REVIEW OF THE GONDWANAN APHIDS

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Summary

Endemic and indigenous aphid species are rare in most Gondwanan countries, being greatly outnumbered by aphids accidentally introduced from Europe or North America, or spreading naturally via Southeast Asia. Our limited knowledge of Gondwanan endemic and indigenous aphids is summarised here, with emphasis on Australia and New Zealand. Many undiscovered species are almost certainly present. Barriers to their discovery are discussed. Associations of aphids with ancient and endemic plants are considered in relation to continental history. Aphids have close functional relationships with a range of other organisms, including ants, wasps, flies and bacteria and some of the obligate relationships may also be Gondwanan. *Neophyllaphis*, *Neuquenaphis* and *Sensoriaphis/Taiwanaphis* have an unquestionable Gondwanan origin, as do southern *Aphis* and *Paradoxaphis* (Australia, New Zealand, South America). The subfamily Lizeriinae may have been the first to diverge from the basal Aphididae and has an exclusively Gondwanan distribution. The subfamily Greenideinae is another early group and is composed of genera with a Gondwanan distribution. Species in these genera occurring in both Australia and Asia/Southeast Asia can be considered native, but not endemic to these areas. *Greenidea* and *Schoutedenia* are thus Australian natives. *Aphis clerodendri* and (less convincingly) *Aphis eugeniae* have a Gondwanan distribution. The genus *Sitobion* (Macrosiphini) has many species probably endemic in various Gondwanan countries and most likely has a Gondwanan origin. Aphidiine wasps (Braconidae), primary parasitoids of aphids, have a well-supported southern origin, and the hyperparasite *Alloxysta*, by virtue of its host-specific relationship with southern aphids and aphidiine wasps, may also have southern roots.

Keywords

INTRODUCTION

Aphid species in Australia have been listed by Eastop (1966), Carver (1998, pers. comm.), Hollis and Eastop (2019) and Brumley (2020). These lists cover all Aphidoidea. The families Phylloxeridae and Adelgidae in Australia each have few species, all of which are introduced to Australia or are cosmopolitan, so the emphasis in this paper is on the remaining family, the Aphididae, made up of 25 sub-families with 30 tribes (Favret, *Aphid Species File)*. Relatively few of these sub-families contribute to the extant aphid fauna of Gondwanan countries.

In this paper I use the term "endemic" for taxa that occur in a particular country but not elsewhere. The term "native" refers to taxa that occur naturally, but are also found in other geographic areas. "Southern" is used as meaning Gondwanan, in all its scattered parts including south and Southeast Asia, but not the Kazakhstan, East Turkey and Saudi Arabia elements which separated earlier.

The total number of aphidoid species known in Australia is approaching 200, but the 20+ endemic species are far outnumbered by adventive and cosmopolitan species. Some known but undescribed species are included among the listed endemics. The situation is similar in New Zealand (Teulon and Stufkens 1998, Teulon *et al.* 2002, Teulon *et al*. 2013) with 15+ endemic species in a total fauna of about 135 species. *Neophyllaphis* occurs in both countries and has been thought to be closest in morphology to the earliest aphids, although some recent molecular studies place the Lachninae as an early branching lineage (and no endemic or native lachnine species are known in Australia or New Zealand). It is considered that the

endemic aphids of these and other southern countries originated in Gondwana before its break-up. In this paper, I collate information on the aphids, their host plants, and some of the endoparasitoids and hyperparasitoids of the aphids, as well as the relevant changes in the geographic environment.

THE CONTINENTS

This section and the following two are not intended to be anything more than a background to the time and place of different events.

The landmass of Pangaea, which coalesced during the Early Carboniferous about 335 mya, began to break up in the Triassic Period (252 to 201 million years ago) leaving Gondwana (the name comes from India) in the south and Laurasia in the north. At this stage, Laurasia was mostly north of the Equator and Gondwana mostly south of the Equator but north of the South Pole. There was climate variation across the supercontinent in terms of temperature and rainfall and a widespread but spatially differentiated fauna, with regions marked by patterns of precipitation. There was also a complex flora, again with some division into provinces, and including cryptogams as well as both gymnosperms and angiosperms (see "The Plants" below). During the Jurassic, about 180 mya[1], Gondwana began to divide forming the current Gondwanan continents, including Australia, Te Riu-a-Māui /Zealandia, Africa, South America, India and some fragments now in the Middle East,

[1] mya= million years ago

western Asia and east and Southeast Asia. Metcalfe (2006, 2013) discussed the origins of southeast Asian areas, including South China, Vietnam, Laos and Thailand, which broke away from Gondwana in the Devonian and Permian, but in more recent times were adjacent to later Gondwanan arrivals such as India and Myanmar. Notably, the Devonian is before the time of land animals, or most seed plant lineages, but they are there by the Permian. Part of Indonesia is Gondwanan. Japan's origin is different, being derived from remnants of the early supercontinent Rodinia. The island of Taiwan formed only 4-5 mya, so its flora and fauna are necessarily recent arrivals, either naturally via land bridges to South China or the Philippines during the Pleistocene glaciation which resulted in periods of low sea level, or introduced by human activity. An approximation of these events is shown in Table 1.

The first separations were in Western Gondwana, with India/Africa and South America dividing from each other and from the remainder of Gondwana. India began to separate from both Africa and Gondwana at as late as the Cretaceous and collided with Asia only 50 mya (Chatterjee *et al*. 2006). Australia separated from eastern Antarctica at about 132 mya. At about 84 mya Zealandia separated. Zealandia has recently been accepted as a continent although now largely submerged. It includes New Zealand and islands such as Lord Howe, Chatham, Norfolk and New Caledonia. Compression forces during the early Eocene pushed the continent upwards and inwards and hence there was a continuous exposed south to north land mass connecting all the components that we know today as widely separated. About 25 mya, the weakened crust sank back again, with the exception of the current emergent elements. The geology and history of Zealandia have been detailed by Mortimer *et al*. (2017).

During the history of continental movement, dramatic changes in climate occurred both globally and locally, leading to mass extinction events in each of which well over 50% of insect species are thought to have become extinct (e.g. Crowley and North, 1988). Major extinctions of land plants may not have accompanied the late Permian extinction of many land animals (Nowak *et al*. 2019, McElwain and Punyesena, 2007). It has been suggested that aphids may have suffered disproportionately. Johnson (1992) showed that there was a substantial loss of plants in north America during the Cretaceous extinction event and Donovan *et al*. (2017) discussed the rapid establishment of insect-plant communities in Patagonia after the Cretaceous extinction. The same might be true for other southern continents. Rehan *et al*. (2013) elucidated the diversification of bees following the Cretaceous extinction. Aphids, like bees, are plant dependent and are considered to have diversified strongly during the Cretaceous (von Dohlen and Moran, 2000) and Miocene, especially in the north. I have attempted to summarise major events in Table 1.

FOSSIL RECORD

The earliest known fossil in the Aphidomorpha is *Triassoaphis cubitus* from pre-Jurassic deposits around Ipswich, Queensland (Evans, 1956). From around the same period, *Creaphis theodora* was described from middle Asia by Scherbarkov and Wegierek (1990). The oldest known aphid fossil from Europe is *Leaphis prima* from the Vosges area of France dating back to 174-163 Mya (Jurassic) (Shcherbakov 2010)). *Koonwarraphis* from early Cretaceous Victoria is another fossil from Australia but it is a relative latecomer (Martin *et al*. 2016). Raynor and Waters (1989) described a fossil aphid from South Africa, but it, too, is a Cretaceous latecomer. They discussed other palaeontological evidence and concluded that the origins of aphids were as far back as the Carboniferous.

Szwedo *et al*. (2013) took the origin of Aphidomorpha back to the Middle Permian following discovery of aphid-like fossils in Southern France. Ole Heie (e.g. 1967, 1987, 1994, 2015) (Denmark) and Żyła and colleagues (Poland) have done extensive work describing new families, genera and species of fossil aphids from Europe (e.g. Żyla and Wegierek 2020, Żyla *et al*. 2020).

THE PLANTS: HISTORY AND EARLY APHID ASSOCIATIONS

The earliest land plants were algae and evolved in the late Silurian, from about 420 mya. The late Devonian saw the development of ferns, seed ferns, horsetails and lycopods. Mosses are known from about 400 mya (Liu *et al.* 2019). McLoughlin (2001) and Kustatscher *et al.* (2018) summarised the flora of Gondwana in relation to geological and climatic events, pointing out that the basic flora, generally associated with lands derived from Gondwana, was present before the breakup of Pangaea, and is assumed to have become extinct in "Laurasia", following climatic extremes. Aphids occur on present-day mosses and horsetails, *Aphis equiseticola* being specific to its horsetail food plant. A range of species in the Northern Hemisphere feed on mosses (e.g. see Müller 1973, Pike *et al*. 2012). Some aphid species are specific to ferns: for example, Robinson (1966) listed seven indigenous and four adventive species in North

Table 1. Approximate chronological sequence of palaeogeography and life forms

Period/Epoch	Time span (Mya)	Geography	Plants	Aphids	Extinctions
Devonian	419-359	North and south China, Indochina split from Gondwana	Horsetails, mosses, seed ferns, ferns, lycopods, tree-like plants	(Earliest land arthropods)	Late Devonian
Carboniferous	359-299	Assembly of Pangaea		Insect diversification	
Permian	299-251	West Burma and Lhasa terranes split from Gondwana	*Glossopteris*, podocarps, early angiosperms	Earliest aphidomorph fossils	End Permian
Triassic	251-200	Split of Gondwana and Laurasia		Earliest aphid fossils	End Triassic
Jurassic	200-145	Separation of India-Africa-South America from Gondwana			
Cretaceous	145-65.5	India separates from Africa, Australia and Zealandia separate from Gondwana, Africa and S. America separate.		Many aphid fossils	End Cretaceous (K-T)
Tertiary/ Paleocene	65.5-55.8				
Tertiary/Eocene	55.8-34	India collides with Asia			
Tertiary/Oligocene	34-23				
Tertiary/Miocene	23-5.3		Radiation of northern angiosperms	Radiation of northern aphids. European fossils of Greenideinae	
Tertiary/Pliocene	5.3-2.4	Taiwan formed			
Quaternary	2.4-present				

America. The seed ferns are extinct. The only record of aphids on a lycopod is of the banana aphid, *Pentalonia nigronervosa* (Singh and Srivastava 2022). It seems unlikely that this is a regular host association.

High forest trees, including the extinct *Glossopteris*, and tree ferns, conifers, ginkgos and podocarps date from the early Permian, *ca* 299 mya, and have living descendants today. Blackman and Eastop, in *Aphids on the World's Plants*, did not record any aphid species on ginkgos. I have used this reference extensively without further attribution for notes on host-aphid relationships and aphid distributions, both online (Favret, 2025, https://aphidsonworldsplants.info/) and in the original books, *Aphids on the World's Crops*, *Aphids on the World's Trees*, and *Aphids on the World's Herbaceous Plants and Shrubs*, the latter typically abbreviated by Victor Eastop to *Aphids on the World's Whatsits*. I have used Colin Favret's *Aphid Species File* (https://aphid.speciesfile.org/) for questions of aphid taxonomic detail. I use the abbreviations B&E and ASF occasionally in the text for these resources, but I have relied heavily on B&E for information on aphid host-plant relationships and distribution, and ASF for nomenclature.

There are extant aphids on *Araucaria* (Araucariaceae) and *Podocarpus* (Podocarpaceae) as well as numerous northern conifers. The Araucariaceae is the oldest family of living conifers, with 13 species of *Araucaria* endemic to New Caledonia and others spread across the southern continents and introduced elsewhere. They are particularly favoured for beachfronts. *Neophyllaphis araucariae* lives on several species with a wide geographic spread including Mauritius (first description), Java, New Guinea, Australia, Hawaii, Costa Rica, Bahamas, Mexico and USA, but it was introduced to Hawaii and probably other North American sites. Surprisingly, it has not been recorded in New Caledonia despite the range of potential hosts (Mille *et al*. (2020). B&E give information for five species of *Araucaria* and *Neophyllaphis araucariae* occurs on all of them. Although *Araucaria* had a world-wide range in the Jurassic and Cretaceous, it became extinct in northern continents. However, it occurs as a cultivated plant in many countries, often taking its aphids with it. In Australia, *Neophyllaphis araucariae* occurs on Norfolk Island pine (*Araucaria heterophylla*, endemic to Norfolk Island but widely cultivated elsewhere including Australia) but there are no records from hoop pine (*A. cunninghamii*) or bunya pine (*A. bidwillii*), both of which are endemic to Australia.

In a sister group to *Araucaria*, *Wollemia* (wollemi pine, recently discovered in New South Wales) has not been reported to host aphids. In the same family is *Agathis* (kauri): *Neophyllaphis rappardi* has been found on *Agathis labillardieri* in West Papua (Indonesia) but surprisingly there are no records from Australia or New Zealand, both of which have kauri forests. The wollemi pine is sometimes described as "a living fossil" but equally, the araucarias and kauri are living fossils. Chen *et al.* (2022) provided a molecular analysis clarifying the relationships of these ancient tree genera.

For Podocarpaceae, 22 species of *Podocarpus* trees harbour 18 different *Neophyllaphis* spp., in Australia, New Zealand, Papua, China, Peru, Africa, Argentina, Brazil, Venezuela, Taiwan, Vietnam, Java, Malaysia. These (except the newcomer Taiwan) are Gondwanan countries. *Neophyllaphis* occurs in other countries where it has been introduced with its host. There is some overlap of aphid species between hosts. On four species of *Afrocarpus*, we have three species of *Neophyllaphis* overlapping with the *Podocarpus* list, *N. varicolor*, *N. viridis* and *N. grobleri*. *Neophyllaphis* also occurs in Japan, on *P. macrophylla.* Possibly both plant and aphid were introduced there. *P. angustifolia*, widespread in South America, is critically endangered by logging but is not reported to have any aphids. But there may be many more podocarp-feeding aphids. Khan *et al*. (2023) have listed 208 extant species of podocarps ranging through the Gondwanan countries. One genus, *Dacrydium* (rimu in New Zealand), is spread through the islands of Zealandia, New Guinea, Indonesia and Southeast Asia, but is extinct in Australia. No aphids are known from *Dacrydium*, but it seems a likely and accessible host.

Based on a time-calibrated molecular phylogeny, Salomo *et al.* (2017) argued that the angiosperms probably arose in the Late Permian, about 275 mya, rather than the later estimate of around 130 mya suggested by fossils alone. Hence, we have a well-developed flora of both angiosperms and gymnosperms before the separation of Pangaea, and thus also before the breakup of Gondwana. And (see above) we have an aphidomorph fossil history in Europe that is older than expected, i.e., preceding the breakup of Pangaea.

Prominent among the Gondwanan angiosperms, the southern beech (*Nothofagus*, Nothofagaceae) occurs in Australia, New Zealand, New Guinea, South America and New Caledonia. Steed-Mundin (2025) has given an overview of the genus, and discusses a "disputed split" proposed by Heenan and Smissen (2013) who raised four well-defined subgenera to generic status. In this paper I will follow Steed-Mundin's example and stick to the original generic name. 36 species are known: 12 from New Guinea, 11 from South America, five from New Caledonia, five from NZ and three from Australia. The New Caledonia and New Guinea species are all in subgenus *Brassospora*; the subgenus *Nothofagus* includes only South American species, and the other two subgenera, *Lophozonia* and *Fuscospora*, each occur in Australia, New Zealand and South America. *Nothofagus* spp. are host to *Taiwanaphis/Sensoriaphis* (Taiwanaphidinae) in South America, Australia, New Guinea, and New Zealand. Three species of *Taiwanaphis* on diverse host plants (not *Nothofagus*) are listed in India by Singh *et al.* (2018). These three species are supported in B&E but not listed in ASF. *Neuquenaphis* spp. (Spicaphidinae) are widespread on *Nothofagus* spp. in South America, but only one species in the Taiwanaphidinae is found there. *Nothofagus* does not occur in India or Africa and there is no fossil evidence (including pollen) for its past occurrence. No aphids have yet been recorded from *N. gunnii* (Tasmania). Plant scientist David Tng (2012) has written a thoughtful account of *Nothofagus*.

The other host plants of presumed southern endemic aphids are dicotyledonous shrubs and herbs, with the possibility of some on native grasses. The hosts (other than podocarps and *Nothofagus*) include small trees, shrubs and herbaceous plants. In New Zealand, *Aristotelia* (Elaeocarpaceae), *Plagianthus* (Malvaceae), *Coprosma* (Rubiaceae), *Hebe* (Plantaginaceae), *Olearia* and *Ozothamnus* (Asteraceae), *Carmichaelia* (Fabaceae, New Zealand broom) and the native climbers *Muelenbeckia* (Polygonaceae) and *Clematis* (Ranunculaceae)are all known to host aphids.

The smaller aphid-bearing plants include *Platylobium* and *Gompholobium* (Fabaceae, yellow bush peas, Australia), low herbaceous plants like *Epilobium* (Onagraceae) (Australia and New Zealand) and *Acaena* (Rosaceae) (Australia and South America). *Aciphylla* (Apiaceae) is a hard leaved rosette plant producing a long flower spike, in Australia, New Zealand and Antarctic islands, but aphids are known on it only in New Zealand. *Dracophyllum* (62 spp., Ericaceae) has a distribution in Australia and the elements of Zealandia but aphids are known from it only in New Zealand. See Table 2 for the Australian aphids and their host plants.

THE APHIDS

Aphids are not ordinary insects. Not for them is the simple life cycle of other hemimetabolous insects: egg, larva (eating and growth), adult (fly around, mate, lay eggs). The complexity of their annual cycles and the terminology of different forms often deters non-specialists from reading or thinking about them, but aspects of their biology form essential components of their ability to colonise new territories.

1. Aphids are parthenogenetic and viviparous, most of the time. They are born with embryos already developing inside them, so can rapidly build up new colonies.
2. The parthenogenetic aphids come in two forms, wingless and winged. The winged ones develop in response to environmental cues, especially crowding. It is an epigenetic process triggered by environment and modified via neural, neurohormonal and hormonal and epigenetic pathways, and enables dispersal.
3. Aphid species may be restricted to a narrow set of host plants (e.g., a single species, genus or family), or they may be able to use a wide range of plants ("polyphagy").
4. Aphids have a sexual generation, usually invoked by thresholds of photoperiod, or more accurately, scotoperiod (dark phase). A consequent epigenetic change causes production of males and females (gynoparae) whose parthenogenetically-produced female offspring will be capable of mating and laying eggs.
5. Many aphid species include clones that are continuously parthenogenetic, i.e. do not and cannot produce sexual forms.
6. The sexual females may occur on the regular host plant/s or may be deposited on a special winter host, e.g. the peach aphid *Myzus persicae*, found on a wide range of plants in summer, but returning to peach to produce overwintering eggs. This is known as host alternation. Usually the sexual females are wingless and the males are winged, but not always. Non-native aphids in Australia, including *M. persicae*, have clones that skip the overwintering process and reproduce parthenogenetically throughout the year.
7. The sexual females mate with males and lay eggs that diapause, avoiding adverse seasons, winter or sometimes summer.

Moran (1988), von Dohlen and Moran (2000) and others have discussed the evolution of host plant alternation in aphids. Hales *et al*. (1997) reviewed evolutionary and genetic aspects of aphid biology including migration and annual cycles.

These unusual biological features can be both advantageous and limiting when considering the ability of aphids to expand their geographic range. Polyphagy is an asset for expansion of range, and diapausing eggs can get a species through extremely cold winters or hot summers. Both strategies can give flexibility to a species. Host alternation has a downside, as not one, but two essential host plants must be found for a coloniser to succeed. Sexual reproduction, of course, also gives the opportunity for genetic recombination, again providing flexibility and potential new opportunities. Genetic change by mutation in parthenogenetic lines also gives opportunities for adapting to new environments and potentially new host plants (e.g. Wilson *et al.*, 2003). Alien aphids can establish on sub-Antarctic islands, where polyphagy and parthenogenesis have been recognised as enabling factors (Hullé *et al*. 2003).
An essential consideration in studying aphid distribution is dispersal. Aphids are small, fragile, soft-bodied insects. Yet winged aphids are capable of wind-assisted flights of over 1000 kilometres. In the 1950s Bruce Johnson, later professor of zoology at the University of Tasmania, worked on *Aphis craccivora* (cowpea aphid) and its migration on high altitude winds from crops in north-western NSW (Coonamble, Walgett, Moree) to the east coast (Johnson, 1957). In August 1966, on a trip from Adelaide to Alice Springs, I observed *A. craccivora* on desert chenopods such as saltbush and bluebush at nearly every stopping point, raising the possibility of even longer flights to the east coast. Few other aphids were seen (White, 1967). European and North American reports were summarised by Robert (1987) including dispersal over 1000 km. Hill *et al*. (2020) proposed that the giant willow aphid *Tuberolachnus salignus* arrived in mainland Australia and Tasmania from infestations in New Zealand, a distance around 1500 km. With these capabilities, aphids would laugh at Wallace's Line, the distance from China to Taiwan, and the distance from Australia to the closest historically exposed parts of Zealandia. Successful establishment at the destination is another matter and depends on ability to find a suitable host plant in the limited time available. Aphids survive only a day or so without feeding, but a single successful female migrant can start a new population, because of the parthenogenetic mode of reproduction.

Aphids contain populations of a symbiotic bacterium, *Buchnera aphidicola*, in specialised cells known as bacteriocytes (= mycetocytes in older literature). The bacteria are essential to the aphid's survival, as they are capable of synthesising amino acids lacking in the aphid's diet of sugar-rich, but nitrogen-poor, phloem sap. The bacteria are passed from mother to embryo (or egg) during development. Older work on bacteriocyte and bacterial structure was summarised by Houk (1987), though unfortunately he does not mention work by Hinde at Sydney University (Hinde, 1971, a, b c.). See Wilson *et al*. (2010), Pers and Hansen (2021) and Hansen and Moran (2011) and references therein for more recent detailed accounts. The relationship of aphids and *Buchnera* dates back to the earliest days of aphids, and bacterial molecular markers can throw light on aphid phylogeny e.g., Martinez-Torres *et al*. (2001). There is extensive literature on the molecular, biochemical and physiological aspects of *Buchnera* and its interaction with its aphid host. One interesting feature is its ability to synthesise Vitamin B5 (pantothenic acid. The holidic[2] aphid diet developed by Dadd and Mittler in the early 1960s (see Dadd and Mittler, 1966) enabled studies of essential nutrients for aphids, and further developments using aposymbiotic aphids (i.e. those with bacterial symbionts killed by antibiotics) allowed recognition of nutrients supplied by the bacteria. Initially it was supposed that the bacteria provided aphids with sterols, as insects cannot synthesise them, but aphids feeding on plants can modify plant sterols to produce their sterol requirements (e.g. the moulting hormone ecdysone is a steroid). On defined artificial diets lacking any sterols, however, only a limited number of generations survive, suggesting a possible role for *Buchnera*, although it is known that most bacteria do not synthesise sterols. Aposymbiotic aphids on sterol-free diets were not able to reproduce (Douglas, 1988), so the role of the symbionts in sterol production is supported.

Sometimes aphids contain additional bacterial symbionts. One is *Hamiltonia*, which appears to deter parasitic wasps from attacking its host aphids (Rothacher *et al.* 2016). Others may support recovery after heat stress of both *Buchnera* and its host aphid (Heyworth *et al*. 2020).

Some aphids have mutualistic relationships with ants. Most of these associations are facultative but a few are obligate (reviewed by Stadler and Dixon, 2005). Unidentified ants were observed forming a cover of vegetation fragments over colonies of the endemic Australian *Aphis acaenovinae* on its ground-hugging host, *Acaena ovina*, in the

[2] A holidic diet is one prepared from defined chemicals, e.g. measured amounts of specific amino acids, sucrose, vitamins, minerals, water. Aphids feed on the diet through a stretched Parafilm membrane.

Table 2. Australian endemic aphids with host plants and distribution

Subfamily	**Genus**	**Species**	**Plant**	
Neophyllaphidinae				
	Neophyllaphis	*araucariae*	*Araucaria heterophylla*	(see text)
		brimblecombei	*Podocarpus elatus*	NSW, QLD
		lanata	*P. spinulosus*	NSW, QLD
		gingerensis	*P. lawrencei*	ACT, NSW
Taiwanaphidinae	*Taiwanaphis*	*tasmaniae*	*Nothofagus cunninghamii*	TAS
		furcifera	*Nothofagus moorei*	NSW
		melaleucica	*Melaleuca lanceolata* (Myrtaceae)	WA
Greenideinae	*Meringosphon*	*paradisicum*	*Gastrolobium dilatatum* (Fabaceae)	WA
	*Anomalaphis**	*casimiri*	*Leptospermum scopiarum* (Myrtaceae)	ACT
		comperei	*Agonis flexuosa (Myrtaceae*	WA
Aphidinae	*Aphis*	*acaenovinae*	*Acaena anserovina* *Geum* (both Rosaceae)	NSW
	Aphis	*carverae*	*Epilobium labillardiereanum* (Onagraceae)	NSW
	Aphis	*platylobii*	*Platylobium formosum* NSW, *Daviesia mimosoides* ACT (Fabaceae)	NSW and ACT
	Casimira	*canberrae*	*Epilobium junceum***	NSW and ACT
Lizeriinae	*Ceriferella*	*leucopogonis*	Leucopogon	NSW
		dossuaria	"native flowers"	WA

* Additional species known but not described

** Very widespread, similar to *E. billierardereanum*.

Brindabellas, but the relationship was not obligate as colonies without ants were common (Hales 2008). Aphids have various general predators such as coccinellid, neuropteran, chamaemyiid and syrphid larvae, and coccinellid and neuropteran adults, and any of these can extinguish local populations.

Northern ladybirds have been introduced from time to time as potential biological control agents to Australia and New Zealand, for example *Adalia bipunctata*, on several occasions dating back to 1895. Its first intended target was the cabbage aphid, a particularly unattractive meal as it has a dense coat of wax filaments and smells like cabbage. It has not been successful (Ślipiński *et al*. 2020). The exotic ladybird *Hippodamia variegata* arrived in Australia seemingly unassisted some 25 years ago (Franzmann, 2002). It is known to prey on pest aphids but could feasibly also attack endemic ones. More insidious, and more successful in biological control, are endoparasitic wasps in the Aphidiinae and Aphelinidae. Some cecidomyiid midges also parasitise aphids. As well as the primary parasites, there are hyperparasites.

More details of life histories of the parasites will be discussed in a later section, as will the proposition that some of these groups have a southern background.

Adventive aphids can cause a definite threat to native aphids, e.g., *Aphis oenotherae* that competes with *Casimira canberrae* and other endemic aphids feeding on *Epilobium*.

ENDEMIC AND NATIVE APHIDS OF AUSTRALIA

Autobiographically, this should be the beginning of the story. In 1965 I had started my PhD on the physiology of polymorphism in aphids, with the cabbage aphid as the experimental animal. I was sharing a flat with friends and we wanted to augment our basic cookery with some herbs, so had small pots of mint and parsley on our 3rd floor windowsill. The parsley got aphids on it. The mint got aphids on it. They were different aphids! So began my interest in aphid diversity, supported initially by Cottier's 1953 book on the aphids of New Zealand.

Eastop's comprehensive work on the Australian Aphidoidea (Eastop 1966) recognised 119 species altogether, 51 genera with 101 species being in the Aphididae as then defined. Eleven species out of the total, all in Aphididae, were noted as native (=endemic). The endemics included two species of *Neophyllaphis*, one *Taiwanaphis*[3] two *Ceriferella*, one *Meringosiphon*, one described and two undescribed *Anomalaphis*, *Aphis acaenovinae*, and *Casimira canberrae*. *Neophyllaphis podocarpi*, known from Asia, was included in the list, but the Australian version has since been described as a separate endemic species *N. brimblecombei*. *Ceriferella* is now classified in the subfamily Lizeriinae, possibly the most ancient subfamily of the Aphididae, and one with an exclusively Gondwanan distribution (see below). The Lizeriinae includes just three genera. *Paoliella* has about 22 species distributed across Africa and one in India and one in Brazil. *Ceriferella* has two species in Australia, *C. dossuaria* and *C. leucopogonis*, both described by Carver and Martyn in 1965. The genus has not been found elsewhere. The third genus, *Lizerius*, has eight species and is confined to South America and the Caribbean.

Mary Carver (pers. comm., 1998) listed 171 species of Australian Aphidoidea including four undescribed *Anomalaphis* species which are probably endemic, and an undescribed *Taiwanaphis* from Western Australia, since described by Quednau (2010) as *T. melaleucica*. Brumley (2020) updated Eastop's list in work based on the aphids in the Australian National Insect Collection plus 24 known species not in the collection, with endemics *Aphis carverae*, *A. platylobii*[4], *Neophyllaphis lanata* and an additional species of *Taiwanaphis* (as *Sensoriaphis*, Carver and Hales, 1974) and of *Anomalaphis*. Brumley (2020) also provided identifications of some specimens in the collection, recognising non-native species and genera not previously recorded here. So the number of recognised Australian endemic aphids has almost doubled since 1966. A species of *Sitobion* on *Smilax* spp. in Australia was listed by Hollis and Eastop (2006) as *S. smilacifoliae*, but morphometric studies did not support this (Hales *et al*. 2010), leading B&E to suspect that it was a new species. *Sitobion* has high numbers of probably endemic species in Africa and India (B&E).

The number of exotic arrivals - at least 18 since Carver's checklist - has easily outstripped the number of newly recognised endemics. Two recent newly-found exotics were *Megoura crassicauda*

[3] It is ironic that the aphids on *Nothofagus* in Australia and neighbouring countries are now named for an island that did not exist when they evolved.

[4] Hille Ris Lambers (*in litt.*) called it "a horrible aphid" because of its differences from northern *Aphis* spp.

and *Sarucallis kahawaluokalani* from the author's northern Sydney garden.

The Australian endemic aphids are shown with their host plants and other data in Table 2. Some species not listed can be considered naturally occurring in Australia ("native" or "indigenous") by way of a Gondwanan linkage via Southeast Asia, particularly Indonesia. These include *Aphis clerodendri*, *Aphis eugeniae*, and Greeneidinae (*Greenidea*, *Schoutedenia*).

Of these, *Aphis clerodendri* is present through east Asia, New Guinea and Australia on *Clerodendrum* (Lamiaceae), a genus found in Africa, South America, India, East and South-East Asia, New Guinea and Australia (but not New Zealand). (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:30002447-2). On the basis of distribution, it is tempting to think of *Aphis clerodendri* as a Gondwanan aphid but it is very similar in morphology to the world-wide highly polyphagous *Aphis gossypii*. Polyphagy leads to easy natural and human-assisted invasion of new areas. *A. gossypii* is said by Blackman and Eastop to be "particularly abundant and well-distributed in the tropics". A southern origin for *A. clerodendri* is probable but more work on *A.gossypii* would be needed before claiming southern origin.

Aphis eugeniae (= *A. hardyi* in Eastop,1966) was found by the author in Sydney on cheese tree (*Glochidion ferdinandii*: Phyllanthaceae). It has other hosts, often in the Euphorbiaceae, and is widely distributed across Asia, including India, east and south-east Asia and Australia, New Guinea and New Caledonia. Like *A. clerodendri*, it could make a hopeful claim to be Gondwanan.

A better claim can be made for the two subfamilies Greenideinae and Lizeriinae. Liu *et al*. (2014) provided an interesting molecular phylogeny showing the relationships among Greenideinae and to other aphid subfamilies, essentially supporting the division of Greenideinae into three tribes, Greenideini, Cervaphidini and Schoutedeniini.

The Greenideini includes *Greenidea* (61 spp. with wide Asian distribution, especially India and east and Southeast Asia, one sp. in Australia), *Allotrichosiphum* (4 spp. from India, South China and Japan), *Eutrichosiphum* (54 spp. mainly India, east Asia including Japan, Indonesia), *Greenideoida* (12 spp., east and southeast Asia), *Mesotrichosiphum* (3 spp., East China, Philippines, Indonesia), *Mollitrichosiphum* (18 spp., India, China, Taiwan, Japan, Indonesia), and *Tritrichosiphum* (1 spp., described from Thailand, listed in *Aphid Species File* but not *Aphids on the World's Plants*). Gao *et al.* (2017) discussed species richness and endemism of the Greenideinae, recognising 192 species/subspecies and found the greatest endemicity was correlated with concentrations of taxa. The distribution has a Gondwanan nature - Himalayas, Southern China, Malay Peninsula and Java. Australia has *G. ficicola* on native figs such as Port Jackson fig *Ficus rubiginosa* (noted in Eastop 1966 as *Ficus hillyi*, a misspelling of *Ficus hillii*).

Cervaphidini includes five extant genera, *Anomalaphis, Brasilaphis, Cervaphis*, *Meringosiphon* and *Sumatraphis* plus the fossil *Quisqueyaaphis heiei* from the Caribbean in Dominican amber (Wegierek, 2001). *Anomalaphis* consists of two species limited to Australia. Carver (pers. comm. 1998) knew of 4 undescribed species, all from Australia. *Brasilaphis* consists of a single species, unsurprisingly in Brazil. *Cervaphis* contains five species mainly in Southeast Asia with *Cervaphis rappardi* reported from Papua New Guinea (PNG) (Lamb,1971). *Meringosiphon* is monotypic and known only from Western Australia. The hostplant, not known at the time of description, has been confirmed as *Gompholobium dilatatum* (Fabaceae). *Sumatraphis* is also monotypic, and known from Indonesia, India, Nepal and Yunnan province in Southern China (B&E, ASF).

The Schoutedeniini contains three genera. *Schoutedenia* has two species, *Schoutedenia emblica* from India, Pakistan, Nepal, China, and Thailand, and *S. ralumensis*, recently revised to include a range of species including *S. lutea*, which is common in eastern Australia on *Breynia oblongifolia* (Euphorbiaceae). *S. ralumensis* is widespread in Southeast Asia, India, and Africa. *Eonaphis* has four species, all in Africa, while *Paulianaphis* is monotypic with a single species in Madagascar. A Gondwanan origin is likely, and was recognised by Remaudière (1988): "Les Schoutedeniini ont une distribution typiquement Gondwanienne." Perkovsky and Wegierek (2018) argued that thermal sensitivity of the bacterial symbiont *Buchnera* restricted aphids, following the northern Tertiary expansion, from crossing the tropics. They took the Greenideinae as an example of the few groups to have made the crossing, but may not have considered their likely southern origin or the extent of Gondwanan fragments in Asia. However, the resolution of Greenideinae origins is equivocal because there are several known European fossils (Wegierek and Peñalva 2002).

The subfamily Lachninae is generally associated with Pinales, another group with early Pangaean ancestors. Eastop (1966) listed six species in Australia, but considered them to be of European or North American origin. There are no known endemic or native species in Australia. The subfamily appears to be an ancient lineage of the Aphididae, supported with molecular studies by von Dohlen and Moran (2000), Martinez-Torres *et al*. (2001), Ortiz-Rivas, Martinez-Torres (2010) and Rebijith *et al*. (2017) using mitochondrial and nuclear genes, as well as Owen and Miller (2022) in a phylogenomic study, although there is variability among the topologies. Heie (2015), however, questioned these conclusions, proposing possible evolutionary mechanisms compatible with his cladistic determinations suggesting that the family is relatively young. None of the analyses using genes of the obligate bacterial endosymbiont *Buchnera aphidicola* found Lachninae to branch near the base of the tree (Nováková *et al*., 2013). Lachninae has no endemic or native species in Australia or New Zealand. Several are present in India. The family thrives in the conifer forests of North America and Europe and several species, some of aboricultural significance, have been accidentally introduced to Australia. It seems our *Callitris* (Cupressaceae) woodlands support no endemic aphids. Lachnines almost certainly evolved during Pangaean times and either inhabited only the sections of the supercontinent that became Laurasia and India, or were generally dispersed throughout Pangaea but became extinct in the rest of the Gondwanan section.

Jacksonia papillata (Aphidinae: Macrosiphini) is known from Macquarie Island but is widespread in the Palaearctic and found particularly on etiolated parts of plants especially grasses (Eastop 1966), but also on mosses (Müller 1973). Despite being found in an Australian Antarctic territory it can be presumed to be an accidental introduction.

In New Zealand, possible additions to the list have been found in native grass turfs, an environment not so far studied in Australia. New Zealand endemic aphids are reported in detail by Teulon *et al*. (2013) and are summarised in the next section.

Singh and Srivastava (2022) listed aphids on various ancient plants in India, including horsetails, ferns and podocarps, but their data seem to include accidental presence on plants and throw no light on the relationship of aphids to plants of early or southern origins. For example, *Idiopterus* on horsetails and *Myzus ornatus* on *Podocarpus* are unlikely relationships. *Cinara atrotibialis* on an unidentified *Araucaria* is more likely but more information is needed.

ENDEMIC AND NATIVE APHIDS OF NEW ZEALAND

Work on the New Zealand endemic aphids has been more comprehensive than that in Australia and at least 15 endemic species are now known out of a total fauna of 135. The endemics are mostly in the Aphidinae, but there are two species of *Neophyllaphis* and one of *Taiwanaphis*. The aphidine species are each specific to particular endemic plants.

Cottier (1953) recognised two species of *Neophyllaphis* (*N. araucariae* and *N. totarae*), *Aphis coprosmae*, *Aphis healyi*, *Aphis nelsonensis*, *Sensoriaphis nothofagi* (*gen. et sp. nov*.) feeding on *Nothofagus truncata* on Little Barrier Island, and *Thripsaphis foxtonensis* from *Carex*. *Aphis nelsonensis* on *Epilobium* may now be rare following introduction of *Aphis oenotherae*, as with *Casimira canberrae* in Australia (Hales *et al*. 2014).

More recently, Teulon and colleagues have written extensively on endemic aphids in New Zealand, e.g. von Dohlen and Teulon (2003), who used molecular phylogeny to establish the early divergence of the NZ aphidines, and Teulon *et al.* (2013) who gave a detailed account of endemic aphids and their biology in NZ. They generally use the term "native aphids", but the species listed are most likely endemic. Their list (see Table 1 in Teulon *et al*. 2013) includes undetermined/undescribed species (*Aphis* on *Hebe*, *Aphis* on *Olearia*, *Aphis* on *Samolus*, *Aphis* on *Clematis*, *Casimira* on *Ozothamnus*, *Schizaphis* on *Aciphylla*, *Schizaphis* on *Dracophyllum*, *Melanaphis* on ?grass, three undescribed *Rhopalosiphum* from grass and cereals. Podmore *et al*. (2019) investigated the genetics of undescribed *Schizaphis* species using mitochondrial markers which supported the distinction between the *Aciphylla* and *Dracophyllum* populations and showed the presence of potentially new species. Teulon (2021) gave details of the biology of *Aphis healyi* and an undetermined *Schizaphis*.

Other species in New Zealand are well-known and described in Teulon *et al.* (2013). They include *Paradoxaphis arisoteliae* and *P. plagianthi*, and *Aphis cottieri* on *Muehlenbeckia* in Aphidini, with *Megoura stufkensi* on Fabaceae being the only apparently endemic member of the Macrosiphini (but see *Sitobion* below.) Specimens of *Carmichaelia* (aphid host plant in NZ) found on Lord Howe Island were noted as probably accidentally transported, but recognition of past land connections presents another interpretation.

Taiwanaphis (*Sensoriaphis*) *nothofagi* is listed on three species of *Nothofagus*. *Neophyllaphis totarae* is listed from four species of *Podocarpus*, and another undescribed *Neophyllaphis* from *P. nivalis* is known in the South Island. This one (collected by author on 4 February 1972 at Arthur's Pass, about 3000 ft altitude) was to have been described by Mary Carver and named *N. sinzi*, following tourist pamphlets advertising the South Island as SINZ. The material consisted of one aptera vivipara, one male, and one ovipara, which was not enough for a full description (White, collection notes). They were scattered on young shoots, not part of a colony. Some Australian *Neophyllaphis* on *Podocarpus* diapause over summer as eggs, (Hales 1976, Hales and Lardner 1988), so the discovery of parthenogenetic and sexual morphs in February is a point of interest. I also collected a *Sitobion* (Aphidinae: Macrosiphini) from *Rhipogonum* (Smilacaceae) at Lake Mapourika on 7 February 1972, which may fall into the same category as the Australian one from *Smilax* - probably native if not endemic.

ENDEMIC AND NATIVE APHIDS OF NEW GUINEA.

Lamb (1971) published a checklist of the 57 aphids known at that time from PNG, based on Moericke yellow trap samples from several contrasting localities (*ca* 6000 specimens) and others in collections, including the British Museum (Natural History). It included cosmopolitan aphids like *Aphis gossypii*, and widespread aphids that were not known in Australia until later such as *A. glycines* and *Hysteroneura setariae*. It further included Asian genera still not known in Australia (*Indomegoura* widespread in Asia, *Macromyzus* which has 5 species on ferns and is widespread in Asia. *Anomalosiphum pithicolobii* and *Cervaphis rappardii* (Cervaphidini) were listed and also occur in Asia. *Greenidea*, discussed above, has species in PNG that have not reached Australia. Lamb (1974) went on to compare the aphid fauna across various countries using numerical analysis and concluded that the PNG aphid fauna was most similar to that of the Philippines and not closely related to the Australian fauna. Probably several of the species listed by Lamb could be regarded as "native", having a continuous distribution from PNG through the Gondwanan countries of India and East and Southeast Asia.

Taiwanaphis niuginii on *Nothofagus carrii* is an endemic addition to the fauna (Carver, 1978, as *Sensoriaphis*). There may be others.

ENDEMIC AND NATIVE APHIDS OF SOUTH AMERICA

The continent of South America consists of multiple countries. There are many species of endemic *Neophyllaphis* on *Podocarpus*. One on *Araucaria* is widespread in Gondwanan countries. *Neuquenaphis* is a genus endemic to South America on *Nothofagus*, and some species may be threatened by incursions of human populations and logging (Figeroa *et al*. 2017). See earlier account for these ancient genera.

Fuentes-Contreras *et al*. (1997) listed 31 native species from Chile alone: of these, four were *Aphis* spp., 10 *Uroleucon* and 12 *Neuquenaphis*. Nieto Nafría, Mier Durante, Ortego and colleagues have written numerous papers on newly-discovered South American aphids, particularly in Chile and Argentina - too many to reference individually, but easily found. Taking a single genus as a proxy for the South American aphid fauna, I went through the genus *Aphis* in Blackman and Eastop's *Aphids on the World's Plants*, and found over 50 recently described species of *Aphis* presumably endemic to South America. Ortego *et al*. (2021) raised the number just of *Aphis* endemic to South America to 56. As in Australia and New Zealand, *Aphis* and related genera are significant among the endemic aphid fauna. Like Australia, South America has an *Aphis* on *Acaena*, but it is not closely related to Australia's *A. acaenovinae* (Mier Durante and Ortego, 1998). South America has not only large numbers of endemic *Aphis* spp., but also endemic genera such as *Delfinoia* (Nieto Nafría *et al*. 2017). Unlike Australia, South America has at least one macrosiphine genus, *Uroleucon*, with 25+ endemic species. *Uroleucon* is otherwise widespread in Europe, Asia, and North America. Two species have recently arrived in Australia. The genus in South America was reviewed by de Carvahlo *et al.* (1998), who described four new species.

It has long been a question for aphidologists "Why are there so few aphids in the tropics"? Dixon, Kindlmann *et al*. (1987) suggested that it might be a question of plant apparency, i.e. the flora is so complex that host-specific insects have (or would have) trouble finding their host-plants. This is especially so if there is a dense canopy obscuring the understory. Like Australia, South America has both rain forest and desert regions which allow few opportunities for aphids. The further question, posed by Heie (1994), is "Why are there so few aphids in temperate areas of the southern hemisphere?" There are more than he thought, and without doubt there are more undiscovered, particularly in South America and Africa.

However, the native vegetation in much of the non-desert area of Australia is dominated by *Eucalyptus* and *Acacia*, neither of which support populations of aphids, although ephemeral colonies of polyphagous non-native aphids are occasionally found on them. Further, agricultural and grazing land are unlikely to support a diverse range of aphids.

In contrast to the aphids, other members of the Sternorrhyncha and of the Auchenorrhyncha are well-adapted to eucalypts and acacias and have radiated extensively in Australia, with some tribes endemic to Australasia. The moss bugs (Peloridiidae) are recognised as a Gondwanan group (Fletcher, pers.comm., see Burckhardt 2009, Ye *et al*. 2019).

ENDEMIC AND NATIVE APHIDS OF AFRICA

The continent of Africa consists of about 48 separate countries, and contains extensive deserts and extensive rain forests. Madagascar, Mauritius and smaller island nations have palaeogeological links to Africa. Eastop, early in his career, wrote about the aphids of East Africa and of West Africa but unfortunately these works are hard to come by. Theobald (1914) reported only 35 species.

I have not been able to get any overall idea of African aphid endemicity. Known endemic aphids include two species of *Protaphis*, a genus with strong diversity in Eastern Europe/ Western Asia, and Gondwanan genera *Paoliella* (Lizeriinae), and *Eonaphis* (Greenideinae) with four species. It was suggested (von Dohlen, pers. comm.) that *Sitobion* might be a guide to endemicity, with 24 species known so far only from Africa (B&E). Another group of *Sitobion* species seems to be indigenous to India and there are others in Southeast Asia and South America. There are probably other undescribed species in Australia and New Zealand, as well. It seems likely to be a Gondwanan genus. Nieto Nafría *et al.* (2024) with their deep knowledge of South American species reached the same conclusion.

ENDEMIC AND NATIVE APHIDS OF INDIA

The *Aphis* as a proxy approach was less successful with the Indian fauna. Only two species fitted the criteria for endemicity (not known from other countries). *Casimira bhutanensis* Ghosh, Basu & Raychaudhuri was described from India in 1971, with the only other described member of the genus being endemic to Australia. Ghosh and Ghosh (2006) reported on the Aphidini of India (not seen). As in South America, there are many apparently endemic members of the genus *Sitobion* in India. Ghosh and Singh (2000) reported on distribution and endemism of insects across India._Later, Singh and Singh (2019) stated that "In India, 794 species of aphids under 208 genera are reported out of which about 385 are endemic". They did not give a list, and did not clearly cite the sources of the figures in their tables.

Indian aphid taxonomists have been very active and if this count is even approximately correct, there is a very high degree of endemism, possibly related to speciation of a Gondwanan fauna during the millions of years between India's departure from Gondwana to the Northern Hemisphere, and its collision with the Asian plate, the south side of the Himalayas being geologically of earlier Gondwanan origin (see Chatterjee *et al.* 2006, for a palaeoclimatic and geological description).

APHID PARASITOIDS AND HYPERPARASITOIDS

Two taxa of small wasps, Braconidae: Aphidiinae and Aphelinidae, contain obligate parasitoids of aphids. The wasp's egg is laid into the aphid and the larva develops and eventually pupates within the host, whose cuticle becomes swollen and hardened. This is known as a "mummy", typically a beige colour if the wasp is an aphidiine and black if it is an aphelinid. Ferrar-Suay *et al*. (2025) recently reviewed the biology and diversity of aphid parasitoids.

Wasps of both groups have a degree of specificity and have been imported for biological control, e.g. *Aphidius ervi* for control of the (introduced) blue-green lucerne aphid *Acyrthosiphon kondoi* in Australia (Milne 1986). Importation for biological control has a risk to the native aphid fauna. Bulman *et al.* (2021) found evidence that aphidiine wasps introduced for biological control did not parasitise native aphids in NZ, but that endemic aphids were parasitised by a suite of endemic aphidiines. In Chile, Tomanović *et al.* (2023) recently described four new endemic South American species of the aphidiine *Pseudephedrus* parasitising *Neuquenaphis* species on *Nothofagus*. And in Australia, a new genus *Parephedrus* was erected containing a species of aphidiine parasitising *Taiwanaphis* (*Sensoriaphis*) on *Nothofagus* in New South Wales (Starý and Carver 1971).

Belshaw *et al*. (2000) conducted phylogenetic molecular studies and concluded that a southern origin was likely for the aphidiines. This agrees with conclusions by others including Stary and Carver (1971), and Schlinger (1974), but has been questioned more recently by Ortego-Blanca *et al*. (2009) on the basis of the morphology of a fossil in amber, found in Spain. Petrović (2022) wrote about the taxonomic impediments to aphidiine studies, which included lack of taxonomists and their uneven geographic spread, and he decried the tendency to rush to molecular methods including bar-coding: "(studying) *Aphidius colemani* group in Eastern Africa and the native Aphidiinae of New Zealand used destructive DNA extraction protocols and lost potentially very valuable information, while those from New Zealand probably also lost several as yet undescribed species".

Less common internal parasitoids are midges in the family Cecidomyiidae (Diptera). The aphid *Schoutedenia ralumensis*[5] is parasitised in NSW by an undescribed gall midge in the genus *Pseudendaphis*[6] (identified by K.M. Harris, pers.comm.) The midge lays its eggs near an aphid colony and the hatching larva enters the young aphid via unsclerotised parts of the cuticle. The larva grows within the body of the aphid and exits via the anus, pupating in the soil (Hales and Carver, 1976). We found that the earliest stage parasitised was the third instar, and that the parasite avoided major organs but destroyed the fat body and embryos (Lardner and Hales (1990). In contrast, Kirkpatrick (2009) found that all instars of *Toxoptera aurantii* were parasitised by *P. maculans* in Trinidad. *Endaphis* is widespread in northern continents.

The wasp larvae and midge larvae can in turn be parasitised by other wasps ("hyperparasitoids"). The gall midge in *Schoutedenia* is parasitised by a polyembryonic wasp, *Tricacis* (Platygastrinae, identification by E. Riek, pers. comm.) that lays its egg in the brain of the developing midge embryo before hatching! In mounted late instar or adult aphids, 2-4 cyclopoid larvae of the hyperparasite can sometimes be seen in the brain of the parasite (Hales and Carver, 1976, Hales unpublished).

Sullivan (1987) mentioned cases where aphids had tertiary parasites, generally hyperparasites attacking each other. Sullivan and Völkl (1999) reviewed the hyperparasitoids of aphids, listing ten different genera in three different superfamilies, but do not give biogeographic information. They indicated that the majority are host specific, either to the aphid species or the primary parasite species. The major hyperparasite of aphids in Australia is *Alloxysta* (Cynipidae: Charipinae). Carver (1992) listed five species occurring here. Ward *et al.* (2021) gave an account of the hymenopterous parasites and hyperparasites in aphids on grain crops in Australia. *Alloxysta* is widespread in northern continents. It is not clear whether there is a Gondwanan history, but Ferrer-Suay *et al*. (2012) listed all the Charipinae by current distribution. By far the majority were northern species, but twelve species were considered Australasian, with another 28 species in the Neotropics, Afrotropics and Oriental regions. These all have more or less clear Gondwanan connections and the host specificity suggests an ancient link with southern aphids and their aphidiine parasites and their hyperparasites. Just as aphids showed rapid radiation in the northern Tertiary, it is likely that the wasps did too.

This story is not about southern aphids but is too good to leave out. The parasitoid wasp *Protaphidius nawaii* parasitises the lachnine *Stomaphis japonica*. The aphid colonies are attended by two subgenera of ants in the genus *Lasius*. The ants of the two subgenera attend different colonies of the aphid. Molecular analysis showed that genetically different strains of the wasp parasite attacked aphids depending on which ant sub-genus was attending them! The ants had different behaviours around the aphids, and this may have caused selective pressure resulting in divergence within the parasite species (Yamamoto *et al*., 2020).

Schlinger (1974) reviewed biological evidence for "continental drift" using the multi-trophic relationship of plant (*Nothofagus*), aphid (*Neuquenaphis* and *Sensoriaphis*[7]) parasitoid and hyperparasitoid (a species of *Alloxysta* that appeared to be host specific) and considered that the associations were too intricate and strong to have arisen in South America by any method other than continental drift. More recent evidence supports the view that Gondwanan plants host Gondwanan aphids, and the major primary parasitoids have a Gondwanan origin. Most likely the host-specific hyperparasites do too.

UNANSWERED QUESTIONS

The sections above have indicated many holes in our understanding of these trophically related groups. A few, just related to possible hosts for Australian and New Zealand aphids, are listed below.

1. Are there aphids on mosses and horsetails in southern continents?

[5] *S. lutea* synonymised under *S. ralumensis*, (Remaudière 1988)
[6] Since noted as a junior synonym of *Endaphis* (Tang *et al*. 1994)

[7] A species of *Sensoriaphis* (now as *Taiwanaphis*) occurs in South America. Schlinger postulated that *Neuquenaphis* would probably occur in Australasia. It might, but it hasn't been found yet.

2. Are there aphids on *Nothofagus gunnii* (Tasmania)?
3. Are there aphids on the Wollemi pine (living fossil related to *Araucaria*, NSW)?
4. Are there aphids on celery-top pine or Huon pine in Tasmania (*Phyllocladus* and *Lagarostrobus*)?
5. Are there aphids on *Agathis* (kauri) in Australia or New Zealand? (*Neophyllaphis rappardi* has been collected from *Agathis labilliardieri* in Papua (B&E)
6. Are there indigenous/endemic aphids on *Dacrydium*, another member of the Podocarpaceae?
7. Are there endemic aphids in Australia on endemic grasses?

Why are the answers to these simple questions (and many others) not already known? The first answer is the elusive nature of aphids - their small size, their rarity, their seasonality, and a lack of perceived charisma for the general entomologist. The second is a lack of search effort. Search effort is limited by availability of informed hunters - many people with knowledge of aphids are tied to research and management relating to agricultural pests, or are working on entirely different aspects of aphid biology. The few aphid taxonomists are often committed to the care and management of large general collections. The second problem is that native aphids are hard to find even if you know they exist, with small, seasonal and transient populations, and often far removed from the cities where the jobs are. Travel is expensive in time and money and unlikely to receive funding. Retired entomologists with an interest in aphids have the time, but there are various hurdles to jump: access to laboratory alcohol becomes difficult, scientific collecting licences need prior planning and may be difficult to obtain, most scientific literature is commercialised and often not available without substantial payment for people without institutional support (my thanks to authors who have provided detailed abstracts). Opportunistic observations, often adjuncts to road trips, have provided a lot of our endemic aphids, but in national parks or state forests collecting is generally illegal without a licence. If you are lucky enough to see what may be a new aphid in a national park, are you going back home to apply for a licence, wait x weeks for it and come back? Not usually feasible and something will probably have eaten the aphids in the meantime. In Australia the licences are different from state to state. Queensland requires separate permission for each national park, or did when I asked. For non-aphidologists, recognising an aphid can be a challenge, let alone deciding on whether it may be new. And most likely they still can't legally collect it to find out. Aphids are complicated and not spectacular, need careful slide mounting for examination (need good stereomicroscope) and identification (need good compound microscope). Identification needs a lot of background knowledge and if you suspect you have a new species, you definitely need a specialist's opinion. Aphid taxonomists are hard to find. This has been an impediment to the descriptions of the new endemic aphids in New Zealand, for example. But there are plenty of opportunities for the courageous!

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REFERENCES

Belshaw, R., Dowton. M., Quicke, D.L.J. and Austin, A.D. (2000). Estimating ancestral geographical distributions: a Gondwanan origin for aphid parasitoids? *Proceedings of the Royal Society of London B* **267:** 491-496.

Blackman, R.L. and Eastop, V.F. *Aphids on the World's Plants.* See Favret, C., below.

Brumley, C. (2020). A checklist and host catalogue of the aphids (Hemiptera: Aphididae) held in the Australian National Insect Collection. *Zootaxa*, *4728*(4), 575-600.

Bulman, S., Drayton, G.M., Cameron, P.J. and two others. (2021). Endemic New Zealand aphids (Hemiptera: Aphididae) parasitised by native Aphidiinae (Hymenoptera: Braconidae), not biological control parasitoids. *Austral Entomology* **60:** 713-721. https://doi.org/10.1111/aen.12564

Burckhardt, D., (2009). Taxonomy and phylogeny of the Gondwanan moss bugs or Peloridiidae (Hemiptera, Coleorrhyncha). *Deutsche Entomologische Zeitschrift*, 56: 173–235. https://doi.org/10.1002/mmnd.200900019

Carver, M. (1978). A new species of *Sensoriaphis* from New Guinea (Homoptera: Aphididae). *Pacific Insects* **19:** 31–38.

Carver, M. (1992). Alloxystinae (Hymenoptera: Cynipoidea: Charipidae) in Australia. *Invertebrate Taxonomy* **6:** 769–785. https://doi.org/10.1071/IT9920769

Carver, M. and Hales, D. (1974). A new species of *Sensoriaphis* Cottier, 1953 (Homoptera: Aphididae) from New South Wales. *Journal of Entomology* (B), **42:** 113-125.

Carver, M. and Martyn, E.J. (1965). Descriptions of a new aphid genus from Australia and of the alate viviparous female of *Sensoriaphis tasmaniae* Carver and Martyn, 1962

(Homoptera: Aphididae). *Proceedings of the Royal Entomological Society of London. Series B, Taxonomy* **34:** 34-37

Chatterjee, S., Goswami, A. and Scotese, C. (2006). The longest voyage: tectonic, magmatic, and Palaeoclimatic evolution of the Indian plate during its northward flight from Gondwana to Asia. *Gondwana Research*, **23**: 238-267.

Chen, L., Jin, W-T., Liu, X-Q. and Wang, X-Q. (2022). New insights into the phylogeny and evolution of Podocarpaceae inferred from transcriptomic data. *Molecular Phylogenetics and Evolution*, **166:** 107341.

Cottier, W. (1953). *Aphids of New Zealand*. New Zealand Department of Scientific and Industrial Research, Bulletin 106, 382 pp.

Crowley, T.J. and North, G.R. (1988). Abrupt climate change and extinction events in earth history. *Science* **240:** 996-1002. DOI: 10.1126/science.240.4855.996

Dadd, R.H. and Mittler, T.E. (1966). Permanent culture of an aphid on a totally synthetic diet. *Experientia* **15:**832-833. doi.10 1007/BFO01897447

De Carvahlo, R.C.Z., Blackman R.L. and Spence, J.M. (1998). The genus *Uroleucon* Mordvilko (Insecta, Aphidoidea) in South America, with a key and descriptions of four new species. *Zoological Journal of the Linnean Society*, **123:** 117-141. doi.org/10.1111/j.1096-3642.1998.tb01296.x

Dixon; A.F.G., P. Kindlmann; P., Leps; J. and. Holman, J. (1987) Why there are so few species of aphids, especially in the tropics *The American Naturalist* **129:**580-592. DOI:10.1086/284659

Donovan, M.P., Iglesias, A., Wilf, P. and two others (2017). Rapid recovery of plant-insect associations after the End-Cretaceous extinction. *Nature Ecology and Evolution*, Article 0012, 2017

Douglas, A.E. (1988). On the source of sterols in the green peach aphid *Myzus persicae*, reared on holidic diets. *Journal of Insect Physiology* **34:** 403-408. doi.org.10.1016/0022-1910(88)90110-2

Eastop, V.F. (1966). A taxonomic study of Australian Aphidoidea (Homoptera). *Australian Journal of Zoology* **14:** 399-592.

Evans, J.W. (1956). Palaeozoic and Mesozoic Hemiptera (Insecta). *Australian Journal of Zoology* **4:** 165- 285.

Favret, C. & Aphid Taxon Community, eds. (2025) Blackman & Eastop's Aphids on the World's Plants, version 1.0. Accessed at *https://aphidsonworldsplants.info/* [accessed October-November 2025]

Favret, C. (2025). *Aphid Species File. http://Aphid.SpeciesFile.org* . [Accessed October-November 2025].

Ferrer-Suay, M., Barreda, M., Rakhshani, E. and three others. (2025). A review of aphid parasitoids, with an identification key to the genera of economic importance. *Insects*, **16:** 648. doi:10.3390/insects16070648

Ferrer-Suay, M., Peretas-Martinez, J., Selfa, J. and Pujada-Villar, J. (2012). Taxonomic and synonymic catalogue of the Charipinae and notes about this subfamily (Hymenoptera: Cynipoidea: Figitidae). *Zootaxa* **3376:** 1-92. doi 10.11646/zootaxa3376.1.1

Figueroa, C.C., Niemeyer, H.M., Cabrera-Brandt, M. and four others (2017). Forest fragmentation may endanger a plant-insect interaction: the case of the highly specialist native aphid *Neuquenaphis staryi* in Chile. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, **107:** 297-310. https://doi.org/10.1111/icad.12283

Franzmann, B.A. (2002). *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae), a predacious ladybird new in Australia. *Australian Journal of Entomology*, **41:** 375-377. https://doi.org/10.1046/j.1440-6055.2002.00318.x

Fuentes-Contreras, E., Muñoz, R. and Niemeyer, H.M. (1997). Diversidad de áfidos (Hemiptera: Aphididae en Chile. *Revista Chilena de Historia Natural*, **70:** 531-542.

Gao, C., Chen, J., Li, Y., Jiang, L-Y. and Qiao G-X (2018). Congruent patterns between species richness and areas of endemism of the Greenideinae aphids (Hemiptera: Aphididae) revealed by global-scale data. *Zoological Journal of the Linnean Society*, **183:** 791–807.'

Ghosh, A.K., Basu, R.C. and Raychaudhuri, D.N. (1971). On a collection of aphids (Homoptera: Aphididae) from Bhutan with descriptions of two new species. *Kontyû, Tokyo Entomological Society*, 39: 120–125.

Ghosh, A.K, and Ghosh, L.K. (2006). Fauna of India and the adjacent countries: Homoptera: Aphidoidea, Part 7/1 Subfamily Aphidinae, Tribe Aphidini. Series: *Fauna of India and the Adjacent Countries* ISBN: 9788181711113

Ghosh, L.K. and Singh, R. (2000). Biodiversity of Indian insects with special reference to aphids (Homoptera: Aphididae). *Journal of Aphidology* **14:** 113-123.

Hales, D.F. (1976) Biology of *Neophyllaphis brimblecombei* Carver (Homoptera: Aphididae) in the Sydney region. *Australian Zoologist* **19:** 77-83.

Hales, D. (2008). Biological observations on the Australian endemic aphid Aphis acaenovinae Eastop (Hemiptera: Aphididae) including a new host record. *Australian Entomologist* **35:** 93-95.

Hales D.F. and Carver, M.(1976). A study of *Schoutedenia lutea* (van der Goot, 1917 (Homoptera: Aphididae). *Australian Zoologist*, **19:** 85- 94.

Hales, D., Foottit , R.G. and Maw, E. (2010). Morphometric studies of the genus *Sitobion* Mordvilko 1914 in Australia (Hemiptera: Aphididae). *Australian Journal of Entomology* **49:** 341–353.

Hales, D, Foottit . R.G. and Maw, E. (2014). 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. doi:10.1111/aen.12125, 2014.

Hales, D., Foottit, R.G. and Maw, E. (2015). **S**exual morphs of *Aphis acaenovinae* Eastop,1961 (Hemiptera: Aphididae: Aphidinae). *Australian Entomologist*, **42:** 19-24.

Hales, D.F. and Lardner, R.M. (1988). Genetic evidence for the occurrence of a new species of *Neophyllaphis* Takahashi (Homoptera: Aphididae) in Australia. *Journal of the Australian Entomological Society* **27:** 81-85.

Hales, D.F., Tomiuk, J., Wöhrmann, K. and Sunnucks, P. (1997). Evolutionary and genetic aspects of aphid biology. *European Journal of Entomology*, **94:** 1-55.

Hansen, A.K. and Moran, N.A. (2011). Aphid genome expression reveals host-symbiont cooperation in the production of amino acids. *Proceedings of the National Academy of Sciences USA*, **108:** 2849-2854.

Heenan, P.B. and Smissen, R.D. (2013). Revised circumscription of *Nothofagus* and recognition of the segregate genera *Fuscospora*, *Lophozonia*, and *Trisyngyne* (Nothofagaceae). *Phytotaxa*, **146:** 1-31

Heie, O.E. (1967). Studies on fossil aphids (Homoptera: Aphidoidea) especially in the Copenhagen collection of fossils in Baltic amber. Reprinted from *Spolia Zoologica Musei Hauniensis* 26, 273 pp.

Heie, O. E. (1970). Lower Eocene aphids (Insecta) from Denmark. *Bulletin of the Geological Society of Denmark,* **20:** 162-168.

Heie, O.E. (1987). Palaeontology and phylogeny. In Minks, A.K. and Harrewijn, P. (eds). *Aphids - Their Biology, Natural Enemies and Control, Vol. 2A*. Elsevier, Amsterdam and New York, pp.367-391.

Heie, O.E. (1994). Why are there so few aphids in the temperate areas of the southern hemisphere? *European Journal of Entomology* **91:** 127-133.

Heie, O.E. (2015). A theory about the evolutionary history of Lachnidae and comments on the results of some molecular phylogenetic studies of aphids (Hemiptera: Aphidoidea).

Polish Journal of Entomology **84:** 275–287. DOI: 10.1515/pjen-2015-0024
Heyworth, E.R., Smee, M.R. and Ferrari, J. (2020) Aphid facultative symbionts aid recovery of their obligate symbiont and their host after heat stress. *Frontiers of Ecology and Evolution*, **8:**56. doi: 10.3389/fevo.2020.00056
Hill, L., Gunawardena, D.N., Flynn, A. and Dominiak, B.C. (2020). Possible windborne transmission of giant willow aphid *Tuberolachnus salignus* (Gmelin) (Hemiptera: Aphididae: Lachninae) westward from New Zealand to Australia. *New Zealand Entomologist*, **43:**1-14. https://doi.org/10.1080/00779962.2019.1707343
Hinde, R. (1971a). The control of the mycetome symbiotes of the aphids *Brevicoryne brassicae*, *Myzus persicae,* and *Macrosiphum rosae*. *Journal of Insect Physiology*, **17:** 1791-1800**.**
Hinde, R. (1971b). The fine structure of the mycetome symbiotes of the aphids *Brevicoryne brassicae*, *Myzus persicae*, and *Macrosiphum rosae*. *Journal of Insect Physiology*, **17:** 2035-20.
Hinde, R. (1971c). Maintenance of aphid cells and the intracellular symbiotes of aphids in vitro. *Journal of Invertebrate Pathology*, **17:** 333-338.
Hollis, D. and Eastop, V.F. (latest version 2019). https://biodiversity.org.au/afd/taxa/Sternorrhyncha/checklist (viewed November 2025)
Houk, E.J. (1987). Symbionts. In Minks, A.K. and Harrewijn, P. (eds). *Aphids - Their Biology, Natural Enemies and Control, Vol. 2A*. Elsevier, Amsterdam and New York, pp.123-129.
Hullé, M., Pannetier, D., Simon, J-P and two others. (2003). Aphids of sub-Antarctic Îles Crozet and Kerguelen: species diversity, host range and spatial distribution. *Antarctic Science*, **15:** 203-209**.**
Johnson, B. (1957). Studies on the dispersal by upper winds of *Aphis craccivora* Koch in New South Wales. *Proceedings of the Linnean Society of New South Wales*, **82:** 191-198.
Johnson, K.R. (1992) Leaf-fossil evidence for extensive floral extinction at the Cretaceous-Tertiary boundary, North Dakota. *Cretaceous Research*, **13:** 91-117.
Khan, R., Hill, R.S, Liu, J. and Biffin, E. (2023). Diversity, distribution, systematics and conservation status of Podocarpaceae. *Plants (Basel)*, **12:**1171. doi: 10.3390/plants12051171
Kirkpatrick, T.W. (2009). Notes on *Pseudendaphis maculans* Barnes, a cecidomyid endoparasite of aphids in Trinidad, B. W. I. *Bulletin of Entomological Research,* **45:** 777-781. https://doi.org/10.1017/S0007485300033393
Kustatscher, E., Ash, S., Karesev, E. and four others. (2018). Flora of the Late Triassic. *Topics in Geobiology*, **46:** 545-622. https://doi.org/10.1007/978-3-319-68009-5_13
Lamb, K.P. (1971). Aphids of Papua New Guinea: an annotated checklist. *Proceedings of the Linnean Society of New South Wales*, **96:** 186-192.
Lamb, K.P. (1974). New Guinea aphids and their biogeographical affinities. *Pacific Insects* **16:** 61-65.
Lardner R.M. and Hales, D.F. (1990). Histopathology of an aphid, *Schoutedenia lutea*, parasitized by a gall midge, *Pseudendaphis* sp. *Entomophaga*, **35:** 557-567.
Liu, Q , Chen, J., Huang, X., Jiang, L. and Qiao, G. (2014). Ancient association with Fagaceae in the aphid tribe Greenideini (Hemiptera: Aphididae: Greenideinae) *Systematic Entomology*, **40:** 230-241. https://doi.org/10.1111/syen.1210001
Liu, Y., Johnson, M.G. Cox, C.J. and seven others (2019). Resolution of the ordinal phylogeny of mosses using targeted exons from organellar and nuclear genomes. *Nature Communications* **10:** Article number:1485.
Martin, S.K ., Skidmore, L.I. and Stilwell, J.D (2016). A first record of Cretaceous aphids (Hemiptera, Sternorrhyncha, Aphidomorpha) in Australia, from the Lower Cretaceous Koonwarra Fossil Bed, Victoria**.** *Zootaxa* **4137:** 95-107. doi: 10.11646/zootaxa.4137.1.7.
Martinez-Torres, D., Buades, C., Latorre, A. and Moya, A. (2001). Molecular systematics of aphids and their primary endosymbionts. *Molecular Phylogenetics and Evolution* **20:** 437-449. https://doi.org/10.1006/mpev.2001.0983
McElwain, J.C. and Punyasena, S.W. (2007). Mass extinction events and the plant fossil record. *Trends in Ecology and Evolution* **22:** 548-57. doi: 10.1016/j.tree.2007.09.003
McLoughlin, S. (2001). The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany,* **49:** 271–300.
Metcalfe, I. (2006). Palaeozoic and Mesozoic tectonic evolution and palaeogeography of
East Asian crustal fragments: The Korean Peninsula in context. *Gondwana Research* **9:** 24- 46.
Metcalfe, I. (2013). Tectonic and palaeogeographic evolution of eastern Tethys. *Journal of Asian Earth Sciences* 66: 1-33**.** https://doi.org/10.1016/j.jseaes.2012.12.020
Mier Durante, M.P. and Ortego, J. (1998). Une nouvelle espèce d'*Aphis* inféodée au genre *Acaena* en Argentine [Hemiptera, Aphididae; Rosaceae]. *Revue Française d'Entomologie* (N.S.) **20:** 121-126.
Mille, C., Jourdan, H., Cazères, S., Maw, E. and Footitt, R. (2020). New data on the aphid (Hemiptera, Aphididae) fauna of New Caledonia: some new biosecurity threats in a biodiversity hotspot. *Zookeys* **22:**943:53–89. doi: 10.3897/zookeys.943.47785
Milne, W.M. (1986) The release and establishment of *Aphidius ervi* Haliday (Hymenoptera: Ichneumenoidea) in eastern Australia. *Journal of the Australian Entomological Society*, **25:** 123-130.
Moran, N. A. (1988). The evolution of host-plant alternation in aphids: evidence for specialization as a dead end. *American Naturalist* **132:** 681-706
Mortimer, N., Campbell, H.J, Tulloch, A.J. and eight others. (2017).) Zealandia: Earth's hidden continent. *Geological Society of America Today*, **27:** 27-35.
Müller, F.P. (1973). Aphiden an Moosen. *Entomologische Abhandlungen* **39:** 203-241.
Nieto Nafría, J.M., Mier Durante, M.P. and López Ciruelos, S.I. (2017) *Delfinoia*, a new South American aphid genus (Hemiptera, Aphididae, Macrosiphini) on *Cayaponia* (Cucurbitaceae). *Zookeys*, **671:** 49-60. doi:10.3897/zookeys.671.12247.
Nieto Nafría, J.M., Ortego, J. and Mier Durante, M.P. (2024). Tres estudios taxonómicos sobre pulgones (Hemiptera, Aphididae) de América del Sur. *Suplementos del bolétin de la asococión español de entomología*, **6:** 1-70.
Nováková, E., Hypŝa, V., Klein, J. and three others. (2013). Reconstructing the phylogeny of aphids (Hemiptera: Aphididae) using DNA of the obligate symbiont *Buchnera aphidicola. Molecular Phylogenetics and Evolution*,.**68:** 42-54. doi.org/10.1016/j.ympev.2013.03.016
Nowak, H., Schneebeli-Hermann, E. and Kustatcher, E. (2019). No mass extinction for land plants at the Permian-Triassic transition. *Nature Communications* **10:** Article 384.
Ortego-Blanco, J., Bennett, D.J., Delclos, X. and Engel, M.S. (2009). A primitive Aphidiine wasp in Albian amber from Spain and a Northern Hemisphere origin for the subfamily (Hymenoptera: Braconidae: Aphidiinae). *Journal of the Kansas Entomological Society*, **82:** 273-282. https://doi.org/10.2317/JKES0812.08.1
Ortiz-Rivas, B. and Martìnez-Torres, D. (2010). Combination of molecular data support the existence of three main lineages in the phylogeny of aphids. *Molecular Phylogenetics and Evolution*.**55:** 305-317. doi.org/10.1016/j.ympev.2009.12.005
Owen, C.L. and Miller, G.L. (2022). Phylogenomics of the Aphididae: deep relationships between subfamilies clouded by gene tree discordance, introgression and the

gene tree anomaly zone. *Systematic Entomology*, **47**(3): 470-486.

Perkovsky, E. and Wegierek, P.(2017). Aphid–*Buchnera*–Ant symbiosis; or why are aphids rare in the tropics and very rare further south? *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, **107:** Issue 2-3: Fossil Insects, Arthropods and Amber, 297 - 310. DOI:https://doi.org/10.1017/S1755691017000147

Pers, D. and Hansen, A.K. (2021). The boom and bust of the aphid's essential amino acid metabolism across nymphal development. *Genes, Genomes, Genetics*. **11:**:jkab115. doi: 10.1093/g3journal/jkab115

Petrović, A. (2022). Sizing the knowledge gap in taxonomy: the last dozen years of Aphidiine research. *Insects* **13:** (No page numbers, available online). https://doi.org/10.3390/insects13020170.

Pike, K.S., Graf, G., Foottit, R.G., and six others. (2012). Eriosomatine aphids (Hemiptera: Aphididae: Eriosomatinae) associated with moss and roots of conifer and willow in forests of the Pacific Northwest of North America. *The Canadian Entomologist*.**144:** 555-576. doi:10.4039/tce.2012.49

Podmore, C., Hogg, I.D., Drayton, G.M. and five others (2019). Study of COI sequences from endemic New Zealand aphids highlights high mitochondrial DNA diversity in Rhopalosiphina (Hemiptera: Aphididae). *New Zealand Journal of Zoology*, **46:** 107-123 (published online 2018) https://doi.org/10.1080/03014223.2018.1510843

Quednau, F W. (1962). A list of aphids so far unrecorded from South Africa, with descriptions of two new species (Homoptera, Aphidoidea). *South African Journal of Agricultural Science* **5:** 253-264

Quednau, F.W. (2010). Atlas of the drepanosiphine aphids of the world part III: *Memoirs of the American Entomological Institute*, **83:** 361 pp.

Raynor, R.J. and Waters, S.B. (1989). A new aphid from the Cretaceous of Botswana. *Palaeontology*, **32:** 669-683.

Rebijith, K.B., Asokan, R., Hande, H.R. and four others. (2017). Reconstructing the macroevolutionary patterns of aphids (Hemiptera: Aphididae) using nuclear and mitochondrial DNA sequences. *Biological Journal of the Linnean Society* **121**(4): 796-814

Rehan, S.M., Leys, R, Schwarz, M.P. (2013). First evidence for a massive extinction event affecting bees close to the K-T boundary. *PLoS ONE* **8:** e76683. https://doi.org/10.1371/journal.pone.0076683Remaudière, G. (1988). Révision des Schoutedeniini et description d'un *Eonaphis* malgache nouveau [Hom. Aphididae Greenideinae]. *Bulletin de la Société Entomologique de France*, **93:** 65-78.

Robert, Y. (1987). Aphids and their environment. 5.1. Dispersion and migration. In Minks, A.K. and Harrewijn, P. (eds). *Aphids - Their Biology, Natural Enemies and Control, Vol. 2A*. Elsevier, Amsterdam and New York.

Robinson, A.G. (1966). Review of the fern aphids in North America with descriptions of a new species and a new genus. *The Canadian entomologist*, **98:** 1252-1259. DOI: https://doi.org/10.4039/Ent981252-12

Rothacher, L., Ferrer-Suay, M. and Vorburger, C. (2016). Bacterial endosymbionts protect aphids in the field and alter parasitoid community composition. *Ecology*, **97:** 1712-1723.https://doi.org/10.1890/15-2022.1

Salomo, K., Smith, J.F., Feild, T.S. and six others (2017). The emergence of the earliest angiosperms may be earlier than fossil evidence indicates. *Systematic Botany*, **42:** 607-619. https://doi.org/10.1600/036364417X696438.

Shcherbakov, D.E. (2010). The earliest true bugs and aphids from the middle Triassic of France (Hemiptera). *Russian entomological journal*, **19:** 179-182.

Shcherbakov, D.E. and Wegierek. P. (1990). A new and the oldest aphid family, Creaphididae from the Triassic of middle Asia. *Psyche*, **90:** 81-85.

Schlinger, E.I. (1974). Continental drift, *Nothofagus*, and some ecologically related insects. *Annual Review of Entomology*, **19:** 323-343.

Singh, G., Prasad, M. and Singh, R. (2018). Updated check-list of Lachninae, Lizeriinae, Mindarinae, Phyllaphidinae, Saltusaphidinae, Taiwanaphidinae and Thelaxinae (Aphididae: Hemiptera) and their food plants in India. *Journal of Entomology and Zoology Studies* 6: 3157-3166. (No doi)

Singh, R. and Singh, G. (2019). Species diversity of Indian aphids (Hemiptera: Aphididae) *International Journal of Biological Innovations* **1:** 23-29. DOI:https://doi.org/10.46505/IJBI.2019.1105

Singh, R. and Srivastava, A. (2022). Association of the aphids (Insecta: Homoptera: Aphididae) with pteridophytes and gymnosperms of India. *Journal of applied entomologist*, **2:** 23-32.

Ślipiński, A., Li, J. and Pang, H. (2020). *Ladybird beetles of the Australo-Pacific region. Coleoptera: Coccinellidae: Coccinellini.* CSIRO Publishing, Bloomsbury Wildlife, Sydney. 240 pp.

Stadler, B. and Dixon, A.F.G. (2005). Ecology and evolution of aphid-ant interactions. *Annual review of ecology, evolution, and systematics* **36:** 345-372. https://doi.org/10.1146/annurev.ecolsys.36.091704.175531

Starý, P. and Carver, M. (1971). A new genus and species of Aphidiidae (Hymenoptera) parasitizing *Sensoriaphis* (Hemiptera) on *Nothofagus* in New South Wales. *Journal of the Australian Entomological Society*, **10:** 175-178. https://doi.org/10.1111/j.1440-6055.1971.tb00028.x

Steed-Mundin, O. (2025). The southern beeches: an introduction to the genus *Nothofagus* Blume. *Curtis's Botanical Magazine* **41:** 439-456.

Sullivan, D.J. (1987**).** Insect hyperparasitism. *Annual Review of Entomology*, **32:**49-70.

Sullivan, D.J. and Völkl, W. (1999). Hyperparasitism: multitrophic ecology and behavior. *Annual Review of Entomology*, **44:** 291-315. https://doi.org/10.1146/annurev.ento.44.1.291315.https://doi.org/10.1146/annurev.ento.44.1.291

Szwedo, J., Lapeyrie, J. and Nel, A. (2015). Rooting down the aphid's tree–the oldest record of the Aphidomorpha lineage from Palaeozoic (Insecta: Hemiptera). *Systematic Entomology*,**40:** 07-214 https://doi.org/10.1111/syen.120992

Tang, Y.Q., Yokomi, R.K. and. Gagné, R.J. (1994). Life history and description of *Endaphis maculans* (Diptera: Cecidomyiidae), an endoparasitoid of aphids in Florida and the Caribbean Basin. *Annals of the Entomological Society of America*, **87:** 523–531. https://doi.org.10.1093/aesa/87.5.523

Teulon, D.A.J. (2021). Distribution and population trends of two New Zealand aphids (Hemiptera, Aphididae, Aphidinae). *New Zealand Entomologist*, **44:** 81-87. doi.org/10.1080/00779962.2022.206377

Teulon, D.A.J. and Stufkens, M.A.W. (1998). Current status of New Zealand indigenous aphids. *Conservation Advisory Service Notes* **216**. pp.1-23

Teulon, D.A., Stufkens, M., Drayton, G., and seven others. (2013) Native aphids of New Zealand—diversity and host associations. *Zootaxa*, 3647 (4), 501–517. https://doi.org/10.11646/zootaxa.3647.4.1

Teulon, D.A.J., Stufkens, M.A.W., von Dohlen, C.D. and Kean, J. (2002). Status of New Zealand indigenous aphids. DOC Science Internal Series **106.**

Theobald, F.V. (1914). African Aphididae. *Bulletin of entomological research*, **4:** 313 - 337. DOI:https://doi.org/10.1017/S0007485300043248

Tng, D. (2012). https//davistng.wordpress.com/2012/05/22/nothofagus-icon-trees-of-gondwanan-botany. Accessed October, 2025.

Tomanivić, Ž., Stanković, S.S., Petrović. A. and four others (2023). Four new species of *Pseudephedrus* (Hymenoptera, Braconidae, Aphidiinae) from Chile with a key to species identification. *Systematics, Morphology and Physiology*, **52:** 909-920.

von Dohlen, C.D. and Moran, N.A. (2000). Molecular data support a rapid radiation of aphids in the Cretaceous and multiple origins of host alternation. *Biological journal of the Linnean Society*, **71:** 689-717.

von Dohlen, C.D. and Teulon, D.A.J. (2003). Phylogeny and historical biogeography of New Zealand indigenous Aphidini aphids (Hemiptera, Aphididae): an hypothesis. *Annals of the Entomological Society of America*, **96:** 107-116**.** DOI: 10.1603/0013-8746(2003)096[0107:PAHBON]2.0.CO;2

Ward, S.E., Umina, P.A., MacFadyen, S. and Hoffmann, A.A. (2021). Hymenopteran parasitoids of aphid pests within Australian grain production landscapes. *Insects* **12:** 44. https://doi.org/10.3390/insects12010044

Wegierek, P. (2001). *Quisqueyaphis heiei* gen and sp. nov. (Hemiptera: Aphidinea: Greenideidae), a new species of aphid from Dominican amber. *Annales Zoologici*, **51:** 409-415.

Wegierek, P. and Peñalva, E. (2002). Fossil representatives of the family Greeneidae from the Miocene of Europe. *Geobios* **35:** 745-757. doi.org/10.1016/S0016-6995(02)00086-4

White, D. (1967). Some aphids occurring on endemic plants in central Australia, with special reference to *Aphis craccivora* Koch. *Journal of the Australian Entomological Society*, **6:** 74-76.

Wilson, A.C.C., Ashton, P. D., Calevro, F. and nine others (2010). Genomic insight into the amino acid relations of the pea aphid, *Acyrthosiphon pisum*, with its symbiotic bacterium *Buchnera aphidicola. Insect Molecular Biology*. **19:** 249-258. https://doi.org/10.1111/j.1365-2583.2009.00942.x

Wilson, A.C.C., Sunnucks, P. and Hales, D.F. (2003). Heritable genetic variation and potential for adaptive evolution in asexual aphids (Aphidoidea). *Biological Journal of the Linnean Society*, **79:** 115-135.

Yamamoto, T., Hasegawa, H., Nakase, Y. and 2 others. (2020). Cryptic diversity in the aphid-parasitizing wasp *Protaphidius nawaii* (Hymenoptera: Braconidae): discovery of two attendant-ant-specific mtDNA lineages. *Zoological Sciences*, **37:** 117-121. DOI:10.2108/zs190093

Żyla, D., Homan, A. and Wegierek, P. (2020). Oviparosiphidae and its implications for inferring aphid evolution (Hemiptera, Sternorrhyncha). *PLOS One,* doi.org/10.1371/journal.pone.0174791 April 26, 20.

Żyla, D. and Wegierek, P. (2013). Early stages of aphid evolution (Hemiptera, Sternorrhyncha: Aphidomorpha) from the Late Jurassic/Early Cretaceous locality of Khohont (Mongolia). *Insect systematics and evolution*, **44:** 149-155.

Żyla, D. and Wegierek, P. (2020). Early stages of aphid evolution (Hemiptera, Sternorrhyncha, Aphidomorpha). Department of Natural History. Upper Silesian Museum. DOI 10.5281/zenodo.4159531

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