FIRST DETECTION OF *MEGOURA CRASSICAUDA* MORDVILKO, (HEMIPTERA: APHIDIDAE) IN AUSTRALIA AND A REVIEW OF ITS BIOLOGY

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Summary

Aphids are important pests of crop production. Australia has been subject to many aphid incursions. In this paper, we describe the first detection in Australia of the bean or vetch aphid *Megoura crassicauda* Mordvilko, a pest of broad beans (*Vicia faba* L.) and related legumes, and provide background information on the insect. The potential to establish and spread is discussed.

Keywords: incursion, establishment, broad beans, aphids, vetch

INTRODUCTION

Aphids are important phloem-feeding plant pests distributed worldwide and cause serious crop production losses in temperate regions. Their mode of feeding and reproduction has led to a close and often specific association with their host plants (Dixon 1998). Aphids also transmit viruses and other disorders, further contributing to lowered production (Plumb 1976; Sylvester 1980). Australia's geographic isolation and stringent biosecurity systems decrease the risks of exotic aphid incursions. In recent decades, however, there have been many aphid incursions with adverse impacts on Australia's plant production systems.

In his seminal review of the Australian aphidoid fauna, Eastop (1966) noted 119 species, broken into groups on the basis of geographic origin as follows: native (11 species), cosmopolitan or otherwise possibly pre-European settlement (44 species) and the rest (64 species) introduced from various parts of the world as a result of European settlement activities. Carver (pers. comm. to DFH 1998) increased this number to 169 species, including a few undescribed natives. Since then there has been a regular stream of at least 15 new incursions, including important pests of agriculture, horticulture, forestry and cut flowers. Examples include the Russian wheat aphid *Diuraphis* noxia Kurdjumov (NSW Department of Primary Industries, 2016), the Monterey Pine aphid Essigella californica Essig (Carver and Kent 2000; Wharton 2005), the currant-lettuce aphid Nasonovia ribisnigri Mosley (Dominiak et al. 2009; Hill 2012), the soybean aphid Aphis glycines Matsumura (Atlas of Living Australia 2017; Plant Health Australia 2017) and the hellebore aphid Macrosiphum hellebori Theobald & Walton (Valenzuela et al. 2009). Other recent establishments with less economic impact include the giant willow aphid Tuberolachnus salignus Gmelin (Dominiak 2017) and the evening

primrose aphid *Aphis oenotherae* Oestlund, which has displaced the native aphids feeding on the family Onagraceae (Hales *et al.* 2015).

Previous responses to aphid incursions often have included an initial but unsuccessful attempt at eradication. In 1977 two lucerne aphids, spotted alfalfa aphid Therioaphis trifolii Monell f. maculata and blue-green lucerne aphid Acyrthosiphon kondoi Shinji, were detected in Queensland and spread through eastern Australia within one year (Clements et al. 1984, Walters and Dominiak 1984). The pea aphid Acyrthosiphon pisum Harris was found shortly afterwards and also rapidly spread through Australia (Dominiak and Walters 1984; Ryalls et al. 2013). Eradication was not achieved and all three aphids became widely established very quickly with adverse effects on lucerne and related industries, including dairy farming. Incursion response turned to management (Bishop et al. 1982; Hughes and Bryce 1984; Walters and Dominiak 1984; Milne 1986). More recently, when the currant-lettuce aphid was detected in February 2004, it became widespread in Tasmania and subsequently in other Australian states in late 2006 (Dominiak et al. 2009). Chemical controls and restrictions on host movements delayed its dispersal and it is now managed as part of lettuce production using resistant varieties, integrated pest management and pesticides (McDougal and Creek 2011).

Some aphid incursions, regardless of initial success, do not continue to maintain high populations. For example the wild service aphid *Dysaphis aucupariae* Buckton, first detected in Australia in October 1981, established high initial populations constituting nearly 70% of all trapped aphids within 6 months of first detection (Carver and Hales 1983), before declining

unaccountably. In Australia, the summer forms occurred on *Plantago lanceolata* L. (plantain) leaves, stems and flower heads. This aphid is holocyclic (having a sexual generation) in Europe and its winter host is the wild service tree (*Sorbus torminalis* (L.) Crantz). Possibly the populations in Australia were holocyclic (*cf.* Carver and Hales *loc. cit.*) and unable to overwinter because of the rarity of the winter host.

Failure to eradicate aphid populations is not surprising when one considers that their biology is characterised by rapid viviparous parthenogenetic reproduction, such that a single female can produce large numbers of genetically identical offspring within a few days of settling on an appropriate food plant. Dispersal is also rapid, since although the colony will initially be composed mainly of wingless females, crowding induces them to switch to producing winged females with a flight range, in suitable meteorological conditions, of hundreds of kilometres (see Ogawa and Miura 2014 for a recent review of aphid polyphenism). Local spread by wingless aphids can also occur, even in the absence of crowding (Hodgson 1991).

The origins of invading aphids are often unknown, though it appears likely that most arrive either on commercial or military aircraft or by sea transport on growing or freshly-cut plants. It is possible to determine invasion pathways by molecular means:

Caron *et al.* (2014) studied another parthenogenetic invader of Southern Hemisphere countries, the willow sawfly *Nematus oligospilus* Förster (Hymenoptera: Tenthredinidae), with the use of multi-locus genotypes based on microsatellite DNA. They successfully identified two invading superclones and determined the probable geographic origins of some populations. Similarly, work on the blackberry-cereal aphid *Sitobion fragariae* Walker populations in New Zealand indicated origins in Asia and in Australia (Wilson *et al.* 1999). This work utilised microsatellite polymorphisms, elongation factor 1 α and single-stranded conformational polymorphisms.

DETECTION AND IDENTIFICATION OF MEGOURA CRASSICAUDA

On 19 October 2016, colonies of large green aphids were detected by the first author on broad beans, *Vicia faba* L. ev. Coles Early Dwarf, in Beecroft, a Sydney suburb, New South Wales (NSW), Australia (-33.754027, 151.059535). They were provisionally identified as *Megoura viciae* Buckton or *Megoura crassicauda* Mordvilko. Samples were sent to Orange Agricultural Institute and verified as *M. crassicauda* (Fig.1). Possible eradication was considered in December 2016 but given the inability to eradicate past aphid incursions, it was decided not to attempt eradication. NSW Department of Primary Industries then moved into a management phase, as it had with other previous aphid incursions.



Figure 1. Megoura crassicauda Mordvilko wingless adult parthenogenetic female: photomicrograph using montaged images.

Continued observations were made on the Beecroft colonies, which reached high population densities and covered the entire stems and basal shoots of infested

plants. Hand-spraying with "Pest Oil" (Petroleum oil) and subsequently "Confidor" (Imidacloprid) was

ineffective in controlling the aphid infestations, and the plant shoots and pods turned black and died. The yield of mature bean pods was almost zero. Natural enemies (unidentified aphidiid wasps, syrphids and coccinellids, for example Coccinella transversalis Fabricius (transverse ladybird) and Coelophora inaequalis (Fabricius), had no noticeable effect on the aphid numbers. Leather (2013) summarised studies indicating that M. viciae, a European pest aphid closely related to M. crassicauda and having a similar host range, is highly toxic to coccinellids, as is the cowpea aphid Aphis craccivora Koch, previously the most common aphid pest of broad beans in NSW. A few late-instar coccinellid larvae were, however, observed on the Beecroft aphid colonies. An aphidiid wasp parasitoid affecting the genus Megoura is known in Europe: Aphidius megourae Starý. The wasp, however, attacks M. viciae only in part of its range (Starý 1964).

BIOLOGY AND DISTRIBUTION OF MEGOURA CRASSICAUDA

The genus Megoura has eight species (Lee et al. 2014), all characterised by well-developed smooth, divergent antennal tubercles and swollen siphunculi and all associated with fabaceous hosts. Using DNA markers, Kim & Lee (2008) showed that M. crassicauda, M. viciae and M. litoralis F.P. Müller form a single clade within the genus. Megoura crassicauda is called bean aphid by Japanese authors, who also sometimes refer to the species as M. japonica (Blackman and Eastop 2000). According to current taxonomic opinion, the name M. japonica Matsumura should be applied only to a species feeding on Vicia unijuga A. Br. in Hokkaido, Japan (Favret, 2017; personal communications from Japanese taxonomists as listed in Acknowledgements). Megoura crassicauda sometimes called the vetch aphid in other countries (Takemura et al. 2002) although this common name is more correctly applied to M. viciae.

Aphids of the genus *Megoura* can be distinguished from other aphids found on broad beans in Australia by the following combination of characters

- Large green aphids
- Antennal tubercles well developed with inner faces divergent dorsally
- Slightly swollen black siphunculi
- · Black cauda.

No other member of the genus *Megoura* is known from Australia (see Lee *et al.* (2014) for a key to known species).

Megoura crassicauda feeds on Vicia spp. including V. amoena Fisch., amurensis Oett., angustifolia (now considered to be V. sativa subsp. nigra (L.) Ehrdt.), cracca L., faba L., flava (?= flavida Schur), megalotropis Lebed., pseudo-orobis Fisch. & C.A Mey, sativa L., sepium L., unijuga A. Br. and venosa (Link) Maxim. (Blackman and Eastop 2000; Asai et al. 2002; Takemura et al., 2002) and Lathyrus spp. including sea pea L. japonicus Willd. and L. davidii Hance (Blackman and Eastop, 2000) – all beans in Fabaceae. These beans are grown widely as a valuable source of human and animal food. Of all these known hosts only V. faba and the common vetch V. sativa are naturalised in NSW (Plantnet, 2017). However, M. viciae has been recorded on many more plant hosts in these two genera, including hairy vetch V. villosa Roth (also naturalised in NSW), which may be considered as another potential field host. Authorities for the above species were not given by Blackman and Eastop (2017) and have been added and updated from The Plant List (2017).

Studies on the biology of M. crassicauda relevant to its pest potential are limited but are briefly summarised below. Asai et al. (2002) reported studies on holocyclic (having a sexual generation) and anholocyclic (continuously parthenogenetic) clones of M. crassicauda and showed that both exhibited very poor cold-hardiness. This implies that sexuallyproduced over-wintering eggs would form an important survival strategy in cold climates. Feeding studies on artificial diets showed that M. crassicauda is stimulated to probe by the presence of two acylated flavonol glycosides in V. angustifolia, suggesting kairomonal roles during host recognition (Takemura et al. 2002). Ohta et al. (2014) identified feeding deterrents in non-host legumes. On many leguminous plants, M. crassicauda, A. pisum and A. craccivora can co-occur and form mixed colonies. Tsuchida et al. (2006) demonstrated that M. crassicauda lacked S (secondary)-endosymbionts, while the other legumefeeding aphids had mixtures of up to four types. Some facultative S-symbionts substantially affect the fitness of their legume-feeding aphid hosts in particular ecological contexts.

Megoura viciae has been the subject of extensive physiological research (many papers by A.D. Lees and students, e.g. Lees 1977; Steel and Lees 1977; Hardie et al. 1981; Hardie 1986) and M. crassicauda seems to be achieving the status of a model aphid in laboratory studies in Japan, probably because it is easy to culture, but field studies are not common. Surprisingly and in contrast to the Beecroft observations, Kasai (2016) found that infestation with

M. crassicauda did not reduce bean production in V. sativa.

In the absence of any study on the intrinsic rate of increase (r_m) and the mean relative growth rate (MRGR) in M. crassicauda, equivalent studies on the closely-related M. viciae may be useful in understanding the rapid population growth of M. crassicauda. Dixon (1987) brought together studies on the rate of increase of aphid populations, indicating that one of the most important determinants was the rate of reproduction in early adult life. Factors influencing this early reproduction rate include adult size and number of ovarioles (the tubes from the ovaries in which successive parthenogenetically produced embryos develop). Megoura adults are large, with up to 20 ovarioles, though there is variation within clones depending on environmental factors such as nutrition (Ward et al. 1983). The most common count is 16-17 ovarioles. In comparison, another aphid pest of broad beans in NSW, cowpea aphid A. craccivora, has relatively small adults and has only a small but variable number of ovarioles (maximum of 12) (Elliott et al. 1975; Elliot and McDonald 1976; Traicevski and Ward 2002, studying winged adults). Hence it is to be expected that M. crassicauda will outstrip the more slowly reproducing A. craccivora on broad beans in Australia. As an example of aphid population studies in Australia, Turak et al. (1998) and Sunnucks et al. (1998) reported r_m and MGRM studies on a group of grass and cereal-feeding Sitobion genotypes from NSW with respect to temperature and host compatibilities.

FINAL COMMENTS

Megoura crassicauda is another example of an aphid incursion into Australia where the decision was made not to contain or eradicate. It is unclear what the long-term impact of this aphid will be on broad (faba) bean production in Australia. Pesticide management options are available for other aphid species already found in Australia on this host. The high frequency of incursion of aphid pests, their importance as pests and disease vectors coupled with their high fecundity and host specificity, should make surveillance for these exotic pests a high priority for all jurisdictions dealing with plant biosecurity. Early detection enables early deployment of management options and reduces potential spread and damage.

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REFERENCES

- Asai, M., Yoshida, H., Honda, K. and Tsumuki, H. (2002). Cold hardiness of three species, *Acyrthosiphon pisum, Megoura crassicauda* and *Aulacorthum solani* (Hemiptera: Aphididae). *Applied Entomology and Zoology* **37**(3): 341-346.
- Atlas of Living Australia (2017).
 - (http://bie.ala.org.au/species/urn:lsid:biodiversity.org.au:afd.t axon:a7d1554e-ff42-4afa-9bb0-31c2a967db99,
 - http://biocache.ala.org.au/occurrences/4b240d0b-45d6-4252-b888-ce4c028ed1e0. Accessed 5 February 2017.
- Bishop, A.L., Walters, P.J., Holtkamp, R.H. and Dominiak, B.C. (1982). Relationships between Acyrthosiphon kondi and damage in three varieties of alfalfa. Journal of Economic Entomology 75: 118-122.
- Blackman, R.L. and Eastop, V.F. (2000). 2nd Edition. Aphids on the World's Crops: An Identification and Information Guide. The Natural History Museum (London, England) Wiley.
- Blackman, R.L. and Eastop, V.F. (2017). http://www.aphidsonworldsplants.info/C_HOSTS_Vac_Vio.htm#Vicia (accessed 20 March 2017).
- Caron, V., Ede, F.J., Sunnucks, P., and O'Dowd, D.J. (2014). Distribution and rapid range expansion of the introduced willow sawfly *Nematus oligospilus* Forster (Hymenoptera: Tenthredinidae) in Australasia. *Austral Entomology* 53: 175-182.
- Carver, M. and Hales, D.F. (1983). Two new additions to the aphid fauna of Australia (Homoptera: Aphididae). *Journal of the Australian Entomological Society* 22: 197-198.
- Carver, M. and Kent, D.S. (2000). Essigella californica (Essig) and Eulachnus thunbergii Wilson (Hemiptera: Aphididae: Lachninae) on Pinus in south-eastern Australia. Australian Journal of Entomology 39: 62-69.
- Clements, R.J., Turner, J.W., Irwin, J.A.G., Langdon, P.W. and Bray, R.A. (1984). Breeding disease resistant, aphid resistant lucerne for subtropical Queensland. Australian Journal of Experimental Agriculture and Animal Husbandry 24: 178-188.
- Dixon, A.F.G. (1987). Parthenogenetic reproduction and the rate of increase in aphids. In *Aphids, Their Biology, Natural Enemies* and Control Vol. 2A, eds A.K. Minks and P.W. Harrewijn. Elsevier, Amsterdam. Pp. 269-287.
- Dixon, A.F.G. (1998). *Aphid Ecology: An optimization approach*. Chapman & Hall, London.
- Dominiak, B.C. and Walters, P.J. (1984). Establishment of Acyrthosipon pisum (Harris) (Hemiptera: Apididae) in New South Wales. Journal of the Australian Entomological Society 23: 269-270.
- Dominiak, B.C., Links, I.J., Fletcher, M.J., Worsley, P. and McDougall, S. (2009). Detection and spread of currant-lettuce aphid *Nasonovia ribisnigri* (Mosley) (Hemiptera: Aphididae) in New South Wales. *General and Applied Entomology* 38: 27-30
- Dominiak, B.C. (2017). Giant willow aphid. Primefact 1514. First edition Plant Biosecurity and Product Integrity. NSW Department of Primary Industries. 2p

- Eastop, V.F. (1966). A taxonomic study of Australian Aphidoidea (Homoptera). *Australian Journal of Zoology* **14**: 399-592.
- Elliot, H.J., McDonald, F.J.D. and Vesk, M. (1975). Germarial structure and function in a parthenogenetic aphid, Aphis craccivora Koch (Hemiptera: Aphididae). International Journal of Insect Morphology and Embryology 4: 341-347.
- Elliott, H. J., and F. J. D. McDonald. (1976). Reproduction in a parthenogenetic aphid, *Aphis craccivora* Koch: Embryology, ovarian development and fecundity of apterae and alatae. *Australian Journal of Zoology* 24: 49-63.
- Hales, D.F., Foottit, R.G. and Maw, E. (2015). Endemic aphids Aphis carverae sp. nov. and Casimira canberrae (Eastop, 1961) on Epilobium (Onagraceae) threatened by introduced Aphis oenotherae Oestlund, 1887 (Hemiptera: Aphididae: Aphidinae). Austral Entomology 54: 278–285.
- Hardie, J., Lees, A.D. and Young, S. (1981). Light transmission through the head capsule of an aphid, Megoura viciae. Journal of Insect Physiology 27: 773-777.
- Hardie, J. (1986). Morphogenetic effects of precocenes on three aphid species. *Journal of Insect Physiology* 32: 813-818.
- Hill, L. (2012). The currant lettuce aphid, Nasonovia ribisnigri arrives in Tasmania: Part 1. Victorian Entomologist 42(2): 29-31.
- Hodgson, C. (1991). Dispersal of apterous aphids (Homoptera: Aphididae) from their host plant and its significance. Bulletin of Entomological Research 81: 417-427.
- Hughes, R.D. and Bryce, M.A. (1984). Biological characterization of two biotypes of pea aphid, one susceptible and the other resistant to fungal pathogens, coexisting on lucerne in Australia. Entomologia Experimentalis et Applicata 36: 225-229
- Kasai, A. (2016). Vetch aphid, Megoura crassicauda (Hemiptera: Aphididae), parasitism does not reduce the bean production of narrow-leaved vetch, Vicia sativa subsp. nigra (Fabaceae). Ecological Research 31: 189–194.
- Kim, H. and Lee, S. (2008). Molecular systematics of the genus Megoura (Hemiptera: Aphididae) using mitochondrial and nuclear DNA sequences. Molecules and Cells 25: 510-22.
- Leather, S. (2013). Not all aphids taste the same. https://simonleather.wordpress.com/tag/megoura-viciae/, Accessed 3 February, 2017.
- Lee, W., Kanbe, T. and Akimoto, S. (2014). A new species of Megoura (Hemiptera, Aphididae) from Japan. ZooKeys 417: 37-44.
- Lees, A.D. (1977). Action of juvenile hormone mimics on the regulation of larval-adult and alary polymorphism in aphids. *Nature* 267: 46-48.
- Lees, A.D. (1984). Parturition and alate morph determination in the aphid Megoura viciae. Entomologia Experimentalis et Applicata 35: 93-100.
- McDougal, S. and Creek, A. (2011). Currant lettuce aphid. Primefact 155, Fourth edition. NSW Department of Primary Industries. 4pp.
- Milne, W.M. (1986). The release and establishment of Aphidius ervi Haliday (Hymenoptera: Ichneumonoidea) in lucerne aphids in eastern Australia. Journal of the Australian Entomological Society 25: 123-130.
- NSW Department of Primary Industries (2016). Russian wheat aphid. Primefact 1489. First edition. Plant Biosecurity and Product Integrity. 3pp.
- Ogawa, K. and Miura, T. (2014). Aphid polyphenisms: transgenerational developmental regulation through viviparity. Frontiers in Physiology 5: Published online Jan. 24, 2014, doi: 10.3389/fphys.2014.00001.
- Ohta, N., Mori, N., Kuwahara, Y. and Nishida, R. (2014) A hemiterpene glucoside as a probing deterrent of the bean

- aphid, Megoura crassicauda, from a non-host vetch, Vicia hirsuta. Phytochemistry 67: 584-588.
- Plant Health Australia (2017)
 - http://www.planthealthaustralia.com.au/wp-content/uploads/2014/06/Insect-transmitted-viruses-of-grains-CP-2014. Accessed 5 February 2017.
- Plantnet. (2017). http://plantnet.rbgsyd.nsw.gov.au/cgibin/NSWfl.pl?page=nswfl&lvl=sp&name=Vicia~sativa. Accessed 12 March 2017.
- Plumb, R.T. (1976). Barley yellow dwarf virus in aphids caught in suction traps, 1969-73. Annals of Applied Biology 83: 53-59.
- Ryalls, J.M., Riegler, M., Moore, B.D. and Johnson, S.N. (2013). Biology and trophic interactions of lucerne aphids. Agricultural and Forest Entomology 15: 335-350.
- Starý, P. (1964). Food specificity in the Aphidiidae. *BioControl* 9: 91-99
- Steel, C.G.H. and Lees, A.D. (1977). The role of neurosecretion in the photoperiodic control of polymorphism in the aphid Megoura viciae. Journal of Experimental Biology 67: 117-135.
- Sunnucks, P., Chisholm, D., Turak, E. and Hales, D.F. (1998). Evolution of an ecological trait in parthenogenetic *Sitobion* aphids. *Heredity* 81: 638-647.
- Sylvester, E.S. (1980). Circulative and propagative virus transmission by aphids. Annual Review of Entomology 25: 257-286.
- Takemura, M., Nishida, R., Mori, N. and Kuwahara, Y. (2002). Acylated flavonol glycosides as probing stimulants of a bean aphid, Megoura crassicauda, from Vicia angustifolia. Phytochemistry 61: 135-140.
- The Plantlist (2017).
 - http://www.theplantlist.org/1.1/browse/A/Leguminosae/Vicia/. Accessed 17 March 2017.
- Traicevski, V. and Ward, S.A. (2002). Probing behaviour of *Aphis craccivora* Koch on host plants of different nutritional quality. *Ecological Entomology* 27: 213–219.
- Tsuchida, T., Koga, R., Sakurai, M. and Fukatsu, T. (2006). Facultative bacterial endosymbionts of three aphid species, Aphis craccivora, Megoura crassicauda and Acyrthosiphon pisum, sympatrically found on the same plants. Applied Entomology and Zoology 41: 129-137.
- Turak, E., Talent, R., Hales, D.F. and Sunnucks, P. (1998). Different responses to temperature in three closely-related sympatric cereal aphids. *Entomologia Experimentalis et Applicata* 86: 49-58.
- Valenzuela, I., Carver, M., Malipatil, M.B. and Ridland, P.M. (2009). Occurrence of *Macrosiphum hellebori* Theobald & Walton (Hemiptera: Aphididae) in Australia. *Austral Entomology* 48: 125-129.
- Walters, P.J. and Dominiak, B.C. (1984). The establishment in New South Wales of *Trioxys complanatus* Quilis (Hymenoptera: Aphididae), an imported parasite of *Therioaphis trifolii* (Monell) f. *maculata*, spotted alfalfa aphid. *General and Applied Entomology* 16: 65-67.
- Ward, S. A., Wellings, P. W. and Dixon, A. F. G. (1983). The effect of reproductive investment on pre-reproductive mortality in aphids. *Journal of Animal Ecology* 52: 305-313.
- Wharton, T., (2005). Biology and Ecology of Essigella californica (Essig) on Pinus radiata D. Don. in Australia. PhD thesis, Australian National University, Canberra, ACT.
- Wilson, A.C.C., Sunnucks, P. and Hales, D.F. (1999). Microevolution, low clonal diversity and genetic affinities of parthenogenetic Sitobion aphids in New Zealand. Molecular Ecology 8: 1655-1666.