

Seedhead tephritids and their parasitoids - can predictions be made about likely parasitism of tephritids introduced into Australia for biological control of Asteraceae?

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Abstract. Tephritids that attack flowerheads are almost entirely restricted to plants in the Asteraceae. Surveys of Asteraceae flowerheads were made in Australia for the presence of tephritids and their parasitoids. The tephritids tended towards host-plant specificity at the level of plant, tribe or below, whereas the parasitoids showed no marked affinities with host tephritid or host plant. The parasitoid complexes were compared with those of *Mesoclanis* species (Tephritidae) on *Chrysanthemoides monilifera* (Asteraceae) in South Africa, and with those of several asteraceous flowerhead communities in Europe and North America. The parasitoid complexes throughout these regions are remarkably constant in taxonomic structure. Comparisons of the Australian fauna with those from elsewhere allow predictions to be made about which species may move onto tephritids introduced into Australia for biological control of asteraceous weeds, particularly *Mesoclanis* species on *C. monilifera*, and allows predictions of their possible impact on the success of this programme.

Introduction

It is an expectation of biological control of weeds programmes that introduced insects will experience a lower level of parasitism than they do in their native environment, and thereby have a greater impact on their host plant. When a biological control agent is released, every effort is made to ensure that it is free of its parasitoids from its country of origin. However, there remains the possibility that native parasitoids will adapt to the novel host, and many examples exist to illustrate that this can occur (Cornell and Hawkins 1993; Julien 1992). Before a new agent is released, the possibility of attack by native parasitoids is rarely considered. It is the aim of this paper to consider this possibility for an agent that is soon to be released in Australia.

Seedhead tephritids (Tephritidae) are more or less restricted to the family Asteraceae (White 1988; Straw 1989), and many species are host specific (White 1988), resulting in their frequent use in biological control programmes (Harris 1989; Julien 1992). Three species of *Mesoclanis* (Tephritidae) are being assessed

as potential biological control agents of *Chrysanthemoides monilifera* (Asteraceae) in Australia. *Mesoclanis polana* has been shown to be specific to *C. monilifera* and has been approved for release. *Mesoclanis magnipalpis* and *M. dubia* are still undergoing specificity testing.

Chrysanthemoides monilifera is native to southern Africa, and in 1987 a survey was commenced for potential biological control agents (Scott and Adair 1990). In addition to the tephritids mentioned above, four species of chrysomelids and one species of geometrid have been released in Australia. A tortricid ("*Tortrix*" sp.) and a rust fungus (*Aecidium osteospermi*), both of which can inflict considerable damage on *C. monilifera*, are also undergoing assessment (Adair and Edwards, this Volume).

Two subspecies of *C. monilifera* have become weedy in Australia, *C. m. rotundata*, or bitou bush, along the eastern coast from southern Queensland to eastern Victoria, and *C. m. monilifera*, or boneseed, in South Australia, Victoria, New South Wales and Tasmania (Weiss 1986). *Chrysanthemoides monilifera* is unusual amongst the Asteraceae in having large

fleshy drupes containing a single woody seed (Bremer 1994), in contrast to the dry achenes normally associated with asteraceous seedheads. The larval stages of all three *Mesoclanis* species being assessed feed within the florets and developing ovules of *C. monilifera*, pupating within the seed or occasionally within the florets or receptacle, depending on species (P.B. Edwards and E.M. Brown unpublished). In South Africa, *M. polana* occurs only on *C. m. rotundata*, whereas *M. magnipalpis* and *M. dubia* occur on *C. m. rotundata*, *C. m. monilifera*, *C. m. pisifera* and *C. incana* (Munro 1950; P.B. Edwards and E.M. Brown unpublished).

The question addressed in this paper is whether we can make informed predictions about the likelihood of *Mesoclanis* species being parasitized by native Australian parasitoids, and if so, to consider which species, genera or families of parasitoids are likely to be involved, and to speculate on the possible impact these species may have on the population dynamics of *Mesoclanis* species. The approach used to develop our answers was: (i) a sampling programme to survey the parasitoids attacking *Mesoclanis* species in South Africa, to determine the species involved and their relative importance; and (ii) a sampling programme in Australia of the tephritids on Asteraceae flowers to ascertain the structure of the parasitoid communities involved. The results were considered in the context of published information on tephritid-parasitoid complexes elsewhere, and the history of other tephritids used in biological control programmes.

Methods

Parasitoids of Mesoclanis species on C. monilifera in South Africa

Chrysanthemoides monilifera flowerheads, from five sites in South Africa where *Mesoclanis* species are

known to be abundant, were sampled regularly for the presence of parasitoids. Sampling was undertaken at St. Lucia, Mtunzini, Durban, St Francis Bay and De Hoop Nature Reserve. Flowerheads at various stages of development were sampled and kept in ventilated containers until all tephritids and parasitoids had emerged. Samples were taken during all seasons, between 1992 and 1994. The total numbers of different species of parasitoids were determined (details on phenology and impact are to be presented elsewhere).

Parasitoids associated with seedhead tephritids in Australia

Collections were made of flowerheads from 64 species (including four subspecies of *Senecio lautus* and two subspecies of *Chrysanthemoides monilifera*) of Asteraceae in New South Wales, Victoria, Queensland and the Australian Capital Territory, the general region of *C. monilifera* distribution in Australia (Weiss 1986). Native and introduced species were included in the survey. Samples were held in the laboratory until all tephritids and parasitoids had emerged. On occasion, if only parasitoids emerged, the samples were dissected to look for evidence of tephritids, such as empty pupal cases, dead larvae or typical feeding damage. Many other flowerhead samples were also dissected, to ensure that neither diapausing tephritids nor diapausing parasitoids were present. Adult tephritids were occasionally collected directly from flowerheads.

Results

Parasitoids of Mesoclanis species on C. monilifera in South Africa

A summary of the total numbers of parasitoids collected at each site in South Africa is presented in Table 1, together with the numbers and identity of

Table 1. Numbers of parasitoids associated with *Mesoclanis* spp. reared from samples of *Chrysanthemoides monilifera* in South Africa. 'Others' includes *Pteromalus* sp. (Pteromalidae), an Encyrtidae, two species of Eulophidae (one an *Aprostocetus*) and a second species of *Torymoides* (Torymidae).

Site	Host plant	Tephritidae	<i>Eurytoma</i> sp. A	<i>Torymoides</i> sp. B	<i>Psytalia</i> sp. A	Others
St Lucia	<i>C. m. rotundata</i>	<i>Mesoclanis polana</i>	359	132	178	84
Mtunzini	<i>C. m. rotundata</i>	<i>Mesoclanis polana</i>	192	198	86	73
Durban	<i>C. m. rotundata</i>	<i>Mesoclanis polana</i>	132	189	59	62
St Francis Bay	<i>C. m. rotundata</i>	<i>Mesoclanis magnipalpis</i>	373	81	143	21
De Hoop	<i>C. m. pisifera</i>	<i>Mesoclanis magnipalpis</i>	268	16	52	2

Mesoclanis species. *Eurytoma* sp. A (Eurytomidae) was the dominant species at three sites, and together with *Psytalia* sp. (Braconidae) and *Torymoides* sp. B (Torymidae) comprised over 85% of the total number of parasitoids at each site. Other species collected included *Eupelmus* sp. (Eupelmidae), *Pteromalus* sp. (Pteromalidae), a species of Encyrtidae, two species of Eulophidae and a second species of *Torymoides* (Torymidae).

All species of *Mesoclanis* and parasitoids emerged within a few weeks of collection, except for *Eurytoma* sp. A, which emerged over a period of up to 10 months after collection. For instance, 32 *Eurytoma* sp. A emerged from a collection of *M. polana* made from *C. m. rotundata* at St Lucia in July 1992: 16% emerged in August, a further 53% by February, 28% by April and the remaining 3% by June 1993. Sixty-six *Eurytoma* sp. A emerged from a collection of *M. magnipalpis* made from *C. m. pisifera* in De Hoop Nature Reserve in July 1993: 2% emerged by September, a further 3% by November, 0% by March and the remaining 95% by May 1994.

Parasitoids associated with seedhead tephritids in Australia

Of the 42 native species of Asteraceae sampled (including four subspecies of *Senecio laetus*), tephritids were reared from 34, and there was evidence of tephritid activity in a further one (parasitoids emerged and adult tephritids collected from flowerheads) (Table 2). Of the 17 introduced Asteraceae species (including two subspecies of *Chrysanthemoides monilifera*), tephritids were reared from four, and collected from flowerheads of a further two (Table 2). A total of 14 tephritid species was collected. None occurred on the introduced plant *Chrysanthemoides monilifera*.

Of the parasitoids reared, the Torymidae were the most widespread in terms of host associations. *Torymoides* sp. A was associated with six species of tephritids from 14 host plants, including two introduced plant species, *Euryops pectinatus* and *Senecio pterophorus* (Table 2). Other widely occurring parasitoids included three species of *Megastigmus* (Torymidae), two species of *Pteromalus* (Pteromalidae), a species of *Systasis* (Pteromalidae), and two species of *Aprostocetus* (Eulophidae). Occasional collections included *Euderus* sp. (Eulophidae), *Eupelmus* sp. (Eupelmidae), an Encyrtidae and *Apanteles* sp. (Braconidae).

Discussion

Host plant associations of seedhead tephritids

The 14 species of tephritids associated with native Australian Asteraceae showed specificity at the level of plant tribe. Some species were only collected from one plant species, although more extensive sampling would be required to ascertain if these were host specific. Tribal specificity of seedhead tephritids has frequently been reported (e.g. Goeden *et al.* 1987; Green *et al.* 1993; Zwölfer and Arnold-Rinehart 1993), although exceptions do occur, such as *Paroxyna genalis* which is known from 38 species in six tribes of Asteraceae (Goeden *et al.* 1994a).

Tephritids were reared from four introduced plant species. *Sphenella ruficeps* was reared from the plants *Euryops pectinatus* and *Senecio pterophorus*, which is consistent with the observed affinity of *S. ruficeps* for Senecioneae. Similarly, *S. ruficeps* and *Trupanea prolata*, which were both reared from *Senecio madagascariensis* have maintained their tribal affinity. *Senecio madagascariensis*, or fireweed, is a noxious weed in eastern Australia, and is taxonomically very close to the native species *S. laetus* (Parsons and Cuthbertson 1992). Our observation of the transfer of these two species of tephritids from the native species to the introduced species is therefore not surprising. It suggests, however, that it may be difficult to find biological control agents for *S. madagascariensis* that are host specific. Our observation of *Spathulina acroleuca* being reared from the introduced plant *Gerbera jamesonii*, is surprising, since not only is the genus *Gerbera* in a different tribe from the other hosts of *S. acroleuca*, but it is in a different subfamily, Lactucoideae. (Of the two subfamilies in Asteraceae, Lactucoideae is poorly represented in Australia, containing approximately 2% of the native species of Asteraceae (from Willis 1964)). *Spathulina acroleuca* has been collected from *Ageratum conyzoides* (tribe Eupatorieae, subfamily Lactucoideae) in Malaysia (Ibrahim and Zakaria 1988), indicating that either *S. acroleuca* does have a wide host range, or that it comprises more than one species.

Parasitoids of seedhead tephritids and their host and host-plant associations

The diversity of parasitoid species associated with the Australian tephritids collected during this study was not as great as that of their hosts, although this may partly be a reflection of our taxonomic knowledge

Table 2. Parasitoids associated with tephritids reared from Asteraceae collected in south-eastern Australia. Unless otherwise indicated, tephritids were reared from flowerheads. (NSW = New South Wales, Vic = Victoria, ACT = Australian Capital Territory, Qld = Queensland). * - Introduced plant species. ** - Adult tephritid collected from flowerhead (none reared).

Host plant	Location	Tephritidae	Eurytomidae	Torymidae	Pteromalidae	Eulophidae	Others
SUBFAMILY LACTUCOIDEAE							
Tribe Mutiseae							
* <i>Gerbera jamesonii</i>	Frankston (Vic)	<i>Spathulina acroleuca</i>					
SUBFAMILY ASTEROIDEAE							
Tribe Senecioneae							
<i>Senecio odoratus</i>	Clayton (Vic)	<i>Sphenella ruficeps</i> <i>Trupanea glauca</i> <i>Sphenella ruficeps</i>		<i>Torymoides</i> sp. A <i>Torymoides</i> sp. A <i>Torymoides</i> sp. A <i>Torymoides</i> sp. A <i>Torymoides</i> sp. A	<i>Systasis</i> sp. A <i>Systasis</i> sp. A		<i>Apanteles</i> sp. (Braconidae)
<i>Senecio quadridentatus</i>	Black Mtn (ACT) Bungendore (NSW) Tamworth (NSW) Mollymook (NSW) Jervis Bay (NSW)	<i>Sphenella ruficeps</i> <i>Sphenella ruficeps</i> **	<i>Eurytoma</i> sp. B <i>Torymoides</i> sp. A				<i>Apanteles</i> sp. (Braconidae)
<i>Senecio linearifolius</i>	Tathra (NSW) Congo (NSW) Bermagui (NSW) Nowendoc (NSW)	<i>Sphenella ruficeps</i> <i>Sphenella ruficeps</i> <i>Trupanea prolata</i> <i>Sphenella ruficeps</i>		<i>Torymoides</i> sp. A <i>Torymoides</i> sp. A <i>Torymoides</i> sp. A			
<i>Senecio biserratus</i>	Barrington Tops (NSW)	<i>Sphenella ruficeps</i>			<i>Systasis</i> sp.		<i>Apanteles</i> sp. (Braconidae) <i>Apanteles</i> sp. (Braconidae)
<i>Senecio amygdalifolius</i>	Gingers Ck (NSW) Gingers Ck (NSW)	<i>Sphenella ruficeps</i> <i>Sphenella ruficeps</i>	<i>Eurytoma</i> sp.	<i>Megastigmus</i> sp. <i>Megastigmus</i> sp.	<i>Systasis</i> sp. A		<i>Apanteles</i> sp. (Braconidae) Braconidae
<i>Senecio bipinnatisectus</i>	Gingers Ck (NSW)	<i>Sphenella ruficeps</i>					
<i>Senecio lautus</i>	Booti Booti NP (NSW)	<i>Trupanea prolata</i>					
subsp. <i>maritimus</i>	Tacking Pt (NSW) Crowdy Bay NP (NSW) Bermagui (NSW) Barrington Tops (NSW)	<i>Trupanea prolata</i> <i>Trupanea prolata</i> <i>Trupanea prolata</i> <i>Trupanea prolata</i>	<i>Eurytoma</i> sp. C	<i>Megastigmus</i> sp. C <i>Torymoides</i> sp. A <i>Megastigmus</i> sp.	<i>Systasis</i> sp.		Braconidae Braconidae
<i>Senecio lautus</i>	Tamworth (NSW)	<i>Sphenella ruficeps</i> <i>Trupanea prolata</i> <i>Trupanea prolata</i> <i>Trupanea prolata</i>		<i>Megastigmus</i> sp.			<i>Apanteles</i> sp. (Braconidae) <i>Psytalia</i> sp. A (Braconidae)
subsp. <i>lanceolatus</i>	Woodsreef (NSW)	<i>Sphenella ruficeps</i> <i>Trupanea prolata</i> <i>Trupanea prolata</i> <i>Trupanea prolata</i>	<i>Eurytoma</i> sp. B	<i>Megastigmus</i> sp.			
<i>Senecio lautus</i>	Biloela (Qld) Kosciusko N.P. (NSW)	<i>Trupanea prolata</i> <i>Sphenella ruficeps</i> <i>Trupanea prolata</i>					
subsp. <i>alpinus</i>							

Table 2 continued 1

Host plant	Location	Tephritidae	Eurytomidae	Torymidae	Pteromalidae	Eulophidae	Others
* <i>Senecio madagascariensis</i>	Grafton (NSW)	<i>Sphenella ruficeps</i>					
	Harrington (NSW)	<i>Sphenella ruficeps</i>					
		<i>Trupanea prolata</i>	<i>Eurytoma</i> sp.				Braconidae
	Ravensworth (NSW)	<i>Sphenella ruficeps</i>					
	Wollongbar (NSW)	<i>Sphenella ruficeps</i>					
	Cell Ck (NSW)	<i>Sphenella ruficeps</i>					
		<i>Trupanea prolata</i>	<i>Eurytoma</i> sp. C	<i>Megastigmus</i> sp.	<i>Systasis</i> sp.		Braconidae
	Krambach (NSW)	<i>Sphenella ruficeps</i>					
		<i>Sphenella ruficeps</i>					
	Menangle (NSW)	<i>Trupanea prolata</i>	<i>Eurytoma</i> sp. C	<i>Megastigmus</i> sp. C	<i>Systasis</i> sp.		<i>Psytalia</i> sp. A (Braconidae)
	Cessnock (NSW)	<i>Sphenella ruficeps</i>					
		<i>Trupanea prolata</i>					
	Mt Seaview (NSW)	<i>Trupanea prolata</i>					
	Buldelah (NSW)	<i>Trupanea prolata</i>					
	Port Macquarie (NSW)	<i>Sphenella ruficeps</i>	<i>Eurytoma</i> sp. C	<i>Megastigmus</i> sp. C	<i>Systasis</i> sp.		Braconidae
		<i>Trupanea prolata</i>					
	Bittern (Vic)	<i>Sphenella ruficeps</i>		<i>Torymoides</i> sp. A	<i>Pteromalus</i> sp. A		
* <i>Euryops pectinatus</i>	Ocean Grove (Vic)	<i>Sphenella ruficeps</i>		<i>Torymoides</i> sp. A			
Tribe Heliantheae							
<i>Melanthera biflora</i>	Coffs Hbr (NSW)	<i>Rhabdochaeta</i> sp. nov.					<i>Eupelmus</i> sp. A (Eupelmidae)
Tribe Inuleae							
<i>Ixiolaena lepholopis</i>	Moree (NSW)	<i>Tephritis pelia</i>					
<i>Helichrysum scorpioides</i>	Bittern (Vic)	<i>Tephritis poenia</i>		<i>Torymoides</i> sp. A	<i>Systasis</i> sp. A	<i>Aprostocetus</i> sp. B <i>Aprostocetus</i> sp. C <i>Euderus</i> sp. A	
<i>Helichrysum rutidolepis</i>	Falls Ck (Vic)	<i>Tephritis poenia</i>					
<i>Ozothamnus turbinatus</i>	Sandy Pt (Vic)	<i>Tephritis</i> sp. nov. C					
<i>Helipterum albicans</i>	Mt Nelse (Vic)	<i>Tephritis poenia</i>		<i>Megastigmus</i> sp. C	<i>Pteromalus</i> sp. A	<i>Aprostocetus</i> sp. A	
<i>Craspedia</i> sp.	Falls Ck (Vic)	<i>Tephritis poenia</i>					
<i>Leptorhyncos panaetioides</i>	Moree (NSW)	<i>Tephritis pelia</i>					
<i>Leptorhyncos tenuiflorus</i>	Bittern (Vic)	<i>Tephritis poenia</i>		<i>Torymoides</i> sp. A	<i>Pteromalus</i> sp. A	<i>Aprostocetus</i> sp. B	
<i>Leptorhyncos squamatus</i>	Falls Ck (Vic)	<i>Tephritis poenia</i>					
	Canberra (ACT)	<i>Tephritis poenia</i>					
<i>Chrysocephalum apiculatum</i>	Sutton (NSW)	<i>Tephritis pelia</i>		<i>Torymoides</i> sp. A	<i>Systasis</i> sp. A	<i>Eulophidae</i>	<i>Encyrtidae</i>
<i>Chrysocephalum semipapposum</i>	Canberra (ACT)			<i>Megastigmus</i> sp. B		<i>Aprostocetus</i> sp. B	
	Narrabri (NSW)	<i>Tephritis pelia</i> **		<i>Torymoides</i> sp. A	<i>Systasis</i> sp. A	<i>Aprostocetus</i> sp. C	

Table 2 continued overleaf

Table 2 continued

Host plant	Location	Tephritidae	Eurytomidae	Torymidae	Peromalidae	Eulophidae	Others
<i>Calocephalus brownii</i>	Pt Lonsdale (Vic)	New Genus A sp. nov.		<i>Megastigmus</i> sp. A			
<i>Annobium alatum</i>	Ebor Falls (NSW) Nimmitabel (NSW)	<i>Tephritis poenia</i> ** <i>Tephritis poenia</i>					
Tribe Anthemideae							
* <i>Leucanthemum vulgare</i>	Ebor Falls (NSW)	<i>Tephritis poenia</i> ** <i>Spathulina acroleuca</i> **					
Tribe Astereae							
<i>Olearia axillaris</i>	Ocean Grove (Vic)	<i>Tephritis</i> sp. nov. A					
<i>Olearia phlogopappa</i>	Falls Ck (Vic)	<i>Tephritis</i> sp. nov. B	<i>Eurytoma</i> sp. B	<i>Megastigmus</i> sp. C			
<i>Olearia tomentosa</i> subsp. <i>flavescens</i>	Tathra (NSW)	<i>Tephritis</i> sp. nov. D		<i>Megastigmus</i> sp. C <i>Torymoides</i> sp. A	<i>Systasis</i> sp. A		
<i>Celmisia astelifolia</i>	Falls Ck (Vic)	<i>Tephritis</i> sp. nov. B		<i>Torymoides</i> sp. A			
<i>Brachycome segmentosa</i>	Bittern (Vic)	<i>Spathulina acroleuca</i>					
<i>Vittadinia ?triloba</i>	Lake Albecutya (Vic)	New Genus B sp. nov. A					
<i>Vittadinia gracilis</i>	Canberra (ACT)	New Genus B sp. nov. A					
<i>Vittadinia cuneata</i>	Yeovil (NSW)	New Genus B sp. nov. A					
<i>Calotis erinacea</i>	Wyperfeld N.P. (Vic)	<i>Spathulina acroleuca</i>		<i>Torymoides</i> sp. A			
<i>Calotis cuneata</i>	Molong (NSW)	<i>Spathulina acroleuca</i>		<i>Torymoides</i> sp. A		<i>Aprostocetus</i> sp. B	
<i>Minuria integerrima</i>	Moree (NSW)	New Genus B sp. nov. B		<i>Torymoides</i> sp. A	<i>Pteromalus</i> sp. B	<i>Aprostocetus</i> sp. B	
	Moree (NSW)	<i>Tephritis pelia</i> **		<i>Torymoides</i> sp. A	<i>Pteromalus</i> sp. A	<i>Aprostocetus</i> sp. B	
		<i>Spathulina acroleuca</i> **					
* <i>Eriogon mucronatus</i>	Bungendore (NSW)	<i>Spathulina acroleuca</i> **					

The following plants produced no tephritids and no parasitoids: Subfamily Lactuioideae (Tribe Lactueae) *Actites megalocarpa*, **Hypochoeris radicata*, **Taraxacum officinale*, **Fragopogon praetensis*, (Tribe Arctodeae) **Gazania rigens*, Subfamily Asteroideae (Tribe Senecioneae) *Senecio hispidulus*, **Senecio cineraria*, (Tribe Heliantheae) **Coreopsis lanceolata*, (Tribe Inuleae) *Bracteantha viscosa*, *Bracteantha bracteata*, *Pseudognaphalium luteoalbum*, (Tribe Anthemideae) **Chrysanthemum anethifolium*, (Tribe Calenduleae) **Chrysanthemoides monilifera*, **Chrysanthemoides monilifera rotundata*, **Osteospermum fruticosum*, (Tribe Astereae) *Olearia stellulata*, *Brachycome multifida*, **Coryza bonariensis*.

of many of these groups. For instance, all of the specimens of the *Torymoides* species have been placed in one species, which is near *T. australiensis*, however, due to the difficulty of distinguishing between some species, it is possible that more than one species may be present (I. Naumann personal communication). The *Torymoides* species reared from *Mesoclanis* species in South Africa is a different species from the one we recorded in Australian samples, although it is barely distinguishable (I. Naumann personal communication). Similarly, the *Megastigmus* species can be difficult to define due to considerable colour variability, although in the present collections at least three species were recognizable.

There were no clear patterns of host specificity or plant specificity exhibited by the Australian parasitoids. For example *Torymoides* sp. A was associated with six species of tephritids in four genera, and from 14 plant species (including two introduced species) from three tribes. Studies by Hoffmeister (1992) on parasitoids associated with tephritids breeding in pulpy fruits showed that, in general, ecological factors such as habitat or host-fruit texture were more important in determining host-parasitoid associations, than were phylogenetic factors, in particular the taxonomic relatedness of the tephritids. This may well be the case with the Australian species. For instance, *Megastigmus* sp. C was only recorded from coastal localities, but from five tephritid hosts and from plants in three tribes. Some parasitoids, such as *Eupelmus* sp., were only reared from one host (*Rhabdochaetes* sp.) on one host plant (*Melanthera biflora*). This may either be an artefact of our sporadic and opportunistic sampling regime, or it may indicate specificity at the host or host-plant level.

A useful categorization of parasitoids is into koinobionts, which allow the host to continue development before completing their own development and killing the host, and idiobionts, which kill their host at the time of oviposition (Askew and Shaw 1986). The former tend to be specialized endoparasitoids, and the latter tend to be generalist ectoparasitoids. The two predominant parasitoids of *Mesoclanis* species in South Africa, *Eurytoma* sp. A (Eurytomidae), and *Psytalia* sp. (Braconidae) are koinobionts. In addition, our results show that *Eurytoma* sp. A has a diapause, which can delay its emergence for up to 10 months. This is particularly important for *C. m. pisifera* at De Hoop, which has a short, but predictable, flowering period of two to three months. The prolonged diapause

of *Eurytoma* sp. A ensures that its emergence is synchronized with that of *Mesoclanis magnipalpis* at the flowering time of *C. m. pisifera*. At St Lucia, there is also a peak of flowering, although sporadic flowering can occur throughout the year, which is consistent with the more variable diapause observed in *Eurytoma* sp. A from that site, leading to emergences throughout the year. This observation of koinobiont species predominating where good synchrony with the host is essential, is consistent with the conclusions of Hoffmeister (1992), who observed the corollary, that only idiobiont species were found where high synchronization with the host was of no advantage.

The biology of the Australian species of parasitoids collected during this study has not been well studied, so it is not known if any are koinobionts. A high degree of specialization between parasitoid and host would suggest that the parasitoid is likely to be host specific, and although this does not appear to be the case for *E. tibialis* in Europe (see Table 3), it has been suggested that *E. tibialis* may be a cluster of sibling species (Schlumprecht, cited in Zwölfer and Arnold-Rinehart 1994).

Comparisons between structure of parasitoid complexes

Examples of some seedhead-tephritid parasitoid complexes from Europe and North America are presented in Table 3. There are marked similarities between many of these complexes, and with the complex associated with *Mesoclanis* species in South Africa. Most striking is the dominance of a koinobiont *Eurytoma* species in almost all these associations. Zwölfer and Arnold-Rinehart (1993) summarized findings on 24 associations between Cardueae (Cynareae), *Urophora* spp. and *Eurytoma* spp. in Europe, and found that the association between a koinobiont *Eurytoma* species (*E. tibialis* of *E. serratulae*), an idiobiont *Eurytoma* species (*E. robusta*), plus idiobiontic species of *Torymus* (Torymidae) and *Pteromalus* (Pteromalidae), was a remarkably constant complex. Zwölfer and Arnold-Rinehart (1994) suggest that this parasitoid guild "is an ancient and stable one."

Our evidence indicates that the genus *Eurytoma* is less important in Australian seedhead communities, where Torymidae, Pteromalidae and Eulophidae predominate. In Australia and South Africa, *Torymoides* species appear to replace the *Torymus* species of Europe and North America. The Eulophidae, in particular *Aprostocetus* spp., were well represented

Table 3. Parasitoids associated with tephritids reared from Asteraceae collected in Europe and North America. Unless otherwise stated, tephritids were reared from flowerheads. *Tephritidae reared from galls on plant stems; ** Tephritidae reared from mimes on branch; *** Most species of *Tetrastichus* now in *Aprostocetus*.

Tephritidae	Host plant	Region	Eurytomidae	Torymidae	Pteromalidae	Eulophidae	Eupelmidae	Braconidae	Reference
<i>Urophora strumaseva</i>	<i>Centaurea solstitialis</i>	Europe	<i>Eurytoma tibialis</i> <i>Eurytoma robusta</i>	<i>Torymus</i> sp.	<i>Pteromalus</i> sp. (as <i>Habrocytus</i>)				Sobhan and Zwölfer 1985
<i>Urophora solstitialis</i>	<i>Carduus nutans</i>	Europe	<i>Eurytoma tibialis</i> <i>Eurytoma robusta</i>	<i>Torymus chloromerus</i> <i>Antistrophophlex cothurnatus</i>	<i>Pteromalus</i> sp. <i>Colotrechnus</i> sp.	<i>Aprostocetus</i> spp.		<i>Bracon</i> spp. <i>Orgilus</i> sp.	Vitou J. Personal communication
<i>Urophora jaceana</i>	<i>Centaurea nemoralis</i>	UK	<i>Eurytoma tibialis</i> (as <i>curta</i>) <i>Eurytoma robusta</i>	<i>Torymus cyanimus</i> (as <i>Habrocytus</i>)	<i>Pteromalus trypetae</i>	<i>Tetrastichus</i> sp.***	<i>Macroneura vesicularis</i>		Vatley 1947
<i>Urophora stylata</i>	<i>Cirsium vulgare</i>	UK	<i>Eurytoma tibialis</i>	<i>Torymus chloromerus</i>	<i>Pteromalus elevatus</i>				Redfern <i>et al.</i> 1992
<i>Urophora cardui</i> **	<i>Cirsium arvense</i>	Europe	<i>Eurytoma serranulae</i> <i>Eurytoma robusta</i>	<i>Torymus chloromerus</i>	<i>Pteromalus elevatus</i>				Eber and Brandl 1994
<i>Tevellia serratulae</i>	<i>Cirsium vulgare</i>	UK		? <i>Glyptomerus</i> sp.	<i>Pteromalus muscaeus</i>	<i>Tetrastichus cristii</i> ***		<i>Bracon</i> sp.	Redfern <i>et al.</i> 1992
<i>Tephritis conura</i>	<i>Cirsium heterophyllum</i>	Europe	<i>Eurytoma</i> sp. nr <i>tibialis</i>		<i>Pteromalus caudiger</i>				Romstök-Völkl 1990
<i>Euaresta stigmatica</i>	<i>Ambrosia</i> spp.	USA	<i>Eurytoma</i> sp.		<i>Pteromalus</i> sp. <i>Heteroschema</i> sp.				Headrick <i>et al.</i> 1995
<i>Paroxyyna genalis</i>	e.g. <i>Eriophyllum lanatum</i>	USA	<i>Eurytoma</i> sp.		<i>Pteromalus</i> sp. <i>Chlorocyrtus</i> sp. <i>Mesopolobus</i> sp. <i>Colotrechnus</i> sp.	<i>Diglyphus</i> sp.			Goeden <i>et al.</i> 1994a
<i>Neotephritis finalis</i>	e.g. <i>Encelia farinosa</i>	USA	<i>Eurytoma veronia</i>		<i>Pteromalus</i> sp.				Goeden <i>et al.</i> 1987
<i>Procecidochares flavipes</i>	<i>Brickellia</i> spp.	USA	<i>Eurytoma</i> sp.		<i>Pteromalus</i> sp. <i>Colotrechnus ignotus</i>				Goeden <i>et al.</i> 1994b
<i>Procecidochares stoneli</i>	<i>Viguiera</i> spp.	USA	<i>Eurytoma</i> sp.	Unknown sp.	<i>Halticoptera</i> sp.	<i>Tetrastichus</i> sp.***			Green <i>et al.</i> 1993
<i>Tomoplagia cressoni</i>	e.g. <i>Perezia microcephala</i>	USA	<i>Eurytoma veronia</i>		<i>Pteromalus</i> sp. <i>Colotrechnus ignotus</i>				Goeden and Headrick 1991
<i>Eutreta diana</i> *	<i>Artemisia tridentata</i>	USA	<i>Eurytoma</i> sp.	<i>Torymus citripes</i>	<i>Zatropis</i> sp.	<i>Euderus</i> sp.	<i>Eupelmus</i> sp.		Emlen 1992
<i>Eurosta solidaginis</i> *	<i>Solidago altissima</i>	USA	<i>Eurytoma gigantea</i> <i>Eurytoma obtusiventris</i>		<i>Halticoptera</i> sp.				Miller 1959
<i>Valentiballa californica</i> *	<i>Chrysothamnus nauseosus</i>	USA	<i>Eurytoma</i> sp.						Goeden <i>et al.</i> 1995

in the Australian samples, particularly those from the plant tribes Inuleae and Astereae. The genus *Aprostocetus* (sometimes as *Tetrastichus*) was also present in several European and North American parasitoid communities, as well as the *Mesoclanis* spp. community from *Chrysanthemoides monilifera* in South Africa.

A dominant species in the South African *Mesoclanis* spp. parasitoid fauna was the koinobiont braconid *Psytalia* sp. This is in contrast to the European fauna on Cynareae, where although braconids do occur in association with tephritids, they are mostly idiobiont *Bracon* species (Capek and Zwölfer 1990). In Australian samples, the braconid *Apanteles* sp. was associated with tephritids in *Senecio* species. Capek and Zwölfer (1990) note that the *Apanteles* species that occur in European thistles are koinobiont, but tend to be associated with lepidopteran hosts.

Fate of seedhead tephritids in biological control programmes

About half of the species of tephritids used as biological control agents have become abundant in their new habitat and are exerting varying degrees of control over the target weed (Harris 1989; Julien 1992). For instance, ten years after *Urophora affinis* and *U. quadrifasciata* were introduced into Canada for the control of *Centaurea diffusa* and *C. maculosa*, no native parasitoids had been acquired and the flies attained population densities five to eighteen times greater than those that occur in Europe (Myers and Harris 1980). Low levels of parasitism have subsequently been detected in these species (P. Harris personal communication). Of the failures, some can be attributed to unsuitability of the target weed as a host (Harris 1989). Of particular interest here is whether any failures, or cases where poor control has been achieved, can be attributed to the transfer of native parasitoids to the introduced host.

Among seedhead tephritids, there are remarkably few records of introduced species being parasitized by native parasitoids. This may in part reflect a lack of detailed follow-up studies, or of reporting cases where parasitism is having only a negligible effect. One published case where an introduced tephritid has acquired parasitoids in its country of introduction, is the tephritid *Orellia ruficauda* and its host *Cirsium arvense* in Canada. The tephritid now has two endoparasitic eulophid parasitoids, although it is not

stated if these are native or whether they arrived with the tephritid (Lalonde and Roitberg 1992). Both the tephritid and the host plant have been in Canada for more than a hundred years. Furthermore, the parasitoids are not implicated in the lack of control of the weed.

Another example is the case of *Procecidochares utilis*, a tephritid used against Crofton Weed *Ageratina adenophora*. It is deemed to have been a success in Hawaii, but not in Australia, New Zealand, India or South Africa. This tephritid is a stem-galling species, in contrast to the seedhead species discussed so far. It is generally accepted that endophagous herbivores, such as galling species, are more prone to parasitism as a consequence of their immobility and high discoverability (Askew and Shaw 1986). *Procecidochares utilis* is specific to *A. adenophora* and, in the absence of parasitoids, is capable of controlling the weed. Even in the presence of parasitoids in Hawaii it is controlling the weed. In four of the five countries where *P. utilis* has been released it has acquired native parasitoids, and in the fifth, New Zealand, it acquired an Australian parasitoid. In Australia, the dominant parasitoid is *Megastigmus* sp. (Torymidae) (Dodd 1961), the same species that later was found in New Zealand (Hill 1989). In South Africa *Torymoides* sp. (= *Dimeromicrus*) (Torymidae), *Eupelmus* sp. (Eupelmidae) and a Pteromalidae were involved (Kluge 1991); in India a *Torymoides* sp. (= *Dimeromicrus*) and *Syntomopus* sp. (Pteromalidae) (Rao *et al.* 1971); and in Hawaii the main species were a *Bracon* sp. (Braconidae), a *Eupelmus* sp. and a *Eurytoma* sp. (Eurytomidae) (Bess and Haramoto 1972). There are no close phylogenetic similarities between the parasitoids acquired in the different regions, other than that *Torymoides* sp. was acquired in two countries, and in all localities except Hawaii, a torymid was included. The *Megastigmus* sp. that parasitized *P. utilis* in Australia is not the same as any of the species collected from our seedhead samples (I. Naumann personal communication).

Other tephritids introduced into Australia include the flowerhead species *Earesta aequalis*, which was released in 1932 and has established on Noogoora burr, *Xanthium strumarium*. No control has been achieved (Haseler 1966), although there have been no records of parasitoids attacking the tephritid. The stem-galling *Procecidochares alana* was released on mistflower, *Ageratina riparia* in 1986, and has established (Julien 1992), and again there is no report of parasitoids attacking this species. More recently the flowerhead

species *Urophora solstitialis* has been released on nodding thistle *Carduus nutans* (Woodburn 1993), and is now established but has not acquired any native parasitoids (Sheppard and Woodburn in press). *Tephritis postica* was released on *Onopordum* spp. in 1994 (D. Briese personal communication), so it is too early to know if establishment has occurred.

Likelihood of Mesoclanis species acquiring Australian parasitoids

The data presented on Australian flowerhead tephritid communities indicate that there is a suite of parasitoids present which could attack *Mesoclanis* species when they are released for the biological control of *Chrysanthemoides monilifera* in Australia. In this final section we consider the likelihood of this occurring, which species may be involved, and their possible impact on the usefulness of *Mesoclanis* species as a biological control agent.

There are several factors in favour of *Mesoclanis* species not acquiring native parasitoids at all. Firstly, the history of flowerhead tephritids used in biological control programmes suggests this. Secondly, *C. monilifera* is in a plant tribe not represented in Australia, and although it has been shown that this is of more relevance to defining the host range of the tephritids than their parasitoids, in the case of *C. monilifera* it may be of some importance. *Chrysanthemoides* species, and many *Calendula* and *Osteospermum* species possess calenic acid which may be unique to the tribe (Bremer 1994), and thus may be involved in defining the host range of specific herbivores, and even parasitoids. Furthermore *C. monilifera* is distinguished, even within the Calenduleae, by the presence of a fleshy drupe and a hard woody seed-coat, a characteristic which could deter generalist parasitoids. It is probable that non-specialized parasitoids would have to attack larvae of *Mesoclanis* species early in development, before they become ensconced within the relative sanctuary of a developing seed. This is perhaps a contributing factor towards the fact that two of the main parasitoids of *Mesoclanis* species in South Africa are koinobionts, which obviously have the capacity to emerge from the woody seed. Thirdly, *C. m. rotundata* is predominantly a coastal species (Weiss 1986), occurring along the New South Wales coast, an area that we found to be depauperate of native Asteraceae. It is therefore possible that there is not the abundance of parasitoids searching on asteraceous flowerheads in coastal

regions that exists in drier inland regions, where species from the Asteraceae are known to be much more diverse and abundant (Willis 1964; Morley and Toelken 1983). *Chrysanthomoides m. monilifera* occurs in both coastal and inland regions (Weiss 1986), and therefore may be more exposed to native parasitoids.

If *Mesoclanis* species do acquire native parasitoids, which parasitoids are likely to be involved? Generalist species are far more likely to be involved than specialists and idiobionts rather than koinobionts. The predominance of Torymidae and Pteromalidae would suggest that these families could be the source of potential parasitoids. *Torymoides* sp. A was the most widespread and abundant parasitoid. *Megastigmus* sp. C, which has a mainly coastal distribution, could be a candidate to parasitize *Mesoclanis* species on *C. m. rotundata* and coastal populations of *C. m. monilifera*. Additional species collected from coastal areas of New South Wales where *C. m. rotundata* is most abundant included *Systasis* sp. A, *Eupelmus* sp. A. and *Apanteles* sp..

If *Mesoclanis* species do acquire one or more of these parasitoids, will their potential success as biological control agents be jeopardized? In South Africa, in the presence of at least two dominant koinobiont species, and several idiobiont species, inflicting between 50% and 90% parasitism for most of the year (P.B. Edwards unpublished), *Mesoclanis* species have a significant impact on seed production, up to 64% seed destruction has been recorded at one site (P.B. Edwards and E.M. Brown unpublished). In most biological control programmes where native parasitoids have been recruited, the overall level of parasitism has been lower than on the host in the country of origin (Cornell and Hawkins 1993), and in many cases the effectiveness of the biological control agent has been little affected (e.g. Manongi and Hoffmann 1995). One reason for this is that generalist parasitoids are usually not capable of having a major impact on a host that has a synchronized seasonality, which would be the case with *Mesoclanis* species associated with *C. monilifera*.

In conclusion, we cannot predict the likelihood of *Mesoclanis* species acquiring native parasitoids in Australia. We are more confident in predicting what these parasitoid species might be, and we are optimistic that if parasitoids do attack *Mesoclanis* species, their impact will be negligible in the biological control programme against *C. monilifera* in Australia.

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