

Beneficial Scale Insects

TAKUMASA KONDO AND PENNY J. GULLAN

All insects play an important role in the natural environment; however, human activities such as cultivation of agricultural crops in monoculture over large areas create ideal conditions for the proliferation of some phytophagous insects. The term ‘pest’ is completely anthropocentric, being defined as any organism that has a harmful impact on humans, their food or their living conditions, including organisms that act as vectors of diseases.

Scale insects can qualify either as beneficials or as ‘pests’, depending on the circumstances. Indeed, some scale insect ‘pests’ can be regarded as beneficial, and vice versa, depending on human perception of the situation. An insect that feeds on a weed or provides a valued resource is considered beneficial, but when it attacks a cultivated plant it is suddenly rated as a ‘pest’. For example, in temperate conifer forests, soft scale insects feeding on the trees may be considered pests by silviculturists; however, apiculturists regard them as beneficial, because honeybees feed on their honeydew (Fig. 1.1f), especially when no flower nectar is available in winter; hence the scale insects are essential for the survival of the bees.

Useful products derived from scale insects include pigments (Fig. 1.1a, b), resins and waxes (Fig. 1.1d). Both the scale insects and their sugary honeydew waste are important sources of food for other animals; scale insect honeydew (Fig. 1.1f) is essential in the production of honeydew honey by bees, and for the survival of other insects, e.g. parasitoid wasps.

The following account covers some scale insect species reported in the scientific literature as beneficial to humans. The scales are grouped according to their useful products (coloured dyestuffs, resins and waxes); their use as a food source for animals, including humans; and for the control of weeds (Fig. 1.1e).

Dyestuffs

Scale insects have a long history of use as sources of red pigments, the most famous being the carmine dye (carminic acid) extracted from the cochineal insects of Central and South America, *Dactylopius* species (Dactylopiidae); this is still used to colour food and cosmetics and, to a lesser extent, textiles. Many other scale insect species are or have been used to produce dyes in different parts of the world.

Family Dactylopiidae

Dactylopius coccus Costa. Commonly known as the cochineal insect, this scale is the commercial source of carmine dye (carminic acid). It is farmed on cultivated prickly pear cactus, *Opuntia ficus-indica*, in the Canary Islands, Chile, Mexico and Peru (Donkin, 1977; Kirby, 1977; Kondo *et al.*, 2008; Cranston and Gullan, 2014).

Dactylopius ceylonicus (Green). This species was introduced from South America to India and Sri Lanka to produce carmine dye for export to England; however, it has a lower carminic acid content than the domesticated species, *D. coccus*, so was less productive. An additional problem was that it eventually kills its host, *Opuntia monacantha* (Zimmermann *et al.*, 2009).

Dactylopius tomentosus (Lamarck). (Fig. 1.1a). A comparative study showed that *D. coccus* produces the largest amount of carminic acid per insect, followed by *D. tomentosus*, *D. opuntiae*, *D. ceylonicus*, and *D. confusus*, in that order (Chávez-Moreno *et al.*, 2010). However, there is no evidence that *D. tomentosus* has ever been cultivated for its dye.

Dactylopius confusus (Cockerell) and *D. opuntiae* (Cockerell). These two species also have been used for production of carmine dye, but they are a poorer source of carminic acid than *D. coccus* (Cardon, 2007).

Family Eriococcidae

Acanthococcus uvaeursi L. Apparently this eriococcid was exploited in the past for its red colour, but there is no evidence of trade in this insect as a dyestuff (Donkin, 1977; Kirby, 1977).

Family Kermesidae

Kermes ilicis L. This scale insect is found on various species of oak, *Quercus* spp. (Fagaceae), in southern France, Spain, the Near East and elsewhere around the Mediterranean Sea (García Morales *et al.*, 2020). The red dye, vermilion, consists principally of kermesic acid (Kirby, 1977). In Europe, before the discovery of the New World which brought the introduction of the cochineal (*Dactylopius* spp.), kermesic acid from *Kermes*

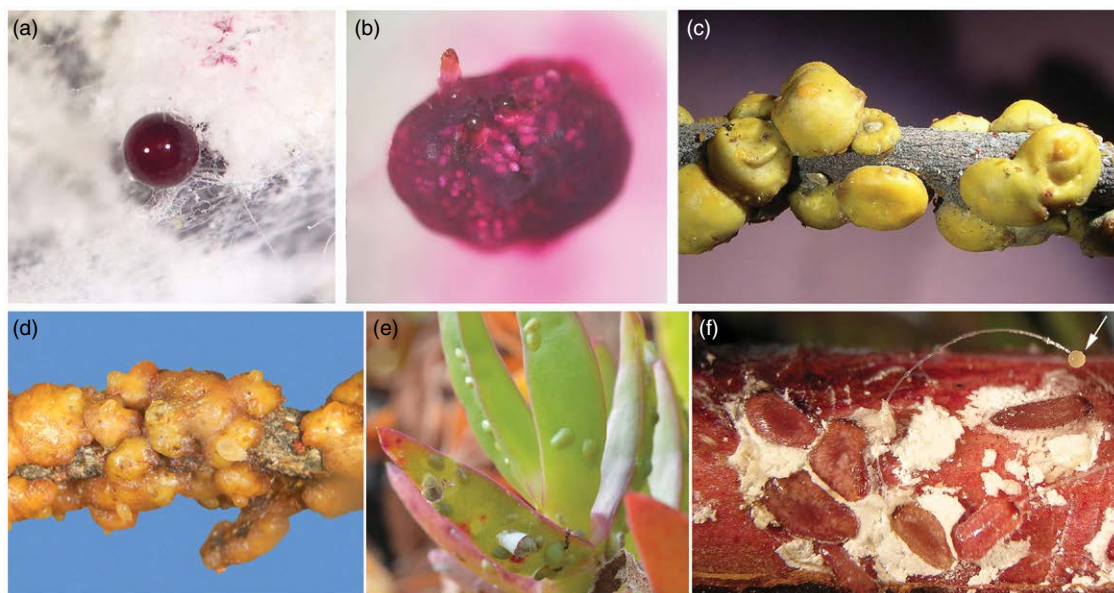


Fig. 1.1. Beneficial scale insects. (a) A drop of haemolymph of *Dactylopius tomentosus* (Lamarck), which is red due to carminic acid. (b) A red dye exuding from a specimen of the commercial lac, *Kerria lacca* (Kerr), when treated in potassium hydroxide. (c) The insects and the wax of *Cerococcus quercus* Comstock were gathered and chewed like gum by native Americans in the USA. (d) The lac scale *Tachardiella fulgens* (Cockerell) is used as stomach medicine and to repair crockery in Mexico. (e) *Pulvinariella mesembryanthemi* (Vallot) is being considered as a biocontrol agent for weedy ice plants. (f) Cysts of *Xylococcus macrocarpae* (Coleman) expel large quantities of honeydew (see arrow) that honeybees collect to make honey. Photographs (a), (b), (c), (d) and (f) by T. Kondo, and (e) by Cristina Vieites-Blanco (Universidade de Lisboa, Campo Grande., Lisbon, Portugal).

spp. and other scale insects' dyes were used in the textile dyeing industry (Kirby, 1977).

***Kermes vermilio* Planchon.** Of the two *Kermes* species used as a source of dyestuff, this was the most commonly utilized. It is found on many species of oaks, *Quercus* spp., in the Palaearctic region, but especially in the Mediterranean region (García Morales *et al.*, 2020). The vermilion dye extracted from this species is known as kermesic acid (Donkin, 1977). In the Middle Ages it was the basis of a valuable industry but is no longer used.

Family Kerriidae

***Kerria lacca* (Kerr).** (Fig. 1.1b). Commonly cultivated for its resin (see section below on resins and waxes), this lac insect is also the source of a red dye known as 'lake' or 'lake pigment'; this natural red dyestuff is used to colour cotton and silk in India and Thailand (Donkin, 1977; Kirby and White, 1996; Kondo, 2012; Wongwad *et al.*, 2012).

Family Margarodidae

The red dye in all *Porphyrophora* species consists mainly of carminic acid and other minor colorants such as flavokermesic acid and kermesic acid (Hofenk de Graaff, 2004; Cardon, 2007; Lech and Jarosz, 2016).

***Porphyrophora crithmi* (Goux).** This ground pearl is used as a source of a red dye (Cardon, 2007). It occurs in France on the roots of *Crithmum maritimum* (Apiaceae) (García Morales *et al.*, 2020).

***Porphyrophora hamelii* Brandt.** The red dye extracted from this ground pearl is known as Armenian red and was used in the textile industry (Donkin, 1977; Vahedi and Hodgson, 2007). The species occurs in Armenia, Iran and Turkey on the roots and lower stems of various grasses (García Morales *et al.*, 2020).

***Porphyrophora hirsutissima* Hall.** It has been suggested that this species of ground pearl probably was a source of crimson dyes in Egypt (Cardon, 2003; Vahedi and Hodgson, 2007).

***Porphyrophora polonica* (Linnaeus).** This ground pearl, known as Polish cochineal, is a source of a red dye used in Poland for colouring textiles (Donkin, 1977; Vahedi and Hodgson, 2007; Lech and Jarosz, 2016). It occurs in many countries in the Palaearctic, on the roots and lower stems of many plants (García Morales *et al.*, 2020).

***Porphyrophora sophorae* Archangelskaya.** This ground pearl is a source of a red dye (Vahedi and Hodgson, 2007). It occurs in China, Kazakhstan and Uzbekistan on the roots of *Glycyrrhiza*, *Hedysarum* and *Sophora* (Fabaceae) (García Morales *et al.*, 2020).

Resins and Waxes

The surface of a scale insect's body is normally covered by resinous or waxy substances, or mealy wax. In the lac insects

(Kerriidae), the body surface is covered by different types of resin (Chamberlin, 1923). Adult female wax scales (Coccidae: Ceroplastinae) produce copious amounts of wax that cover the dorsum (Hodgson and Peronti, 2012). The following are several scale insect species exploited commercially for their resins and waxes.

Family Coccidae

Ericerus pela (Chavannes). Males of the pela scale, *Ericerus pela* (Coccidae), occur in large numbers; their puparia are made of abundant wax that is the main ingredient of a high-quality wax produced in China. The scales are farmed commercially (Qin, 1997). Pela wax is used for the insulation of electrical cables, anti-corrosive coating on ammunition, as a shining agent for paper, a polishing ingredient for automobiles, tyres, leather products and wood furniture and for coating pills, making candles, etc. (Qin, 1997).

Waxiella africana (Green). The wax of the adult female of this scale insect is used for mending cracks and holes in porcelain and metal in Egypt (Kamel and Afifi, 1970).

Family Kerriidae

The resins of some *Kerria* spp. (Kerriidae) are used as the main ingredient of shellac (Varshney, 1977). Shellac is a natural resinous oligomer, consisting of polyesters, i.e., aleuritic acid, shellolic acid and a small amount of free aliphatic acids (Gately and Kennedy, 2017). It has multiple uses but is primarily known as a high-quality varnish on wood furniture and musical instruments (Licchelli *et al.*, 2013) such as guitars. Shellac is used also to give glossiness to candies and as a coating on medicinal capsules to slow the release of the medicine (Schad *et al.*, 2013).

Kerria lacca (Kerr). Shellac is a purified product of the resin of this lac insect, which is grown commercially on various host trees in India, Thailand and Myanmar (Farg and Leopold, 2009). Shellac extracted from *K. lacca* is currently used in many industries, for example as an insulating material for electrical cables due to non-transmission of electricity, and in paints and surface coatings (Licchelli *et al.*, 2013).

Kerria chinensis (Mahdihassan). This scale insect species is the main source of commercial lac in Thailand (Chen *et al.*, 2011).

Kerria nepalensis Varshney. This is a species of lac insect farmed for commercial shellac production in Myanmar (Chen *et al.*, 2011).

Kerria pusana (Misra). This species is the most widely used commercial lac insect in Myanmar (Chen *et al.*, 2011).

Kerria (*Kerria*) *ruralis* (Wang, Yao, Teiu & Liang). A source of commercial lac in China (Chen *et al.*, 2011).

Kerria yunnanensis Ou & Hong. This lac insect is the main commercial source of shellac resin in China (Chen *et al.*, 2011).

Tachardiella fulgens (Cockerell). (Fig. 1.1d). This lac insect species, under the name of ‘Gomilla’ or ‘Gomea’, was used medicinally to treat stomach troubles and for repairing crockery and utensils in Mexico and the southwestern USA (Chamberlin, 1923).

Family Monophlebidae

Llaveia axin (Llave). In Guatemala and Mexico, fat from the body of the giant monophlebid, *L. axin*, is used in lacquer work for decorating gourds, wood and ceramic objects. The natural compounds give a smooth, shiny and durable finish (Williams and MacVean, 1995; Suazo-Ortuño *et al.*, 2013).

Llaveia mexicanorum (Cockerell). The body fat of this species is used to coat cups and bowls made from gourds, sold throughout Guatemala; also as a base coat for lacquer work in Mexico (Williams and MacVean, 1995).

Weed Control

Scale insects have been successful in controlling invasive weeds within a classical biological control framework. Examples are given below.

Family Coccidae

Pulvinariella mesembryanthemi (Vallot). (Fig. 1.1e). This soft scale may be used as a biocontrol agent for the weedy ice plants of the genus *Carpobrotus* (Aizoaceae) in the coastal regions of Spain (Vieites-Blanco *et al.*, 2020) and elsewhere where ice plants are weeds.

Family Dactylopiidae

Dactylopius austrinus De Lotto. This is used as a biocontrol agent for the weedy cactus *Opuntia aurantiaca* in Australia and South Africa (Moran and Cobby, 1979; Hosking, 1984).

Dactylopius ceylonicus (Green). This scale insect was used successfully as a control agent of *Opuntia vulgaris* (Cactaceae) in Sri Lanka in 1863 (Tyron, 1910).

Dactylopius opuntiae (Cockerell). This scale insect is an important biological control agent used against invasive *Opuntia stricta* (Cactaceae) in Australia, Kenya and South Africa (Volchansky *et al.*, 1999; Mathenge *et al.* 2010). It has been introduced recently to Kenya (Laikipia province) as a successful biological control agent of invasive *O. stricta* on pastureland (Witt *et al.*, 2020). It has also been used successfully to control invasive *Opuntia littoralis*, *O. oricola* and their hybrids in Santa Cruz island off the coast of southern California, USA (Goeden *et al.*, 1967, 1968; Goeden and Ricker 1980).

Dactylopius tomentosus (Lamarck). (Fig. 1.1a). This species is an important biological control agent against invasive species of *Cylindropuntia* spp. (Cactaceae) in Australia and South Africa (Moran and Zimmermann, 1984; Mathenge *et al.*, 2009).

Family Eriococcidae

Tectococcus ovatus Hempel. Since 2014, this gall-inducing eriococcid has been released on the islands of Hawaii and Oahu

for the control of the highly invasive strawberry guava, *Psidium cattleianum* (Myrtaceae) (Johnson, 2016).

Family Kerriidae

Austrotachardia sp. There is potential for *Austrotachardia* sp. to control native weeds of the genus *Cassinia* in the central region of New South Wales, Australia (Campbell *et al.*, 1994).

Paratachardina sp. There is potential for *Paratachardina* sp. to control native weeds of the genus *Cassinia* in the northern region of New South Wales, Australia (Campbell *et al.*, 1994).

Family Pseudococcidae

Antonina australis Froggatt. In Australia, attempts were made to introduce this mealybug into parts of Queensland from New South Wales to control *Cyperus rotundus*, a weed of economic significance; however, this project halted due to the fear that the mealybug might become a pest of cultivated crops (Froggatt, 1904).

Trabutina mannipara (Hemprich & Ehrenberg). The manna mealybug, *T. mannipara*, has been used as a biological control agent against invasive *Tamarix* spp. in warm desert regions in the south-western USA (DeLoach *et al.*, 1996).

Food and Medicines

Scale insects are an important food for animals in the environment; some species also being consumed by humans. They also are used as additives in foodstuffs and in medicines. Some examples are presented below.

Family Cerococcidae

Cerococcus quercus Comstock. (Fig. 1.1c). The insects and their wax were gathered and chewed like gum by native Americans in the USA (Miller and Kosztarab, 1979).

Family Eriococcidae

Cystococcus spp.: *C. pomiformis* (Froggatt), *C. echiniformis* Fuller and *C. campanidorsalis* Semple, Cook & Hodgson. In Australia, Aboriginal people eat the adult females and nymphs of these gall-inducing eriococcids. The galls, commonly known as Australian ‘bush coconuts’, occur on bloodwood trees, *Corymbia* spp. (Gullan and Cranston, 2014; Yen *et al.*, 2016). Both the insects and galls serve as a food source for other insects (e.g. moths) and birds (Turner, 1942; Semple *et al.*, 2015).

Family Kerriidae

Kerria lacca (Kerr). Shellac resin from this insect is a natural polymer used for coating applications in the food,

pharmaceutical and nutraceutical industries. It is an approved food additive in the USA and Europe, known as E904 (Schad *et al.*, 2013).

Tachardiella fulgens (Cockerell). (Fig. 1.1d). This lac insect species, under the name ‘Gomilla’ or ‘Gomea’, was used to treat stomach troubles in Mexico (Chamberlin, 1923).

Family Margarodidae

Heteromargarodes chukar (La Rivers). This North American ground pearl is an important food source for an introduced gamebird, the chukar partridge, *Alectoris graeca* (Galliformes: Phasianidae) (Christensen, 1970).

Family Monophlebidae

Icerya seychellarum (Westwood). The Aldabra flying fox, *Pteropus aldabrensis* (Chiroptera: Pteropodidae) and the black rat, *Rattus rattus* (Rodentia: Muridae), have been observed licking the upper surfaces of leaves infested with this scale (Roberts and Seabrook, 1989; Hutson, 2004), probably for honeydew deposits (since the insects themselves are mostly on the leaf undersides).

Llaveia spp. Giant monophlebs, *Llaveia* spp., have been used for centuries in Mesoamerica as a source of wood lacquer, and for medicinal purposes (Williams and MacVean, 1995).

Nietnera sp. In Sakorn Nakorn Province, Thailand, this giant monophlebid is cooked with sticky rice. The local people call this scale Kai-Jackchian, meaning cicada eggs (Kondo, 2001).

Family Pseudococcidae

Trabutina spp.: *T. mannipara* (Hemprich & Ehrenberg) and *T. serpentina* (Green). The biblical ‘manna from heaven’, the food consumed by the Israelites during their wanderings in the Sinai desert, is the dried honeydew of these two mealybug species (Ben-Dov, 1988).

Family Stigmaticocidae

Stigmaticoccus spp. The honeydew of these scale insects, eliminated through a long wax anal tube, is a crucial source of carbohydrate for numerous bird and insect species in natural ecosystems in the Dominican Republic, Mexico and Brazil (Hodgson *et al.*, 2007).

Honeydew Honey from Honeybees

Honeydew (Fig. 1.1f) is the excess sugary liquid that phytophagous insects of the order Hemiptera, suborder Sternorrhyncha, eliminate from the anus after imbibing large amounts of phloem sap to satisfy their nutritional needs (Malumphy,

1997). Scale insect honeydew is high in carbohydrates, which provides an important food source for honeybees, birds and many other organisms, including ants, bumblebees, flies, small beetles and wasps (Moiler, 1987). Although most of the world's honey is derived from floral nectar (flower honeys), bees can make honey from other sources of sugars such as honeydew (honeydew honeys). In some regions, honeydew honey may represent a significant percentage of the total production, even exceeding the amount of floral honeys (Kunkel, 1997). The main scale insect families reported as sources of honeydew used by honeybees are Aclerididae, Coccidae, Coelostomidiidae, Eriococcidae, Kermesidae, Monophlebidae, Pseudococcidae, Stigmaticoccidae and Xylococcidae (Fig. 1.1f), and the scale insect species involved are usually found on the bark of trees. Several scale insects that are important sources of honeydew for honeybees are listed below.

Family Aclerididae

Aclerda berlesii Buffa. In Greece, this flat grass scale produces large quantities of honeydew, which bees exploit as a source for honey production (Santas, 1989).

Family Coccidae

Eulecanium sericeum (Lindinger); *Physokermes hemicryphus* (Dalman), *Physokermes piceae* (Schränk); *Parthenolecanium corni* (Cockerell), *P. corni* (Bouché), *P. fletcheri* (Cockerell); *Phyllostoma myrtilli* (Kaltenbach). In temperate regions of Europe, numerous soft scales are sources of honeydew for honeybees when flower sources are scarce (Kunkel, 1997).

Family Coelostomidiidae

Ultracoelostoma spp.: *U. assimile* (Maskell) and *U. brittini* Morales. The honeydew of these two scale species is a sugar source for honeybees in the *Nothofagus* (southern beech) forests of New Zealand (Crozier, 1981; Morales, 1991).

Family Kermesidae

Kermes quercus (L.). In Europe, the honeydew of this oak-feeding scale insect is exploited by honeybees (Kunkel, 1997).

Family Marchalinidae

Marchalina hellenica (Gennadius). In Greece, around 15,000 t of honeydew honey (60% of their national honey production) are collected annually, mainly derived from the honeydew of this scale insect, which feeds on *Pinus* spp. (Pinaceae) (Santas, 1983; Gounari, 2003).

Family Putoidae

Puto israelensis Ben-Dov. In Turkey, during spring, honeybees gather copious honeydew from this scale insect for making honey (Ünal *et al.*, 2016).

Family Stigmaticoccidae

Stigmaticoccus asper Hempel. The honeydew of this scale insect, eliminated through a long wax anal tube, is an important source for honey production from the oak tree *Quercus humboldtii* (Fagaceae), in the Oriental Cordillera of Colombia (Chamorro *et al.*, 2013) and from leguminous trees in Brazil (Hodgson *et al.*, 2007).

Family Xylococcidae

Xylococcus macrocarpa (Coleman). (Fig. 1.1f). This scale insect lives under the bark of *Calocedrus decurrens* and produces a long waxy tube from the anus to eliminate copious honeydew that is the source of 'white cedar honey' in California (USA) (White *et al.*, 1962).

Conclusions

Scale insect products such as dyestuffs, resins and waxes have long been exploited by people and continue to be in daily life. Red dye (carminic acid) from the cochineal insect can be found in cosmetics (e.g. lipsticks and rouge), foodstuffs (e.g. processed meats, drinks and ice-cream) and sometimes in clothing. Shellac has multiple uses, mainly in coating various foodstuffs (including candies, fruits), pills, wooden musical instruments, furniture, etc. Scale insect honeydew can be an important food source for honeybees, and is a crucial source of carbohydrates for birds and insects in many natural ecosystems.

Of the more than 8000 species of scale insects, 7.6% have been considered as pests (present study); however, other species, and even those considered as pests, play an important role in their natural ecosystems, forming an integral part of the food web.

References

- Ben-Dov, Y. (1988) Manna scale, *Trabutina mannipara* (Hemprich & Ehrenberg) (Homoptera: Coccoidea: Pseudococcidae). *Systematic Entomology* 13, 387–392.
- Campbell, M.H., Holtkamp, R.H., McCormick, L.H., Wykes, P.J., Donaldson, J.F., Gullan, P.J. and Gillespie, P.S. (1994) Biological control of the native shrubs *Cassinia* spp. using the native scale insects *Austrotachardia* sp. and *Paratarchardia* sp. (Hemiptera: Kerriidae) in New South Wales. *Plant Protection Quarterly* 9, 64–68.

- Cardon, D. (2003) *Le monde des teintures naturelles*. Belin, Paris.
- Cardon, D. (2007) *Natural Dyes. Sources, Tradition, Technology and Science*. Archetype Publications, London.
- Chamberlin, J.C. (1923) A systematic monograph of the Tachardiinae or lac insects (Coccidae). *Bulletin of Entomological Research* 14, 147–212.
- Chamorro, F.J., Nates-Parra, G. and Kondo, T. (2013) Mielato de *Stigmatococcus asper* (Hemiptera: Coccoidea: Stigmatococcidae): recurso melífero de los bosques de roble *Quercus humboldtii* (Fagaceae) en los Andes orientales de Colombia. *Revista Colombiana de Entomología* 39(1), 61–70.
- Chávez-Moreno, C.K., Tecante, A., Fragoso-Serrano, M. and Pereda-Miranda, R. (2010) Metabolic profiling of *Dactylopius* (Hemiptera: Dactylopiidae) species pigments by geographical origin and hosts using multivariate data analysis. *Biochemical Systematics and Ecology* 38(4), 671–679.
- Chen, X., Chen, H., Feng, Y., He, R. and Yang, Z. (2011) Status of two species of lac insects in the genus *Kerria* from China based on morphological, cellular, and molecular evidence. *Journal of Insect Science* 11(106), 1–14.
- Christensen, G.C. (1970) *The Chukar Partridge. Its Introduction, Life History, and Management*. Biology bulletin No. 4. Nevada Department of Wildlife, Reno, Nevada, USA.
- Cranston, P.S. and Gullan, P. J. (2014) A dyeing business. Canary cochineal insects. *Antenna* 38(4), 202–207.
- Crozier, L.R. (1981) Beech honeydew: forest produce. *New Zealand Journal of Forestry* 26, 200–209.
- DeLoach, C.J., Gerling, D., Fornasari, L., Sobhian, R., Myartseva, S. et al. (1996) Biological control programme against saltcedar (*Tamarix* spp.) in the US: progress and problems. In: Moran, V.C. Moran and Hoffman, J.H. (eds) *Proceedings of 9th International Symposium on Biological Control of Weeds*, January 1996, Stellenbosch, South Africa, pp. 253–260.
- Donkin, R.A. (1977) The insect dyes of Western and West-Central Asia. *Anthropos* 72(5/6), 847–880.
- Farag, Y. and Leopold, C.S. (2009) Physicochemical properties of various shellac types. *Dissolution Technologies* 16, 33–39.
- Froggatt, W.W. (1904) The nut grass coccid (*Antonina australis* Green). *Agricultural Gazette of New South Wales* 15, 407–410.
- García Morales, M., Denno, B., Miller, D.R., Miller, G.L., Ben-Dov, Y. and Hardy, N.B. (2020) *ScaleNet: A literature-based model of scale insect biology and systematics*. Database. Available at: <http://scalenet.info>
- Gately, N.M. and Kennedy, J.E. (2017) Processing stability and the significance of variation in extrusion speeds and temperatures on SSB® 55 Pharma Grade Shellac for oral drug delivery. *Journal of Manufacturing and Materials Processing* 1(1), 1–14.
- Goeden, R.D., Fleschner, C.A. and Ricker, D.W. (1967) Biological control of prickly pear cacti on Santa Cruz Island, California. *Hilgardia* 38, 579–606.
- Goeden, R.D., Fleschner, C.A. and Ricker, D.W. (1968) Insects control prickly pear cactus. *California Agriculture* 22, 8–10.
- Goeden, R.D. and Ricker, D.W. (1980) Santa Cruz Island – revisited. Sequential photography records the causation, rates of progress, and lasting benefits of successful biological weed control. In: *Proceedings of the 5th International Symposium on the Biological Control of Weeds*, pp. 355–365.
- Gounari, S. (2003) Seasonal development and ovipositing behavior of *Marchalina hellenica* (Hemiptera: Margarodidae). *Entomologia Hellenica* 15, 27–37.
- Gullan, P.J. and Cranston, P.S. (2014) *The Insects: An Outline of Entomology*. 5th edn. Wiley-Blackwell, Chichester, UK.
- Hodgson, C.J. and Peronti, A.L.B.G. (2012) A revision of the wax scale insects (Hemiptera: Sternorrhyncha: Coccoidea: Ceroplastinae) of the Afrotropical Region. *Zootaxa* 3372, 1–265.
- Hodgson, C.J., Gamper, H.A., Bogo, A. and Watson, G.W. (2007) A taxonomic review of the Margarodid genus *Stigmatococcus* Hempel (Hemiptera: Sternorrhyncha: Coccoidea: Stigmatococcidae), with some details on their biology. *Zootaxa* 1507, 1–55.
- Hofenk de Graaff, J.H. (2004) *The Colorful Past. Origins, Chemistry, and Identification of Natural Dyestuffs*. Archetype Publications, London.
- Hosking, J.R. (1984) The effect of temperature on the population growth potential of *Dactylopius austrinus* De Lotto (Homoptera: Dactylopiidae), on *Opuntia aurantiaca* Lindley. *Journal of the Australian Entomological Society* 23, 133–139.
- Hutson, A.M. (2004) The bats of Aldabra atoll, Seychelles. *Phelsuma* 12, 126–132.
- Johnson, M.T. (2016) Managing conflict over biological control: the case of strawberry guava in Hawaii. In: Van Driesche, R.G., Simberloff, D., Blossey, B., Causton, C., Roddie, M.S. et al. (eds) *Integrating Biological Control into Conservation Practice*, 1st edn. John Wiley & Sons, Chichester, UK, pp. 264–276.
- Kamel, A.H. and Afifi, S.A. (1970) A remarkable use for the scale insect *Ceroplastes africanus* Green in Egypt. *Entomologist's Monthly Magazine* 106, 32.
- Kirby, J. (1977) A spectrophotometric method for the identification of lake pigment dyestuffs. *National Gallery Technical Bulletin* 1, 35–45.
- Kirby, J. and White, R. (1996) The identification of red lake pigment dyestuffs and a discussion of their use. *National Gallery Technical Bulletin* 17, 56–80.
- Kondo, T. (2001) Las cochinillas de Colombia (Hemiptera: Coccoidea). *Biota Colombiana* 2(1), 31–48.
- Kondo, T. (2012) Introduction to the study of entomology. In: UNESCO-EOLSS Joint Committee (eds) *Encyclopedia of Life Support Systems*. Animal and Plant Productivity. EOLSS Publishers, Paris, France. Available at: <http://www.eolss.net/sample-chapters/c10/E5-25-47.pdf> (accessed 26 September 2021)
- Kondo, T., Gullan, P.J. and Williams, D.J. (2008) Coccidology. The study of scale insects (Hemiptera: Sternorrhyncha: Coccoidea). *Revista Corpoica – Ciencia y Tecnología Agropecuaria* 9(2), 55–61.
- Kunkel, H. (1997) 1.2.3.1. Scale insect honeydew as forage for honey production. In: Ben-Dov, Y. and Hodgson, C.J. (eds) *Scale Insects: Their Biology, Natural Enemies and Control*. World Crop Pests, Vol. 7A. Elsevier, Amsterdam and New York, pp. 291–302.
- Lech, K. and Jarosz, M. (2016) Identification of Polish cochineal (*Porphyrophora polonica* L.) in historical textiles by high-performance liquid chromatography coupled with spectrophotometric and tandem mass spectrometric detection. *Analytical and Bioanalytical Chemistry* 408(12), 3349–3358.
- Licchelli, M., Malagodi, M., Somaini, M., Weththimuni, M. and Zanchi, C. (2013) Surface treatments of wood by chemically modified shellac. *Surface Engineering* 29(2), 121–127.
- Malumphy, C. (1997) Honeydew. In: Ben-Dov, Y. and Hodgson, C. (eds) *Soft Scale Insects: Their Biology, Natural Enemies and Control*. World Crop Pests, Vol. 7A. Elsevier, Amsterdam and New York, pp. 269–274.
- Mathenge, C.W., Holford, P., Hoffmann, J.H., Zimmermann, H.G., Spooner-Hart, R. and Beattie, G.A.C. (2009) Distinguishing suitable biotypes of *Dactylopius tomentosus* (Hemiptera: Dactylopiidae) for biological control of *Cylindropuntia fulgida* var. *fulgida* (Caryophyllales: Cactaceae) in South Africa. *Bulletin of Entomological Research* 99(6), 619–627.
- Mathenge, C.W., Holford, P., Hoffmann, J.H., Zimmermann, H.G., Spooner-Hart, R.N. and Beattie, G.A.C. (2010) Determination of biotypes of *Dactylopius tomentosus* (Hemiptera: Dactylopiidae) and insights into the taxonomic relationships of their hosts, *Cylindropuntia* spp. *Bulletin of Entomological Research* 100, 347–358.
- Miller, D.R. and Kosztarab, M.P. (1979) Recent advances in the study of scale insects. *Annual Review of Entomology* 24, 1–27.
- Moiler, H. (1987) Honeydew – a South Island beekeeper's bounty. *New Zealand Beekeeper* 195, 31–33.
- Morales, C.F. (1991) *Margarodidae (Insecta: Hemiptera)*. Fauna of New Zealand / Ko te Aitanga Pepeke o Aotearoa, No. 21. DSIR Plant Protection, Auckland, New Zealand.

- Moran, V.C. and Cobby, B.S. (1979) On the life history and fecundity of the cochineal insect, *Dactylopius austrinus* De Lotto (Homoptera: Dactylopiidae), a biocontrol agent for the cactus *Opuntia aurantiaca*. *Bulletin of Entomological Research* 69, 629–636.
- Moran, V.C. and Zimmermann, H.G. (1984) The biological control of cactus weeds: achievements and prospects. *Biocontrol News and Information* 5, 297–320.
- Qin, T.K. (1997) 1.2.3.2. The pela wax scale and commercial wax production. In Ben-Dov, Y. and Hodgson, C.J. (eds) *Soft Scale Insects: Their Biology, Natural Enemies and Control*. World Crop Pests, Vol. 7A. Elsevier, Amsterdam and New York, pp. 303–321.
- Roberts, P. and Seabrook, W.A. (1989) A relationship between black rats (*Rattus rattus*), Seychelles fruit bats (*Pteropus seychellensis aldabrensis*) and the coccoid (*Icerya seychellarum*) (Insecta, Homoptera) on Aldabra Atoll, Seychelles. *Journal of Zoology, London* 218, 332–334.
- Santas, L.A. (1983) Insects producing honeydew exploited by bees in Greece. *Apidologie* 14(2), 92–103.
- Santas, L.A. (1989) Species of honeydew producing insects useful to apiculture in Greece. *Entomologia Hellenica* 7, 47–48.
- Schad, B., Smith, H., Cheng, B., Scholten, J., VanNess, E. and Riley, T. (2013) *Coating and Taste Masking with Shellac*. Pharmaceutical Technology, Vol. 2013 Supplement, Issue 5. Available at: <http://www.pharmtech.com/coating-and-taste-masking-shellac> (accessed 26 September 2021)
- Semple, T.L., Gullan, P.J., Hodgson, C.J., Hardy, N.B. and Cook, L.G. (2015) Systematic review of the Australian ‘bush coconut’ genus *Cystococcus* (Hemiptera: Eriococcidae) uncovers a new species from Queensland. *Invertebrate Systematics* 29(3), 287–312.
- Suazo-Ortuño, I., Val-De Gortari, E. del and Benítez-Malvido, J. (2013) Rediscovering an extraordinary vanishing bug: *Llaveia axin axin*. *Revista Mexicana de Biodiversidad* 84(1), 338–346. doi:10.7550/rmb.31286
- Turner, A.J. (1942) Fragmenta lepidopterologica. *Proceedings of the Royal Society of Queensland* 53(4), 61–96.
- Tyron, H. (1910) The ‘wild cochineal insect’, with reference to its injurious action on prickly pear (*Opuntia* spp.) in India, etc. and to its availability for the subjugation of this plant in Queensland and elsewhere. *Queensland Agricultural Journal* 25, 188–197.
- Ünal, S., Ayan, S., Karadeniz, M. and Yer, E.N. (2017) Some Forest Trees for Honeydew Honey Production in Turkey. *Siberian Journal of Forest Science* 4, 101–110.
- Vahedi, H.A. and Hodgson, C.J. (2007) Some species of the hypogaeal scale insect *Porphyrophora* Brandt (Hemiptera: Sternorrhyncha: Coccoidea: Margarodidae) from Europe, the Middle East and North Africa. *Systematics and Biodiversity* 5(1), 23–122.
- Varshney, R.K. (1977) Taxonomic studies on lac insects of India (Homoptera: Tachardiidae). *Oriental Insects (Supplement)* 5 (1976), 1–97.
- Vieites-Blanco, C., Retuerto, R., Rodríguez Lado, L. and Lema, M. (2020) Potential distribution and population dynamics of *Pulvinariella mesembryanthemi*, a promising biocontrol agent of the invasive plant species *Carpobrotus edulis* and *C. aff. acinaciformis*. *Entomologia Generalis* 40(2), 173–185. doi: 10.1127/entomologia/2020/0758
- Volchansky, C.R., Hoffmann J.H. and Zimmermann H.G. (1999) Host-plant affinities of two biotypes of *Dactylopius opuntiae* (Homoptera: Dactylopiidae): Enhanced prospects for biological control of *Opuntia stricta* (Cactaceae) in South Africa. *Journal of Applied Ecology* 36(1), 85–91.
- White, J.W. Jr, Riethof, M.L., Subers, M.H. and Kushnir, I. (1962) *Composition of American Honeyes*. Technical Bulletin 1261. US Department of Agriculture, Washington, DC, USA.
- Williams, M.L. and MacVean, C.M. (1995) Ethnococcidology: use of the giant margarodids, *Llaveia* spp. (Homoptera: Coccoidea: Margarodidae), by indigenous peoples of Mesoamerica in their culture, medicine and arts. *Israel Journal of Entomology* 29, 147–148.
- Witt, A.B., Nunda, W., Makale, F. and Reynolds, K. (2020) A preliminary analysis of the costs and benefits of the biological control agent *Dactylopius opuntiae* on *Opuntia stricta* in Laikipia County, Kenya. *BioControl* 1–9.
- Wongwad, E., Jimtaisong, A., Saewan, N. and Krisadaphong, P. (2012) Preparation of lake pigment from Thai lac dye. *International Conference on Biomedical Engineering and Technology* 34, 73–78
- Yen, A., Flavel, M., Bilney, C., Brown, L., Butler, S. et al. (2016) The bush coconut (scale insect gall) as food at Kiwirrkurra, Western Australia. *Journal of Insects as Food and Feed* 2(4), 293–299.
- Zimmermann, H.G., Moran, V.C. and Hoffmann, J.H. (2009) Invasive cactus species (Cactaceae). In: Muniappan, R., Reddy, G.V. and Raman, A. (eds) *Biological Control of Tropical Weeds Using Arthropods*. Cambridge University Press, Cambridge, UK, pp. 108–129.