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REVIEW

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The worldwide status of phasmids (Insecta: Phasmida) as pests of agriculture and forestry, with a generalised theory of phasmid outbreaks

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Abstract

Stick insects have been reported as significant phytophagous pests of agricultural and timber crops since the 1880s in North America, China, Australia and Pacific Islands. Much of the early literature comes from practical journals for farmers, and even twentieth Century reports can be problematic to locate. Unlike the plaguing Orthoptera, there has been no synthesis of the pest status of this enigmatic order of insects. This paper provides a literature synthesis of those species known to cause infestation or that are known to damage plants of economic importance; summarises historical and modern techniques for infestation management; and lists known organisms with potential for use as biological control agents. A generalised theory of outbreaks is presented and suggestions for future research efforts are made.

Keywords: Pests, Infestation, Agriculture, Forestry

Background

> *"The unexampled multiplication and destructiveness of this insect at Esperance farm is but one of the many illustrations of the fact, long since patent to all close students of economic entomology, that species normally harmless may suddenly become very injurious".* Riley [1]

Compared to their close relatives, the Orthoptera (sensu stricto) the Phasmida (=Phasmatodea, Phasmatoptera, Cheleutoptera) are not well known as agricultural or forest pests, despite sharing a number of key traits: large body size [2]; kentromorphism [3]; and having a widespread history of considerable damage to forests and crops [4]–[5]. The existence of kentromorphic (density-dependant) forms of some species may be homologous to the solitary and gregarious forms of the plaguing locusts. The fecundity of females is likely to be a significant factor in the scale of phasmid outbreaks—in most species, females lay several hundred eggs [6]. In addition, their wasteful eating habits [7] and their often rapid growth [8] means they consume a large quantity of vegetation [9]. Considerable efforts have been put into controlling the three species of Australian phasmid known to cause periodic infestation [10].

Phasmid outbreaks are occasionally still reported [11] although it appears that nothing from these outbreaks has yet reached the scientific literature. This work compiles the current knowledge on phasmid outbreaks and those species known to threaten economically important forests or crops, along with what little is currently known on methods for biological control. It is hoped that such a work will allow future authors to more easily place phasmid outbreaks in a worldwide scientific context and encourage their reporting in the literature, as well as providing a concise background to the importance of studying species that either parasitise or predate these insects.

This introduction provides a high-level overview of what is currently known about phasmid biology

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relating to their pest status. This is followed by individual accounts of pest species, and new conclusions on what causes phasmid outbreaks.

Aspects of phasmid biology potentially relevant to pest status

Kentromorphism

Density-dependent polymorphism (kentromorphism) is well studied in the members of the Acrididae (Orthoptera) colloquially known as 'locusts'. Perhaps the best known example of kentromorphism is the two phases of *Locusta migratoria* [12]. In *L. migratoria,* the kentromorphic changes are both morphological and behavioural, creating the cryptic solitary phase and gregarious swarming phase of this species (it should be noted that intermediate forms do exist). Key [3] provides evidence of kentromorphic phases in three species of Australian phasmid known to be pests: *Didymuria violescens, Podacanthus wilkinson*, and *Ctenomorphodes tessulatus* although there is no noticeable change in activity pattern and no obvious tendency to gregariousness [13]. The solitary phases are heavily camouflaged, while the gregarious phases have aposematic colouration.

Fecundity

Phasmids generally lay a large number of eggs, so a high mortality of the egg and nymphal stages is expected. Indeed, many new phasmid hobbyists find themselves overrun after a single generation. While a number of generalist and insectivore predators attack phasmids, there are a number of phasmid egg specialist parasitoids in both the Diptera and Hymenoptera.

Foodplant choice

In general, the diet of phasmids can be considered to be polyphagous, with many species not having a unique host plant, or being capable of switching to alternative hosts if the favoured host is unavailable [14]. Blüthgen and Metzner [15] show a relationship between the age of leaf favoured and the degree of polyphagy of the phasmid, with more host-specific phasmids favouring younger leaves and vice versa. Campbell [7] agrees with this result describing host-plant preference within the genus *Eucalyptus* for species that feed on young foliage.

Experiences of rearing phasmids in captivity [16] and with invasive species [17] show many species are highly polyphagous.

Damage to crops

Campbell [7] reports that the Australian species *Didymuria violescens* and *Podacanthus wilkinsoni* exhibit strong negative geotaxis from the first nymphal stage—climbing trees and feeding on the growing tips of *Eucalyptus.* Prathapan et al. [18] report similar findings in India of *Sipyloidea stigmata* feeding on the terminal shoots of *Piper nigrum*. The damage caused is increased in the words of Campbell by "the insects' habit of biting through the leaf near the petiole, resulting in the excision of a large part of the leaf blade. An insect may fall with the excised portion of the leaf, which it then abandons and climbs to another branchlet where it resumes feeding".

Shepherd [19] showed that severe defoliation of *Eucalyptus delegatensis* by *Didymuria violescens* leads to significant mortality and decreased rate of increase in trunk diameter of this timber tree. Mazanec [20] showed that trunk diameter growth is decreased by moderate defoliation. Long-term effects of repeated defoliation (many phasmids have a 2-year cycle of high population density) were shown to cause high mortality and decrease in trunk diameter [21]. Subsequently, Mazanec [22] showed even a light defoliation caused significant reduction of diameter growth for two growing seasons. These findings led Readshaw and Mazanec [23] to show for timber crops that the history of outbreaks may be studied using tree rings.

Table 1 provides a list covering the species attacked by phasmids during outbreaks, as well as plants of economic importance known to be attacked by phasmids. Table 2 provides a geographic breakdown of phasmid infestations.

Infestation vs outbreak

The terminology of pest levels of phasmid varies between authors. In this work, outbreaks are considered to be a sudden increase in phasmid population, as exemplified by *Diapheromera femorata* in the USA and *Didymuria violescens* in Australia. Species which maintain fairly constant population densities that have economically important effects on crops or timber are considered to be an infestation.

Control of pest phasmids

Abiotic factors affecting phasmids in the wild

For species not capable of flight, the slow movement of the adults limits the spread of an infestation. The maximum rate of spread of *Diapheromera femorata* during infestation was 1/8th of a mile per year [5]. This minimal spread plus natural barriers contains the infestations, and also makes treatment much easier than it would otherwise be. Indeed, Butler [24] commented that the "extremely local character of the infestation was a curious feature". Although in this case the insects did begin to cross a road so that "every passing carriage or motor crushed them by hundreds".

O'Connor [25] suggests similar localisation in infestations of *Graeffea crouanii* on coconut in Tonga, "Normally, heavy attack by the stick insect begins in a small,

Table 1 Plants of economic importance attacked by Phasmids

Plant family	Plant species	Species	Locality	References
Anacardiaceae	*Mangifera indica*	*Trachyaretaon echinatus*	Philippines	[106]
		Pharnacia magdiwang	Philippines	[106]
Araceae	*Xanthosoma sagittifolia*	*Eubulides taylori*	Philippines	[106]
Arecaceae	*Cocos nucifera*	*Graffea crouanii*	Fiji	[46, 95]
			Tonga	[25]
			Samoa (Upolu Island)	[93]
			Micronesia: Pohnpei; American Samoa	[133]
			Pacific Islands: Caroline; Marquesas; Vanuatu; New Caledonia	[134]
		Acanthograeffea denticulata	Micronesia	[133]
		Acanthograefeea modesta	Micronesia: Chuuk	[133]
		Graeffea minor	Samoa	[130]
		Graeffea lifuensis	Loyalty Islands	[102]
		Ophicrania leveri	Solomon Islands	[26]
		Hermarchus pythonius	Fiji	[95]
		Graeffea seychellensis (check PSF)	Seychelles	[102]
		Graeffea liuensis	Loyalty Islands	[102]
	"Oil palm"	*Eurycantha insularis*	Papua New Guinea Northern (Oro) Province	[114]
		Eurycantha calcarata	Papua New Guinea West New Britain	[112]
Burseraceae	*Canarium ovatum*	*Pharnacia ponderosa*	Philippines	[106]
Cannabaceae	*Celtis* sp.	*Diapheromera femorata*	USA: Wisconsin	[74]
Casuarinaceae	*Casuarina equisetifolia*	*Phasmotaenia elongata*	Philippines	[106]
Combretaceae	*Terminalia microcarpa*	*Pharnacia ponderosa*	Philippines	[106]
Cupressaceae	*Cuprous funebris*	*Baculonistria alba*	China: Sichuan	[117]
			China: Yangtze River, Three Gorges Area Chongqing	Guowei [115]
Euphorbiaceae	*Alueites fordii*	*Baculonistria alba*	China: Sichuan	[117]
	Sapium sebiferum	*Baculonistria alba*	China: Sichuan	[117]
Fabaceae	*Robinia pseudoacacia*	*Diapheromera femorata*	USA: Wisconsin	[74]
			USA: New York	[66]
Fagaceae	*Castanopsis fissa*	*Micadina yingdensis*	China: Guangdong	[119]
	Castanopsis cuspidata Castanopsis hicklii	Sinophasma maculicruralis and Sinophasma pseudomirabile	China: Guangxi Region: Bobai County	[4]
	Cyclobalanopsis sp.	*Baculonistria alba*	China: Sichuan	[117]
	Quercus liaotungensis	*Ramulus chongzinense*	China: Gansu Province: Chingxin and Huating Counties	[120]
	Carpinus cordata	*Ramulus chingzinense*	China: Gansu Province: Chingxin and Huating Counties	[120]
	Fagus sp.	*Ramulus pingliense*	China: Gansu Province: Wenxian County	[4]
Juglandaceae	*Platycarya strobilacea*	*Baculonistria alba*	China: Sichuan	[117]
	Platycarya orientalis	*Baculoinstria alba*	China: Sichuan	[117]
Myrtaceae	*Eucalyptus* spp. Various species are valuable timber trees (Rentz 1996)	*Didymuria violescens*	Australia: New South Wales, Victoria	[7, 27]
		Podacanthus wilkinsoni	Australia	[7]
	Psidium guajava	*Trachyaretaon echinatus*	Philippines	[106]
		Rhamphosipyloidea philippa	Philippines	[106]
		Pharnacia magdiwang	Philippines	[106]
		Pharnacia ponderosa	Philippines	[106]

Table 1 continued

Plant family	Plant species	Species	Locality	References
Pandanaceae	*Pandanus tectorius*	*Graffea crouanii*	Micronesia: Tonga	[25]
	Pandanus sp.	*Megacrania batesi* (?)	Philippines: Capiz Province	[106]
		Acanthograeffea denticulata	Micronesia: Marianas	[133]
Pinaceae	*Pinus patula*	*Libethroidea inusitata*	Colombia	[126]
Piperaceae	*Piper nigrum*	*Sipyloidea stigmata*	India: Western Ghats	[18]
Poaceae	*Miscanthus floridulus*	*Graffea crouanii*	Fiji	[97]
	Zea mays	*Baculonistria alba*	China: Sichuan	[117]
Rosaceae	*Prunus cerasus*	*Diapheromera femorata*	USA: West Virginia	[44]
	Prunus domestica	*Ramulus pingliense*	China: Gansu Province: Wenxian County	[4]
Rubiaceae	*Gardenia jasminoides*	*Mnesilochus mindanaense*	Philippines	[106]
Salicaceae	*Salix heilophilia*	*Baculonistria alba*	China: Sichuan	[117]
Sapotaceae	*Palaquium* sp. (?)	*Lonchodes brevipes*	Malay Peninsular	[135]
Solanaceae	*Solanum tuberosum*	*Baculonistria alba*	China: Sichuan	[117]

Question marks indicate potential ambiguities that are discussed in the text in the case of Phasmid species. In the case of plant species they are the likely scientific name based on vernacular names given in the reference

localized area". This observation was confirmed by Paine [26]: "Outbreaks seem to occur on certain islands, in certain situations, and not always very frequently, so that while over the whole range of this insect the loss of copra [the dried kernel of the coconut used to extract oil] resulting from its ravages is inconsiderable, losses to individual planters and village communities can be serious". This slow spread is also reported for *Didymuria violescens* outbreaks in Australia [27].

Butler [24] recorded the males of *Diapheromera femorata* spreading faster than females in the United States, and opined this was due to "greater sluggishness". This can be attributed to the greater bulk of a gravid female (both sexes of this species are apterous). The proportion of females at a distance from the focus of an infestation increased throughout the year.

Craighead [28] reports that environmental conditions may also reduce the level of infestation by *Diapheromera femorata*, "Under dry conditions many of the young fail to extricate themselves completely from the egg capsule and die". The source of this is likely to be the work of Severin and Severin [29]. This is likely to be true of many temperate species that have a springtime emergence.

Predators

Bragg [30] showed that ladybirds (Coleoptera: Coccinellidae) ate young phasmids in culture conditions although there appear to be no reports of this from the wild.

Several records have been made of phasmids being predated by spiders. Robinson and Robinson [31] report a species of *Eurycnema* being predated by *Nephila maculata*. Robinson and Lubin [32] found several phasmid nymphs in the web of a species of *Fecenia*. Bragg [33] gives an account of the phasmid *Asceles margaritatus* being predated by a spider in Kinabalu National Park, Sabah. Laboratory tests confirm that phasmids are palatable to spiders [34]. The jumping spider *Ascyltus pterygotes* (Salticidae) was reported attacking the stick insect *Graeffea crounaii* by Rapp [35].

Other pests of phasmids include lizards [36]. In the old Primates gallery at the Natural History Museum, London (UK) there was a photo of a slow loris (*Nycticebus coucang*) feeding on a species of *Eurycnema* (date and location of photograph unknown).

Human usage of phasmids

Bragg [37] gives an account of the eggs of phasmids (*Haaniella*) being eaten by the Bideyuh tribe in Sarawak. Bragg [38] also reports the Iban tribe in Sarawak eat *Haaniella echinata*, not just the eggs. Stone [39] reports *Extatosoma tiaratum* is eaten by natives of Papua New Guinea (although as *E. tiaratum* is not found in this region the author probably refers to *Eurycantha* or *Extatosoma popa*). The insects eat the leaves of the sago palm, which are used as a thatching material. When the leaves are collected, any phasmids found are skewered on pointed sticks pushed from the abdomen up through the head. The insects are then spit roasted on an open fire until the legs fall off.

The hind legs of *Eurycantha latro* Redtenbacher, 1908 have been used as fishing hooks on Goodenough Island [40].

Non-biological control

O'Connor [25] recommends the banding of coconut palms as a defence against *Graeffea crouanii*, and smoking down the adult insects from the canopy. As bands were

Table 2 Economically important plants attacked by phasmids (by geography)

Continent	Country	Locality	Host plant	Species	References
Asia	China	Guangdong Province	*Castanopsis fissa*	*Micadina yingdensis*	[119]
		Jilin Province	Unknown	*Ramulus minutidentatus*	[123]
			Tilia mandshurica	*Ramulus minutidentatus*	[136]
		Shaanxi Province	Various	*Ramulus pingliense*	[9]
		Gansu Province	*Fagus* sp. *Rosa domestica*	*Ramulus pingliense*	[4]
		Guangxi Autonomous Region	Castanopsis cuspidata Castanopsis hicklii	*Sinophasma maculicruralis*, Sinophasma pseudomirabile	[4]
		Hubei Province	Orange orchards (241 hectares, loss of over 2100 tons of fruit)	Unknown	[115]
	India	Thenmala, Kerala, Western Ghats	Black Pepper *Piper nigrum*	*Sipyloidea stigmata*	[18]
	Malay Peninsular		"Gutta-percha"	*Lonchodes brevipes*	[135]
	Philippines		Gabing San Fernando *Xanthosoma sagittifolia*	*Eubulides taylori*	[106]
			Mango *Mangifera indica*	*Trachyaretaon echinatus* Pharnacia magdiwang	[106]
			Guava Psidium guajava	Trachyaretaon echinatus *Rhamphosipyloidea philippa* Pharnacia magdiwang	[106]
			Pandan *Pandanus* sp.	*Megacrania batesi* (?)	[106]
			Rosal *Gardenia jasminoides*	*Mnesilochus mindanaense*	[106]
			Pili *Canarium ovatum*	*Pharnacia ponderosa*	[106]
			Kalumpit *Terminalia microcarpa*	*Pharnacia ponderosa*	[106]
			Agoho *Casuarina equisetifolia*	*Phasmotaenia elongata*	[106]
	Solomon Islands		Coconut *Cocos nucifera*	*Ophicrania leveri*	[26]
North America	USA	*Wisconsin*	Montmorency sour cherry *Prunus cerasus*	*Diapheromera femorata*	[44]
		West Virginia	Black Locust *Robinia pseudoacacia* Hackberry *Celtis* sp.	*Diapheromera femorata*	[74]
		New York	Black, red and chestnut-oaks	*Diapheromera femorata*	[65]
		New York	Locust	*Diapheromera femorata*	[66]
		Michigan	Oaks	Diapheromera femorata	[70]
		Iowa	Hazel, oak	Diapheromera femorata	[24]
South America	Colombia	El Tambo	*Pinis patula*	*Libethroidea inusitata*	126
Oceania	Australia	South-East	*Eucalyptus* spp.	*Didymuria violescens*	[7]
			Eucalyptus spp.	*Podacanthus wilkinsoni*	[7]
		New South Wales		*Anchiale austrotesselata*	[48]
		near Brisbane		*Anchiale austrotessulata*	[88]
	Cook Islands	*Atiu*	Coconut *Cocos nucifera*	*Graeffea crouanii*	[47]
	Fiji		Coconut *Cocos nucifera*	*Graeffea crouanii*	[46, 94, 95]
				Hermarchus pythonius	[95]
			Miscanthus floridulus	*Graeffea crouanii*	[97]
	Micronesia	*Tonga*	*Pandanus tectorius*	*Graffea crouanii*	[25]

Table 2 continued

Continent	Country	Locality	Host plant	Species	References
	Papua New Guinea	Northern (Oro) Province, Higaturu	"Oil palm"	*Eurycantha insularis*	[114]
		Northern (Oro) Province, Saiho Division (Tunana)			
		West New Britain, Malilimi Plantation (New Britain Palm Oil)	"Oil palm"	*Eurycantha calcarata*	[112]
	Samoa		*Cocos nucifera*	*Graeffea minor*	[130]
	Samoa		*Cocos nucifera*	*Graeffea crouanii*	[93]

Check all host plant reports are in here and vice versa

Question mark indicates potential ambiguities that are discussed in the text in the case of Phasmid species. In the case of plant species they are the likely scientific name based on vernacular names given in the reference

not commercial available at the time on Tonga, instructions are given for making them, "two to three parts by weight of resin are mixed with one by weight of linseed, coconut or castor oil, the oil being heated and the resin added gradually until it is all dissolved. To this may be added one ounce of technical DDT per pound of banding material". The banding material so made is allowed to cool and painted by hand around the trunks of the palms.

The use of systemic insecticide (Monocrotophos) injected into the trunks of coconut palms has been demonstrated to be an effective method for controlling *Graeffea crouanii* [41, 42]. Aerial application of Malathion was considered effective in controlling an outbreak of *Didymuria violescens* [43].

The migration of insects from neighbouring habitats onto crops [44] means that a repeated theme in successful control of phasmid outbreaks for wingless species is the creation of barriers between host plants. Wilson [45] reports on *Diapheromera femorata* outbreaks in the United States: "Because the walkingstick does not fly, infestations are often localized and expand only a few hundred yards during the season. A stream or road separating parts of a stand often retards the spread of the insect. One side of such barriers can have completely denuded trees while the other might have little or no injury". Similar advice, clearing the areas between coconut trees, is given to farmers controlling *Graffea crouanii* on Fiji [46] and Atui [47].

Hadlington and Hoschke [48] and Campbell [7] show that bush fires dramatically curbed the extent of a phasmid outbreak in Australia. It has been suggested [49] that phasmid eggs may survive forest fires, although in reduced numbers, so there is still potential for infestations to recur. Burning of forest may also cause a short-term spike in the phasmid density [48].

'Smoking' is the technique of burning palm fronds underneath infested palms to disturb the insects and cause them to fall to the ground. Reports from collectors suggest a similar effect from cigarette smoke [50] and Australian wildfires [51].

Potential for biological control

The Hymenopteran subfamilies Loboscelidiinae and Amiseginae (Chrysididae) are obligate egg parasitoids of phasmids [52]. Several hundred species are known from the American, African and Oriental regions. Later works [53] show that mimicking seeds may cause the eggs to be attractive to ants, encouraging them to take them to their nests which offer some protection from egg parasitoids. Very few associations are known between parasitoid and host [54], and it is not known how host-specific individual parasitoid species are. Severin [55] discusses the resemblance of the eggs of *Diapheromera femorata* to seeds, but does not conclude that this resemblance protects them from parasitoids.

Phasmophaga antennalis (Diptera: Tachinidae) appears to be a phasmid specialist feeding on several species across the United States [56, 57]. It feeds on adults, and parasitisation may be indicated by a scar on the phasmids abdomen. *Perilampus hyalinus* (Hymenoptera: Perilampidae) is a hyperparasitoid of phasmids via *P. antennalis* [57].

The adaptation of several species of phasmid to develop capitula [58] on their eggs which are attractive to ants could be an evolutionary response to the predation and parasitisation of their eggs. O'Connor [25] lists the ant *Tapinoma melanocephalum* as devouring the eggs of *Graeffea crouanii*, but it is possible the ants took the eggs to their nest. Compton and Ware [59] show that the capitula of phasmid eggs can perform the same function as the elaiosome of seeds—encouraging them to be taken, dispersed and protected by ants.

Studies by Campbell [7] looking for eggs parasitised by Cleptid wasps found that for the plaguing species *Didymuria violescens* and *Podacanthus wilkinsoni*, the level of parasitism depended on the dominant vegetation with *Eucalyptus delegatensis* resulting in lower levels of parasitism than *Eucalyptus dalrympleana*—although neither showed signs of being promising in controlling outbreaks.

The lethal parasitisation of several Bornean phasmids by mermithid larvae was demonstrated by Bragg [60]. Although the species of mermithid was not identified, it is believed the same species attacked various species of collected. Yeates and Buckley [61] also describe records of mermithid nematodes attacking phasmids.

Table 3 provides an overview of potential biological control agents.

Monitoring

Campbell [7] gives two methods for monitoring phasmids in outbreak proportions. The first is to count eggs in a sample area of soil under the canopy and scale up to an acre taking account of the proportion of canopy cover (adult insects of the species studied are canopy dwellers). The second method (to estimate numbers of nymphs and adults) was to catch the frass using suspended traps and dry it to constant mass before calculating the frass fall per hour. Both methods were deemed satisfactory for estimating populations.

A solved problem?

While phasmid outbreaks can be efficiently controlled using injected or aerially applied insecticides, a deeper understanding of the causes of phasmid outbreaks (Table 4) will allow for more targeted control and mitigation, perhaps without resorting to the use of insecticides. The problem faced is similar to that faced in controlling the pest Orthoptera [62].

Accounts of phasmids attacking economically important plants

Species where the only literature record is a foodplant association are not discussed further, details are given in the preceding tables. A partial list of synonyms is given—synonyms not used in publications in the References are ignored. Taxonomic names have been checked and updated using the Phasmida SpeciesFile [63].

Species accounts

***Diapheromera femorata* (Say, 1824)**

= *Spectrum femoratum* Say, 1824 [64]

This species is widespread in the United States east of the Rocky Mountains [28], but rarely in levels likely to cause concern.

Riley [1] reports an unusual number of this species feeding on rose bushes and other shrubs while he was lecturing at Cornell University (Ithaca, NY, USA). Riley's report goes on to describe the earliest documented infestations of this species, also in New York State, starting in 1874. Reproductions from two letters ([65, 66]) to the *American Agriculturalist* are given in [67].

Ferrisborough (1874) reports a case of the insects attacking locust (*Robinia pseudoacacia*) used to "furnish the farm with posts and stakes" in New York State [68]. The insects entirely stripped the trees of their leaves every second year. Over a period of 15 years, the increasing infestation resulted in nearly all of the locust being killed, and the insects spreading to nearby native trees.

Snow's account [69] from Yates County, New York is perhaps the earliest one with which we have the most complete history of infestation. The site of the infestation was Esperance Farm [1]. The insects attacked second-growth plantations of white oak and hickory, as well as his peach orchard. The first signs of infestation were described in his report: "I noticed about August 15th, in the reservation of young timber, mostly white oak and hickory, a few trees having the appearance of being burned just enough to kill the leaves. On closer investigation I found many of these insects devouring the leaves".

The American Agriculturist [65] continues the reporting of the infestation on Snow's land. The reported case in 1874 develops until the phasmids "appeared in such numbers as to denude of their foliage … some 25 acres". After a year of relatively little damage in 1876, the infestation returned: "the trees on some 30 acres were stripped of their leaves. So thorough was the work of these insects, that from a distance the woods appeared as if a fire had gone through them". The destruction caused by the insects continued until they were stopped by frost, and resulted in many dead branches. The numbers during an infestation "are almost beyond comprehension: they cluster upon a limb or fence-rail so thickly that they pile up upon one another, and one cannot enter the wood where they are, without having numbers on his clothing".

A response to the American Agriculturalist request [66] reports a similar story from Conklin from Cumberland County, Pennsylvania. The insects had been seen on his land for 40 years, but 10 years previously (circa 1877) had reached infestation densities. "In this instance … these insects denuded a row of locust trees that formed the shelter on the northwest side of a peach orchard. For half a dozen rods from this locust row the peach trees were also stripped of their leaves".

Riley, as the Entomologist of the US Commission for Agriculture, continued his investigation [1] reporting that "the underbrush was also very effectually cleaned of its foliage". Riley continued to investigate the pest phasmid, calculating that captive females were capable of laying "upwards of a hundred" eggs.

Butler [24] records an infestation in predominantly oak woodland in the area around Peterson, Iowa (USA). They spread from the forest to an orchard where "they infested particularly one tree of early apples, devouring nearly all the leaves; on a single twig six inches in length I counted sixteen clustered together and they were equally numerous over the entire tree". Butler goes on to describe the effect of

Table 3 Potential biological control agents

Higher class.	Species	Phasmid	Notes	References
Insecta Diptera Tachinidae	*Biomya genalis*	*Diapheromera femorata* Nymphs		[45]
	Phasmophaga anetannalis	*Diapheromera femorata* Nymphs	Phasmid consumes egg laid on foliage	[45]
	Mycteromyiella laetifica	*Graeffea leveri* nymphs/adults	Also a species of *Megacrania* is parasitised	[26, 137]
	Mycteromyiella phasmatophaga	*Graeffea leveri* Nymphs/adults	Probably not usual host	[26, 137]
	Thrixion halidayanum	*Leptynia hispanica*		[138, 139]
	Euhallidaya sverinii	*Diapheromera femora* Eggs		[140]
Insecta Hymenoptera Chrysididae	*Mesitiopterus kahlii*	*Diapheromera femorata* Eggs	Never recovered in sufficient number to be considered an important means of control	[45]
	Cladobethylus insularis	*Eurycantha insularis* Eggs		[114]
	Exova tunana	*Eurycantha insularis* Eggs		[114]
Cleptidae	*Myrmecomimesis* spp.	*Didymuria violescens* Egg *Podacanthus wilkinsoni* Egg		[7]
	Myrmecomimesis sp.	Anchiale austotesselata		[48]
		Ctenomorphodes tessulatus egg	305 emerged from a field collected sample of 11,694	[88]
	Myrmecomimesis nigripedicel	Ctenomorphodes tessulatus Egg	At much lower density than M. striata	[88]
	Myrmecomimesis rubrifemur	Graeffea crouanii	In Australia attacks *Anchiale austrotesselata*. Unsuccessfully introduced to Fiji.	[99]
	Loboscelidia sp.	Anchiale austrotesselata		[48]
	Loboscelidia sp.	Ctenomorphodes tessulatus	Only 6 from sample of 11,694 eggs	[88]
Eupelmidae	Paranastatus nigricutellatus Eady, 1956 Paranastatus verticalis Eady, 1956	Graffea crouanii eggs	Controls up to 50 % of eggs. Seems effective on Fiji but not western Samoa [100]	[46, 101, 141]
	Anastatus (Anastatus) eurycanthae Gibson, 2012	*Eurycantha calcarata* eggs		[112]
	Anastatus gratidiae Risbec, 1951	*Gratidia* sp.		[142]
Formicidae	Tapinoma melanocephalum	*Graeffea crouanii* Eggs		[25, 143]
	Pheidole megacephala	*Graeffea crouanii* Eggs		[143]
Mecoptera Bittacidae	Harpobittacus sp.	Anchiale austrotesselata		[48]
Aves	*Gymnorhina tibicen*	Graeffea crouanii		Paine [26] from Hinckley (unpublished)
	Acridotheres tristis	Graeffea crouanii		[47]
Mammalia	*Rattus exulans*	Graeffea crouanii All instars and eggs		[144]
	Rattus rattus	Graeffea crouanii all instars and eggs		[143]

Table 3 continued

Higher class.	Species	Phasmid	Notes	References
Fungus Deuteromycetes Hyohomycetaceae	Beauveria bassiana	Unknown	Used in China to control infesting phasmids	[115]

This table shows host-specific parasites and specific examples of wild predators. Laboratory studies of generalist predators (e.g. [145]) and non-economically important generalist insectivores (e.g. Hamilton and Pollack 1961) are not included

the infestation on his family, "The woods had become forbidden ground to us; if one was sufficiently brave to start through them, the walking-sticks fell to the ground from every tree in such numbers to sound like hail".

The largest reported outbreak of *D. femorata* is from Ogemaw County, Michigan (USA), where several smaller infestations merged in the autumn of 1936 to cover approximately 2500 acres [70]. All of the infestations were in second-growth stands of oak. The insects were first discovered in the area in 1921 and first caused major defoliation in 1928. During 1931, no adults were found but the density of eggs in leaf litter was measured at 36.5 per square foot. In 1932, the largest Michigan report was 1600 acres south of Grayling. The same infestation was mapped in 1936 and covered upwards of 1900 acres. Graham reports that "without exception these outbreaks are located in the same type of forest… these hills were formerly covered, for the most part, with a forest of white and Norway pine mixed with apsen, oak, cherry, and, in places, paper birch". The prevailing forestry management of the time, following logging and repeated burning, allowed mature oaks to dominate and caused the phasmid infestation. The rate of defoliation observed by Graham shows that "trees may be completely stripped by the middle of July, but usually this stage occurs much later". Graham also notes that the large infestations seem to be created by the merging of smaller ones, commenting that "the original foci are sometimes easily located by an examination of the condition of the trees, especially when years of infestation have been followed by the death of the favourite host trees".

Many subsequent authors state that this species is capable of causing infestations within the continental United States and giving the areas more likely to have infestations as the "Lake States" [71] or south of a line drawn between southern Nebraska and Delaware [45, 72] but few detailed reports can be traced in the literature. Wilson [45] while not giving details of individual infestations does detail the effect on trees infested with this species "The entire leaf blade, except the basal parts of the stout veins, is consumed. During heavy outbreaks large stands are often completely denuded. Trees may be defoliated two times in the same season in some outbreaks. Three or four heavy infestations are usually sufficient to cause some branch mortality". Helfer [73] describes walking through an infested area; "Eggs and faecal pellets are dropped to the ground in great numbers, producing a pattering sound, like rain, accompanied by a peculiar seething sound of thousands of jaws chewing the leaves". Over 100 eggs per square foot of ground have been recorded in severe infestations [45].

Oatman [44] describes a 1959 request from a Door County, Wisconsin cherry grower asking for advice on chemical control of this species. Interestingly, their main concern was not damage to the crop but the unwillingness of contracted Jamaican labour to work in infested areas due to superstitions relating to the insects. The infestation increased through 1960 until in 1961, "within seconds after a person stopped under or near a tree, walkingsticks dropped onto and crawled upon his body so that even to an experienced entomologist it was an uncomfortable, creepy feeling".

An 'Event Notification Report' from the Smithsonian Institution's Centre for Short-Lived Phenomena (25 September 1973; [74]) details: "Millions of walking sticks, *Diapheromera femorata*, have infested an area in the Knobley Mountains about 3–4 miles from Keyser, West Virginia. When the infestation was first observed on 7 September, five acres (0.04 km^2) of black locust and hackberry trees had been affected. At present 10 acres of these trees have been completely defoliated and the trees and ground are covered with these insects".

Natural control might include the wasp *Mesitiopterus kahliix* which has been recovered from eggs of this species [45]. Wilson also reports two parasitic flies that attack the nymphs, *Biomya genalis* and *Phasmophaga antennalis*—the later being interesting as the phasmid is parasitised by eating eggs the fly has laid on the foliage. Wilson again reports that birds including crows and robins concentrated in heavily infested areas and feed on the insects. Riley [1] reports that turkeys and chickens feed upon nymphs while they remain close to the ground, and that various species of Heteroptera feed on nymphs and adults (*Arma spinosa*, *Poisus cynicus* and *Acholla multispinosa*). Graham [70] reports robins and crows feeding on the insects with "large flocks of these birds … observed day after day on each of the major infestations. Although the birds were numerous, the insects were so much more so that the effect on the walking-stick population seemed insignificant".

Table 4 Comparison of phasmid species known to outbreak

Species	Host plants	Eggs laid	Body length	Life cycle
Diapheromera femorata	Young nymphs on low growing plants: beaked hazel, rose, juneberry, sweetfern, blueberry, strawberry. older nymphs/adults: black oaks, basswood, wild cherry and less preferred: quaking aspen, paper birch, hickory, locust, apple, chestnut [45].	150 3 per day [45]	2.5″–3.5″ [45]	Eggs hatch May/June, Adulthood late July/August, mating a week later, egg lying until October. In north of range eggs double diapause and there are two broods, further south eggs hatch year following oviposition [45]
Didymuria violescens	Various species of *Eucalyptus* (see species report)	200 1–5 per day [27] 357 (mated) 401 (virgin) ([146] laboratory)	Approx 3″ [27]	Egg hatches in spring (October–December) after 6–18 month diapause. Five nymphal stages from 1 to 3 weeks each [27]
Podacanthus wilkinsoni	Various species of *Eucalyptus*		120 mm [85]	Eggs remain dormant until spring, or spring the following year. Insects mature the same year they emerge from the egg

The first recommended chemical treatment was Paris Green Water [copper(II) acetate triarsenite in aqueous solution] [1], for treatment of young nymphs near ground level. Riley's preferred method was destruction of eggs, either by digging and turning them into the ground, or by burning over the dead leaves during winter. Graham [70] views replanting of native trees as the preferred method of control, and advises against burning: "It should be remembered … that forest fires have been responsible for setting the stage for walking-stick outbreaks by killing out all tree growth except that of the oaks". The use of calcium arsenate, either by spraying or dusting is also recommended "where the presence of the insects becomes objectionable". Wilson [45] recommended the use of DDT application in the later half of July for control, or a barrier strip 100ft wide sprayed with lead arsenate at 4 pounds per 100 gallons of water per acre to prevent infestation from neighbouring areas. A revised edition of the publication [72] states "As this publication goes to press, there are no chemical insecticides registered for use in control of the walkingstick".

Rivers et al. [75] showed that the venom of *Nasonia vitripennis* (Hymenoptera: Pteromalidae) was tolerated by adults of *Diapheromera femorata*.

Didymuria violescens **(Leach, 1814)**

= *Phasma violescens* Leach, 1814

This Australian species feeds on various species of Eucalyptus, preferring *E. robertsoni*, *Eucalyptus radiata*, *E. dives*, *E. dalrympleana*, *E. maculosa*, *E. viminalis* and *E. bicostata*. Other eucalypts are less favoured but also used as hosts, including the economically valuable alliances where *E. delegatensis* (alpine ash) or *E. regnans* (mountain ash) dominate [27]. The species can be univoltine or semi-voltine depending on environmental conditions, achieved through one of two stages of diapause in the egg stage [76, 77].

Outbreaks have been recorded in State Forests around Nundle (Nundle, Hanging Rock, Tomalla, Nowendoc and Tuggolo State Forests), Jenolan (Jenolan and Konangaroo State Forests) and the southern highlands of New South Wales (Bago State Forest) and Victoria (Mt Bogong, Mt Stabley, Mt Pinnibar).

The outbreak in the Nundle area started in the summer of 1949–50. The outbreak continued 2 years later and in the summer of 1951–1952 extensive defoliation occurred, followed by a sudden, but temporary, reduction in phasmid numbers over extensive areas. In the Tuggolo State Forest, extensive defoliation occurred in the 1955–1956 season and most of the remaining forested area (except for areas burnt late in 1957) in the 1957–1958 season. In the Jenolan area, large numbers of trees were killed over thousand of acres [7]. A widespread fire in the summer of 1957 in this area also destroyed large numbers of phasmids.

In the Nundle and Jenolan areas, two species of phasmid, *D. violescens* and *P. wilkinsoni*, occur in plague numbers, though the latter is probably responsible for the greater part of the defoliation. In the southern highlands area, violescens alone is involved. Adults of *P. wilkinsoni* are most abundant during the even numbered years and those of *D. violescens* during the odd numbered years.

Population densities of *D. violescens* were noticed to be higher than usual in the areas infested by *Podacanthus wilkinsoni* from 1947 to 1948 onwards. The dating of the first major outbreak was confirmed using tree ring data [23] to occur in 1951 rather than in 1953 as stated by previous authors. This outbreak occurred outside of the range of *Podacanthus wilkinsoni*. Infestations continued every year until 1962–1963 [27]. No defoliation was reported by 1967 [23].

Newman and Endacott [43] report on the treatment of an infestation in the catchment area of the Kiewa Hydroelectric scheme, Victoria. Defoliation by phasmids was first noted in this area in 1956–1957 with subsequent infestation levels in 1958–59. Treatment was required as death of the forest in the catchment area could reduce the stability of soil on mountain slopes which are stabilised by tree roots, increase the risk of forest fire and 'draw adverse comment from a community which is making increasing use of the area for recreation'. Control was with Malathion with 4.5 oz of active ingredient in 3 gallons of light diesel fuel per acre. Delivery was by helicopter. Spraying was at a time after the majority of the insects had hatched and before oviposition to reduce negative effects on the Hymenopteran egg parasites of the phasmids. The frass-fall method used by Campbell [7] was used to determine the effectiveness of treatment, which was determined to be highly successful.

The pattern of infestation [27] does not involve long-range dispersal. In the initial stages, the insects increase in density, sporadically getting to densities that cause severe defoliation in small groups of trees, generally at elevations of 2000–4000 ft on ridge tops and Western facing slopes. Two years later the next generation, the areas of severe infestation expand to several square miles, and occasionally joining. In following generations, areas around the original epicentres may be completely defoliated. During the decline of an outbreak, severe defoliation becomes diffuse, then patchy until only small pockets of high phasmid density are left, which generally fail to persist. The decline of outbreaks is demonstrated by Readshaw to be due to an increased predation and parasitisation of the egg stage as outbreaks progress. The lack of Chrysid (Hymenoptera) parasites in the alpine conditions where outbreaks occur is postulated to be a reason why these populations of *D. violescens* are prone to outbreak.

In 1963, *Didymuria violescens* defoliated 650 square miles of *Eucalyptus* forest, an event deemed serious not only for direct negative effects of tree growth and survival but also the potential threat this might cause to the stability and efficiency of important water catchments [27, 43].

Although present in mountain and coastal forest throughout New South Wales and Victoria, large outbreaks are confined to "the inland slopes of the Great Dividing Range, between Canberra, A.C.T., and west Gippsland, Victoria. Typically, outbreaks occur at elevations between 2000 and 4000 ft in forests with tall trees, an almost continuous canopy, and a shrubby understory containing a sprinkling of sapling eucalypts. The forest floor usually comprises a loosely packed layer of undecomposed litter and varying amounts of grass and herbaceous vegetation" [20]. In the areas where this species reaches plague proportions, this species has a two-yearly life cycle apart from populations in the Mt Warning area [7]. In some stands, 80 % of trees were killed after two severe defoliations in alternate years [21].

A further outbreak [78] at the Corin Dam (nera Canberra) was initially suspected to be fire damage but was revealed to be an outbreak of this species in 1988. It was likely to have started in the wet and cool summer of 1983–1984. Very small nymphs travelling on air currents are considered as a means of an outbreak spreading.

Males of this species fly sporadically from elevated positions and can travel a significant distance over their lifetime. Females do not fly but can glide short distances. This can lead to differential dispersal between males and females [7]. The spread of this species is thus slow, and might be the cause of outbreaks occurring predominantly in areas where the tree canopy is largely continuous.

Some natural control may be achieved by *Indomyrmex* ants and the birds *Colluricincla harmonica* and *Cinclosoma punctatum* [27]. The bird *Strepera graculina* is considered to be an important predator of this species [79].

***Podacanthus wilkinsoni* Macleay, 1882** [80]

= *Didymuria violescens* nymph sensu Froggatt (1923)*

*Froggatt confuses Didymuria violescens as the nymphs of *Podacanthus wilkinsoni*. See [7].

The first report of this species causing infestation is from Mr C. S. Wilkinson (in [80]) and is the first report of pest phasmids in Australia (nr Binda Caves, Westmoreland). Macleay speculates that phasmids may be the cause for other large areas of eucalypt deaths in the vicinity of Australian colonies. Further reports of mass defoliation from Murphy's Creek, nr Walcha, New South Wales were made by Oliff [81] and Froggatt [82] states that continued every alternate year. The common name of 'Ringbarker' comes from the similar effect on trees as ringbarking (removing a complete ring of bark around the tree to cause death—a technique used by foresters to thin woodland).

The species can be uni-voltine or semi-voltine depending on environmental conditions, achieved through one of two stages of diapause in the egg stage [76]. In the areas where this species reaches plague proportions, this species has a two-yearly lifecycle [7].

A note in the Proceedings of the Linnean Society of New South Wales [83] reports Mr Froggatt "showed a series of specimens of the gregarious phasmids *Podacanthus wilkinsoni* Macleay, showing remarkable colouration varying from deep green to bright red. There were hundreds of thousands of these stick insects crawling over the scrub about 20 miles east of Glen Innes, where these were taken in the middle of March". Whether the insects were correctly identified in this instance is unknown.

Outbreaks that began in the cool summer of 1947–1948 in New South Wales (Nundle and Jenolan) continued every second summer until 1959–1960 when the outbreak suddenly declined. Hadlington (in [84]) reports that these forests were being converted to *Pinus radiata* which is not susceptible to attack.

Campbell [7] reports a 1957 study of soil egg density of areas completely defoliated by this species estimating densities of over 1,200,000 eggs per acre. Studying the viability of these eggs suggested a maximum population of over 350,000 phasmid per acre (50,000 per acre is considered enough for serious defoliation). Severe fires in late 1957 were shown to have a dramatic effect in reducing the phasmid outbreak.

Elliott et al. [85] "has causes periodic, ever defoliation in the highland forests of south–eastern Australia. It os distributed from Northern New South Wales down to areas south west of Sydney. Several species of eucalypts are acceptable hosts and *E. radiata, E. robertsonii, E. dives, E. viminalis, E. huberiana, E. dalrympleana, E. stellulata* and *E. Pauciflora* are favoured species".

***Anchiale austrotessalata* (Brock and Hasenpusch, 2007)** [86]

= *Ctenomorphodes tessulatus* Gray, 1835 [87]

Unlike *Didymuria violescens* and *Podacanthus wilkinsoni* which have been known to reach plague densities since at least 1880, the first record of this Australian species causing infestation is in 1956 [48]. High-density populations were reported from Toonumbar, Wedding Bells, Tanban, Ingalba and Colombatti State Forests.

While many species of trees were eaten (*Syncarpia, Acacia, Casuarina*), there is preference for *Eucalyptus* species. *E. maculata* that had been completely defoliated were found adjacent to *E. microcorys* with intact crowns. The areas of forest with pest levels of phasmids consisted of *E. punctata, E. triantha, E. paniculata, E. maculata, E. gummifera, Syncarpia laurifolia*. These regions consistently had an understory of *Casuarina torulosa* and *E. microcorys* [48].

The species can be uni-voltine or semi-voltine depending on environmental conditions, achieved through one of two stages of diapause in the egg stage [76]. Laboratory studies showed females could lay up to 900 eggs over a period of 5 months [48].

Heather (1965) studied the egg parasites of this species from Slacks Creek State Forest Reserve (near Brisbane) where this species had been 'varying to plague proportions' in recent years [88]. The mortality of first instar nymphs was found to increase in dry conditions [48].

Further outbreaks in coastal Queensland between 1974 and 1976 caused extensive tree damage and some tree fatality [89, 90].

***Graeffea crouanii* (Le Guillou, 1841)**

= *Bacillus crouanii* Le Guillou, 1841 [91]

= *Graeffea coccophaga* (Newport, 1844) [92]

= *Graeffia coccophaga* incorrect subsequent spelling of genus by Hopkins [93]

= *Graeffia coccophagus* incorrect subsequent spelling by Simmonds [94]

Unlike the early reports of *Diapheromera femorata* that are in their own way poetic, the earliest reports of *Graeffea crouanii* are short and terse, perhaps due to them being reported by visiting and stationed entomologists rather than the landowners directly. Veitch and Greenwood [95] list the species "as being of some considerable importance" on the cocoanut[sic], *Cocos nucifera* on Fiji. The eggs of this species have been shown to survive floating in seawater [96] so could potentially disperse among islands naturally.

Hopkins [93] spent 2 years on Samoa working on filariasis for the London School of Hygiene and Tropical Medicine with P.A. Buxton, studying agricultural pests that came their way, admitting their "observations make no claim to completeness, they are perhaps worthy of publication in view of the scarcity of records from this group of islands". *G. crouanii* was found to be "a serious pest of coconuts in some districts, entirely stripping the leaves and leaving only the mid-ribs. They are almost entirely nocturnal in their habits and may easily be collected on the smaller trees by searching for them with a lantern at night".

Simmonds [94] reports from Fiji: "One of the periodic occurrences of damage by stick insects (*Graffea coccophagus*) was reported in May, this time from the Macuata coast".

O'Connor [25] reports an outbreak of this species on Tonga and reports additional foodplants of *Pandanus tectorius* (used as food, thatch and in the manufacture of mats and baskets) and Miscanthus japonicus (=Miscanthus floridulus, incorrectly reported as a rush—correctly reported as grass in Lever [97]—edible). The outbreak was on Fofoa island, Vavau, with the infestation covering 50 of 180 acres. Hundreds of coconut palms had been killed by the feeding activity of the phasmid and "many more were stripped, except for a few stunted and distorted central fronds, and the remainder retained about half or a third of their normal foliage". O'Connor visited in April–May 1949 at the end of the outbreak.

Paine [26] gives details of an outbreak on the island of Taveuni (Fiji group) which "began to reach serious dimensions in 1958, and by April 1959 100 acres of coconuts were affected. By the end of 1961 the outbreak had extended over 500 acres in which the older fronds were at least 50 per cent defoliated and nearly 400 palms had been killed".

This species was introduced to the island of Atiu (Cook Islands) by the ancient Polynesians. Reports from the 1800s from missionaries and visitors noted it could be extremely common and was capable of destroying groups of Coconut Palms [47]. The Common Myna bird (*Acridotheres tristis*), also introduced to the island, is an effective predator of the insect introduced to the island to control the phasmid [98]. Populations of the insect increased in response to plans enacted to first control (May 2009) then eradicate (November 2010) the Myna population. Paine (1968) lists predation from "turkeys, domestic fowl and Australian Magpie (*Gymnorhina tibicen*) will attack *Graffea* on the ground (Hinckley, unpublished) and the Mantid *Tenodera aridifolia* (Stoll) on coconut leaves (Singh, unpublished)". Singh's unpublished report to the Director of the Department of Agriculture, Fiji also states that an introduced toad, *Bufo marinus*, is not considered an effective predator.

O'Connor [25] found that the eggs of caged stick insects were devoured overnight by the "minute and rapidly moving" ant *Tapinoma melanocephalum*, although it is possible the eggs were just carried to their nest and not consumed. The Fijian Ministry of Primary Industries recommends a number of biological and mechanical methods of controlling *G. crouanii* in Fiji [46]. Recommended biological controls are the egg parasite wasps *Paranastatus nigriscutellatus* Eady, 1956 and *P. verticalis* Eady, 1956. Paine (1968) gives the level of parasitism by these species from unpublished reports from Hinckley (10 %) and Pillai (52 %).

Paine [26] also reports of an unsuccessful attempt to control this species by establishing populations of the tachinids *Mycteromyiella letifica* and *M. phasmatophaga*. One of the tachinid flies (Diptera) thought to control *Graeffea leveri*, *Mycteromyiella laetifica* on the Solomon Islands were imported to Fiji to try and control this species. 960 puparia were shipped, with half used for experiments and the remainder released on Taveuni. The fly could be reared in lab conditions but not maintained in culture [99]. No evidence was found for persistence in the wild of those released. Waterhouse and Norris [100] suggest a reason for the limited control exerted by these predators is that the maggots can feed inside and emerge from larger hosts without damaging vital organs. Similarly, the hymenopteran *Myrmecomimesis rubrifemur* from eggs of *Anchiale austrotessulata* could not be bred on this species.

Biological control is more effective when combined with using cattle, goats or sheep to clear weeds around the base of infected trees to expose eggs to sun and other predators (including poultry). Crooker [101] and Lever [102] report high levels of infestation in farms with dense ground cover in Tonga, while Singh (1981) reports plantations almost free from infestation with little ground cover. The effect of desiccation on reducing the survival of eggs was discussed by Rapp [35]. Inter-cropping with non-host plants such as *Theobroma cacao* or *Colocasia esculenta* may help reduce damage to coconuts by up to 90 %.

O'Connor [25] gives a recipe for making sticky bands using "two or three parts by weight of resin are mixed with one part by weight of linseed, coconut or castor oil, the oil being heated and the resin added gradually until it is all dissolved". The recommendation of adding DDT to the banding mixture is no longer applicable. The banding mixture is applied around the trunk of the palm to trap nymphs climbing the trunk. Debris from the floor of the plantation piled near the palms and set on fire removes insects from the coconut crown, and these too are caught on the band as they climb the tree.

Deesh, Swamy and Khan [103] summarise the problems of chemical control of this species. The problems relate to the high crown of the adult trees (circa 25 m above the ground) which makes physical application of insecticide difficult, and mist sprays can only reach heights of around 12 m. Aerial application is effective [104] but expensive [96]. Chemical control is effective when the crowns are reachable [105]. Injection of systematic insecticides is possible and routinely used [41] although fungal infection via the bored holes in the trunk can kill the tree [42].

***Graeffea leveri* (Günther, 1937)**

= *Ophicrania leveri* Günther, 1937

This species feeds on coconut palms. In the Solomon Islands (except Savo), flies of the Tachinid genus *Mycteromyiella* prey on nymphs of this species and it may be due to the lack of *Mycteromyiella* on Savo that this island is the only one to get major infestations of this phasmid [102].

Mycteromyiella laetifica attacks *Graeffea leveri* and a species of *Megacrania* at all nymphal stages and as adults. Generally, only one egg is oviposited on each phasmid, but more (up to 7) is not uncommon. The eggs are laid externally, and those laid on more heavily chitinised sections of the host have significantly increased mortality. Most hosts died within 5 days of parasite emergence—although some went on to successfully reproduce [26].

Parasitised hosts were shipped to Fiji in 1963–1964 in an effort to establish this species as a parasite of *Graeffea crouanii*. Mycteromyiella phasmatophaga also attacks *Graeffea leveri* although its usual host is likely to be *Sipyloidea poeciloptera*. Again usually only one egg is oviposited on each phasmid, although one specimen had 9 parasite eggs.

***Megacrania batesii* Kirby, 1896**

This species is thought [106] to be the culprit of an "unusually high population of an undetermined stick insect that infested pandan plants that are used for matweaving in Capiz Province on Panay Island [Philippines]".

***Carausius morosus* (Sinéty, 1901)**

This species has been introduced accidentally on a number of occasions. Generally, it is not considered a pest, but an outbreak in the San Diego (California, USA) area was a cause of concern for a number of years. A project to record hostplants of the species in San Diego Zoo [17] showed the species to be widely polyphagous. The species is now regarded as a pest in the local area [107]. Headrick and Wilen [108] summarise the history of this invasive species in the area: "the precise time of its establishment in California is unknown; the first official finding occurred in San Diego County in 1991 and shortly thereafter in San Luis Obispo County. There has been an increase in homeowner reports of walking stick damage in the last 10 years along the Central and Southern coasts of the state".

Due to its popularity as both a pet and laboratory animal, there have been several other unintentional introductions of this species. Its spread in the Azores is discussed by Borges et al. [109]. Brock [110] confirms the identity of a non-native species in the Cape Suburbs, South Africa, as *C. morosus*, where it seems to have become a minor garden pest. "One lady had telephoned him, distressed that pest control people had recently killed all the adults on ivy (often mentioned as a foodplant), but she now had lots of nymphs". The species does not currently appear to be a pest after accidental introduction to Madeira [111].

***Eurycantha calcarata* Lucas, 1869**

Gibson et al. [112] refer to this species as an important pest of oil palm in Papua New Guinea and a Eupelmid (Hymenoptera) egg parasite they are rearing in the laboratory for field studies.

***Eurycantha insularis* Lucas, 1869**

Outbreaks of this species in Oro Province, Papua New Guinea have been treated by the organophosphate insecticide monocrotophos [113]. Kimsey et al. [114] describe two new Amisegine wasps (Hymenoptera: Chrysididae) as egg parasites of this species, reared from eggs collected from infested oil palms.

***Sipyloidea stigmata* Redtenbacher, 1908**

Reported to be an increasing pest of *Piper nigrum* (Black Pepper) [18] and reaching economically important levels in Thenmala and Kulathupuzha, India where it has a preference for eating tender leaves on plagiotropic stems of the vine.

***Baculonistria alba* (Chen and He, 1990)** [2, 115]

= *Baculum alba* Chen and He, 1990 [116]

= *Phobaeticus sichuanensis* Cai and Liu, 1993 [117]

A 1986 infestation of this species destroyed several hundred hectares of forest in Wushan County and Zhongxian County (Sichuan Province) through 1986, with densities of several hundred individuals per tree [4].

Another infestation of 800 hectares happened in the Three Gorges area of the Yangtze River green-shelter, in March–April 2005. Around 40 hectares of trees were killed and defoliation was predominantly restricted to *Cupressus funebris*. The infestation reached an average density of 120 individuals per tree, and was controlled in early May by the application of insecticide. Reported with photographs of defoliation by Xiang Guowie [115].

This species has a 3-year life cycle [116].

***Micadina yingdensis* Chen and He, 1992** [118]

= *Micadina yingdeensis* incorrect subsequent spelling [119]

Around 2000 hectares of *Castanopsis ifs* were damaged by this species in Guangdong Province, China during 1989, around 400 hectares of trees were killed. The next year nearly 3000 hectares in the same region were infested, with the area of destroyed trees (50,000 m^3 of timber valued at $560,000) reaching 850 hectares. The density reached more than 450 specimens on a 2–3-year-old tree with less than 100 leaves, more than 1000 insects were found on a 6–7-year-old tree with a crown diameter of <1.5 m^3 [119].

This species is unusual as it may be up to tri-voltine [115].

***Ramulus chongxinense* (Chen and He, 1991)** [120]

= *Baculum chongxinense* Chen and He, 1991 [121]

In Gansu Province (Chongxin and Huatin Counties), China this species attacked over 20 species in 1998, with the infestation covering over 2600 hectares (2,100 hectares were destroyed) at densities estimated as 1000–5000 individuals per plant. *Quercus liaotungensis* and *Carpinus cordata* were the most affected species. The infestation recurred on a two-year cycle.

***Ramulus minutidentatus* (Chen and He, 1994)** [122]

= *Baculum minutidentatum* Chen and He, 1994 [123]

This species defoliated several areas of forest in Yongji County (Jinlin Province) in 1991, killing all younger trees and making older trees dry and withered (Xu and Zhang, 1994 from Hennemann et al., 2008). Infestation occurred 1998–2001 in Tonghua (Jinlin Province) where 2000–5000 insects per tree (*Tilia mandshurica*) were found, along with a leaf-litter egg density of 1000–3000/m^2. This species has a three-year life cycle ([124] in [115]).

***Ramulus pingliense* (Chen and He, 1991)** [4]

= *Baculum pingliense* Chen and He, 1991 [121]

This species reached damaging levels in Ankang (Shaanxi Province) during 1985. The insects are long lived and individuals can eat remarkable quantities of both young and old foliage. (Ji et al. 2000 in Hennemann et al. 2008). July 1985 saw this species, along with *R. intersulcatus* which caused less damage, infest forests and gardens in Pingli (Shaanxi Province), the total area was 1400 hectares, including 360 hectares of crops and over 1000 hectares of forest.

Chen [4] reports considerable damage by this species affecting 2,000 hectares of forest and plantation, including *Fagus* sp. and *Prunus domestica* in Gansu Province.

This species is uni-voltine [115].

***Sinophasma brevipenne* Günther, 1940** [125]

Zeng et al. (2002 in [115]) report up to 500 of these insects infesting the crowns of trees in Guiyang (Guizhou Province) in 1983, with many trees in the centre of the city being completely defoliated.

***Sinophasma maculicruralis* Chen, 1986**

***Sinophasma pseudomirabile* Chen and Chen, 1996**

Chen [4] reports both species have been known to cause regular harm in the Guangxi Autonomous Region. In 1984, the population density reached 2000–5000 individuals per tree. Hundreds of hectares of *Castanopsis cuspidata* and *C. hicklii* were almost totally defoliated. *S. maculicruralis* is uni-voltine [115].

***Libethroidea inusitata* Hebard, 1919**

This species has been known to cause damage to *Pinus patula* in Colombia, where up to 80 hectares were destroyed in 1992–3 [126].

Conclusions and remarks

Theory of phasmid outbreak release

Readshaw [27] proposed a theory for the occurrence of phasmid outbreaks based on a study of *Didymuria violescens*. Campbell [127] also summarised conditions that make an outbreak likely. The theory presented here combines these two theories and provides supporting evidence from other outbreaks reported in this paper. Several of the criteria suggested by Readshaw are rejected, at least for a general theory, through comparison to North American infestations.

Rejected criteria:

1. Periodicity

   Readshaw [27] puts emphasis on the semi-voltine life cycle of *Didymuria violescens* as being important to sustaining infestation, giving the trees a year to recover between outbreaks. The uni-voltine life cycle of *Diapheromera femorata*, and the up to tri-voltine *Micadina yingdensis* show that alternating years of low and high density are not critical in creating or sustaining an outbreak.

2. Kentromorphism

   While kentromorphism is important in the plague locusts, it appears not to be crucial in phasmid outbreaks, only being present in the Australian species that cause periodic infestation. It seems likely this is an evolutionary response to naturally occurring outbreaks caused by forest fires, whereas the other species cause infestation as a response to recent human modification of their environment.

Accepted criteria:

1. Habitat disturbance

   Readshaw [27] requires outbreaks to be infrequent. This point is expanded upon by Campbell [127] as 'Freedom from Catastrophe' and 'Forest Stand Conditions'. In Australia, the criterion is a period of absence of forest fire or other catastrophe (between 10 and 80 years). The condition of forest is also a factor in the Michigan and other infestations of *Diapheromera femorata* where younger second-growth forest was closely linked to high phasmid densities. The introduction of the phasmid may itself be the disturbance, such as the case of *Carausius morosus* in San Diego [17], and potentially some introductions of *Graeffea corona* onto new islands [100].
2. Inability of predators and parasitoids to contain infestation
   When phasmids occur at normal population densities, the equilibrium is maintained by a number of predators and parasitoids. During an outbreak the phasmid population increases to a level where these natural enemies are incapable of controlling their numbers. Readshaw [27] used the periodicity criterion to explain why these species did not also increase significantly inline with the phasmid population. Given the rejection of this criterion, it seems likely that the inability of these species to control the phasmid population is in fact due to the 'Habitat disturbance' criterion: rapid ecological disturbance has either removed or temporarily reduced the population of phasmid predators and parasitoids.
3. High fecundity
   Readshaw [27] required a "relatively rapid and massive development around epicentres of high density" for infestations to occur and expand. The species known to cause infestation are known to be highly fecund, all laying in excess of 100 eggs over their lifetime. This high level of reproduction suggests that phasmids in general are heavily predated and/or parasitised. The absence of these enemies is likely therefore to cause a rapid, continued, increase in their abundance until predation/parasitisation is restored, the forest is destroyed through defoliation, or a catastrophic event such as a forest fire. Neumann [6] demonstrated that crowding and food shortage reduced fecundity of females of *Didymuria violescens* in laboratory conditions.
4. Slow migration
   Phasmids are generally slow moving insects, and the species known to cause periodic infestation are known to migrate slowly from the epicentres. In the case of *Diapheromera femorata,* even a road has been known to create a break between infested and non-infested areas. In the conditions of an outbreak, this slow migration causes the population density to rise significantly generation-on-generation. Readshaw [27] suggests that localised outbreaks may cause further outbreaks by acting as foci for predators and allowing other areas to reach outbreak density. While Readshaw suggests bird predation may act to produce this effect, Campbell [127] notes that birds have been known to completely control early outbreaks of phasmids.

Geographic remarks

While recent decades have seen major phasmid outbreaks, there are still many questions that are unanswered in this aspect of phasmid biology. First, while some Australian species have kentromorphic phases no American species are known to. This strongly suggests a long history of outbreaks in Australia and thus an entirely natural cause of outbreaks. So far nobody has reported kentromorphic morphological or behavioural changes in *Diapheromera femorata*, the sole species prone to infestation levels in the USA or any of the Chinese phasmid fauna.

Further work

The method of Hadlington and Hoschke [48] for measuring damage by these insects (measuring the dry weight of faeces and fallen foliage as a result of feeding) applied to laboratory cultures of these insects could provide baseline data for the severity of infestations for different species.

The study of historical infestations, even when they are ongoing, could be improved using the tree ring technique of Readshaw and Mazanec [23]—and could help the study of the current regular infestations in China and elsewhere. While dendrochronology had been thought impractical for work on Eucalypts, a new body of work shows that it is possible [128].

As the author of the American Agriculturist [65] closed their work, I hope this summary will encourage further work on the importance of phasmids and I would welcome any references that I have overlooked.

> *"Here is an opportunity for [an entomologist] to do useful work—in tracing the habits of this insect, and in suggesting the means for staying its progress. We call attention to this case in the hope of calling out information. If any readers have knowledge of similar ravages, or any experience in the destruction of the insects, we hope they will communicate it". Anon. [65]*

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Competing interests
The author declares that he has no competing interests.

Appendix: Bibliographical notes

The report in Packard [129] on The Thick-Thighed Walking-Stick (*Diapheromera femorata*) is said to be taken verbatim from Riley [1] but there are minor variations in the text. In this work, I have used Riley's account directly, and attribute authorship to him.

Paine [26] gives the following reference:

Swezey (1924) notes on insect pests in Samoa—Hawaii Plrs' Rec. 28 pp. 214–219. This publication could not be traced. The reference used in this paper as Swezey (1924) [130] has the same title but was published in a different journal, *Proc Hawaiian Entomol Soc*, in the same year, and appears to contain the same content, although it is longer than Paine indicated.

The works of Severin [55], Severin and Severin [29] and Butler [24] are reproduced, along with other early studies of the phasmids of the United States and Canada, in Arment [131].

Hennemann et al. [115] provides a summary in English of many of the Chinese language papers referenced in this text. While efforts have been made to fact check where possible, some translated details have been taken directly from this work. These are listed as (Original Author, XXX in [115].

Access to works on Chalcidoidean parasites of phasmids was aided by the Universal Chalcidoidea Database [132].

The taxonomy and nomenclature of the phasmids follows Brock [63].

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