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Endemic aphids *Aphis carverae* sp. nov. and *Casimira canberrae* (Eastop, 1961) on *Epilobium* (Onagraceae) threatened by introduced *Aphis oenotherae* Oestlund, 1887 (Hemiptera: Aphididae: Aphidinae)

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Abstract We describe the wingless viviparae and sexual forms of *Aphis carverae* sp. nov., a new endemic species of *Aphis* Linnaeus, 1758 from Australia. The species is holocyclic and monoecious on *Epilobium* (Onagraceae). No winged individuals have been found. *Casimira canberrae* (Eastop, 1961) is another endemic aphidine species from *Epilobium*. We describe the winged viviparous and wingless sexual female morphs of this aphid, which is also shown to be holocyclic and monoecious. Native aphids feeding on Onagraceae in Australia are under serious competitive threat from the recently introduced *Aphis oenotherae* Oestlund, 1887.

Key words Australian endemic aphids, competition, extinction, invasive species, principal components analysis.

INTRODUCTION

The native aphid fauna of Australia encompasses only about 20 known species spread over five subfamilies of the family Aphididae (M. Carver pers. comm. 1998). Only three endemic Aphidinae have been described from Australia: *Aphis platylobii* Carver & White, *Aphis acaenovinae* Eastop and *Casimira canberrae* (Eastop).

We describe here a new species of *Aphis* Linnaeus found on *Epilobium* near Thredbo Village in the alpine region of New South Wales.

Casimira canberrae has been recorded in Sydney and Canberra on *Epilobium*, and has also been collected in Victoria and South Australia (M. Carver pers. comm. 1998). The type series of *C. canberrae* was collected on willow herb identified as *Epilobium junceum* (Onagraceae). The aphid was readily found in and near the type locality (Sullivan's Creek, Australian National University, Canberra) during the 1950s–1980s, and also on the Macquarie University campus (North Ryde, Sydney) in the 1970s–1980s, but has not been found during the present study. We describe the winged vivipara and wingless ovipara of *C. canberrae*.

These species are threatened (*C. canberrae* possibly now extinct) by the introduced Nearctic *Aphis oenotherae* Oestlund, and their current status is discussed.

Abbreviations

Depositories

ANIC	Australian National Insect Collection, Canberra
BMNH	British Museum of Natural History (now Natural History Museum, London)
CNC	Canadian National Collection of Insects

Anatomical features

A 1 . . . 6	Antennal segments 1 . . . 6
Ab1 . . . 8	Abdominal segment 1 . . . 8
ht2	Second segment of hind tarsus
Th1	First thoracic segment
URS	Rostral segment iv + v ('ultimate rostral segment')

Other

DFH	Dinah F Hales

MATERIALS AND METHODS

Specimens were mounted in Canada Balsam and measured for 40 characteristics (see descriptions). Lists of material examined are provided below for each species. Measurements for holotype wingless vivipara of *A. carverae sp. nov.* are given, with range for other specimens in parentheses. In descriptions of other morphs, the range of measurements is given.

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Measurements of tubercles and setae are given in micrometres, and measurements for other variables in millimetres. Measurements and ratios are rounded to two decimal places. Patterns of morphological variation were analysed using principal components analysis (PCA; procedure PRINCOMP, SAS 9.3, SAS Institute Inc., Cary, NC, USA).

SYSTEMATICS

Genus *Aphis* Linnaeus, C. 1758: 451–453

Type species. *Aphis sambuci* Linnaeus, 1758 by subsequent designation

Aphis carverae sp. nov.
http://zoobank.org/urn:lsid:zoobank.org:act:12D9C970-9DAC-4D5D-AF54-48932A943234

Material examined

Holotype female. Specimen 10.3, Thredbo NSW, roadside E of village, (coordinates −36.505 and 148.308, altitude 1380 m above sea level) ex *Epilobium* sp., 6.iii.2008, coll. DFH (ANIC). Paratypes: all other specimens (wingless viviparae, oviparae and males) as listed below, with the exception of those from Goolwa and Jenolan Caves.

Holotype and paratypes to be deposited in ANIC (13 wingless viviparae, 3 oviparae, 1 male), other paratypes in CNC (19 wingless viviparae, 3 oviparae, 1 male) and BMNH (10 wingless viviparae, 2 oviparae).

Fig. 1. Holotype wingless viviparous female of *Aphis carverae* sp. nov.

Wingless viviparae. ex *Epilobium billardierianum* (Thredbo NSW, roadside E of village, (coordinates -36.505 and 148.308, altitude 1380 m above sea level) 6.iii.2008, coll. DFH, 28 specimens; same data, 17.iv.2008, 1 specimen; same data 5.ii.2004, 7 specimens; culture 27.xii.2006 ex Thredbo, 1 specimen; Thredbo Valley (nr village, NW of river) 5.ii.2004, 5 specimens. With proposed name '*Aphis matris*': (ANIC): left-hand label Aphis matris sp.nov.? ?? nelsonensis, right-hand label *Ludwigia peploides* (=*Jessicua repens* L.) Onagraceae S. Aust.: on banks R. Murray nr Goolwa Barrages 24.v.63 M. Carver, 1 specimen, slide numbered 161 on left-hand label and 159 on right-hand label; ex *E. billardierianum* ssp. *cinereum*, nr Jenolan Caves NSW, 17.xii.1974, coll. DFH, 2 specimens (slides in poor condition and could be measured only for some data points).

Oviparae. ex *Epilobium billardierianum*, Thredbo roadside, 17.iv.2008, coll. DFH, 8 specimens.

Males. ex *Epilobium billardierianum*, Thredbo roadside, 17.iv.2008, coll. DFH, 2 specimens.

Wingless vivipara (Fig. 1)**.** Small to medium, body length 1.36 (0.93–1.52) mm excluding cauda. Black in life with antennal segment 3, and femora and tibiae of all legs whitish proximally. Head with small antennal tubercles, median frontal prominence slightly protruding and somewhat flattened, with two pairs of setae. Ventral surface of head capsule divided medially. Macerated specimens pale except as follows. Head, subgenital plate, subanal plate, cauda, siphunculi, spiracular plates, coxae, distal parts of femora (75%) and tibiae (25%) and tarsi pigmented. All outer precoxal plates, and inner precoxal plates of mid- and hind legs pigmented. Light pigmentation on rostrum, antennal segments 1 and 2, 5 and 6 and spiracular plates. Without segmental pigmentation on tergites or sternites. Antennae imbricated, 6- or occasionally 5-segmented, without secondary rhinaria; 0.53 (0.45–0.73) times the length of the body excluding the cauda. Three individuals (body lengths 1.47, 1.50 mm and unmeasured) from Thredbo Valley with larger measurements for most antennal and leg segments: measurements for these if outside the range for other specimens given in square brackets. Antennal segment lengths: A3 0.16 (0.12–0.21) mm [0.21–0.27], A4 0.08 (0.06–0.13) mm [0.14–0.17], one specimen with fused A3 + 4, 0.22 mm, A5 0.10 (0.09–0.14) mm [0.14–0.17], A6 (5) base 0.09 (0.09–0.12) mm. Processus terminalis 0.19 (0.15–0.23) mm, 2.02 (1.46–2.16) times the length of base of the last segment. Base of antennal segment 3 constricted, approximately half the maximum thickness of the segment. Antennal setae short, 11 (8–14) µm. Mesothoracic furca broad-based (0.11 mm) with long diverging arms (0.07 mm, measurements from holotype only). Rostrum

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Fig. 2. Oviparous female of *Aphis carverae* sp. nov.

ending approximately at the middle of the mid-coxae. URS 0.10 (0.09–0.11) mm, 1.06 (0.82–1.25) times the length of the second segment of the hind tarsi, and bearing 2 secondary setae about 15–30 µm in length. Primary setae 6. Prothorax with a pair of lateral tubercles 16 (11–33) µm in height and 20 (10–31) µm in width at base. Similar lateral tubercles on abdominal segments 1 and 7, those on Ab1 being 18 (11–22) µm high and 14 (12–20) µm wide. Hind tibia 3 0.52 (0.46–0.58) mm [0.73–0.87], hind femur 3 0.32 (0.21–0.41) mm [0.41–0.45], hind tarsal segment 2 0.10 (0.08–0.11) mm [0.11–0.12]. First tarsal chaetotaxy 3-3-2. Longest setae on hind coxa 18 (14–26) µm, on hind trochanter 24 (16–52) µm, on ventral surface of hind femur 16 (12–22) µm, and on hind tibia 28 (14–30) µm at mid-length and 48 (24–48) µm distally. Siphunculi 0.16 (0.13–2.0) mm, 0.12 (0.09–0.16) times body length, tapering gradually from base to apex, base/apex ratio 2.06 (1.0–2.25). Cauda black, 0.19 (0.15–0.20) mm with 4 (3–6) setae. Subgenital plate with 2 (2–5) setae on the anterior part and 8 (6–12) on the posterior margin. Eighth tergite with two setae 14 (8–16) µm long. Setae on third abdominal tergite 10 (8–12) µm. Measured on 42 specimens with data above.

Alate vivipara. None collected and none reared from a culture maintained from February to May 2014.

Ovipara (Fig. 2)**.** Body length 1.16–1.58 mm excluding cauda, dusky black in life, basal three quarters of fore- and mid-tibiae whitish. Eyes dark. Femora and hind tibiae black, slightly paler at bases of femora. Macerated specimens similar to wingless viviparae in pigmentation, except hind tibiae pigmented throughout length. Hind tibiae thickened, each bearing 33–112 scent plaques. Antennae 6-segmented, A3 0.12–0.16 mm, A4 0.05–0.10 mm, A5 0.08–0.18 mm, base A6 0.08–0.11 mm, processus terminalis 0.15–0.18 mm. Antenna 0.44–0.52 times the length of the body excluding the cauda. Processus terminalis 1.21–2.08 times the length of base of A6. Longest setae on antennal segment 3 9–11 µm. Without secondary rhinaria. Rostrum extending to half way between bases

Fig. 3. Male of *Aphis carverae* sp. nov.

of mid- and hind coxae. URS 0.09–0.10 mm, 1.10–1.19 times the length of the second segment of the hind tarsi, and bearing 2 secondary setae about 18–22 µm in length. Primary setae 6 lateral tubercles on Th1 6–10 µm in height, 10–24 µm in width; on Ab1 14–16 µm in height and 10–14 µm in width. Length of hind femur 0.25–0.32 mm, of hind tibia 0.40–0.52 mm, of second segment of hind tarsus 0.08–0.09 mm. First tarsal chaetotaxy 3-3-2. Longest setae on hind trochanter 8–15 µm, longest dorsal seta on hind femur 12–18 µm, longest ventral seta on hind femur 12–20 µm, and longest setae on hind tibiae 20–32 µm (distal), 20–24 µm (middle). Siphunculi 0.13–0.17 mm, 0.10–0.12 times body length, tapering gradually from base to apex (base/apex ratio1.50–1.88). Cauda with 4–6 setae, subgenital plate broad, black, with 10–21 setae on the anterior part and 6–14 on the posterior margin. Setae on eighth abdominal tergite 6–14 µm long, and on third abdominal tergite 7–12 µm long. Measured from eight specimens, data below.

Male (Fig. 3)**.** Wingless, body length 0.94–1.02 mm excluding cauda, shiny black in life, basal three quarters of tibiae whitish. Femora black, slightly paler at bases. Eyes dark. Macerated specimens similar to wingless viviparae in pigmentation, but with broken bars of pigmentation on abdominal tergites and continuous pigmentation on 3 sternites anterior to genitalia; genitalia black. Antennae 6-segmented in available specimens, with secondary rhinaria on segments 3 (7–17), 4 (4–5) and 5 (1–4). Antennal segment lengths A3 0.18–0.19 mm, A4 0.11–0.17 mm, A5 0.13 mm, base A6 0.10–0.11 mm, processus terminalis 0.15 mm. Antenna 0.73–0.85 times the length of the body excluding the cauda. Processus terminalis 1.42–1.47 times the length of base of the last segment. Longest setae on A3 10 µm. Rostrum extending just beyond bases of hind coxae. URS 0.09–0.10 mm, 1.05–1.07 times the length of the second segment of the hind tarsi, and

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bearing 2–3 secondary setae about 14–18 µm in length. Th1 tubercle 10 µm in height, 12 µm in width (one measurement only), Ab1 12–16 µm high by 12–14 µm wide. Lengths of hind leg segments: femur 0.27–0.28 mm, tibia 0.42 mm, second segment of hind tarsus 0.08–0.09 mm. First tarsal chaetotaxy 3-3-2. Setae on hind trochanters 16–18 µm, on hind femora 14–15 µm (dorsal), 16–18 µm (ventral) and on hind tibiae 18–22 µm (middle) and 18–28 µm (distal). Siphunculi 0.12–0.15 mm, approximately 0.12–0.16, times body length, somewhat constricted at mid-length, base/apex ratio 1.16–1.67). Cauda 0.11 mm with 4–5 setae. Setae on eight abdominal tergite 10–12 µm long, and on third abdominal tergite 10 µm long. Claspers with about 24 setae on the ventral and anterior surfaces. Basal part of aedeagus pigmented; the membranous part not everted in available specimens. Measured from two specimens, data below.

Mitochondrial cytochrome oxidase subunit 1 (COI, 'DNA barcode') sequence is available as GenBank accession numbers KJ372758 and KJ372759.

History of collections

Carver collected a black *Aphis* resembling the Thredbo specimens on *Ludwigia peploides* near the Goolwa Barrages in South Australia on 24.v.63, and DFH subsequently collected specimens believed to be the same species (M. Carver pers. comm. 1974) from *Epilobium billardierianum* ssp. *cinereum* near Jenolan Caves NSW on 17.xii.1974. Carver proposed a manuscript name '*Aphis matris*' for the species, but lack of material prevented completion of a description. Material from both collections is in ANIC but is in poor condition. DFH found black *Aphis* on shoots of *E. billardierianum* at Thredbo NSW by the roadside near the entrance to Thredbo Village in 2004. Further searching provided a few more specimens from the Thredbo River Valley. Additional trips in 2006 and 2008 gave more specimens from the initial site, with sexual forms discovered in May 2008. The Thredbo specimens may be the same species as '*A. matris*', but the material of the latter is insufficient to verify this, and the description is based on the Thredbo material. Ideally, specimens from additional locations should be included in the data set, but extensive fieldwork has failed to discover more material, including at the Goolwa and Jenolan cave sites where '*A. matris*' was found. No winged specimens have been collected or reared in culture, and observed populations were always small.

Etymology. The species is named in honour of Dr Mary Carver, in appreciation of her work on aphids in Australia and her encouragement of DFH.

Aphis canberrae Eastop, V.F. 1961

Casimira canberrae (Eastop) This species was described in the genus *Aphis* from the wingless vivipara, no other morphs being available (Eastop 1961, pp. 175–176). No illustrations were provided. Material from the type series was said to be deposited in the collection now known as ANIC, but was not found. Eastop (1966) created the new genus *Casimira*, differing from *Aphis* in lacking tubercles on Ab7 and having first tarsal segment chaetotaxy 2-2-2, with *C. canberrae* as type species. Among the materials examined in this study were other specimens collected and determined by Eastop (see below).

Fig. 4. Winged viviparous female of *Casimira canberrae*.

Material examined

Wingless viviparae Epilobium cinereum 7.v.76, Macquarie University North Ryde NSW, coll. DFH, 3 specimens, on 2 un-numbered ANIC slides; 5.viii.82, same data, 1 specimen. Ex *Epilobium*, 17.iv.89, coll. VF Eastop, base of Black Mountain, ACT, 1 specimen, VFE 18505; 29.iv.89, same data, 3 specimens VFE 18545.

Winged viviparae E. cinereum 14.iv.78, North Ryde NSW, coll. DFH, 6 specimens (ANIC slides numbered 20 1721 1168); Black Mountain ACT, 29.iv.1989, VFE, 2 specimens, slides numbered 18545; Vic: Kilmore, 17.ii.70; y. t., 1 specimen; Ginninderra, A.C.T.; Feb.'66. C.R. Lindsay. Ex M.y.T, 1 specimen.

Oviparae ex *E. cinereum*, 6.v.80, Macquarie University North Ryde NSW, coll. DFH, 2 specimens (ANIC slide in poor condition); 7.v.76, same data, 2 specimens.

Winged vivipara (Fig. 4)**.** Body length 1.36–1.67 mm excluding cauda, colour in life not available. Macerated specimens are pigmented on head, antennae (less so on segments 3 + 4), rostrum (segments iii-v), legs (tibiae lighter except at ends), siphunculi, cauda, anal plate and genital plate. Light pigmentation surrounding spiracles and bases of dorso-lateral abdominal setae. Forewing media once-branched. Antennae 5- or 6-segmented. Antennae 0.64–0.83 times the length of the body excluding the cauda. Antennal segment lengths A3 0.23–0.27 mm, A4 0.16–0.19 mm, A3 + 4 0.23 mm ($n = 1$) A5 0.16–0.18 mm, base A6 0.11–0.19 mm, processus terminalis 0.36–0.41 mm. Processus terminalis about 3.17–3.68 times the length of base of the last segment. Longest setae on antennal

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Fig. 5. Oviparous female of *Casimira canberrae*.

segment 3 13–22 µm. 2–4 secondary rhinaria on A3, none on A4. Rostrum extending to hind coxae. URS 0.14–0.15 mm, 1.30–1.38 times the length of the second segment of the hind tarsi, and bearing 4 secondary setae about 16–30 µm in length. Lateral tubercles on Th1 16 µm in height, 16 µm in width ($n = 1$); on Ab1 16–30 µm in height and 11–21 µm in width. Lengths of hind leg segments: femur 0.39–0.42 mm, tibia 0.75–0.80 mm, second segment of hind tarsus 0.10–0.11 mm. First tarsal chaetotaxy 2-2-2. Longest seta on hind trochanter 14–29 µm, longest dorsal seta on hind femur 14–22 µm, longest ventral seta on hind femur 23–28 µm, and longest setae on hind tibiae 19–26 µm (distal), 30–33 µm (middle). Siphunculi 0.12–0.14 mm, 0.07–0.10 times body length, 0.81–0.90 times cauda length, tapering gradually from base to apex (base/apex ratio 1.53–2.05). Cauda 0.15–0.18 mm long, with 5–6 setae, subgenital plate black, with 2 setae on the anterior part and 5–8 on the posterior margin. Setae on eight abdominal tergite 49–63 µm long, and on third abdominal tergite 41–48 µm long. Measured from eight specimens, with data as below. (Note: Slides are affected by crystallisation of mounting medium, and not all characters could be measured on all specimens.)

Wingless ovipara (Fig. 5)**.** Body length 1.12–1.26 mm excluding cauda, grey in life, lightly dusted with wax. Eyes dark. Macerated specimens pigmented on head, antennae (less so on segments 3 + 4), rostrum (segments iii-v), legs (tibiae lighter except at ends), siphunculi, cauda, anal plate and genital plate. Hind tibiae thickened, each bearing 11–41 scent plaques. Antennae 5-segmented. Antennal segment lengths A3 + 4 0.20–0.23 mm, A5 0.09–0.10 mm, base A 6 0.08–0.09 mm, processus terminalis 0.28 mm. Antennae 0.52–0.73 times the length of the body excluding the cauda. Processus terminalis 3.15–3.54 times the length of base of the last segment. Longest setae on A3-4 14–18 µm. Without secondary rhinaria. Rostrum extending to hind coxae. Rostral segment iv + v 0.13 mm, 1.35–1.59 times the length of the second segment of the hind tarsi, and bearing 4 secondary setae about 8–18 µm in length. Lateral tubercles on Th1 16 µm in height, 14–16 µm in width; on Ab1 16–23 µm in height and 12–14 µm in width. Lengths of hind leg segments: femur 0.27–0.29 mm, tibia 0.45–0.50 mm, second segment of hind tarsus 0.08–0.10 mm. First tarsal chaetotaxy 2-2-2. Longest setae on hind trochanter 24–26 µm, longest dorsal seta on hind femur 16–28 µm, longest ventral seta on hind femur 25–30 µm, and longest setae on hind tibiae 19–34 µm (distal), 26–35 µm (middle). Siphunculi 0.12 mm, approximately 0.09–0.11 times body length and 0.68–0.74 times cauda length, tapering gradually from base to apex (base/apex ratio 2.0–2.3). Cauda 0.16–0.17 mm long, with 5–6 setae, subgenital plate broad, black, with 2–3 setae on the anterior part and 8–12 on the posterior margin. Setae on eight abdominal tergite 40–56 µm long, and on third abdominal tergite 40–52 µm long. Measured from 3 specimens, data below. (Note: Specimens from 6.v.80 are on a single slide and are affected by crystallisation of mounting medium.)

Additions to description of wingless vivipara

We measured eight wingless viviparae. Some measurements fell outside the range reported in the initial description, e.g. body length as low as 1.02 mm, cauda 0.14 mm, A3 + 4 up to 0.32 mm, A4 up to 0.16 mm, A6 base as low as 0.08 mm, and ht2 as low as 0.09 mm. Longest seta on A3 to 20 µm, dorsal cephalic setae to 35 µm, prothoracic tubercles maximum height 24 µm, maximum width 16 µm, siphuncular proportions 0.05–0.08 mm basal diameter, 0.02–0.04 mm apical diameter; base to apex ratio 1.74–2.63. We can add some measurements to the description: hind tibia 0.48–0.70 mm, hind femur 0.29–0.39 mm, siphunculus/body length 0.08–0.11. Two specimens had 4 secondary setae on URS and one had 3. Seta on the hind coxa up to 42 µm in length, on hind trochanter 20–30 µm, dorsally on the hind femur 13–24 µm, ventrally 20–29 µm; 32–45 µm at mid-length of hind tibia, 28–36 µm distally on hind tibia. Tubercle on Ab1 16–24 µm in height, and 10–20 µm in width. We found most specimens had setae on Ab3 longer than in Eastop's (1961) description ranging from 38–50 µm (one specimen only outside this range, with 23 µm). Specimens collected in Sydney were not black, but a pinkish grey colour lightly dusted with wax. The populations are similar morphometrically.

Males. Not known.

Notes on host plants

Eastop (1961) recorded the host plant of *C. canberrae* as *Epilobium junceum*, now called *E. hirtigerum* or *E. billardierianum* depending on subspecies of *E. junceum*. *Epilobium hirtigerum* is common in the type locality at present (February 2014).

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Epilobium cinereum is now regarded as *E. billardierianum* ssp. *cinereum*. In Thredbo, the host plant is *E. billardierianum* ssp. *hydrophilum* (keys and distribution in PlantNet, http://plantnet.rbgsyd.nsw.gov.au, http://www.anbg.gov.au). The name *billardierianum* has been misspelt on some slide labels. Additionally, two spellings are current: *billardiereanum* and *billardierianum*; the former is listed in the Australian Plant Name Index (http://www.cpbr.gov.au/cgi-bin/apni), with the latter as an 'orthographic variant'. However, the latter is much more frequent elsewhere, including in PlantNet, which places the alternative spelling as a synonym. It is also the form used by ITIS (*Integrated Taxonomic Information System*, http://www.itis.gov), as well as by Raven and Engelhorn (1971), who revised *E. cinereum.*

Ludwigia peploides was previously known as *Jussiaea repens*. Slides show different spellings of the latter genus.

Principal components analysis

Patterns of variation among wingless viviparae were examined using principal components analysis. PCA transforms a set of variables into a new set of uncorrelated variables (components) formed as linear combinations of the original variables, such that each successive variable accounts for the maximum amount of remaining total variation in the data set (Tabachnick & Fidell 2006). Measurement variables examined were those available for the specimens collected at Jenolan Caves, NSW, and Murray River, SA. The length of hind tibia, and lengths of A 4 and 5, were correlated with the length of A 3 and were excluded as redundant.

Correlations of the original variables with the first three principal components for an analysis that included specimens of *Aphis oenotherae* and *Casimira canberrae* are given in Table 1a. Component 1 corresponds to generalised size (contribution for all variables positive and of similar magnitude). Representatives of *C. canberrae* are clearly distinguished by component 2 (Fig. 6a), which contrasts (opposite signs) antennal and leg with caudal and siphuncular lengths, and *A. oenotherae* by component 3 (Fig. 6b) reflecting a contrast between the length of base of antennal segment 6 against the length of ultimate rostral segment and siphunculus. Specimens from Jenolan Caves and Murray River fall at the periphery (larger size end) of the scatter representing specimens from Thredbo on component axis 1 (Fig. 6a) but fall among the Thredbo specimens on axis 2. This was confirmed in a second analysis excluding specimens of *C. canberrae* and *A. oenotherae* (Fig. 7, Table 1b).

Table 1 Principal components analysis: contribution of components to total variation and loadings (correlations between original variable and component) for components 1–3

Component	1	2	3
(a) Analysis including *Aphis oenotherae* and *Casimira canberrae*			
Proportion of variance explained	52%	20%	16%
Loadings:			
Hind tarsus segment 2	0.47	–0.16	–0.03
Cauda	0.36	0.50	0.03
Siphunculus	0.24	0.63	–0.34
Antennal seg 3	0.46	–0.64	0.18
Terminal process	0.41	–0.48	0.07
Antennal seg 6 base	0.22	0.21	0.79
Ultimate rostral segment	0.42	–0.18	–0.47
(b) Analysis excluding *A. oenotherae* and *C. canberrae*			
Proportion of variance explained	67%	9%	7%
Loadings:			
Hind tarsus segment 2	0.37	–0.35	–0.44
Cauda	0.38	–0.27	–0.42
Siphunculus	0.40	–0.09	–0.10
Antennal seg 3	0.39	0.43	0.19
Terminal process	0.38	0.08	0.47
Antennal seg 6 base	0.36	0.65	–0.25
Ultimate rostral segment	0.36	–0.43	0.55

DISCUSSION

Carver (slide label) considered that the aphid she collected in South Australia might be *A. nelsonensis* Cottier 1953 described from New Zealand, also on *Epilobium*. However, *A. nelsonensis* as described has 5-segmented antennae, with A3–5 illustrated as thin relative to A 1 and 2. Mean measurements provided in Cottier's description fall within the range for the Thredbo species in body length, total antenna length, antenna to body length ratio, number of setae on genital plate and cauda, but the cauda and siphunculi are considerably shorter in *A. nelsonensis. Aphis nelsonensis* has been collected only twice, in 1946 and 1965, and intensive recent searches have failed to rediscover it (Teulon & Stufkens 2002; Teulon *et al*. 2003, 2013). Jon Martin (BMNH) kindly provided basic measurements of material in his care from each collection, and the siphunculi and cauda were shorter than in Thredbo specimens. Specimens from both *A. nelsonensis* collections had 5-segmented antennae, possibly as a result of crowding and nutritional stress: the host plants from the 1946 collection were distorted to the extent that they could not be identified to species (Cottier 1953). The slides from the 1963 and 1974 collections of '*A. matris*' are in poor condition, and many features could not be measured. Although the available measurements fall within the range of the Thredbo material, their conspecificity could not be conclusively demonstrated.

Blackman & Eastop's key to aphids on *Epilobium* does not identify any aphid with the features of *A. carverae* (Blackman & Eastop 2006). The closest species is *Aphis mirifica*, but this is clearly different, having 5–11 setae on the cauda, a greater ratio of antennal length to body length and a different colour. However, the other measurements and ratios given by Heie (1986) for *A. mirifica* fall within the same range as those for *A. carverae.* Couplet 22 of the key could be modified as follows:

22. SIPH pale. RIV+V 0.9-1.0x HT II *Aphis* sp. (Washington, USA, BMNH colln)
SIPH dark. RIV+V 0.82-1.25xHT II 22A
22A. Body in life yellowish, green, bluish-green, femora pale in macerated specimens. 5–11 hairs on cauda *Aphis mirifica*
Body in life black, femora pigmented in macerated specimens, 4–6 hairs on cauda *Aphis carverae*

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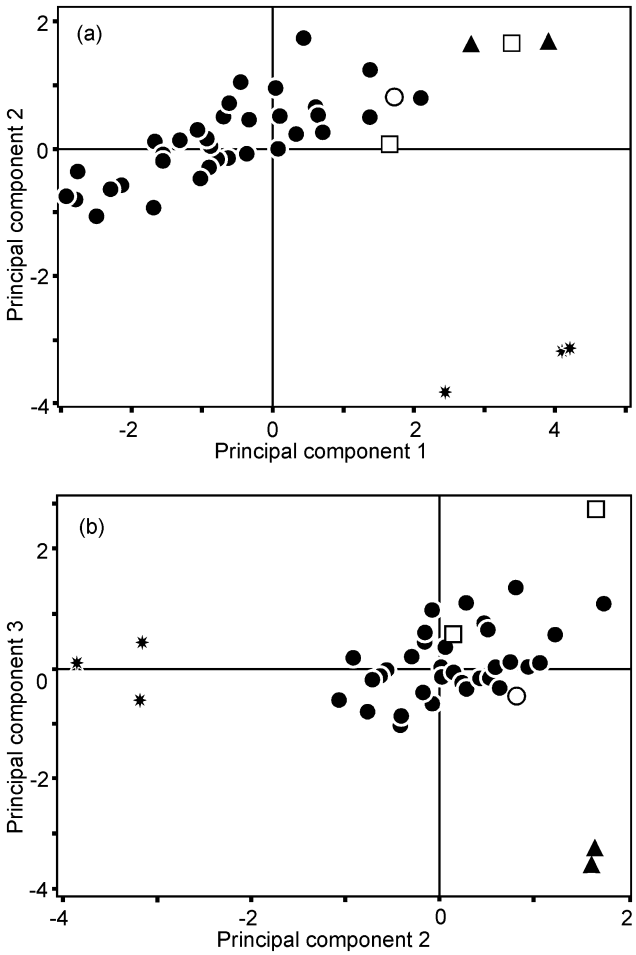

Fig. 6. Projection of specimens onto principal component axes, including specimens of *Aphis oenotherae* and *Casimira canberrae*: (a) Components 1 and 2, (b) components 2 and 3. Specimens from Thredbo (●), Jenolan Caves (□), Murray River (○), *A. oenotherae* (▲), *C. canberrae* (*).

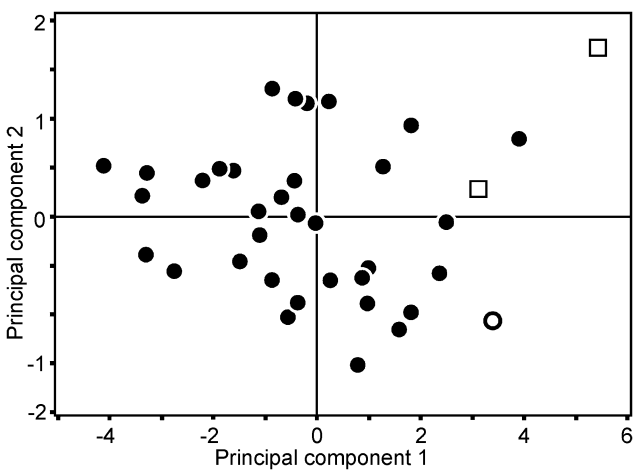

Fig. 7. Projection of specimens onto principal component axes, excluding *A. oenotherae* and *C. canberrae*, components 1 and 2. Specimens from Thredbo (●), Jenolan Caves (□), Murray River (○).

Like many Australasian aphids, *A. carverae* is rare and patchy in distribution (see Teulon *et al*. 2003 for the situation in several New Zealand species, including *A. nelsonensis*). Disregarding the 1963 and 1974 samples, *A. carverae* has been found only in a restricted area in the vicinity of Thredbo Village, in the alpine region of southern NSW. The aphids are found in small colonies on the growing tips of the host plant *E. billardierianum* and have been collected from December (but could be present earlier) to mid-April, when few viviparae remain among the sexual individuals. The aphid is shown to be holocyclic and monoecious by the fact that males and oviparae occur on the summer host and are wingless. In the Thredbo area, the perennial herbaceous host plants die back and are snow-covered from approximately June to October. The host range could potentially be wider, including other species of *Epilobium*, *Ludwigia* and perhaps other cultivated or naturalised genera within the Onagraceae. No alates of the species have been found: the three winged specimens caught in the Thredbo area conformed to the introduced Nearctic evening primrose aphid, *Aphis* (*Bursaphis*) *oenotherae* Oestlund, a recognised invasive species (CABI 2013), which arrived in Australia in or before the 1990s and was first collected here by DFH in 1995.

Casimira canberrae has also been shown to be holocyclic and monoecious by the presence of oviparae on the summer host. Notably, the oviparae were collected in Sydney, which has a relatively mild winter climate, in which the majority of exotic Aphidinae are continuously parthenogenetic. While the species is noted as black in the original description, the North Ryde (Sydney) specimens (all morphs) were relatively pale, greyish in appearance and lightly wax-covered. The Canberra and Sydney sites have both undergone considerable modification since the material was collected, but *Epilobium* is still present. However, no aphids other than *A. oenotherae* can be found on *Epilobium* at either site. *C. canberrae* has not been collected at all in recent years, despite targeted and opportunistic searching over the past decade.

Extensive searching on Onagraceae within the alpine region and elsewhere within eastern Australia (Sunshine Coast in Queensland, ACT, Sydney) has failed to find aphids other than *A. oenotherae* on Onagraceae, apart from *A. carverae* at the Thredbo site. DFH returned in 2013 to the Jenolan Caves area and found no aphids other than *A. oenotherae* on *Epilobium*, at many sites at altitudes between about 800 and 1200 m asl. In October 2013, *A. oenotherae* was found on evening primroses 17 km from Goolwa SA and on Hindmarsh Island, SA, less than 1 km from Carver's initial discovery at the Goolwa Barrages. Potential host plants (*Ludwigia*, *Epilobium*, *Oenothera*) were not found on the mainland side of the Goolwa Barrages. *Aphis oenotherae* is also known from Melbourne (collected by John Wainer, Department of Environment and Primary Industries, Victoria) and from Perth (collected by Cameron Brumley, Department of Agriculture and Food, Western Australia), hence is now known from all mainland states of Australia. Around Lake Jindabyne (altitude 915 asl) near Thredbo in the alpine region, evening primroses were covered in massive colonies of *A. oenotherae* including winged

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viviparae, and they have also been collected, albeit so far in small numbers, in the Thredbo Valley. Clearly, the native species, with their small populations, apparent low rate of increase and lack of vagility, are critically threatened by the American invader. Estoup and Guillemaud (2010) used the following definition of an invasive population: 'we consider an invasive population to be a set of individuals that has been introduced into a new area, in which these individuals have established themselves, increased in number and spread geographically'. *A. oenotherae* in Australia exhibits these characteristics.

Competitive exclusion was proposed to occur when species inhabiting the same niche compete for resources: the species with an overall competitive advantage will displace the other(s) (Gause 1934). In practice, there may be trade-offs of various kinds such that a perceived advantage is balanced out, and few examples of actual exclusion have been observed. For example, the widespread sympatric coexistence of *A. carverae* and *C. canberrae* on a few related *Epilobium* species over many millennia appears to contradict Gause's principle. In contrast, *A. oenotherae*, with its rapid reproductive rate, ready production of winged individuals, and wider host range is well placed to drive the native species to extinction, and in the case of *C. canberrae* (and *A. nelsonensis* in New Zealand) may have already done so in large areas of its previous distribution, providing an example consistent with Gause's principle.

A possible advantage for *A. carverae* in the mountains may be its monoecious holocycly. Holocyclic *A. oenotherae* in the northern hemisphere are host-alternating with *Ribes* spp. as a primary host (Blackman & Eastop 2006). *Ribes uva-crispa* (=*R. grossularia*) is naturalised in the Southern Tablelands of New South Wales, which includes the area of occurrence of *A. carverae* (http://plantnet.rbgsyd.nsw.gov.au). If *A. oenotherae* is holocyclic and host-alternating, spring generations on the primary host may delay its colonisation of herbaceous host plants, allowing *A. carverae* to maintain a slight advantage in areas exposed to rigorous winter temperatures. If anholocyclic in Australia, *A. oenotherae* may not survive winter in the mountains and need to reinvade annually. Global warming over coming decades, with either scenario, would disrupt the balance and enable *A. oenotherae* to displace *A. carverae.* The collection of possibly conspecific specimens from South Australia is the only sample so far seen from a low-altitude, coastal environment, wherein an anholocyclic existence would be feasible.

We conclude that *A. carverae* and *C. canberrae* are at risk of extinction as a result of competition for feeding sites by *A. oenotherae*.

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