

Evolutionary and Taxonomic Relationships Between Fruit-piercing Moths and the Menispermaceae

H. A. C. Fay

Department of Primary Industries, PO Box 1054, Mareeba, Qld 4880, Australia.

Abstract

Twining vines of the family Menispermaceae provide the food for larvae of the principal fruit-piercing moths in Australia, and in most of the Old World tropics and near tropics. These large noctuid moths are adult pests of a range of commercial fruits, and can cause crop losses of more than 50%. In Australia, the Menispermaceae are represented by 13 genera and 24 species, which predominantly occur through coastal and subcoastal regions in the east and north of the continent. Their density and diversity is greatest in the wet tropical forest areas of north-east Queensland. Around 60% of the Australian menisperm species are now known to support fruit-piercing moth larvae to various extents. While moth species–menisperm associations range from species specific (i.e. monophagy) to genera generalist (i.e. polyphagy), polyphagy appears to contribute less to a moth's status as a pest than habitat diversity. *Tinospora smilacina* and *Stephania japonica* are the two most widely occurring Australian menisperms, with forms or varieties occupying habitats from wet tropical forest to semi-desert, and these species are particularly important to the fruit-piercing moth problem. Some moth species–host plant associations appear to be dynamic, as indicated by the dietary expansion of the moth *Othreis fullonia* in recent centuries onto *Erythrina* spp. (Fabaceae) in New Guinea and the Pacific. The perceived relationship between *Erythrina* spp. and the Menispermaceae is through the similar alkaloids they possess (i.e. the tetracyclic *Erythrina*-type), which are found particularly in certain species within the tribe Menispermeae. Variation in the alkaloids associated with certain menisperm genera may explain specific moth–host plant relationships, which in turn support alternative tribal associations for some menisperm taxa to those currently recognised.

Introduction

Fruit-piercing moths are large noctuids of the subfamily Catocalinae (including the Ophiderinae) (Kitching 1984). As adults, they attack a wide range of ripening fruits using a saw-like proboscis to obtain the juice (Tryon 1898; Cochereau 1977; Bänziger 1982). They frequently inflict damage to levels higher than 50% in crops such as citrus, lychees and carambolas (Fay and Halfpapp 1991, 1993a). While fruit-piercing moths range through most of the world's tropics and some subtropics, the most damaging species occur in the Old World from Africa to the Pacific. Species from the genera *Othreis*, *Eudocima*, *Khadira* and *Rhytia* in Australia, together with *Adris* in Asia, are capable of piercing most fruits (Bänziger 1982) while others, such as *Phyllodes* and *Oraesia*, feed only on softer or previously damaged fruits. All of these genera utilise twining vines of the family Menispermaceae as the host plants for their larvae, most of them exclusively (Bänziger 1982, 1987; Common 1990; Fay and Halfpapp 1993b). In this paper, the taxonomic and evolutionary relationships between fruit-piercing moths and their larval host plants (particularly in Australia) is discussed. A plausible basis for these relationships is provided and their value to menisperm taxonomy is interpreted.

Australian Menispermaceae—Distribution and Moth Utilisation

The Menispermaceae in Australia are represented by 13 genera (with the recent restoration of *Echinostephia* and generic segregation of *Pachygone longifolia* F.M.Bailey) and 24 species (Forman 1982, 1986, pers. comm.; Queensland Herbarium 1994). As with fruit-piercing moths, species diversity reaches a maximum in wet tropical rainforest in north-east Queensland (Fig. 1), particularly in complex mesophyll vine forest (Tracey 1982), but the family is represented through most of the summer rainfall area of the continent. At least one species, *Tinospora smilacina* Benth., extends into the semi-arid zone across northern Australia (Fig. 1) where the average annual rainfall is as low as 300 mm. A maximum of about half the Australian menisperm species can be found co-existing in a single habitat. It is now known that around 60% of the menisperms in Australia, including all genera, are utilised by fruit-piercing moths for oviposition and/or food for their larvae. This is probably a conservative figure as laboratory feeding tests suggest more species are likely to be involved (Fay and Halfpapp 1993b) (Table 1). Larvae of some moth species will accept only a single species or genus of menisperm, others will feed on a range of genera (Fay and Halfpapp 1993b). Despite this, there is reasonably equal utilisation of menisperms by fruit-piercing moths within the three tribes (after Forman 1986) represented in Australia (Table 1).

The pest status of individual moth species is believed to be related partly to menisperm polyphagy but, more importantly, to the diversity of habitats in which menisperms occur and can be utilised (Fay and Halfpapp 1993b). For example, although *Khadira aurantia* (Moore) has a range of hosts and breeding is confined to tropical rainforest, it has a lower pest status than *Othreis materna* (L.) which will utilise only *Tinospora* (Table 1). *Tinospora smilacina* and *Stephania japonica* (Thunb.) Miers occupy the most diverse range of habitats of the Australian menisperms (Forman 1981; Queensland Herbarium 1994) and these two species play a major role in the pestilence of fruit-piercing moths in this country (Sands and Schotz 1989; Fay and Halfpapp 1993b; Fay 1994).

Evolutionary Trends

In the Australian and Asian regions, the major species of fruit-piercing moth can be found associated with four families within the Order Ranunculales (Table 2). Most moth species associations are confined to the Menispermaceae, but those of the genera *Adris* and *Oraesia* extend to the closely related families, Berberidaceae, Lardizabalaceae and Ranunculaceae (Kim and Lee 1986; Bänziger 1987). Apart from their morphological similarities to the Menispermaceae, the Berberidaceae and Ranunculaceae at least are known to share benzyloisoquinoline, protoberberine and aporphine alkaloids (Thorner 1970). It is well known that secondary plant compounds can play an important role in the selection, avoidance, utilisation or tolerance of certain plants by insects (Bernays and Chapman 1994). The alkaloids, in particular, appear to have been significant in the expansion of the host range of some fruit-piercing moth species beyond the Menispermaceae.

In New Guinea and the Pacific Islands, *Othreis fullonia* (Clerck) (the species known to utilise the largest number of menisperm hosts, see Table 1) has increased the range of its larval food to include unrelated *Erythrina* spp. (Fabaceae) (Table 2). This adaptation is thought to be relatively recent as the species utilised in islands such as Fiji and New Caledonia, for example *Erythrina variegata* L., *Erythrina fusca* Lour. and *Erythrina lithosperma* Miq., were introduced or have proliferated over the past few centuries (Cochereau 1977; Kumar and Lal 1983; Waterhouse and Norris 1987). Within the Menispermaceae, the tribe Menispermeae contains a few species which possess tetracyclic *Erythrina*-type alkaloids, for example cocculolidine and dihydroerysodine (Amer *et al.* 1991). The Menispermaceae are thought to be the only family outside the genus *Erythrina* containing this type of alkaloid. The genus *Cocculus* notably, but also some *Pachygone*, produce these tetracyclic alkaloids and both are known from the Pacific but are now rare or absent (Forman 1986; Amer *et al.* 1991). Both genera support larvae of *O. fullonia* in either Asia or Australia (Bänziger 1982; Fay and Halfpapp 1993b). *Stephania japonica* var. *timoriensis* (DC) Forman (= *forsteri*) is now the only or principal menisperm in some Pacific Islands (Cochereau 1977), and while it supports some larval development in *O. fullonia*, it is

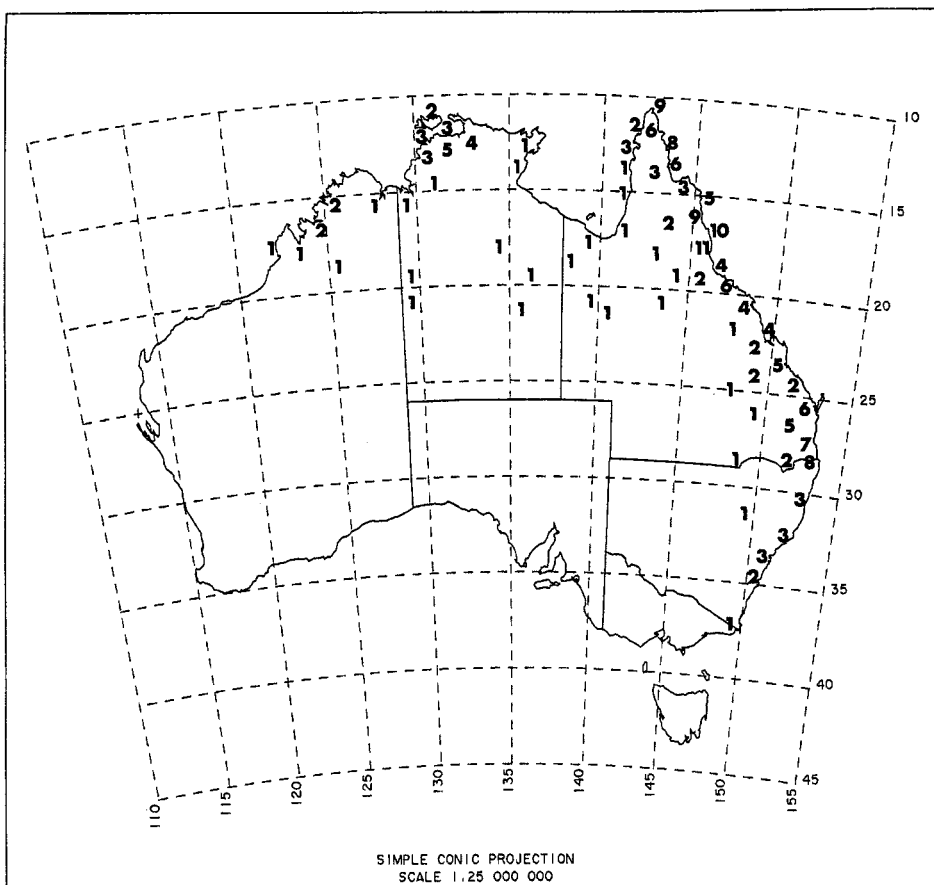


Fig. 1. Distribution of Menispermaceae in Australia as indicated by species numbers through a range of localities. Data are based on records of the Queensland Herbarium, CSIRO Tropical Forest Research Centre (Atherton), the Conservation Commission of the Northern Territory, Forman (1981, 1982, 1984) and personal observations.

Table 1. Associations between some Australian fruit-piercing moth species and menisperm tribes

The numbers of menisperm species utilised are based on field observations and laboratory testing

Moth species	Possible number of menisperm spp. utilised	Menisperm Tribes		
		Tinosporeae	Tiliacoreae	Menispermeae
<i>Othreis fullonia</i>	17+	#	#	#
<i>Khadira aurantia</i>	8+	#	#	#
<i>Othreis jordani</i>	5+	#	#	#
<i>Othreis iridescens</i>	3+		#	#
<i>Phyllodes imperialis</i>	2+		#	#
<i>Eudocima salamina</i>	1 or 2			#
<i>Othreis materna</i>	1	#		
<i>Rhytia cocalus</i>	1	#		

considered to be a poor host in regions where a larger range of menisperms is available (Fay 1994). Loss of, or a reduction in, preferred Menispermaceae may well have contributed to *O. fullonia* adopting *Erythrina* spp. as hosts in the Pacific, and may explain the absence of this phenomenon in Australia. Polyphagous fruit-piercing moths, such as *O. fullonia* and *Adris tyrannus* (Guen.), might well be dynamic species which can adapt to new hosts, having evolved from those moths specifically associated with either *Tinospora* or *Stephania*.

Moth–Menisperm–Alkaloid Associations and their Taxonomic Significance

The above observations lend weight to the view that the general associations between fruit-piercing moths and the plant hosts of their larvae are explainable in terms of the alkaloid-types encountered. Elsewhere (Fay 1994), differences in the larval growth characteristics of *O. fullonia* on three menisperm hosts could not be interpreted on nutritional grounds, but was considered to be allelochemic-, and particularly alkaloid-, associated. However, can more specific associations between moth species and particular menisperms be similarly interpreted?

Amongst the main fruit-piercing moths in Australia, *O. materna* and *Rhytia cocalus* (Cramer) will only accept *Tinospora* while *Eudocima salamina* feeds almost exclusively on *Stephania japonica* (Sands and Schotz 1989; Fay and Halfpapp 1993b) (Table 3). *Othreis jordani* Holl. prefers menisperms within the tribes Tinosporeae and Tiliacoreae, while *K. aurantia* tends towards the Menispermeae. Although *O. fullonia* has a confirmed preference for *Tinospora* (Bänziger 1982; Fay 1994), it can utilise *Tiliacora* (Tiliacoreae) and *Sarcopetalum* (Menispermeae) with almost the same efficiency. Virtually all the Australian menisperm genera contain biscoclaurine alkaloids (Table 3). However, there is considerable variation in the representation of the other alkaloid groups, or in the presence of dibenzo-*p*-dioxin type bases within the biscoclaurines (Thornber 1970; Hart *et al.* 1972; Forman 1975, 1984, 1986). Certainly, there is sufficient variation in the major alkaloids represented in particular menisperms to explain some preferences and/or associations individual moth species have for their hosts (Table 3). For example, moths with a narrow host range utilise those plant genera (*Stephania* and *Tinospora*) which evidently contain the largest range of alkaloid types. It would follow then that polyphagous moths, such as *O. fullonia*, have also evolved to tolerate plants with less diverse, and/or specific, alkaloid components. Nevertheless, it should be noted that some menisperm genera are better known phytochemically than others (Thornber 1970) and therefore some caution must be observed when making assumptions.

Some moth–host plant affinities add doubt to certain tribal assignments (Forman 1986) amongst menisperm taxa. The strongest case in point is probably the genus *Tiliacora*. Of the Tiliacoreae in Table 3, *Pycnarrhena novoguineensis* Miq. is utilised by larvae of *Othreis jordani*, *O. iridescens* (Lucas) and *Phyllodes imperialis* Druce, whereas *Tiliacora australiana* Forman is not known to support any of these moths (Fay and Halfpapp 1993b). *Tiliacora* can be considered as being unique amongst the Australian Tiliacoreae in possessing biscoclaurine alkaloids with dibenzo-*p*-dioxin bases which are generally associated with species within the Menispermeae (Table 3). *Tiliacora* is also recognised as being morphologically distinct from the remainder of its tribe. Some Asian *Tiliacora* possess an endosperm, whereas other Tiliacoreae lack one, and their pollen morphology is different (Forman 1975). It is interesting that in 1871, Miers placed *Tiliacora* in a tribe separate from the other Tiliacoreae (= Triclisieae) (Forman 1975).

In a similar vein, the relatively recent generic change of *Stephania aculeata* F.M.Bailey to *Echinostephia aculeata* (F.M.Bailey) Domin (Queensland Herbarium 1994) would be supported by its association with fruit-piercing moths. *Othreis fullonia* is the only moth species recorded from *Echinostephia aculeata* (Sands and Schotz 1989). *Eudocima salamina*, whose principal host is *S. japonica*, might have been expected to utilise *Echinostephia aculeata* had this plant been allelochemically typical of the genus *Stephania*. In fact, the morphinoid amurine has recently been isolated from *E. aculeata* (Blanchfield *et al.* 1993), an alkaloid from a group not known in the genus *Stephania* (Thornber 1970; Matsui *et al.* 1982).

Table 2. Plant family affinities of some species of fruit-piercing moths in the Asia-Pacific region
Data from Wada and Munakata (1968), Bänziger (1982, 1987), Kim and Lee (1986), Fay and Halpapp (1993b)

Menispermaceae	Order Ranunculales			Order Fabales
	Lardizabalaceae	Berberidaceae	Ranunculaceae	
<i>Adris tyrannus</i>	<i>Adris okurai</i>	<i>Adris tyrannus</i>		
<i>Eudocima salamania</i>				
<i>Khadiira aurantia</i>				
<i>Oraesia excavata</i>			<i>Oraesia excavata</i>	
<i>Othreis</i> spp. (all)				
<i>Phylloides imperialis</i>				<i>Othreis fullonia</i>
<i>Rhytia</i> spp. (all)				
+ others				

Table 3. Generalised associations between some menisperm genera, alkaloid groups and specific fruit-piercing moths

Men. = Menispermaceae, Tin. = Timosporaeae, Til. = Tiliaceae. Alkaloid groups marked with 'd' contain dibenzo-p-dioxin type bases. Es = *Eudocima salamania*, Ka = *Khadiira aurantia*, Of = *Othreis fullonia*, Om = *Othreis materna*, Rc = *Rhytia coccalis*, Oj = *Othreis jordanii*, Oi = *Othreis iridescens* and Pi = *Phylloides imperialis*. Species in lighter type are considered not as strongly associated or utilisation is unconfirmed in the field

Genus (Tribe)	Alkaloid Group					Associated moth species
	Biscoclaurine	Aporphine	Protoberberine	Prooporphine	Hasubanan	
<i>Stephania</i> (Men.)	#d	#	#	#	#	Es, Ka, Of
<i>Tinospora</i> (Tin.)	#	#	#			Om, Rc, Of, Oj, Ka
<i>Pachygone</i> (Men.)	#d					Of, Oj
<i>Legnephora</i> (Men.)		#				Of, Ka
<i>Tiliacora</i> (Til.)	#d					Of, Ka
<i>Pycnarhena</i> (Til.)	#					} Oj, Oi, Pi,
<i>Hypserpa</i> (Men.)	#					} Of, Ka

In 1975, Forman acknowledged that most genera within the tribe Triclisieae (= Tiliacoreae) could be distinguished on the alkaloid composition of their species. The diagnostic value of alkaloids at the generic level has also been recognised by other authors for other plant families (Greinwald *et al.* 1992). In 'Flora Malesiana', Forman (1986) indicates 'a clear need for a complete review of the generic classification and delimitation in the Menispermaceae from a multidisciplinary approach'. Fruit-piercing moths almost certainly have a role to play in this.

Acknowledgments

Thanks are due to John Clarkson (Queensland Herbarium, Mareeba) for encouraging me to present this paper.

References

- Amer, M.E., Shamma, M., and Freyer, A.J. (1991). The tetracyclic *Erythrina* alkaloids. *Journal of Natural Products* **54**, 329–363.
- Bänziger, H. (1982). Fruit-piercing moths (Lep., Noctuidae) in Thailand: a general survey and some new perspectives. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **55**, 213–240.
- Bänziger, H. (1987). Biological and taxonomic studies on immature and adult fruit-piercing moths in Nepal, with reference to Thailand. *Natural History Bulletin, Siam Society* **35**, 1–17.
- Bernays, E.A., and Chapman, R.F. (1994). 'Host-plant Selection by Phytophagous Insects.' (Chapman and Hall: New York.)
- Blanchfield, J.T., Kitching, W., Sands, D.P.A., Thong, Y.H., Kennard, C.H.L., and Byriell, K.A. (1993). Alkaloids from some Australian *Stephania* (Menispermaceae) species. *Natural Product Letters* **3**, 305–312.
- Cochereau, P. (1977). Biologie et écologie des populations en Nouvelle-Calédonie d'un papillon piqueur de fruits: *Othreis fullonia* Clerck (Lepidoptera, Noctuidae, Catocalinae). *Travaux et Documents de L'O.R.S.T.O.M.* No. **71**, 322 pp.
- Common, I.F.B. (1990). 'Moths of Australia.' (Melbourne University Press: Melbourne.)
- Fay, H.A.C. (1994). The relative acceptabilities of three Australian Menispermaceae as food plants for larvae of the fruit-piercing moth, *Othreis fullonia*. *Entomologia Experimentalis et Applicata* **72**, 67–75.
- Fay, H.A.C., and Halfpapp, K.H. (1991). Potential methods for the control of fruit-piercing moths (Lepidoptera: Noctuidae) in tropical Australia. In 'Proceedings of the First Asia-Pacific Conference of Entomology, Chiang Mai, Thailand, November 1989'. pp. 204–208. (Entomology and Zoology Association of Thailand: Bangkok.)
- Fay, H.A.C., and Halfpapp, K.H. (1993a). Non-odorous characteristics of lychee (*Litchi chinensis*) and carambola (*Averrhoa carambola*) pertaining to fruit-piercing moth susceptibility. *Australian Journal of Experimental Agriculture* **33**, 327–331.
- Fay, H.A.C., and Halfpapp, K.H. (1993b). Differential habitat affinities of five species of fruit-piercing moths (Lepidoptera: Noctuidae) in their utilization of *Tinospora smilacina* Benth. as a larval host plant in north Queensland. *Australian Journal of Ecology* **18**, 451–462.
- Forman, L.L. (1975). The tribe *Triclisieae* Diels in Asia, the Pacific and Australia. The Menispermaceae of Malesia and adjacent areas: VIII. *Kew Bulletin* **30**, 77–100.
- Forman, L.L. (1981). A revision of *Tinospora* (Menispermaceae) in Asia to Australia and the Pacific. The Menispermaceae of Malesia and adjacent areas: X. *Kew Bulletin* **36**, 375–421.
- Forman, L.L. (1982). New Australian Menispermaceae. *Kew Bulletin* **37**, 369–373.
- Forman, L.L. (1984). A revision of tribe *Tinosporeae* (Menispermaceae) in Asia, Australia and the Pacific. *Kew Bulletin* **39**, 99–116.
- Forman, L.L. (1986). Menispermaceae. *Flora Malesiana* **10**, 157–253.
- Greinwald, R., Bachmann, P., Witte, L., Acebes-Grinoves, J.R., and Czygan, F.-C. (1992). Taxonomic significance of alkaloids in the genus *Adenocarpus* (Fabaceae–Genisteae). *Biochemical Systematics and Ecology* **20**, 69–73.
- Hart, N.K., Johns, S.R., Lamberton, J.A., and Soares, H. (1972). Alkaloids of *Pachygone pubescens* (Menispermaceae). *Australian Journal of Chemistry* **25**, 2289–2290.
- Kim, K.C., and Lee, T.S. (1986). Identification, larval host plant range, and damage of the fruit sucking moths to the major fruit in Cheonnam Province. *The Korean Journal of Plant Protection* **24**, 183–190. (In Korean.)
- Kitching, I.J. (1984). A historical review of the higher classification of the Noctuidae (Lepidoptera). *Bulletin of the British Museum of Natural History, Entomology* **49**, 153–234.

- Kumar, K., and Lal, S.N. (1983). Studies on the biology, seasonal abundance and host-parasite relationship of fruit sucking moth *Othreis fullonia* (Clerck) in Fiji. *Fiji Agricultural Journal* **45**, 71-77.
- Matsui, M., Kabashima, T., Ishida, K., Takebayashi, T., and Watanabe, Y. (1982). Alkaloids of the leaves of *Stephania japonica*. *Journal of Natural Products* **45**, 497-500.
- Queensland Herbarium (1994). 'Queensland Vascular Plants: Names and Distribution.' (Queensland Department of Environment and Heritage: Indooroopilly.)
- Sands, D.P.A., and Schotz, M. (1989). Advances in research on fruit piercing moths of subtropical Australia. In 'Proceedings of the 4th Australasian Conference on Tree and Nut Crops'. pp. 378-383. (Exotic Fruit Growers Association: Lismore.)
- Thorner, C.W. (1970). Alkaloids of the Menispermaceae. *Phytochemistry* **9**, 157-187.
- Tracey, J.G. (1982). 'The Vegetation of the Humid Tropical Region of North Queensland.' (CSIRO Division of Plant Industry: Melbourne.)
- Tryon, H. (1898). Orange-piercing moths. *Queensland Agricultural Journal* **2**, 308-315.
- Wada, K., and Munakata, K. (1968). Naturally occurring insect control chemicals. Isoboldine, a feeding inhibitor, and cocculolidine, an insecticide in the leaves of *Cocculus trilobus* DC. *Journal of Agricultural and Food Chemistry* **16**, 471-474.
- Waterhouse, D.F., and Norris, K.R. (1987). 'Biological Control: Pacific Prospects.' (Inkata Press: Melbourne.)

Manuscript received 10 March 1995, accepted 17 August 1995