zasięgiem występowania. W jej ramach wyznaczono czynniki determinujące szeroką ekspansję tego gatunku. Zasięg *D. acerifoliae* jest ściśle skorelowany z **występowaniem roślin żywicielskich** (*A. saccharinum*, *A. saccharum*, *A. rubrum*), co

kładzie nacisk na istotność uwzględniania ich podczas prowadzenia badań monitoringowych.

W regionach, gdzie klony te zostały wprowadzone sztucznie (np. w Europie czy Ameryce Południowej), istnieje wysokie ryzyko kolonizacji przez *D. acerifoliae*, który został już odnotowany w Europie. Analizy sugerują, że introdukcje te mogły mieć niezależny charakter, a bariery górskie ograniczają rozprzestrzenianie gatunku (Figure 9).

Model wskazał dodatkowo, że terytoria, na których *D. acerifoliae* może się pojawić w najbliższej przyszłości, obejmują Francję i Turcję. Istnieje także potencjał do zasiedlania obszarów, w których uprawiany jest *A. saccharinum*, m.in. w Azji Zachodniej, Afryce Północnej i Ameryce Południowej.

Tym samym na podstawie uzyskanych wyników badań **pozytywnie zweryfikowano hipotezę H1:** *Drepanaphis acerifoliae* wykazuje potencjał inwazyjny, przejawiający się możliwością zasiedlania obszarów poza rodzimym zasięgiem nearktycznym, których warunki klimatyczne oraz dostępność roślin żywicielskich są zbliżone do warunków występujących w jego naturalnym obszarze występowania.

Warto podkreślić, że rozprzestrzenienie *D. acerifoliae* jest powiązane z działalnością człowieka, taką jak transport roślin ozdobnych czy handel. W warunkach europejskich gatunek może stanowić potencjalne zagrożenie dla drzewostanów miejskich, parkowych i leśnych, szczególnie tam, gdzie uprawia się klony północnoamerykańskie. Wyniki modelowania niszy ekologicznej trafnie wskazały obszary, na których w ostatnim czasie odnotowano nowe stanowiska badanego gatunku (Martynov i inni, 2025), co potwierdza wiarygodność opracowanego modelu w świetle aktualnych badań terenowych.

Wyniki pracy ukazują, że postępujący sukces ekologiczny i dalsze drogi ekspansji *Drepanaphis acerifoliae* są zależne przede wszystkim od rozprzestrzenienia jego roślin żywicielskich, a zmiany klimatu promują poszerzanie jego obszaru występowania na świecie, czego dowodzi pierwsze stwierdzenie tego gatunku z Azji (Japonia) (Sugimoto, 2024).

7.2 Publikacja 2: Rewizja taksonomiczna mszyc z rodzaju *Drepanaphis* na podstawie danych morfologicznych wraz z wyznaczeniem zasięgów występowania znanych gatunków.

Malik, K., Bugaj-Nawrocka, A., Wieczorek, K. (2024). Taxonomic revision of the Nearctic genus *Drepanaphis* Del Guercio (Hemiptera: Aphididae: Drepanosiphinae). *Insects*, 15(7), 1–71. https://doi.org/10.3390/insects15070553

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Materiały uzupełniające dostępne online:

https://www.mdpi.com/article/10.3390/insects15070553/s1

Supplementary file S1: Dane metryczne i cechy morfologiczne uskrzydlonych samic partenogenetycznych z rodzaju *Drepanaphis*;

Supplementary file S2: Dane metryczne i cechy morfologiczne samców oraz samic jajorodnych z rodzaju *Drepanaphis*;

Supplementary file S3: Wyniki analiz statystycznych dla uskrzydlonych samic partenogenetycznych z rodzaju *Drepanaphis*;

Supplementary file S4: Wyniki analiz statystycznych dla samców z rodzaju *Drepanaphis*;

Supplementary file S5: Wyniki analiz statystycznych dla samic jajorodnych z rodzaju *Drepanaphis*;

Supplementary file S6: Materiał porównawczy gatunków z rodzaju *Drepanaphis*.

Efektem publikacji pt. „Taxonomic Revision of the Nearctic Genus *Drepanaphis* Del Guercio (Hemiptera, Aphididae: Drepanosiphinae)" jest kompleksowa rewizja taksonomiczna rodzaju *Drepanaphis*.

Na potrzeby przeprowadzonej rewizji zweryfikowano 652 preparaty obejmujące 1382 osobników, w tym 1055 uskrzydlonych samic partenogenetycznych, 61 samic jajorodnych oraz 42 samców. Efektem badań była szczegółowa redeskrypcja uskrzydlonych samic pokolenia dzieworodnego 17 znanych gatunków należących do rodzaju *Drepanaphis* oraz opis nowego dla nauki gatunku *D. robinsoni* Malik, 2024. Ponadto, sporządzono deskrypcje samic amfigonicznych 14 gatunków oraz deskrypcje samców trzech gatunków *Drepanaphis*. Oprócz szczegółowych opisów, praca dostarcza również ilustracje 44 znanych morf pokolenia partenogenetycznego i obupłciowego wraz z oryginalnymi kluczami do ich identyfikacji.

W pracy zweryfikowano i zdefiniowano zestaw kluczowych cech diagnostycznych rodzaju *Drepanaphis,* wykorzystując technikę mikroskopii świetlnej i skaningowej mikroskopii elektronowej (SEM). Najważniejszą z nich są cztery pary wyrostków na grzbietowej części odwłoka (zwykle największa jest trzecia para), przy czym ich układ, wielkość i barwa mogą istotnie różnić się między gatunkami (Figure 1; Figure 6[G]). Czułki są 6-członowe, z najdłuższym ostatnim segmentem, na podstawie którego występuje 1 rynarium główne i od 4 do 11 rynariów dodatkowych (Figure 2; Figure 6[E]). Na trzecim członie czułka znajdują się rynaria wtórne w zróżnicowanej liczbie (Figure 6[D]). Odnóża pokryte są nielicznymi, drobnymi szczecinkami, z ciemnymi lub jasnymi udami (Figure 6[C]) i w przypadku niektórych gatunków paskami na udach trzeciej pary odnóży. Syfony mają kształt kolby lub są cylindryczne z rozetą na końcach (Figure 6[J, K]). Ogonek w kształcie kopuły z 4–6 długimi, cienkimi szczecinkami (Figure 6[L]). Istotnym uzupełnieniem pracy było także szczegółowe przedstawienie po raz pierwszy budowy genitaliów samców (Figure 14), które dostarczyło dodatkowych cech diagnostycznych.

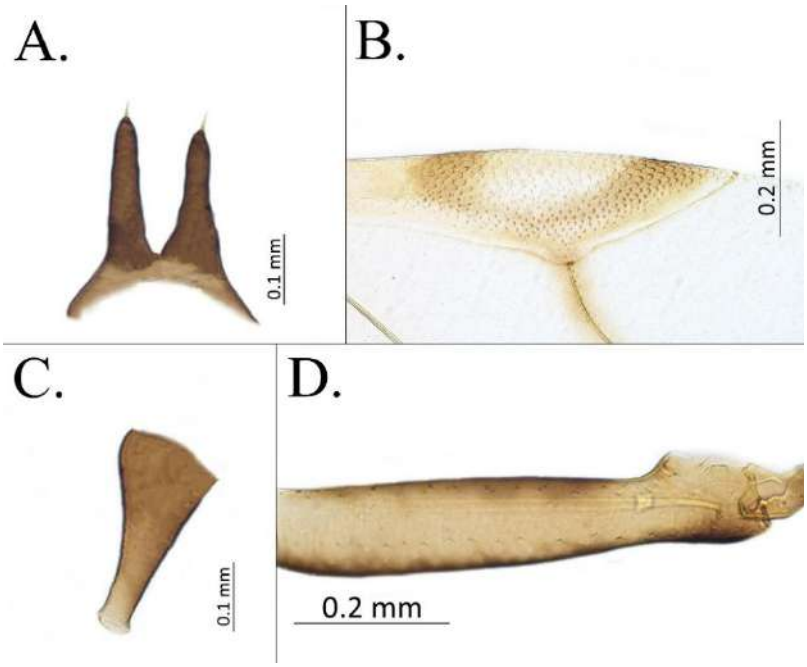
Przeprowadzona analiza wielowymiarowa (PCA) oparta na danych morfologicznych i morfometrycznych, pozwoliła wskazać, które cechy najlepiej różnicują taksony. U 213 uskrzydlonych samic partenogenetycznych reprezentujących wszystkie gatunki *Drepanaphis* wykazano, że najwięcej informacji diagnostycznej niesie zestaw cech związanych z ubarwieniem przednich ud oraz układem wyrostków na grzbietowej części

odwłoka. Cechy te najsilniej porządkują zmienność w danych. Drugi najważniejszy zestaw cech obejmował przepaski na udach tylnych odnóży oraz barwę syfonów.

Podobne wyniki uzyskano dla 30 samców (12 gatunków), gdzie kluczowe znaczenie miały ponownie barwa przednich ud, przepaski na udach tylnych odnóży oraz ubarwienie czułków, a w dalszej kolejności cechy takie jak wielkość syfonów czy dobrze rozwinięte wyrostki na grzbietowej części odwłoka.

Z kolei dla 43 samic jajorodnych (14 gatunków) decydująca okazała się proporcja ostatniego członu czułka (stosunek długości jego części końcowej do podstawy), a w dalszej kolejności ubarwienie czułków, goleni pierwszej pary odnóży oraz syfonów.

Analizy wykazały, że w przypadku wszystkich badanych morf cechy jakościowe (kształt i barwa struktur) są bardziej rozstrzygające niż same wartości metryczne, ponieważ wartości cech ilościowych często się nakładają i nie istnieje pojedynczy, uniwersalny wskaźnik pozwalający jednoznacznie rozdzielić wszystkie gatunki. Do kluczowych cech jakościowych zaliczono: kształt i wielkość wyrostków grzbietowych (Rycina 3[A]), kształt pterostigmy (Rycina 3[B]), kształt i ubarwienie syfonów (Rycina 3[C]), a także ubarwienie uda pierwszej pary odnóży (Rycina 3[D]).



Rycina 3. Morfologiczne cechy diagnostyczne gatunków z rodzaju *Drepanaphis*.

Źródło: opracowanie własne. Rycina stworzona przy wykorzystaniu programu PhotoScape X. A. Wyrostki na grzbietowej części odwłoka; B. Kształt i ubarwienie pterostigmy; C. Kształt i wielkość syfonów; D. Ubarwienie uda pierwszej pary odnóży.

Przeprowadzone analizy wskazały, że przedstawiciele rodzaju *Drepanaphis* charakteryzują się ograniczoną zmiennością cech morfometrycznych, przy jednoczesnym kluczowym znaczeniu cech morfologicznych o charakterze jakościowym, **co potwierdza założenia hipotezy (H2).**

W toku rewizji zidentyfikowano błędne oznaczenia materiału dla siedmiu gatunków (*D. acerifoliae*, *D. carolinensis*, *D. choanotricha*, *D. kanzensis*, *D. sabrinae*, *D. parva*, *D. tissoti*). Szczególnie ważne było rozpoznanie grupy osobników odbiegających układem wyrostków grzbietowych od typowego wzorca wśród okazów oznaczonych pierwotnie jako *D. choanotricha* i *D. parva*. Analizy statystyczne potwierdziły ich odrębność morfologiczną, co umożliwiło opisanie nowego gatunku, *D. robinsoni*, wcześniej błędnie klasyfikowanego w obrębie tych taksonów. Analizy genetyczne w dalszym etapie badań potwierdziły jego odrębną tożsamość gatunkową.

Analizy statystyczne pozwoliły również rozwiązać problem taksonomiczny dotyczący *D. nigricans* i *D. tissoti*, traktowanych jako tożsame gatunki (Remaudière i Remaudière 1997). Wyniki niniejszej pracy wskazują, że są to gatunki odrębne, a kluczową cechą diagnostyczną okazała się liczba dodatkowych rynariów na podstawie ostatniego członu czułka: u *D. nigricans* wynosi 4, natomiast u *D. tissoti* 5–11. Dodatkowo stwierdzono różnice w liczbie pseudosensoriów na goleni trzeciej pary odnóży (u *D. nigricans* 62, u *D. tissoti* 30–31) oraz w barwie syfonów u samic jajorodnych. Wyniki analizy PCA potwierdziły status gatunkowy *D. tissoti* i jednocześnie wsparły synonimizację dwóch innych gatunków: *D. pallida* i *D. simpsoni*.

Wyniki analizy PCA (Figure 38) w dużej mierze wspierają podział gatunków Smith'a i Dillery'ego na grupy morfologiczne, wskazując jednak na konieczność wyłączenia z tych grup dwóch gatunków – *D. kanzensis* i *D. sabrinae*.

Grupa „*acerifoliae*" obejmuje gatunki z czterema parami wyrostków grzbietowych u uskrzydlonych samic partenogenetycznych (pierwotnie: *D. acerifoliae*, *D. carolinensis*, *D. sabrinae*). *Drepanaphis sabrinae* wyróżnia się jednak nietypowym układem wyrostków (II i III para tej samej długości) oraz większą liczbą rynariów dodatkowych (5–6), a jego pozycja w analizach PCA sugeruje charakter pośredni między pozostałymi gatunkami tej grupy.

Gatunki z grupy „*monelli*" mają widoczną głównie trzecią parę wyrostków i ciemne pręgi na udach trzeciej pary odnóży (*D. keshenae*, *D. knowltoni*, *D. monelli*, *D. spicata*). Choć Smith i Dillery (1968) włączali tu także *D. kanzensis*, analizy morfologiczne i PCA wskazują na jego odrębność (m.in. jasne udo przedniej pary odnóży i jaśniejsze syfony), dlatego zaproponowano, aby nie przypisywać go do żadnej grupy, podobnie jak *D. sabrinae*.

Pozostałe grupy są zgodne z wcześniejszym podziałem: „*nigricans*" (*D. choanotricha*, *D. nigricans*, *D. tissoti*) wyróżnia się bardzo długimi czułkami, „*parva*" (*D. idahoensis*, *D. parva*, *D. robinsoni*, *D. saccharini*) jasno ubarwionymi przednimi udami, a „*utahensis*" (*D. granovskyi*, *D. simpsoni*, *D. utahensis*) dwiema parami szczecinek czołowych na głowie.

Ponadto, włączenie do analiz cech morfologicznych samic amfigonicznych i samców (Figures 39–41) dostarcza dodatkowych informacji umożliwiających weryfikację zasadności podziału rodzaju na morfologiczne grupy gatunków zaproponowane przez Smith'a i Dillery'ego (1968), **jednoznacznie wspierając hipotezę (H2)**.

Ważną częścią pracy była również analiza biogeograficzna i troficzna. Wszystkie gatunki rodzaju *Drepanaphis* stwierdzono w Stanach Zjednoczonych, a około połowę także w Kanadzie (*D. acerifoliae*, *D. carolinensis*, *D. kanzensis*, *D. knowltoni*, *D. monelli*, *D. parva*, *D. saccharini*, *D. simpsoni*, *D. spicata*). W USA wyróżniono wzorce rozmieszczenia: w zachodniej części notowane są m.in. *D. granovskyi*, *D. idahoensis*, *D. utahensis* związane z *Acer grandidentatum*, część gatunków występuje zarówno na zachodzie, jak i na wschodzie (np. *D. acerifoliae*, *D. knowltoni*, *D. spicata*), a pozostałe zasiedlają głównie wschodnią część kraju, co odpowiada rozmieszczeniu roślin żywicielskich i może wskazywać, że rodzaj *Drepanaphis* wyewoluował we wschodniej części Ameryki Północnej wraz z dywersyfikacją i rozprzestrzenianiem się klonów.

Rewizja pozwoliła też poszerzyć wiedzę o roślinach żywicielskich omawianej grupy mszyc. Potwierdzono, że przedstawiciele rodzaju *Drepanaphis* są zasadniczo związani z klonami (*Acer*), przy czym *D. monelli* pozostaje jedynym gatunkiem żerującym na kasztanowcu gładkim *Aesculus glabra*. Jednocześnie wykazano, że spektrum żywicieli części gatunków jest szersze niż dotąd zakładano, również u taksonów wcześniej uznawanych za monofagiczne. W kolekcji entomologicznej w Illinois (USA) potwierdzono okazy *D. monelli* z *A. saccharum* i *A. saccharinum* (po weryfikacji

wykluczono błędne etykietowanie). *Drepanaphis kanzensis* jest związany głównie z *A. saccharum* (potwierdzone badaniami terenowymi), ale odnotowano go także na *A. rubrum* i *A. saccharinum*, przy czym pokolenie obupłciowe obserwowano na *A. saccharinum*. Wykazano również duże różnice w częstości występowania gatunków: od bardzo pospolitych (np. *D. acerifoliae*) po bardzo rzadkie, znane z nielicznych stanowisk (np. *D. choanotricha* i *D. robinsoni*).

Opublikowana rewizja stanowi najbardziej aktualne źródło informacji dotyczące morfologicznej różnorodności gatunków w rodzaju *Drepanaphis*. Po raz pierwszy opracowano w niej szczegółowe opisy samic jajorodnych z pokolenia obupłciowego, których cechy przyczyniły się rozwiązania tożsamości gatunkowej taksonów problematycznych. Na podstawie cech samic z pokolenia partenogenetycznego opisano nowy gatunek *D. robinsoni*. Przeprowadzone analizy statystyczne wsparły podział rodzaju na grupy morfologiczne. Przedstawiono aktualny zasięg występowania rodzaju *Drepanaphis* w Ameryce Północnej, a analiza troficzna wykazała szersze spektrum roślin żywicielskich niż dotychczas wykazywano, co może ukierunkować przyszłe badania terenowe, dotyczące w szczególności zebrania przedstawicieli pokolenia obupłciowego gatunków, dla których morfy te nadal pozostają nieznane.

7.3 Publikacja 3: Analiza filogenetyczna rodzaju *Drepanaphis* w oparciu o dane molekularne wraz z charakterystyką konsorcjów endosymbiotycznych.

Malik, K*., Jousselin, E., Clamens, A.-L., Sugimoto, S., Wieczorek, K. (2025). Molecular phylogeny of the *Acer*-feeding aphid subfamily Drepanosiphinae (Insecta: Hemiptera: Aphididae) and the evolution of its endosymbiotic consortia. *Zoological Letters*, 11, 9, https://doi.org/10.1186/s40851-025-00255-2

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Trzecia publikacja z cyklu, pt. „Molecular phylogeny of the *Acer*-feeding aphid subfamily Drepanosiphinae (Insecta: Hemiptera: Aphididae) and the evolution of its endosymbiotic consortia", poświęcona jest filogenezie podrodziny Drepanosiphinae w której szczególną uwagę poświęcono pokrewieństwom wśród gatunków w rodzaju *Drepanaphis*, a także konsorcjom endosymbiotycznym zidentyfikowanym u przedstawicieli całej podrodziny.

W pracy przeprowadzono analizę filogenetyczną opartą na mitochondrialnych markerach molekularnych (COI, Cytb), obejmującą 10 (spośród 18 znanych) gatunków z rodzaju *Drepanaphis*, oraz analizę filogenetyczną opartą na jądrowych markerach molekularnych (EF-1α, PGD) obejmującą 7 gatunków omawianego rodzaju.

Analizy filogenetyczne oparte na połączonym zestawie markerów mitochondrialnych i jądrowych, przeprowadzone z wykorzystaniem metody największej wiarygodności (Maximum Likelihood, ML) oraz interferencji bayesowskiej (BI), wykazały zasadniczo podobną topologię w obrębie grupy, z drobnymi różnicami pomiędzy wynikami uzyskanymi dla poszczególnych typów markerów.

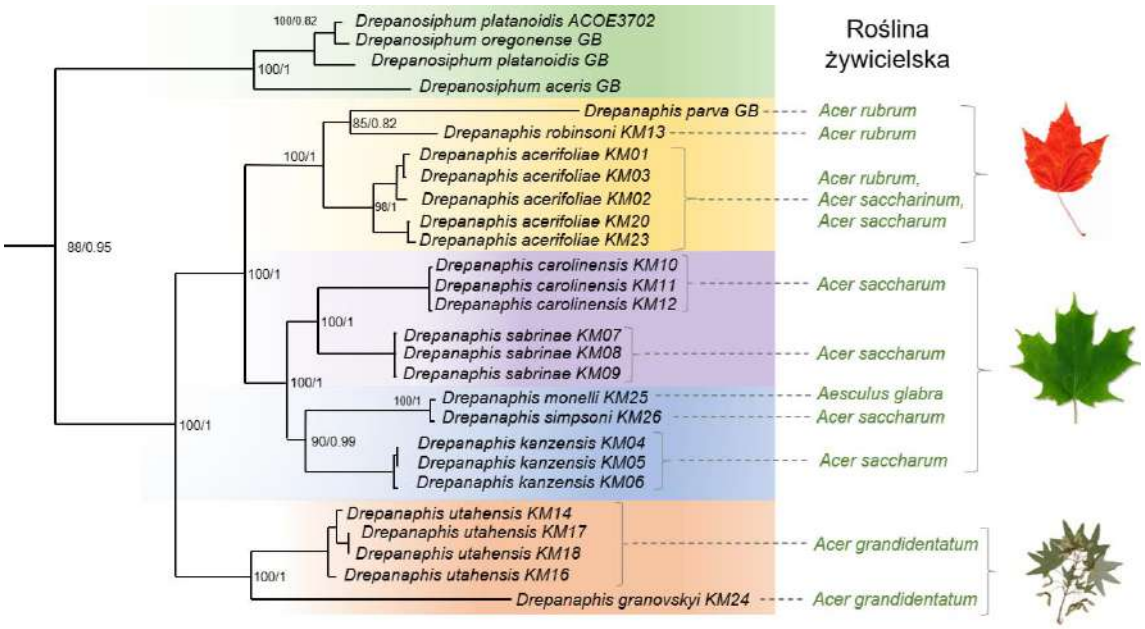
Wyniki świadczą o tym, że rodzaj *Drepanaphis* tworzy dobrze wsparty klad monofiletyczny w obrębie podrodziny Drepanosiphinae, siostrzany względem rodzaju *Drepanosiphum*. Topologia kladogramów uzyskana na podstawie genów mitochondrialnych (COI, Cytb) była zgodna z topologią uzyskaną z pełnego zestawu markerów molekularnych (Rycina 4). Natomiast geny jądrowe (EF-1α, PGD) zostały

zsekwencjonowane dla mniejszej liczby taksonów niż mitochondrialne, a sekwencji nie uzyskano dla: *D. granovskyi*, *D. parva*, *D. simpsoni*, dlatego zaobserwowano pewne rozbieżności w sposobie grupowania gatunków.

W analizach opartych wyłącznie na markerach jądrowych *D. monelli* zajmował pozycję pomiędzy *D. carolinensis* i *D. sabrinae*, tworzącymi wspólny klad siostrzany względem *D. kanzensis*. W analizach z wykorzystaniem wszystkich markerów molekularnych *D. monelli* stanowił linię siostrzaną względem *D. kanzensis*, a te dwa taksony tworzą klad siostrzany względem *D. carolinensis* i *D. sabrinae*.

W oparciu o połączone dane wykorzystanych markerów molekularnych w rodzaju *Drepanaphis* możemy wyróżnić trzy klady obejmujące następujące gatunki:

1. *D. granovskyi* i *D. utahensis*;
2. *D. acerifoliae*, *D. parva*, *D. robinsoni*;
3. *D. kanzensis*, *D. monelli*, *D. simpsoni*, *D. carolinensis* i *D. sabrinae*.



Rycina 4. Kladogram uzyskany na podstawie łącznej analizy genów mitochondrialnych i jądrowych, z uwzględnieniem roślin żywicielskich analizowanych gatunków mszyc z rodzaju *Drepanaphis*.

Źródło: opracowanie własne. Na podstawie: Malik i inni, 2025 **(P3)**, zmodyfikowano. Przedstawiona topologia odpowiada kladogramowi uzyskanemu w analizie bayesowskiej, opartej na czterech markerach molekularnych (COI, Cytb, EF-1α, PGD). Wartości przy węzłach oznaczają poziom wsparcia bootstrapowego z analizy metodą największej wiarygodności (ML) oraz prawdopodobieństwo a posteriori z analizy bayesowskiej (BI) dla węzłów zgodnych **(P3)**.

Badania filogenetyczne pozwoliły na zweryfikowanie, jak kształtują się relacje między gatunkami w rodzaju *Drepanaphis*, a uzyskane wyniki skonfrontowano z danymi morfologicznymi, rozmieszczeniem i roślinami żywicielskimi. Przeprowadzona analiza filogenetyczna częściowo potwierdziła ugrupowania gatunków wyodrębnionych na podstawie zestawu danych morfologicznych proponowane przez Smith i Dillery (1968) oraz Malik i inni, 2024 **(P2)**.

Gatunki z grupy „*acerifoliae*" (*D. acerifoliae* i *D. carolinensis*) według podziału bazującego na sekwencjach genetycznych nie tworzą wspólnego kladu siostrzanego, jak wskazały przeprowadzone analizy morfologiczne **(P2)**, lecz **należą do dwóch różnych kladów** (w których możemy wyznaczyć odmienną roślinę żywicielską):

W analizach filogenetycznych *D. acerifoliae* tworzy klad siostrzany z *D. parva* i *D. robinsoni* żerującymi na *A. rubrum*.

Natomiast *D. carolinensis* stanowi klad siostrzany względem *D. sabrinae*, związanym troficznie z *A. saccharum*.

W grupie „*utahensis*" wyraźnie wyróżnia się klad *D. granovskyi* i *D. utahensis*, dwóch gatunków monofagicznych żerujących na *Acer grandidentatum*, które występują na zachodzie USA. *Drepanaphis simpsoni* również należy do morfologicznej grupy „*utahensis*", jednak jako gatunek związany z *Acer saccharum* tworzy odrębny, wschodnioamerykański klad, co wskazuje na wpływ zarówno specjalizacji żywicielskiej, jak i izolacji geograficznej na proces specjacji.

Nowy podział, wyznaczony w oparciu o dane molekularne oraz powiązania troficzne, obejmuje następujące trzy grupy: ***rubrum*, *grandidentatum* i *saccharum*** – w konfrontacji do wyznaczonych w przeprowadzonych badaniach morfologicznych pięciu grup (Tabela 4).

W świetle uzyskanych wyników, **zasadne jest więc przyjęcie hipotezy (H3)**, zakładającej, że rodzaj *Drepanaphis* stanowi klad monofiletyczny, a w jego obrębie możliwe jest wyróżnienie grup gatunków powiązanych z rozmieszczeniem geograficznym oraz specjalizacją względem roślin żywicielskich.

Tabela 4. Podział na grupy gatunków w rodzaju *Drepanaphis*

Źródło / Grupa	Smith i Dillery 1968	Malik i inni, 2024 (P2)	Malik i inni, 2025 (P3)	
Grupy morfologiczne	Grupa *acerifoliae*		**Grupy troficzne**	Grupa *rubrum*
	D. acerifoliae *D. carolinensis* *D. sabrinae**	*D. acerifoliae* *D. carolinensis*		*D. acerifoliae* *D. parva* *D. robinsoni*
	Grupa *monelli*			
	D. monelli *D. kanzensis** *D. keshenae* *D. knowltoni* *D. spicata*	*D. monelli* *D. keshenae* *D. knowltoni* *D. spicata*		
	Grupa *nigricans*			Grupa *saccharum*
	D. nigricans *D. tissoti* *D. choanotricha*	*D. nigricans* *D. tissoti* *D. choanotricha*		*D. carolinensis* *D. sabrinae* *D. simpsoni* *D. monelli* *D. kanzensis*
	Grupa *parva*			
	D. parva *D. idahoensis* *D. saccharini*	*D. parva* *D. idahoensis* *D. saccharini* *D. robinsoni*		
	Grupa *utahensis*			Grupa *grandidentatum*
	D. granovskyi *D. simpsoni* *D. utahensis*	*D. granovskyi* *D. simpsoni* *D. utahensis*		*D. granovskyi* *D. utahensis*

Źródło: opracowanie własne. Gatunki niesklasyfikowane do żadnej z grup w podziale Malik i inni, 2024: *D. kanzensis**, *D. sabrinae**.

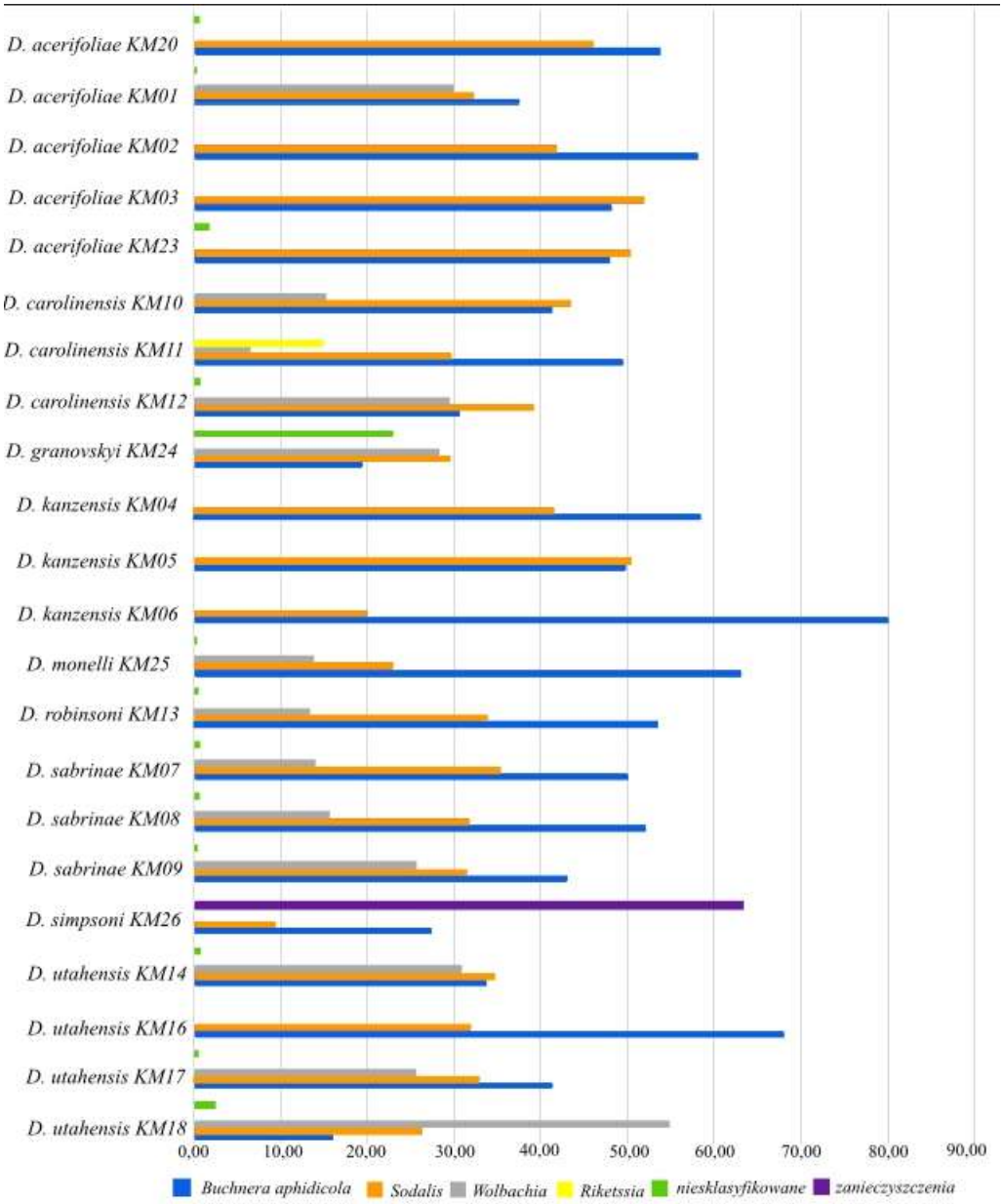
Istotny aspekt badań molekularnych stanowiła także charakterystyka konsorcjów endosybiotycznych podrodziny Drepanosiphinae, w tym w rodzaju *Drepanaphis*. Sekwencjonowanie fragmentu genu bakteryjnego 16S rDNA umożliwiło uzyskanie średnio 15 098 odczytów sekwencyjnych na próbkę (o długości 251 pz), co pozwoliło na szczegółowe zbadanie różnorodności mikrobioty mszyc.

U 22 badanych osobników, należących do 10 gatunków, endosymbiont obligatoryjny *Buchnera aphidicola* został stwierdzony we wszystkich badanych gatunkach i osobnikach, podobnie jak endosymbiont fakultatywny *Sodalis*, jednak proporcje co do ich wzajemnej liczebności różnią się między próbkami (Rycina 5). *Wolbachia* została wykryta u 13 osobników, a pozostałe symbionty zostały zidentyfikowane w pojedynczych próbkach. Badania nie wykazały różnic w składzie endosymbiontów w populacjach *D. acerifoliae* z USA i Europy. U osobnika *D. simpsoni* został ponadto stwierdzony duży procent bakterii kontaminacyjnych, co może być wynikiem wieku próbki (1976 rok).

Wyniki analiz mikrobiologicznych w obrębie całej podrodziny ujawniły przede wszystkim, że rodzaj *Drepanaphis* odznacza się występowaniem endosymbionta *Sodalis* u wszystkich analizowanych osobników. Może to świadczyć o tym, że *Sodalis* w rodzaju *Drepanaphis* pełni funkcję drugiego endosymbionta obligatoryjnego, przejmując tym samym część funkcji metabolicznych od *Buchnera aphidicola*.

Podobną tendencję w występowaniu tego endosymbionta odnotowano w rodzajach *Drepanosiphum* i *Drepanosiphoniella*, natomiast nie zaobserwowano jej w azjatyckim rodzaju *Yamatocallis*.

Należy przy tym zaznaczyć, że ze względu na ograniczoną dostępność materiału badania molekularne objęły jedynie około połowę (56%) obecnie znanych gatunków, co skutkowało brakiem materiału porównawczego dla części grup (np. „*nigricans*"). W związku z tym formułowane wnioski nie dają pełnego obrazu pokrewieństw pomiędzy gatunkami z rodzaju *Drepanaphis* i konieczne są dalsze analizy obejmujące szerszy zestaw gatunków.



Rycina 5. Wynik sekwencjonowania NGS fragmentu genu 16S rDNA.

Źródło: opracowanie własne przy wykorzystaniu programu Excel. Na podstawie: Malik i inni, 2025 **(P3)**, zmodyfikowano. Oś X przedstawia procentowy udział odczytów przypisanych do poszczególnych endosymbiontów w każdej próbce, oś Y osobniki poszczególnych gatunków.

8. Wnioski

Na podstawie przeprowadzonych badań wyciągnięto następujące wnioski:

1. Modelowanie niszy ekologicznej wykazało, że najbardziej sprzyjające warunki dla *D. acerifoliae* poza naturalnym zasięgiem jego występowania zlokalizowane są w krajach basenu Morza Śródziemnego.
2. Temperatura najcieplejszego kwartału, opady zimowe oraz średnie opady roczne stanowią główne czynniki ekologiczne wpływające na ekspansję *D. acerifoliae* na świecie.
3. Modele uwzględniające potencjalne przyszłe zmiany klimatu wskazują, że *D. acerifoliae* może znajdować dogodne nisze siedliskowe na północ od obecnego zasięgu, przy czym wpływ zmian klimatu będzie szczególnie widoczny na drogi jego ekspansji w Europie Środkowej i Wschodniej oraz w azjatyckiej części Rosji.
4. Gatunki w rodzaju *Drepanaphis* charakteryzują się niewielką zmiennością cech morfometrycznych, dlatego jakościowe cechy morfologiczne okazały się kluczowe w klasyfikacji.
5. Na podstawie przeprowadzonych analiz morfometrycznych i morfologicznych opisano nowy dla nauki gatunek *D. robinsoni*, co zostało również potwierdzone przez analizy molekularne.
6. Cechy morf z pokolenia obupłciowego są morfologicznie informatywne i rozstrzygające w przypadku gatunków, których pozycja taksonomiczna była wątpliwa (*D. nigricans*, *D. tisotti*).
7. Najwięcej znanych stanowisk gatunków z rodzaju *Drepanaphis* występuje na wschodnim wybrzeżu Ameryki Północnej, co pokrywa się z naturalnym zasięgiem ich roślin żywicielskich.
8. Rodzaj *Drepanaphis* stanowi klad monofiletyczny.
9. W rodzaju *Drepanaphis* gatunki żerujące na tych samych (lub blisko spokrewnionych) roślinach żywicielskich są zwykle blisko spokrewnione. Na tej podstawie zaproponowano nowy podział na grupy gatunków: *rubrum*, *saccharum*, *grandidentatum*.
10. U przedstawicieli rodzaju *Drepanaphis* bakterie z rodzaju *Sodalis* pełnią rolę drugiego endosymbionta obligatoryjnego.

9. Piśmiennictwo

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10. Wykaz aktywności i osiągnięć naukowych

10.1 Pozostałe publikacje

1. Wieczorek, K., Chłond, D., Chajec, Ł., **Malik, K**., Świątek, P., Jaroszewicz, J., Coulson, S. J., Jousselin, E. (2025). Integrative approach to the systematics of the endemic Svalbard aphid species *Macrosiphum calvulum* (Hemiptera: Aphididae) using molecular, morphological and reproductive system analysis. *Scientific Reports*, 15, 26960. https://doi.org/10.1038/s41598-025-12913-8

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2. Wegierek, P., **Malik, K.**, Hutyra, P., Depa, Ł. (2025). What does the morphological diversity of siphunculi tell us about the evolution of aphids (Insecta: Hemiptera: Aphidoidea)? *The European Zoological Journal*, 92, 85–96. https://doi.org/10.1080/24750263.2024.2434124

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   IF_{2023}: 0.89, MNiSW: 100 pkt

Łączna suma IF = 8,59

Łączna suma punktów MNiSW = 450

10.2 Konferencje naukowe

1. **Malik K.**, Wieczorek K. Filogeneza molekularna i charakterystyka konsorcjów endosymbiotycznych mszyc z rodzaju Drepanaphis (Hemiptera, Aphididae, Drepanosiphinae). 11–14.09.2025. 54. Walny Zjazd Polskiego Towarzystwa Entomologicznego oraz Konferencja Naukowa PTEnt., Lublin, Polska, poster naukowy.

2. Kušková K., Dajdok Z., Hejda M., Kapusta P., Kanka R., Kollár J., Kubáčková L., Kutlvašr J., Lučanová A., **Malik K**., Palaj A., Pergl J., Perglová I., Pyšek P., Sádlo J., Stanek M., Stefanowicz A., Sułowicz S., Tokarska-Guzik B., Vítková M., Wiatrowska B. Impact of alien and native woody plants on vegetation and soil. 02–05.09.2025. 17th International Conference on the Ecology and Management of Alien Plant Invasions 2025 (EMAPI), Christchurch, Nowa Zelandia, poster naukowy.

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6. **Malik K.**, Wieczorek K. Nearktyczny rodzaj *Drepanaphis* Del Guercio (Hemiptera, Aphididae) – przegląd morf pokolenia obupłciowego. 15–17.09.2023. Nadzwyczajny Zjazd Polskiego Towarzystwa Entomologicznego z okazji jubileuszu 100-lecia i Konferencja Naukowa „Nowe horyzonty entomologii", Karkonoski Park Narodowy, Jelenia Góra-Sobieszów, Polska, poster naukowy.

7. **Malik K.**, Bugaj-Nawrocka A., Wieczorek K. Taxonomical study of the genus *Drepanaphis* Del Guercio (Hemiptera, Aphididae: Drepanosiphinae) based on morphological analysis. 25.06–01.07.2023. 9th European Hemiptera Congress, Kurdějov, Czechy, poster naukowy.

8. **Malik K**., Bugaj-Nawrocka A., Wieczorek K. Analysis of the distribution of the genus *Drepanaphis* Del Guercio, 1909 based on museum data. 11–17.09.2022. XI International Anniversary Symposium on Aphids, Targanice, Polska, poster naukowy.
9. **Malik K.** *Drepanaphis acerifoliae* – can the Nearctic aphid take over Europe? 11–17.09.2022. XI International Anniversary Symposium on Aphids, Targanice, Polska, prezentacja ustna.

10.3 Staże i szkolenia

1. Weryfikacja okazów mszyc z rodzaju *Drepanaphis* Del Guercio (Hemiptera, Aphididae: Drepanosiphinae) zdeponowanego w kolekcji Muzeum Historii Naturalnej w Paryżu. 19.11-22.11.2024, Francja.
2. Szkolenie bioinformatyczne z zakresu analizy filogenetycznej. 20-26.10.2024, Uniwersytet w Bergen, Norwegia. Finansowanie w ramach konkursu Mobilność studentów i doktorantów UŚ w ramach projektu HarSval.
3. Weryfikacja okazów mszyc z rodzaju *Drepanaphis* Del Guercio (Hemiptera, Aphididae: Drepanosiphinae) zdeponowanego w kolekcji Muzeum Historii Naturalnej w Londynie. 24-27.09.2024, Wielka Brytania.
4. Staż naukowy w laboratorium UMR CBGP, Centre de Biologie pour la Gestion des Populations. Montpellier sur Lez cedex (INRAE). 18-25.05.2024, Francja.
5. Staż naukowy w laboratarium UMR CBGP, Centre de Biologie pour la Gestion des Populations. Montpellier sur Lez cedex (INRAE). 16-21.04.2023, Francja.
6. Staż naukowy w Stanach Zjednoczonych, w kolekcji entomologicznej the Smithsonian National Museum of Natural History (Washington D.C.) oraz the Systematic Entomology Laboratory (Beltsville) w ramach konkursu PROM programu Narodowej Agencji Wymiany Akademickiej (NAWA) – międzynarodowa wymiana stypendialna doktorantów i kadry akademickiej UŚ, 15.09-14.10.2022, USA.
7. Weryfikacja okazów mszyc z rodzaju *Drepanaphis* Del Guercio (Hemiptera, Aphididae: Drepanosiphinae) zdeponowanego w kolekcji Lund Museum of Zoology (MZLU), 17.05-24.05.2022, Szwecja.

10. 4 Projekty badawcze

Beneficjentka stypendium naukowego w projekcie (Weave-UNISONO: 2022/04/Y/NZ8/00057) pt.: Impact of alien and native woody plants on vegetation and soil (IMPAWOS): two sides of the same coin? Udział w projekcie w roli stypendysty na okres 24 miesięcy (wrzesień 2022 – październik 2025).

10.5 Nagrody i wyróżnienia

1. Zajęcie **I miejsca w konkursie na najlepszy poster dla młodych naukowców** podczas 54. Walnego Zjazdu Polskiego Towarzystwa Entomologicznego oraz Konferencji Naukowej PTEnt w Lublinie 11–14.09.2025, poster naukowy pt.: Filogeneza molekularna i charakterystyka konsorcjów endosymbiotycznych mszyc z rodzaju *Drepanaphis* (Hemiptera, Aphididae, Drepanosiphinae).
2. Stypendium projakościowe na rok akademicki 2024/2025, Szkoła Doktorska, Uniwersytet Śląski w Katowicach.

11. Prace naukowe wchodzące w skład cyklu stanowiącego podstawę rozprawy doktorskiej

Publikacja 1

Malik, K., Bugaj-Nawrocka, A., Wieczorek, K. (2023). Distribution of *Drepanaphis acerifoliae* – aphid pest of *Acer* trees – faced with global climate change. *Folia Biologica* (Kraków), 71, 115–130. https://doi.org/10.3409/fb_71-3.12

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Distribution of *Drepanaphis acerifoliae* – aphid pest of Acer trees – faced with global climate change

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Original article

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The genus *Drepanaphis* del Guercio currently includes 16 species, all of which are found in North America. Representatives of this genus are narrow oligophages associated mainly with plants of the genus *Acer*. Previous studies have focused only on the morphology of selected species, while not considering their geographical distribution. Among all species, the painted maple aphid *Drepanaphis acerifoliae* deserves particular attention, because it represents the broadest range in North America and is the only species of this genus to be found outside of its natural range, i.e. in Europe. Thanks to suitable niche modelling based on a maximum entropy model, we were able to present maps with the potential distribution of *D. acerifoliae* in its natural range. In North America, its distribution coincides with the natural range of the host plants (native to the eastern part), as well as the areas where they are planted (the western part). An extrapolation of these results to the area of Europe allowed for the designation of places where the aphids can find suitable climatic conditions for developing and expanding their spatial distribution. The model indicated the Mediterranean basin, almost all of Italy, excluding mountainous areas, Spain, Portugal, France, Belgium, the Netherlands, the western part of Germany, the southeast and central part of Great Britain, Hungary and the Balkan Peninsula. In a more continental view, the model pointed to areas stretching from the middle of eastern Ukraine, including Crimea, through Russia, to northern parts of Kazakhstan along the border with Russia. Additionally, the impact of climate change on the spread of the species within the next 80 years was analysed, both in North America and Europe. Models considering the potential future climate changes indicate that *D. acerifoliae* may find suitable niches further north of its current ranges. In North America, this is mostly areas of eastern Canada, while in Europe it includes the central and eastern part and the Asian part of Russia.

Key words: ecological niche modelling, climate change simulations, maple, biological control, pest risk.

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The *Acer* genus, also known as the maple, is a diverse taxon of trees found mainly in the northern hemisphere (Grimm *et al*. 2007). Trees of this genus reach a height of 42 m and are characterised by oppositely arranged leaves, as well as open, irregular crowns, and a long or short trunk (Geyer *et al*. 2010). The ancestor of this group of plants probably came from eastern Asia, where as many as 130 out of approximately 150 known species originated (Li *et al*. 2019; Areces-Berazain *et al*. 2020). Other species are present in Europe, western Asia and North America (Li *et al*. 2019). A reconstruction of the evolutionary unfolding of the *Acer* species showed that in North America, the species in the western and eastern parts probably had two independent sources of migration (Renner *et al*. 2008; Areces-Berazain *et al*. 2021). The current *Acer* classification divides the group into 18 sections, some of which are also

subdivided into series (Davis 2021). Phylogenetic analyses indicate that most sections of the *Acer* are monophyletic, but the relationship between the sections is still unclear (Li *et al*. 2019). Maples stand out owing to their variety of growth habits, cold resistance and adaptability. That is why they are often chosen for planting in urban spaces, and they sometimes do very well in such environments (i.e. Uhrin *et al*. 2018; McDermot *et al*. 2020). For example, the silver maple (*Acer saccharinum* L.), which occurs mainly in North America, is one of the fastest growing deciduous trees in the eastern and mid-western forests, it competes well with other plants and its seeds germinate rapidly (Geyer *et al*. 2010). The sugar maple (*Acer saccharum* Marsh.), which is also abundant in North America, is a source of the popular maple syrup and is one of the most important tree species in this region (Minorsky 2003).

Because of the valuable nutritional properties of the sweet phloem sap, maples are often attacked by various groups of insects, including aphids. The aphid genera that are specific to *Acer* spp. are mainly from the subfamilies Chaitophorinae and Drepanosiphinae (Blackman & Eastop 2022). The subfamily Drepanosiphinae includes five genera and 37 species related to different geographic regions (Remaudière & Remaudière 1997; Favret 2022). *Drepanaphis* del Guercio, 1909 is the most speciose genus in this subfamily, represented by 16 species that are distributed in its natural range in North and Central America. This genus consists of monoecious, holocyclic species whose sexual generations develop in the autumn. All species of the genus *Drepanaphis* are associated with different *Acer* spp., except *D. monelli* (Davis, 1909) which feeds on *Aesculus* spp. (Smith & Dillery 1968; Blackman & Eastop 2022).

The most common species in this genus, the painted maple aphid *D. acerifoliae* (Thomas, 1878) (Fig. 1), has also been recorded in Europe. Its occurrence has been reported in Italy (Lozzia & Binaghi 1992; Colombo *et al*. 1996; Barbagallo *et al*. 2008; Barbagallo & Cocuzza 2014), Spain (Perez Hidalgo *et al*. 2008), Hungary (Ripka 2010) and Serbia (Petrović-Obradović *et al*. 2018, 2021). *Drepanaphis acerifoliae* is the only species to be associated with more than one species of the genus *Acer*: *A. saccharinum, A. saccharum* and *A. rubrum* L. (Smith & Dillery 1968; Blackman & Eastop 2022). However, in Europe, this species has been found exclusively on *A. saccharinum* (Petrović-Obradović 2021), which was introduced to the area by Sir Charles Wager in 1725. *Acer saccharinum* spread quickly as an ornamental species (Harris 1991) and was naturalised, i.e. in Belgium (Ronse 2011), France (Tison & de Foucault 2014), Germany (Aas *et al*. 2010) and the British Isles (Stace 2010).

Since maples also occur naturally in Europe, particularly from the same section as *A. saccharum*, and considering the fact that *D. acerifoliae* is an oligophagous species with the potential to change its host, we cannot exclude the risk that it may also feed on other *Acer* species. This provides an additional justification for interest in the invasive potential of this species. In its natural range, the painted maple

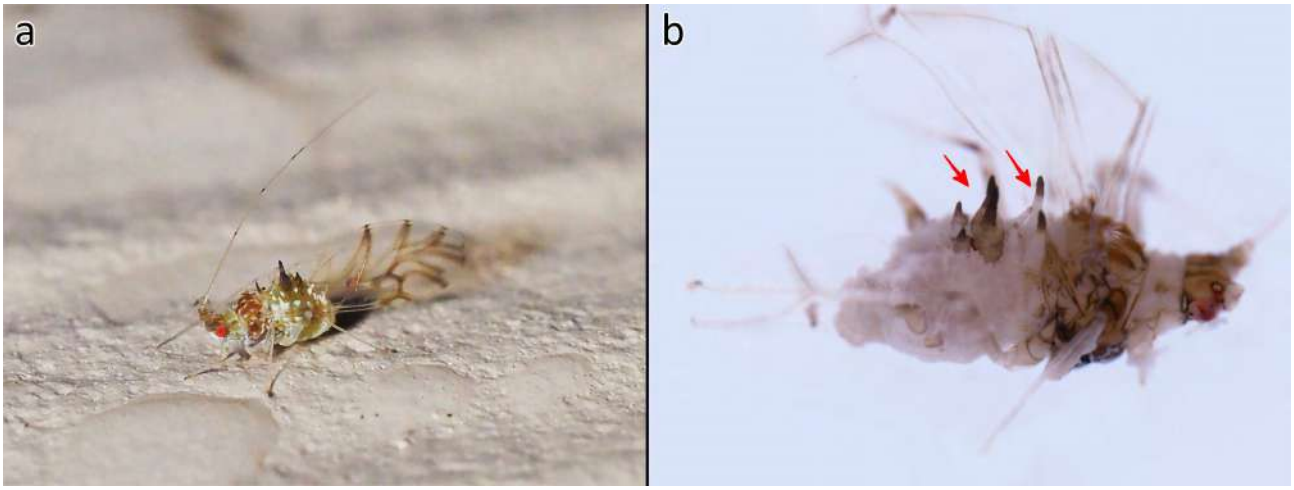

Fig. 1. *Drepanaphis acerifoliae* (Thomas, 1878). Alate viviparous ♀. (a) Live specimen. Image copyright V. Charny, under the Creative Commons 3.0 Licence; and (b) lateral general view. The lateral view reveals the long, finger-like dorsal abdominal tubercles that are characteristic of the *Drepanaphis* species (indicated by arrows).

aphid is considered to be a common pest of maples growing in urban areas. Infestations result in dieback and aesthetic damage, i.e. leaf discolouration and premature leaf drop. Severe infestations can also lead to the production of large amounts of honeydew, which covers the leaves and the surfaces and objects (i.e. cars) beneath the trees. It also facilitates the production of sooty mould fungi, which can injure plants (Dreistadt & Flint 1995). The problems with invasive species are becoming more and more noticeable in the context of climate change. For many insect species, increased levels of atmospheric greenhouse gases and a higher temperature may increase the probability of their spreading to new habitats (i.e. Dukes & Mooney 1999; Bergant *et al*. 2005; Bale and Hayward 2010). Global climate change can significantly impact the species' survival, reproduction, spread and population dynamics. It can also modify the relationships between the environment, pests and their natural enemies (Prakash *et al*. 2014).

Due to the pest status that this aphid has in its natural range and its expansion in Europe, we decided: (I) to evaluate the range of *D. acerifoliae* in relation to the natural range of its host plants; (II) to predict the potential current distribution of *D. acerifoliae* in its natural range and additionally in Europe, from which it is already listed; (III) to predict the potential past distribution of *D. acerifoliae*, to determine where its place of origin could potentially be, and whether it is consistent with the assumption of the evolutionary unfolding of the *Acer* species; and (IV) to indicate areas potentially at risk of invasion by this species on a global scale, significantly beyond its Nearctic range, using modelling for future climate scenarios.

Materials and Methods

Occurrence data

The occurrence data was obtained from the scientific literature, as well as specimens studied in museum collections and biodiversity databases. The search was based on keywords, i.e. the name of the species and its synonyms. Museum curators were asked to provide information about their collections. Photographs of the preparations were provided from the collections in which specimens of the discussed species were identified. Some of them were also examined in the collections during a personal stay. We excluded the records with unspecified or unknown localities. The Geographic Distance Matrix Generator 1.2.3 was used to calculate the geographic distance between each pair of localities (Boria *et al*. 2014; Ersts 2016). To reduce the inherent geographic biases (the effect of spatial autocorrelation) associated with the collecting methods, we removed points closer to each other than 10 km. Overall, 90 unique occurrence localities were compiled for the representatives of *D. acerifoliae* in North America and 22 in Europe. All the localities were georeferenced using Google Earth 7.3.2.5776 (Google Inc. 2022; http://www.google.com/earth/index.html) (coordinates were collected in decimal degrees, datum: WGS84). Details of the occurrence localities used during the modelling process are available in Supplementary Material 1 (SM.01).

Environmental predictors, climate classification and terrestrial ecoregions

We used 19 current bioclimatic variables obtained from the WorldClim 2.0 dataset (SM.02) (Fick & Hijmans 2017; http://www.worldclim.org) and downscaled the paleoclimate data for the Last Interglacial (LIG; ~120,000−140,000 years ago), the Last Glacial Maximum (LGM; between 26,500 and 19,000-20,000 years ago) and the Mid-Holocene (about 6,000 years ago) from the WorldClim 1.4 dataset (Hijmans *et al*. 2005). The influence of possible global climate change on the potential distribution of *D. acerifoliae* was estimated for four different periods (2021-2040, 2041-2060, 2061-2080 and 2081-2100) and for four future representative shared socioeconomic pathways (SSPs) (SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5). The mean values of the modelling results for the three future climate scenarios were obtained from the Coupled Model Intercomparison Project Phase 6 (CMIP6): ACCESS-ESM1-5, CNRM-ESM2-1 and MIROC-ES2L.

Since only climate variables were used in the modelling, to help in understanding which types of climate are most favourable for the occurrence of *D. acerifoliae*, we used the Köppen-Geiger climate classification system (Peel *et al*. 2007). The places where representatives of the species occurred were plotted on a raster with the climate classification data, and the raw data was obtained. Using SAGA GIS, the resulting rasters from MaxEnt were plotted on a raster of the Köppen-Geiger climate classification.

The natural range outlines for the major host plants were taken from http://databasin.org (Fig. 2) (Conservation Biology Institute (CBI) 2023; the maps are a digital

representation of the tree species range maps from the Atlas of the United States Trees by Little (1971)).

To determine which main plant communities *D. acerifoliae* is associated with, we used terrestrial ecoregions which were based on Olson and Dinerstein (2002), Bailey (1995) and Wiken (1986), modified by The Nature Conservancy (TNC – an American charitable environmental organisation). This biogeographic regionalisation contains 814 terrestrial ecoregions classified into 14 different biomes.

We used SAGA GIS 7.8.2 (Conrad *et al*. 2015; SAGA Development Team 2022) to extract raw environmental data from all raster layers of the species occurrence records. We performed a Spearman rank correlation test in the Excel (ver. 2207) add-in program Analysis ToolPak (Microsoft Corporation 2022), to minimise the number of variables by discarding those that were highly correlated ($r \geq 0.75$) (SM.02).

Ecological niche modelling

We used MaxEnt (version 3.4.1; http://www.cs.princeton.edu/~schapire/maxent) to model the *D. acerifoliae* niches and distribution. MaxEnt is a machine learning software based on a maximum entropy algorithm (Phillips *et al*. 2006). As the default settings in MaxEnt may not produce the best predictions (Merow *et al*. 2014; Kumar *et al*. 2014; Samy *et al*. 2016; Bugaj-Nawrocka *et al*. 2021), a different combination of feature types (auto features; or linear, quadratic and product features together (LQP)) and regularisation multiplier values (ranging from 0.5 to 1.75) were used (SM.03).

If the models resulted in biologically nonsensical curves (i.e., highly jagged or multimodal), they were removed or were ranked low. It was difficult to distinguish environmentally-unsuitable areas from those that were under-sampled. Therefore, to deal with the likelihood that certain areas had fewer records and that some places were poorly sampled, we decided to use a method that gave meaning to the records with few neighbours in the geographic space. To weigh the selection of the background points, to account for the sampling intensity and any potential sampling bias, a bias file was implemented in the MaxEnt modelling. A bias grid file was created in SAGA GIS, and all the distribution records of *D. acerifoliae* were weighted by a Gaussian kernel with a standard deviation (SD) of 200 km (using the kernel density estimation). A range of 200 km was chosen, because we assumed that this aphid could easily spread by several kilometres a year, sometimes with short periods of irregular spreads. However, tak-

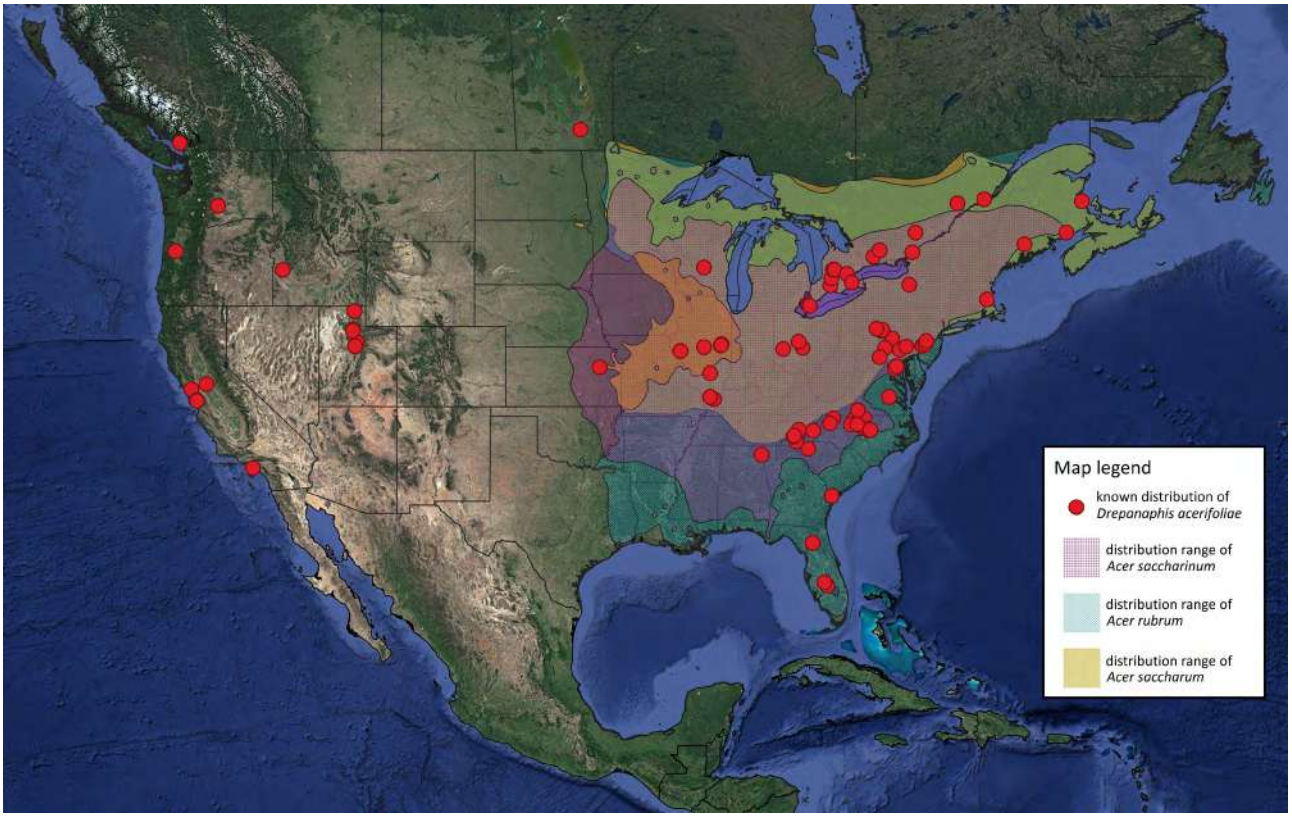

Fig. 2. Known distribution of *Drepanaphis acerifoliae* (Thomas, 1878) in North America (red dots), with the distribution ranges of its host plants.

ing into account the years from which most of that reports came from (the 1930s to 1960s), we assumed that over 60 years, a representative of this species could have travelled 200 km or more in its natural habitat. This was confirmed by the data collected in Europe, where within a few years, *D. acerifoliae* spread several hundred kilometres from the place of its first finding. The resulting grid was then scaled to have a minimum value of 1 and a maximum value of 20 (using grid normalisation) (see Elith *et al*. 2010; Syfert *et al*. 2013). A ten-fold cross-validation was performed, so all of the data was used for the validation, thus making better use of small data sets (Phillips *et al*. 2006; Phillips & Dudík 2008). The logistic output of MaxEnt with prediction values from 0 (unsuitable habitat) to 1 (optimal habitat) was selected.

We used the sample size corrected Akaike's information criterion (AICc and ΔAICc) (measures of the relative quality of models for a given dataset; calculated using ENMTools (Warren *et al*. 2010)), the area under the receiver operating characteristic (ROC) curve (AUC) (the performance of the model and the weight of the omission and commission errors) and the partial area under the ROC curve (pAUC) (calculated using Niche Analyst 3.0 (Qiao *et al*. 2015)) for the evaluation of the models (SM.03).

The models were used to predict suitable niches in present, past and future conditions. The resulting maps for the potential past and present distribution were prepared on a continental scale, where a spatial resolution of 30 arc seconds (~1 km^2) was selected. A global scale was used for the potential future distribution with a spatial resolution of 60 arc seconds (~2 km^2) (downloaded from WorldClim; 30 arc seconds spatial resolution grids were interpolated to a 60 arc seconds spatial resolution). All of the maps were prepared in QGIS 3.26.0 (QGIS Development Team 2022; http://www.qgis.org) using the WGS84 datum and EPSG: 4326 or 3857 (Web Mercator).

Results

Evaluation of the models and importance of the environmental predictors

In this study, we analysed the results from three prediction periods: past (LIG, LGM and Mid-Holocene), present and future (four time periods and four SSPs (SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5)). The training and test AUC values differed from random for all of the models. The setting selection for the model was mainly chosen based on the results of pAUC, AICc and ΔAICc (SM.03). We observed higher values of pAUC, AICc and ΔAICc when we used the auto features, regardless of the number of iterations. The regularisation multiplier settings were also analysed, and we found that a default value of 1 worked fine. For the maximum number of iterations, the best results were obtained with the value of 750 (SM.03).

A jackknife test (refer to SM.04 for more details and MaxEnt outputs) showed that the mean temperature of the warmest quarter (Bio10) was the environmental variable that was the most informative by itself, and it had a significant amount of information that was not contained in the other variables (Fig. 3). The warmest quarter in North America and Europe mostly covered June to August. For humid subtropical climates and subtropical highland climates, in the hottest months the mean temperature is about 26.5°C; while for con-

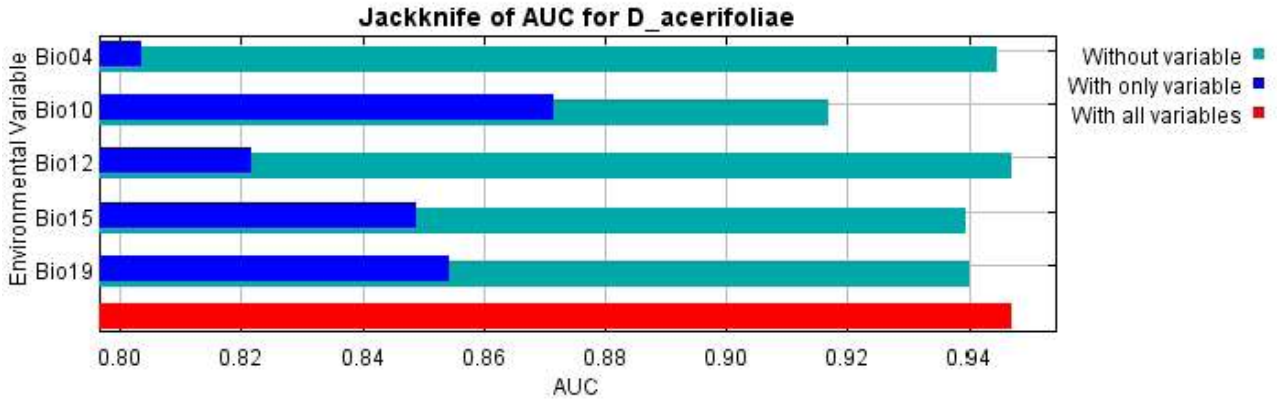

Fig. 3. Results of a jackknife test of the variable importance using AUC on the test data for *Drepanaphis acerifoliae* (Thomas, 1878). The jackknife test, in blue bars, shows the individual environmental variable importance relative to the red bar that shows all environmental variables. The light blue bar represents the Area Under the Curve (AUC) when a specific variable is excluded from the model. It demonstrates the information that the variable carries which is not present in other variables. A lower bar indicates that the variable is more informative by itself. The values shown are averages over replicate runs.

tinental climates it is about 22°C (and below). The mean temperature in the places where *D. acerifoliae* has been found is 21.8°C (min. 14.9°C in Mount Mitchell, North Carolina, USA; and max. 27.3°C in Lake Placid, Florida, USA). The precipitation during the coldest quarter (Bio19) was also significant, and the average rainfall for the studied areas from December to February was 238 mm (min. 55 mm in Winnipeg, Manitoba, Canada; and max. 540 mm in Corvallis, Oregon, USA). The mean precipitation seasonality (Bio15), a measure of the variation in the monthly precipitation totals over the year, fluctuated by around 24%. The most considerable fluctuations were recorded in Los Angeles, California, USA; and the smallest were recorded in Boston, Massachusetts, USA. The mean values for the variable annual precipitation (Bio12) were around 1040 mm/m^2/year (min. 211 mm in Yakima, Washington, USA; and max. 1801 mm in Mount Mitchell, North Carolina, USA). The temperature seasonality (Bio04) had a minor significance among the selected variables, but still was important for the models. It is calculated as the standard deviation of the weekly mean temperatures and expressed as a percentage of the mean of those temperatures. In the case of our research, it fluctuated around 8.6%, which means that the standard deviation of the weekly mean temperatures in the occurrence places was relatively small.

Potential species distributions and localities vulnerable to potential invasion

All the resulting maps show the median of the output grid of ten model replicates. For the present period in North America (Fig. 4) – the native range of *D. acerifoliae* – the results suggest that the most suitable areas for this species are located mainly in the areas where it is already present. In the United States, these include all eastern states to the border of the eastern half of Wisconsin and Iowa, the whole of Missouri, part of Kansas, and the eastern halves of Oklahoma and Texas. Conversely, in the west of the United States there are fewer favourable areas, mainly limited to Washington without the area of the Cascade Range, the west coast of Oregon to the border with the Cascade Range, California without the Sierra Nevada and the Mojave Desert, the Snake River Plain in Idaho, regions of Great Salt Lake and the western parts of the Wasatch Mountains in Utah, and the central part of Arizona within the Arizona transition zone. In Canada, these areas are the Great Lakes regions, the most southern areas of Ontario including Ottawa, the southern regions near Montreal

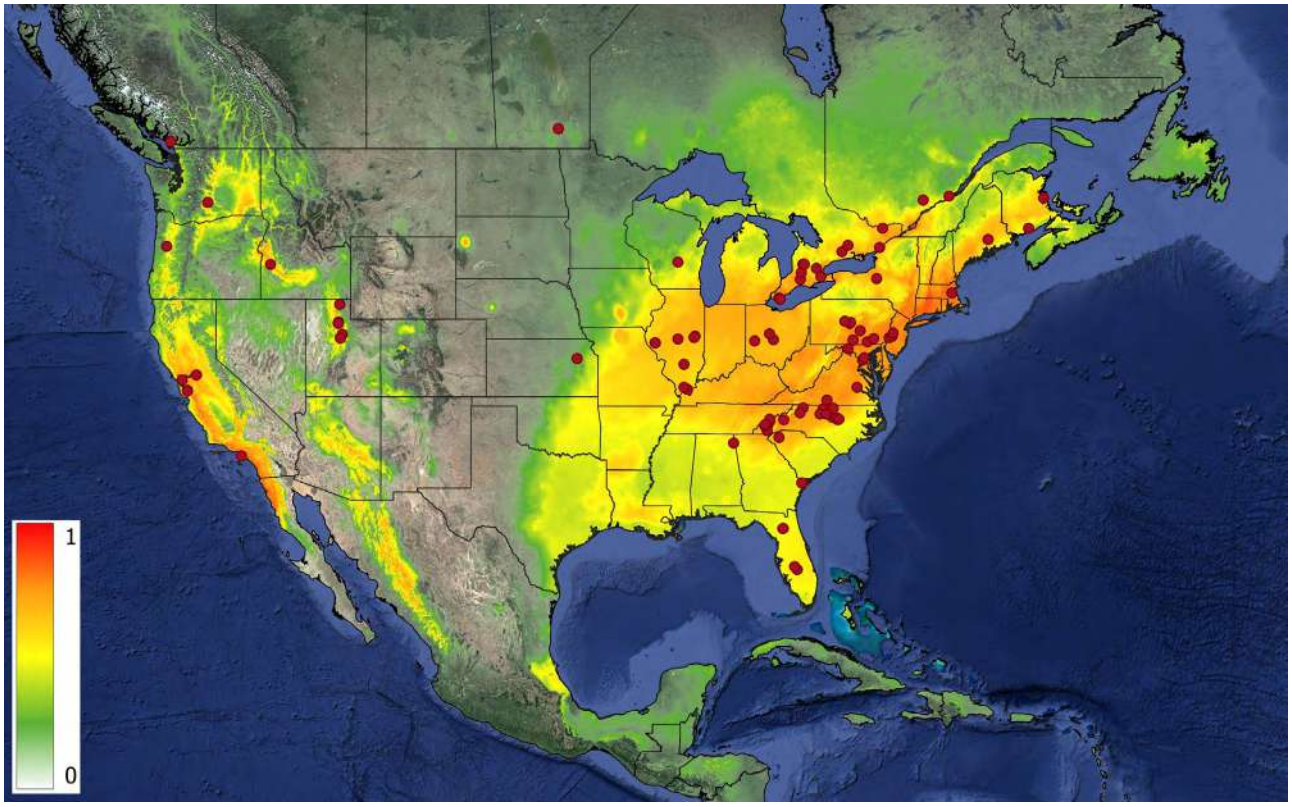

Fig. 4. Model result of a potentially suitable ecological niche for *Drepanaphis acerifoliae* (Thomas, 1878) in North America at present. Red dots represent the currently-known sites of the occurrence of the species. The colour scale shows the probability of a suitable ecological niche. Black lines represent the current national boundaries and the internal divisions into states.

in Quebec, and almost the entire area of New Brunswick. By contrast, the southernmost areas in North America are located in Mexico, along the Sierra Madre Occidental range.

In Europe (Fig. 5), the model indicated the Mediterranean basin as the main area with a suitable ecological niche. It also indicated almost all of Italy, excluding the mountainous areas in the north of the country, Spain, Portugal, France, Belgium, the Netherlands, the west part of Germany, the southeast and central parts of Great Britain, Hungary and the Balkan Peninsula. In all of the aforementioned areas, mountainous areas were shown to be unfavourable. From a more continental standpoint, the model also pointed to areas stretching from the middle of eastern Ukraine, including Crimea, through Russia (the oblasts: Belgorod, Voronezh, Rostov, Krasnodar, Volgograd, Saratov and Orenburg), to northern parts of Kazakhstan along the border with Russia. They also included the territories of Georgia and Azerbaijan.

In West Asia, the model suggested almost the entire territory of Türkiye, Iran (excluding desert areas), northern parts of Iraq, the north and west coasts of Syria, Lebanon, Israel, Palestine and western Jordan. It also indicated the northern part of the African countries lying on the Mediterranean Sea – Morocco, Algeria, Tunisia, Libya and Egypt (Fig. 5).

The results obtained for the last interglacial period (~ 120,000–140,000 years ago) (Fig. 6) largely pointed to the northern part of the east coast as the area potentially most suitable for the development of aphids (based on the conditions that are favourable for these insects at present). The results for later periods showed that the conditions prevailing during the last glacial maximum may have forced the aphids to migrate south (Fig. 7). In turn, the conditions during the Mid-Holocene favoured the further spread of *D. acerifoliae* (Fig. 8).

The results for potential future climate changes indicated that *D. acerifoliae* may find suitable niches further north of its current ranges (SM.05). In North America, areas of eastern Canada including Ontario, Quebec, New Brunswick, Nova Scotia and Newfoundland will be the most vulnerable. In the scenarios for higher CO_2 concentrations (SSP3-7.0 and SSP5-8.5), areas of British Columbia in the west of Canada will also be exposed. Climate changes may primarily affect the occurrence of *D. acerifoliae* in central and eastern Europe and in the Asian part of

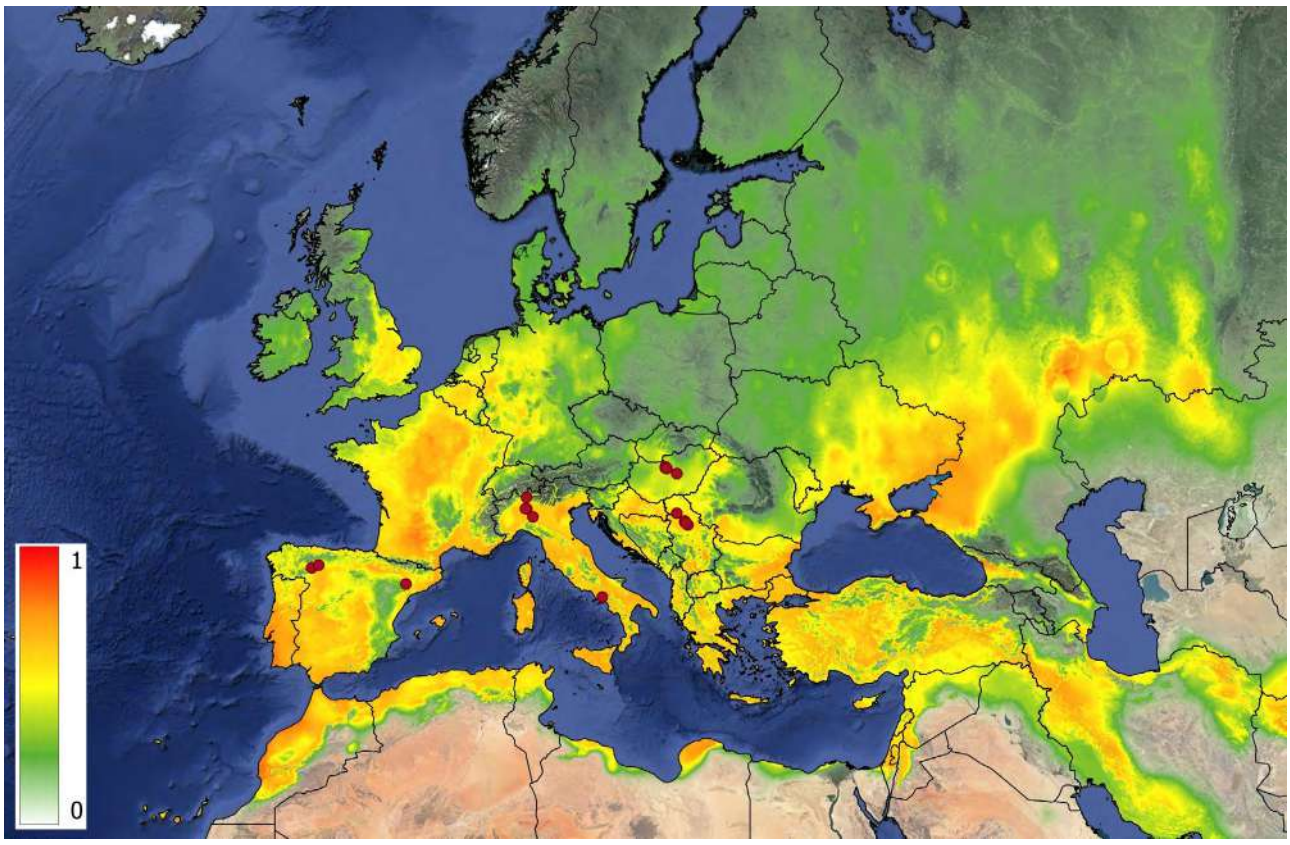

Fig. 5. Model result of a potentially suitable ecological niche for *Drepanaphis acerifoliae* (Thomas, 1878) in Europe, and partly for Africa and Asia at present. Red dots represent the currently known sites of the occurrence of the species. The colour scale shows the probability of a suitable ecological niche. Black lines represent the current national boundaries.

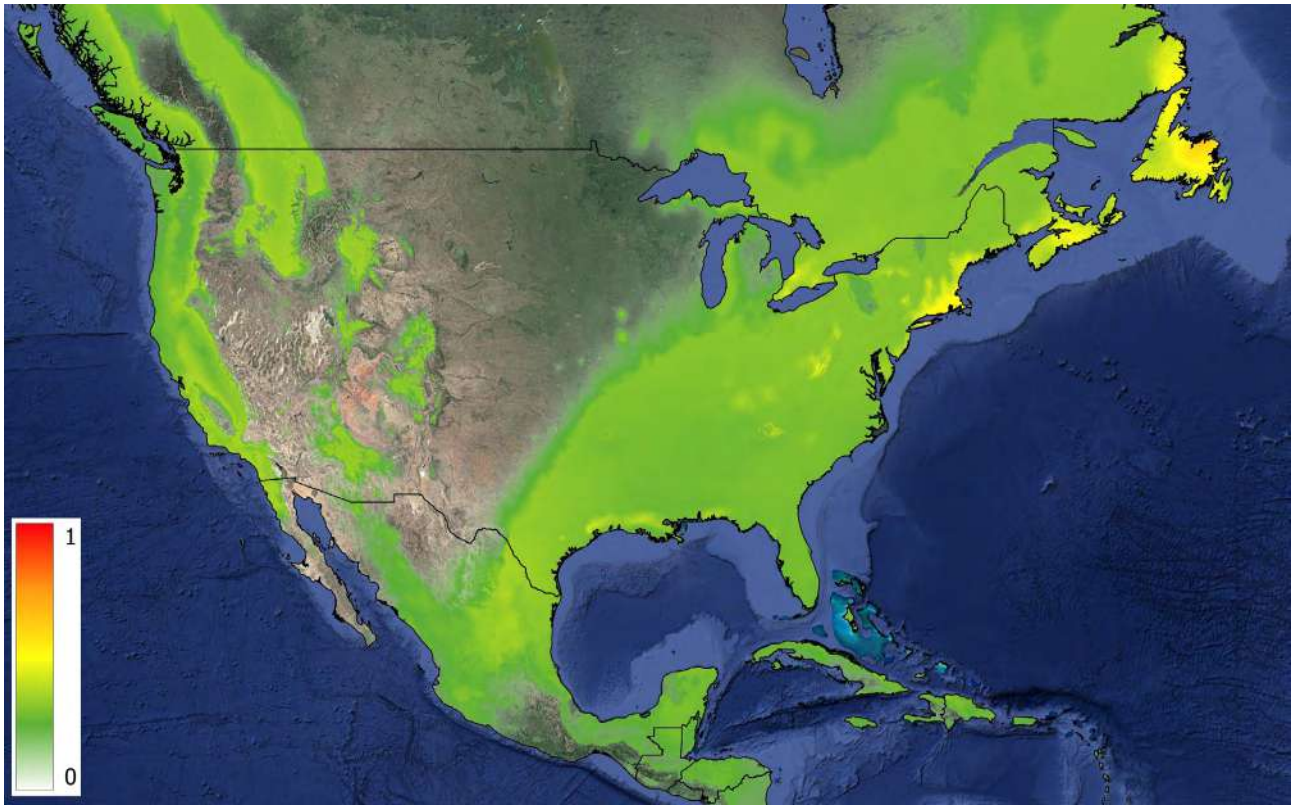

Fig. 6. Model result of the potentially suitable ecological niches for *Drepanaphis acerifoliae* (Thomas, 1878) in North America during the last interglacial period. The colour scale shows the probability of a suitable ecological niche. Black lines represent the current national boundaries.

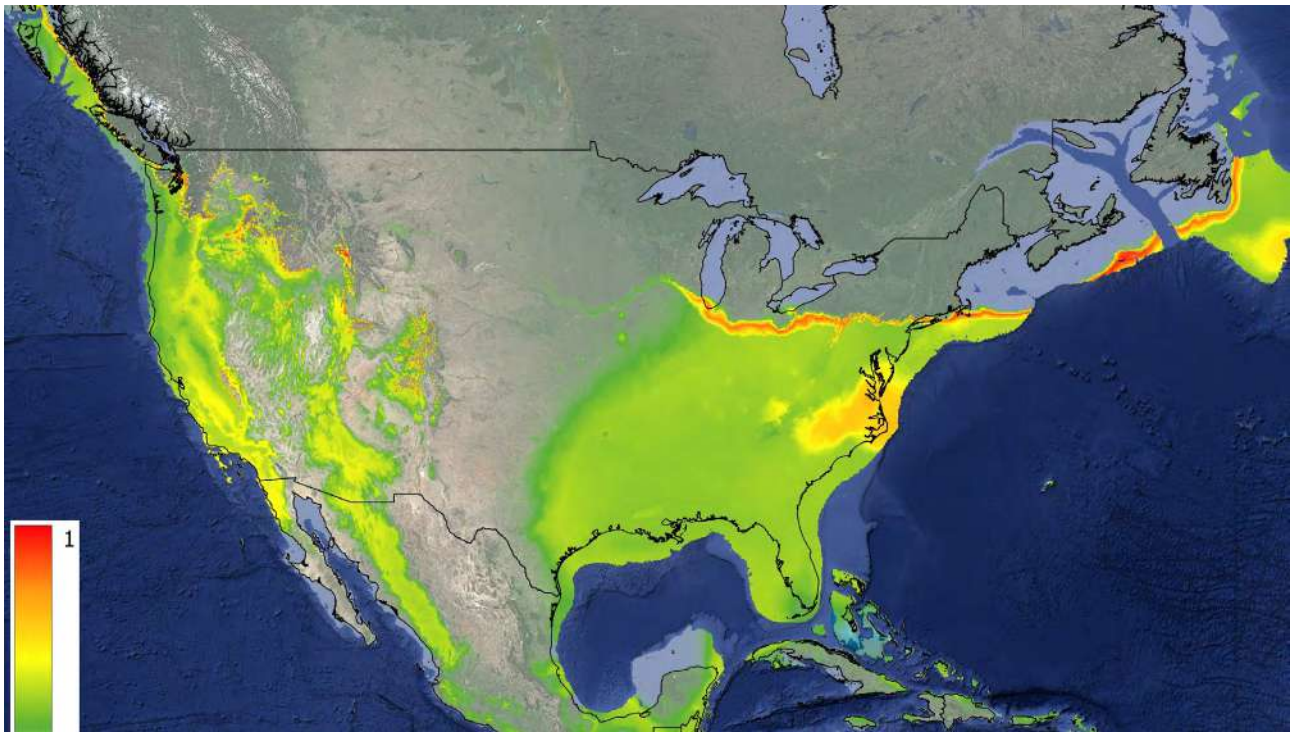

Fig. 7. Model result of the potentially suitable ecological niches for *Drepanaphis acerifoliae* (Thomas, 1878) in North America during the last glacial maximum. The colour scale shows the probability of a suitable ecological niche. Brighter areas mark the boundary of the continental land during the last glacial maximum (between 26,500 and 19,000-20,000 years ago). Black lines represent the current national boundaries.

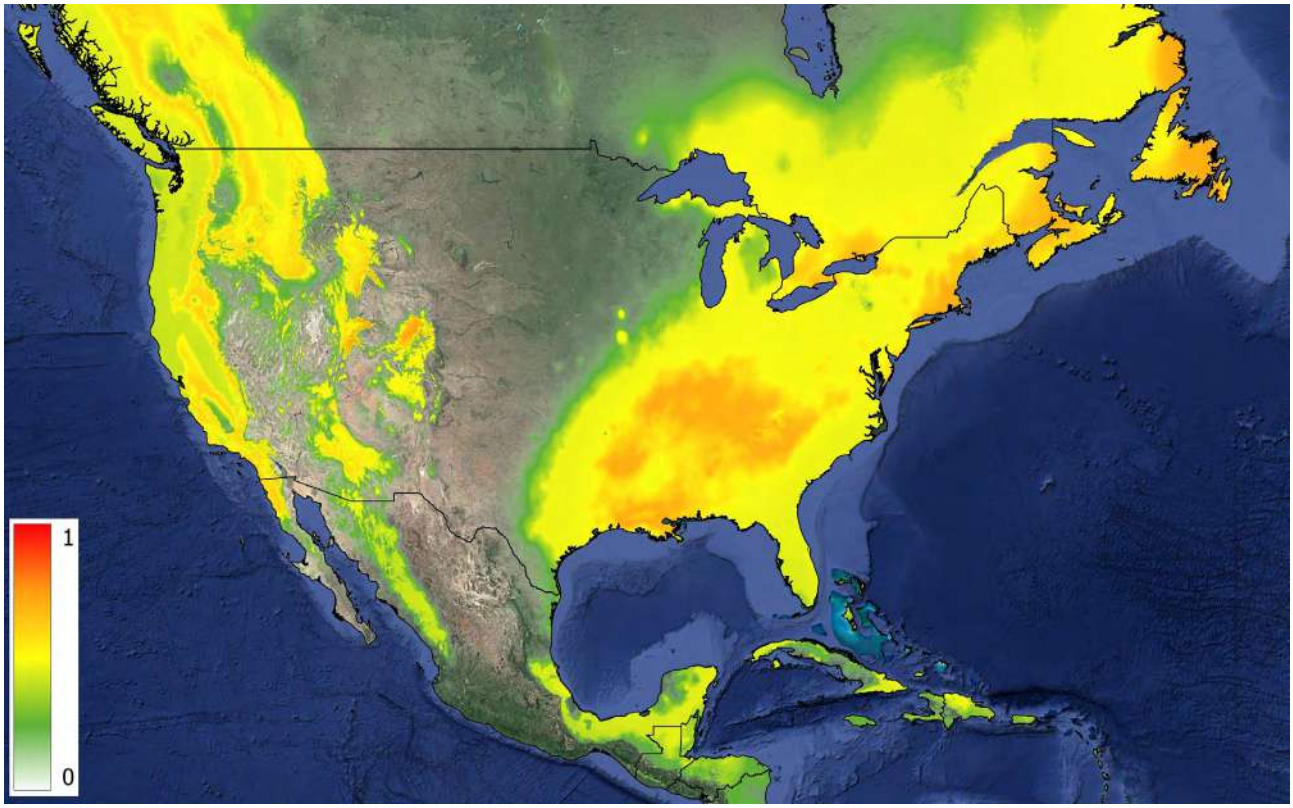

Fig. 8. Model result of the potentially suitable ecological niches for *Drepanaphis acerifoliae* (Thomas, 1878) in North America during the Mid-Holocene period. The colour scale shows the probability of a suitable ecological niche. Black lines represent the current national boundaries.

Russia. The maps also showed a clear shift in the suitable niche to the territories of Great Britain, Germany, Denmark, Poland, the Czech Republic, Slovakia, Ukraine, Belarus, Lithuania, Latvia, Estonia, Finland and the south of Sweden.

Climatic preferences and terrestrial ecoregions

The present potentially-suitable ecological niches of *D. acerifoliae* were compared with the Köppen-Geiger climate classification, to determine the possible climatic preferences of the species (SM.04 – Fig. 3). An analysis of the climate types of the known locations indicated that the representatives of *D. acerifoliae* prefer a temperate (humid subtropical) and continental climate (hot summer and warm summer humid continental). A humid subtropical climate (Cfa) is characterised by a mean temperature during the coldest month above 0°C (32°F), with at least one month when the mean temperature is above 22°C (71.6°F) and about four months above 10°C (50°F). Such climatic conditions prevail in the southeastern part of the United States.

A hot summer humid continental climate (Dfa) has the coldest month with temperatures below 0°C (32°F), but at least one month with the mean temperature above 22°C (71.6°F) and about four months above 10°C (50°F). Within North America, this climate includes the central and eastern United States. In the warm summer subtype (Dfb), the average temperatures in the warmest month are below 22°C (71°F), and the winters are cold, with temperatures usually well below -3°C (27°F). This subtype covers areas from about 42°N to 50°N latitude in North America, but it can be found further west in the Canadian Prairie Provinces and below 40°N in the high Appalachians. It is also found in much of Central and Eastern Europe, southern and central parts of Scandinavia, all the Baltic States, and parts of Romania, Bosnia and Herzegovina, and Türkiye. For all the climate types mentioned above, there is no significant precipitation difference between the seasons.

Among all the individuals of *D. acerifoliae* we examined, 69% inhabited a temperate broadleaf and mixed biome. Other inhabited areas include temperate coniferous forests (10%), temperate grasslands, savannas and shrublands (10%), Mediterranean forests, woodlands and scrub (6%), and last of all deserts and xeric shrublands (3%) as well as boreal forests/taiga (2%) (SM.04 – Fig. 4). As can be seen, this

species is strongly associated with temperate forest areas where, above all, the *Acer* species with which this species is associated occur in their natural state.

Discussion

In our study, we predicted possible suitable ecological niches and the climate change impact on the global distribution of *D. acerifoliae*. We managed to obtain 90 occurrence points for this purpose. On the scale on which the modelling was carried out (continents and the whole world), this amount may be insufficient to consider these results as final. Nevertheless, the research conducted on the impact of the number of samples on the quality of models shows that when using the algorithm implemented in MaxEnt (which uses regularisation to avoid over-fitting), such research attempts should not be rejected. Research also shows that the data quality is often more important than the quantity (Wisz *et al*. 2008; Mateo *et al*. 2010; Støa *et al*. 2019). In order to conduct our research as well as possible, we additionally used a bias file and tested various settings of the MaxEnt software, as recommended by the authors of other studies (Elith *et al*. 2010; Merow *et al*. 2013; Morales *et al*. 2017). Because many species are known from relatively few records, our results highlight the need to develop databases of specimen occurrences in museums or herbaria, and to raise awareness among field researchers of the importance of sharing data in open repositories.

In North America, the distribution of *D. acerifoliae* coincides with the natural range of the host plants (which are native to the eastern part of the continent; Fig. 2) and the areas where they are planted (like the western part; Fig. 2). As the pest is directly dependent on its host, the model's prediction of a potential ecological niche also implies favourable climatic conditions for the host plants (Fig. 4). In Europe, the climatic conditions seem very suitable, and the settleable area is extensive. Europe has been a place where trade exchanges have taken place for centuries, and as a result, it has been exposed to the introduction of alien species that would not normally have had such an opportunity without human participation (DAISIE 2009; Keller *et al*. 2011). For example, the introduced *A. saccharinum* has become a plant host for the parasitic European mistletoe *Viscum album* L., contributing to the spread of this species throughout Europe (Kołodziejek *et al*. 2013; Varga *et al*. 2014). The spread of this species outside cities and parks entails, among other things, the threat of new pests. There are already reports about the presence of the gall mite species *Vasates quadripedes* Shimer, 1869, which is native to North America and forms pouch galls on maple leaves. It has spread across Europe and attacks only *A. saccharinum* (Bruun & Soika 2013). The same scenario is possible for *D. acerifoliae*, as has been shown by the introduction of other American aphids – *Prociphilus fraxinifolii* (Riley, 1879), a pest of ash trees (*Fraxinus* spp.); *Myzocallis* (*Lineomyzocallis*) *walshii* (Monell, 1879), associated with the red oak *Quercus rubra* (L.); and *Appendiseta robiniae* (Gillette, 1907), a pest of *Robinia pseudoacacia* L. Those are examples of alien species that have been able to occupy the whole of Europe in less than two decades, after the first record of their presence in the continent (Mier Durante & Nieto Nafría 1997; Petrović 1998; Ripka *et al*. 1998; Osiadacz & Wieczorek 2006; Havelka & Starý 2007; Barbagallo *et al*. 2008; Borowiak-Sobkowiak, Durak & Wilkaniec 2008; Tasheva-Terzieva 2008; Piron 2009; Modic 2010; Petrović-Obradović *et al*. 2010; Çalışkan *et al*. 2012; Hałaj *et al*. 2016; Wojciechowski *et al*. 2016; Orlova-Bienkowskaja & Bieńkowski 2021). Their spread is especially likely when the foreign host plant is expansive, as in the case of the red oak, which is treated as one of the most frequent invasive trees from North America in temperate European forests (Chmura 2020). We described a similar scenario for species representing the genus *Eulachnus*, except that these taxa are native to Europe and are invasive in North America and Africa (Kanturski *et al*. 2016).

Since all the *Acer* species that are host plants for *D. acerifoliae* are native to eastern North America (*A. saccharinum*, *A. saccharum* and *A. rubrum*), the model obtained for the last interglacial period seems to be consistent with our assumption that the place of origin for this species may be in the region of the northeast United States, or around the Great Lakes. However, a question remains about whether the presence of this species in the west of North America is the result of its independent migration or the effect of human interference, as in the case of its presence in Europe. We are inclined to suspect the latter, as the natural range of the host plants does not extend to western areas. Instead, they are plantings, and because the local climatic conditions in the west are similar to those in the east of North America, there was no problem with adapting for both plants and aphids. From the history of *Acer* spreading around the world, it can be concluded that there are two groups of *D. acerifoliae* host plants. Renner *et al*. (2008) tried to reconstruct the evolutionary unfolding of the *Acer* species (North American/Asian disjunctions) based on combined data from up to seven

chloroplast loci and relaxed-clock rooting. They established that the North American taxa probably started to split from their Asian sister taxa at about 40 Ma, and kept up the rate of this speciation about once per 5 Ma. Areces-Berazain *et al*. (2021) estimated the divergence times between the New World and Old World lineages to be 15 Ma earlier. *Acer* species appeared first on the west coast of North America, and migrations from the Eastern Palearctic region to the Nearctic have occurred at least seven times – starting from the early Eocene (*A. glabrum* Torr. lineage) to the early Miocene (*A. rubrum* L. + *A. saccharinum* L.). The ancestor of the sugar maple species (series Saccharodendron) known from eastern North America probably reached from Europe via Iceland-Greenland by the beginning of the Miocene (Areces-Berazain *et al*. 2021). Therefore, *A. rubrum* and *A. saccharinum* represent the Rubra section, and *A. saccharum* with its subspecies represent the Acer section. In Europe, the Acer section is represented by *A. garnatense*, *A. monspessulanum*, *A. opalus*, *A. pseudoplatanus* and *A. sempervirens*. If *D. acerifoliae* has evolved along with the host plant, there may be biological indications for it to adapt to feeding on other species of the Acer section in Europe.

Our model for the current period indicates areas where *D. acerifoliae* has already been recorded, such as Milan, Nola, Calendasco, Como and Carlazzo in Italy (Lozzia & Binaghi 1992; Colombo *et al*. 1996; Barbagallo *et al*. 2008; Barbagallo & Cocuzza 2014), Lleida and León in Spain (Perez Hidalgo *et al*. 2008), Budapest and Cegléd in Hungary (Ripka 2010), and Novi Sad and Belgrade in Serbia (Petrović-Obradović *et al*. 2018, 2021). However, the introduction in Italy and Spain could have occurred in two independent ways, as the map clearly shows that mountainous areas may constitute a natural barrier to species dispersion (Fig. 9). France is a potential area where the species can be expected to be present already, or will occur soon. The presence of mountainous areas limits both of the roads from Italy and Spain. Nevertheless, both now and in the future, the area of France is one of the most favourable for the occurrence of the aphid. We therefore recommend that appropriate French institutions and researchers scan planted *A. saccharinum* for the presence of *D. acerifoliae*.

In general, the coastal region of the entire Mediterranean Sea seems to have favourable climatic conditions for *D. acerifoliae*, which means that when

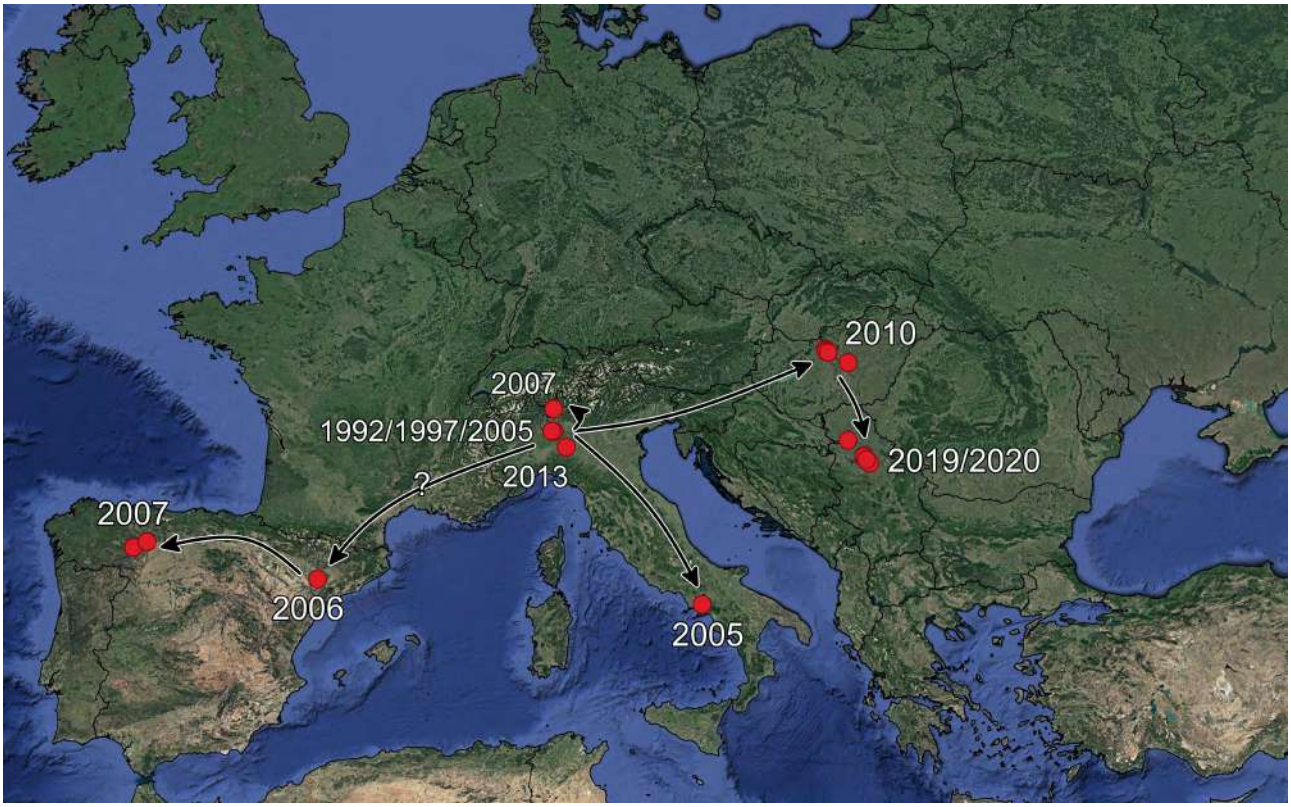

Fig. 9. Known places of the occurrence of *Drepanaphis acerifoliae* (Thomas, 1878) in Europe (red dots) with the year of its identification. The arrows indicate the possible directions of the spread of the species in Europe. The direction from Italy to Spain is marked with a question mark, because the mountainous areas present on the path may have constituted a geographical barrier. Black lines represent the current national boundaries.

a host plant is found, the species may be present not only in Europe but also in northern Morocco, Algeria, Tunisia, Libya and Egypt. In addition, the model shows suitable climatic conditions in the Middle East, particularly in Israel, Palestine, Lebanon, Syria and Türkiye. It is also highly recommended to monitor the presence of *D. acerifoliae* throughout the Balkan Peninsula, because the model shows the most suitable climatic conditions there – the presence of the host plants there may guarantee the dispersion in this part of Europe and will also open the way east to Türkiye. Moreover, this species is already present in Serbia (Petrović-Obradović *et al*. 2018, 2021). Interestingly, the best climatic conditions extend from the middle of eastern Ukraine through Russia to Kazakhstan. They also include the territories of Georgia, Azerbaijan, and Iran. It is therefore worthwhile for local biodiversity control services to pay attention to the planting of *A. saccharinum*, because it may introduce the aphid and lead to its rapid dispersion. This is perhaps not the most realistic scenario due to the presence of the Ural range, which is a good geographical barrier, but the future introduction to this area could also present a threat of the spread of this species to East Asia.

Our models under future climate conditions indicated that suitable areas for *D. acerifoliae* in the northern hemisphere can be projected to expand northward. This phenomenon appears to be common for many other insect species – not only introduced ones. Many studies have shown that over the past decades, species inhabiting Europe and/or North America are increasingly moving northward, expanding their range in that direction (e.g. Régnière *et al*. 2012; Delava *et al*. 2014; Klementová & Svitok 2014; Kistner 2017; Fält-Nardmann *et al*. 2018; Rimšaitė *et al*. 2022). On the other hand, *A. saccharinum* is also grown in temperate parts of the southern hemisphere such as Argentina, Brazil and Uruguay (Di Iorio & Farina 2009; www.gbif.org). Our results of the impact of climate change on the spread of *D. acerifoliae* show the results for South America and include the abovenamed countries and Paraguay. Thus, those countries should also control the condition of aphid species and react to the possible introduction of *D. acerifoliae*, even if it seems that the current conditions in the southern hemisphere may be too demanding.

The spreading of *D. acerifoliae* in future may be limited by the lack of planting *A. saccharinum* in Europe and Asia. However, there is a risk that this aphid will change or expand its host plants over time. Due to the climatic conditions, there is also a chance of phenological asynchrony between the host and the insect (van Asch & Visser 2007). Another worrying phenomenon is that many invasive insects have a wider range of thermal tolerance, beyond their natural niche (Jarošík *et al*. 2015). Natural methods of biological control by using predators may also be a solution, but unfortunately, only a few are known for *D. acerifoliae*. Pérez Hidalgo *et al*. (2008) mentioned predation by *Adalia bipunctata* (Linnaeus, 1758), *Anthocoris pilosus* (Jakovlev, 1877) and *Passer domesticus* (Linnaeus, 1758). As previous authors have also mentioned, we still need to gain a better understanding of the biology of *D. acerifoliae* and the factors influencing the dynamics of its population. Additionally, as many indigenous natural enemies as possible should be identified in order to implement a sustainable conservation scenario. Nevertheless, prevention is crucial, as global trade presents the main risk of introducing and spreading this invasive insect species.

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Author Contributions

Research concept and design: K.M., A.B.-N.; Collection and/or assembly of data: K.M.; Data analysis and interpretation: A.B.-N.; Writing the article: K.M., A.B.-N., K.W.; Critical revision of the article: K.W.; Final approval of article: K.M., A.B.-N., K.W.

Conflicts of Interest

The authors declare no conflict of interest.

Supplementary Material

Supplementary Materials to this article can be found online at: http://www.isez.pan.krakow.pl/en/folia-biologica.html

Supplementary files:

SM.01. Details of all of the occurrence sites used in the MaxEnt model.

SM.02. The list of bioclimatic variables considered as predictors with a correlation coefficient.

SM.03. The results of the evaluation methods for the different MaxEnt settings.

SM.04. MaxEnt model outputs and climatic diagrams.

SM.05. Modelling results for future climate scenarios.

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Publikacja 2

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Taxonomic Revision of the Nearctic Genus *Drepanaphis* Del Guercio (Hemiptera, Aphididae: Drepanosiphinae)

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Simple Summary: This study explores the aphid genus *Drepanaphis*, focusing on its diverse species and their relationships with host plants across North America. The research includes a comprehensive taxonomic revision, identifying 18 species with the addition of *Drepanaphis robinsoni* sp. nov. Detailed descriptions and illustrations cover 44 morphs, including alate viviparous females, oviparous females and males, accompanied by new identification keys. For the first time, sexual morphs of 15 species, particularly oviparous females, are documented. Current range maps for all species and microscopy images of key morphological features contribute to a more comprehensive understanding of this genus, which has received limited study in the past.

Abstract: The Nearctic aphid genus *Drepanaphis* Del Guercio, 1909, the largest within the subfamily Drepanosiphinae (Hemiptera: Aphididae), is characterised by distinctive dorsal abdominal tubercles. This study presents a comprehensive taxonomic revision of the genus, expanding the recognised species to 18, including the newly described *Drepanaphis robinsoni* Malik sp. nov. Detailed descriptions and figures for 44 morphs, encompassing alate viviparous females, oviparous females and males, are provided, with new identification keys for all known species and morphs. The sexual morphs of 15 species, particularly oviparous females, are documented for the first time. Morphometric and principal component analyses (PCA) are employed to distinguish the studied taxa. This study identifies and corrects numerous misidentifications in museum collections, previously labelled as *D. acerifoliae*, *D. choanotricha*, *D. kanzensis*, *D. knowltoni*, *D. parva*, *D. sabrinae* or *D. tissoti*. Furthermore, it revalidates the distinct status of *D. nigricans* and *D. tissoti*, which had been synonymised in earlier works. Current range maps for all species and images of key morphological features obtained through light and scanning electron microscopy are also presented, providing a more complete understanding of this understudied genus.

Keywords: *Acer*; aphids; North America; SEM; sexual morphs

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1. Introduction

Aphids (Hemiptera: Aphididae) are a diverse group of insects, encompassing around 5600 species divided into 24 subfamilies [1]. They are widespread in temperate regions, with some species exhibiting seasonal alternation between unrelated groups of host plants, including angiosperms, gymnosperms and herbaceous plants [2]. Their life cycles, involving both sexual and asexual reproduction driven by adaptive radiation, contribute to their variable phenotypic features [3]. This great diversity makes aphids a fascinating research model with a complex role in ecosystems. On the one hand, aphids produce honeydew and engage in mutualistic relationships with ants [4]. They also contribute to bioaccumulating chemical elements from plants and contaminated soil [5]. However, they are significant crop and ornamental plant pests, causing damage through direct feeding or the transfer of plant pathogens [6].

The subfamily Drepanosiphinae is a widely distributed group of aphids, currently containing 40 species belonging to five genera. Research on the systematics of Drepanosiphinae has mainly focused on the external morphology and molecular biology of the genera *Drepanosiphoniella* Davatchi, Hille Ris Lambers and Remaudière, 1957 [7]; *Drepanosiphum* Koch, 1855 [8]; *Yamatocallis* Matsumura, 1917 [9]; and *Shenahweum* Hottes & Frison, 1931 [10–15]. The genus *Drepanaphis* Del Guercio, 1909 [16], is the most numerous genus within the subfamily, here revised to include 18 species with 44 known morphs. Species from this genus are characterised by distinct dorsal tubercles on the abdominal segments, very long antennae and reduced legs chaetotaxy. All *Drepanaphis* species are regarded as Nearctic, with *D. acerifoliae* (Thomas, 1878) [17] also introduced to Europe [18]. Most species in this genus are similar in the body size and wax arrangement of the dominant morph, alate viviparous females, making them difficult to distinguish. Species of this genus are mostly monophagous, feeding primarily on different maple trees (*Acer* spp.), although some are oligophagous. Exceptionally, the host plant of *D. monelli* (Davis, 1909) [19] is buckeye (*Aesculus glabra*).

Thomas described the first species of the current genus *Drepanaphis* in 1878 as *Siphonophora acerifoliae* [17]. At the end of the description of the new species, he included the following sentence: "It is possible that this Aphis should be placed in *Drepanosiphum*, or a new genus be formed for its reception". Just a year later, in 1879, Monell classified *S. acerifoliae* in the genus *Drepanosiphum*, changing the species name to *Drepanosiphum acerifolii*. For years, most researchers hesitated to determine whether this species also belonged to the genus *Drepanosiphum*. Finally, on 15 September 1909, Del Guercio [16], in "Revista di Patologia Vegetale", proposed a new genus for *S. acerifoliae—Drepanaphis*. At the same time, in September 1909, Davis proposed the genus *Phymatosiphum* for the same species in the "Annals of the Entomological Society of America". Davis referred to the suggestions of H. Schouteden and H. F. Wilson that this was not a representative of *Drepanosiphum*. Interestingly, Del Guercio described the new genus from material he received from Davis himself. His footnote at the end of the article proves this: "Gli insetti esaminati ed in base ai quali ho stabilito il genere indicato mi sono stati spediti gentilmente dal chiaro collega J. J. Davis, al quale porgo anche in questa occasione sentiti ringraziamenti." [transl. "The insects examined and on the basis of which I established the indicated genus were kindly sent to me by my good colleague J. J. Davis, to whom I also offer heartfelt thanks on this occasion."]. Therefore, if Davis had not shared the material mentioned with Del Guercio, we would probably now be discussing the genus *Phymatosiphum*. Nevertheless, according to the International Code of Zoological Nomenclature (ICZN), Art. 21.3, Del Guercio was the first to describe the genus because its publication date is specified to the day.

Once the systematic position of this genus was established, new species were subsequently described. Davis described *Phymatosiphum monelli* (1909) [19], which Gillette synonymised as *Drepanaphis monelli* (1910) [20]. In 1931, Granovsky [21] described *D. keshenae*; in 1937, Miller [22] proposed *D. sabrinae*. In 1941, Smith [23] described *D. carolinensis*, *D. kanzensis*, *D. nigricans*, *D. parvus*, *D. rubrum* and *D. spicata*. However, in 1943, Smith and Knowlton [24] described two more species—*D. granovskyi* and *D. utahensis*—and at the same time concluded that *D. rubrum* is a synonym of *D. parvus*. Smith described two additional species—*D. tissoti* in 1944 [25] and *D. simpsoni* in 1959 [26]. Then, in 1968, Smith and Dillery [27] carried out the first revision of the genus *Drepanaphis*, describing four more new species—*D. choanotricha*, *D. idahoensis*, *D. knowltoni* and *D. saccharini*. The last species, described by Richards in 1969, was *D. pallida* [28].

As already mentioned, this genus was revised by Smith and Dillery in 1968 [27], and since then, this has been the most reliable source of information about the *Drepanaphis* species. The publication provided important information about the morphology of winged viviparous females, but little attention was given to the descriptions of oviparous females and males. The authors primarily studied interspecific relationships and categorised morphological groups to represent differences between species within a genus. However, they focused extensively on the features of the nymphs without considering the morphological

characteristics of the adults. Due to the high similarity of winged forms and the lack of distinct morphological characters between species, the species identity of *D. nigricans* and *D. tissoti* has been questioned, as has that of *D. pallida* and *D. simpsoni* [29].

Therefore, the aim of this study is to perform a comprehensive revision of the genus *Drepanaphis* that considers the variability in species across different regions of North America. This study seeks to document the sexual morphs of 15 species for the first time, including the description of all oviparous females, and to provide comprehensive identification keys for all known species and morphs. A principal components analysis (PCA) is utilised to elucidate relationships among species within the various morphological groups identified in the genus, clarifying the status of the most similar species. Additionally, by examining museum specimens, a new species is described, *Drepanaphis robinsoni* sp. nov., which was previously confused with two other species. It also aims to correct numerous misidentifications of specimens previously mislabelled. Lastly, this study intends to present updated range maps for all species and provide images of key morphological features using light and scanning electron microscopy, thereby contributing to a more complete understanding of this historically understudied genus.

2. Materials and Methods

2.1. Study Material and Light Microscopy

A total of 652 microscopic slides and 1382 individuals were examined (1055 alate viviparous females, 61 oviparous females, 42 males and 223 undetermined specimens). Freshly collected samples were preserved in 70% ethanol. Insects were slide mounted using the method of Wieczorek [30]; examined using light microscopes: a Nikon Ni-U, equipped with a phase contrast system and a Leica DM 3000 LED; and photographed using a Leica MC 190 HD camera (Leica Microsystems GmbH, Wetzlar, Germany). The measurements were taken according to Ilharco and van Harten [31] and are given in millimetres. Voucher specimens were deposited in the entomological collection of the University of Silesia in Katowice, Poland (DZUS). Actual host plant names are given according to the WFO Plant List [32]. Final figure processing was performed using Photoscape X 4.2 (photoscape.org, accessed on 20 June 2024). The drawings were prepared manually and then scanned and processed in Photoscape. The dimensions are the average value of several/dozen measurements of individual appendages.

The following abbreviations (in the descriptions, re-descriptions, tables and Supplementary Materials) were used: ABD—abdominal tergite or tergites; ANT—antennae or their lengths; ANT I–VI—antennal segments from I to VI or their lengths (ratios between antennal segments are given as "III/IV"); BASE—basal part of the last antennal segment or its length; BL—body length; DAT—dorsal abdominal tubercles; FEMUR I—fore femur length; FEMUR II—middle femur length; FEMUR III—hind femur length; HW—head width across compound eyes; HT II—second segment of hind tarsus or its length; PT—processus terminalis of the last antennal segment or its length; SIPH—siphunculi sclerite width; TIBIA III—hind tibia length; URS—ultimate segments of rostrum (IV + V) or their lengths.

The material studied was loaned from the following depositories: Biologické centrum IECA—The Biology Centre of the Czech Academy of Sciences; INHS Insect Collection—Illinois Natural History Survey Champaign, Illinois; MNHN—Muséum national d'Histoire naturelle, Paris, France; MZLU—Museum of Zoology, Lund University, Sweden; MZPW—Museum of the Zoological Institute of the Polish Academy of Sciences, Warsaw; NHMUK—Natural History Museum, London, United Kingdom; USNM—United States National Museum, Smithsonian Institution, Washington, DC, United States; ZMUC—Zoological Museum, University of Copenhagen, Copenhagen, Denmark; A. Jensen's private collection.

The holotype of the new species is deposited at the NHMUK. Paratypes will be deposited at the NHMUK and DZUS.

Quoting the labels of the specimens, a double slash (//) is used to divide data on different labels. Notes and information about the collection are in square brackets [ ].

2.2. Scanning Electron Microscopy

Specimens for scanning electron microscopy (SEM) analysis (five individuals) were preserved in 70% ethanol. The samples were dehydrated using serial baths of 80%, 90% and 96% ethanol—20 min for 80% ethanol, 15 min for 90% ethanol, 10 min for 96% ethanol and two baths of absolute alcohol for 10 min each. Dehydrated samples were dried using a Leica EM CPD300 automated critical point dryer (Leica Microsystems, Vienna, Austria). Dry samples were mounted on aluminium stubs with double-sided adhesive carbon tape and sputter coated with a 30 nm gold layer in a Safematic CCU-010 high-vacuum sputter coater (Safematic GmbH, Zizers, Switzerland). The specimens were imaged with Hitachi SU8010 (Hitachi High-Technologies Corporation, Tokyo, Japan) and Phenom XL (Phenom-World B.V., Eindhoven, The Netherlands) field emission scanning electron microscopes. Final figure processing was performed using Photoscape X 4.2 (photoscape.org, accessed on 20 June 2024).

2.3. Statistical Analysis

A principal components analysis (PCA) was conducted based on the data recorded from individual specimens. Data sets (Tables S1 and S2) with morphometric variables, morphometric ratios and morphological characters for alate viviparous females (52 characters), males (51 characters) and oviparous females (46 characters) were tested with multiple correlation analysis, and the variables with the lowest redundancy values were finally selected. Six morphometric variables, ten morphometric ratios and eight morphological characters were selected for the 213 alate viviparous females of the genus *Drepanaphis* (see Table S3 for details). For the 30 males (see Table S4 for more information), four morphometric variables, 11/12 morphometric ratios and nine morphological characters were selected. In turn, for the 43 oviparous females (see Table S4 for more information), five morphometric variables, 13 morphometric ratios and six morphological characters were selected (all variables are listed in Tables S1 and S2). Before the PCA, each character was converted to zero mean and unit standard deviation within reduced data sets, so the same weight was given to all of them. The PAST software ver. 4.13 [33] was used for multivariate analyses. Since we have already analysed distinctiveness at the generic level with representatives of *Drepanaphis* and the closely related genera *Drepanosiphum* and *Drepanosiphoniella*, we will not repeat it here and will refer to the previous publication [12].

2.4. Occurrence Data and Preparation of Maps

The occurrence data were obtained from the scientific literature, specimens studied in museum collections, fieldwork in the USA in September 2022, iNaturalist (www.inaturalist.org, accessed on 12 June 2024) [34] and biodiversity databases (GBIF Occurrence Download [35], https://doi.org/10.15468/dl.nsv6vq, accessed on 12 June 2024). Museum curators were asked to provide information about their collections (photographs of the preparations were provided). Some specimens were also examined in the collections during the personal stay of the first author. Databases were searched based on keywords, i.e., the name of the species and its synonyms. All records with unspecified or unknown localities were excluded.

All localities of the studied species were georeferenced using Google Earth ver. 10.38.0.0 (Google Inc. [36], Mountain View, CA, USA) (geographical projection, decimal degrees, datum: WGS84). The ranges of host plants were based on data obtained from http://databasin.org, accessed on 12 June 2024 (Conservation Biology Institute (CBI) [37]; the maps are a digital representation of the tree species range maps from the Atlas of the United States Trees by Little [38]). Maps were prepared using Quantum GIS ver. 3.30.1 (QGIS Development Team [39]) using the WGS84 datum and EPSG: 4326 or 3857 (Web Mercator). The data on the distribution of individual species will be published in the GBIF.

3. Results

3.1. Taxonomy

Genus *Drepanaphis* Del Guercio, 1909

Type species *Siphonophora acerifoliae* Thomas, 1878, by original designation.

Diagnosis: Dominant morph is alate viviparous female, characterised by distinct dorsal abdominal tubercles, variably developed on ABD I–IV (Figure 1). Oviparous females apterous, males alate. All morphs with rounded secondary rhinaria on ANT III. Primary and accessory rhinaria on BASE ciliated (Figure 2). Pterostigma distinct, darkly pigmented, with small area inside without pigmentation or palely pigmented, large area inside without pigmentation (Figure 3). Fore femora pale, dark or darker dorsally (Figure 4). Siphunculi tubular or flask-shaped (Figure 5), placed on ABD VI, swollen at base, without subapical reticulation. Almost all species are associated with species of *Acer*, except for *D. monelli*, which is found on species of *Aesculus*. They usually do not form dense colonies and are not attended by ants.

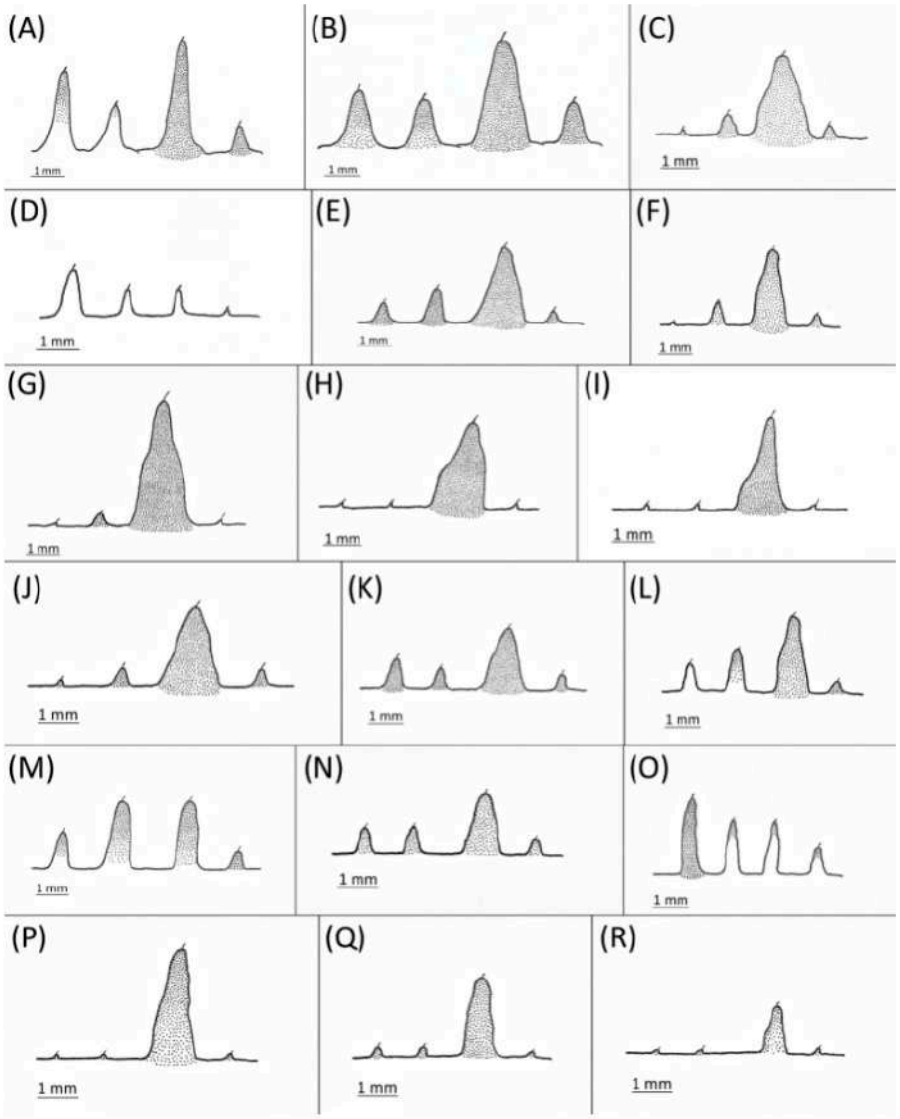

Figure 1. Lateral arrangement of dorsal abdominal tubercles of alate viviparous females of the genus *Drepanaphis*: (**A**) *D. acerifoliae*, (**B**) *D. carolinensis*, (**C**) *D. choanotricha*, (**D**) *D. granovskyi*, (**E**) *D. idahoensis*, (**F**) *D. kanzensis*, (**G**) *D. keshenae*, (**H**) *D. knowltoni*, (**I**) *D. monelli*, (**J**) *D. nigricans*, (**K**) *D. parva*, (**L**) *D. robinsoni* sp. nov., (**M**) *D. sabrinae*, (**N**) *D. saccharini*, (**O**) *D. simpsoni*, (**P**) *D. spicata*, (**Q**) *D. tissoti*, (**R**) *D. utahensis*.

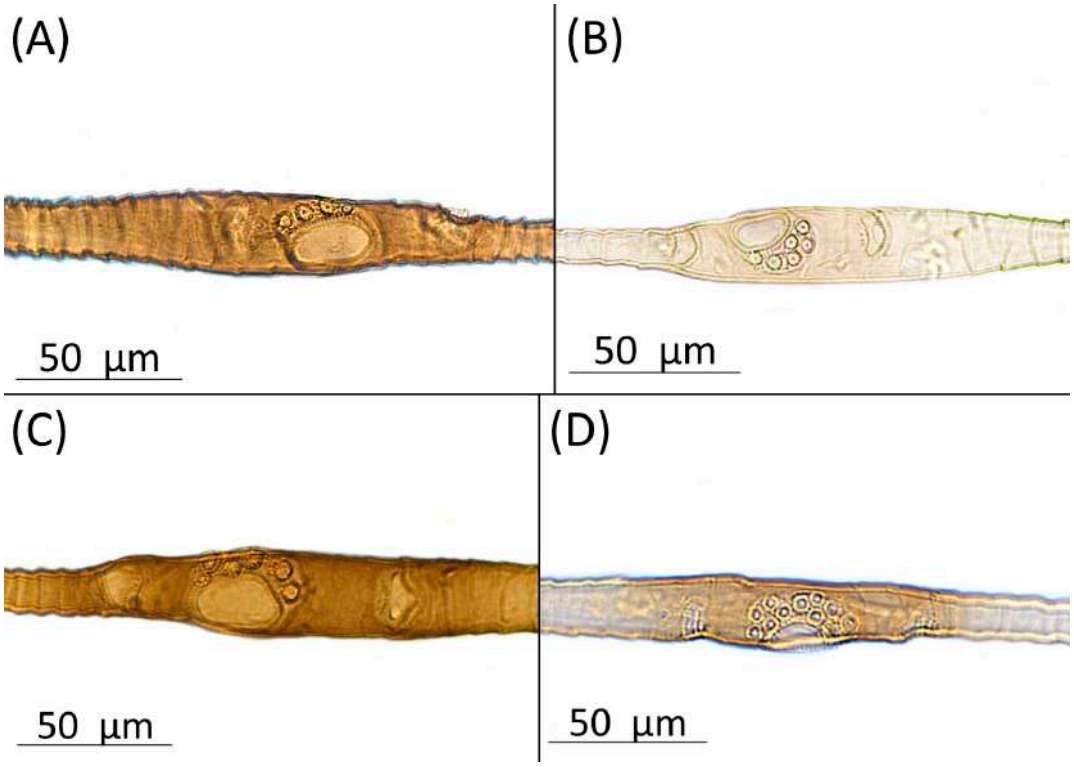

Figure 2. Antennal segment VI base with primary rhinarium (bigger) and accessory rhinaria (smaller) of alate viviparous females of the genus *Drepanaphis*: (**A**) *D. acerifoliae*, (**B**) *D. choanotricha*, (**C**) *D. sabrinae*, (**D**) *D. tissoti*.

Shared morphological characters of alate viviparous females of the genus *Drepanaphis*

Body slender, pale, with various pigmentation patterns on legs. Head separated from pronotum, abdominal segments not separated from one another. Head with little-developed antennal tubercles, with postero-dorsal, latero-dorsal and fronto-orbital setae (Figure 6A). Compound eyes with numerous ommatidia and well-developed triommatidia (Figure 6A). Rostrum ends between fore and middle coxae. Ultimate rostral segments with two pairs of primary setae and four to seven pairs of accessory setae, variable within species (Figure 6B). Antennae six-segmented. Antennal segment II shortest; antennal segments IV and V similar in length; processus terminalis longest. Antennae covered with pointed, short, colourless setae. On ANT I–II 0.01–0.02 mm long (on ANT I more abundant on apical part of segment); on ANT III–VI 0.005–0.01 mm long. ANT I with 8–12 setae, ANT II with 2–5 setae, ANT III with 40–50 setae, ANT IV with 12–18 setae, ANT V with 7–9 setae, BASE with 2–3 setae (type I trichoid sensilla), PT with 2 subapical and 1 apical setae (type II trichoid sensilla). ANT III with 2–22 rounded secondary rhinaria (small multiporous placoid sensilla; Figure 6D). Apical part of antennal segment V with one primary rhinarium (big multiporous placoid sensillum; Figure 6F). Base of antennal segment VI with 1 primary (major) rhinarium (big multiporous placoid sensillum) and 4–11 accessory rhinaria (small multiporous placoid sensilla) adhering to primary rhinarium, number of which may vary between species. Above and below major rhinarium, additional primary rhinaria present (Figure 6E). All rhinaria with ciliated cuticle edges (Figure 6D–F). Fore wings with radius strongly curved, media twice branched. Hind wings with media present. Dorsal abdominal tubercles (Figure 6G) with trichoid sensilla type I at ends (Figure 6H). Dorsal setae pointed, blunt or forked. Siphunculi flask-shaped or tubular (Figure 6J). Apex of siphunculi with well-developed, strong flange and well-developed operculum on siphuncular pore (Figure 6K). Fore femora dark dorsally or pale, hind femora pale, smudged or with dark stripes on distal parts. Legs covered by not numerous, 0.01–0.05 mm long, fine setae with pointed apices. Femora with smaller amount of setae, and tibiae with more abundant setae, especially at

end (Figure 6C). First tarsal segments 4:4:4, empodial setae spatulate (Figure 6I). Cauda knobbed, with 4–6 long, fine and pointed setae (Figure 6L). Anal plate and genital plate covered by numerous fine and pointed setae.

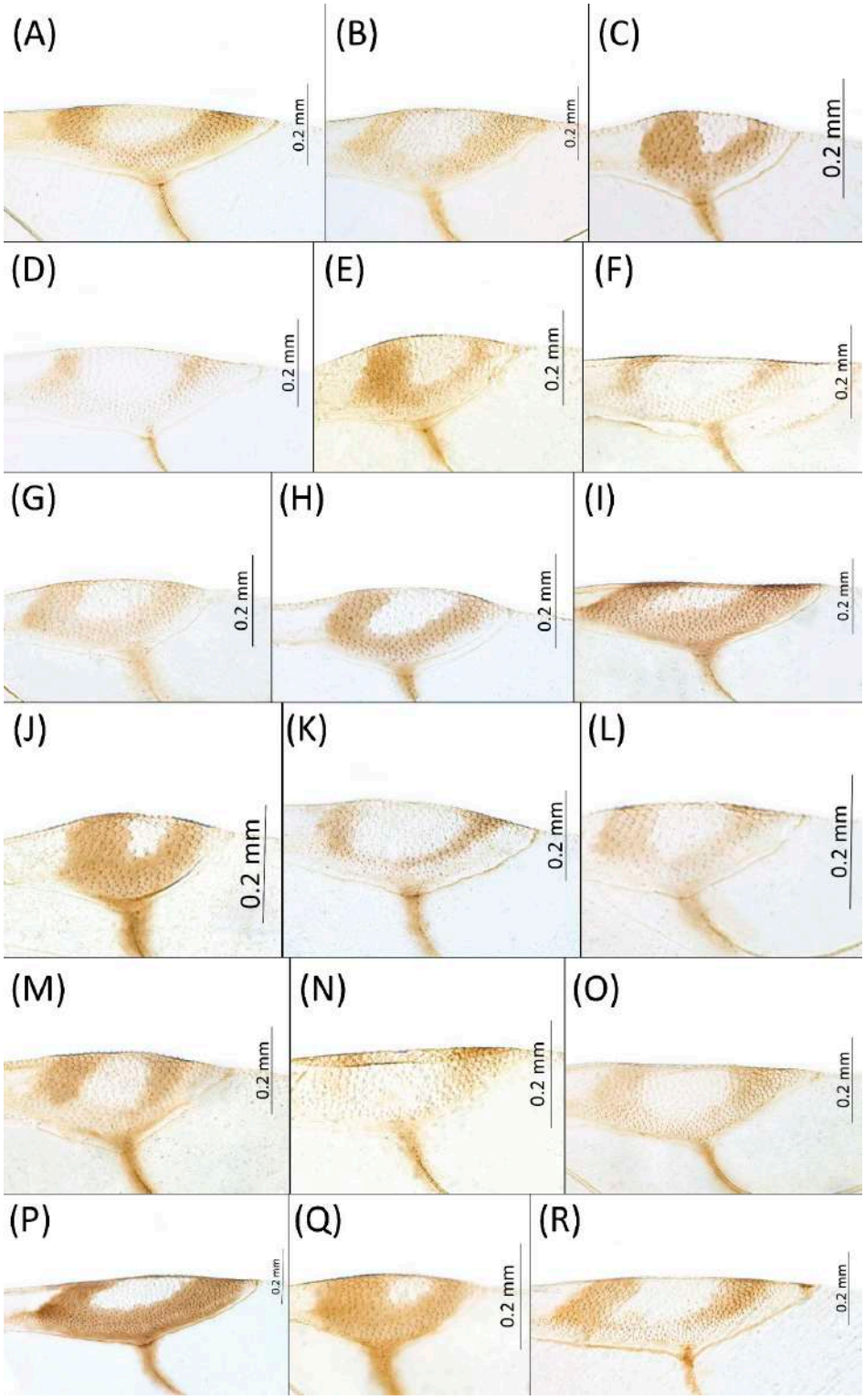

Figure 3. Pterostigma of the fore wing of alate viviparous females of the genus *Drepanaphis*: (**A**) *D. acerifoliae*, (**B**) *D. carolinensis*, (**C**) *D. choanotricha*, (**D**) *D. granovskyi*, (**E**) *D. idahoensis*, (**F**) *D. kanzensis*, (**G**) *D. keshenae*, (**H**) *D. knowltoni*, (**I**) *D. monelli*, (**J**) *D. nigricans*, (**K**) *D. parva*, (**L**) *D. robinsoni* sp. nov., (**M**) *D. sabrinae*, (**N**) *D. saccharini*, (**O**) *D. simpsoni*, (**P**) *D. spicata*, (**Q**) *D. tissoti*, (**R**) *D. utahensis*.

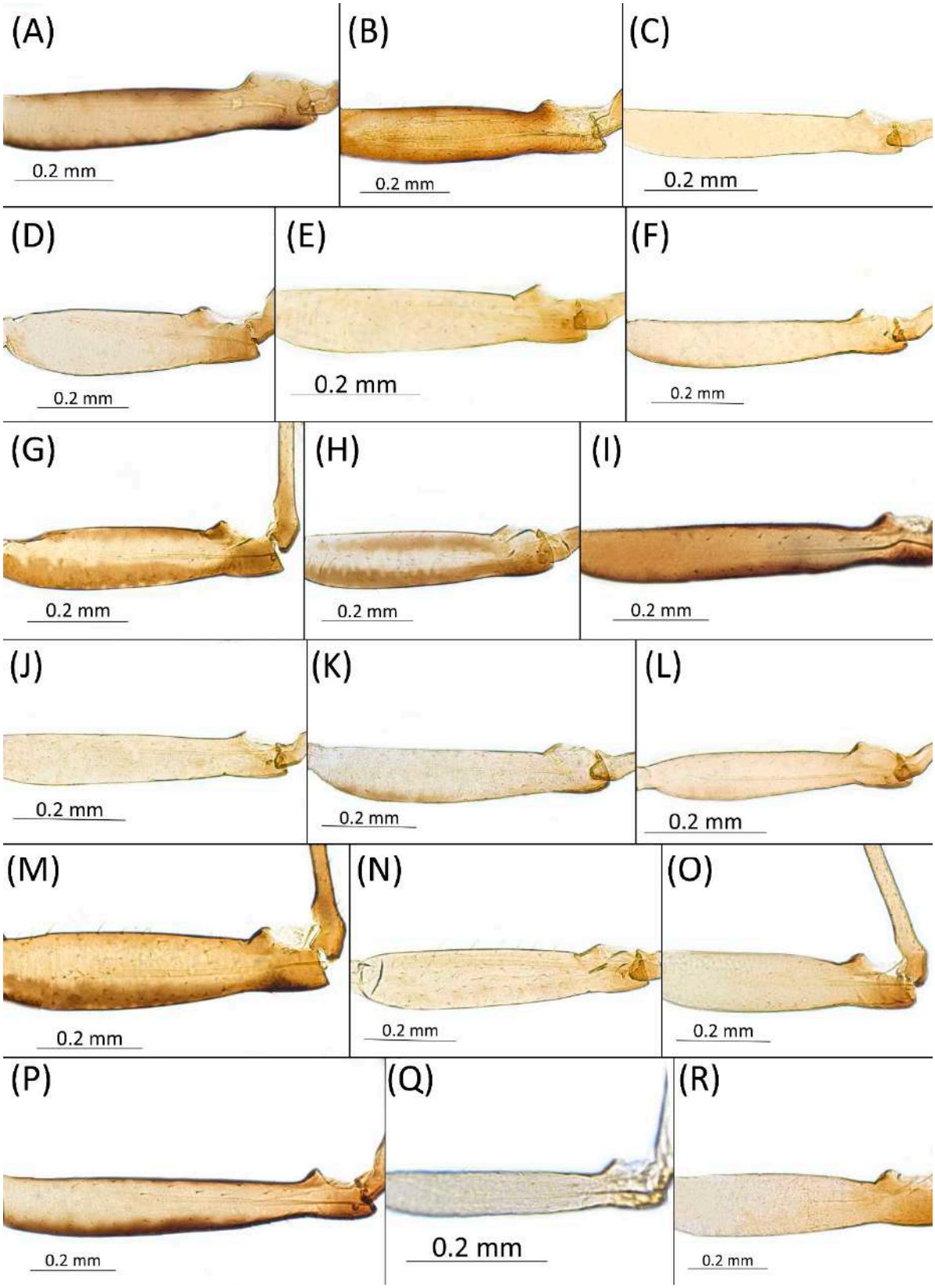

Figure 4. Fore femora of alate viviparous females of the genus *Drepanaphis*: (**A**) *D. acerifoliae*, (**B**) *D. carolinensis*, (**C**) *D. choanotricha*, (**D**) *D. granovskyi*, (**E**) *D. idahoensis*, (**F**) *D. kanzensis*, (**G**) *D. keshenae*, (**H**) *D. knowltoni*, (**I**) *D. monelli*, (**J**) *D. nigricans*, (**K**) *D. parva*, (**L**) *D. robinsoni* sp. nov., (**M**) *D. sabrinae*, (**N**) *D. saccharini*, (**O**) *D. simpsoni*, (**P**) *D. spicata*, (**Q**) *D. tissoti*, (**R**) *D. utahensis*.

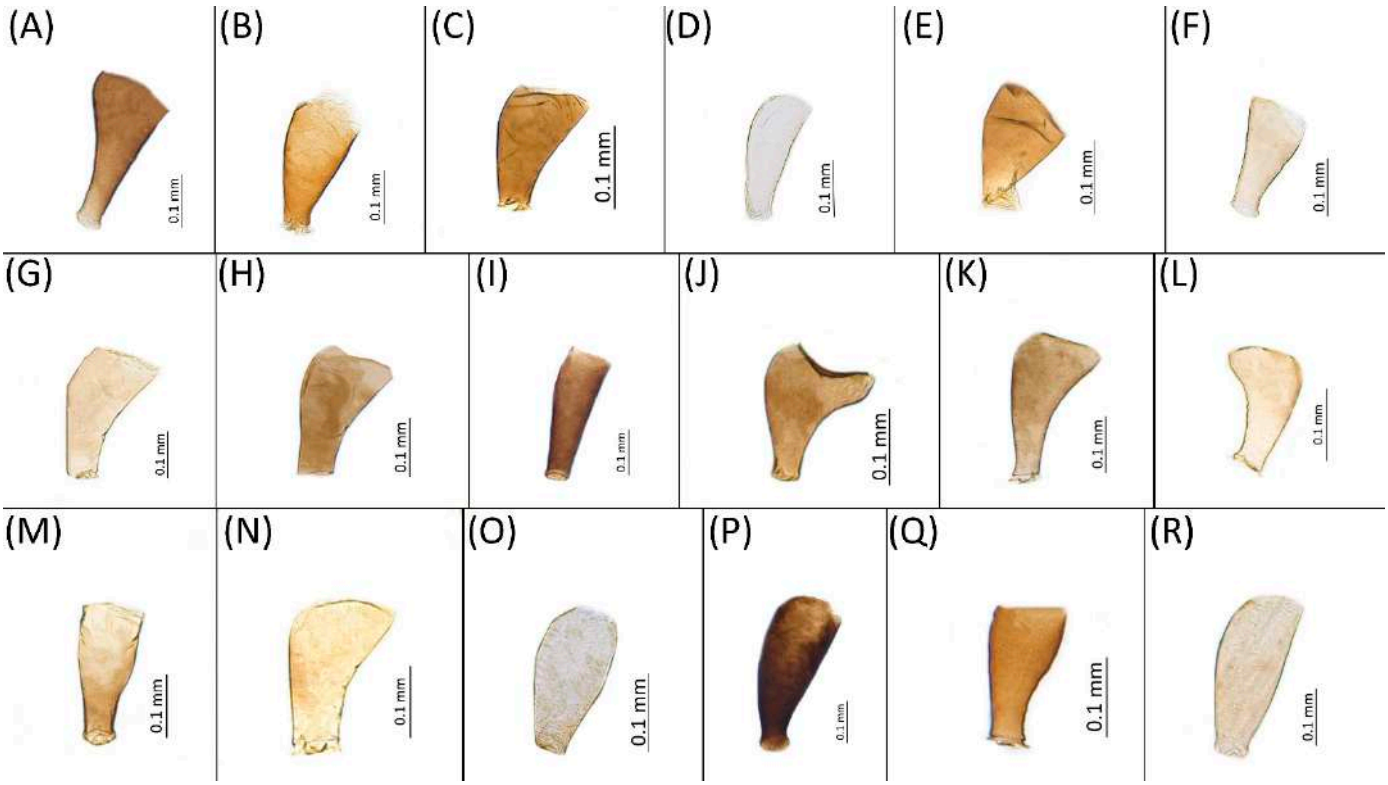

Figure 5. Siphunculi of alate viviparous females of the genus *Drepanaphis*: (**A**) flask-shaped in *D. acerifoliae*, (**B**) flask-shaped in *D. carolinensis*, (**C**) flask-shaped in *D. choanotricha*, (**D**) tubular in *D. granovskyi*, (**E**) flask-shaped in *D. idahoensis*, (**F**) flask-shaped in *D. kanzensis*, (**G**) flask-shaped in *D. keshenae*, (**H**) flask-shaped in *D. knowltoni*, (**I**) tubular in *D. monelli*, (**J**) flask-shaped in *D. nigricans*, (**K**) flask-shaped in *D. parva*, (**L**) flask-shaped in *D. robinsoni* sp. nov., (**M**) tubular in *D. sabrinae*, (**N**) flask-shaped in *D. saccharini*, (**O**) tubular in *D. simpsoni*, (**P**) flask-shaped in *D. spicata*, (**Q**) flask-shaped in *D. tissoti*, (**R**) tubular in *D. utahensis*.

Shared morphological characters of oviparous females of the genus *Drepanaphis*

Body pear-shaped or oval with elongated end of abdomen. Dorsal abdominal tubercles absent. ANT III without or with single, small, rounded secondary rhinaria. BASE with 1 rounded primary rhinarium with ciliated edge and 6–7 very small accessory rhinaria, adhering to primary rhinarium. Dorsal setae arranged in marginal, pleural and spinal rows. ABD I–VI with blunt setae distributed on well-developed sclerites. ABD VII–VIII with pointed setae. Hind tibiae with rounded pseudosensoria, mostly arranged along almost their entire lengths. Cauda knobbed with numerous setae.

Shared morphological characters of alate males of the genus *Drepanaphis*

General characters like in alate viviparous females. ANT III–V with numerous, small, rounded secondary rhinaria. BASE with 1 rounded primary rhinarium with ciliated edge and 4–5 very small accessory rhinaria, adhering to primary rhinarium. Abdomen with well-developed dorsal sclerotisation, especially on ABD IV–V. Dorsal abdominal tubercles smaller and less visible than in alate viviparous females. In some species inconspicuous. Cauda more or less knobbed, with five long, fine, pointed setae. Genitalia dusky, except for *D. granovskyi*, with genitalia distinctly darkly pigmented. In all known males parameres large, lobate, except *D. simpsoni*, with parameres much smaller and elongated. Parameres and basal part of phallus covered with numerous short setae. Distal part of sclerotised arms rather long and thin, whereas proximal part shorter and wider.

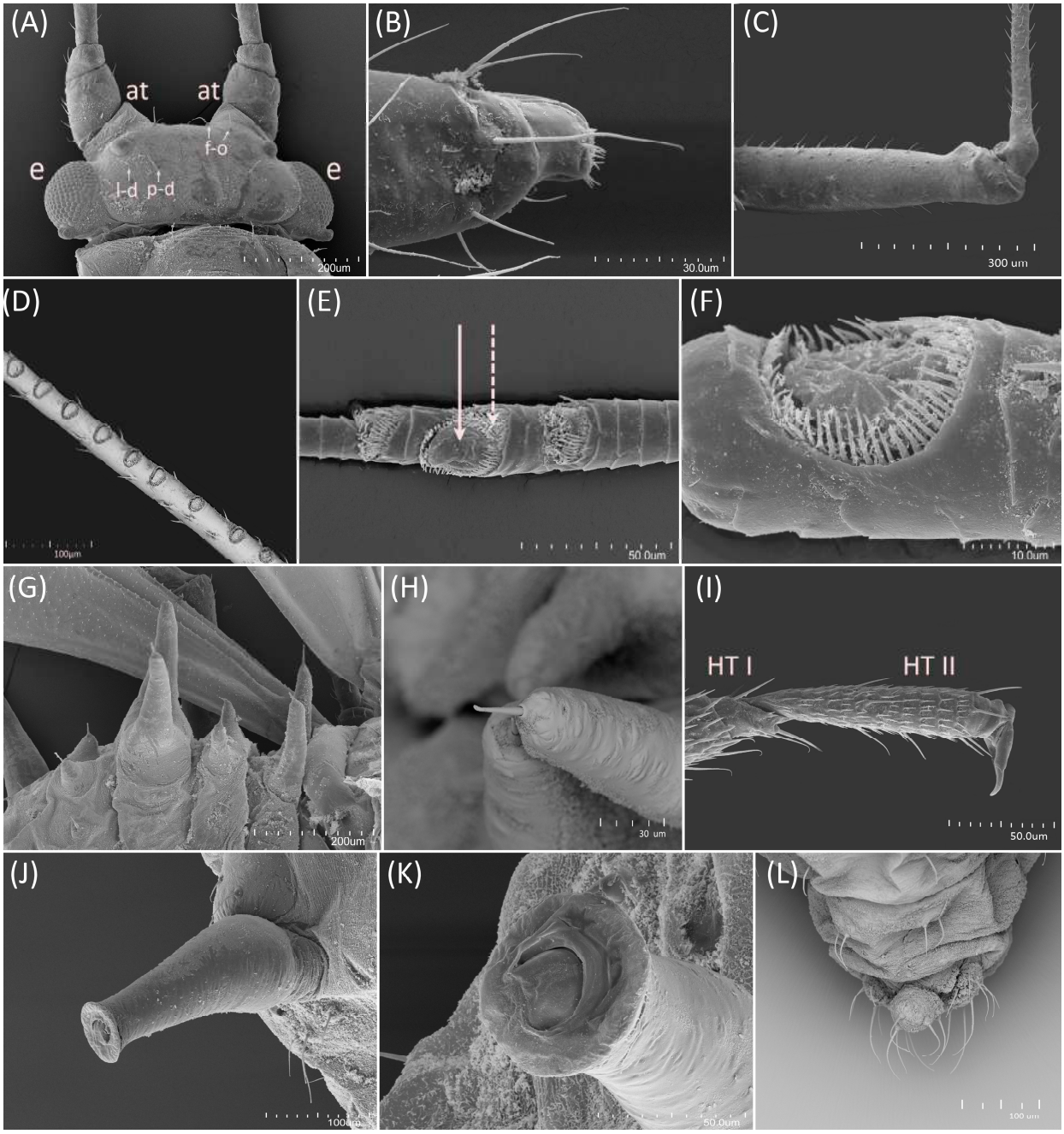

Figure 6. Scanning electron microscopy (SEM) of the most important generic features of the genus *Drepanaphis* on the basis of the type species *D. acerifoliae*: (**A**) dorsal view of head showing compound eyes (e), little-developed antennal tubercles (at), fronto-orbital setae (f-o), postero-dorsal head setae (p-d) and latero-dorsal head setae (l-d); (**B**) ultimate rostral segments with trichoid sensilla (solid arrow), apex of rostrum with basiconic sensilla (dotted arrow); (**C**) ultrastructure of fore femora; (**D**) ANT III with secondary rounded and ciliated rhinaria; (**E**) ANT VI sensilla, big multiporous placoid sensillum: primary rhinarium (solid arrow) and sunken coeloconic sensilla: accessory rhinaria (dotted arrow); (**F**) apical part of ANT V with big multiporous placoid sensillum; (**G**) arrangement of dorsal tubercles on abdomen; (**H**) basiconic sensilla at the end of tubercles; (**I**) hind tarsus with short first segment (HT I) and longer second segment (HT II) with claws; (**J**) lateral side of end of abdomen with siphunculus (SIPH); (**K**) apical part of siphunculus with wide flange; (**L**) dorsal side of end of abdomen with knobbed cauda.

3.2. Keys to Species of the Genus Drepanaphis

3.2.1. Key to the Identification of Alate Viviparous Females of the Genus *Drepanaphis*

1. Femur I pigmented for its full length, especially dorsally (Figure 4A,B,G–I,M,P) 2
- Femur I pale, slightly pigmented basally (Figure 4C–F,J–L,N,O,Q,R) 8
2. Wing veins distinctly bordered (Figure 7A) 3
- Wing veins clear (Figure 7B). 4
3. Conspicuous four pairs of dorsal abdominal tubercles. ABD I pale at base and darker at tips, ABD II pale, ABD III–IV dark brown; third pairs of tubercles biggest (Figure 1A) . . . . . *D. acerifoliae*
- Conspicuous one pair of dark brown dorsal abdominal tubercles on tergite III (Figure 1G) . . . . . *D. keshenae*
4. Conspicuous four pairs of dorsal abdominal tubercles. 5
- Conspicuous one pair of dorsal abdominal tubercles on tergite III. 6
5. First and second pair of dorsal abdominal tubercles equal, third pair biggest, fourth pair smallest (Figure 1B); BASE with 4 accessory rhinaria; ANT III with 9–15 secondary rhinaria . . . . . *D. carolinensis*
- Second and third pairs of dorsal abdominal tubercles equal, first and fourth pairs smallest (Figure 1M); BASE with 5–6 accessory rhinaria (Figure 2C); ANT III with 6–10 secondary rhinaria. . . . . *D. sabrinae*
6. Fore femora > 0.8 mm long, frontal setae 0.09–0.12 mm long. . . . . *D. spicata*
- Fore femora < 0.8 mm long, frontal setae > 0.09 mm long. 7
7. Fore femora dark (Figure 4I), BASE always with four accessory rhinaria, on *Aesculus glabra*. . . . . *D. monelli*
- Fore femora darker dorsally (Figure 4H), BASE with four or five accessory rhinaria, on *Acer grandidentatum*. . . . . *D. knowltoni*
8. Wing veins diffusely bordered (Figure 7C). 9
- Wing veins clear (Figure 7B). 10
9. BL > 1.85 mm long; body with brown dorsal sclerotisation; SIPH shaded or dark (Figure 5K) . . . . . *D. parva*
- BL < 1.85 mm long; body without brown dorsal sclerotisation; SIPH pale (Figure 5L) . . . . . *D. robinsoni* sp. nov.
10. Two pairs of frontal setae. 11
- One pair of frontal setae. 13
11. Conspicuous one pair of dorsal abdominal tubercles on tergite III (Figure 1R) . . . . . *D. utahensis*
- Conspicuous more than one pair of dorsal abdominal tubercles. 12
12. Entire body pale; DAT I–III short, first pair larger than second and third (Figure 1D) . . . . . *D. granovskyi*
- DAT I biggest, darker than others (Figure 1O). . . . . *D. simpsoni*
13. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation; SIPH completely dark; dorsal setae blunt. 14
- Pterostigma palely pigmented with large area inside without pigmentation, SIPH shaded or pale, dorsal setae pointed. 17

14. BASE with more than four accessory rhinaria. 15
- BASE with four accessory rhinaria. 16
15. ANT III with 2–5 secondary rhinaria, frontal setae 0.06–0.08 mm long, dorsal setae 0.03–0.05 mm long . . . .*D. choanotricha*
- ANT III with 8–14 secondary rhinaria, frontal setae 0.05–0.06 mm long, dorsal setae 0.01–0.02 mm long. . . . .*D. tissoti*
16. ANT III with 6–9 secondary rhinaria, dorsal setae 0.02–0.04 mm long. . . . .*D. idahoensis*
- ANT III with 12–18 secondary rhinaria, dorsal setae 0.01–0.02 mm long. . .*D. nigricans*
17. Conspicuous four pairs of dorsal abdominal tubercles (Figure 1N). . . . . .*D. saccharini*
- Conspicuous three pairs of dorsal abdominal tubercles, on ABD III biggest, on DAT II and IV very small (Figure 1F). . . . . .*D. kanzensis*

3.2.2. Key to the Identification of Known Oviparous Females of the Genus *Drepanaphis*

1. BASE with more than four accessory rhinaria. 2
- BASE with four accessory rhinaria. 4
2. ANT segment ratio PT/BASE < 12; >70 pseudosensoria on hind tibiae; legs and antennae very dark, siphunculi tubular. . . . .*D. sabrinae*
- ANT segment ratio PT/BASE > 12, siphunculi flask-shaped. 3
3. ANT III > 0.9 mm long; > 30 pseudosensoria; SIPH/BL 0.07–0.09. . . . . .*D. tissoti*
- ANT III < 0.9 mm long; < 30 pseudosensoria; SIPH/BL 0.12. . . . . .*D. choanotricha*
4. Two pairs of frontal setae. 5
- One pair of frontal setae. 7
5. ANT III < 0.05 mm long; dorsal setae evidently forked. . . . . .*D. granovskyi*
- ANT III > 0.05 mm long. 6
6. URS/ANT III < 0.13 mm long. . . . .*D. utahensis*
- URS/ANT III > 0.13 mm long. . . . .*D. simpsoni*
7. Legs and SIPH dark. 8
- Legs and SIPH pale. 11
8. SIPH/BL > 0.09; HT II/ANT VI < 0.1. . . . .*D. monelli*
- SIPH/BL < 0.09; HT II/ANT VI > 0.1 9
9. URS/BASE < 0.07 . . . . . .*D. carolinensis*
- URS/BASE > 0.07 10
10. ANT > 2.6 mm long; SIPH > 0.2 mm long . . . . . .*D. acerifoliae*
- ANT < 2.6 mm long; SIPH < 0.2 mm long . . . . . .*D. keshenae*
11. ANT segment ratio PT/BASE > 12 . . . . . .*D. nigricans*
- ANT segment ratio PT/BASE < 12 12
12. SIPH/BL < 0.08; URS < 0.09 . . . . . .*D. kanzensis*
- SIPH/BL > 0.08; URS > 0.09 13
13. ANT segment ratio VI/III < 1; 22–23 pseudosensoria . . . . . .*D. idahoensis*
- ANT segment ratio VI/III > 1; 59–71 pseudosensoria . . . . . .*D. spicata*

3.2.3. Key to the Identification of Known Alate Males of the Genus *Drepanaphis*

1. Femur I pigmented for its entire length, two pairs of frontal setae, dorsal abdominal tubercles inconspicuous . . . . . *D. granovskyi*
- Femur I pigmented dorsally 2
- Femur I pale, slightly pigmented basally 7
2. Wing veins distinctly bordered, conspicuous one pair of dorsal abdominal tubercles on tergite III 3
- Wing veins clear 4
3. Hind tibiae with dark area in apical part; PT/BASE < 0.09 . . . . . *D. acerifoliae*
- Hind tibiae pale; PT/BASE > 0.09 . . . . . *D. keshenae*
4. Dorsal abdominal tubercles inconspicuous, BL 2.8 mm long . . . . . *D. spicata*
- Conspicuous one pair of dorsal abdominal tubercles on tergite III 5
5. URS/ANT III > 0.12 . . . . . *D. monelli*
- URS/ANT III < 0.12 6
6. ANT III with > 80 rhinaria, hind tibiae < 1.2 mm long; SIPH < 0.25 . . . . . *D. carolinensis*
- ANT III with < 80 rhinaria, hind tibiae > 1.2 mm long; SIPH > 0.25 . . . . . *D. knowltoni*
7. Conspicuous more than one pair of dorsal abdominal tubercles, wing veins diffusely bordered, body with brown dorsal sclerotisation . . . . . *D. parva*
- Wing veins clear. 8
8. Dorsal abdominal tubercles inconspicuous, two pairs of frontal setae. 9
- Conspicuous one pair of dorsal abdominal tubercles on tergite III. 10
9. ANT segment ratio PT/BASE < 6; SIPH/BL < 0.09. . . . . *D. simpsoni*
- ANT segment ratio PT/BASE > 6; SIPH/BL > 0.09. . . . . *D. utahensis*
10. ANT segment ratio PT/BASE > 6; SIPH pale. . . . . *D. kanzensis*
- ANT segment ratio PT/BASE < 6; SIPH dark.. . . . . *D. choanotricha*

3.3. Checklist of Species in the Genus Drepanaphis

Family: Aphididae Latreille, 1802
Subfamily: Drepanosiphinae Herrich-Schaeffer, 1857
Genus: *Drepanaphis* Del Guercio, 1909
Drepanaphis Del Guercio, 1909: 4: 49
= *Phymatosiphum* Davis, 1909: 2: 196
= *Drepanphis* Takahashi, 1923: 4: 66 (subsequent misspelling)
1. *Drepanaphis acerifoliae* (Thomas, 1878)
2. *Drepanaphis carolinensis Smith*, 1941
3. *Drepanaphis choanotricha* Smith & Dillery, 1968
4. *Drepanaphis granovskyi* Smith & Knowlton, 1943
5. *Drepanaphis idahoensis* Smith & Dillery, 1968
6. *Drepanaphis kanzensis* Smith, 1941
7. *Drepanaphis keshenae* Granovsky, 1931
8. *Drepanaphis knowltoni* Smith & Dillery, 1968
9. *Drepanaphis monelli* (Davis, 1909)
10. *Drepanaphis nigricans* Smith, 1941
11. *Drepanaphis parva* Smith, 1941
12. *Drepanaphis robinsoni* Malik sp. nov.
13. *Drepanaphis sabrinae* Miller, 1937
14. *Drepanaphis saccharini* Smith & Dillery, 1968

15. *Drepanaphis simpsoni* Smith, 1959
16. *Drepanaphis spicata* Smith, 1941
17. *Drepanaphis tissoti* Smith, 1941 stat. rev.
18. *Drepanaphis utahensis* Smith & Knowlton, 1943

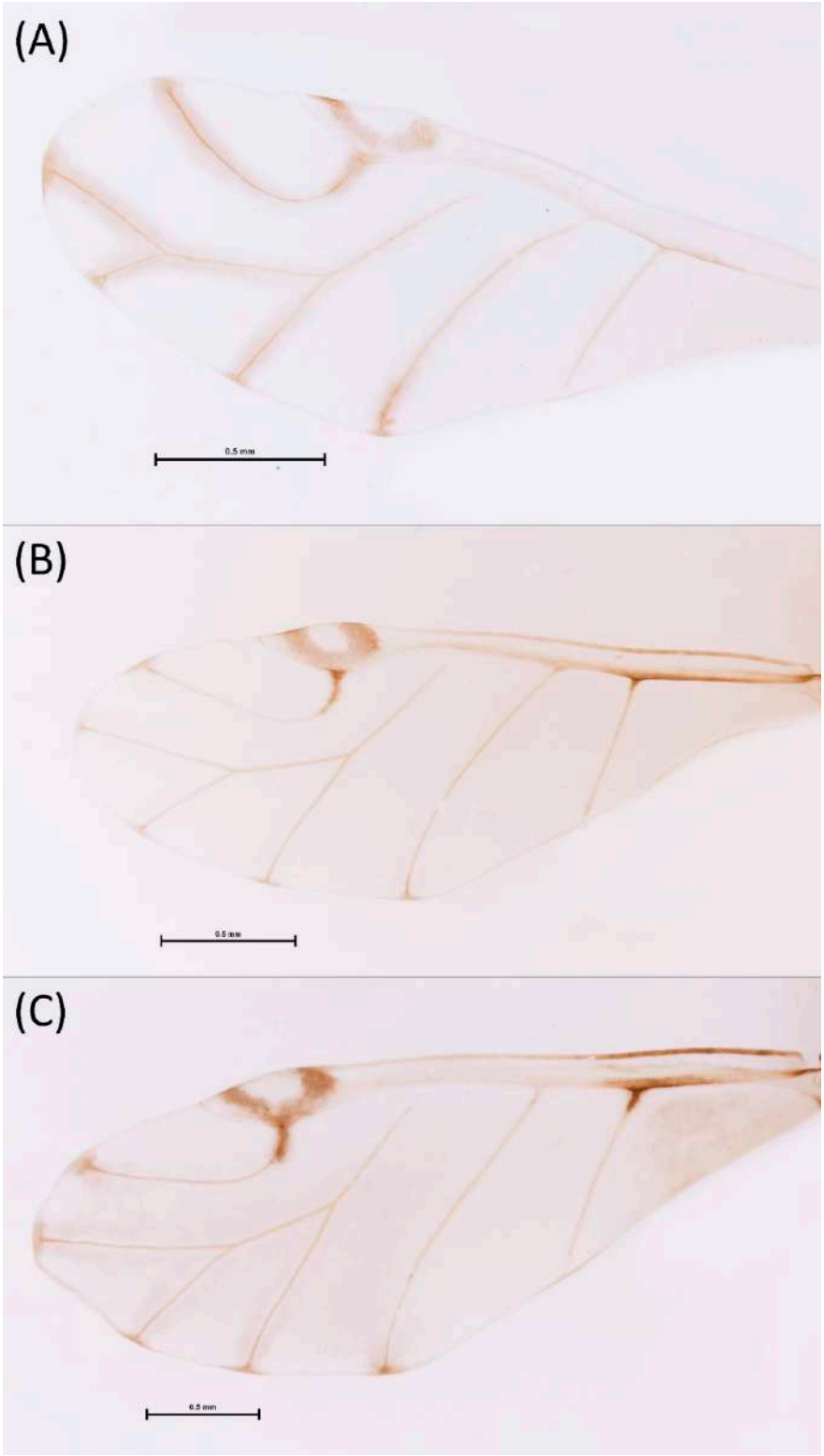

Figure 7. Wing pigmentation: (**A**) wing veins distinctly bordered in *D. acerifoliae*, (**B**) wing veins clear in *D. carolinensis*, (**C**) wing veins diffusely bordered in *D. parva*.

3.4. Review of Species

3.4.1. *Drepanaphis acerifoliae* (Thomas, 1878)

Type species *Siphonophora acerifoliae* Thomas, 1878 by original designation
Type species *Siphonophora acerifoliae* Thomas, 1878 by original designation
= *Siphonophora acerifoliae* Thomas, 1878: 1(2): 4 [17]
= *Siphonophora acericola* Thomas, 1878: 1(2): plate 1 (subsequent misspelling) [17]
= *Drepanosiphum acerifolii* Monell, 1879: 5(1): 27 [40]
= *Drepanosiphum acerifoliae* Davidson, 1909: 2(4): 303 [41]
Drepanaphis acerifoliae Del Guercio, 1909: 2 4(4): 50 [16]
= *Drepanaphis acerifolii* Davis, 1910: 3(5): 419 (subsequent misspelling) [42]
= *Drepanaphis allegheneyensis* Miller, 1936: 68: 81 [43]
Figures 1A, 2A, 3A, 4A, 5A, 7A, 8A, 9A, 10A, 11A, 11A, 12A, 13A, 14A and 15; Tables 1–3

Table 1. Measurements (in mm) of alate viviparous females of *Drepanaphis* (part 1).

Character	*D. acerifoliae* n = 26	*D. carolinensis* n = 16	*D. choanotricha* n = 13	*D. granovskyi* n = 13	*D. idahoensis* n = 10	*D. kanzensis* n = 17	*D. keshenae* n = 11	*D. knowltoni* n = 24	*D. monelli* n = 11
BL	1.55–2.68	1.57–2.5	1.15–1.63	1.37–2.21	1.41–2.19	1.24–2.83	1.05–2.43	1.4–2.46	1.58–2.46
HW	0.28–0.4	0.28–0.39	0.2–0.27	0.21–0.31	0.22–0.3	0.2–0.38	0.25–0.35	0.25–0.35	0.28–0.35
ANT I-VI	3.19–5.29	3.02–4.11	2.04–4.1	1.77–2.94	3.17–4.68	3.26–4.7	3–4.75	3.54–4.8	3.34–4.76
ANT III	0.71–1.11	0.75–1.01	0.56–0.76	0.53–0.77	0.82–1.03	0.77–1.17	0.7–1.1	0.68–1.16	0.83–1.1
ANT IV	0.47–0.90	0.53–0.73	0.36–0.6	0.32–0.52	0.65–0.79	0.51–0.9	0.45–0.86	0.49–0.8	0.67–0.8
ANT V	0.5–0.87	0.53–0.7	0.41–0.57	0.32–0.53	0.62–0.92	0.51–0.87	0.47–0.85	0.49–0.85	0.66–0.8
ANT VI	1.06–1.76	0.71–1.36	1.35–2.11	0.44–1.03	0.83–1.88	0.97–2	1.04–1.8	1.3–2.1	0.97–2.06
BASE	0.11–0.16	0.13–0.18	0.11–0.14	0.08–0.14	0.12–0.17	0.12–0.19	0.1–0.15	0.11–0.17	0.14–0.16
PT	0.94–1.61	0.53–1.21	1.21–1.99	0.35–0.9	0.70–1.72	0.82–1.84	0.93–1.66	1.16–1.94	0.83–1.92
FEMUR I length	0.51–0.85	0.54–0.72	0.31–0.54	0.34–0.59	0.54–0.79	0.53–0.78	0.47–0.79	0.48–0.87	0.62–0.77
FEMUR I width	0.11–0.18	0.1–0.15	0.05–0.08	0.09–0.15	0.1–0.13	0.09–0.37	0.1–0.15	0.1–0.16	0.1–0.16
FEMUR III	0.42–0.76	0.43–0.65	0.31–0.48	0.31–0.54	0.49–0.7	0.45–0.80	0.37–0.66	0.41–0.8	0.52–0.7
TIBIA III	0.84–1.54	0.96–1.28	0.71–0.99	0.65–1.1	1.1–1.40	1–1.5	0.9–1.40	1–1.69	1.2–1.4
HT II	0.07–0.14	0.09–0.14	0.08–0.09	0.07–0.12	0.08–0.12	0.1–0.13	0.08–0.12	0.09–0.12	0.09–0.11
URS	0.09–0.11	0.09–0.10	0.09–0.1	0.07–0.09	0.08–0.10	0.08–0.1	0.08–0.09	0.07–0.1	0.1–0.12
SIPH	0.17–0.38	0.16–0.26	0.12–0.19	0.13–0.24	0.18–0.28	0.15–0.26	0.14–0.3	0.2–0.39	0.21–0.3
CAUDA	0.08–0.13	0.09–0.17	0.04–0.08	0.09–0.14	0.09–0.12	0.09–0.18	0.07–0.13	0.07–0.13	0.09–0.18

Material examined: Paratype. Siphonophora acerifoliae Thomas, 757, Ft. Dodge, Iowa, Dubuque, Iowa, Peoria, Ill. Sept. I, 1887, SI. 7169, Ill. Nat.Hist. Sur.//Aphididae, Drepanaphis acerifoliae Thomas, See slide by Davis, Det. F. C. Hottes, Ill. Nat. Hist. Sur.//PARATYPE, Siphonophora acerifoliae Thomas//INHS Insect Collection 1058753—15 alate viv. fem. [INHS]. Lectotype. Aphididae, Drepanaphis acerifoliae (Thomas), acerifolae, Ft. Dodge + Dubuque, Iowa, also Peoria, Ill., 757, Sept. I, 1897, Det. F.C. Hottes, Ill. Nat. Hist Sur. '28, SI 7168//Lecto-type, Siphonophora acerifoliae Thomas, Viviparous ♀♀//INHS, Insect Collection 457903—five alate viv. fem. [INHS].
Additional material examined—Table S6.

Alate viviparous female—re-description (n = 26)
Colour. In life: Head and thorax brown to dark brown with white wax stripes. Eyes

red. Antennae pale with dark apices of ANT III–V. Fore femora darker than middle and hind femora, dark brown dorsally. Middle and hind femora pale brown to brown. Tibiae pale brown. Wing veins dark bordered, pterostigma dark brown. Abdomen covered by white wax dots. Tergites I–V brown, tergites I–II slightly lighter than tergites III–V. Tergites VI–VIII fully covered by wax. Siphunculi dark (Figure 8A).

Table 2. Measurements (in mm) of oviparous females of *Drepanaphis*.

Character	*Drepanaphis*													
	acerifoliae **n = 6**	***carolinensis*** **n = 8**	***choanotricha*** **n = 2**	***granovskyi*** **n = 1**	***idahoensis*** **n = 1**	***kanzensis*** **n = 5**	***keshenae*** **n = 2**	***monelli*** **n = 5**	***nigricans*** **n = 1**	***sabrinae*** **n = 2**	***simpsoni*** **n = 3**	***spicata*** **n = 1**	***tissoti*** **n = 1**	***utahensis*** **n = 5**
BL	2.74–3.08	1.82–2.81	1.77–2	2.15	2.12	2.44–3.32	2.22–2.3	1.99–2.7	2.14	2.42–2.44	2.78–2.85	2.87	2.43	2.64–3.24
HW	0.36–0.41	0.29–0.38	0.28–0.3	0.3	–	0.31–0.4	0.3–0.36	0.28–0.38	0.31	0.35–0.36	0.35–0.38	–	0.3	0.3–0.4
ANT I-VI	2.65–3.1	2.47–2.75	3.29–3.41	1.92–1.96	2.6–2.63	2.17–3.61	1.61–2.55	1.38–1.83	3.62–3.67	3.24–3.37	2.11–.3.3	3.44	3.87–3.92	2.56–3.24
ANT III	0.59–0.7	0.52–0.64	0.61–0.68	0.41–0.44	0.73–0.74	0.7–0.84	0.49–0.51	0.62–0.8	0.71–0.72	0.74–0.8	0.72–0.78	0.86–0.87	0.91	0.52–0.74
ANT IV	0.42–0.53	0.42–0.46	0.41–0.45	0.32–0.33	0.5–0.51	0.51–0.62	0.36–0.42	0.49–0.6	0.47–0.5	0.51–0.58	0.54–0.61	0.66–0.68	0.57–0.58	0.46–0.52
ANT V	0.46–0.58	0.43–0.49	0.47–0.49	0.35	0.58	0.56–0.61	0.41–0.45	0.57–0.64	0.6	0.55–0.59	0.51–0.67	0.66–0.7	0.6	0.5–0.55
ANT VI	0.88–1.2	0.86–1.05	1.59–1.72	0.66–0.75	0.64–0.67	1.18–1.52	0.89–1.06	1.17–1.7	1.65–1.74	1.2–1.31	0.71–1.31	1.02	1.62–1.66	0.9–1.16
BASE	0.12–0.14	0.13–0.15	0.12	0.11	0.12–0.13	0.13–0.15	0.11–0.12	0.13–0.16	0.12–0.13	0.14–0.16	0.12–0.14	0.13	0.12	0.12–0.14
PT	0.75–1.08	0.72–0.91	1.47–1.6	0.55–0.64	0.51–0.55	1.04–1.39	0.78–0.94	1.01–1.55	1.53–1.61	1.06–1.15	0.57–1.19	0.89	1.5–1.54	0.77–1.02
URS	0.1–0.11	0.09–0.1	0.09–0.1	0.08	0.1	0.08–0.09	0.08–0.12	0.11–0.12	0.1	0.12	0.08–0.09	0.1	0.08	0.09–0.1
FEMUR III	0.59–0.65	0.46–0.6	0.5–0.54	0.42–0.45	0.53–0.55	0.64–0.72	0.51–0.52	0.55–0.72	0.55–0.59	0.58–0.59	0.61–0.62	0.68–0.73	0.56–0.57	0.53–0.64
TIBIA III	1.08–1.26	0.91–1.12	0.9–0.95	0.84	1.08–1.09	1.21–1.38	1–.1.03	1.1–1.37	1.1	1.12–1.15	1.12–1.16	1.39–1.41	1.02	1.03–1.23
HT II	0.12–0.13	0.1–0.13	0.09–0.1	0.09	0.09–0.1	0.1–0.13	0.11–0.12	0.11–0.12	0.1	0.11–0.12	0.11–0.12	0.11–0.12	0.09–0.1	0.11–0.12
SIPH	0.2–0.25	0.13–0.19	0.21–0.24	0.17–0.2	0.17–0.19	0.17–0.19	0.14–0.17	0.2–0.27	0.18–0.19	0.2–0.24	0.15–0.18	0.23–0.27	0.18–0.21	0.14–0.21

Table 3. Measurements (in mm) of males of *Drepanaphis*.

Character	*Drepanaphis*											
	acerifoliae **n = 3**	***carolinensis*** **n = 3**	***choanotricha*** **n = 1**	***granovskyi*** **n = 1**	***kanzensis*** **n = 3**	***keshenae*** **n = 4**	***knowltoni*** **n = 2**	***monelli*** **n = 4**	***parva*** **n = 1**	***simpsoni*** **n = 3**	***spicata*** **n = 1**	***utahensis*** **n = 4**
BL	2.09–2.21	1.75–2.26	1.44	1.82	1.85–2.44	1.67–2.11	2.01–2.1	1.96–2.16	2.48	1.62–2.19	2.82	1.7–2.47
HW	0.33–0.38	0.33–0.37	0.24	0.28	0.33–0.37	0.33–0.34	0.28–0.34	0.3–0.35	–	0.28–0.36	0.38	0.27–0.35
ANT I-VI	2.33–3.5	2.82–3.51	3.37–3.4	1.74–1.75	3.04–3.89	3.37–3.81	3.45–3.97	3.73–4.28	4.54–4.79	2.39–3.04	4.97–5.48	2.74–3.2
ANT III	0.72–0.94	0.73–1	0.69–0.71	0.71–0.73	0.86–1.05	0.77–1.05	0.92–1.0	0.96–1.02	1.12–1.1	0.66–0.87	1.27–1.29	0.75–0.82
ANT IV	0.59–0.64	0.5–0.67	0.43–0.44	0.41–0.42	0.53–0.71	0.53–0.64	0.6–0.64	0.66–0.78	0.79–0.81	0.47–0.63	0.98–1.0	0.46–0.62
ANT V	0.55–0.65	0.42–0.61	0.41–0.43	0.37–0.38	0.48–0.66	0.51–0.6	0.63–0.65	0.63–0.75	0.8–0.82	0.37–0.49	0.94	0.47–0.58
ANT VI	1.21	1.01–1.08	1.67–1.73	–	0.96–1.73	1.28–1.49	1.03–1.64	1.3–1.68	1.65–1.88	0.73–0.9	1.57–2.04	0.9–1.14
BASE	0.13–0.14	0.12–0.15	0.12	0.1–0.11	0.12–0.13	0.11–0.13	0.13–0.14	0.13–0.16	0.13	0.11–0.14	0.15	0.12–0.14
PT	1.08	0.88–0.95	1.55–1.61	–	0.83–1.61	1.17–1.36	0.89–1.51	1.15–1.55	1.52–1.75	0.62–0.76	1.42–1.89	0.78–1.0
URS	0.09	0.08–0.09	0.09	0.08	0.08	0.09–0.13	0.09–0.1	0.11–0.12	0.09	0.08–0.09	0.11	0.09
FEMUR III	0.55–0.63	0.46–0.63	0.41–0.44	–	0.56–0.7	0.49–0.65	0.58–0.65	0.63–0.67	0.73–0.74	0.43–0.59	0.82	0.48–0.64
TIBIA III	1.14–1.28	1.01–1.2	0.83–0.85	–	1.1–1.35	1.01–1.32	1.24–1.37	1.23–1.41	1.52	0.81–1.09	1.75	1.06–1.27
HT II	0.09–0.12	0.1–0.12	0.09	–	0.1–0.12	0.1–0.11	0.1–0.11	0.1–0.12	0.12	0.1–0.11	0.12	0.1–0.12
SIPH	0.23–0.27	0.16–0.23	0.17	0.16–0.17	0.19–0.23	0.17–0.28	0.25–0.26	0.25–0.28	0.19–0.23	0.15–0.16	0.39–0.4	0.17–0.23

Pigmentation of mounted specimens: Head and pronotum brown, rest of thorax dark brown (Figure 9A). ANT I–II brown, ANT III–VI pale brown with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation (Figure 3A). Wing veins brown bordered (Figure 7A). Abdomen pale brown, marginal sclerites dark brown. DAT I pale at base, darker at tips; DAT II pale; DAT III–IV dark brown (Figure 1A). Siphunculi brown to dark brown; cauda, subgenital and anal plate pale. Fore femora darker dorsally (Figure 4A). Middle and hind femora brown with dark brown smudge. Tibiae brown with darker distal parts. Tarsi dark brown.

Figure 8. Live specimens of the genus Drepanaphis: (**A**) *D. acerifoliae*, (**B**) *D. carolinensis*, (**C**) *D. keshenae*. Image copyright V. Charny, under a Creative Commons 3.0 License.

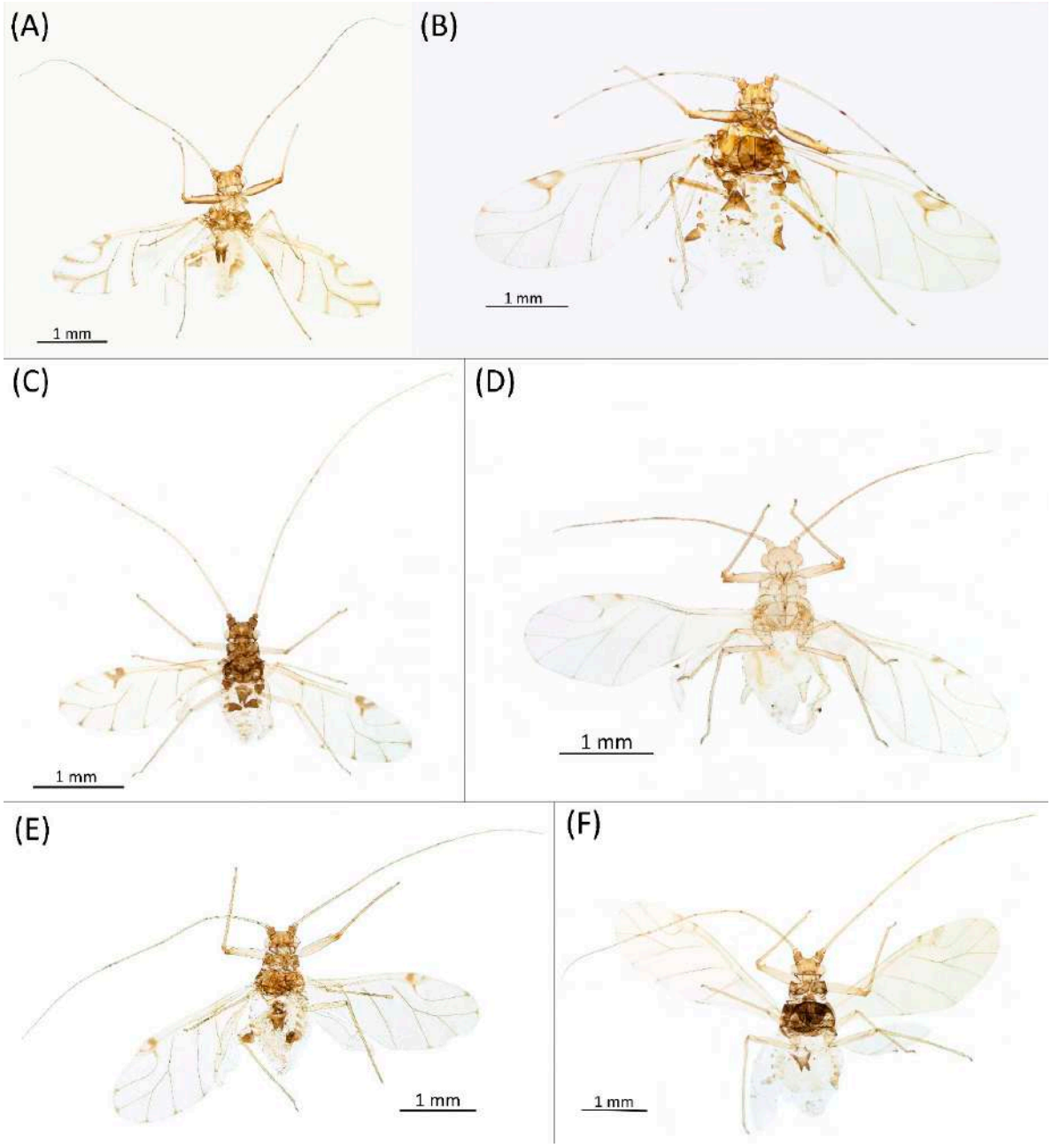

Figure 9. Alate viviparous females of the genus Drepanaphis: (**A**) *D. acerifoliae*, (**B**) *D. carolinensis*, (**C**) *D. choanotricha*, (**D**) *D. granovskyi*, (**E**) *D. idahoensis*, (**F**) *D. kanzensis*.

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.04–0.05 mm long with pointed apices, one pair of pointed frontal setae on ventral side 0.09–0.1 mm long. ANT/BL 1.57–2.26; ANT/HW 9.23–13.74; PT/BASE 6.93–12.02. ANT III with 9–14 secondary rhinaria, BASE with 4 accessory rhinaria (Figure 2A), URS with 4–8 accessory setae (Figure 10A). Other ratios: ANT IV/ANT III 0.64–0.85; ANT V/ANT III 0.64–0.83; ANT VI/ANT III 1.12–1.74; URS/ANT III 0.08–0.13; URS/BASE 0.59–0.88; URS/SIPH 0.25–0.52; HT II/ANT III 0.09–0.14; HT II/BASE 0.62–0.9; TIBIA III/BL 0.49–0.73; SIPH/BL 0.1–0.15; SIPH/CAUDA 1.5–2.9. Dorsal abdominal segments with four pairs of distinct tubercles. DAT I 0.14–0.28 mm long, DAT II 0.07–0.14 mm long. DAT III largest, 0.23–0.37 mm long (Figure 11A). DAT IV smallest, 0.04–0.06 mm long. Pointed setae at ends of tubercles, 0.02–0.03 mm long. Dorsal setae with pointed apices, 0.04–0.06 mm long, on small sclerites on ABD I–V. Marginal sclerites with 3–10 setae. Siphunculi flask-shaped (Figure 5A).

Figure 10. Ultimate rostral segments with trichoid sensilla of selected species of the genus Drepanaphis: (**A**) *D. acerifoliae*, (**B**) *D. monelli*, (**C**) *D. utahensis*.

Oviparous female—re-description (n = 6)

Colour. In life: Head, thorax and abdomen reddish brown. Last segments of abdomen slightly darker. Marginal sclerites dark brown. Eyes red. Antennae dark brown. Siphunculi dark with lighter area on bases. Femora dark dorsally [10].

Pigmentation of mounted specimens: Head brown, pronotum pale brown. ANT brown to dark brown with darker apices of segments. Cauda, subgenital and anal plate pale. Femora, tarsi and siphunculi brown. Tibiae dark brown with darker knee areas and distal parts. Abdominal sclerites brown (Figure 12A).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, 0.1–0.12 mm long; one pair of latero-dorsal setae, one pair of postero-dorsal setae, 0.05–0.06 mm long with blunt apices on dorsal side; one pair of pointed frontal setae on ventral side, 0.1 mm long. ANT/BL 0.93–1.04. Other ratios: ANT VI/ANT III 1.28–1.83; PT/BASE 5.77–9.0; SIPH/BL 0.07–0.08; FEMUR III/BL 0.2–0.22; TIBIA III/BL 0.37–0.43; HT II/ANT VI 0.11–0.14; URS/ANT III 0.14–0.17; URS/BASE 0.71–0.92; URS/SIPH 0.44–0.5. ANT III without secondary rhinaria. URS with 4–8 accessory setae. Hind tibiae with 50–110 pseudosensoriae distributed along almost their entire lengths. Dorsal setae 0.07–0.14 mm long. Pleural and spinal setae on ABD I–V, placed on small dark sclerites. Marginal sclerites on ABD I–V bigger. Siphunculi tubular.

Alate male—re-description (n = 3)

Colour. In life: Head and thorax brown to dark brown with white wax stripes. Eyes red. Antennae pale with dark apices of segments. Wing veins dark brown bordered. Abdomen covered by white wax dots. ABD I–II and VI–VII more intensively covered by wax. Siphunculi dark. Femora pale brown. Tibiae pale brown with darker knee areas.

Pigmentation of mounted specimens: Head brown, thorax dark brown. Abdomen pale with brown spinal and marginal sclerites. ANT dark brown with darker apices of segments. ANT III slightly lighter at base. Wing veins brown bordered. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation. Dorsal abdominal tubercles and

siphunculi dark brown. Cauda and anal plate pale. Fore femora brown, darker dorsally. Middle and hind femora brown with dark brown smudge. Tibiae brown with darker knee areas and distal parts. Tarsi brown (Figure 13A).

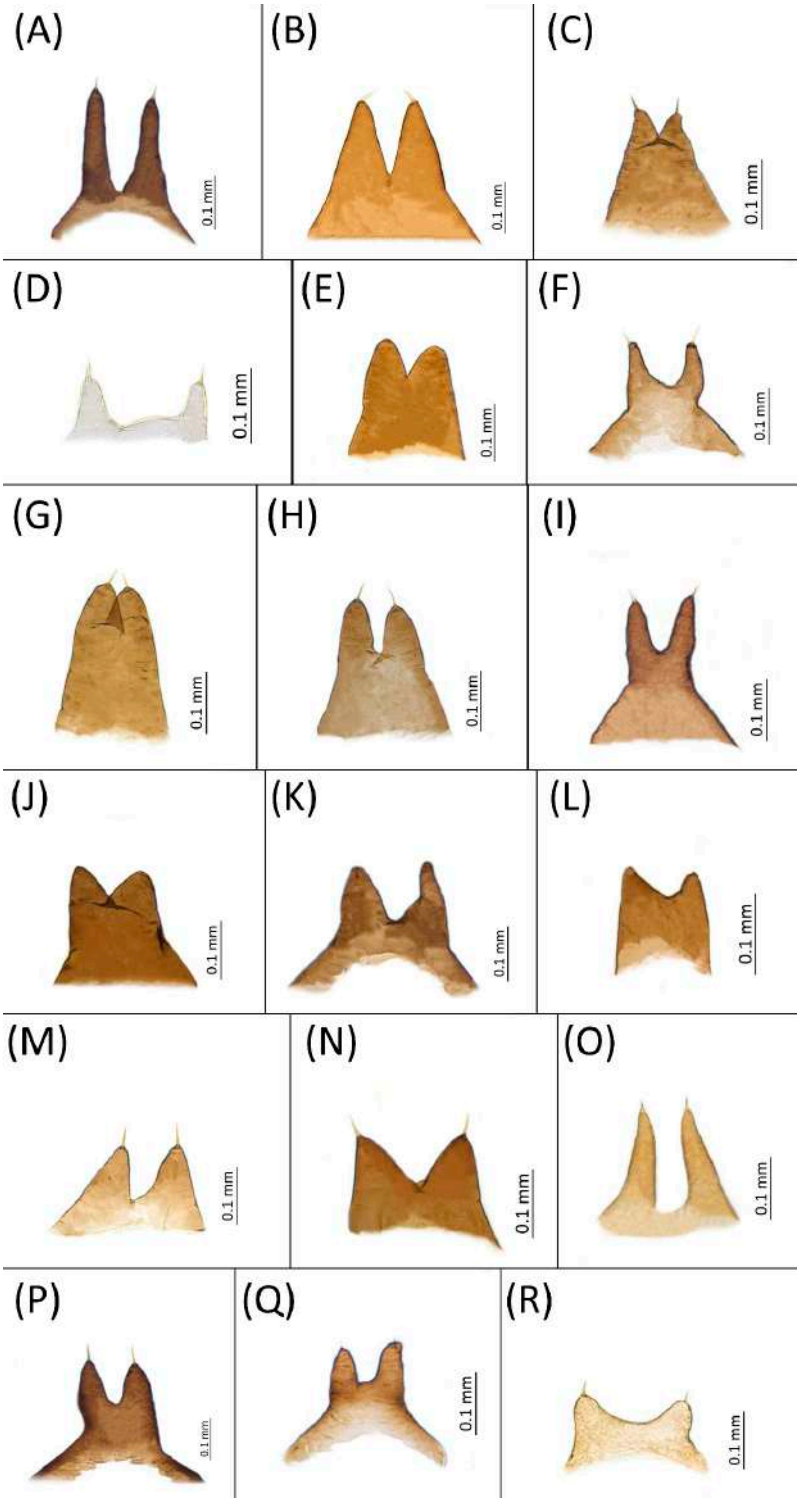

Figure 11. Shape of the third pair of dorsal abdominal tubercles of alate viviparous females of the genus Drepanaphis: (**A**) *D. acerifoliae*, (**B**) *D. carolinensis*, (**C**) *D. choanotricha*, (**D**) *D. granovskyi*, (**E**) *D. idahoensis*, (**F**) *D. kanzensis*, (**G**) *D. keshenae*, (**H**) *D. knowltoni*, (**I**) *D. monelli*, (**J**) *D. nigricans*, (**K**) *D. parva*, (**L**) *D. robinsoni sp. nov.*, (**M**) *D. sabrinae*, (**N**) *D. saccharini*, (**O**) *D. simpsoni*, (**P**) *D. spicata*, (**Q**) *D. tissoti*, (**R**) *D. utahensis*.

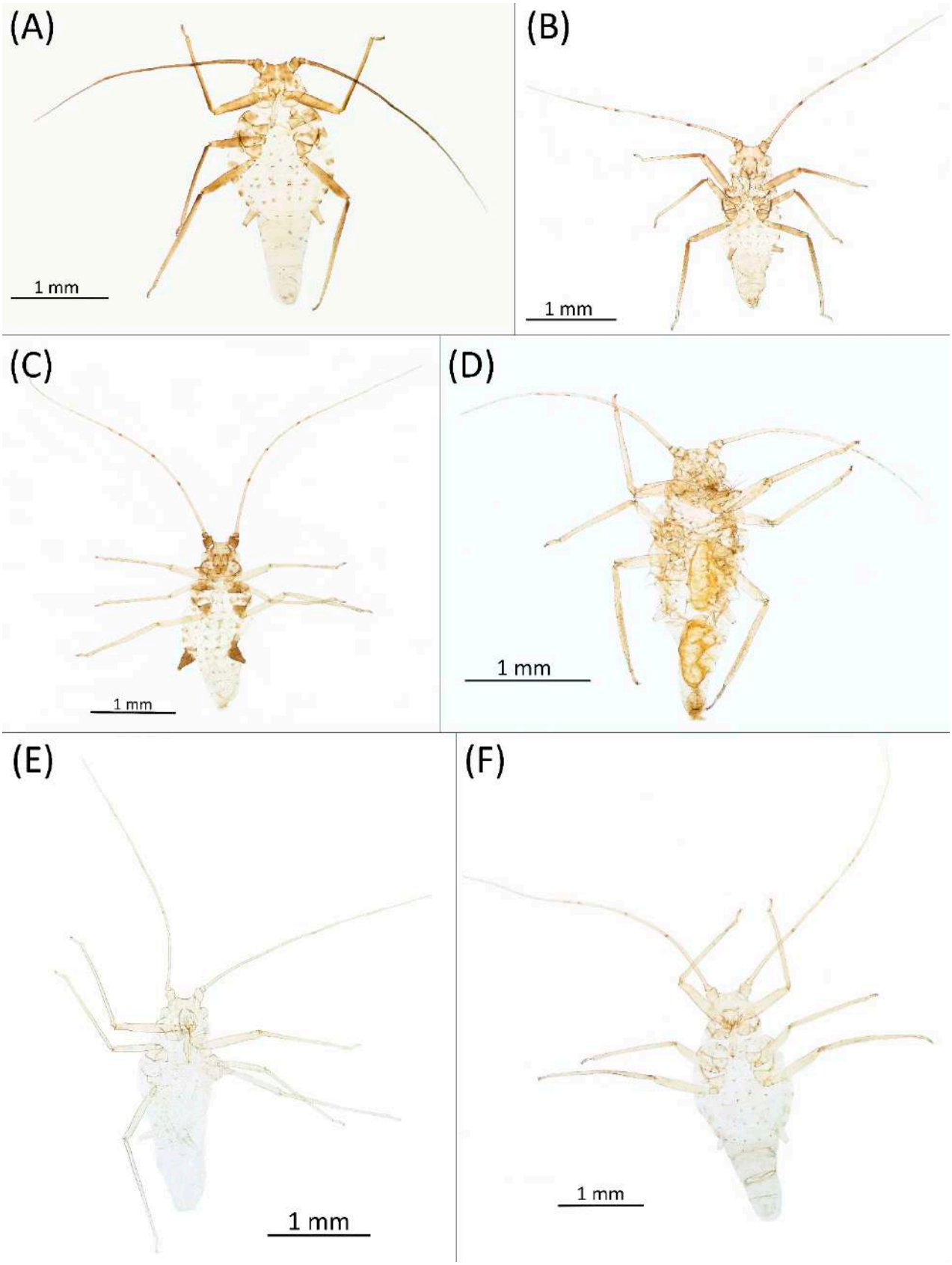

Figure 12. Oviparous females of the genus Drepanaphis: (**A**) *D. acerifoliae*, (**B**) *D. carolinensis*, (**C**) *D. choanotricha*, (**D**) *D. granovskyi*, (**E**) *D. idahoensis*, (**F**) *D. kanzensis*.

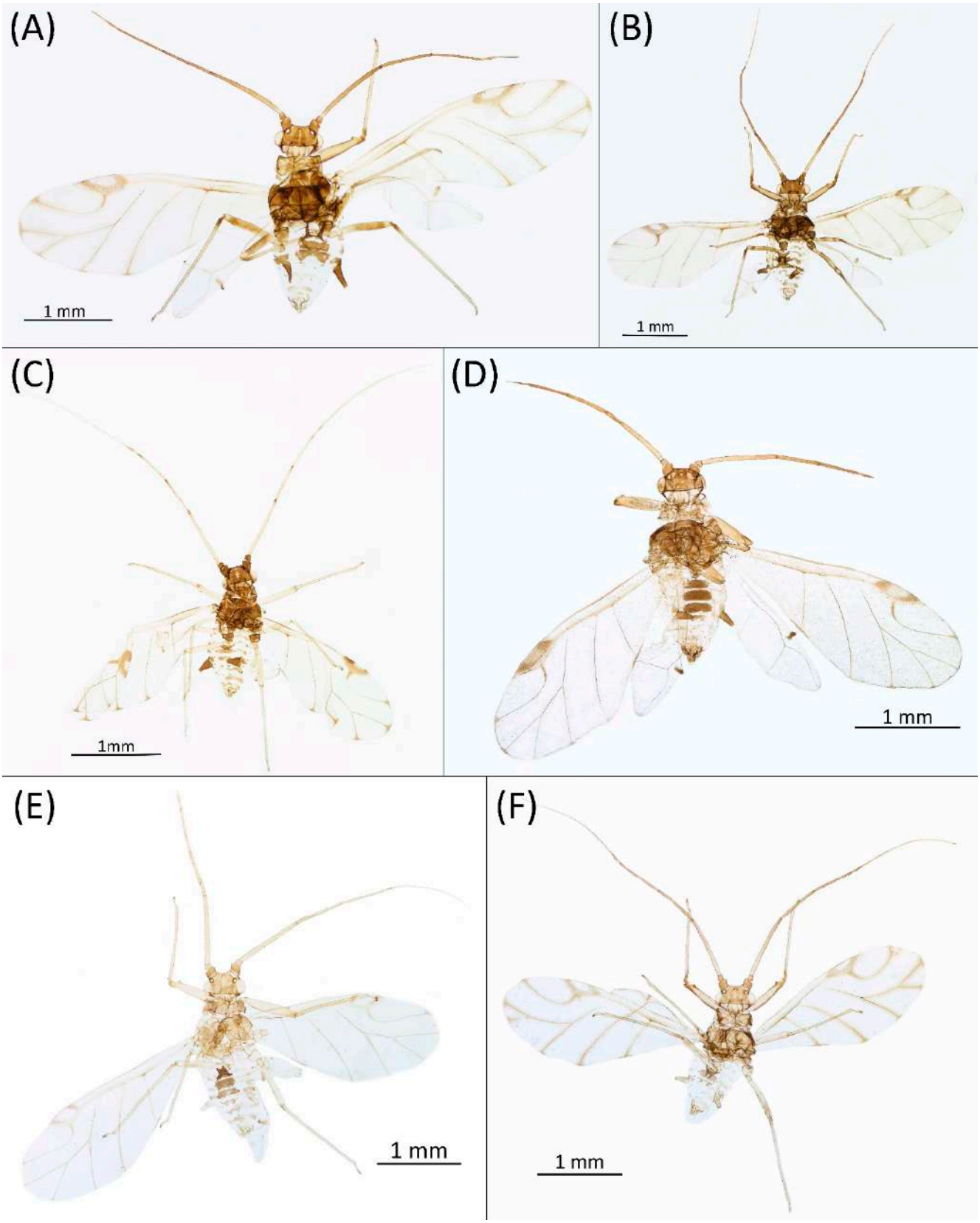

Figure 13. Alate males of the genus Drepanaphis: (**A**) *D. acerifoliae*, (**B**) *D. carolinensis*, (**C**) *D. choanotricha*, (**D**) *D. granovskyi*, (**E**) *D. kanzensis*, (**F**) *D. keshenae*.

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.03–0.05 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.07 mm long. ANT/BL 1.58. Other ratios: ANT VI/ANT III 1.4; PT/BASE 8.3; SIPH/BL 0.1–0.13; FEMUR III/BL 0.26–0.3; TIBIA III/BL 0.54–0.61; URS/ANT III 0.1–0.13; URS/SIPH 0.33–0.39. ANT III with 80–100 rhinaria, ANT IV with 38–50 rhinaria, ANT V with 17–21 rhinaria. URS with 6–8 accessory setae. DAT I inconspicuous or very small, 0.05–0.07 mm long. DAT III distinct, 0.15–0.18 mm long with setae 0.03 mm long at end. Dorsal setae 0.03–0.05 mm long, on small sclerites, bigger on ABD II–V. ABD IV–V with two spinal sclerites, each with two setae 0.03–0.04 mm long. Marginal sclerites with 3–10 setae 0.03–0.05 mm long. Siphunculi flask-shaped. Genitalia with basal part of phallus elongated, with broadly rounded apices (Figure 14A).

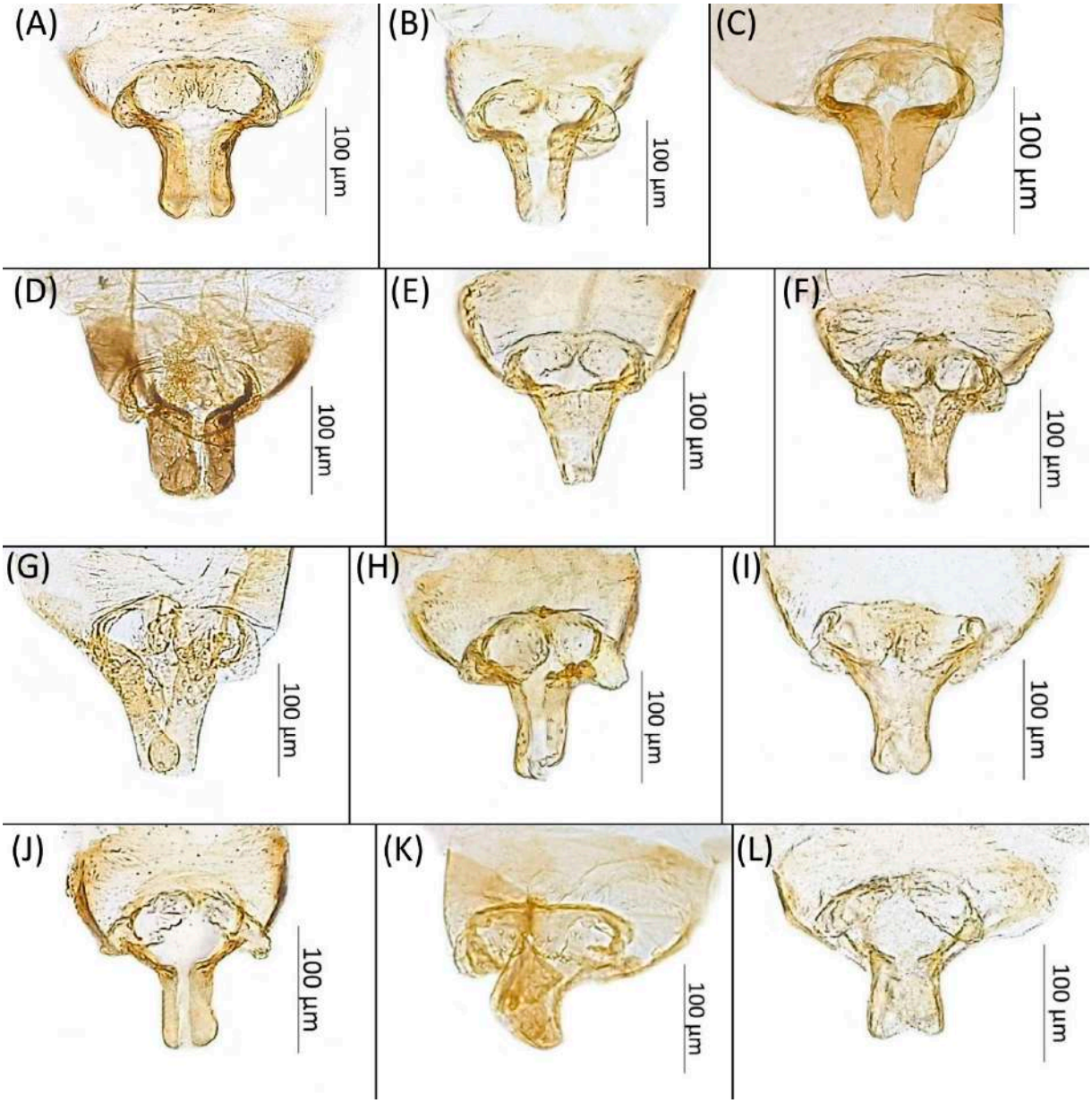

Figure 14. Genitalia of the known males of the genus Drepanaphis: (**A**) *D. acerifoliae*, (**B**) *D. carolinensis*, (**C**) *D. choanotricha*, (**D**) *D. granovskyi*, (**E**) *D. kanzensis*, (**F**) *D. keshenae*, (**G**) *D. knowltoni*, (**H**) *D. monelli*, (**I**) *D. parva*, (**J**) *D. simpsoni*, (**K**) *D. spicata*, (**L**) *D. utahensis*.

Remarks: The locus typicus is not designated since the type slides bear three locality names—Fort Dodge and Dubuque in Iowa and Peoria in Illinois (after Hottes and Frison [10], as well as Smith and Dillery [27]).
Host plants: *Acer rubrum*, *Acer saccharinum*, *Acer saccharum*, also found on plantings of *Acer platanoides* (in North America), occasionally on *Acer nigrum*.
Distribution: Canada: British Columbia (North Vancouverˆ); Manitoba (Winnipeg); New Brunswick (Middle Kouchibouguac‡, Rothesay‡); Ontario (Front of Yonge‡, Hamiltonˆ, Havelock-Belmont-Methuenˆ, Leamington, London, North Perth‡, Perth South‡, Puslinchˆ, Smith-Ennismore-Lakefield‡); Quebec (Orsainville in Quebec City, Shawinigan (Lac Wapizagonke)‡). USA: California (Berkeley, Lodi, Palo Alto (vicinity of Stanford University), San Jose); Colorado (Boulder, Denver, Fort Collins, Greeley); Connecticut (Hamden, Hartford, New Haven); Florida (Gainesville, Highlands Hammock State Park, Lake Placid); Idaho (Eagle); Illinois (Albion, Alma*, Alton, Augerville, Bloomfield Precinct*, Cairo, Carbondale, Catlin, Danville, Dixon Springs, Edwardsville, Elizabethtown, Fairmount Township, Golconda, Grayville, Havana, Herod, Kankakee, Le Roy, Macomb, MURShall, Mattoon, Metropolis, Mount Carmel, Mount Carroll, Mount Pulaski*, Newton, Normal, Oregon, Pekin, Peoria, vicinity of Perry*, Rock Island, Quincy, Shawneetown, Starved Rock State Park, Springfield, Tonti, Urbana); Iowa (Dubuque, Fort Dodge); Kansas (Maple Hill*); Maine (Orono); Maryland (Beltsville, Laurel†); Minnesota (Saint James); Missouri (Columbia, Crane, Kansas City, Saint Louis, Steelville); Nebraska (Ashland, Lincoln, Weeping Water); North Carolina (Alamance, Tunnel Bypass Trail near Bryson City, Burlington, Chapel Hill, Cherokee, Franklin, Great Smoky Mountains National Park, Greensboro, Raleigh, Reidsville, Roaring Gap, Roxboro, Wilkesboro); Ohio (Columbus, Ostrander); Oregon (Corvallis); Pennsylvania (Bryn Athyn, Chambersburg, Houserville, Lancaster, Loganville, Miquon, New Bloomfield, Philipsburg, Pittsburgh, State College); South Carolina (Easley, Hardeeville); Tennessee (Cosby Horse Trail near Cosby); Utah (Bountiful, East Canyon Cashe Co., Logan, Payson, Provo, Salt Lake City); Virginia (Chatham); Washington (Yakima); Washington, D.C.; West Virginia (Martinsburg“); Wisconsin (Montello*, Shields in Marquette County). Europe: Hungary (Cegléd, Gazdagrét, Pesterzsébet, Tabán, Törökvész); Italy (Calendasco, Carlazzo, Milan (Bosco in Città, Sempione Parc), Nola); Serbia (Belgrade (Banjica, New Belgrade, Vrčin, Zemun near Danube), Novi Sad (Bistrica, Novo Naselje)); Spain (Astorga, León, Lleida) (Figure 15) ([10,17,21,23,24,27,41,44–57]; Centre for Biodiversity Genomics—Canadian Specimens [‡]; Illinois Natural History Survey Insect Collection [*]; International Barcode of Life project (iBOL) [ˆ]; Natural History Museum of Denmark Entomology Collection [“]; new record in this publication [†]).
Additional distribution from iNaturalist (www.inaturalist.org, accessed on 12 June 2024): Canada: Ontario (LaSalle, Ottawa); Quebec (Dorval Island). USA: Alabama (Fort Payne, Hoover); California (Albany); Florida (Parkland); Georgia (Cashes Valley, Kennesaw, LaFayette); Illinois (New Lenox); Indiana (Zionsville); Iowa (Cedar Rapids); Kentucky (eastern outskirts of Louisville); Massachusetts (Williamstown); North Carolina (vicinity of Barnardsville, Charlotte, Durham); Ohio (Rest Area Southbound Wapakoneta); Pennsylvania (Bethel Park, Buckingham Springs, vicinity of Strickersville, Villanova University); Virginia (Dulles, Far Hills, Forest Lakes, Holly Knoll Cir near Great Falls, Great Falls Park, Herndon, Woodbridge); Wisconsin (Cross Plains). Europe: Spain (Santiago de Compostela).

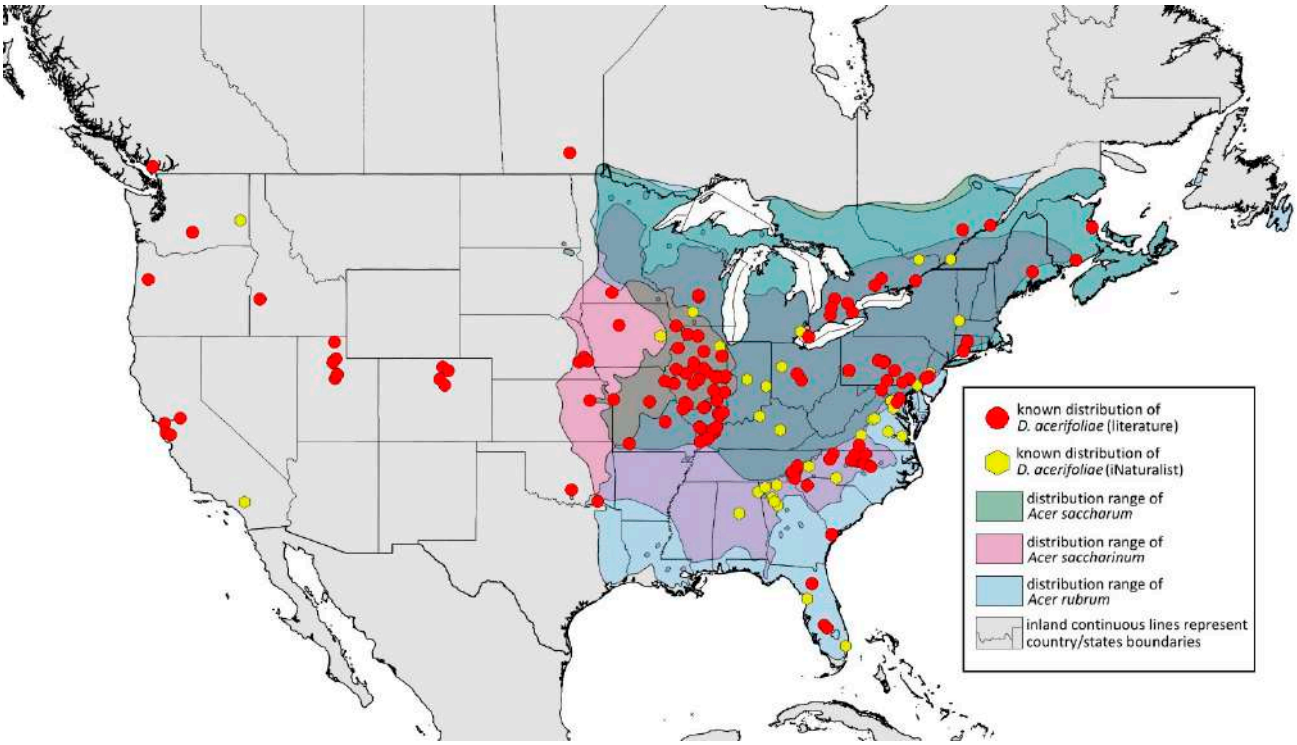

Figure 15. Known distribution of *Drepanaphis acerifoliae* in North America, with distribution ranges of its host plants.

3.4.2. *Drepanaphis carolinensis* Smith, 1941

Drepanaphis carolinensis Smith, 1941: 57(2): 228, 231 [23]

Figures 1B, 3B, 4B, 5B, 7B, 8B, 9B, 11B, 12B, 13B, 14B and 16; Tables 1–3

Material examined: Holotype. Drepanaphis carolinensis Smith, Holotype Type No 55834. D.D.N.N.M.//N.C, Aphids, Host Acer, Raleigh, N.C. 193. Date 4–28-40. C.F. Smith—six alate viv. fem. (USNM) Paratype. Drepanaphis carolinensis Smith//N. C. Aphids, Host Maple, Raleigh, N.C. Date 4-26-40, 193, C. F. Smith//INHS, Insect Collection 1,058,855—four alate viv. fem. Paratype. Drepanaphis carolinensis Smith//N. C. Aphids, Host Acer, Raleigh, N.C. Date 4-30-40, 193, C. F. Smith//INHS, Insect Collection 1,058,858—four alate viv. fem. Paratype. Drepanaphis carolinensis Smith//N. C. Aphids, Host Sugar Maple, Milburnie, NC, Date 21 May 1940, C. F. Smith//INHS, Insect Collection 1,058,859—three alate viv. fem. Paratype. Drepanaphis carolinensis Smith//N. C. Aphids, Host Acer, Raleigh, N.C. Date 4-30-40, 193, C. F. Smith (IECA).

Additional material examined—Table S6.

Alate viviparous female—re-description (n = 16)

Colour. In life: Head, thorax and abdomen reddish brown. Head and pronotum with longitudinal white wax stripes. Abdomen covered by white wax dots, more intensively on ABD I–II and VI–VIII. Eyes red, antennal segments pale with dark apices. Wings clear with small area of dark brown pigmentation at end, radius veins brown. Pterostigma brown. Femora and siphunculi dark. Tibiae pale. DAT dark brown (Figure 8B).

Pigmentation of mounted specimens: Head, pronotum, ANT I–II brown. Rest of thorax dark brown (Figure 9B). ANT III–VI pale brown with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wings clear with small area of dark brown pigmentation at end, radius veins dark brown (Figure 7B). Pterostigma distinct, darkly pigmented, with small area inside without pigmentation (Figure 3B). Abdomen pale brown, marginal sclerites dark brown. DAT (Figure 1B) and siphunculi dark brown. Cauda, subgenital and anal plate pale. Fore femora brown darker dorsally (Figure 4B). Middle and hind femora brown with darker smudge. Hind femora with darker stripes at margins.

Tibiae brown with darker knee areas and distal parts. Tarsi brown.
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.02–0.04 mm long with pointed apices; one pair of pointed frontal setae on ventral side 0.07–0.08 mm long. ANT/BL 1.44–2.07; ANT/HW 9.3–13.25; PT/BASE 5.56–8.1. ANT III with 9–15 secondary rhinaria, BASE with 4 accessory rhinaria, URS with 4–8 accessory setae. Other ratios: ANT IV/ANT III 0.64–0.82; ANT V/ANT III 0.62–0.75; ANT VI/ANT III 1.02–1.6; URS/ANT III 0.09–0.12; URS/BASE 0.56–0.71; URS/SIHP 0.38–0.56; HT II/ANT III 0.11–0.14; HT II/BASE 0.6–0.89; TIBIA III/BL 0.5–0.66; SIPH/BL 0.08–0.14; SIPH/CAUDA 1.33–2.63. DAT with four pairs of distinct tubercles. DAT I 0.13–0.16 mm long, slightly larger than DAT II 0.1–0.13 mm long. DAT III largest, 0.23–0.32 mm long (Figure 11B). DAT IV smallest, 0.06–0.1 mm long. Dorsal setae with pointed apices, 0.02–0.04 mm long, on small sclerites on ABD I–V. Marginal sclerites with 3–6 setae. Siphunculi flask-shaped (Figure 5B).
Oviparous female—description (n = 8)
Colour. In life: Unknown.
Pigmentation of mounted specimens: Head and thorax brown, abdomen pale. ANT I–II brown. ANT III–VI pale brown with darker apices on ANT III–V. Siphunculi, subgenital, anal plate and cauda brown. Fore, middle and hind femora dark brown. Tibiae pale brown with darker knee areas and distal parts. Tarsi pale brown. Dorsal sclerites brown (Figure 12B).
Morphometric characters: Head setae: two pairs of fronto-orbital setae, 0.07–0.1 mm long; one pair of postero-dorsal setae, 0.05–0.06 mm long; one pair of latero-dorsal setae, 0.03–0.04 mm long with blunt apices on dorsal side; one pair of pointed frontal setae on ventral side, 0.09–0.1 mm long. ANT/BL 0.94–1.42. Other ratios: ANT VI/ANT III 1.5–2.0; PT/BASE 5.14–7.0; SIPH/BL 0.06–0.08; FEMUR III/BL 0.2–0.26; TIBIA III/BL 0.38–0.5; HT II/ANT VI 0.1–0.14; URS/ANT III 0.14–0.17; URS/BASE 0.64–0.71; URS/SIPH 0.5–0.64. ANT III with one or without secondary rhinaria. URS with 4–8 accessory setae. Hind tibiae with 27–54 pseudosensoria distributed along almost their entire length. Dorsal setae 0.04–0.1 mm long. Marginal sclerites on ABD I–V distinct. Siphunculi tubular.
Alate male—re-description (n = 3)
Colour. In life: Unknown.
Pigmentation of mounted specimens: Head, ANT I–II, IV–VI brown; ANT III light brown with darker apices. Thorax, DAT and siphunculi dark brown. Abdominal sclerotisation dark brown. Wings clear with small area of dark brown pigmentation at end, radius veins brown. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation. Cauda and anal plate pale. Fore femora brown darker dorsally. Middle and hind femora brown with darker smudge. Hind femora with darker stripes at margins. Tibiae brown with darker knee areas and distal parts. Tarsi brown (Figure 13B).
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae, 0.02–0.03 mm long on dorsal side; one pair of frontal setae on ventral side, 0.05 mm long. ANT/BL 1.53–1.55. Other ratios: ANT VI/ANT III 1.08–1.42; PT/BASE 6.64–7.67; SIPH/BL 0.09–0.1; FEMUR III/BL 0.25–0.3; TIBIA III/BL 0.53–0.63; URS/ANT III 0.09–0.1; URS/SIPH 0.45–0.5. ANT III with 69–102 rhinaria, ANT IV with 43–56 rhinaria, ANT V with 25–38 rhinaria. URS with 4–6 accessory setae. DAT I and II inconspicuous or very small, 0.03–0.04 mm long. DAT III distinct, 0.1–0.15 mm long; DAT IV on spinal sclerites, 0.04–0.05 mm long. Dorsal setae on abdomen with pointed apices, 0.02–0.03 mm long, on small sclerites. Spinal sclerites on ABD V with 4–5 setae, 0.03–0.04 mm long. Marginal sclerites with 3–6 setae. Siphunculi flask-shaped. Genitalia with basal part of phallus short, hook-shaped (Figure 14B).
Host plants: *Acer saccharum*, occasionally on *Acer nigrum* and *Acer rubrum*.
Distribution: Canada: Ontario (Algonquin Provincial Parkˆ, Bon Echo Provincial Parkˆ, Guelph (Clairfields)ˆ, Ottawaˆ, Owen Soundˆ). USA: Florida (Waccasassa River in Levy County); Illinois (Arlington Heights*, Palatine*, Urbana*); Maine (Orono); Massachusetts (Amherst, Taunton); Minnesota (Walsh); Michigan (Albion); New Jersey (Rahway†); North

Carolina (Chapel Hill, Greensboro, Moravian Falls, Raleigh—locus typicus); Ohio (Columbus); Pennsylvania (Harrisburg, State College); Tennessee (Gatlinburg^, Great Smoky Mountains National Park); Washington, D.C.; Wisconsin (Saint Croix Falls) (Figure 16) ([23,24,27,58]; Illinois Natural History Survey Insect Collection [*]; International Barcode of Life project (iBOL) [^]; new record in this publication [†]).

Additional distribution from iNaturalist (www.inaturalist.org, accessed on 12 June 2024): USA: Alabama (Birmingham Botanical Gardens); Arkansas (Jonesboro); Illinois (Bloomington); Indiana (South Bend); Maryland (North Bethesda); Massachusetts (Groton); New Hampshire (Dixville); New York (Onondaga); North Carolina (Durham (Trinity Park)); Vermont (Essex Junction); Virginia (Williamsburg (York River State Park)).

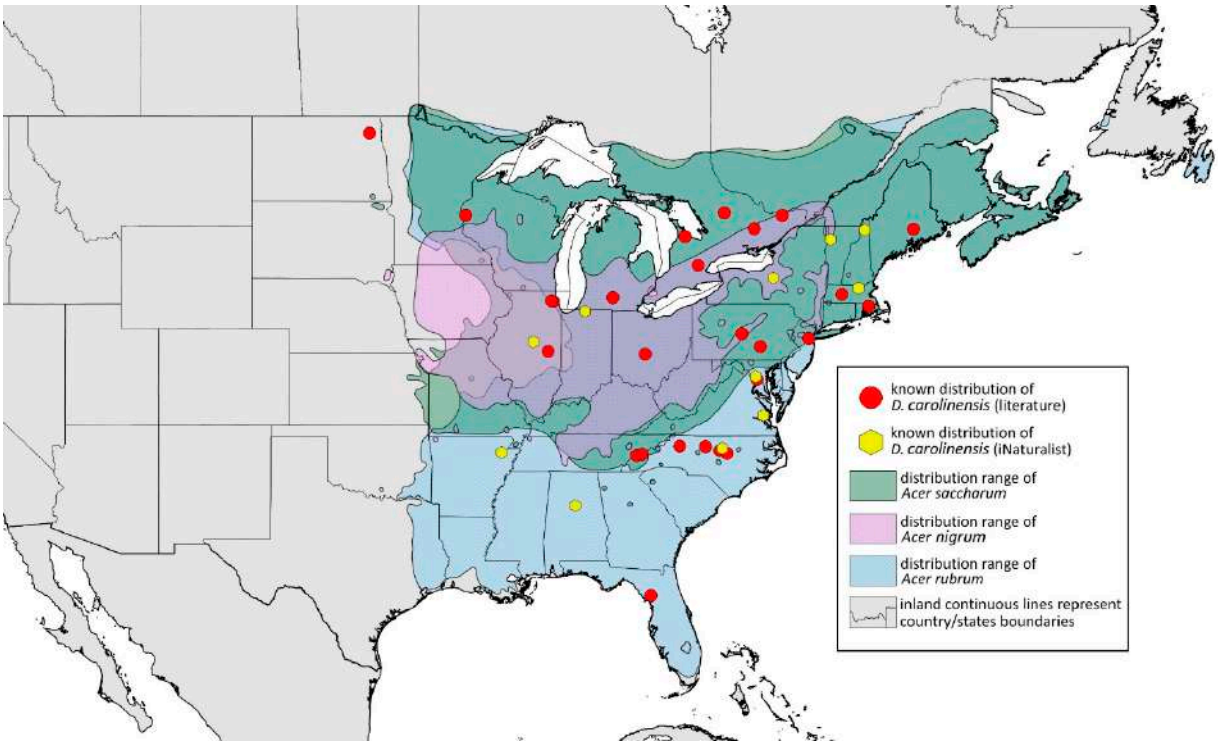

Figure 16. Known distribution of *Drepanaphis carolinensis* in North America, with distribution ranges of its host plants.

3.4.3. *Drepanaphis choanotricha* Smith & Dillery, 1968

Drepanaphis choanotricha Smith & Dillery, 1968: 61(1): 186, 190 [27]
Figures 1C, 2B, 3C, 4C, 5C, 9C, 11C, 12C, 13C, 14C and 17; Tables 1–3
Material examined: Holotype. Drepanaphis choanotricha Smith & Dillery Det. Smith & Dillery, 60-1060 Southern sugar maple, Paratype (blue)//Umstead PK. Raleigh, N. C. 9•11•60, Holotype Red, CFS—two alate viv. fem. [USNM] Paratype. Drepanaphis choanotricha Smith & Dillery Det. Smith & Dillery, 60-1060 Southern Sugar maple//Umstead PK. Raleigh, N. C. 9•11•60, Paratype//INHS, Insect Collection 1058862—four alate viv. fem. Paratype. Drepanaphis choanotricha Smith & Dillery, paratype, BM 1984-340, Det: Smith & Dillery//N.U.S.A, Pl. Southern Sugar maple, Loc. Umstead Pk, Raleigh, N.C., Date II.IX.1960, Leg. C. F. Smith, 60.1060//NHMUK 014314711—three alate viv. fem. Paratype. Drepanaphis choanotricha Smith & Dillery Det. Smith & Dillery, 60-1060 Southern Sugar maple//Umstead PK. Raleigh, N. C. 9•11•60, Paratype//08107//Museum Paris MNHN 25145—three alate viv. fem.
Additional material examined—Table S6.
Alate viviparous female–re-description (n = 13)
Colour. In life: Black with pale legs. Head bearing three longitudinal and one anterior

transverse white wax stripes. Pronotum with two or three medial longitudinal stripes. Mesonotum with one pair of latero-anterior and one pair of medio-posterior wax dots. Metanotum with one pair of lateral wax dots. Abdomen with rows of white wax dots, denser at posterior end [27].

Pigmentation of mounted specimens: Head, ANT I, II, thorax dorsal abdominal tubercles and siphunculi dark brown (Figures 1C and 9C). ANT III–VI pale brown with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wings clear, with dark brown pigmentation of end of veins, radius veins brown. Pterostigma distinct, darkly pigmented, oval with small area inside without pigmentation (Figure 3C). Abdomen pale, dorsal sclerotisation brown. Cauda, subgenital and anal plate pale. Fore femora pale brown (Figure 4C).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.02–0.05 mm long with blunt apices; one pair of pointed frontal setae on ventral side, 0.06–0.08 mm long. ANT/BL 1.79–3.35; ANT/HW 11.73–19.99; PT/BASE 9.04–16.31. ANT III with 2–5 secondary rhinaria, BASE with 5–6 accessory rhinaria (Figure 2B). URS with 6–10 accessory setae. Other ratios: ANT IV/ANT III 0.61–0.99; ANT V/ANT III 0.67–0.83; ANT VI/ANT III 1.81–3.48; URS/ANT III 0.12–0.16; URS/BASE 0.69–0.86; URS/SIPH 0.5–0.76; HT II/ANT III 0.11–0.15; HT II/BASE 0.58–0.79; TIBIA III/BL 0.57–0.74; SIPH/BL 0.1–0.15; SIPH/CAUDA 2.06–4.02. DAT II–IV clearly visible, DAT I inconspicuous. DAT II 0.04–0.06 mm long, DAT III 0.13–0.24 mm long (Figure 11C). DAT IV smallest, 0.01–0.03 mm long. Setae at ends of tubercles 0.03–0.04 mm long with blunt apices. Marginal sclerites with 2–4 blunt setae 0.02–0.04 mm long. Distinct spinal setae 0.04–0.05 mm long with blunt apices on small sclerites. Siphunculi flask-shaped (Figure 5C).

Oviparous female—description (n = 2)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, thorax and coxa brown. ANT I, II and siphunculi dark brown. ANT III–VI pale brown with darker apices on ANT III–V. Abdomen pale. Dorsal sclerotisation brown. Fore, middle and hind femora; tarsi subgenital; anal plate; and cauda pale brown (Figure 12C).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, 0.1–0.12 mm long; one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.06–0.08 mm long with blunt apices; one pair of pointed frontal setae on ventral side, 0.1 mm long. ANT/BL 1.67–1.93. Other ratios: ANT VI/ANT III 2.34–2.7; PT/BASE 12.25–13.3; SIPH/BL 0.12; FEMUR III/BL 0.27–0.29; TIBIA III/BL 0.48–0.51; HT II/ANT VI 0.05–0.06; URS/ANT III 0.13–0.16; URS/BASE 0.75–0.83; URS/SIPH 0.38–0.48. ANT III without secondary rhinaria. URS with 6–7 accessory setae. Hind tibiae with 23–29 pseudosensoria, more abundant in distal parts of tibiae. Dorsal setae 0.1–0.13 mm long. ABD I–VI with setae on small dark sclerites. ABD I–V with marginal sclerites. Siphunculi flask-shaped.

Alate male—re-description (n = 1)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, ANT I, II, thorax, coxa, dorsal abdominal tubercles and siphunculi dark brown. ANT III–VI pale brown with darker apices on ANT III–V. Wings clear with distinct area of dark brown pigmentation at end, radius veins brown. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation. Abdomen pale, dorsal sclerotisation brown. Cauda and anal plate brown. Fore, middle, hind femora and tarsi pale brown (Figure 13C).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.03–0.04 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.07–0.08 mm long. ANT/BL 2.34–2.36. Other ratios: ANT VI/ANT III 2.35–2.51; PT/BASE 12.9–13.4; SIPH/BL 0.12; FEMUR III/BL 0.28–0.31; TIBIA III/BL 0.58–0.59; URS/ANT III 0.13; URS/SIPH 0.53. ANT III with 43–44 rhinaria, ANT IV with 21–23 rhinaria, ANT V with 16–18 rhinaria. BASE with seven very small accessory rhinaria. URS with six accessory setae. DAT III 0.05 mm

long with pointed setae 0.02 mm long at end. Dorsal setae 0.02–0.04 mm long with pointed apices. Spinal sclerites on ABD IV with two setae, ABD V with one seta. Marginal sclerites with 3–6 setae, spinal setae on small sclerites. Siphunculi flask-shaped. Genitalia with basal part of phallus elongated, robust, with pilled inner edges (Figure 14C).
Host plant: *Acer saccharum*.
Distribution: USA: Illinois (Starved Rock State Park); North Carolina (Raleigh (William B. Umstead State Park)—locus typicus); Tennessee (along Low Gap Trail in Great Smoky Mountains National Park*) (Figure 17) ([27]; Illinois Natural History Survey Insect Collection [*]).

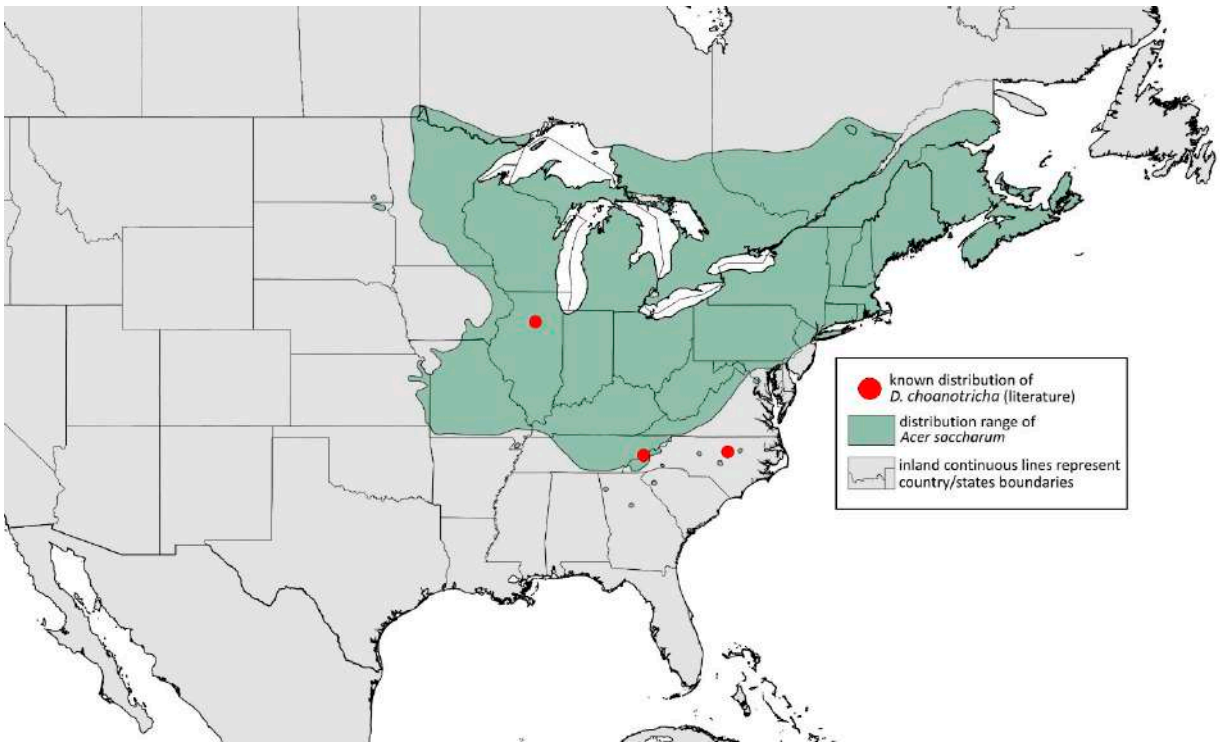

Figure 17. Known distribution of *Drepanaphis choanotricha* in North America, with distribution ranges of its host plants.

3.4.4. *Drepanaphis granovskyi* Smith & Knowlton, 1943

Drepanaphis granovskyi Smith & Knowlton, 1943: 59(2): 172, 173 [24]
Figures 1D, 3D, 4D, 5D, 9D, 11D, 12D, 13D, 14D and 18; Tables 1, 3 and 4
Material examined: Type. Drepanaphis granovskyi S-K//Mt. Acer grandidentatum, Liberty, Ut., Aug. 13, 1942, GF. Knowlton—three alate viv. fem. (USNM) Paratype. Drepanaphis granovskyi S-K//Mt. *Acer grandidentatum*, Spanish Fork, Ut., Aug. 10, 1942, Whitish freen, C F Knowlton//INHS, Insect Collection 1058866—three alate viv. fem. Additional material examined—Table S6.
Alate viviparous female—re-description (n = 13)
Colour. In life: Pale white, appendages clear; without conspicuous wax [27].
Pigmentation of mounted specimens: Head, thorax, ANT pale brown (Figure 9D). Wings clear with palely pigmented pterostigma, with large area inside without pigmentation (Figure 3D). Abdomen, dorsal abdominal tubercles (Figure 1D) and siphunculi pale. Fore femora pale brown (Figure 4D).
Morphometric characters: Head setae: two pairs of pointed fronto-orbital setae, 0.02–0.05 mm long; one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.01–0.02 mm long with pointed apices; two pairs of pointed frontal setae on ventral side, 0.02–0.05 mm long. ANT/BL 1.23–1.47; ANT/HW 8.19–10.79; PT/BASE 3.48–8.08.

ANT III with 9–13 secondary rhinaria, BASE with 4 accessory rhinaria. URS with 4–6 accessory setae. Other ratios: ANT IV/ANT III 0.55–0.72; ANT V/ANT III 0.5–0.75; ANT VI/ANT III 0.81–1.51; URS/ANT III 0.1–0.14; URS/BASE 0.57–0.96; URS/SIPH 0.33–0.54; HT II/ANT III 0.11–0.18; HT II/BASE 0.82–1.0; TIBIA III/BL 0.46–0.54; SIPH/BL 0.08–0.12; SIPH/CAUDA 1.17–2.62. Dorsal abdominal segments with distinct three pairs of tubercles. DAT I biggest, 0.09–0.12 mm long; DAT II 0.04–0.06 mm long; DAT III 0.03–0.06 mm long. DAT IV inconspicuous (Figures 1D and 11D). Setae at ends of tubercles, 0.02–0.03 mm long. Abdominal dorsal setae 0.02–0.04 mm long with pointed apices. Siphunculi tubular (Figure 5D).

Oviparous female—description (n = 1)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Body in general pale brown or with slightly darker hind tibiae and slightly lighter abdomen (Figure 12D).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, 0.07–0.09 mm long; one pair of postero-dorsal setae, 0.09 mm long; one pair of latero-dorsal setae, 0.05–0.06 mm long on dorsal side with forked apices. Two pairs of pointed frontal setae on ventral side, 0.04–0.06 mm long. ANT/BL 0.89–0.91. Other ratios: ANT VI/ANT III 1.5–1.83; PT/BASE 5.0–5.82; SIPH/BL 0.08–0.093; FEMUR III/BL 0.2–0.21; TIBIA III/BL 0.39; URS/ANT III 0.19; URS/BASE 0.73; URS/SIPH 0.4. ANT III without secondary rhinaria. URS with four accessory setae. Hind tibiae with 42–45 pseudosensoria, more abundant in middle part and on ends of tibiae. Dorsal setae 0.08–0.11 mm long with forked apices. Siphunculi tubular.

Alate male—description (n = 1)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, thorax, ANT I dark brown. Pronotum, ANT II, III pale brown; ANT IV–VI brown. Wings clear, pterostigma distinct, darkly pigmented, with small area inside without pigmentation. Abdomen pale, spinal sclerites and siphunculi dark brown. Cauda and anal plate dark brown. Fore femora brown (Figure 13D).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, two pairs of frontal setae on ventral side, 0.02–0.04 mm long with pointed apices. ANT/BL 0.96. Other ratios: SIPH/BL 0.09; URS/SIPH 0.47. ANT III with 66–68 rhinaria, ANT IV with 34–35 rhinaria, ANT V with 19–20 rhinaria. URS with four accessory setae. DAT absent. Dorsal setae 0.02–0.03 mm long with pointed apices. Spinal sclerites on ABD II–V with two pointed setae 0.02 mm long. Marginal sclerites with 1–3 setae, most distinct on ABD IV. Siphunculi tubular. Genitalia with basal part of phallus short, robust, rectangular (Figure 14D).

Host plant: *Acer grandidentatum*.

Distribution: USA: Idaho (Birch Creek (Cub River Canyon), Franklin, Mink Creek, Strawberry Creek); Utah (Avon Canyon, Beaver Canyon, Big Cottonwood Canyon, Blacksmith Fork Canyon, Bountiful, Brigham Canyon, East Canyon (Cache County), Eden, Farmington Canyon, Green Canyon, Heber, Liberty—locus typicus, Logan Canyon, Mantua, Mount Nebo, North Ogden, Richmond, Rolapp, Sardine Canyon, Wellsville Canyon, Willow Creek) (Figure 18) [24,27].

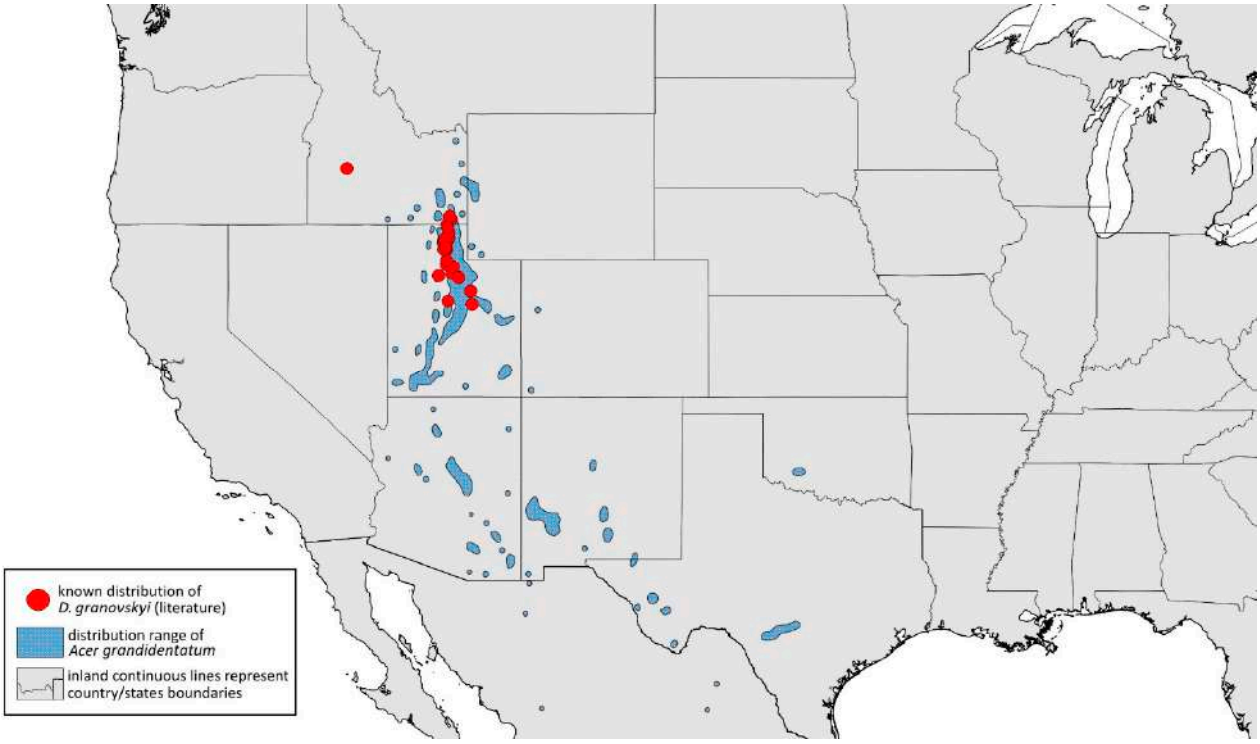

Figure 18. Known distribution of *Drepanaphis granovskyi* in North America, with distribution ranges of its host plants.

3.4.5. *Drepanaphis idahoensis* Smith & Dillery, 1968

Drepanaphis idahoensis Smith & Dillery, 1968: 61(1): 186, 193 [27]
Figures 1E, 3E, 4E, 5E, 9E, 11E, 12E and 19; Tables 1 and 2
Material examined: Holotype. Drepanaphis idahoensis Smith & Dillery Det. Smith & Dillery, 60-887, Acer grandidentatum, Paratype (blue)//Cub River Cany, Ida., 8●16●60, Al. dK transverse area between cornicles, Holotype (red) K-S—two alate viv. fem. (USNM) Paratype. Drepanaphis idahoensis Smith & Dillery Det. Smith & Dillery, 60-887, Acer grandidentatum, Paratype//Cub River Cany, Ida., 8●16●60, Al. dK transverse area between cornicles//Museum Paris MNHN 25147—two alate viv. fem.
Additional material examined—Table S6.
Alate viviparous female—re-description (n = 10)
Colour. In life: Body entirely frosted with white wax except for dark, U-shaped line more or less connecting DAT III to siphunculi. Legs pale [27].
Pigmentation of mounted specimens: Head, thorax, ANT I brown (Figure 9E). ANT II–VI pale brown with slightly darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wings clear with distinct area of dark brown pigmentation at end of veins. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation (Figure 3E). Abdomen pale with brown abdominal sclerites. Dorsal abdominal tubercles (Figure 1E) and siphunculi dark brown. Cauda, subgenital and anal plate pale. Fore femora pale brown (Figure 4E).
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.02–0.03 mm long with blunt apices; one pair of pointed frontal setae on ventral side, 0.05–0.06 mm long. ANT/BL 1.8–2.54; ANT/HW 11.65–20.98; PT/BASE 5.31–11.99. ANT III with 6–9 secondary rhinaria, BASE with 4 accessory rhinaria. URS with 6–8 accessory setae. Other ratios: ANT IV/ANT III 0.70–0.85; ANT V/ANT III 0.68–0.99; ANT VI/ANT III 0.83–2.02; URS/ANT III 0.09–0.11; URS/BASE 0.58–0.75; URS/SIPH 0.34–0.49; HT II/ANT III 0.08–0.12; HT II/BASE 0.6–0.86; TIBIA III/BL 0.6–0.81; SIPH/BL 0.11–0.16; SIPH/CAUDA 1.7–2.45. DAT I 0.03–0.06 mm

long; DAT II 0.05–0.1 mm long; DAT III biggest, 0.18–0.26 mm long. DAT IV inconspicuous (Figure 11E). Dorsal setae 0.02–0.03 mm long with blunt apices, on ABD I–V on small sclerites. Marginal sclerites with 2–4 blunt setae. Siphunculi flask-shaped (Figure 5E).

Oviparous female—description (n = 1)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Body in general pale brown or yellowish with slightly lighter abdomen (Figure 12E).

Morphometric characters: Head setae: two pairs of blunt fronto-orbital setae, 0.09–0.1 mm long; one pair of blunt postero-dorsal setae, 0.08 mm long; one pair of blunt latero-dorsal setae on dorsal side, 0.04 mm long; one pair of pointed frontal setae on ventral side, 0.07 mm long. ANT/BL 1.23–1.24. Other ratios: ANT VI/ANT III 0.86–0.92; PT/BASE 3.92–4.58; SIPH/BL 0.08–0.09; FEMUR III/BL 0.25–0.26; TIBIA III/BL 0.51; HT II/ANT VI 0.13–0.16; URS/ANT III 0.14; URS/BASE 0.77; URS/SIPH 0.53. ANT III without secondary rhinaria. URS with eight accessory setae. Hind tibiae with 22–23 pseudosensoria abundant, distributed in central part of tibiae. Dorsal setae 0.08–0.11 mm long. Siphunculi tubular.

Male: Unknown.

Remarks: Some specimens from Lawrence in Kansas come from the collection of the J.B. Wallis/R.E. Roughley Museum of Entomology, Canada, and the Museum of Zoology, Lund University, Sweden. However, we did not have the opportunity to verify the slides and confirm whether they are indeed individuals representing this species. Moreover, *Acer nigrum* is listed as a host plant on those slides.

Host plant: *Acer grandidentatum*, occasionally found on *Acer negundo* and *Acer saccharum*.

Distribution: USA: Idaho (Cub River Canyon—locus typicus, Franklin, Stanley (between Thompson Creek and Tennell Creek‴)); Oregon (Corvallis (Benton County)); Utah (Cub River Canyon, Hobble Creek Canyon, Providence, Salt Lake City, Vivian Park in Provo Canyon); Washington (Pullman (Whitman County)) (Figure 19) ([27]; NMNH Extant Specimen Records (USNM, US) [‴]).

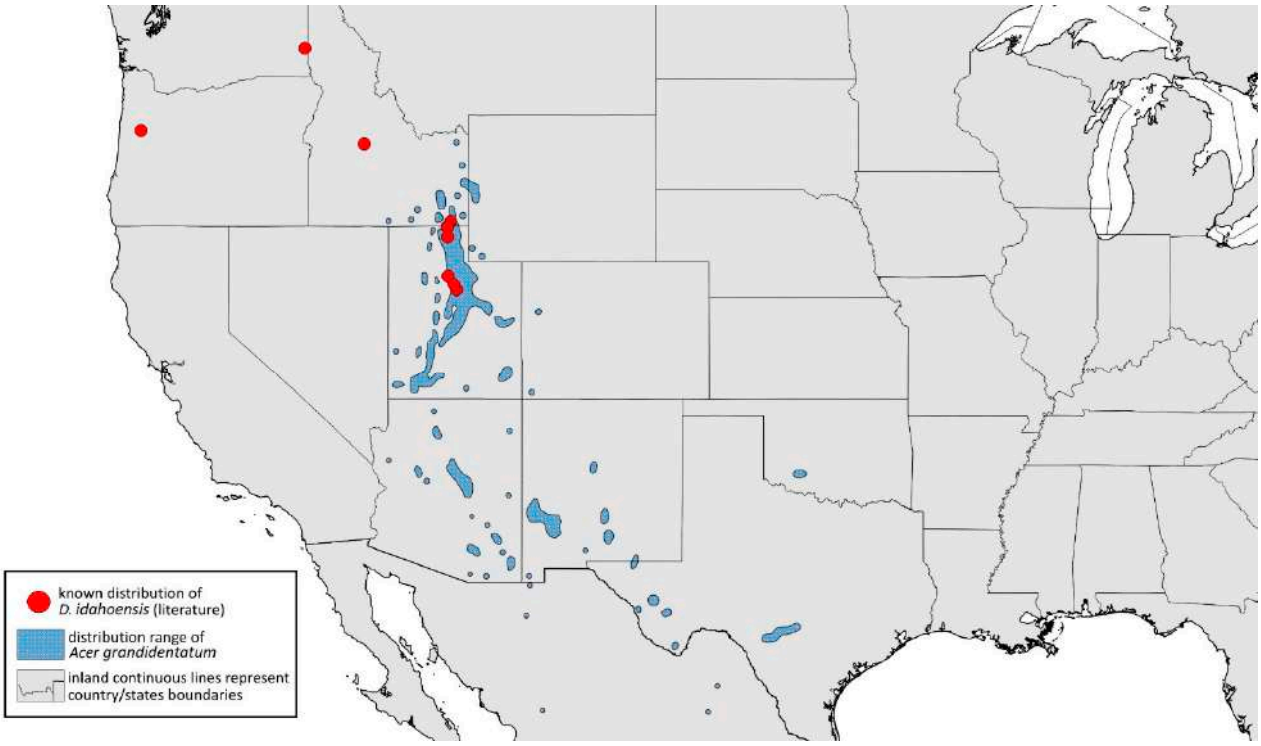

Figure 19. Known distribution of *Drepanaphis idahoensis* in North America, with distribution ranges of its host plants.

3.4.6. *Drepanaphis kanzensis* Smith, 1941

Drepanaphis kanzensis Smith, 1941: 72(2): 228, 232 [23]
= *Drepanaphis kansensis* Leonard, 1959: 32(1): 12 [59]
Figures 1F, 3F, 4F, 5F, 9F, 11F, 12F, 13E, 14E and 20; Tables 1–3
Material examined: Drepanaphis kanzensis Smith Holotype Type No 55838. D.D.N.N.M.//Ka. Aphids, Host Sugar maple, Ft. Scott, Date 6-17 1940, C.F. Smith. Type—five alate viv. fem. (USNM) Paracotype. Drepanaphis kanzensis C. F. Smith//Ka. Aphids, Host Sugar maple, Ft. Scott, Ka, Date 6-17-40, C.F. Smith//08109//Museum Paris MNHN 25148—five alate viv. fem.
Additional material examined—Table S6.
Alate viviparous female—re-description (n = 17)
Colour. In life: Head, thorax and abdomen covered by white wax. ANT and legs pale, eyes red. Dorsal abdominal tubercles dark brown. Wings clear with pale pterostigma.
Pigmentation of mounted specimens: Head and pronotum brown, rest of thorax dark brown (Figure 9F). ANT I–II brown, ANT III–VI pale brown with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wings clear with palely pigmented pterostigma, with large area inside without pigmentation (Figure 3F). Abdomen pale with brown sclerites. Dorsal abdominal tubercles dark brown (Figure 1F). Siphunculi pale brown with darker smudge. Cauda, subgenital and anal plate pale. Fore femora pale brown (Figure 4F).
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.03–0.05 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.08–0.09 mm long. ANT/BL 1.44–2.56; ANT/HW 9.35–14.43; PT/BASE 5.6–12.98. ANT III with 10–15 secondary rhinaria, BASE with 4 accessory rhinaria. URS with 6–8 accessory setae. Other ratios: ANT IV/ANT III 0.6–0.8; ANT V/ANT III 0.59–0.84; ANT VI/ANT III 0.76–1.086; URS/ANT III 0.087–0.108; URS/BASE 0.56–0.68; URS/SIPH 0.38–0.63; HT II/ANT III 0.16–0.24; HT II/BASE 0.59–0.87; TIBIA III/BL 0.52–0.73; SIPH/BL 0.084–0.137; SIPH/CAUDA 0.94–2.33. Dorsal abdominal segments with distinct three pairs of tubercles. DAT I inconspicuous. DAT II 0.09–0.11 mm long, DAT III biggest 0.2–0.28 mm long (Figure 11F), DAT IV smallest 0.05–0.06 mm long. Pointed setae at end of tubercles 0.03–0.04 mm long. Dorsal setae 0.04–0.05 mm long with pointed apices, on small sclerites. Marginal sclerites with 2–5 setae. ABD VIII with two spinal sclerites, each with two setae. Siphunculi flask-shaped (Figure 5F).
Oviparous female—description (n = 5)
Colour. In life: Unknown.
Pigmentation of mounted specimens: Head, thorax, ANT pale brown. ANT with darker apices on ANT III–V. Abdomen and siphunculi pale. Dorsal sclerotisation pale brown. Femora, tibiae pale brown. Tibiae with slightly darker apical areas. Tarsi brown (Figure 12F).
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.07–0.1 mm long with blunt apices; one pair of pointed frontal setae on ventral side, 0.1 mm long. ANT/BL 0.75–1.4; PT/BASE 7.43–10.66. Other ratios: ANT VI/ANT III 1.51–2.17; SIPH/BL 0.05–0.07; FEMUR III/BL 0.21–0.28; TIBIA III/BL 0.38–0.52; HT II/ANT VI 0.07–0.1; URS/ANT III 0.098–0.13; URS/BASE 0.62–0.69; URS/SIPH 0.44–0.53. ANT III without secondary rhinaria. URS with eight accessory setae. Hind tibiae with 41–67 pseudosensoria distributed in central part of tibiae. Dorsal setae 0.09–0.13 mm long. Siphunculi tubular.
Alate male—description (n = 3)
Colour. In life: Unknown.
Pigmentation of mounted specimens: ANT pale with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wings clear with palely pigmented pterostigma, with large area inside without pigmentation. Abdomen pale with brown to dark brown sclerotisation. Siphunculi pale; cauda and anal plate brown. Legs pale, tibiae with slightly darker apical parts (Figure 13E).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.03–0.04 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.05–0.06 mm long. ANT/BL 1.45–2.36. Other ratios: ANT VI/ANT III 0.92–1.5; PT/BASE 6.38–10.0; SIPH/BL 0.09–0.11; FEMUR III/BL 0.28–0.33; TIBIA III/BL 0.54–0.67; URS/ANT III 0.08–0.09; URS/SIPH 0.35–0.42. ANT III with 94–127 rhinaria, ANT IV with 38–62 rhinaria, ANT V with 18–32 rhinaria. URS with six accessory setae. DAT III 0.13–0.15 mm long with pointed setae 0.03 mm long at end. DAT I, II and III inconspicuous. Dorsal setae 0.03–0.04 mm long with pointed apices. Spinal sclerites with two setae on ABD I, V, VI, VII, ABD VIII with four setae. Marginal sclerites with 3–4 setae. Siphunculi tubular. Genitalia with basal part of phallus elongated, triangular (Figure 14E).
Remarks: One slide with two individuals, previously misidentified as *Drepanaphis kanzensis* from the NHMUK collection (BM 1958-454; NHMUK 014314720) is correctly identified as *Drepanaphis idahoensis*. The material was collected in Hobble Creek Canyon, Utah, USA, from *Acer grandidentatum*.
Host plant: *Acer rubrum*, *Acer saccharum*.
Distribution: Canada: New Brunswick (Fredericton); Ontario (Brockville°, Guelph°, Ottawa, Puslinch, Toronto°, Unionville); Quebec (Orsainville (Zoo), Sainte-Foy). USA: Kansas (Fort Scott—locus typicus, Hiawatha); Maine (Presque Isle); Michigan (East Lansing); Missouri (Butler, Columbia); New Jersey (Rahway†); New York (Geneva, Lockport", Niagara County); Ohio (Columbus); Pennsylvania (State College (Botany Bldg.)); Wisconsin (Sturgeon Bay); Washington DC (Figure 20) ([23,24,27,58]; International Nucleotide Sequence Database Collaboration [°]; Natural History Museum of Denmark Entomology Collection ["]; new record in this publication [†]).

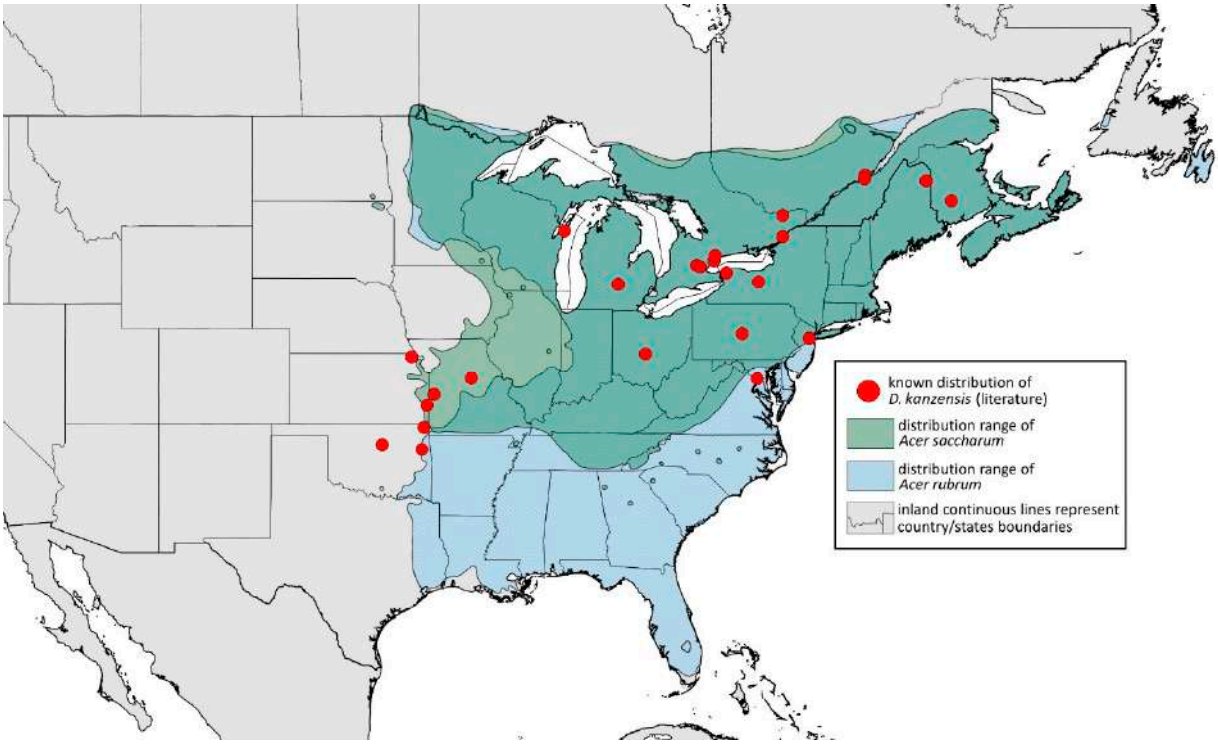

Figure 20. Known distribution of *Drepanaphis kanzensis* in North America, with distribution ranges of its host plants.

3.4.7. *Drepanaphis keshenae* Granovsky, 1931

Drepanaphis keshenae Granovsky, 1931: 19: 246, 248 [21]
Figures 1G, 3G, 4G, 5G, 8C, 11G, 13F, 14F, 21A, 22A and 23; Tables 1–3

Material examined: Lectotype. APHIDIDAE. Drepanaphis keshenae Granovskyi, Det. Granovsky 1929, Sl. 7617, Det. F. C. Hottes, 29, ILL. NAT. HIST. SUR, lectotype//Elizabethtown Ill., VI-20-1929, coll. Frison + Hottes. On *Acer saccharum*. ILL. NAT. HIST. SUR.//INHS, Insect Collection 459,587—three alate viv. fem.
Additional material examined—Table S6.
Alate viviparous female—re-description (n = 11)
Colour. In life: Head and thorax covered with white wax. Antennae pale with dark apices of segments. Eyes red. Abdomen covered with white wax, apart from ABD V with distinct black dorsal tubercles. Fore femora dark; middle and hind femora, tibiae and tarsi pale brown. Wing veins distinctly brown bordered. Siphunculi dark (Figure 8C).
Pigmentation of mounted specimens: Head, thorax, ANT I brown (Figure 21A). ANT II–VI pale brown to brown with darker apices on ANT III–V. Wing veins distinctly brown bordered. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation (Figure 3G). Abdomen pale with brown sclerotisation. DAT dark brown (Figure 1G). Siphunculi pale brown to brown. Cauda, subgenital and anal plate pale. Fore femora darker dorsally (Figure 4G). Middle and hind femora, tibiae and tarsi pale brown to brown. Hind femora with brown smudge.

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.02–0.04 mm long with pointed apices; one pair of pointed frontal setae on ventral side 0.07 mm long. ANT/BL 1.5–3.12; PT/BASE 7.2–13.82. ANT III with 10–16 secondary rhinaria, BASE with 4 accessory rhinaria. URS with 6–8 accessory setae. Other ratios: ANT IV/ANT III 0.56–0.79; ANT V/ANT III 0.61–0.81; ANT VI/ANT III 0.99–2.15; URS/ANT III 0.09–0.13; URS/BASE 0.61–0.9; URS/SIPH 0.33–0.64; HT II/ANT III 0.08–0.13; HT II/BASE 0.62–1.00; TIBIA III/BL 0.53–0.82; SIPH/BL 0.096–0.15; SIPH/CAUDA 1.75–3.38. DAT III distinct, 0.24–0.47 mm long (Figure 11G) with pointed setae, 0.02–0.03 mm long at ends. DAT II 0.04 mm long or inconspicuous. DAT I and IV inconspicuous. Dorsal setae 0.02–0.03 mm long, with pointed apices, on ABD I–V on small sclerites. Siphunculi flask-shaped (Figure 5G).
Oviparous female—description (n = 2)
Colour. In life: Unknown.
Pigmentation of mounted specimens: Head, thorax, ANT brown. ANT with darker apices on ANT III–V. Abdomen pale with brown sclerotisation. Siphunculi dark brown. Legs brown, tibiae with slightly darker apical parts (Figure 22A).

Morphometric characters: Head setae: two pairs of blunt fronto-orbital setae 0.09 mm long, one pair of blunt postero-dorsal setae 0.08 mm long, one pair of blunt latero-dorsal setae 0.05 mm long on dorsal side, one pair of pointed frontal setae 0.08 mm long on ventral side. ANT/BL 1.04–1.15. Other ratios: ANT VI/ANT III 1.78–2.08; PT/BASE 7.09–7.83; SIPH/BL 0.06–0.07; FEMUR III/BL 0.22–0.23; TIBIA III/BL 0.44–0.46; HT II/ANT VI 0.11–0.13; URS/ANT III 0.16–0.24; URS/BASE 0.73–1.1; URS/SIPH 0.48–0.86. ANT III without secondary rhinaria. URS with 6–8 accessory setae. Hind tibiae with 56–67 pseudosensoria distributed along almost their entire lengths. Dorsal setae 0.7–0.11 mm long. Siphunculi tubular, 0.14 mm long.
Alate male—description (n = 4)
Colour. In life: Unknown.
Pigmentation of mounted specimens: Head, thorax, ANT I, II, IV, V, VI brown. ANT III pale brown with darker apices of segments. Wing veins brown bordered. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation. Abdomen pale with brown sclerites. Dorsal abdominal tubercles dark brown. Siphunculi, cauda and anal plate brown. Fore femora brown, darker dorsally. Middle and hind femora, tibiae and tarsi brown. Hind femora with brown smudge (Figure 13F).
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.02–0.03 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.07 mm long. ANT/BL 1.74–2.2. Other ratios: ANT VI/ANT III 1.22–1.93; PT/BASE 9.2–11.1; SIPH/BL 0.1–0.14; FEMUR

III/BL 0.3–0.31; TIBIA III/BL 0.59–0.64; URS/ANT III 0.1–0.17; URS/SIPH 0.42–0.76. ANT III with 71–101 rhinaria, ANT IV with 29–46 rhinaria, ANT V with 25–31 rhinaria. URS with six accessory setae. DAT III 0.08–0.24 mm long with pointed setae 0.02–0.03 mm long at end. Dorsal setae 0.02–0.03 mm long with pointed apices. Siphunculi tubular. Genitalia with basal part of phallus elongated, finger-like (Figure 14F).

Remarks: Smith and Dillery [27] claimed they could not locate any of the slides from Keshena, Wisconsin. Therefore, they suggested Elizabethtown, Illinois, as locus typicus. Additionally, there is a slide no. 95/58 (Biologické centrum AV ČR) from Logan, Utah, dated 16.09.1962, from *Acer grandidentatum*, but it is dark and unverifiable.

Host plant: *Acer saccharum*.

Distribution: USA: Alabama (Aldridge Gardens in Hoover, Old Rocky Ridge (Jefferson County)); Florida (High Springs, Waccasassa River (Levy County)); Illinois (Bell Smith Springs Scenic Area, Dixon Springs, Eddyville (Bell Smith Springs National Natural Landmark), Elizabethtown); North Carolina (Raleigh); Ohio (Hocking County); Wisconsin (Keshena) (Figure 23) [23,27].

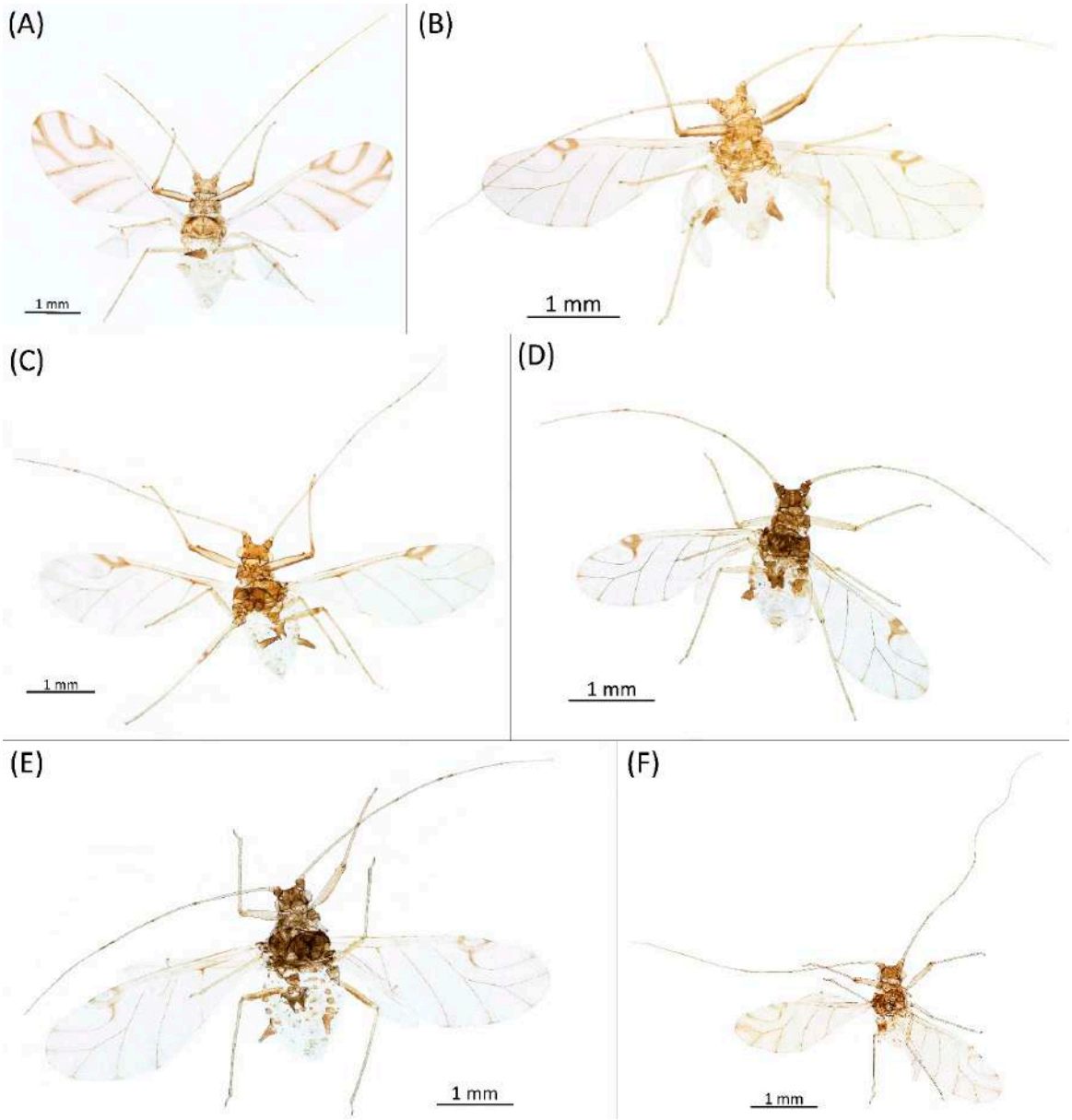

Figure 21. Alate viviparous females of the genus Drepanaphis: (**A**) *D. keshenae*, (**B**) *D. knowltoni*, (**C**) *D. monelli*, (**D**) *D. nigricans*, (**E**) *D. parva*, (**F**) *D. robinsoni* sp. nov.

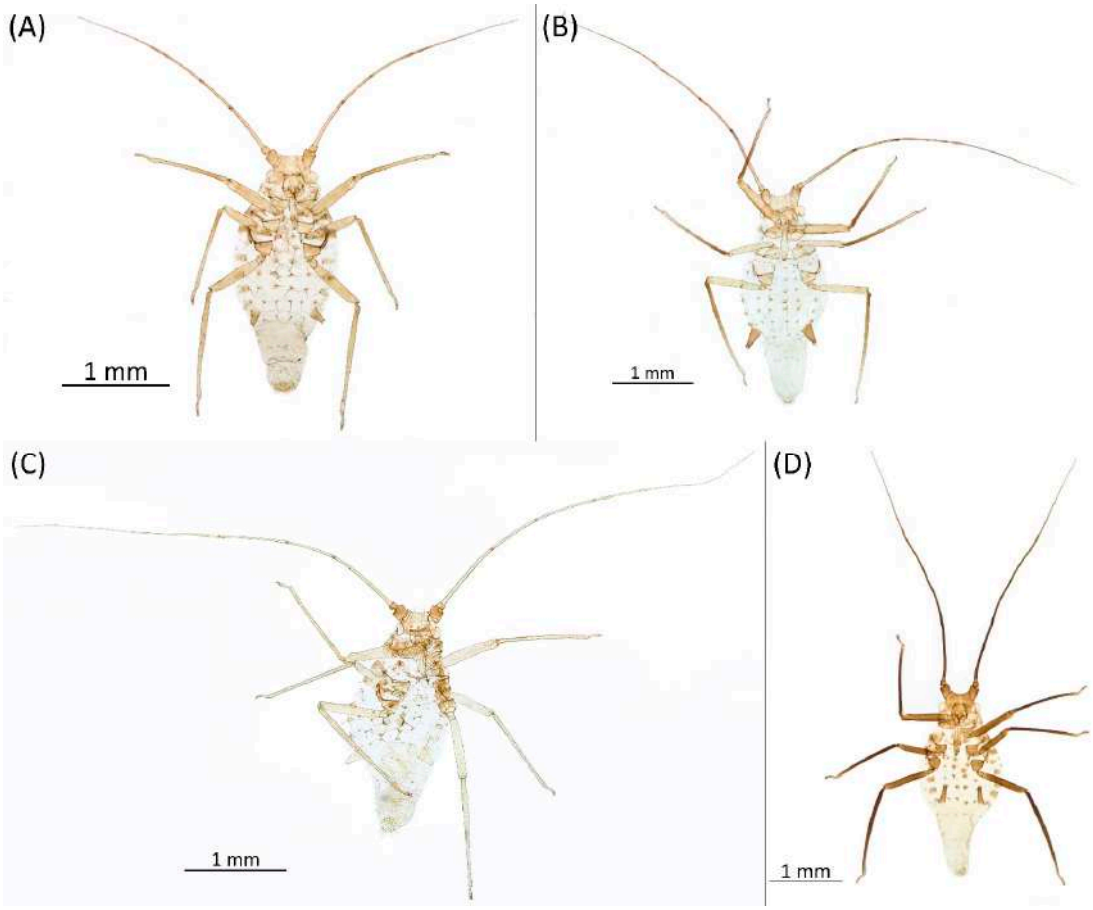

Figure 22. Oviparous females of the genus Drepanaphis: (**A**) *D. keshenae*, (**B**) *D. monelli*, (**C**) *D. nigricans*, (**D**) *D. sabrinae*.

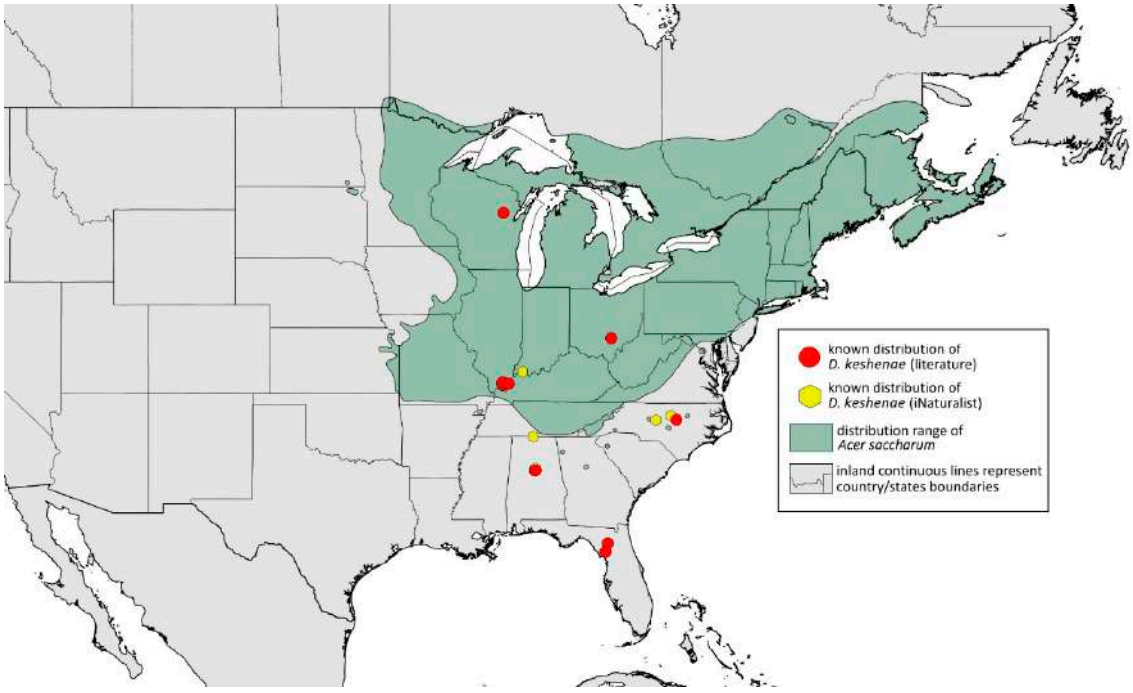

Figure 23. Known distribution of *Drepanaphis keshenae* in North America, with distribution ranges of its host plants.

Additional distribution from iNaturalist (www.inaturalist.org, accessed on 12 June 2024): Alabama (Birmingham Botanical Gardens, Hoover); Indiana (Evansville); North Carolina (Asheboro, Durham); Tennessee (vicinity of Ardmore).

3.4.8. *Drepanaphis knowltoni* Smith & Dillery, 1968

Drepanaphis knowltoni Smith & Dillery, 1968: 61(1): 186, 195 [27]
Figures 1H, 3H, 4H, 5H, 11H, 14G, 21B, 24A and 25; Tables 1 and 3
Material examined: Holotype. Drepanaphis knowltoni Smith & Dillery Det. Smith & Dillery, 60-886, Acer grandidentanum//Cub River Cany., Ida. 8•15•60, Alate whitish, holotype—K-S—one alate viv. fem. (USNM). Paratype. Drepanaphis knowltoni Smith & Dillery Det. Smith & Dillery, 60-886, Acer grandidentanum//Cub River Cany., Ida. 8•15•60, Alate whitish, holotype—K-S//Museum Paris MNHN 25149—one alate viv. fem. Additional material examined—Table S6.
Alate viviparous female—re-description (n = 24)
Colour. In life: Body white with wax; may be entirely white, or thoracic lobes and V-shaped area connecting siphunculi with DAT III may be exposed and dark. Front femora, DAT III and siphunculi always dark [27].
Pigmentation of mounted specimens: Head, thorax, ANT I brown (Figure 21B). ANT II–VI pale brown, with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wing veins clear with small area of dark brown pigmentation on end. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation (Figure 3H). Abdomen pale with brown sclerotisation. DAT III (Figure 1H) and siphunculi dark brown. Cauda, subgenital and anal plate pale. Fore femora brown, darker dorsally (Figure 4H). Middle and hind femora, tibiae and tarsi pale brown to brown. Hind femora with brown stripes at margins.
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side; one pair of pointed frontal setae on ventral side; 0.02–0.05 mm long with pointed apices. ANT/BL 1.73–2.59; PT/BASE 7.1–12.93. ANT III with 10–15 secondary rhinaria, BASE with 4–5 accessory rhinaria. URS with 6–8 accessory setae. Other ratios: ANT IV/ANT III 0.64–0.79; ANT V/ANT III 0.69–0.85; ANT VI/ANT III 1.23–2.20; URS/ANT III 0.09–0.12; URS/BASE 0.47–0.72; URS/SIPH 0.29–0.42; HT II/ANT III 0.09–0.14; HT II/BASE 0.56–0.85; TIBIA III/BL 0.59–0.82; SIPH/BL 0.12–0.18; SIPH/CAUDA 2.2–3.6. DAT III distinct 0.18–0.28 mm long (Figure 11H), with setae 0.03–0.04 mm long at end. Dorsal setae 0.03–0.04 mm long, with pointed apices. ABD VI with marginal sclerites and 2–5 setae each. Siphunculi flask-shaped (Figure 5H).
Oviparous female: Unknown.
Alate male—re-description (n = 2)
Colour. In life: Unknown.
Pigmentation of mounted specimens: Head, thorax, ANT I, II brown. ANT III–VI pale brown, with darker apices on ANT III–V. Wings clear, pterostigma distinct, darkly pigmented, with small area inside without pigmentation. Abdomen pale with brown sclerotisation. Siphunculi, cauda and anal plate brown. Fore femora pale brown, darker dorsally. Middle and hind femora, tibiae, apices of tarsi pale brown. Hind femora with brown stripes at margins. Tibiae with slightly darker apical parts (Figure 24A).

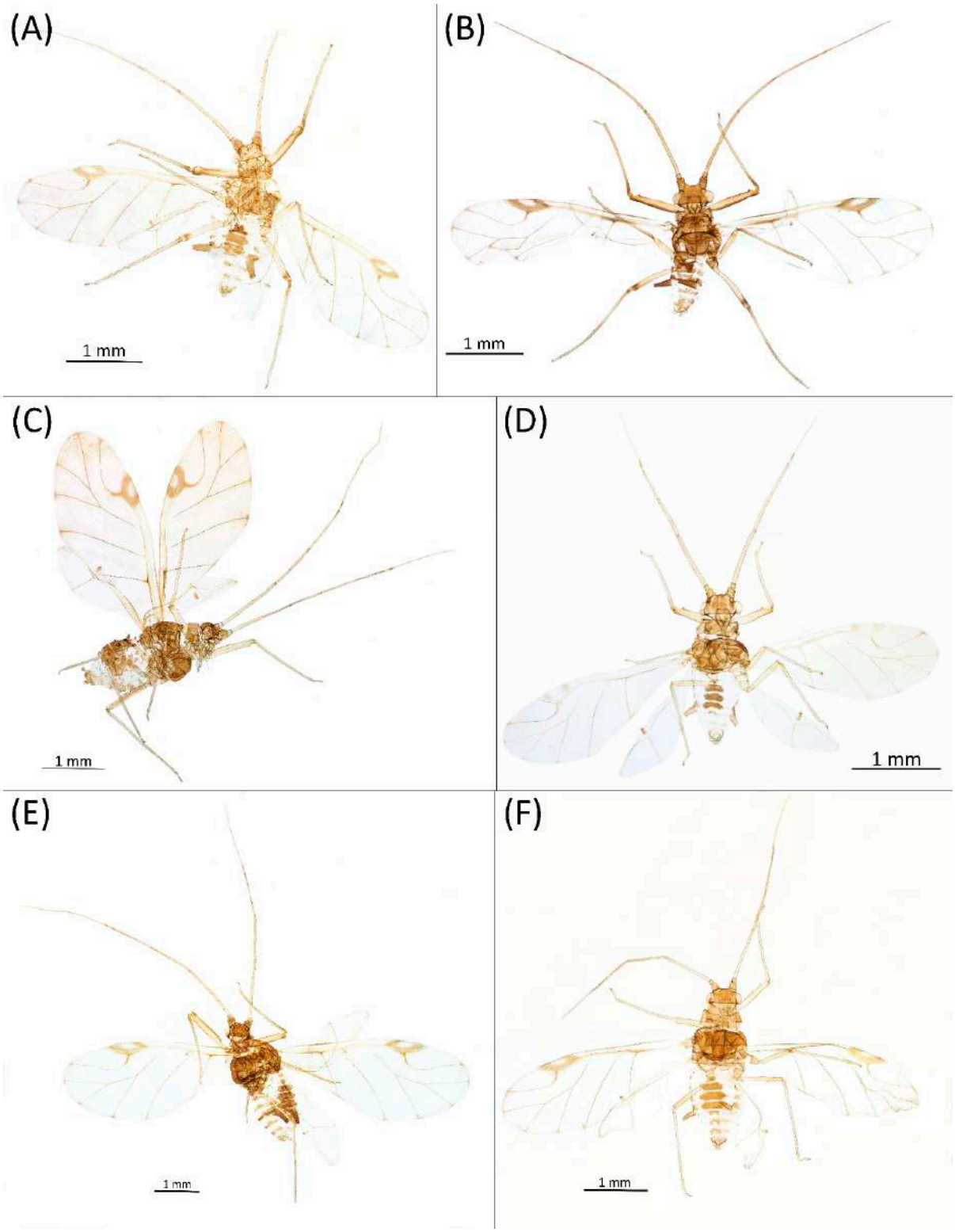

Figure 24. Alate males of the genus Drepanaphis: (**A**) *D. knowltoni*, (**B**) *D. monelli*, (**C**) *D. parva*, (**D**) *D. simpsoni*, (**E**) *D. spicata*, (**F**) *D. utahensis*.

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.03–0.04 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.06 mm long. ANT/BL 1.64–1.91. Other ratios: ANT VI/ANT III 1.03–1.78; PT/BASE 6.36–11.65; SIPH/BL 0.12; III FE-

MUR/BL 0.29–0.31; TIBIA III/BL 0.62–0.65; URS/ANT III 0.1; URS/SIPH 0.37. ANT III with 71–79 rhinaria, ANT IV with 29 rhinaria, ANT V with 22 rhinaria. BASE with five accessory rhinaria. URS with eight accessory setae. DAT III 0.1–0.11 mm long with pointed setae 0.04–0.05 mm long at end. Dorsal setae 0.04–0.05 mm long with pointed apices. Spinal sclerites with 2 setae, marginal sclerites with 3–5 setae. Siphunculi tubular. Genitalia with basal part of phallus elongated, robust with capitate apices (Figure 14G).
Male: Unknown.
Host plants: *Acer grandidentatum*, *Acer nigrum*, *Acer rubrum*, *Acer saccharum*.
Distribution: Canada: New Brunswick (Fredericton). USA: Connecticut (Wallingford); Idaho (Cub Creak, Cub River Canyon—locus typicus, Deer Cliff Lodge, Franklin, Mink Creek, Stanley, Strawberry Creek, Thomas Spring); Michigan (Midland); Minnesota (Saint Paul); New York (Mount Kisco); North Carolina (Grandfather Mountain); Rhode Island (Providence); Tennessee (vicinity of Cosby* (0.4 mi up Low Mount Cammerer Trail, Great Smoky Mountains National Park)); Utah (Blacksmith Fork Canyon, Cub River Canyon, Daniel's Canyon, Logan Canyon, Mantua, Parley's Canyon, Providence, Provo Canyon, Richmond, Smithfield Canyon, Weber Canyon, Wellsville Canyon); Virginia (Richmond) (Figure 25) [27]; Illinois Natural History Survey Insect Collection [*].

Additional distribution from iNaturalist (www.inaturalist.org, accessed on 12 June 2024): New York (Columbia, Syracuse).

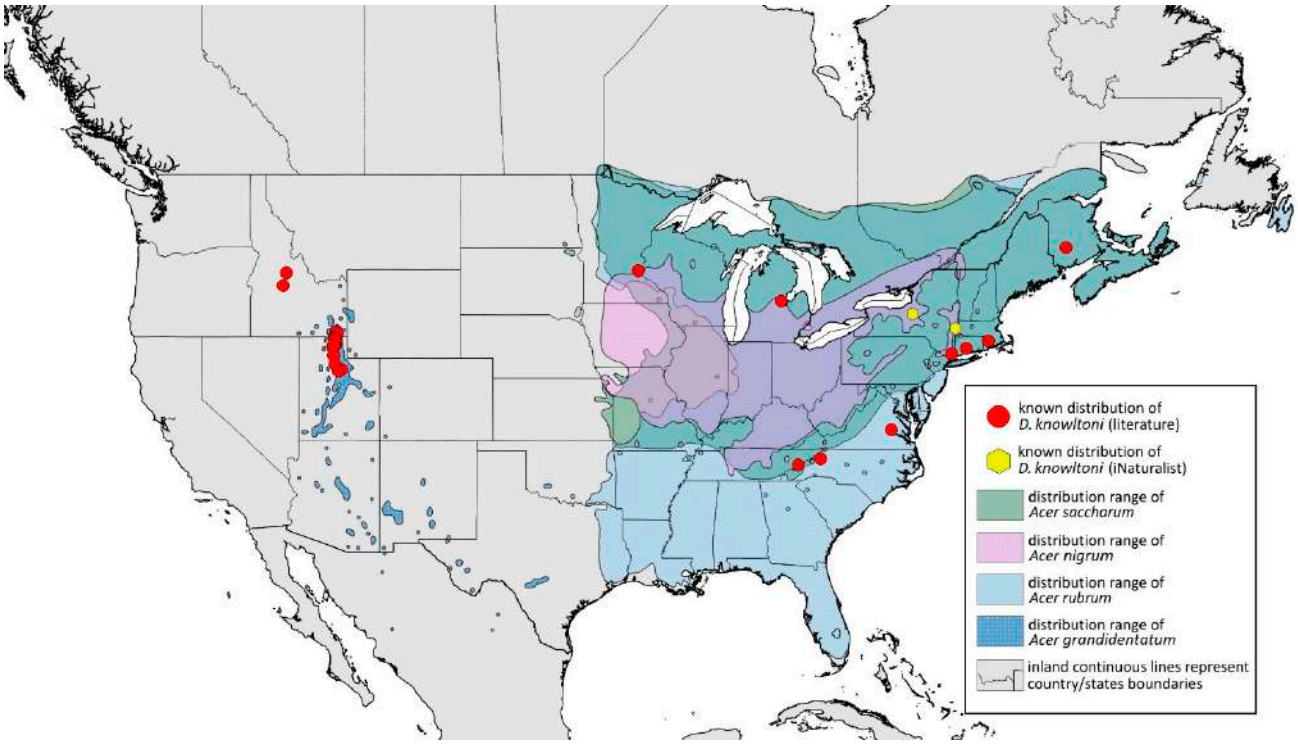

Figure 25. Known distribution of *Drepanaphis knowltoni* in North America, with distribution ranges of its host plants.

3.4.9. *Drepanaphis monelli* (Davis, 1909)

= *Phymatosiphum monelli* Davis, 1909: 2(3): 197 [19]
Drepanaphis monelli Gillette, 1910: 3(4): 371 [20]
= *Drepanosiphum monelli* Burnham, 1938: 70(9): 184 [60]
Figure 1I, Figure 3I, Figure 4I, Figure 5I, Figure 10B, Figure 11I; Figures 14H, 21C, 22B, 24B and 26; Tables 1–3
Material examined: Type. Phymatosiphum monelli n.g.e t n.sp., Type, Occ.# 40469. 2n. dt. Zab. Nat. Hist. sz. 3120, John J. Davis.//Phymatosiphum 670 monelli n. sp. -Type-

Byckeye, St. Louis, Mo. 30 June'08. J. T. Monell Col. Mounted from alcoholic specimens. John J. Davis.//INHS, Insect Collection 1058879—three alate viv. fem.
Additional material examined—Table S6.

Alate viviparous female—re-description (n = 11)

Colour. In life: Powdery white over entire body, except dark fuscous thoracic lobes. Brownish-yellow, U-shaped line more or less connecting DAT III to siphunculi. Front femora, DAT III and siphunculi dark [27].

Pigmentation of mounted specimens: Head, thorax, ANT I dark brown (Figure 21C). ANT II–VI pale brown with darker apices on ANT III–V. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation (Figure 3I). Abdomen pale with brown sclerotisation. Dorsal abdominal tubercles (Figure 1I) and siphunculi dark brown. Cauda, subgenital and anal plate pale. Fore, middle and hind femora pale brown to brown. Fore femora darker dorsally (Figure 4I); hind femora with brown stripes at margins. Fore tibiae with darker apical part.

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.02–0.03 mm long; one pair of pointed frontal setae on ventral side, 0.06 mm long. ANT/BL 1.9–2.74; PT/BASE 5.51–13.91. ANT III with 9–12 secondary rhinaria, BASE with 4 accessory rhinaria. URS with 6–12 accessory setae (Figure 10B). Other ratios: ANT IV/ANT III 0.66–0.94; ANT V/ANT III 0.72–0.92; ANT VI/ANT III 1.11–2.24; URS/ANT III 0.1–0.13; URS/BASE 0.71–0.86; URS/SIPH 0.34–0.48; HT II/ANT III 0.09–0.13; HT II/BASE 0.62–0.86; TIBIA III/BL 0.55–0.82; SIPH/BL 0.11–0.16; SIPH/CAUDA 1.65–2.78. DAT III distinct, 0.16–0.22 mm long (Figure 11I), with setae 0.02–0.03 mm long at end. ABD I–V with dorsal setae 0.02–0.03 mm long with pointed apices, on small sclerites. Marginal sclerites with 3–5 setae. Siphunculi tubular (Figure 5I).

Oviparous female—description (n = 5)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, thorax pale brown. ANT brown to dark brown with darker apices on ANT III–V. Abdomen pale with brown sclerotisation. Siphunculi dark brown. Femora and tarsi pale brown. Tibiae dark brown, lighter on ends (Figure 22B).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.07–0.12 mm long with blunt apices; one pair of pointed frontal setae on ventral side, 0.01 mm long. ANT/BL 1.38–1.83. Other ratios: ANT VI/ANT III 1.64–2.21; PT/BASE 6.29–10.85; SIPH/BL 0.09–0.11; III FEMUR/BL 0.25–0.29; III TIBIAE/BL 0.48–0.55; HT II/ANT VI 0.07–0.1; URS/ANT III 0.14–0.19; URS/BASE 0.75–0.86; URS/SIPH 0.44–0.6. ANT III without secondary rhinaria. URS with 8–10 accessory setae. Hind tibiae with 32–62 pseudosensoria more abundant in middle part of tibiae. Dorsal setae 0.08–0.11 mm long. Siphunculi flask-shaped.

Alate male—re-description (n = 4)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, thorax, ANT I, II dark brown. ANT III–VI brown with darker apices on ANT III–V. Wings clear with small area of dark brown pigmentation on end. Pterostigma distinct, very darkly pigmented, with small area inside without pigmentation. Abdomen pale with brown sclerotisation. Siphunculi dark brown, cauda and anal plate brown. Fore femora brown, darker dorsally. Middle and hind femora, tibiae and tarsi pale brown. Hind femora with dark brown stripes on ends. Tibiae with slightly darker apical parts (Figure 24B).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.03–0.05 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.06–0.07 mm long. ANT/BL 1.73–2.13. Other ratios: ANT VI/ANT III 1.36–1.66; PT/BASE 7.16–11.92; SIPH/BL 0.11–0.13; FEMUR III/BL 0.29–0.33; TIBIA III/BL 0.58–0.69; URS/ANT III 0.11–0.12; URS/SIHP 0.48–0.79. ANT III with 91–98 rhinaria, ANT IV with 38–45 rhinaria, ANT V with 21–26 rhinaria. URS with eight accessory setae. DAT III distinct, 0.1–0.12 mm

long, with pointed setae, 0.03–0.04 mm long at end. Dorsal setae 0.03 mm long on small sclerites. ABD IV–V with two setae on spinal sclerites. Marginal sclerites with 3–4 setae. Siphunculi tubular. Genitalia with basal part of phallus smooth, elongated, hook-shaped (Figure 14H).

Host plants: *Aesculus glabra*, occasionally found on *Aesculus pavia* and *Acer saccharum*.

Distribution: Canada: Quebec (Senneville). USA: Florida (Gainesville, High Springs); Illinois (Havana, Kankakee, Mount Carroll, Oakwood, Rock Island, Urbana); Missouri (Columbia, Saint Louis—locus typicus); North Carolina (Bryson City, Cullowhee, Grandfather Mountain, Raleigh (Umstead Park)); Ohio (Columbus); Pennsylvania (State College); Wisconsin (Milwaukee) (Figure 26) [19,21,23,27,49,58].

Additional distribution from iNaturalist (www.inaturalist.org, accessed on 12 June 2024): Alabama (Birmingham Botanical Gardens); Pennsylvania (Penn Hills).

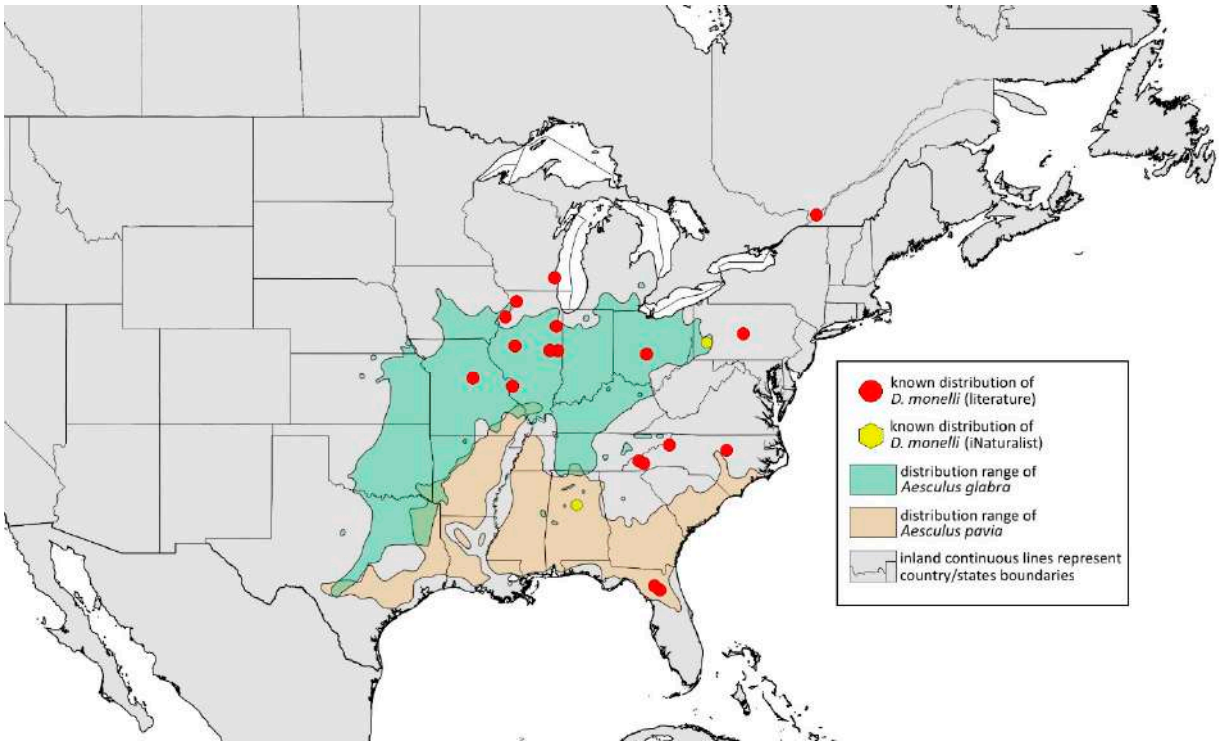

Figure 26. Known distribution of *Drepanaphis monelli* in North America, with distribution ranges of its host plants.

3.4.10. *Drepanaphis nigricans* Smith, 1941

Drepanaphis nigricans Smith, 1941: 57(2): 228, 236 [23]

Figures 1J, 3J, 4J, 5J, 11J, 21D, 22C and 27; Tables 2 and 4

Material examined: Holotype. Drepanaphis nigricans Smith Holotype Type No 55835. D.D.N.N.M.//N.C. 41-151, Acer rubrum, Busick, N.C., (Park Way), 2 July 1941, CF. Smith—five alate viv. fem. (USNM). Paratype. Drepanaphis nigricans C. F. Smith//N. C. Aphids, Host Acer rubrum, Blowing Roak, N. C., Date June 12 1940, C. F. Smith, Black light spots//INHS, Insect Collection 1058449—three alate viv. fem. Paracotype. Drepanaphis nigricans C. F. Smith//N. C. 41-151, Acer rubrum, Busick, NC., Park Way, July 2, 1941, CF Smith//Museum Paris MNHN 25153—six alate viv. fem.

Additional material examined—Table S6.

Alate viviparous female—re-description (n = 51)

Colour. In life: Black with pale legs, wings with noticeable dark spots at ends of veins. Head and pronotum with three longitudinal white wax stripes, median pronotal stripe interrupted, often faint. Mesonotum with two transverse rows of four small wax dots

anteriorly (medial pairs sometimes missing) and one pair of elongated dots posteriorly. Metanotum with two wax dots laterally. Abdomen with many wax dots, most dense at posterior end [27].

Pigmentation of mounted specimens: Head, thorax, ANT I dark brown (Figure 21D). ANT II–VI pale brown with darker apices on ANT III–V. Wings clear with dark pigmentation at end of veins. Pterostigma distinct, darkly pigmented, oval with small area inside without pigmentation (Figure 3J). Abdomen pale with brown dorsal sclerotisation. Dorsal abdominal tubercles (Figure 1J) and siphunculi dark brown. Cauda, subgenital and anal plate brown. Fore femora pale brown (Figure 4J).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.01–0.02 mm long; one pair of pointed frontal setae on ventral side, 0.06–0.07 mm long. ANT/BL 2–3.38; PT/BASE 7.5–15.8. ANT III with 11–20 secondary rhinaria, BASE with 4 accessory rhinaria. URS with 6–10 accessory setae. Other ratios: ANT IV/ANT III 0.63–0.79; ANT V/ANT III 0.64–0.84; ANT VI/ANT III 1.18–2.26; URS/ANT III 0.09–0.15; URS/BASE 0.6–0.94; URS/SIPH 0.45–0.7; HT II/ANT III 0.09–0.13; HT II/BASE 0.6–1.02; TIBIA III/BL 0.55–0.86; SIPH/BL 0.077–0.14; SIPH/CAUDA 1.03–2.63. DAT I inconspicuous. DAT II 0.02–0.04 mm long, DAT III biggest 0.14–0.25 mm long (Figure 11J), DAT IV 0.2–0.6 mm long. Ends of tubercles with very short setae, about 0.01 mm long. ABD I–V with dorsal setae 0.01–0.02 mm long, on small sclerites. Marginal sclerites with 3–6 setae. Siphunculi flask-shaped (Figure 5J).

Oviparous female—description (n = 1)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head and thorax pale brown. ANT I–II brown; ANT III–VI pale brown. ANT II–VI with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Siphunculi, cauda, subgenital and anal plate pale brown. Legs pale (Figure 22C).

Morphometric characters: Head setae: two pairs of fronto-orbital setae 0.08–0.1 mm long, one pair of postero-dorsal setae 0.08 mm long, one pair of latero-dorsal setae on dorsal side 0.04–0.05 mm long with blunt apices; one pair of pointed frontal setae on ventral side, 0.09–0.1 mm long. ANT/BL 1.69–1.71. Other ratios: ANT VI/ANT III 2.29–2.45; PT/BASE 12.38–12.72; SIPH/BL 0.08–0.09; FEMUR III/BL 0.26–0.28; TIBIA III/BL 0.51–0.52; HT II/ANT VI 0.06; URS/ANT III 0.14; URS/BASE 0.77; URS/SIPH 0.53. ANT III with 3–4 secondary rhinaria. URS with 12 accessory setae. Hind tibiae with 53–62 pseudosensoria more abundant in middle part of tibiae, closer to distal part of femur. Dorsal setae 0.07–0.09 mm long, on ABD VIII slightly shorter. Siphunculi flask-shaped.

Male: Unknown.

Host plant: *Acer rubrum*.

Distribution: USA: Florida (Gainesville); New York (Sparta); North Carolina (Blowing Rock, Bolton, Busick—locus typicus, Cashiers, Chapel Hill, Durham, Great Smoky Mountains National Park* (Goldmine Loop Trail), Mount Mitchell, Raleigh (Umstead Park), Sunburst); Pennsylvania (State College); Tennessee (Great Smoky Mountains National Park* (Low Mount Cammerer Trail)) (Figure 27) ([23,27]; Illinois Natural History Survey Insect Collection [*]).

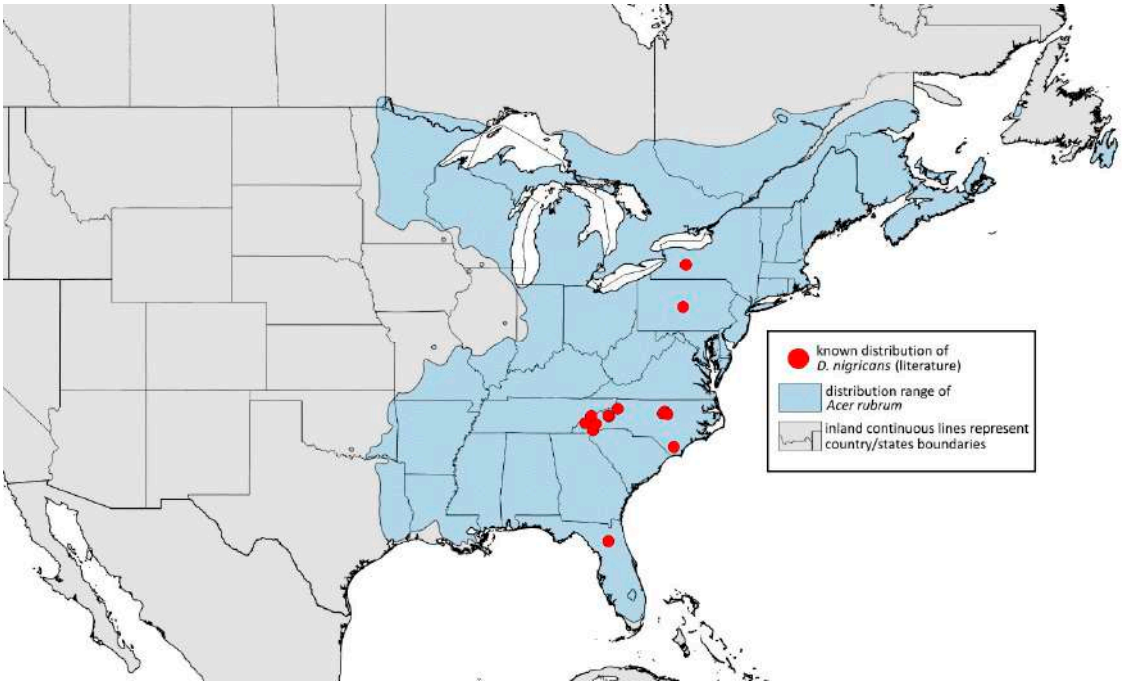

Figure 27. Known distribution of *Drepanaphis nigricans* in North America, with distribution ranges of its host plants.

3.4.11. *Drepanaphis parva* Smith, 1941

Drepanaphis parva Smith, 1941: 57(2): 228, 237 [23]
= *Drepanaphis rubrum* Smith, 1941: 57(2): 228, 238 [23]
= *Drepanaphis parvus* Smith & Knowlton, 1943: 59(2): 173 [24]
Figures 1K, 3K, 4K, 5K, 7C, 11K, 14I, 21E, 24C and 28; Tables 3 and 4
Material examined: Holotype. Drepanaphis parvus Smith Holotype Type No 55836. D.D.N.N.M.//N. C. Aphids, Host Acer, Greensboro, N. C. 193, Date 5-3-40, C. F. Smith—three alate viv. fem. (USNM). Paratype. Drepanaphis parvus C. F. Smith//N. C. Aphids, Host Acer rubrum, Raleigh, NC, Date May 12 1941, C. F. Smith//INHS, Insect Collection 1058907—six alate viv. fem. Paracotype. Drepanaphis parvus C. F. Smith//N. C. Aphids, Host Acer, Greensboro, N. C. 193, Date 5-3-40, C. F. Smith//INHS, Insect Collection 1058906—six alate viv. fem. Paracotype. Drepanaphis parvus C. F. Smith//N. C. Aphids, Host Acer, Greensboro, N. C. 193, Date 5-3-40, C. F. Smith//Museum Paris MNHN 22493—six alate viv. fem.
Additional material examined—Table S6.
Alate viviparous female—re-description (n = 15)
Colour. In life: Head and thorax reddish brown; head and pronotum with five longitudinal white wax stripes; pronotal wax pattern as in *D. acerifoliae*. Abdomen green–grey–brown with white tip, white wax dots in longitudinal rows in line with those on thorax [27].
Pigmentation of mounted specimens: Head, ANT I, thorax brown to dark brown (Figure 21E). ANT II–VI pale brown with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wing veins diffusely bordered. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation (Figures 3K and 7C). Abdomen pale with DAT I–IV (Figure 1K) and sclerotisation dark. Siphunculi brown, cauda, subgenital and anal plate pale brown. Fore femora pale brown (Figure 4K). Hind femora with darker smudge.
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.02–0.03 mm long with blunt apices; one pair of pointed frontal setae on ventral side, 0.05–0.06 mm long. ANT/BL 1.41–1.94; PT/BASE 6.36–11.31. ANT III with 9–15 secondary rhinaria, BASE with 4 accessory rhinaria. URS with 4–8 accessory setae. Other ratios: ANT IV/ANT III 0.55–0.79;

ANT V/ANT III 0.52–1.16; ANT VI/ANT III 1.05–1.7; URS/ANT III 0.08–0.11; URS/BASE 0.67–0.77; URS/SIPH 0.35–0.43; HT II/ANT III 0.09–0.14; HT II/BASE 0.67–1.08; TIBIA III/BL 0.46–0.59; SIPH/BL 0.08–0.13; SIPH/CAUDA 1.61–2.46. DAT I 0.07–0.11 mm long; DAT II 0.05–0.08 mm long; DAT III biggest, 0.14–0.19 (Figure 11K); DAT IV smallest, 0.04–0.07 mm long. Dorsal setae 0.01–0.03 mm with blunt apices, on small sclerites. ABD VII–VIII with setae pointed and slightly longer, 0.03–0.05 mm long. Siphunculi flask-shaped (Figure 5K).

Oviparous female: Unknown.

Alate male—re-description (n = 1)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, ANT I, thorax brown. ANT II–VI pale brown. ANT III–V with slightly darker apices on ends and dark area with primary rhinarium on ANT VI. Wing veins diffusely bordered. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation. Abdomen pale with dark tubercles and sclerotisation. Cauda and anal plate brown. Legs pale; hind femora with brown smudge (Figure 24C).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.03–0.05 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.05–0.06 mm long. ANT/BL 1.83–1.93. Other ratios: ANT VI/ANT III 1.47–1.71; PT/BASE 11.69–13.46; SIPH/BL 0.08–0.09; FEMUR III/BL 0.29–0.3; TIBIA III/BL 0.61; URS/ANT III 0.11; URS/SIPH 0.69. ANT III with 91–97 rhinaria, ANT IV with 38–41 rhinaria, ANT V with 21–26 rhinaria. URS with eight accessory setae. DAT I–II inconspicuous. DAT III 0.13–0.15 mm long, DAT IV 0.04–0.05 mm long. Dorsal setae 0.04–0.06 mm long, with pointed apices. ABD I–V with 2–4 setae on spinal sclerites. Marginal sclerites with 2–6 setae. Genitalia with basal part of phallus robust, elongated, hook-shaped (Figure 14I).

Host plants: *Acer rubrum*, *Acer saccharum*.

Distribution: Canada: New Brunswick (Middle Kouchibouguac‡); Nova Scotia (Jakes Landingˆ, Kejimkujik Main Parkway‡, Upper Hammonds Plains‡); Ontario (Callander, Cambridge°, Corwhinˆ, Front of Yonge‡ (44°30′00.0″ N 75°54′00.0″ W), Griffithˆ, Kitchener‡, Marentette Beach in Wheatleyˆ); Prince Edward Island (Stanhope); Quebec (Shawinigan (Lac Wapizagonke‡)). USA: Florida (Gainesville, Sebring (Highlands Hammock State)); Georgia (Savannah); Maine (Presque Isle); Massachusetts (Mount Grace (Warwick)); North Carolina (Andrew's Bald in Great Smoky Mountains National Park* (35°32′16.8″ N 83°29′38.4″ W), Blue Ridge Parkway, Greensboro—locus typicus, Purchase Knob in Great Smoky Mountains National Park* (35°35′16.2″ N 83°03′53.4″ W), Raleigh, Sparta‴); Michigan (Chippewa Township° (46°18′00.0″ N 85°06′00.0″ W), Eckerman Cornerˆ); Pennsylvania (Bethayres, Center Hall, Cooksburg, Miquon, Philipsburg, Pleasant Gap, State College); Tennessee (Bote Mountain Trail in Great Smoky Mountains National Park* (35°34′37.1″ N 83°44′02.3″ W), Gatlinburg°); Wisconsin (Sturgeon Bay) (Figure 28) ([23,24,27]; Centre for Biodiversity Genomics—Canadian Specimens [‡]; Illinois Natural History Survey Insect Collection [*]; International Barcode of Life project (iBOL) [ˆ]; International Nucleotide Sequence Database Collaboration [°]; NMNH Extant Specimen Records (USNM, US) [‴]).

Additional distribution from iNaturalist (www.inaturalist.org, accessed on 12 June 2024): Pennsylvania (Wyndmoor); Virginia (Dulles).

3.4.12. *Drepanaphis robinsoni* Malik sp. nov.

urn:lsid:zoobank.org:act:3C2B4AAD-E06A-410B-940D-AEA4E96662FC

Figures 1L, 3L, 4L, 5L, 11L, 21F and 29; Table 4

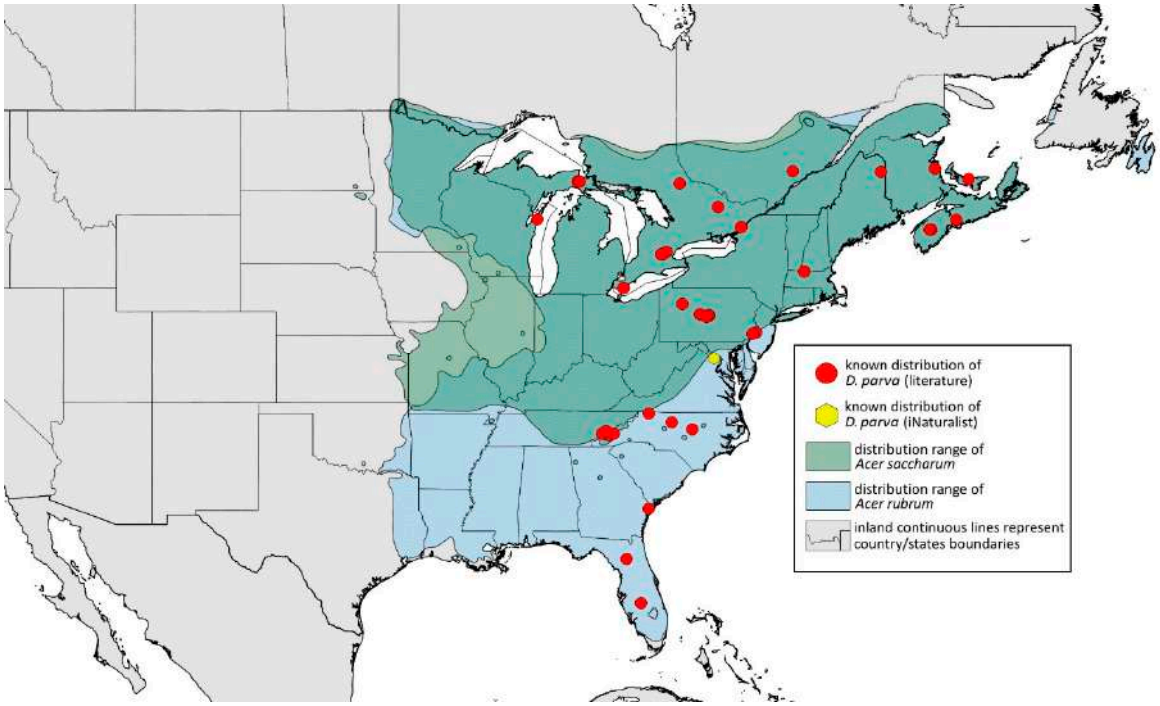

Figure 28. Known distribution of *Drepanaphis parva* in North America, with distribution ranges of its host plants.

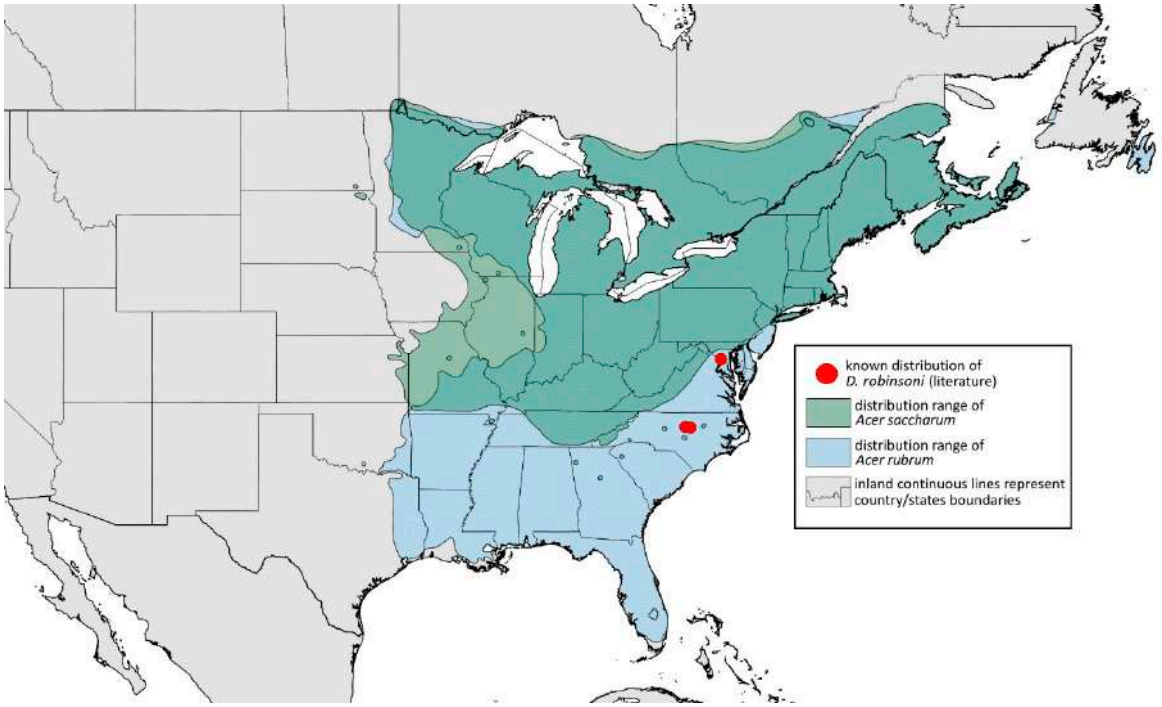

Figure 29. Known distribution of *Drepanaphis robinsoni* in North America, with distribution ranges of its host plants.

Material examined: Holotype. *Drepanaphis choanotricha* Dillery & Smith [MS], Al. Viv ♀, US/153 HLGS det.//Acer saccharum, Umstead Park, Raleigh N.C., U.S.A, 19●VI●1966, HLGS leg. BM 1982-492//NHMUK 14314713—one alate viv. fem. PARATYPES *Drepanaphis choanotricha* Dillery & Smith [MS], Al. Viv ♀, US/153 HLGS det.//Acer saccharum, Umstead Park, Raleigh N.C., U.S.A, 19●VI●1966, HLGS leg. BM 1982-492//NHMUK

14314714—one alate viv. fem. *Drepanaphis parva* Smith, BM 1984-340 Det: Dillery & Smith//N.U.S.A, Acer rubrum, Chapel Hill N.C., 2●VII●1965, Dillery and Smith leg. 65.127//NHMUK 12821447—three alate viv. fem. *Drepanaphis parva* Smith, BM 1984-340 Det.: C. F. Smith//N.U.S.A, Acer rubrum, Raleigh N.C., 5●VII●1959, Leg: C. F. Smith. 59.394 O//NHMUK 12821448—three alate viv. fem; SA02-385-05-001 DZUS—one alate viv. fem., 22 September 2022, Washington, D.C., USA, Acer rubrum, K. Malik leg. & det.
Additional material examined—Table S6.

Alate viviparous female—description (n = 11)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, ANT I, thorax brown (Figure 21F). ANT II–V pale brown with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wings clear with smudge-bordered ends of veins. Pterostigma distinct, darkly pigmented, with small area inside without pigmentation (Figure 3L). Abdomen pale with DAT I pale, DAT II and IV brown and DAT III dark brown (Figure 1L). Siphunculi, cauda, subgenital and anal plate pale. Legs pale brown, fore femora slightly darker at margins (Figure 4L).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.01–0.02 mm long with blunt apices; one pair of pointed frontal setae on ventral side, 0.05–0.06 mm long. ANT/BL 2–3.2; PT/BASE 9.39–15.7. ANT III with 9–13 secondary rhinaria, BASE with 4 accessory rhinaria. URS with six accessory setae. Other ratios: ANT IV/ANT III 0.66–0.81; ANT V/ANT III 0.69–0.85; ANT VI/ANT III 1.54–2.67; URS/ANT III 0.09–0.12; URS/BASE 0.67–0.84; URS/SIPH 0.44–0.62; HT II/ANT III 0.09–0.12; HT II/BASE 0.64–0.86; TIBIA III/BL 0.54–0.85; SIPH/BL 0.09–0.17; SIPH/CAUDA 1.63–2.12. DAT I 0.06–0.08 mm long; DAT II 0.05–0.11 mm long; DAT III biggest, 0.14–0.22 mm long (Figure 11L); DAT IV smallest, 0.04–0.06 mm long. Dorsal setae 0.02–0.03 mm long with blunt apices. Marginal sclerites with 3–4 setae. Siphunculi flask-shaped (Figure 5L).

Oviparous female: Unknown.

Male: Unknown.

Remarks: The new species *D. robinsoni* was designated based on two other incorrectly designated species of the *Drepanaphis* genus. These species include *D. choanotricha* (NHMUK 14314713, NHMUK 14314714) and *D. parva* (NHMUK 12821445, NHMUK 12821447, INHS Insect Collection 1058904). The fresh material of this new species was also collected in Washington, D.C.

Diagnosis: Alate viviparous females of the new species can be easily distinguished from the closely related *D. parva* by their pale siphunculi and lack of sclerotisation on the abdomen and from *D. choanotricha* by the presence of only four accessory rhinaria.

Etymology: We are pleased to name this new species in honour of Arthur Grant Robinson, an eminent Canadian aphidologist, who collected specimens of this species.

Host plants: *Acer rubrum*, *Acer saccharum*.

Distribution: USA: North Carolina (Chapel Hill, Doughton, Raleigh—locus typicus (Umstead Park)); Washington, D.C. (Figure 29).

3.4.13. *Drepanaphis sabrinae* Miller, 1937

Drepanaphis sabrinae Miller, 1937: 69(5): 111 [22]

Figures 1M, 2C, 3M, 4M, 5M, 11M, 22D, 30A and 31; Tables 2 and 4

Material examined: See Table S6.

Alate viviparous female—re-description (n = 14)

Colour. In life: Abdomen orange brown, sometimes yellowish. Small flecks of white wax present, three to five on head; four antero-medial, two antero-lateral and two postero-medial on mesonotum; two lateral on metanotum; some on abdomen. Pronotum with three longitudinal wax stripes, median stripe interrupted and faint [27].

Pigmentation of mounted specimens: Head, ANT, thorax and legs brown to dark brown (Figure 30A). ANT II–VI with darker apices on ANT III–V and dark area with primary

rhinarium on ANT VI. Wings clear, pterostigma distinct, darker pigmentation on ends, with small area inside without pigmentation (Figure 3M). Abdomen pale with dark dorsal tubercles, lighter on bases, darker on tips (Figure 1M), and pale brown sclerotisation. Siphunculi pale brown to brown, slightly darker on ends (Figure 5M). Fore femora dark dorsally (Figure 4M). Tibiae with slightly darker knee apical parts on ends. Cauda, subgenital and anal plate pale.

Table 4. Measurements (in mm) of alate viviparous females of *Drepanaphis* (part 2).

Character	*D. nigricans* n = 51	*D. parva* n = 15	*D. robinsoni* sp. nov. n = 11	*D. sabrinae* n = 14	*D. saccharini* n = 15	*D. simpsoni* n = 12	*D. spicata* n = 19	*D. tissoti* n = 25	*D. utahensis* n = 26
BL	1.04–2.12	1.85–2.7	1.22–1.73	1.75–2.76	1.58–2.40	1.69–2.41	2.12–3	0.99–1.8	1.55–2.8
HW	0.2–0.33	0.29–0.39	0.25–0.29	0.33–0.39	0.29–0.33	0.3–0.36	0.3–0.43	0.21–0.29	0.27–0.39
ANT I-VI	3.29–5.16	3.22–4.9	3.15–3.91	3.2–5	3.65–4.57	2.62–3.43	4.7–5.86	3.11–4.19	2.32–4.17
ANT III	0.6–1.04	0.81–1.31	0.73–0.88	0.77–1.19	0.80–1.1	0.69–0.85	1.04–1.37	0.7–1.11	0.74–1
ANT IV	0.52–0.73	0.52–0.87	0.52–0.67	0.59–0.99	0.58–0.89	0.51–0.61	0.78–1.07	0.46–0.63	0.48–0.78
ANT V	0.56–0.78	0.51–0.84	0.57–0.72	0.61–0.97	0.58–0.85	0.44–0.58	0.76–1.04	0.47–0.71	0.44–0.73
ANT VI	1.02–1.99	0.95–1.85	1.51–1.95	1.04–1.85	1.16–1.68	0.73–0.97	1.54–2.33	1.03–2.11	0.76–1.5
BASE	0.1–0.16	0.12–0.16	0.1–0.14	0.13–0.2	0.1–0.14	0.12–0.15	0.12–0.19	0.09–0.13	0.12–0.17
PT	0.9–1.84	0.83–1.7	1.03–1.83	0.9–1.66	1.04–1.56	0.6–0.85	1.37–2.17	0.9–1.98	0.62–1.33
FEMUR I length	0.45–0.72	0.53–0.66	0.45–0.55	0.6–0.88	0.53–0.79	0.5–0.59	0.74–1.03	0.44–0.6	0.51–0.87
FEMUR I width	0.07–0.13	0.08–0.15	0.09–0.12	0.11–0.18	0.11–0.15	0.14–0.17	0.09–0.18	0.05–0.09	0.1–0.18
FEMUR III	0.41–0.65	0.4–0.67	0.39–0.47	0.51–0.83	0.46–0.7	0.49–0.65	0.65–0.9	0.4–0.59	0.5–0.73
TIBIA III	0.84–1.34	1.03–1.45	0.9–1.05	1.11–1.61	1.03–1.51	0.92–1.04	1.36–1.89	0.82–1.16	1.05–1.48
HT II	0.08–0.12	0.1–0.13	0.08–0.09	0.10–0.13	0.10–0.12	0.10–0.12	0.11–0.14	0.08–0.1	0.1–0.14
URS	0.08–1	0.09–0.11	0.08–0.09	0.12–0.13	0.09–0.11	0.08–0.09	0.1–0.12	0.08–0.1	0.08–0.1
SIPH	0.12–0.22	0.21–0.3	0.14–0.21	0.19–0.34	0.19–0.21	0.16–0.21	0.24–0.43	0.13–0.21	0.18–0.3
CAUDA	0.07–0.96	0.09–0.15	0.08–0.1	0.09–0.13	0.08–0.14	0.1–0.13	0.1–0.15	0.07–0.11	0.1–0.17

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.02–0.04 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.07–0.01 mm long. ANT/BL 1.18–2.51; PT/BASE 5.82–9.66. ANT III with 6–10 secondary rhinaria, BASE with 5–6 accessory rhinaria (Figure 2C). URS with 8–14 accessory setae. Other ratios: ANT IV/ANT III 0.65–0.88; ANT V/ANT III 0.67–0.93; ANT VI/ANT III 1.25–1.9; URS/ANT III 0.11–0.14; URS/BASE 0.68–0.95; URS/SIPH 0.42–0.65; HT II/ANT III 0.09–0.14; HT II/BASE 0.53–0.77; TIBIA III/BL 0.52–0.78; SIPH/BL 0.09–0.16; SIPH/CAUDA 2.01–2.54. DAT I 0.09–0.15 mm long; DAT II and III equal, 0.12–0.23 mm long (Figure 11M); DAT IV smallest, 0.03–0.07 mm long. Dorsal setae 0.03–0.04 mm long with pointed apices, on small sclerites. Marginal sclerites with 2–5 setae. Siphunculi tubular (Figure 5M).

Oviparous female—description (n = 2)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head and thorax brown, abdomen pale. ANT I–II brown. ANT III–VI dark brown with lighter apices on ANT VI. Abdomen pale with dark sclerotisation. Siphunculi, subgenital, anal plate and cauda brown. Fore, middle, hind femora and siphunculi brown. Tibiae dark brown. Tarsi brown (Figure 22D).

Morphometric characters: Head setae: two pairs of fronto-orbital setae 0.08–0.09 mm long, one pair of postero-dorsal setae mm long, one pair of latero-dorsal setae 0.05–0.7 mm long with pointed apices on dorsal side; one pair of pointed frontal setae on ventral side 0.09 mm long. ANT/BL 1.33–1.39. Other ratios: ANT VI/ANT III 1.5–1.76; PT/BASE 7.19–7.57; SIPH/BL 0.08–0.1; FEMUR III/BL 0.24; TIBIA III/BL 0.46–0.47; HT II/ANT VI 0.09; URS/ANT III 0.15–0.16; URS/BASE 0.75–0.86; URS/SIPH 0.5–0.6. ANT III with

one or without secondary rhinaria. URS with 8–10 accessory setae. Hind tibiae with 70–76 pseudosensoria distributed along almost their entire lengths. Dorsal setae 0.04 -0.09 mm long. Siphunculi tubular.

Male: Unknown.

Remarks: Smith [23] lists Hardeeville as a place of occurrence, along with Raleigh and Chapel Hill, and located all of them in North Carolina. However, the locality of Hardeeville occurs only in South Carolina and is thus classified in this work as such a locality for this species.

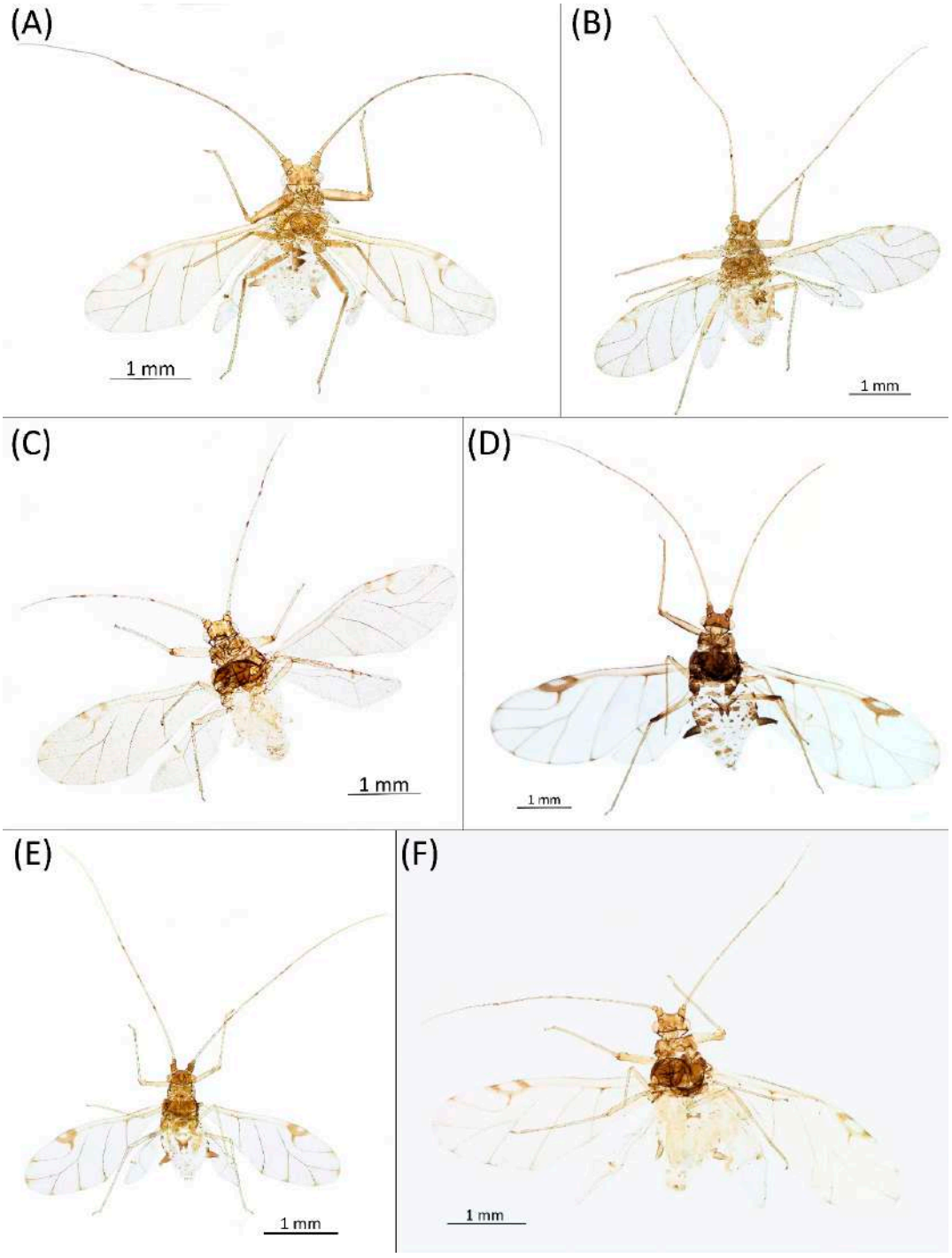

Figure 30. Alate viviparous females of the genus *Drepanaphis*: (**A**) *D. sabrinae*, (**B**) *D. saccharini*, (**C**) *D. simpsoni*, (**D**) *D. spicata*, (**E**) *D. tissoti*, (**F**) *D. utahensis*.

Host plant: *Acer saccharum*.
Distribution: USA: Maine (Orono); Massachusetts (Amherst—locus typicus, Groton); Michigan (Albion (College Campus)); Minnesota (Saint Paul); New York (Ithaca); North Carolina (Chapel Hill, Laurinburg (Jaycee Park†), Raleigh (Fred Fletcher Park)); Pennsylvania (State College); South Carolina (Hardeeville) (Figure 31) ([23,27]; new record in this publication [†]).

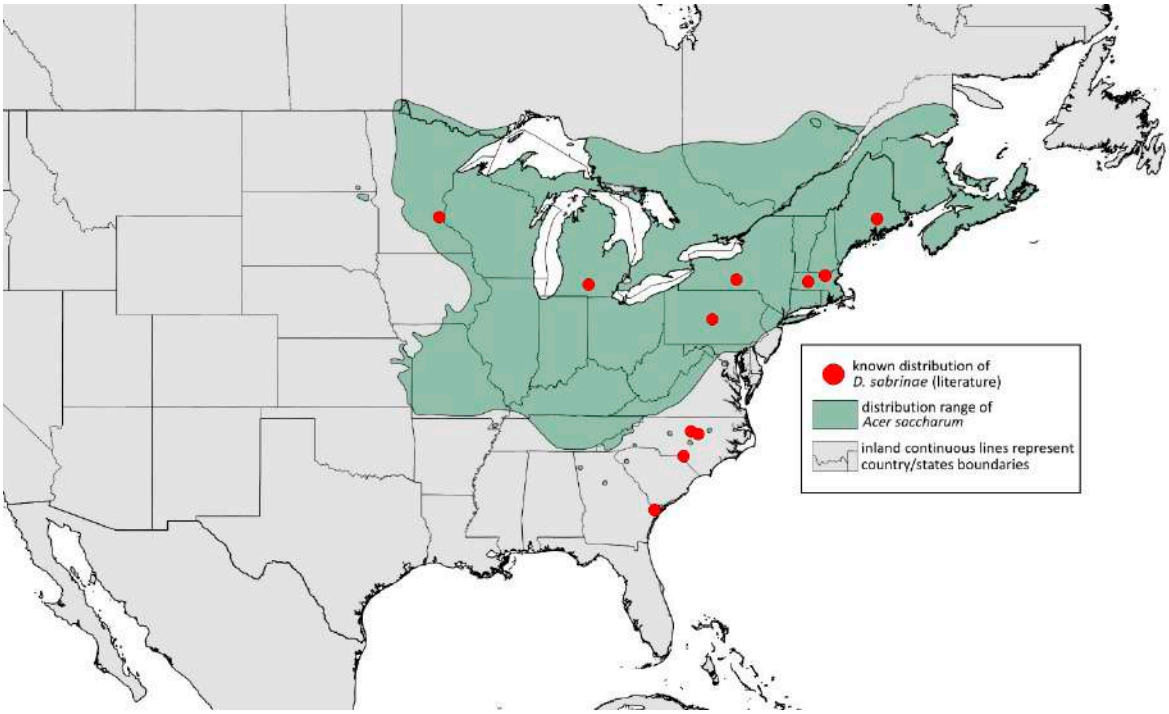

Figure 31. Known distribution of *Drepanaphis sabrinae* in North America, with distribution ranges of its host plants.

3.4.14. *Drepanaphis saccharini* Smith & Dillery, 1968

Drepanaphis saccharini Smith & Dillery, 1968: 61(1): 186, 198 [27]
Figures 1N, 3N, 4N, 5N, 30B and 32; Table 2
Material examined: Holotype. Drepanaphis saccharini S & D Det. Smith & Dillery, 60-887, Silver Maple//St. James, Minn, 8●3●60, Holotype, S●S—one alate viv. fem. (USNM). Paratype. Drepanaphis saccharini S & D Det. Smith & Dillery, 60-887, Silver Maple, Paratype//St. James, Minn, 8●3●60, S●S//INHS, Insect Collection 1058912—one alate viv. fem. Paratype. Drepanaphis saccharini Smith & Dillery, paratype, Det: Smith & Dillery, BM 1984-340//N.U.S.A., Pl. Silver maple, Loc. St. James, Minn., Date 3.VIII.1960, Leg. S. S. S//NHMUK 12821470—three alate viv. fem.
Additional material examined—Table S6.
Alate viviparous female—re-description (n = 15)
Colour. In life: Abdomen greenish with white tip [27].
Pigmentation of mounted specimens: Head, ANT I and thorax brown (Figure 30B). ANT II–VI pale brown with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wings clear, pterostigma palely pigmented, with large area inside without pigmentation (Figure 3N). Abdomen pale with dorsal abdominal tubercles dark (Figure 1N) and sclerotisation pale brown. Siphunculi, cauda, subgenital and anal plate pale brown. Legs pale brown. Fore femora slightly darker on margins (Figure 4N), hind femora with smudge.
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.02–0.05 mm long with pointed

apices; one pair of pointed frontal setae on ventral side, 0.08 mm long. ANT/BL 1.2–2.4; PT/BASE 8.68–14.04. ANT III with 6–10 secondary rhinaria, BASE with 4 accessory rhinaria. URS with 6–8 accessory setae. Other ratios: ANT IV/ANT III 0.69–0.87; ANT V/ANT III 0.69–0.83; ANT VI/ANT III 1.27–1.97; URS/ANT III 0.11–0.13, URS/BASE 0.78–0.91; URS/SIPH 0.46–0.57; HT II/ANT III 0.1–0.14; HT II/BASE 0.8–1.1; TIBIA III/BL 0.56–0.66. SIPH/BL 0.09–0.12; SIPH/CAUDA 1.48–2.34. DAT I and II equal 0.03–0.08 mm long; DAT III biggest, 0.08–0.17 mm long (Figure 11N); DAT IV smallest, 0.02–0.04 mm long. ABD I–V with dorsal setae 0.03–0.04 mm long with pointed apices, on small sclerites. Marginal sclerites with 2–6 setae. Siphunculi flask-shaped (Figure 5N).
Remarks: Sexual generation remains unknown.
Host plants: *Acer saccharinum*, *Acer rubrum*.
Distribution: Canada: Ontario (Toronto). USA: Georgia (Oakwood); Illinois (Chemung, Oakwood); Iowa (Decorah); Kansas (Wathena); Maryland (Beltsville, Plummers Island); Minnesota (Cannon Falls, Saint James—locus typicus, Savage); New York (Chemung); North Carolina (Burlington, Hendersonville, Moravian Falls); Ohio (Gallipolis) (Figure 32) [27].

3.4.15. *Drepanaphis simpsoni* Smith, 1959

Drepanaphis simpsoni Smith, 1959: 52(6): 647 [26]
= *Drepanaphis pallida* Richards, 1969: 101(1): 107 [28]
Figures 1O, 3O, 4O, 5O, 11O, 14J, 24D, 30C, 33A and 34; Tables 2–4
Material examined: Holotype. Drepanaphis simpsoni Smith, Holotype + Allotype C. F. S. Det: D. H. R. L. C. F. SMith//N. U. S. A. Pl. Acer saccharum, Loc. Presque Isle (Maine), Date 10.IX.1956, Leg. Simpson & H. R. L. 465, BM1984-340—two alate viv. fem., one alate viv. male. Paratype. Drepanaphis simpsoni Smith + kanzenis Smith, oviparae, Det. C. F. Smith//N. U. S. A. Pl. Acer saccharum, Loc. Presque Isle (Maine), Date 10.IX.1956, Leg. Simpson & H. R. L. 465, BM1984-340—three Viviparous ♀♀. Paratype. Drepanaphis simpsoni Smith, Acer saccharum//Presque Isle, Me., Oct. 9, 1958, Simpson//INHS, Insect Collection 1058916—one alate viv. fem.
Additional material examined—Table S6.
Alate viviparous female—re-description (n = 12)
Colour. In life: Head and thorax reddish brown, somewhat darker dorsally with short, fine, longitudinal, white wax stripes. Abdomen light yellow to white with DAT I reddish brown [27].
Pigmentation of mounted specimens: Head, ANT I–II and pronotum brown (Figure 30C). Rest of thorax dark brown. ANT II–VI pale brown with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wings clear, pterostigma distinct, darkly pigmented, with small area inside without pigmentation (Figure 3O). DAT I dark; DAT II, III and IV pale brown on apices (Figure 1O). Cauda, subgenital and anal plate brown. Legs, abdomen and siphunculi pale. Fore femora darker on ends (Figure 4O).
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.01–0.03 mm long with pointed apices; two pairs of pointed frontal setae on ventral side, 0.04–0.05 mm long. ANT/BL 1.17–1.61; PT/BASE 4.62 -7.08. ANT III with 8–13 secondary rhinaria, BASE with 4 accessory rhinaria. URS with 4–6 accessory setae. Other ratios: ANT IV/ANT III 0.66–0.83; ANT V/ANT III 0.58–0.76; ANT VI/ANT III 0.98–1.33; URS/ANT III 0.1–0.12; URS/BASE 0.59–0.67; URS/SIPH 0.42–0.48; HT II/ANT III 0.13–0.17; HT II/BASE 0.77–1.0; TIBIA III/BL 0.42–0.56; SIPH/BL 0.07–0.11; SIPH/CAUDA 0.63–2.16. DAT I biggest, 0.17–0.22 mm long, DAT II 0.1–0.16 mm long, DAT III 0.08–0.16 mm long (Figure 11O), DAT IV smallest, 0.05–0.11 mm long. End of tubercles with setae 0.02 mm long. Dorsal setae 0.02–0.03 mm long with pointed apices. Siphunculi tubular (Figure 5O).
Oviparous female—description (n = 3)
Colour. In life: Unknown.
Pigmentation of mounted specimens: Head, thorax, siphunculi pale. ANT and legs pale

brown, ANT II–VI with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Cauda, subgenital and anal plate brown (Figure 33A).

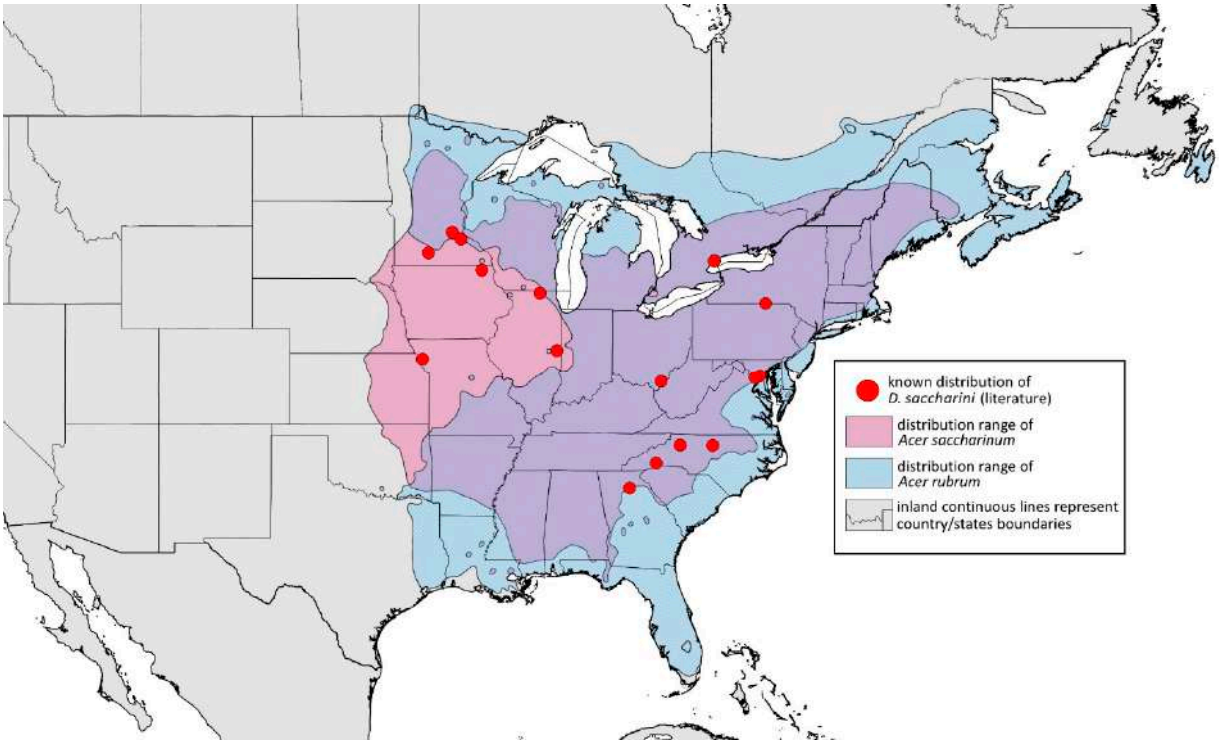

Figure 32. Known distribution of *Drepanaphis saccharini* in North America, with distribution ranges of its host plants.

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.07–0.1 mm long with blunt apices; two pairs of pointed frontal setae on ventral side, 0.08–0.1 mm long. ANT/BL 1.04–1.17. Other antennal ratios: ANT VI/ANT III 0.93–1.82; PT/BASE 4.07–9.92; SIPH/BL 0.05–0.06; III FEMUR/BL 0.21–0.22; TIBIA III/BL 0.4–0.41; HT II/ANT VI 0.08–0.17; URS/ANT III 0.11–0.12; URS/BASE 0.57–0.75; URS/SIPH 0.53. ANT III without secondary rhinaria. URS with 6–9 accessory setae. Hind tibiae with 43 pseudosensoria more abundant in middle part of tibiae, closer to distal part. Dorsal setae 0.08–0.12 mm long, on ABD VIII slightly shorter. Siphunculi tubular.

Alate male—re-description (n = 3)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, ANT I–II, thorax and siphunculi brown. ANT III–VI pale brown, ANT II–V with slightly darker apices on ends of segments and dark area with primary rhinarium on ANT VI. Wings clear, pterostigma palely pigmented, with large area inside without pigmentation. Cauda and anal plate brown. Abdomen pale with dark sclerotisation. Legs pale brown (Figure 24D).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.01–0.03 mm long with pointed apices; two pairs of pointed frontal setae on ventral side, 0.03–0.04 mm long. ANT/BL 1.33–1.62. Other ratios: ANT VI/ANT III 0.99–1.14; PT/BASE 5.16–5.85; SIPH/BL 0.07–0.09; III FEMUR/BL 0.24–0.31; TIBIA III/BL 0.45–0.56; URS/ANT III 0.55–0.56; URS/SIPH 0.64–0.73. ANT III with 92–118 rhinaria, ANT IV with 62–82 rhinaria, ANT V with 30–38 rhinaria. URS with six accessory setae. DAT inconspicuous. Dorsal setae 0.02–0.03 mm long, with pointed apices. ABD II–VI with distinct spinal sclerites, each with 2–4 setae. Marginal sclerites with 1–3 setae. Siphunculi tubular. Genitalia with basal part of phallus rectangular, with broadly rounded apices (Figure 14J).

Remarks: The analysis of type material of *D. pallida* confirmed its identity with *D. simpsoni*.
Host plant: *Acer saccharum*.
Distribution: Canada: New Brunswick (Fredericton); Ontario (New Castle, Ottawa). USA: Connecticut (Windsor); Maine (Orono, Presque Isle—locus typicus); Massachusetts (Amherst); New York (Ithaca); Pennsylvania (State College) (Figure 34) [26,27].

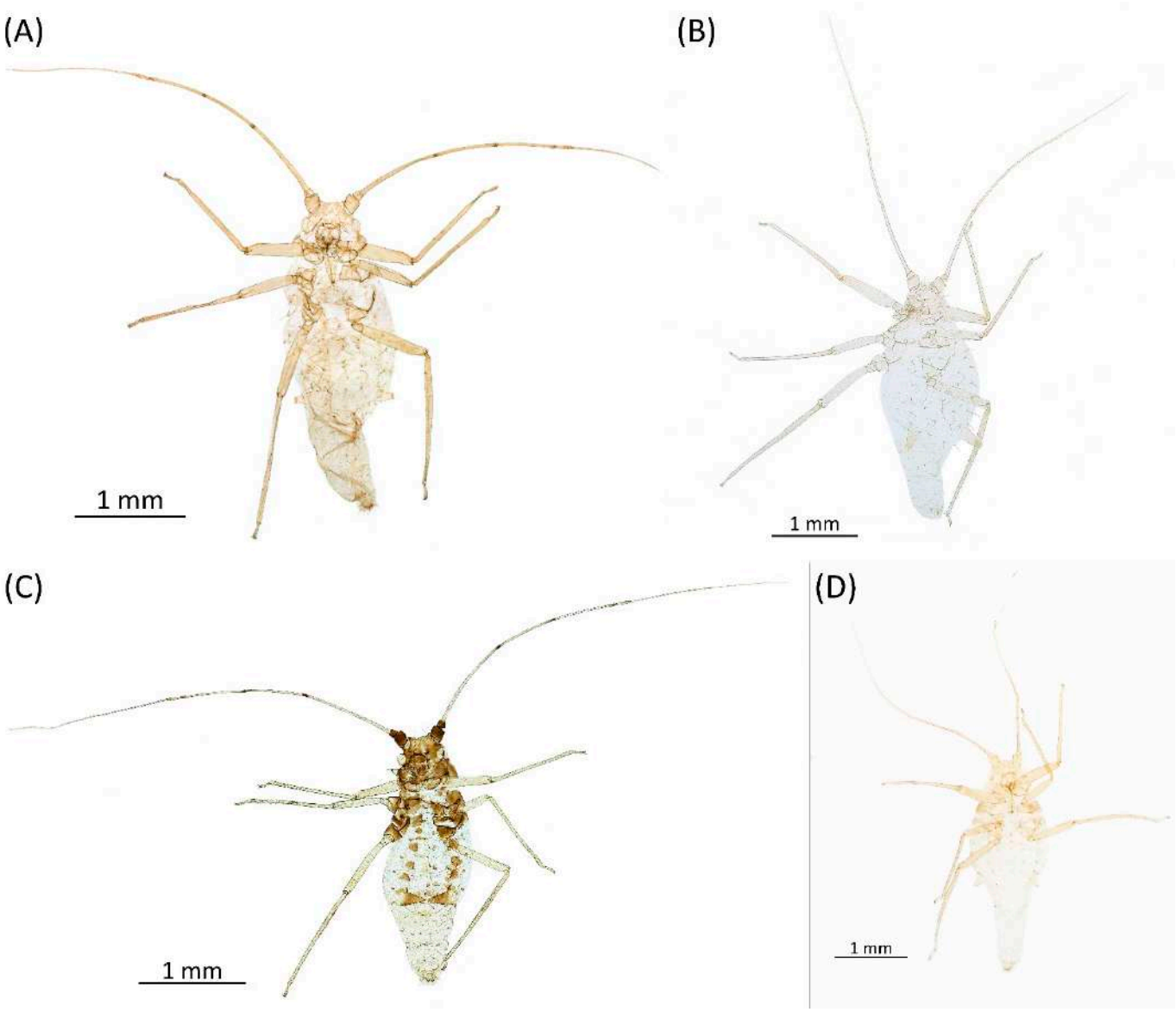

Figure 33. Oviparous females of the genus *Drepanaphis*: (**A**) *D. simpsoni*, (**B**) *D. spicata*, (**C**) *D. tissoti*, (**D**) *D. utahensis*.

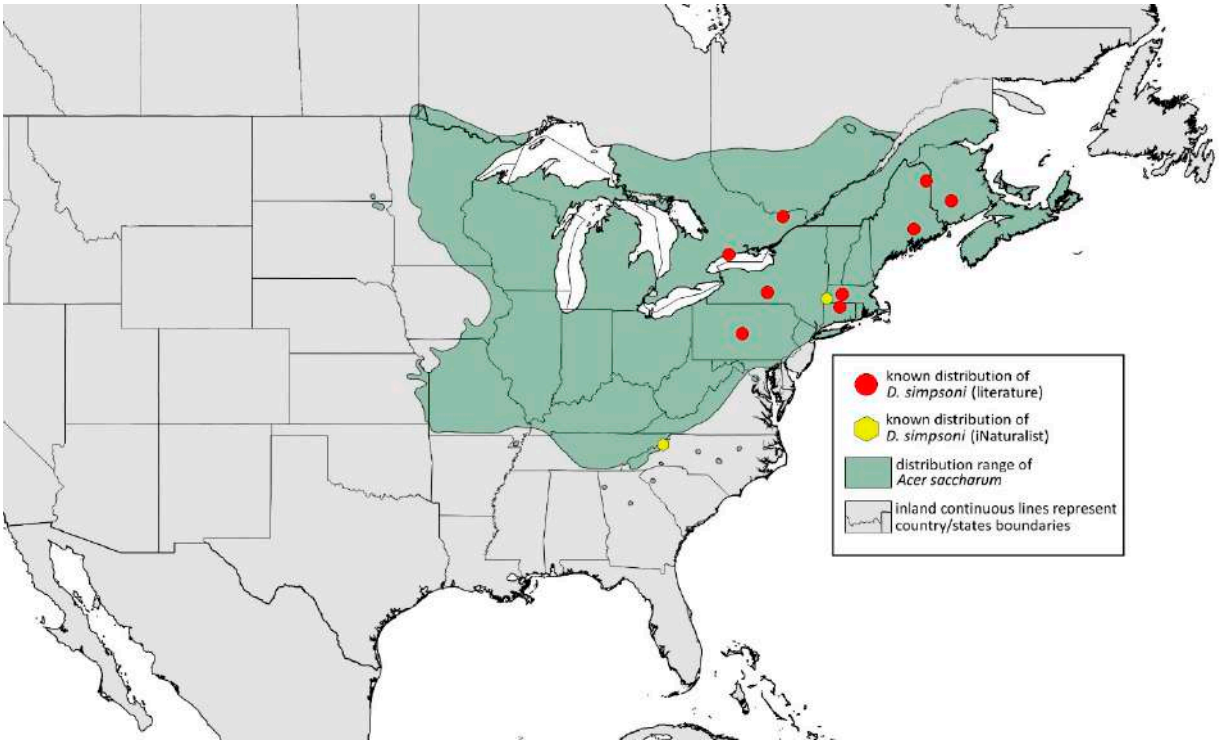

Figure 34. Known distribution of *Drepanaphis simpsoni* in North America, with distribution ranges of its host plants.

Additional distribution from iNaturalist (www.inaturalist.org, accessed on 12 June 2024): Massachusetts (Great Barrington); Tennessee (Roan Mountain).

3.4.16. *Drepanaphis spicata* Smith, 1941

Drepanaphis spicatum Smith, 1941: 57(2): 228, 241 [23]
= *Drepanaphis spicata* Palmer, 1952: 5:87 [51]
Figures 1P, 3P, 4P, 5P, 11P, 14K, 24E, 30D, 33B and 35; Tables 2 and 4
Material examined: Holotype. Drepanaphis spicatum Smith Holotype Type No 55839. D.D.N.N.M.//N. C. 41-150, Acer spicatum, Mt. Mitchell, (Camp Alice), July 2, 1941, C. F. Smith, Remounted June 7,00—two alate viv. fem. (USNM). Paratype. Drepanaphis spicatum C. F. Smith//N. C. 41-188, Acer spicatum, On Park Way, Busic, N. C. 7-31-41, C. F. S.//INHS, Insect Collection 1058917—five alate viv. fem.
Additional material examined—Table S6.
Alate viviparous female—re-description (n = 19)
Colour. In life: Entire body powdery white except dark fuscous thoracic lobes, DAT III, siphunculi and brownish-yellow, U-shaped line more or less connecting DAT III to siphunculi. Fore femora dark [27].
Pigmentation of mounted specimens: Head, ANT I–II and pronotum brown (Figure 30D). Rest of thorax dark brown. ANT II–VI pale brown with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wing veins clear, pterostigma distinct, very darkly pigmented, with small area inside without pigmentation (Figure 3P), radius veins dark brown. Abdomen pale with DAT III dark (Figure 1P) and dorsal sclerotisation dark. Cauda, subgenital and anal plate pale brown to brown. Fore femora brown, darker dorsally (Figure 4P). Middle femora pale brown, hind femora pale brown with dark stripes at margins.
Morphometric characters: Head setae: two pairs of fronto-orbital setae 0.05–0.07 mm long, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.03–0.05 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.09–0.012 mm long. ANT/BL 1.77–2.35; PT/BASE 7.86–14.63. ANT III with 9–15 secondary rhinaria,

BASE with 4 accessory rhinaria. URS with 6–8 accessory setae. Other ratios: ANT IV/ANT III 0.67–0.95; ANT V/ANT III 0.6–0.88; ANT VI/ANT III 1.19–2.06; URS/ANT III 0.08–0.1; URS/BASE 0.6–0.8; URS/SIPH 0.26–0.41; HT II/ANT III 0.08–0.11; HT II/BASE 0.63–0.85; TIBIA III/BL 0.54–0.73; SIPH/BL 0.1–0.18; SIPH/CAUDA 1.87–3.17. DAT III significant, 0.22–0.31 mm long (Figure 11P). Dorsal setae with pointed apices, 0.04–0.06 mm long, on small sclerites. Marginal sclerites with 3–6 setae. Siphunculi flask-shaped (Figure 5P).

Oviparous female—description (n = 1)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Body in general pale brown, with slightly darker hind tibiae and ends of siphunculi (Figure 33B).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.08–0.12 mm long with blunt apices; one pair of pointed frontal setae on ventral side, 0.11 mm long. ANT/BL 1.2. Other ratios: ANT VI/ANT III 1.19; PT/BASE 6.85; SIPH/BL 0.08–0.09; FEMUR III/BL 0.24–0.25; TIBIA III/BL 0.48–0.49; HT II/ANT VI 0.12; URS/ANT III 0.12; URS/BASE 0.77; URS/SIPH 0.43. URS with 10 accessory setae. Hind tibiae with 59–71 pseudosensoria distributed in central part of tibiae. Dorsal setae 0.1–0.13 mm long, on ABD VIII slightly shorter, to 0.09 mm long. Siphunculi flask-shaped.

Alate male—re-description (n = 1)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, ANT I–II, thorax and siphunculi brown. ANT III–VI pale brown, ANT II–V with slightly darker apices on ends of segments and dark area with primary rhinarium on ANT VI. Wings clear, pterostigma distinct, darkly pigmented, with small area inside without pigmentation. Abdomen pale with dark sclerotisation. Cauda and anal plate brown. Legs pale, fore femora darker dorsally, hind femora with dark stripes on the apical parts (Figure 24E).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.03–0.05 mm long with pointed apices; one pair of pointed frontal setae on ventral side, 0.07 mm long. ANT/BL 1.76–1.94. Other ratios: ANT VI/ANT III 1.58–1.24; PT/BASE 9.47–12.6; SIPH/BL 0.14; FEMUR III/BL 0.29; TIBIA III/BL 0.62; URS/ANT III 0.09; URS/SIPH 0.73. ANT III with 106–107 rhinaria, ANT IV with 46 rhinaria, ANT V with 23–25 rhinaria. URS with 12 accessory setae. Dorsal tubercles inconspicuous. Dorsal setae 0.04–0.06 mm long, with pointed apices. ABD I–VI with spinal sclerites and 2–4 setae. Marginal sclerites with 1–3 setae. Siphunculi flask-shaped. Genitalia with basal part of phallus short, robust and almost square-shaped (Figure 14K).

Remarks: Smith and Knowlton [24] note in their article that individuals from Utah and Idaho are slightly different from other representatives of this species. They note the difference in abdominal dorsal tubercule III, usually longer, and with fewer and smaller dark areas around the hairs on the dorsal side of the abdomen.

Host plant: *Acer spicatum*, specimens from Utah and Idaho known from *Acer grandidentatum*.

Distribution: Canada: Manitoba (Caddy Lake, Camp Morton, Grand Beach); Quebec (Chute Panet, Saint-Nicolas). USA: Idaho (Franklin, Mink Creek); North Carolina (Buck Creek Gap, Grandfather Mountain, Mount Mitchell—locus typicus); Pennsylvania (Philipsburg, Pleasant Gap, Sprace Creek (Colerain Park), State College (Poe Paddy Laken Tussey Tower), Woodward); Utah (Big Cottonwood Canyon, Blacksmith Fork Canyon, City Creek Canyon, Logan Canyon, Mantua, Mount Nebo, Mount Sterling in Smithfield Canyon, Provo Canyon, Strawberry Creek, Weber Canyon) (Figure 35) [23,24,27].

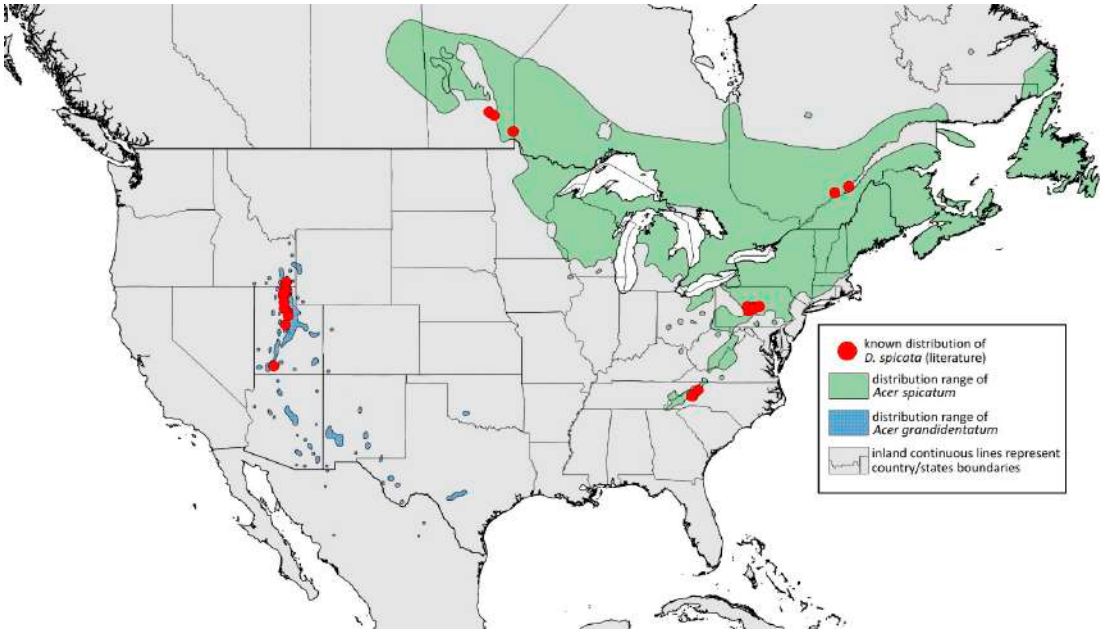

Figure 35. Known distribution of *Drepanaphis spicata* in North America, with distribution ranges of its host plants.

3.4.17. *Drepanaphis tissoti* Smith, 1944 stat. rev.

Drepanaphis tissoti Smith, 1944: 27(3): 55 [25]

Figures 1Q, 2D, 3Q, 4Q, 5Q, 11Q, 30E, 33C and 36; Tables 2 and 3

Material examined: Holotype. Drepanaphis tissoti Smith, Det. CFSmith, Acer rubrum//Gainesville, Florida, Hatchetcreek, 5-5-1941, A. N. Tissot coll. F-2207-41. Paracotype. Drepanaphis tissoti Smith, Acer rubrum,//Gainesville, Florida, Hatchetcreek, 5-5-1941, A. N. Tissot coll. F-2207-41//Museum Paris MNHN 25154—one alate viv. fem. Paracotype. Drepanaphis tissoti Smith, Acer rubrum,//Gainesville, Florida, Hatchetcreek, 5-5-1941, A. N. Tissot coll. B. M.1967-340. F-2207-41//NHMUK 12821452—one alate viv. fem.
Additional material examined—Table S6

Alate viviparous female—re-description (n = 25)

Colour. In life: Black with pale legs, wings with noticeable dark spots at end of veins. Head with three, pronotum with two longitudinal white wax stripes. Mesonotum with two antero-lateral wax dots; two anteromedial dots usually connected to two postero-medial dots to make two longitudinal stripes. Metanotum with two wax dots laterally. Abdomen with many wax dots, most dense at posterior end [27].

Pigmentation of mounted specimens: Head, thorax, ANT I–II dark brown (Figure 30E). ANT III–VI pale brown with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wings clear with dark pigmentation of ends of veins, radius veins dark brown. Pterostigma distinct, darkly pigmented, oval with small area inside without pigmentation (Figure 3Q). Abdomen pale with brown dorsal sclerotisation. Dorsal abdominal tubercles (Figure 1Q) and siphunculi dark brown. Cauda, subgenital and anal plate pale. Femora (Figure 4Q), tibiae and tarsi pale brown.

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.01–0.02 mm long with blunt apices. One pair of pointed frontal setae on ventral side, 0.05–0.06 mm long. ANT/BL 1.95–3.64; PT/BASE 7.2–16.8. ANT III with 8–11 secondary rhinaria, BASE with 5–11 accessory rhinaria (Figure 2D). URS with 6–9 accessory setae. Other ratios: ANT IV/ANT III 0.61–0.73; ANT V/ANT III 0.53–0.83; ANT VI/ANT III 1.18–2.72; URS/ANT III 0.11–0.13; URS/BASE 0.67–0.9; URS/SIPH 0.44–0.69; HT II/ANT III 0.1–0.13; HT II/BASE 0.65–0.85; TIBIA III/BL 0.57–0.88; SIPH/BL 0.09–0.18; SIPH/CAUDA 1.4–2.45. DAT I, II and IV inconspicuous. DAT III 0.15–0.19 mm long (Figure 11Q). Dorsal setae 0.01–0.02 mm long

with blunt apices, on small sclerites. Siphunculi flask-shaped (Figure 5Q).

Oviparous female—description (n = 1)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, ANT I–II, thorax, siphunculi dark brown. ANT and legs pale brown, ANT II–VI with darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Abdomen pale with dark sclerotisation. Cauda, subgenital and anal plate pale brown (Figure 33C).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.06-.0.07 mm long with blunt apices; one pair of pointed frontal setae on ventral side, 0.09 mm long. ANT/BL 1.6. Other ratios: ANT VI/ANT III 1.78–1.82; PT/BASE 12.5–12.8; SIPH/BL 0.074–0.086; FEMUR III/BL 0.23; TIBIA III/BL 0.42; HT II/ANT VI 0.05–0.06; URS/ANT III 0.088; URS/BASE 0.67; URS/SIPH 0.44. URS with eight accessory setae. Hind tibiae with 30–31 pseudosensoria more abundant on the middle part of tibiae, closer to knee area. Dorsal setae 0.08–0.1 mm long, marginal sclerites with 1–4 setae each. Siphunculi flask-shaped.

Male: Unknown.

Remarks: Remaudière and Remaudière, based on personal communication from F.W. Quednau [29], establish the synonymisation of *D. tissoti* with *D. nigricans* without sufficient morphological study. However, the analysis and comparison of both species indicate differences (particularly the significant differences between oviparous females of these species). The main features that differentiate the alate viviparous females of these species are the number of secondary rhinaria on ANT III (in the case of *D. nigricans*, more than 11, in the case of *D. tissoti*, never more than 11) and the number of accessory rhinaria on BASE (*D. nigricans* always with 4, *D. tissoti* with 5–11). However, the features between oviparous females are also significant: hind tibiae with 53–62 pseudosensoria (*D. nigricans*) and 30–31 pseudosensoria (*D. tossoti*). Differences are also present in the respective ratios: ANT VI/ANT III, TIBIA III/BL, URS/BASE.

Host plants: *Acer rubrum*, occasionally on *Acer saccharum*.

Distribution: USA: Florida (Hatchet Creek near Gainesville—locus typicus); North Carolina (Chapel Hill, Hope Valley Forest); Pennsylvania (Black Moshannon State Park, State College); South Carolina (Easley) (Figure 36) [25,27].

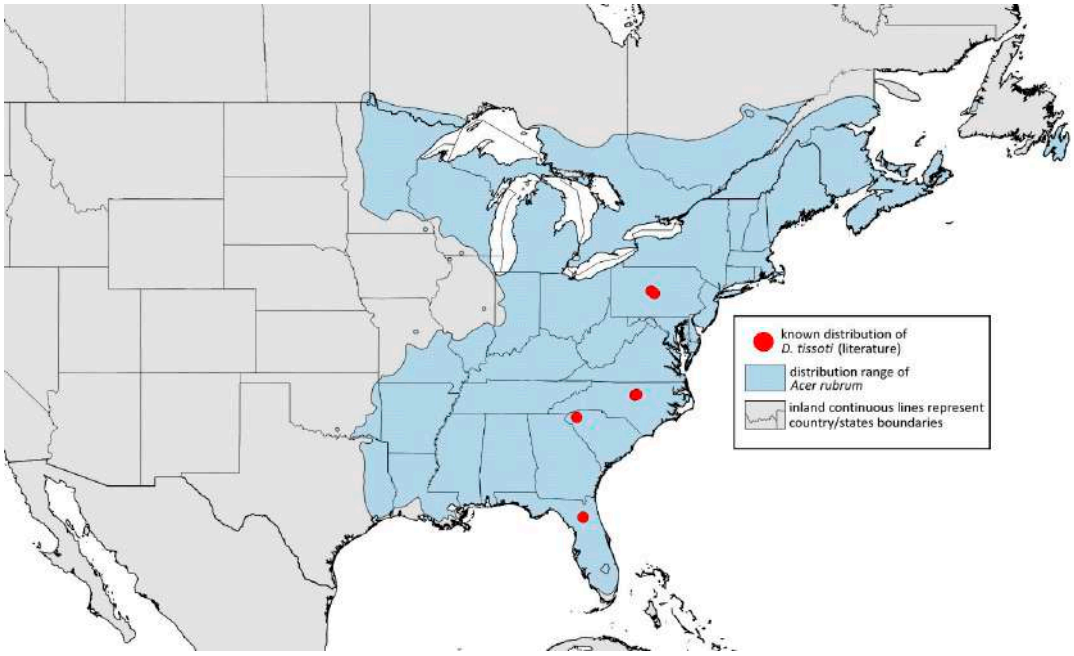

Figure 36. Known distribution of *Drepanaphis tissoti* in North America, with distribution ranges of its host plants.

3.4.18. *Drepanaphis utahensis* Smith & Knowlton, 1943

Drepanaphis utahensis Smith & Knowlton, 1943: 59(2): 172, 174 [24]
Figures 1R, 3R, 4R, 5R, 10C, 11R, 14L, 25F, 30F, 33D and 37; Tables 2–4

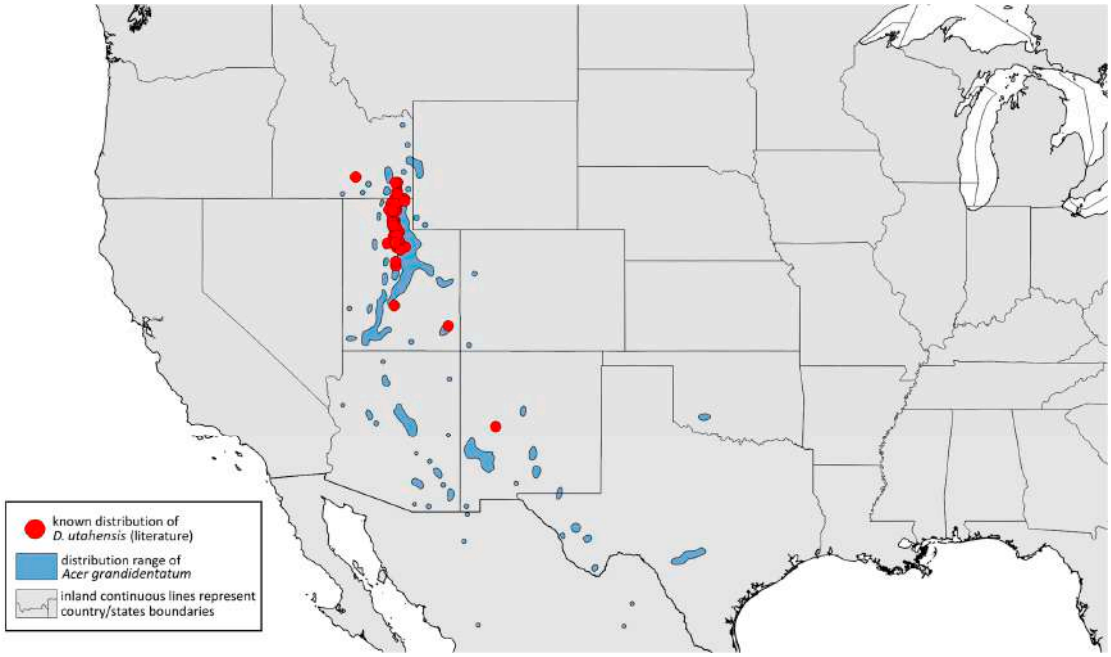

Figure 37. Known distribution of *Drepanaphis utahensis* in North America, with distribution ranges of its host plants.

Material examined: Holotype. Drepanaphis utahensis K.-S.//Type Utah Aphids, Host maple, Drepanaphis utahensis K.-S. Brigham Canyon, Date 7-1-1937, C. F. Smith, C.K.S.—five alate viv. fem. (USNM). Paratype. Mt. Maple—Paratype., APHIDIDAE OF UTAH, Host Acer glabrum, Aphid Drepanaphis utahensis K-S, Locality Ogden Cany; Ut., May-20-1930, GEORGE F. KNOWLTON, Coll. very active. Heavy whitish pruinose, over head, thorax + abdomen. Ground color of abdomen green (not to dark)////INHS, Insect Collection 1058919—one alate viv. fem.
Additional material examined—Table S6.
Alate viviparous female—re-description (n = 26)
Colour. In life: Body yellow, head and pronotum edged in black, prescutum and thoracic lobes brown, DAT III dark; entire body frosted with white wax [27].
Pigmentation of mounted specimens: Head, ANT I, pronotum and siphunculi brown (Figure 30F). Rest of thorax dark brown. ANT II–VI pale brown with slightly darker apices on ANT III–V and dark area with primary rhinarium on ANT VI. Wings clear with small area of dark brown pigmentation at end. Wings clear, pterostigma distinct, pigmented darker on ends, with small area inside without pigmentation (Figure 3R). Abdomen pale. DAT III dark (Figure 1R). Cauda, subgenital and anal plate pale brown. Legs pale brown. Fore femora darker on ends (Figure 4R).
Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.03–0.04 mm long with pointed apices; two pairs of pointed frontal setae on ventral side 0.06–0.08 mm long. ANT/BL 0.94–2.05; PT/BASE 4.27–9.04. ANT III with 12–22 secondary rhinaria, BASE with 4 accessory rhinaria. URS with 6–10 accessory setae (Figure 10C). Other ratios: ANT IV/ANT III 0.57–0.88; ANT V/ANT III 0.5–0.87; ANT VI/ANT III 0.87–1.68; URS/ANT III 0.09–0.13; URS/BASE 0.49–0.73; URS/SIPH 0.33–0.46; HT II/ANT III 0.12–0.18; HT II/BASE 0.69–0.95; TIBIA III/BL 0.41–0.66; SIPH/BL 0.08–0.13; SIPH/CAUDA 1.51–2.36. DAT I, II and IV inconspicuous. DAT III distinct, 0.09–0.14 mm long (Figure 11R). Dorsal setae 0.03–0.04 mm

long with pointed apices. Siphunculi tubular (Figure 5R).

Oviparous female—description (n = 5)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Body generally pale brown with abdomen slightly lighter. Legs and dorsal sclerotisation slightly darker (Figure 33D).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae 0.07–0.01 mm long, one pair of latero-dorsal setae on dorsal side 0.05–0.07 mm long with blunt apices; two pairs of pointed frontal setae on ventral side, 0.05–0.07 mm long. ANT/BL 0.88–1.04. Other ratios: ANT VI/ANT III 1.31–1.2; PT/BASE 5.92–7.77; SIPH/BL 0.05–0.066; FEMUR III/BL 0.19–0.21; TIBIA III/BL 0.36–0.42; HT II/ANT VI 0.1–0.12; URS/ANT III 0.12–0.17; URS/BASE 0.69–0.83; URS/SIPH 0.47–0.64. ANT III without secondary rhinaria. URS with 6–8 accessory setae. Hind tibiae with 13–52 pseudosensoria more abundant in middle part of tibiae. Dorsal setae 0.08–0.09 mm long. ABD I–II with large marginal sclerites. Siphunculi tubular.

Alate male—re-description (n = 4)

Colour. In life: Unknown.

Pigmentation of mounted specimens: Head, pronotum, ANT and siphunculi brown. Rest of thorax dark brown. Wings clear with closed, wide, brown pterostigma. Abdomen pale with dark sclerotisation. Cauda, anal plate and genitalia brown. Legs pale, hind femora with light brown smudge (Figure 24F).

Morphometric characters: Head setae: two pairs of fronto-orbital setae, one pair of postero-dorsal setae, one pair of latero-dorsal setae on dorsal side, 0.02–0.03 mm long with pointed apices; two pairs of pointed frontal setae on ventral side, 0.03–0.06 mm long. ANT/BL 1.29–1.68. Other antennal ratios: ANT VI/ANT III 1.2–1.44; PT/BASE 6.14–7.3; SIPH/BL 0.09–0.11; FEMUR III/BL 0.26–0.3; TIBIA III/BL 0.51–0.64; URS/ANT III 0.11–0.12; URS/SIPH 0.47–0.53. ANT III with 78–83 rhinaria, ANT IV with 46–52 rhinaria, ANT V with 27–30 rhinaria. URS with eight accessory setae. DAT inconspicuous. Dorsal setae 0.02–0.03 mm long, with pointed apices. ABD II–V with spino-pleural sclerites with two setae each. Marginal sclerites with 3–6 setae. Siphunculi tubular. Genitalia with basal part of phallus short, robust, with broadly rounded apices (Figure 14L).

Remarks: Archibald [61] reported an individual of this species from Nova Scotia on sugar maple, *A. saccharum* [27]. However, when analysing its range of occurrence, Archibald probably incorrectly identified this individual. The databases analysed also included records from Illinois and North Carolina. But the host plant was never *A. grandidentatum*, and we could not analyse these individuals, so we do not include their occurrence on the map. Smith and Knowlton [24] also mention that they had over 100 other slides from Utah and Idaho, but these specimens were brighter. However, they did not notice any other significant differences apart from colour. These individuals come from the following locations: Idaho (Boise (Minidoka National Forest), Franklin, Mink Creek); Utah (American Fork Canyon, Beaver Canyon, Big Cottonwood Canyon, Brigham Canyon, Eden, Emigration Canyon, Lakota, Mantua, Millville, Mt. Nebo, Oak Creek Canyon, Parley's Canyon, Providence Canyon, Provo Canyon, Richmond, Sardine Canyon, Uinta).

Host plant: *Acer grandidentatum*.

Distribution: USA: Idaho (Bench^, Caribou-Targhee National Forest, Cub River Canyon); New Mexico (Cibola National Forest); Utah (Abajo Mountains, Blacksmith Fork Canyon, Bountiful (Skyline Drive), Brigham Canyon—locus typicus, City Creek Canyon, Cutler Dam, Daniels Canyon, Farmington Canyon, Honeyville, Huntsville, Liberty, Logan (Green Canyon), Mantua, Mount Nebo, Mount Timpanogos, Muller's Park (Davis County), North Ogden, Ogden Canyon, Peterson, Pinecrest, Providence Canyon, Provo Canyon, Salt Lake City‴, Santaquin, Smithfield Canyon, Weber Canyon, Wellsville Canyon (also Mount Sterling), West Hodges Canyon) (Figure 37) [24,27]; International Barcode of Life project (iBOL) [^]; NMNH Extant Specimen Records (USNM, US) [‴].

3.5. Results of the Statistical Analysis

Based on the morphological and morphometric data, in the PCA results for the group consisting of the 213 alate viviparous females representing all species of the genus *Drepanaphis*, the first two axes of the PCA represent 70.8% of the total variance (the first three axes represent 80.9%). The first component (axis 1) is characterised mostly by the fore femora colour and the arrangement of conspicuous dorsal abdominal tubercles. The second component (axis 2) reflects the characteristics of the presence of stripes on the hind femora, dorsal sclerites and siphunculi colour (Figure 38; Table S3). In the case of all analysed morphs, qualitative features were decisive due to the fact that metric features often overlap, and there is no single clear feature that would allow for distinguishing individual species from each other.

For 30 males representing 12 species of the genus *Drepanaphis*, the first two axes of the PCA represent 67.3% of the total variance (the first three axes represent 75.8%) in the variant where the antennal segment ratio VI PT/BASE variable is not used. When this characteristic is used, then the value increases to 86.9% (the first three axes represent 91.2%). The first component (axis 1) is characterised by the fore femora colour, the presence of the stripes on the hind femora and the antenna colour. The second component (axis 2) reflects mainly the length-to-height ratio in the middle part of the siphunculi, the number of frontal setae and the visible appearance of a third pair of tubercles on the abdomen segment (Figure 39; Table S4). In the analysis where the ratio of the length of the processus terminalis of the last antennal segment to that of its basal part was also used, this feature is dominant in the characterisation for axis 1 (Figure 40).

For 43 oviparous females representing 14 species of the genus *Drepanaphis*, the first two axes of the PCA represent 91.3% of the total variance (the first three axes represent 94.4%). The first component (axis 1) is characterised by the ratio of the length of the processus terminalis of the last antennal segment to that of its basal part. The second component (axis 2) reflects mainly the colour of antennae, fore tibiae, dorsal sclerites and siphunculi (Figure 41; Table S5).

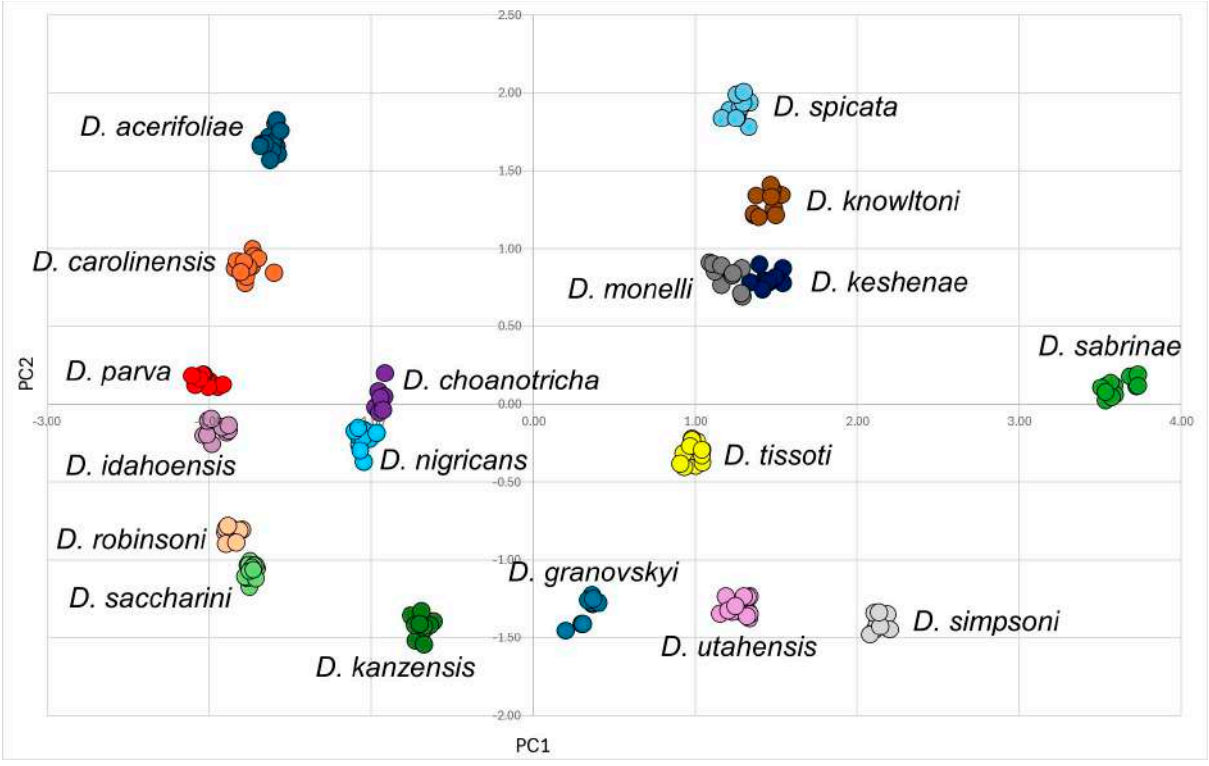

Figure 38. Plots of the first two components of a principal components analysis (PCA) for alate viviparous females of the genus *Drepanaphis*. Plots demonstrate the separation of individual species.

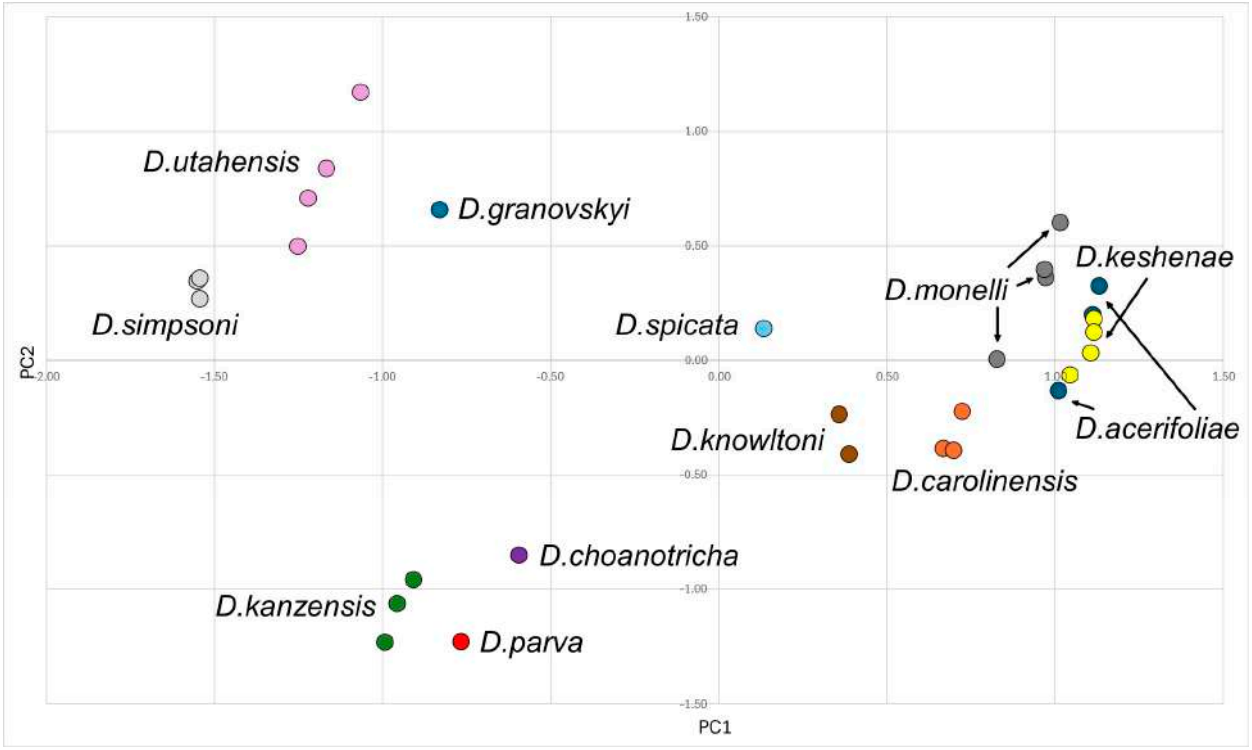

Figure 39. Plots of the first two components of a principal components analysis (PCA) for males of the genus *Drepanaphis* (without antennal segment ratio VI PT/BASE). Plots demonstrate the separation of individual species.

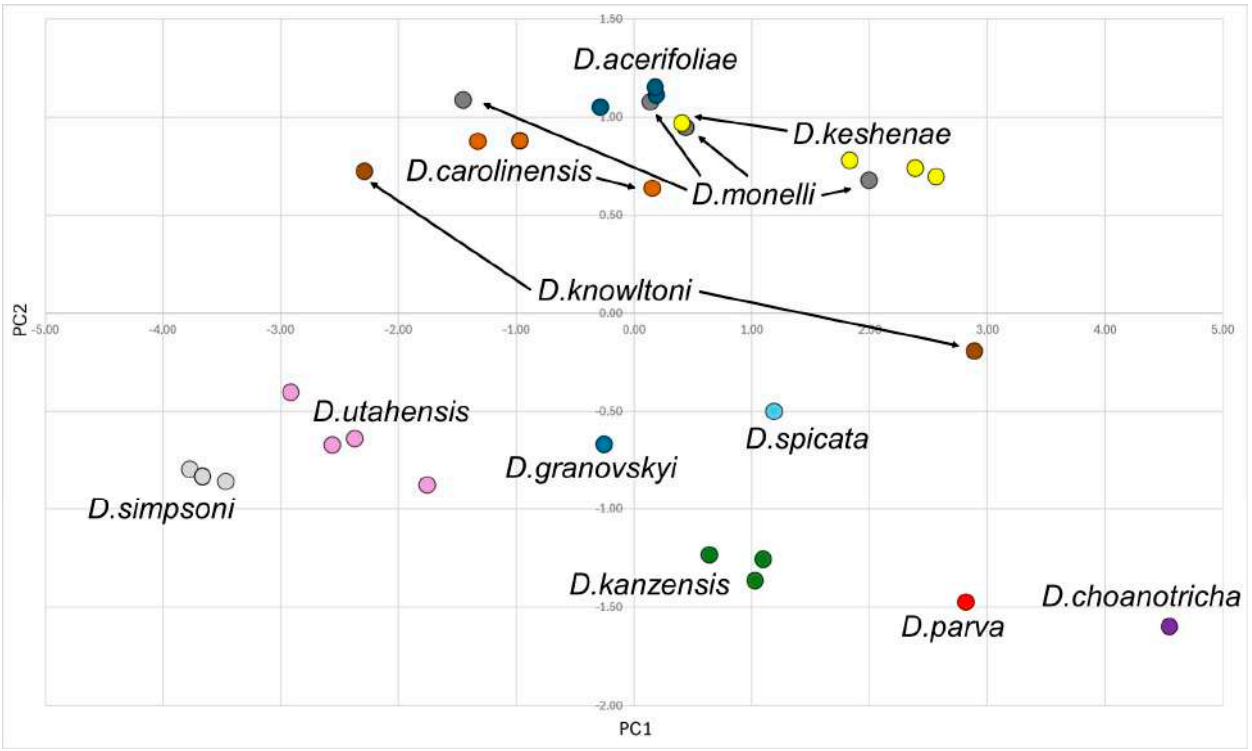

Figure 40. Plots of the first two components of a principal components analysis (PCA) for males of the genus *Drepanaphis* (with antennal segment ratio VI PT/BASE). Plots demonstrate the separation of individual species.

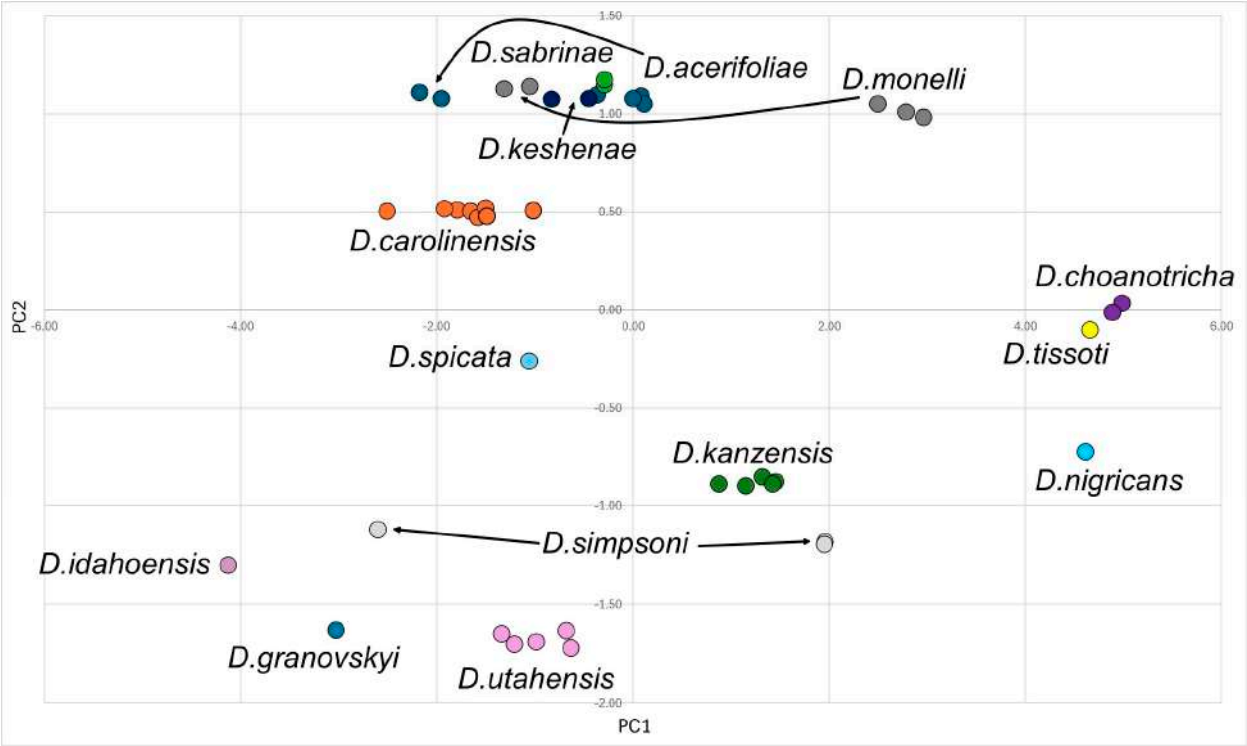

Figure 41. Plots of the first two components of a principal components analysis (PCA) for oviparous females of the genus *Drepanaphis*. Plots demonstrate the separation of individual species.

The PCA results confirm the full species status of *D. tissoti* within the genus *Drepanaphis*. Moreover, according to previously proposed species groups by Smith and Dillery [27], most of these proposals are justified. In the genus under study, we can distinguish the "*acerifoliae*" group, characterised by four clearly visible pairs of dorsal abdominal tubercles in alate viviparous females. Originally, species such as *D. acerifoliae*, *D. carolinensis* and *D. sabrinae* were included here. However, *D. sabrinae* has a unique tubercle pattern, its siphunculi are light brown and unlike the other two species, which have four accessory rhinaria each, this species has five to six of them. This species is plotted for alate viviparous females at the far end of axis 1, but for oviparous females, it is shown close to *D. acerifoliae* and *D. carolinensis*. Species in the "*monelli*" group have only the third pair of tubercles visible and dark stripes on the hind femora. This group includes *D. keshenae*, *D. knowltoni*, *D. monelli* and *D. spicata*. Smith and Dillery [27] also proposed *D. kanzensis* here, although they also indicated some doubts about its position in this group. Based on the morphological analysis of this species, we propose not assigning it to any existing group, similar to the approach taken with *D. sabrinae*. The position of *D. kanzensis* outside the previously designated group is confirmed in the analyses of all generations—alate viviparous females and sexuales, oviparous females and males. In the case of sexual generation, species from the "*acerifoliae*" and "*monelli*" groups partially overlap, which is primarily due to the very similar metric ratio of the analysed characters and, especially in the case of males, the inability to measure some features in *D. acerifoliae* and *D. carolinensis* individuals (Figures 39–41). For the correct analysis of the results, it is also important to mention that in oviparous females, the measurement values of the processus terminalis (ANT VI PT) for two individuals from *D. acerifoliae* and two from *D. monelli* were lower than those in the others, which resulted in some disturbance in the analyses and the separation of these individuals on the plot. This is the only reason for this situation.

The remaining groups coincide with the previous proposal. Therefore, we have a "*nigricans*" group, with *D. choanotricha*, *D. nigricans* and *D. tissoti*, mostly characterised by very long antennae; a "*parva*" group, where all species have a light-coloured front femora,

i.e., *D. idahoensis*, *D. parva*, *D. robinsoni* sp. nov. and *D. saccharini*; and a fifth "*utahensis*" group, with *D. granovskyi*, *D. simpsoni* and *D. utahensis*, where all species have two pairs of frontal setae on the head.

4. Discussion

4.1. Morphological Groups within the Genus Drepanaphis

The most significant character of species belonging to the genus *Drepanaphis* is the presence of distinctive tubercles on dorsal abdominal tergites I–IV. The size and shape of dorsal abdominal tubercles have great importance in the systematics of this group of aphids. Smith and Dillery [27] pointed out the importance of this feature for distinguishing species belonging to five morpho-groups. However, in their original descriptions, they did not consider qualitative features such as the colour of the fore femora or the shape of the siphunculi. Additionally, when determining the groups, the authors paid great attention to the characteristics of the nymphs and the host plant associations, which may not provide sufficient information about the morphological similarities within the designated groups. They also did not consider the characteristics of the sexual generation, which were relatively poorly known. By analysing the morphological characters in the genus *Drepanaphis*, five distinct species groups can be distinguished. Species with four distinct pairs of dorsal abdominal tubercles, with the third pair being the largest, first femora dark around the edges and four accessory rhinaria are characteristic of the "*acerifoliae*" group, consisting of *D. acerifoliae* and *D. carolinensis*. The original division also included *D. sabrinae*, but due to different proportions of tubercles (the second and third pairs of equal length) and five accessory rhinaria, this species is not classified into any group. Additionally, *D. sabrinae* is the only species with an ultimate rostral segment 0.12–0.14 mm long. The second group of species morphologically similar to each other and distinguished by having only a third pair of tubercles is the "*monelli*" group (*D. keshenae*, *D. knowltoni*, *D. monelli* and *D. spicata*). Species in this group are very similar and are often incorrectly marked in museum collections; e.g., *D. knowltoni* was marked incorrectly as *D. monelli* and vice versa; *D. knowltoni* and *D. spicata* are also frequently confused species. In the case of this group, similarly to the "*acerifoliae*" group, another species, *D. kanzensis*, was originally included. Variability resulting from the colour of the fore femora and the lack of black stripes on the third pair of hind femora means that this species is also not classified into any group. A group of individuals characterised by relatively small body size, long antennae and a variable number of accessory rhinaria creates the "*nigricans*" group (*D. choanotricha*, *D. nigricans*, *D. tissoti*). Remaudière and Remaudière [29], after personal communication from Quednau, established the synonymisation of *D. tissoti* with *D. nigricans*, but our analysis indicates differences between them. A significant feature was the number of rhinaria, both secondary (*D. nigricans* with more than 11, *D. tissoti* never with more than 11) and accessory (*D. nigricans* always with 4, *D. tissoti* with 5–11). Species belonging to the "*parva*" group (*D. idahoensis*, *D. parva*, *D. robinsoni* sp. nov., *D. saccharini*) differ by pale fore femora. *Drepanaphis parva* and *D. robinsoni* sp. nov. have wing veins with slightly dusky areas. Apart from the similarity in the smudge on the wings, they differ in the presence of sclerotisation on the abdomen (Figure 21E,F) or the different shapes of the dorsal abdominal tubercles (Figure 11K,L). Representatives with two frontal setae in adults belong to the "*utahensis*" group (*D. granovskyi*, *D. simpsoni*, *D. utahensis*). *Drepanaphis granovskyi* and *D. utahensis* are light-coloured species with relatively small tubercles, which in the case of *D. simpsoni* are larger, and this species is the only one with the first pair of tubercles, the largest concerning the remaining pairs.

4.2. Morphometric Similarities in the Genus Drepanaphis

The phenomenon of morphological similarity in aphids is common and can be distinguished in many genera of hemipterans. An example is the genus *Aphis* L., where the species generally appear very similar due to convergence toward particular morphological types [62]. To distinguish some of them (*A. glycines*, *A. gossypii*, *A. rhamnicola*), it is necessary

to use DNA barcoding because morphological comparative studies are insufficient [63]. While species in the *Drepanaphis* genus may initially appear different, primarily due to the varied arrangement of dorsal abdominal tubercles, and constitute a distinct group within the subfamily Drepanosiphinae [14], the morphometric features of most species overlap, making it impossible to establish clear differentiation ranges. The range of sizes of individuals in the genus is very wide, especially considering that the specimens analysed encompass forms from each season (from early spring to late autumn), which may vary substantially in body size. Additionally, the morphological plasticity of aphids [64] can affect a wide spectrum of ranges of dimensions. The morphometric feature that often carries significant taxonomic information is the length of the appropriate segments of the antennae. In some species of the genus *Drepanaphis*, the length of the processus terminalis of the last antennal segment may serve as a distinguishing feature, visible in well-preserved specimens. However, in the case of most mounted specimens, the last segment is often broken or destroyed, which can lead to erroneous conclusions regarding interspecies differences based on this feature [18]. Another qualitative feature is the number of rhinaria on antennal segment III, which should be relatively constant. In the case of some species, such as *D. choanotricha*, the number of rhinaria is small, which facilitates initial verification. However, the ranges of rhinaria numbers overlap for many species, rendering this feature less significant for identification purposes. The number of setae on the ultimate rostral segment is also a questionable diagnostic character.

Although SEM can provide excellent imaging of detailed morphological features in aphids [65], this method does not enable accurate counting of this character (Figure 10). Therefore, we included ranges of numerical intervals in the key rather than specific values in this case. Although quantitative features such as the number of accessory rhinaria on the base of antennal segment VI may differentiate species like *D. choanotricha*, *D. sabrinae* and *D. tissoti* (Figure 2), most morphometric features overlap. When verifying individuals in this genus, attention should primarily be given to qualitative features, which can aid in identifying living specimens. These features include dark-bordered wings in the case of *D. acerifoliae* and *D. keshenae* (Figure 8) and the colour of the fore femora. When analysing individuals using light microscopy, the qualitative features that hold the greatest diagnostic importance are the shape and size of the dorsal abdominal tubercles. Although in some species, their shape and size may be distorted by the incorrect positioning of individuals on the mounted specimen [18], this feature remains valuable, especially in morphologically very similar species.

4.3. Host Plant Ambiguity

After analysing specimens from various entomological collections, it was found that *Drepanaphis* species are associated with a much broader range of host plant species than previously believed. This applies in particular to species that were classified as monophagous. *Drepanaphis monelli* is the only species in this genus that feeds on *Aesculus glabra*; the remaining species feed on maples. Host plant associations were also used as a diagnostic feature in the key and differentiated the examined specimens. Among the analysed specimens of this species in the INHS collection, a series of specimens of *Drepanaphis monelli* were also found on *A. saccharum* and *A. saccharinum*. Following thorough analysis, the taxonomic identity of this species was confirmed, thereby rejecting the possibility of mislabelling the specimens. In this case, we suspect two phenomena: (I) accidental drift from a host plant to a neighbouring tree species or (II) a genuinely broader species range of the host plant. While we do not discount the possibility of drift, which is common in groups of small insects [66], it has been observed accidentally in other species within this genus, such as on ferns (*D. acerifoliae*) and mosses (*D. utahensis*). However, we are more inclined to claim that the number of host plant species is greater than expected, a conclusion supported by numerous other examples. *Drepanaphis kanzensis*, which mainly occurs on *A. saccharum* (confirmed by field research conducted in September 2022 in the USA), may also appear on *A. rubrum* or *A. saccharinum*. It is noteworthy that the sexual generation of this species primarily occurs on

A. saccharinum rather than *A. saccharum*, contrary to common assumption. The question arises of whether the sexual generation in this genus is so difficult to collect because of the omission of host plants. An interesting example is the new species *D. robinsoni* sp. nov., initially misidentified as both *D. choanotricha*, associated with *A. saccharum*, and *D. parva*, which primarily feeds on *A. rubrum*. In this case, we face difficulties in determining the primary host plant of the new species. Although designating a single host plant facilitates initial verification and provides a reliable source of information about the species [67], the analysis of a representative number of specimens from the genus *Drepanaphis* reveals that they are more narrowly oligophagous than monophagous. This fact should be considered when using the identification key.

4.4. Distribution

Among all identified *Drepanaphis* species, *D. granovskyi*, *D. idahoensis* and *D. utahensis* stand out most prominently due to their distribution. They are the only ones associated exclusively with the western part of North America, and they all feed on *Acer grandidentatum*. However, morphological analysis indicates that *D. idahoensis* is less similar to other species. A similar distinction can be observed with *D. knowltoni*, which also inhabits the same geographical area and feeds on *A. grandidentatum* but exhibits distinct morphological characteristics. The case of *D. spicata* is also noteworthy. Representatives of this species occur in the northernmost part of the continent among all those analysed (with only *D. acerifoliae* also recorded above latitude 49°). Similar to *D. knowltoni*, *D. spicata* shows range fragmentation, although further field confirmation of these findings is necessary.

The ranges of the other species overlap, corresponding to the natural ranges of their host plants. There are strong indications that the original habitat of the first representatives of this genus was the eastern part of North America, and their evolution is closely linked to the spread of trees within the *Acer* genus [68].

5. Conclusions

The study of the genus *Drepanaphis* highlights its taxonomic complexity and the diverse host plant associations among its species. Morphological analyses reveal distinctiveness even among closely related species, underscoring the importance of comprehensive revision and accurate species identification tools. The geographical distribution patterns suggest evolutionary ties to the *Acer* genus, particularly in eastern North America.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/insects15070553/s1, Table S1: Metric data and morphological characters for alate viviparous females of the genus *Drepanaphis*; Table S2: Metric data and morphological characters for males and oviparous females of the genus *Drepanaphis*; Table S3: Results of statistical analysis for alate viviparous females of the genus *Drepanaphis*; Table S4: Results of statistical analysis for males of the genus *Drepanaphis*; Table S5: Results of statistical analysis for oviparous females of the genus *Drepanaphis*; Table S6: Examined material of the *Drepanaphis* species.

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Publikacja 3

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Molecular phylogeny of the *Acer*-feeding aphid subfamily Drepanosiphinae (Insecta: Hemiptera: Aphididae) and the evolution of its endosymbiotic consortia

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Abstract

The Drepanosiphinae is a Holarctic subfamily of Aphididae comprising six genera: *Drepanaphis, Drepanosiphoniella, Drepanosiphum, Megalosiphonaphis, Shenahweum,* and *Yamatocallis*, all of which exhibit strict host plant associations, primarily with *Acer* species. Despite long-standing taxonomic attention, evolutionary relationships within the group remain poorly resolved, and some important aspects of their biology, such as their patterns of association with symbionts, have been unexplored despite evidence that species in the subfamily might be involved in atypical nutritional symbioses. Here, we present a molecular phylogenetic reconstruction of this subfamily and investigate the evolution of its endosymbiotic consortia. Phylogenetic analyses were conducted using multiple DNA markers, employing both Bayesian inference (BI) and maximum likelihood (ML) approaches. Endosymbionts were characterized using high-throughput sequencing of a fragment of the bacterial 16S rRNA gene. The resulting phylogenies are largely congruent across markers and methods and consistently support the monophyly of Drepanosiphinae. *Drepanaphis* and *Drepanosiphum* form a well-supported clade as sister to *Drepanosiphoniella*, while *Yamatocallis* and *Megalosiphonaphis* form a distinct, more distantly related clade. Within *Drepanaphis*, species group according to host plant use rather than traditional morphological groupings, revealing three host-associated clades: *rubrum*, *saccharum*, and *grandidentatum*. Endosymbiont characterization revealed that, in addition to the obligate symbiont *Buchnera aphidicola*, most Drepanosiphinae species also host a *Sodalis*-like bacterium, consistent with previous genomic evidence for a dual nutritional symbiosis with this bacterium. However, *Sodalis* was absent in most *Yamatocallis* species, indicating a complex and potentially dynamic evolutionary history of symbiotic relationships within the subfamily. Patterns of association with *Wolbachia*, *Rickettsia, Fukatsuia, Serratia* and *Arsenophonus* suggest a limited role in nutrition. By integrating phylogenetic reconstruction with symbiont profiling, this study provides the most comprehensive evolutionary framework to date for Drepanosiphinae and reinforces the view that nutritional symbioses in aphids are evolutionarily dynamics.

Keywords Aphid microbiome, *Drepanaphis*, Dual symbiosis, Maple, *Sodalis*, *Yamatocallis*

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Background

Drepanosiphinae is a morphologically and biogeographically diverse subfamily within Aphididae [1]. It comprises 42 recognized species within six genera: *Drepanaphis* Del Guercio, 1909 (18 species), *Drepanosiphoniella* Davatchi, Hille Ris Lambers & Remaudière, 1957 (three species), *Drepanosiphum* Koch, 1855 (10 species), *Megalosiphonaphis* Sugimoto, 2024 (one species), *Shenahweum* Hottes & Frison, 1931 (one species), *Yamatocallis* Matsumura, 1917 (nine species) [2, 3]. Drepanosiphinae are distributed across most major biogeographic regions. *Drepanosiphum* is Holarctic and well-represented in Europe, while *Drepanosiphoniella* occurs mainly in the Mediterranean. The Nearctic genera *Shenahweum* and *Drepanaphis* account for much of North American diversity, with *Drepanaphis* being the most speciose; only *D. acerifoliae* (Thomas, 1878) occurs outside North America, also reaching Europe and Japan. In Asia, *Yamatocallis* occurs in India, China, Korea, and Japan, whereas *Megalosiphonaphis* has only been recorded in Japan [3–11]. Across all regions, these aphids exhibit strong host specificity, primarily associating with *Acer* species [3]. Morphologically, representatives of Drepanosiphinae are distinguished by features such as enlarged fore or mid femora and the presence of rastral spines on the hind tibiae, which are considered synapomorphies for the group [1]. All genera within the subfamily are morphologically well characterized and have been the subject of detailed taxonomic studies [1, 4, 6, 8, 9, 11, 12].

Despite this, evolutionary relationships within Drepanosiphinae remain poorly resolved due to limited taxon sampling [1]. In particular, high morphological similarity among species in the largest genus, *Drepanaphis*, has long complicated species delimitation [13]. To address this, five morpho-groups have been proposed based on diagnostic traits such as the shape and color of the pterostigma, the form of the siphunculi, and the presence and structure of abdominal tubercles [9, 13]. However, several species remain difficult to place confidently within these morpho-groups, suggesting that morphology alone may be insufficient for accurate species delimitation. Furthermore, the phylogenetic position of the Asiatic genera *Yamatocallis* and *Megalosiphonaphis* remain unresolved, emphasizing the need for broader molecular phylogenetic analyses.

Thus, a comprehensive molecular phylogeny is needed to resolve evolutionary relationships within Drepanosiphinae, clarify the placement of Asiatic genera and test the validity of *Drepanaphis* morpho-groups. Given the strong host specificity toward *Acer* species, mapping host associations onto a robust phylogeny can reveal whether ecological traits correspond to evolutionary lineages and help explain patterns of diversification.

In addition, Drepanosiphinae species are potentially characterized by atypical dual nutritional symbioses [14]. While most aphid species are associated with a single obligate symbiont, *Buchnera aphidicola*, which supplies essential amino acids and vitamin B that are limited or absent in the aphid diet, several studies using microbial metagenomic data have shown that this mutualistic relationship is not as exclusive as previously thought across the aphid phylogeny [14–16]. In several aphid subfamilies, *Buchnera* lacks essential metabolic functions, most notably the ability to synthesize biotin and riboflavin, and is complemented by other microbial symbionts that rescue or replace one or more of its roles. By compensating for the evolved auxotrophies of their *Buchnera* partners, these secondary symbionts provide essential nutrients and become co-obligate associates [14]. Such dual nutritional symbioses, in which *Buchnera* is complemented by an additional symbiont, have also been identified in members of the subfamily Drepanosiphinae. Notably, Fukatsu [17] discovered a secondary intracellular symbiotic bacterium in the genus *Yamatocallis* (in *Y. tokyoensis* Takahashi, 1923 and *Y. hirayamae* Matsumura, 1917), referred to as YSMS (*Yamatocallis* Secondary Mycetocyte Symbiont). Phylogenetically affiliated with the γ-Proteobacteria, this symbiont's patterns of association and tissue tropism suggest a potential role in aphid nutrition. More recently, Manzano-Marín et al. [14] uncovered co-obligate associations involving *Sodalis*-like bacteria in other Drepanosiphinae members, i.e. *Drepanosiphum platanoidis* Schrank, 1801 and *Drepanosiphoniella fugans* Remaudière and Leclant, 1972. Genomic data from this study show that *Sodalis*-like symbionts, characterized by highly reduced genomes indicative of long-term obligate associations, appear to compensate for metabolic deficiencies in *B. aphidicola*, particularly the loss of B-vitamin biosynthesis. Although only four of the 42 recognized Drepanosiphinae species have been investigated for the presence of symbionts, the subfamily may represent an alternative example of a diversified obligate dual-symbiotic system, comparable to that observed in Chaitophorinae, Hormaphidinae or Lachninae [18, 19]. In order to investigate this hypothesis, a more thorough exploration of symbiont diversity across and within species is needed. A comprehensive phylogenetic framework will then help determining whether *Sodalis* is involved in a long-term association with this group and whether YSMS is restricted to certain species or genera.

In light of Drepanosiphinae's strong host specificity, morphological complexity, and potential dual symbiotic systems, the overarching aim of this study is to provide the first comprehensive evolutionary framework for the group by integrating multilocus molecular phylogeny with endosymbiont characterization. Specifically, we aim to: 1. Reconstruct the phylogeny of 20 Drepanosiphinae

species, representing five of the six recognized genera and nearly half of all known species; 2. Clarify the phylogenetic positions of the Asiatic genera *Yamatocallis* and *Megalosiphonaphis*, which exhibit unique morphological traits and restricted distributions; 3. Resolve relationships within *Drepanaphis*, the largest and most problematic genus, and assess whether the phylogenetic clustering of species reflects their host–plant associations with *Acer*; 4. Characterize endosymbiotic consortia across Drepanosiphinae, and map their distributions onto the host phylogeny in order to identify potential co-obligate symbionts.

Material and methods

Sample collection, fixation and storage

The study used 20 of 42 species from the subfamily Drepanosiphinae. Eight species belonging to the genus *Drepanaphis* [*D. acerifoliae*; *D. carolinensis* Smith, 1941; *D. granovskyi* Smith & Knowlton, 1943; *D. kanzensis* Smith, 1941; *D. monelli* (Davis, 1909); *D. robinsoni* Malik, 2024; *D. sabrinae* Miller, 1937; *D. utahensis* Smith & Knowlton, 1943] were collected in USA from 2022 to 2023, *D. acerifoliae* was also collected in Belgrade, Serbia in 2023. *D. simpsoni* Smith, 1959, collected in USA in 1976, was obtained from the MNHN collection (Paris, France). Four species belonging to the genus *Yamatocallis* [*Y. acericola* Higuchi, 1975; *Y. hirayamae*; *Y. nikkoensis* Sugimoto, 2017; *Y. tokyoensis*] were collected in Japan in 2023. *Megalosiphonapis nigrostriata* Sugimoto, 2024 was collected in Japan in 2024. *Drepanosiphoniella fugans* and *Drepanosiphum platanoidis* were collected in France in 2016. For each sample collected, a preliminary classification of individuals was carried out through observation under the Nikon SMZ 25 stereoscopic microscope. Subsequently, some specimens were mounted on slides and identified using a Nikon Ni-U light microscope equipped with a phase contrast system. All voucher specimens were preserved in 70% or 99.8% ethanol, stored at –20∘C and deposited in the entomological collection of the University of Silesia in Katowice, Poland (DZUS) and INRAe, Montpellier, France. Detailed collection data for all studied species are presented in Table S1.

DNA extraction, polymerase chain reaction amplification and sequencing

For each collected aphid individual, total genomic DNA was conducted with a non-destructive DNA extraction as advised by [20]. We used the DNeasy Blood & Tissue Kit (Qiagen, Germany) and followed the manufacturer's recommendations, except that that samples were left in the lysis buffer overnight and the final elution volume was 80 µl. During the extraction procedure, a negative control (i.e. a 'blank template' of ultrapure water) was processed with the same extraction kit. All DNA samples were stored at –20 °C. Polymerase chain reaction (PCR) amplifications were conducted for two mitochondrial gene fragments: a 700-bp region of the cytochrome oxidase I (COI), using primer pairs LepF (5'-ATTCAACC AATCATAAAGATATTGG-3') LepR (5'-TAAACTTCT GGATGTCCAAAAAATCA-3') [21] and 780 bp of the cytochrome b (Cytb) using primer pair CB1 (5'-GATGA TGAAATTTTGGATC-3') and CB2 (5'-ATTACACCT CCTAATTTATTAGGAAT –3') [22]. We also amplified two nuclear gene fragments: 900 bp of the elongation factor-1a (EF1a) using primer pair EF3 (5'-GAACGTGA ACGTGGTATCAC –3') and EF6 (5'-TGACCAGGGTG GTTCAATAC-3') [23] and 700 bp of the 6-phosphogluconate dehydrogenase PGD using primer pair PGD531 (5'-GGTGCTGGYCATTTYGTDAAAATG –3') and PGD1097 (5'-CAKCCTCCACGCCACATDAG –3') [24].

The PCR mixture included 12.5 µL of Master Mix with, 1.25 µL of each primer (10 µM), 7 µL of nuclease-free water and 2 µL of DNA template. Amplification included 30 s denaturation at 98 °C followed by 35 cycles each consisting of 30 s denaturation at 98 °C, 30s of annealing at temperature between 48 and 50°C°C and 1 min extension at 72 °C. A final extension was carried out at 72 °C for 5 min. PCR products were electrophoresed on 1% agarose to check for PCR success. Resulting PCR products were processed by the Eurofins sequencing society (Germany) using a BigDye v3.1 sequencing kit and Applied Biosystems 3730xl sequencers. Both strands were sequenced for all specimens to minimize PCR artefacts and ambiguities. Sequences of complementary strands were edited and reconciled using Geneious v11 (available at: http://www.geneious.com/).

Additional sequences were downloaded from GenBank (http://www.ncbi.nlm.nih.gov/Genbank): *Drepanaphis parva* Smith, 1941 (the only *Drepanaphis* available in GenBank prior to our study); *Drepanosiphum oregonense* Granovsky, 1939; *Yamatocallis sauteri* Takahashi, 1927. Two closely related Chaitophorinae species - *Chaitophorus salicti* Schrank, 1801 and *Periphyllus testudinaceus* (Fernie, 1852) were used as outgroup. In addition, we used a more distantly related Aphidinae species - *Brachycaudus helichrysi* (Kaltenbach, 1843) as an outgroup. GenBank sequence numbers for all studied species, including newly generated are presented in Table S1.

Phylogenetic analyses

We aligned each gene fragment using ClustalW in MEGA v11 [25]. Sequences were then translated to check for any frameshift or stop codon. Then the two mitochondrial genes were concatenated in one alignment, and the nuclear gene fragments were concatenated in another alignment. Each of this dataset was analyzed separately to check for convergence of phylogenetic signal between maternally inherited DNA (mitochondrial data) and

biparentally inherited data (nuclear DNA data). We then analyzed a complete data partition made of the concatenation of mitochondrial and nuclear genes.

For all DNA datasets we followed the same analytical protocol. In order to choose the most appropriate partitioning schemes and best substitution models, for each DNA matrix, we built a pre-partition file: we divided each protein–coding sequence into three partitions one for each codon position. We then ran ModelFinder as implemented in IQ-TREE v2.1.3 [26] with option MFP+MERGE which both tests, models for each DNA partition and test if partitions can be merged. Once models and partitions were selected, we ran Maximum Likelihood (ML) analyses in IQ-TREE v2.1.3 with 1000 ultrafast bootstrap replicates (-bb option), using the best fitting models and partitions found based on BIC (Bayesian information criterion) model selection.

Bayesian phylogenetic inference (BI) was further conducted using MrBayes v3.2. [27]. We partitioned the dataset by codon position, defining three partitions corresponding to the first, second, and third codon positions for mitochondrial genes and a single partition for the nuclear genes. For each partition, we applied a GTR substitution model with gamma-distributed rate variation among sites. Model parameters, including state frequencies, substitution rates, and gamma shape parameters, were unlinked across partitions to allow independent estimation. The analysis was run with four independent Markov chain Monte Carlo (MCMC) chains for 100 million generations, sampling every 1,000 generations. A temperature parameter of 0.07 was used to improve mixing. Convergence and stationarity were assessed by monitoring the standard deviation of split frequencies and effective sample sizes. The first 25% of samples were discarded as burn-in before summarizing parameter estimates and the posterior tree distribution.

16S rDNA endosymbiont characterization

Using the same DNA extractions as for aphid DNA sequencing, we amplified a 251-bp portion of the V4 region of the 16S rRNA gene [28] and used targeted sequencing of indexed bacterial fragments on a MiSeq (Illumina) platform using the dual-index sequencing strategy developed by [29], following the protocol described in Jousselin et al. [30]. DNA extracts were amplified twice along with negative controls. PCR replicates were conducted on distinct 96-well microplates.

The PCR products were pooled with samples from other microbiome studies, purified and quantified with the Kapa Library Quantification Kit (Kapa Biosystems). The DNA pool was then paired-end sequenced on an Illumina MiSeq flow cell with a 500-cycle Reagent Kit v2 (Illumina). We then followed the procedure of Manzano-Marín et al. [14] to analyze sequencing results and infer presence and absence of aphid endosymbionts. Briefly, sequencing results were first filtered through Illumina's quality control procedure. We then used FLASH v1.2.11 [31] to merge paired sequences into contigs and CUTADAPT v1.9.1 to trim primers. The FROGS pipeline [32] was then used to generate an abundance table of symbiont lineages across samples. Taxonomic assignments of clusters was carried out using RDPtools v2.0.3 3(https://github.com/rdpstaff-/RDPTools, last accessed March, 2025 [33];) and, BLASTn+ against the Silva database release 138 [34] as implemented in FROGS. Following taxonomic affiliation, we aggregated clusters when they shared the same taxonomy with at least 98% of identity (FROGS' affiliation postprocess step). We refined taxonomic assignation using phylogenetic placement of clusters using reference sequences of known facultative and obligate symbionts of aphids identified through genomic studies (Fig. S1). From the abundance table of clusters across samples, we transformed read numbers per aphid samples into percentages and sequences accounting for <0.5% of all the reads for a given sample were excluded using an R script following Jousselin et al. [30]. Clusters were kept only if present in both PCR replicates of the same sample. For final description of endosymbiont diversity, we only kept the PCR replicate that yielded the highest number of reads. We used relative abundance data to produce a heatmap in R of endosymbiotic taxa across aphid samples.

Results

Phylogenetic reconstructions within the subfamily Drepanosiphinae

Phylogenetic analyses conducted using both ML and BI methods on a combined dataset (COI, Cytb, EF-1α and PGD genes) resulted in a largely similar topology within the ingroup (Fig. 1A). The Drepanosiphinae was found to be sister to the Chaitophorinae subfamily and retrieved as monophyletic but with quite low support (bootstrap support, BS = 55 posterior probability, PP = 0.64). The Drepanosiphinae representatives were split into two clades. One clade included all species of the monophyletic *Drepanaphis* (Fig. 1B) and representative species of *Drepanosiphum* (Fig. 1C) and *Drepanosiphoniella*, as sister groups to *Drepanaphis*. A second clade included all species of *Yamatocallis*. The genus *Megalosiphonaphis* (Fig. 1D) was either placed as a sister lineage of *Yamatocallis* (Fig. 1E) (in ML analysis) or sister to all other Drepanosiphinae (in the Bayesian inference).

The genus *Drepanaphis* was recovered as monophyletic with strong support (bootstrap support, BS = 100; posterior probability, PP = 1). Three clades included the following species of *Drepanaphis*: i) *D. granovskyi* and *D. utahensis* ii) *D. acerifoliae*, *D. parva*, *D. robinsoni* iii) *D. kanzensis*, *D. monelli*, *D. simpsoni*, *D. carolinensis* and

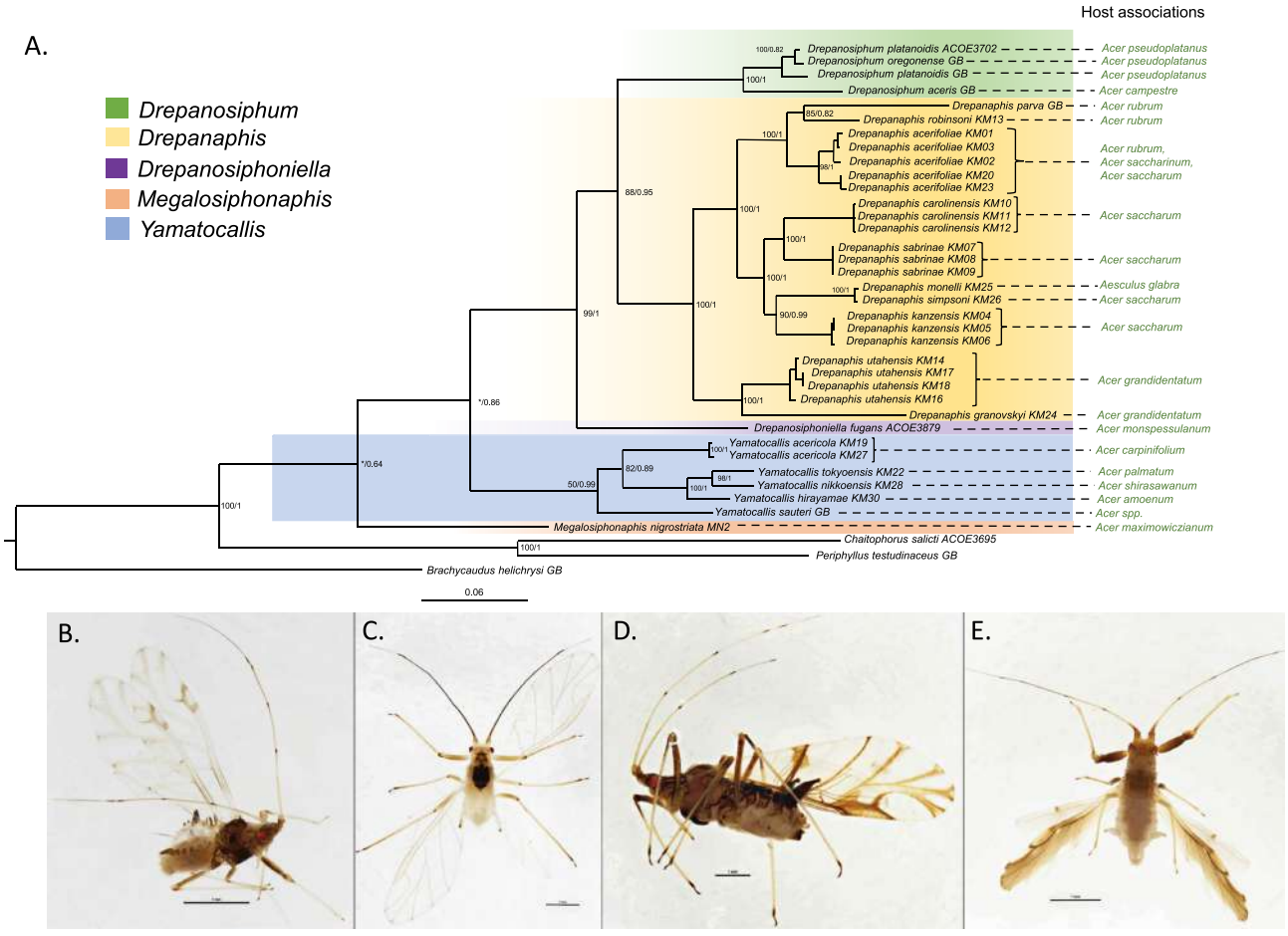

Fig. 1 (**A**). Phylogenetic tree obtained from the combined analysis of mitochondrial and nuclear genes, with indication of host associations of analyzed aphid species of the Drepanosiphinae subfamily. The topology shown represents the tree inferred under Bayesian analyses based on four molecular markers: a 700-bp region of cytochrome oxidase I (COI), 780 bp of cytochrome b (cytb), 900 bp of elongation factor-1α (EF1α), and 700 bp of 6-phosphogluconate dehydrogenase (PGD). Values at nodes indicate bootstrap support from maximum likelihood (ML) analyses and posterior probabilities from Bayesian inference (BI) for congruent nodes. An asterisk ('*') indicates that the corresponding node was not recovered in the other analysis. Visual representation of species studied: fluid-preserved specimen of (**B**). *Drepanaphis acerifoliae*; (**C**). *Drepanosiphum oregonense*; (**D**). *Megalosiphonaphis nigrostriata*; (**E**). *Yamatocallis tokyoensis*

D. sabrinae. The species belonging to the genus *Drepanosiphum* with *D. aceris*, *D, oregonense* and *D. platanoidis* formed a monophyletic group (bootstrap support, BS = 100; posterior probability, PP = 1). However, the analyzed *D. platanoidis* sequences come from distant populations that exhibit genetic variability. The genus *Yamatocallis* was recovered as monophyletic (BS = 82 PP = 0.99). *Y. tokyoensis*, *Y. nikkoensis* and *Y. hirayamae* constitute one clade, sister to species *Y. acericola* and *Y. sauteri*. As mentioned above, the position of *Megalosiphonaphis nigrostriata* varied and was poorly supported: it was found as a sister lineage to *Yamatocallis* (BS = 51) or sister to all other Drepanosiphinae (PP = 0.64).

Indicating host plant associations for each aphid species on the phylogenetic tree based on combined markers reveals that closely related species often utilize the same host plant (Fig. 1A). For example, *Drepanaphis utahensis* and *D. granovskyi*, which are sister species, are both associated with *Acer grandidentatum*. Overall, the distribution of host plant usage across the Drepanosiphinae phylogeny suggests that species feeding on similar hosts tend to be more closely related.

Analysis of mitochondrial genes (COI, Cytb) retrieved a tree (Fig. 2A) that was broadly congruent with the topology obtained from the full set of molecular markers, except for the placement of *Drepanosiphoniella fugans* (sister species to *Drepanaphis* in the mitochondrial tree but with low support: BS = 60 PP = 0.64). Nuclear genes (EF-1α, PGD) were sequenced for fewer taxa than mitochondrial ones and no sequences were obtained from the species: *D. granovskyi, D. parva*; *D. simpsoni* and *M. nigrostriata*. However, based on this limited sampling, our EF-1α and PGD tree (Fig. 2B) confirmed the monophyly of Drepanosiphinae (BS: 100; PP: 1).

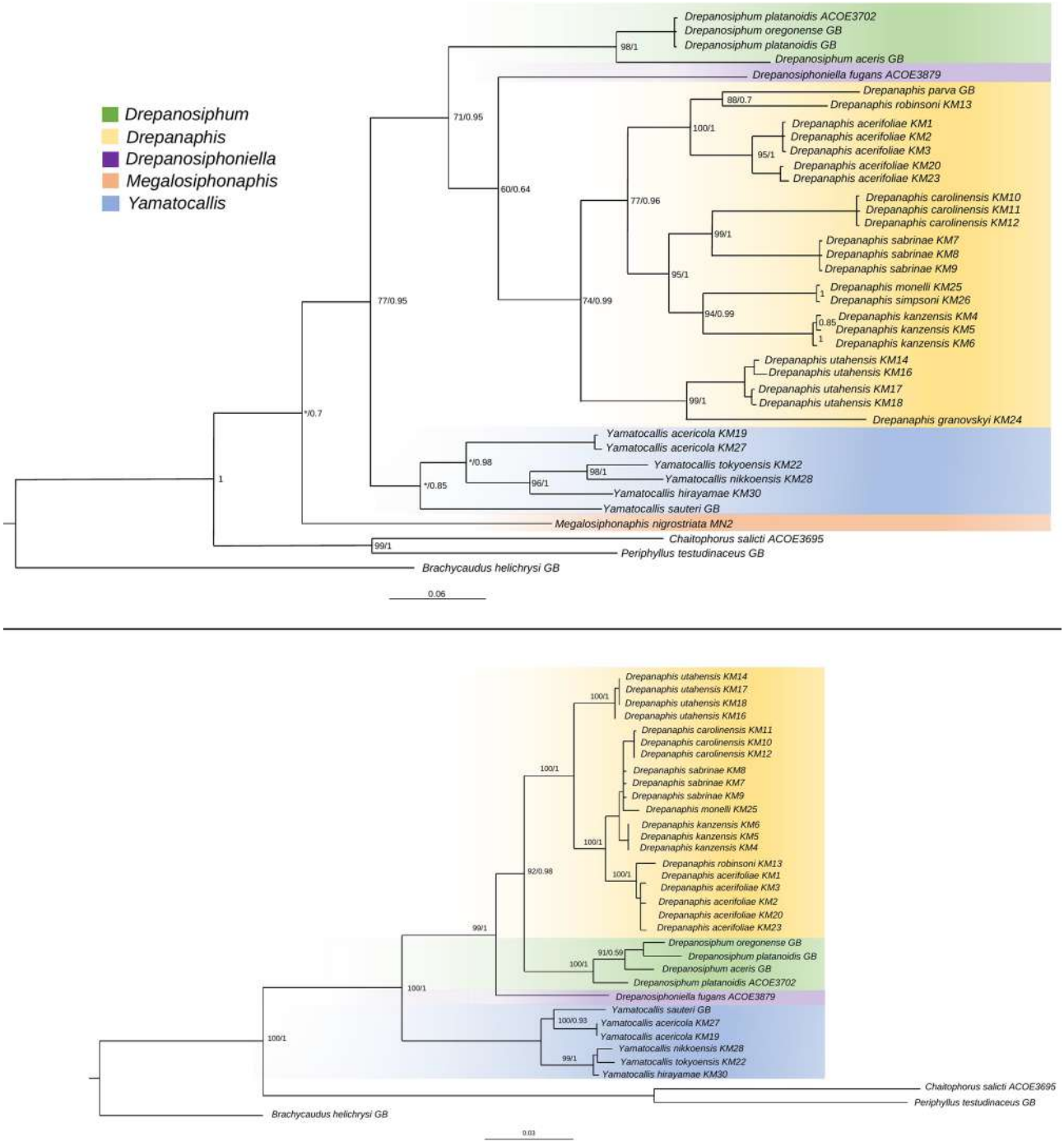

Fig. 2 A. Phylogenetic tree obtained under Bayesian inference of mitochondrial markers: a 700-bp region of cytochrome oxidase I (COI), 780 bp of cytochrome b (cytb) of analyzed aphid species of the Drepanosiphinae subfamily. Values at nodes indicate bootstrap support (ML) and posterior probabilities (Bayesian inference) for congruent nodes. An asterisk ('*') indicates that the node was not recovered in the corresponding analysis. B. Phylogenetic tree obtained under Bayesian inference of nuclear markers: 900 bp of elongation factor-1α (EF1α), and 700 bp of 6-phosphogluconate dehydrogenase (PGD) of analyzed aphid species of the Drepanosiphinae subfamily. Values at nodes indicate bootstrap values obtained with posterior probabilities (Bayesian inference)

Similarly to the mitochondrial tree, one clade included genera *Drepanaphis, Drepanosiphum* and *Drepanosiphoniella*, but the position of *D. fugans* was different (sister to all others with strong support (BS: 100, PP: 1). *Yamatocallis* was found as a sister group to the remaining Drepanosiphinae.

There are differences in species groupings within the genus *Drepanaphis*. Phylogenetic analysis performed on

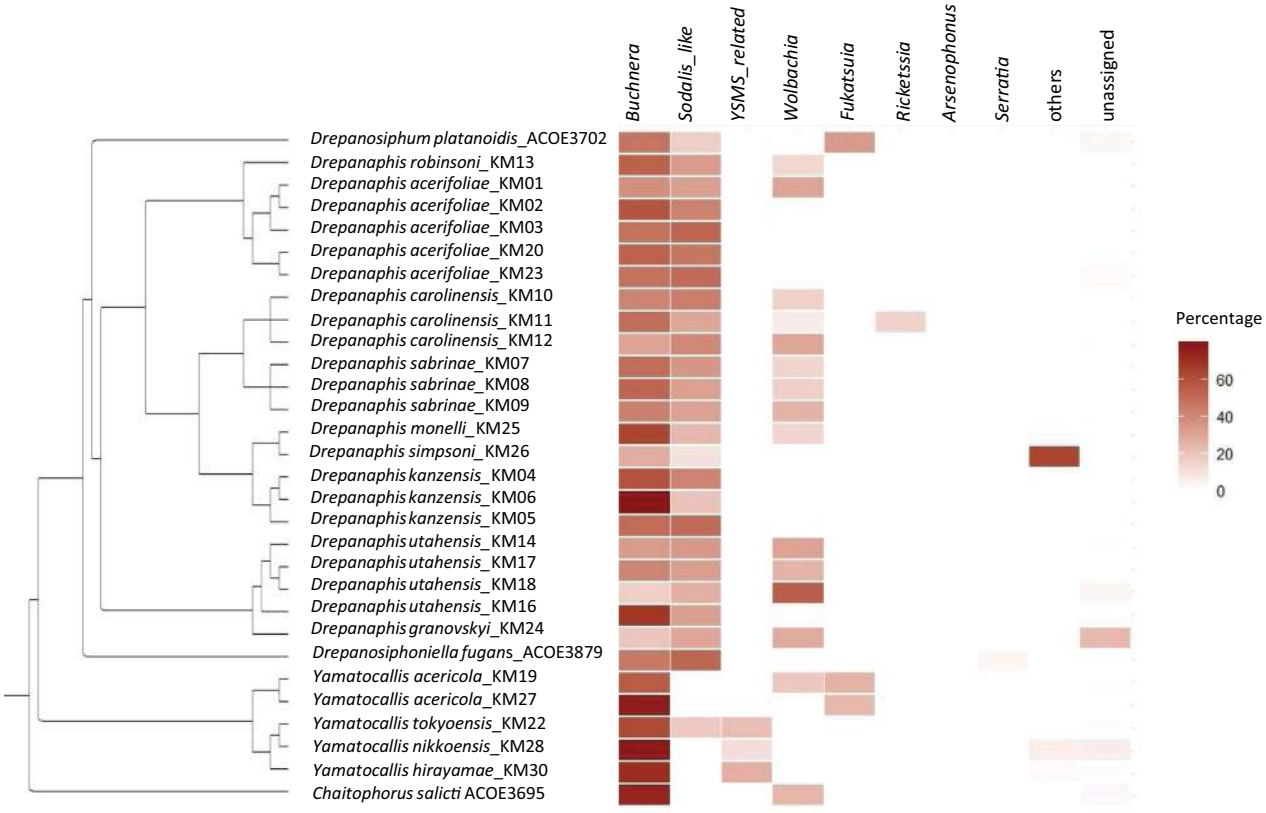

Fig. 3 Phylogenetic tree and heatmap illustrating the distribution of endosymbionts among analyzed aphid species of the Drepanosiphinae subfamily. The tree topology used is the tree obtained with Bayesian analyses of combined markers. The heatmap (right) shows the relative 16S rDNA gene read abundance (in percentage) of different bacteria, identified as typical aphid endosymbionts (columns), detected in each species (rows). Gradient fill represents endosymbiont read relative abundance (in percentages), with darker colors indicating higher proportions. "Others" generally correspond to diverse bacteria that are ubiquitous and could represent environmental contaminations (all reads were added together for representation). "Unassigned" represent reads assigned to clusters that were in very low abundance (less than 0.5% of the reads found in a sample). The results are further detailed in additional files - Tables S1 and S2

nuclear markers clustered *D. monelli* between *D. carolinensis* and *D. sabrinae* which constitute a sister clade to *D. kanzensis*. Phylogenetic analyses performed on the combined data, groups *D. monelli* as a sister branch to *D. kanzensis*, constituting a sister clade to *D. carolinensis* and *D. sabrinae*.

Diversity of symbionts associated with Drepanosiphinae

High-throughput sequencing of 16s rDNA bacteria gene fragment yielded on average 15216 sequencing reads per sample, those were 251 bp long. This allowed uncovering the diversity of the aphid microbiota (Fig. 3; Table S2). In our 29 specimens from 16 species (*Drepanaphis acerifoliae*; *D. carolinensis*; *D. granovskyi*; *D. kanzensis*; *D. monelli*; *D. robinsoni*; *D. sabrinae*; *D. simpsoni*; *D. utahensis*; *Drepanosiphum platanoidis*; *Drepanosiphoniella fugans*; *Yamatocallis acericola*, *Y. hirayamae*; *Y. nikkoensis*; *Y. tokyoensis, Chaitophorus salicti*), 96 to 99% of the reads were assigned to the primary symbiotic partner of aphids, *Buchnera aphidicola* and several known aphid facultative symbionts: mainly a *Sodalis*-like bacterium, *Wolbachia*, *Ricketssia*, *Fukatsuia* and *Arsenophonus*. Using sequences from NCBI previously analyzed in Fukatsu [17], we also retrieved a cluster that was assigned to the so-called YSMS based on BLAST and phylogenetic analyses (Fig. S1, Table S3). Although results are represented as relative read abundances in the heatmap (Fig. 3), these values should not be interpreted as accurate estimates of symbiont abundance within specimens [30]. We therefore report and discuss only the presence or absence of symbionts. The obligate symbiont *Buchnera aphidicola* was consistently present across all species and individuals, whereas the presence of other symbionts varied among species and populations. A *Sodalis*-like symbiont was detected in 25 individuals, from Drepanosiphinae including all 22 individuals from *Drepanaphis* (*D. acerifoliae, D. carolinensis, D. granovskyi, D. kanzensis, D. monelli, D. robinsoni, D. sabrinae, D. simpsoni, D. utahensis*), the representative of *Drepanosiphoniella fugans*, *Drepanosiphum platanoidis* included here and a single individual from the *Yamatocallis* genus among the

five included in our survey, namely *Yamatocallis tokyoensis*. Several sequence clusters had showed high sequence similarity with *Sodalis*-like symbionts previously identified in *Drepanosiphum platanoidis* [14] or Lachninae aphids [19] (Fig. S1, Table S3). Each aphid species always hosted a single *Sodalis* cluster, which suggests some kind of host specificity in *Sodalis*. Three *Yamatocallis* species, *Y. nikkoensis*, *Y. hirayamae* and *Y. tokyoensis* were found associated with a bacterial strain that showed genetic similarity with the YSMS, sequenced by Fukatsu [17]. This strain was not diversified across species, as it was represented by single genetic cluster in our sampling (Table S3, Fig S1). A more robust taxonomic affiliation of this strain would necessitate sequencing more genes and not just a short 16S rDNA gene fragment. Indeed, for instance, based on this fragment alone, *Sodalis* is not a monophyletic genus (Fig. S1). In any case, the heatmap of symbiont occurrence puts into phylogenetic perspective suggests acquisition of *Sodalis*-like in a common ancestor of *Drepanaphis*, *Drepanosiphoniella* and *Drepanosiphum* genera. *Wolbachia* strains are also largely distributed across Drepanosiphinae species: *Wolbachia* was detected in 14 individuals, including 13 individuals of *Drepanaphis* (*D. acerifoliae, D. carolinensis, D. granovskyi, D. monelli, D. robinsoni, D. sabrinae, D. utahensis)* and a single individual of *Yamatocallis acericola*. *Fukatsuia* endosymbionts was detected in both individuals of *Y. acericola* and *Drepanosiphum platanoidis. Ricketssia*, *Arsenophonus* and *Serratia symbiotica* were all detected in a single individual from our sampling. A comparison of geographically distant populations from the native and introduced ranges revealed no differences in the composition of *Drepanaphis acerifoliae* populations from the USA and Europe. The complete composition of the microbiota (in relative read abundance) is available in Tables S2 and S3.

Discussion

Phylogenetic relationships within the subfamily Drepanosiphinae

Our phylogenetic analyses confirm the monophyly of Drepanosiphinae and its sister relationship to Chaitophorinae, consistent with the molecular framework proposed by Wieczorek et al. [1]. This result reinforces the monophyly of currently established subfamilies (sensu Remaudière and Remaudière) within Aphididae [24]. In contrast to the earlier study by Wieczorek et al. [1], which included only single mitochondrial or nuclear genes (COI and EF-1α) and a limited number of species, our research analyzed four gene regions and incorporated 20 species from five of the six recognized Drepanosiphinae genera (the lacking *Shenahweum* is a monotypic genus rarely collected in its Nearctic range). This broader dataset allowed for more robust resolution of internal relationships within the subfamily. The position of *Yamatocallis,* in particular has been clarified. While previously represented only by *Y. tokyoensis* and considered an independent lineage within Drepanosiphinae, our study included four additional species (*Y. acericola, Y. nikkoensis, Y. hirayamae*, and *Y. sauteri*). The results strongly support *Yamatocallis* as a sister clade to the main Drepanosiphinae lineages, which includes *Drepanaphis*, *Drepanosiphum* and *Drepanosiphoniella*. This finding aligns with analyses of morphological features and supports the inclusion of *Yamatocallis* within the subfamily, rather than as a separate lineage. The newly described monotypic genus *Megalosiphonaphis* [11], was retrieved as part of the Drepanosiphinae clade, but with low branch support (below 0.7). This uncertainty is likely due to the limited data available, as only mitochondrial markers were successfully sequenced for this genus. Morphologically, *Megalosiphonaphis* shares traits with other Drepanosiphinae, such as elongated siphunculi with a reticulated apex (similar to *Yamatocallis*) and the arrangement of accessory rhinaria on antennal segment VI (as in *Drepanosiphum*), suggesting a close relationship. However, more comprehensive molecular data are needed to confirm its systematic placement. Our results also support the monophyly of *Drepanosiphum*. However, two populations of *D. platanoidis* were placed in separate positions on the phylogenetic tree, likely reflecting intraspecific genetic variability rather than species-level divergence. The genus *Drepanosiphoniella* was also recovered within the core Drepanosiphinae clade, confirming its close relationship with *Drepanosiphum* and *Drepanaphis*, as previously suggested [1]. These findings emphasize the importance of combining broader taxon sampling with multilocus molecular data to refine the systematics within aphid subfamilies and to resolve longstanding taxonomic uncertainties within the group. Thorough molecular phylogenetic investigations have been conducted for several aphid subfamilies (Calaphidinae [35]; Chaitophorinae [36]; Lachninae [37]), but many aphid lineages still lack such analyses. Thus, we provide here the most comprehensive phylogenetic reconstruction to date for Drepanosiphinae.

Morphological affinities, versus phylogenetic relationships in *Drepanaphis* with insight into their biogeographical history and host-plant associations

Drepanaphis, is the most diverse genus within the subfamily Drepanosiphinae, as it includes 18 species [9]. Winged viviparous females are distinguished by the tubercles on the dorsal part of the abdomen, which are the most remarkable features in this group. Over the last decades, the most reliable source of information about the *Drepanaphis* species has been the revision conducted by Smith and Dillery [13]. Although they did not incorporate all critical diagnostic features of the winged viviparous females necessary for determining morpho-groups,

the revision also overlooked the descriptions of all known oviparous females and males. Recently, Malik et al. [9] conducted a comprehensive morphological revision of *Drepanaphis*, using a matrix of 52 characters and broad comparative material. This study clarified previously problematic taxa such as *D. nigricans* Smith, 1941 and *D. tissoti* Smith, 1944, enabled the identification of all morphs, and resulted in the delineation of five morpho-groups: "acerifoliae," "monelli," "nigricans," "parva," and "utahensis". Present molecular phylogenetic analyses partly supported the morphological groupings but also revealed some inconsistencies. Only 10 of the 18 known species of *Drepanaphis* were available for molecular study, leaving some groups - such as "nigricans" - unrepresented. Phylogenetic trees based on mitochondrial and nuclear markers were mostly congruent, with the exception of a few taxa. Species in the "acerifoliae" group, though morphologically similar, did not form a monophyletic clade. Instead, *D. acerifoliae*, *D. parva*, and *D. robinsoni* appeared in closely related yet distinct lineages. All three species are associated with *Acer rubrum*, and while *D. parva* and *D. robinsoni* were previously grouped morphologically, molecular results indicate they form a sister clade to *D. acerifoliae*, an oligophagous species on the same host. This clustering of species using the same range of host-plants, suggests that host plant specialization triggers speciation events in this aphid group [38]. Host plant associations also help clarify relationships in the "utahensis" group. *D. granovskyi* and *D. utahensis*, both monophagous on *Acer grandidentatum* and restricted to the western United States, form a distinct clade. In contrast, *D. simpsoni*, also in the "utahensis" morpho-group and associated with *Acer saccharum*, belongs to a separate, distributed in the eastern United States lineage. These phylogenetic splits likely reflect both host specificity and geographic isolation as triggering factor of speciation events as observed in other Nearctic aphids [39, 40]. Notably, *D. monelli*, the only species in the genus associated with *Aesculus glabra* rather than maples, showed inconsistent phylogenetic placement. Mitochondrial data clustered it with *D. simpsoni*, forming a sister group to *D. kanzensis*, while nuclear data placed it with *D. sabrinae* and *D. carolinensis*. The lack of nuclear data for *D. simpsoni* may explain this incongruence. Morphologically, *D. monelli* has been linked to species such as *D. keshenae*, *D. knowltoni*, and *D. spicata*, which were not included in the molecular dataset due to limited material. Some species not assigned to any morphological group, like *D. sabrinae* and *D. kanzensis* are clustered with species sharing the same host plant in molecular analyses, further supporting the value of host association as a taxonomic criterion. Additionally, several monophagous species that are grouped together phylogenetically also share morphological traits, suggesting convergence under similar ecological pressures. Thus, based on the combined morphological, molecular, and ecological evidence, we propose a revised species grouping system for *Drepanaphis*, centered on host plant affiliation. Three major host-associated groups are recognized: the *rubrum*, *saccharum*, and *grandidentatum*. This host-based classification more accurately reflects the evolutionary history and highlights the conserved nature of host plant associations in the genus *Drepanaphis*.

Drepanosiphinae's endosymbiotic consortia

Our results provide new insight into the diversity of microbial communities associated with Drepanosiphinae, highlighting the complexity and variability of endosymbiotic relationships in this aphid subfamily. As expected, the obligate endosymbiont *Buchnera aphidicola* was present in all individuals. However, significant variation was observed in the composition of secondary symbionts across species and populations. The dominant facultative symbiont identified was a *Sodalis*-like bacterium, detected in 86% of Drepanosiphinae individuals. It was present in all species of *Drepanaphis*, *Drepanosiphoniella*, and *Drepanosiphum*, and in all individuals sampled from these genera. Its occurrence did not vary with host plant association or geographic distribution. A single strain was found per aphid species which suggests some kind of host specificity in *Sodalis*. Previous genomic studies on *Drepanosiphum platanoidis* showed that its *B. aphidicola* lacks essential biosynthetic capacities, which appear to be complemented by a *Sodalis*-like symbiont that shows genomic characteristics typical of long-term obligate symbiosis (i.e., highly reduced genome and high GC content). These findings led to the suggestion that *Sodalis*-like bacteria may act as co-obligate partners of *Buchnera* in *D. platanoidis* and potentially in other Drepanosiphinae species [14].

The symbiont distribution patterns observed in our study support this hypothesis and suggest that the acquisition of a *Sodalis*-like symbiont occurred early in the evolutionary history of Drepanosiphinae. However, species of the genus *Yamatocallis* do not show a systematic association with a *Sodalis*-like partner. Fukatsu [17], based on limited sampling of *Y. tokyoensis* and *Y. hirayamae*, proposed that these species harbor a distinct intracellular symbiont, YSMS, suggesting an ancient association dating back to the origin of the genus. We detected YSMS-like sequences in three *Yamatocallis* species, but a robust taxonomic placement of this bacterium will require sequencing of additional genetic markers. Based solely on the 16S rRNA gene fragment, we cannot rule out the possibility that YSMS also belongs to the *Sodalis* lineage (Fig. S1). Regardless of its precise taxonomic status, we did not detect YSMS or any *Sodalis*-like symbiont in *Yamatocallis acericola*, which argues against

Fukatsu's hypothesis [17] and instead points to two alternative scenarios: a more recent acquisition of YSMS in a subset of species, or a lineage-specific secondary loss. A further possibility is that *Yamatocallis* initially harbored *Buchnera* together with *Fukatsuia*, and that *Fukatsuia* was later replaced by YSMS. Additional data, particularly from *Y. sauteri*, will be essential to discriminate among these hypotheses. Endosymbiont profiling using multiple markers or whole endosymbiont genome data across species are also needed to: 1) elucidate the taxonomic affiliation of YSMS; 2) reconstruct the phylogenetic history of *Drepanosiphinae* main symbionts (*Sodalis* and YSMS) and evaluate aphid/symbiont codiversification scenarios (as [41]). In addition to *Sodalis*, the facultative symbiont *Wolbachia* was detected in 48% of Drepanosiphinae individuals, a notably high prevalence compared to other aphids [42, 43]. However, unlike *Sodalis*, *Wolbachia* was not present in all individuals of a given species and thus cannot be considered an obligate partner. Understanding its ecological role in Drepanosiphinae will require further genomic and ecological research. Given aphids' reproductive biology, it is unlikely that *Wolbachia* functions as a reproductive manipulator. Nonetheless, it has been shown to protect aphids from fungal pathogens in *Pentalonia nigronervosa* (Coquerel, 1859) [44]. Thus, Drepanosiphinae may provide a promising system for comparative studies of *Wolbachia* in aphids, given the relatively high and recurrent detection of this symbiont in multiple species. Unlike *Cinara cedri* Mimeur, 1936 [45] or *P. nigronervosa,* where infection can reach nearly 100% of samples, Drepanosiphinae species exhibit variable prevalence of *Wolbachia*, making them particularly valuable for studying the evolutionary dynamics and ecological correlates of symbiont maintenance and loss [30, 42].

Other symbionts, including *Fukatsuia*, *Rickettsia*, *Serratia*, and *Arsenophonus*, were found only in a few individuals, suggesting transient or facultative associations. These rare occurrences reflect the dynamic nature of aphid microbiomes, where facultative symbionts may be gained or lost in response to environmental pressures, host plant use, or other ecological factors [46, 47].

Overall, our findings emphasize the value of combining high-throughput sequencing with ecological and taxonomic context to better understand the evolution of symbiotic associations in aphids. In Drepanosiphinae, *Sodalis*-like bacteria potentially play a central role in compensating for *Buchnera* deficiencies. However, symbiont diversity differs markedly between lineages, as illustrated by the contrasting profiles of *Yamatocallis*. Similar differences in co-obligate associations have been observed in Chaitophorinae [14, 15, 48], the sister group to Drepanosiphinae, where *Serratia symbiotica* appears to have been independently gained or lost multiple times. Such evolutionary lability in nutritional symbioses was first highlighted in Lachninae [18, 19, 49]. The significant role of endosymbionts in various insect groups is supported not only by molecular studies but also by morphological analyses, revealing their diversity and intergenerational transmission strategies [50].

Thus, our results further highlight the diversity of nutritional symbiotic consortia in aphids and emphasize the potential of Drepanosiphinae as an alternative model system for exploring the evolution of dual symbiotic associations in aphids.

Conclusions

This study provides a comprehensive phylogenetic framework for the subfamily Drepanosiphinae, confirming its monophyly and clarifying relationships among its genera. Phylogenetic analyses consistently support a close relationship between *Drepanaphis* and *Drepanosiphum*, with *Drepanosiphoniella* forming a sister lineage, while *Yamatocallis* and *Megalosiphonaphis* represent distinct evolutionary branches. Within *Drepanaphis*, host plant association emerges as a key factor shaping species groupings, leading to the definition of three host-associated groups: *rubrum*, *saccharum*, and *grandidentatum*, which correspond to specific *Acer* host affiliations. The widespread occurrence of a *Sodalis*-related bacterium across Drepanosiphinae, along with previous genomic evidence, suggests a long-standing co-obligate symbiosis within the subfamily. *Wolbachia* is also recurrently associated with members of the subfamily, contrasting with earlier reports of its low prevalence in aphids, and raising questions about its ecological role in this group. Additional facultative symbionts, including *Rickettsia*, *Fukatsuia*, *Serratia* and *Arsenophonus*, exhibit limited and sporadic distributions, possibly reflecting transient or non-established, rather than stable, long-term coevolutionary associations. Together, these findings significantly enhance our understanding of phylogenetic relationships within Drepanosiphinae and provide new insights into the diversity and evolutionary dynamics of aphid-symbiont interactions.

Supplementary Information

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Supplementary Material 1

Supplementary Material 2

Supplementary Material 3

Supplementary Material 4

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KM, KW and EJ designed the study. KM and SS collected aphid samples. KM, EJ and A-LC performed molecular and microbial data. KM and EJ prepared figures. KM, KW and EJ analyzed the data and drafted manuscript. All authors read and accepted the final manuscript.

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Data availability
All data generated or analyzed during this study are included in this published article [and its supplementary information files]. Genetic data are deposited in GenBank, NCBI.

Declarations

Ethics approval and consent to participate
Aphids (invertebrates) were used for this study. No vertebrate or human individuals or tissues were used.

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Katowice, 05.01.2026

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Oświadczam, że w pracy:

Malik, K., Jousselin, E., Clamens, A.-L., Sugimoto, S., Wieczorek, K. (2025). Molecular phylogeny of the Acer-feeding aphid subfamily Drepanosiphinae (Insecta: Hemiptera: Aphididae) and the evolution of its endosymbiotic consortia. Zoological Letters 11, 9. https://doi.org/10.1186/s40851-025-00255-2

Mój udział polegał na opracowaniu koncepcji badań, przeprowadzeniu analiz laboratoryjnych, bioinformatycznej analizie danych, interpretacji wyników, wykonaniu tabel i figur, przygotowaniu manuskryptu oraz formułowaniu odpowiedzi na uwagi recenzentów. Jestem autorem korespondencyjnym.

Kamila Malik

podpis

Załącznik nr 10
do pisma okólnego nr 2
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OŚWIADCZENIE

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Afiliacja

Miejsce Katowice, dnia 05.01.2026

OŚWIADCZENIE

Oświadczam, że w pracy:

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https://doi.org/10.1186/s40851-025-00255-2

Mój udział polegał na opracowaniu koncepcji badań, planowaniu oraz nadzorowaniu badań, interpretacji otrzymanych wyników, udziale w przygotowaniu i pisaniu manuskryptu na każdym etapie.

.....

Podpis współautora publikacji

A STATEMENT OF THE APPLICANT'S CO-AUTHOR OF THEIR CONTRIBUTION TO THE WORK

Montferrier sur lez, 29/12/2025

Emmanuelle Jousselin

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STATEMENT

I declare that for the following work:

Malik, K., Jousselin, E., Clamens, A.-L., Sugimoto, S., Wieczorek, K. (2025). Molecular phylogeny of the Acer-feeding aphid subfamily Drepanosiphinae (Insecta: Hemiptera: Aphididae) and the evolution of its endosymbiotic consortia. Zoological Letters 11, 9.
https://doi.org/10.1186/s40851-025-00255-2

My participation consisted of laboratory work (isolation of genetic material and PCR), conducting phylogenetic analyses, and characterizing the composition of endosymbiont consortia, as well as visualization of the obtained results, preparing and reviewing the final version of the manuscript.

Signature of the co-author of the publication

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A STATEMENT OF THE APPLICANT'S CO-AUTHOR OF THEIR CONTRIBUTION TO THE WORK

Montferrier sur Lez (France), date 05/01/2026

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https://doi.org/10.1186/s40851-025-00255-2

My participation consisted of preparing the material for analysis, performing laboratory work (including the isolation of genetic material and PCR), and preparing and processing the results of genetic analyses and endosymbiont characterization.

Signature of the co-author of the publication

* applies to co-authors

A STATEMENT OF THE APPLICANT'S CO-AUTHOR OF THEIR CONTRIBUTION TO THE WORK

Yokohama, Dec.29, 2025

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Malik, K., Jousselin, E., Clamens, A.-L., Sugimoto, S., Wieczorek, K. (2025). Molecular phylogeny of the Acer-feeding aphid subfamily Drepanosiphinae (Insecta: Hemiptera: Aphididae) and the evolution of its endosymbiotic consortia. Zoological Letters 11, 9.
https://doi.org/10.1186/s40851-025-00255-2

My participation consisted of fieldwork (collecting representatives of the genus *Yamatocallis* and *Megalosiphonaphis* used for genetic analyses).

Signature of the co-author of the publication

* applies to co-authors