Basic Biology and Host Use Patterns of Tephritid Flies (Phytalmiinae: Acanthonevrini, Dacinae: Gastrozonini) Breeding in Bamboo (Poaceae: Bambusoidea)

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ABSTRACT   We report results of field collections, laboratory rearing, and behavioral observations of tephritids belonging to the tribes Acanthonevrini and Gastrozonini in Malaysia and Thailand. The focus of the study was on general biology, seasonal history, mating, oviposition, larval biology, larval habits, and microhabitats. Host association with bamboo was unequivocally established for 31 species. Adult flies fed on liquids oozing from plants or other sources. Most species developed in the rainy season, when bamboo shoots were available. In Thailand, adult flies gathered along streams in the dry season. Observed sexual behavior patterns appeared to be simple in Gastrozonini, whereas in some Acanthonevrini, the males produced a foamy "nuptial gift," which was offered to females during courtship. Eggs were laid under sheaths or in injuries to the bamboo surface. The main obstacle to oviposition and penetration of shoots appeared to be the hard culm sheaths. The larvae entered feeding substrates via injuries, holes created by other insects, or by squeezing in between culm sheaths and bamboo walls. Larvae of Gastrozonini and *Rioxoptilona* (Acanthonevrini) fed on living or dead bamboo shoots. Larvae of other Acanthonevrini developed in water-filled internode cavities, scraping particles from walls or collecting them from the water surface. Bamboo growth stages and degree of protection by culm sheaths were used to classify microhabitats. These determined to a large extent which guilds of flies could be found. While larvae of some bamboo tephritids destroyed thin bamboo shoots or branches, most acted as secondary pests and did not cause substantial economic losses.

KEY WORDS   bamboo fly, behavior, habitat preference, economic importance

Fruit flies breeding in bamboo (Poaceae: Bambusoidea) are one of the least studied groups of tephritids (Aluja and Norrbom 2000). Almost nothing had been published on their basic biology and ecology before our investigations (Kovac and Azarae 1994, Dohm and Kovac 2001, Dohm et al. 2008, Kovac et al. 2010, Kovac et al. 2013).

There are two subfamilies of Tephritidae that harbor species exploiting bamboos: the Dacinae and the Phytalmiinae (sensu Korneyev 2000). In the Dacinae, only the tribe Gastrozonini has acquired bamboo as a host. The Asian species with known host records all breed in bamboo, whereas the African species breed in other Poaceae (e.g., *Panicum*, *Sorghum*, and *Zea*; Hancock 1999, Hancock and Drew 1999a, Copeland 2007). The Gastrozonini comprise 137 described species (Kovac et al. 2005/6) and several undescribed species. They are regarded as a monophyletic entity, although to date there is no consistent unambiguous morphological synapomorphy that would permit proper definition of clades.

The subfamily Phytalmiinae hosts a cluster of genera which, at least in part, exploit bamboo in various stages and conditions. All of them are assigned to the tribe Acanthonevrini (Korneyev 2000). Some of these species breed in bamboo shoots in an advanced state of decay, while the larvae of others live semiaquatically in the internodes of older shoots or dead culms (Hardy 1973, 1974; Hancock and Drew 1995, 1999b; Kovac and Streit 1996; Dohm and Kovac 2001; Dohm et al. 2008). The Phytalmiinae breeding in bamboo do not form a monophyletic group. Korneyev (2000) treats them in different subgroups of the Acanthonevrini, which also harbor species breeding in substrates other than bamboo (e.g., fruits and dead wood).

Bamboos have several striking features, of which size (up to 30 m high) and fast growth of shoots in some species are prominent (Kovac and Azarae 1994). The mechanical properties of the bamboo stems make them an important material for durable and lightweight constructions and for use in handicrafts (Farrelly 1984, Recht and Wetterwald 1992, Wong 1995). The shoots are widely used as food in Asian cuisine. The basic morphology of bamboo is similar to that of

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other grasses: the bamboo stem or "culm" is a rod divided into segments by transverse septae or "nodes," and the sections in between these are called "internodes." In most bamboo species, the internodes are hollow, which allows the development of phytotelmata when the internode wall is perforated, for example, by boring insects, or otherwise damaged (Kovac and Streit 1996).

The shoots are clad in robust overlapping sheaths inserted at the nodes, which serve as a shelter for the soft growing tissue and protect it from insects or mechanical damage. Growth is achieved by lengthening of the internodal wall between subsequent nodes. Usually, the sheaths dry out at some point and fall off.

Given that bamboo represents a resource of growing economic importance, research to identify host use patterns and the potential impact of the bamboo-breeding tephritids could be useful for identifying and managing pest species. From a more basic perspective, given that most of our knowledge on fruit flies stems from studies on a handful of species of economic importance, acquiring data on little-known taxonomic groups can improve our understanding of evolutionary patterns and life history strategies within the Tephritidae in particular and among phytophagous insects in general (Sivinski 2000, Sivinski et al. 2000).

Materials and Methods

Study Sites. Field work was carried out during several field trips between 1998 and 2003 in Malaysia (P.D. and D.K.) and between 2001 and the present in Thailand (D.K. and A.F.). In Malaysia, the main study site was located at the Ulu Gombak Field Study Centre (UFSC) of the University of Malaya (West-Malaysia, Selangor Darul Ehsan), ≈30 km north of Kuala Lumpur in the western foothills of the Genting Highlands (3° 19′32″ N and 101° 45′16″ E; altitude: 250 m; Kovac and Streit 1996). Additional collecting sites (P.D.) were close to Kampung Kemensah and Hulu Langat (Selangor Darul Ehsan, near Kuala Lumpur), near Labis (Johore, 30 September to 3 October 2003), and near Pokok Sena (Kedah, 29 October to 6 November 2003) (Table 1).

The Ulu Gombak area is covered with lowland dipterocarp forests. Owing to past selective logging, bamboo was abundant in the vicinity of the UFSC (Kovac and Streit 1996). The dominant bamboo species was *Gigantochloa scortechinii* Gamble, which is endemic to the Malay Peninsula (Fig. 1). It reaches a height of up to 25 m, with internodes of 20–60 cm in length and 8–10 cm in diameter, and a wall thickness of ≈1 cm (Kovac and Azarae 1994, Kovac 1998). The shoots of *G. scortechinii* grow at a rate of up to 15–20 cm/d (Kovac and Azarae 1994). *G. scortechinii* sprouts from August to November, with the occasional appearance of thin shoots during the rest of the year. Other bamboos occurring in the area included *Dendrocalamus pendulus* Ridley, one stand of *Dendrocalamus giganteus* Munro, and additional unidentified species.

In Thailand, observations were carried out in the Province of Mae Hong Son (NW Thailand), district of Pangmapha (19° 28,189′ N, 98° 17,741′ E; altitude ≈900 m), during several field trips between 2001 and the present. The mountainous Pangmapha district is primarily covered with dipterocarp monsoon forests; however, bamboos are common in disturbed areas. About 15 species of bamboo were recorded in the area: *D. giganteus*, *Dendrocalamus hamiltonii* Nees and Arnott ex Munro, *Dendrocalamus strictus* (Roxburgh) Nees, *Dendrocalamus.* sp., *Bambusa polymorpha* Munro, *Bambusa tuldoides* Munro, *Cephalostachyum pergracile* Munro, *Thyrsostachys siamensis* Gamble, *Melocalamus compactiflorus* (Kurz) Bentham, and additional unidentified species. In Pangmapha, bamboo shoots of most species were present between May and October, with shoots of the largest species appearing in July or later.

Collecting and Preservation. To gauge species composition and distribution of tephritids in the study area, we collected the adults by selective net sweeping from different types of bamboo microhabitats or by net sweeping from surrounding vegetation. A parang (machete) was used to create cuts in the shoots to increase their attraction to bamboo tephritids. The adults were either pinned or preserved in 70% ethanol. Larvae were boiled for 2–3 min and then preserved in 70% ethanol to obtain suitable material for descriptions. Voucher specimens of adult flies are stored in the collection of Entomology I at the Senckenberg Museum in Frankfurt am Main, Germany (SMF).

Obtaining Eggs and Larvae to Rear to Adults. The methods used to obtain larvae to rear to adults comprised: 1) collecting dead bamboo shoots cut by locals or damaged by *Cyrtotrachelus* beetles, followed by laboratory examination; 2) cutting young shoots and placing them on the ground or in an upright position for 1 to 2 wk, followed by transfer to the laboratory; 3) felling shoots or culms and breaking open the internodes to collect the larvae developing in internode cavities; 4) collecting eggs from locations where egg laying was observed or from field-collected material; and 5) placing field-collected females in containers provided with bamboo material for the "breeding experiments."

Another source of larvae developing inside the internode cavities of dead culms was the experimental internodes, which were prepared according to the method of Kovac and Streit (1996): a bamboo culm was felled and the top part cut off. The basal part of the culm comprising 10–15 internodes was stripped of branches and fixed horizontally ≈1.5 m above the ground. Two cuts were sawn near the nodes approximately halfway through each internode. The tip of a parang was then inserted into an end of one of these slits and, using a hammer, driven lengthwise along the internode to the other slit. The blade was then fully inserted into this cut and tilted, thus creating a lid on the upper side of the internode. The lid could be opened and closed for inspection or for collection of material (Fig. 2).

Rearing of Larvae in the Laboratory and Breeding Experiments. Bamboo shoots collected in the field were either temporarily stored in 40- by 20- by 30-cm

Table 1. List of tephritids collected or reared from bamboo during the present study and used in breeding experiments (see "Materials and Methods")

Species	Collected from bamboo	Reared from field-collected bamboo substrate	Breeding experiments in the lab in Malaysia
Dacinae, Gastrozonini			
Acroceratitis bilineata (Meijere)	M	M	−(11)
Acroceratitis ceratitina (Bezzi)	T		
Acroceratitis distincta (Zia)	T	T	
Acroceratitis hardyi Hancock and Drew	M	M	
Acroceratitis histrionica (Meijere)	T	T	
Acroceratitis incompleta Hardy	T	T	
Acroceratitis nigrifacies Meijere	M	M	−(6)
Acroceratitis septemmaculata Hardy	T	T	
Acroceratitis n. sp.	T		
Acrotaeniostola fuscinotum Hering	M		
Acrotaeniostola longicauda Wang	T	T	
Acrotaeniostola quinaria (Coquillett)	M		−(1)
Acrotaeniostola cf. *spiralis* Munro	M		−(1)
Acrotaeniostola n. sp. aff. *quinaria*	T	T	
Anoplomus rufipes Hardy	T		
Carpophthorella cf. *capillata* (Bezzi)	M, Sabah[a]		
Carpophthorella sookae Chua	M		+(11)
Chaetellipsis bivittata (Hardy)	M	M	+(3)
Chaetellipsis maculosa Hancock and Drew	M, T	M	+(11)
Chaetellipsis paradoxa Bezzi	T		
Cyrtostola limbata (Hendel)	M, T	M, T	−(1)
Enicoptera gigantea Enderlein	M	M	−(7)
Enicoptera sumatrana (Hering)	M	M[b]	
Gastrozona balioptera Hardy	T		
Gastrozona fasciventris (Macquart)	M, T	M, T	+(9)
Gastrozona selangorensis Chua	M	M	−(3)
Ichneumonopsis burmensis Hardy	T	T	
Ichneumonopsis n. sp.	M		
Paraxarnuta anephelobasis Hardy	T	T	
Paraxarnuta extorris (Hering)	M		−(1)
Paraxarnuta sp.	M		−(1)
Taeniostola vittigera Bezzi	M, T	M	+(9)
Xanthorrachis annandalei Bezzi	M, T	T	−(1)
Phytalmiinae, Acanthonevrini			
Felderimyia flavipennis Hancock and Drew	M		−(3)
Felderimyia fuscipennis Hendel	M, T	M	−(5)[c]
Felderimyia gombakensis Hancock and Drew	M, T	M, T	−(2)
Kambangania ypsilon (Rondani)	M, T		
Langatia setinerva Hancock and Drew	M	M	
Ptilona confinis (Walker)	M, T	M	
Ptilona conformis Zia	M	M	
Ptilona sp.	M, Sabah[a]		
Rioxoptilona dunlopi (Wulp)	M, T	M, T	−(5)
Rioxoptilona gravelyi (Munro)	T	T	
Rioxoptilona hemileina (Hering)	T	T	
Rioxoptilona ochropleura (Hering)	M	M	−(7)
Rioxoptilona soluta (Bezzi)	T		
Rioxoptilona vaga (Wiedemann)	M, T	M, T	−(8)
Themara cf. *hirtipes* Rondani	M, T		
Themara cf. *maculipennis* (Westwood)	M		
Trypetinae, Adramini			
Adrama determinata (Walker)	M		

The collected specimens were resting on stems, shoots, or leaves of different bamboo species.

M, Malaysia; T, Thailand; +, breeding experiment successful in at least one trial; −, breeding experiment failed; in brackets, number of breeding experiments.

[a] This species was only observed, not caught.

[b] The specimens did not eclose properly, but most probably were *Enicoptera sumatrana*.

[c] One specimen resulted from a breeding experiment. This is regarded as an artefact.

plastic fish tanks covered with fine-mesh gauze, or immediately dissected to retrieve larvae. Larvae were sorted based on morphological characters (e.g., shape, size, and color) and then placed into 18- by 12.5- by 6.5-cm plastic boxes along with uncontaminated shoot material. Larvae developing in internode cavities were kept in cut internodes with openings sealed with gauze and rubber bands. Internodes were placed upright in a sink or large plastic containers, containing 1–2 cm of water as protection against ants. Temperature and light conditions approximated those in the field (no environment control). In the rainy season in the forest, the daily minimum temperature was 18°C and maximum temperature was 31°C.

Fig. 1. Bamboo habitat at the Ulu Gombak Studies Center in West Malaysia. Note the different developmental stages of *G. scortechinii*: shoots (center), mature upright culms, and dead toppled down bamboo culms.

Breeding boxes were inspected daily. Larvae leaving the substrate to pupate were collected and transferred to pupation boxes containing layers of moistened tissue. Pupation boxes were inspected daily, and puparia were separated and transferred to labeled vials for eclosion. Pupation vials were stored in a fish tank containing 2 cm of water to provide a humid atmosphere. Eclosed flies were isolated for ≈3 d and allowed to develop until fully pigmented. For breeding experiments in Malaysia, females of 21 species of Gastrozonini and Acanthonevrini were placed in containers equipped with a piece of freshly cut bamboo shoot to enable oviposition.

Attraction of Tephritids to Cut Bamboo Shoots (Table 2). On 29 August 1998, five shoots of *G. scortechinii* were cut from different locations in the vicinity of the UFSC and observed daily for 5 min. At 1-min intervals, tephritid species arriving on the shoot, their gender, and abundance were recorded. The observations were repeated over 15 consecutive days (no observation available for day 11).

Nomenclature of Bamboo Shoot Parts and Classification of Microhabitats (Fig. 2). When a bamboo shoot emerges from the soil, it is protected by tightly overlapping culm leaves, also called "culm sheaths" (Holttum 1958, McClure 1966) or "sheaths." The shoot apex consists of apical meristem (tissue consisting of undifferentiated cells) and a condensed series of internodes, which elongate through cell division and extension at their basal parts.

A new shoot always emerges with the same basal diameter as it will have when full height is reached (no stem thickening). After the internodes have elongated, the culm sheaths mainly encase the soft tissues

of the basal growth region of each internode. The culm sheath consists of the sheath proper and the "blade." The blade is a small leaf-like protrusion from the tip of the sheath. Small projections at the junction of blade and sheath are called "auricles." In some bamboo species, they contain "extrafloral nectaries" (Schellerich–Kaaden and Maschwitz 1998). When the elongation period of the bamboo shoot nears completion and the internode walls have hardened, branches start to grow from lateral or "branch buds" and the culm sheaths dry up and fall off (terminology after McClure 1966, Recht and Wetterwald 1992, Wong 1995, Judziewicz et al. 1999).

Larval microhabitats were classified as follows (Fig. 2): (A) dead (felled) bamboo shoot lying on the ground, including stump; (B) dead upright shoot or felled shoot in an upright position; (C) apical (soft) part of an upright shoot (large bamboo species, internodes short, and culm sheaths overlapping); (D) basal, partly hardened part of an older upright shoot (internodes elongated, only basally covered by culm sheaths); (E) thin shoot of a small bamboo species or side branch of a large bamboo species (both symbolized in Fig. 2 as side branch of a large bamboo culm); (F) mature, upright culm; and (G) dead (felled) mature culm.

Results

Adult Biology: Adult Habitat, Activity, and Food Sources (Table 3). Bamboo-breeding Gastrozonini and Acanthonevrini were commonly sighted on bamboo or under leaves of the surrounding vegetation. The flies were active during daytime and left the
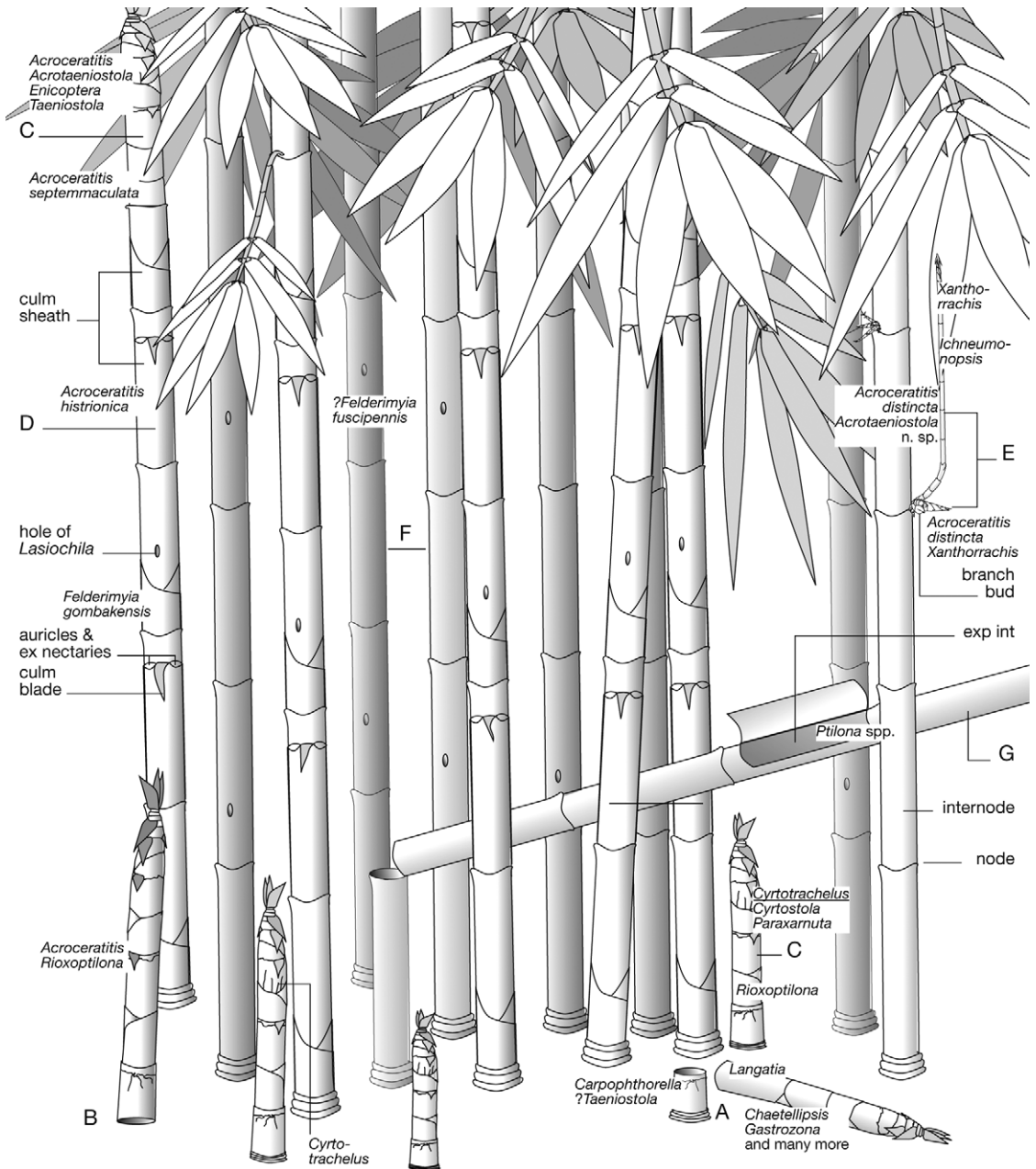
Fig. 2. Schematic drawing of a bamboo stand illustrating culms at different stages of development (A–G), describing technical terms and indicating larval microhabitats of Gastrozonini and Acanthonevrini. (A) Dead (felled) shoot lying on the ground. (B) Dead upright shoot. (C) Apical part of an upright shoot. (D) Basal part of an older upright shoot. (E) Thin shoot of a small species or side branch of a large bamboo species. (F) Mature, upright culm. (G) Dead (felled) mature culm; ex nectaries, extrafloral nectaries; exp int, experimental internode; ?, presumed larval habitat, (see "Material and Methods" for further information).

breeding sites before dawn. Only *Cyrtostola limbata* (Hendel) was observed at night, waiting on the back of *Cyrtotrachelus* weevils to bore an egg-laying hole (Kovac and Azarae 1994). Most Gastrozonini and Acanthonevrini were encountered on bamboo shoots. In contrast, the Acanthonevrini *Felderimyia* spp., *Ptilona* spp., and *Langatia setinerva* Hancock and Drew usu-

ally remained on upright or fallen culms throughout the entire year. *Felderimyia* specimens moved on upright older shoots (*Felderimyia gombakensis* Hancock and Drew) or mature culms (*F. gombakensis*, *Felderimyia flavipennis* Hancock and Drew, and *Felderimyia fuscipennis* Hendel), whereas *Ptilona* and *Langatia* preferred fallen bamboo culms. *Ptilona* typically ran in

Table 2. Frequency of tephritid specimens arriving on five freshly cut bamboo shoots lying on the ground in the vicinity of the Ulu Gombak FSC, West Malaysia

Species	Days													
	1	2	3	4	5	6	7	8	9	10	12	13	14	15
Acroceratitis bilineata	7♀	1♀	2♀	—	1♀	—	—	—	—	—	—	1♀*	—	—
Acroceratitis nigrifacies	6♀	1♀	3♀	—	—	—	—	—	—	—	—	—	—	—
Chaetellipsis maculosa	1♀	1♀	—	—	—	—	—	—	—	—	—	—	—	—
Enicoptera gigantea	6♂ 6♀	3♂ 2♀	4♂ 1♀	—	2♂	—	—	—	—	—	—	—	—	—
Gastrozona fasciventris	7♀	2♀	2♀	—	—	—	—	—	—	—	—	—	—	—
Taeniostola vittigera	1♂ 3♀ 1	—	—	—	—	—	—	—	—	—	—	—	—	—
Rioxoptilona dunlopi	—	—	—	?1♂	—	?1♀	1♂	1♀	?1♂	?2♂	—	—	—	—
Rioxoptilona ochropleura	—	—	—	—	—	?1♀	1♀	—	—	—	—	1♀	—	—
Rioxoptilona sp.	—	—	—	—	—	1♀	1♀	—	—	—	—	—	—	—
Rioxoptilona vaga	?1	?1	4♀	1♀	3♀	1♀	1♀	1♀	1♀	—	—	—	—	—
Adrama determinata	1	—	—	—	—	—	—	—	—	—	—	—	—	—

The gender of the specimens was recorded, whenever possible.
Doubtful species are marked with "?".
Rioxoptilona sp. belongs to *R. dunlopi* or *R. ochropleura.*
The female *Acroceratitis bilineata* marked with "*" remained on the bamboo shoot for just a few seconds.

a wiggly line, alternately stretching out a wing to the left or right; while *Langatia* often flapped its wings while walking. All these Acanthonevrini hid on the opposite side of the culm when approached.

We have classified the bamboo microhabitats inhabited by different guilds of tephritids according to the life stages of the bamboo and the degree of protection offered by the culms sheaths (Microhabitats A–G, Fig. 2; see also "Materials and Methods").

Certain Gastrozonini were attracted by freshly cut bamboo shoots lying on the ground or cut into pieces (Table 2). During the peak of the shooting season, they arrived almost immediately or within minutes after the shoot was cut, frequently in high numbers. The first Gastrozonini species arriving at cut shoots of *G. scortechinii* at the UFSC were usually *Chaetellipsis* spp. (*maculosa* Hancock and Drew or *bivittata* (Hardy)), *Gastrozona fasciventris* (Macquart) (Fig. 3A) or, less often, *Taeniostola vittigera* Bezzi (Fig. 3B). The next Gastrozonini to arrive were *Acroceratitis* and *Enicoptera* spp. (Fig. 3C). Cut shoots attracted the Gastrozonini for only ≈3 d. Acanthonevrini (*Rioxoptilona dunlopi* (Wulp) (Fig. 4A), *Rioxoptilona ochropleura* (Hering) and *Rioxoptilona vaga* (Wiedemann)) preferred older cut shoots, mostly between the 3rd and 10th d after the shoot was felled (see Table 2). For some Gastrozonini and Acanthonevrini, only females were attracted by cut shoots (Table 2).

In northern Thailand, bamboo-breeding tephritids of several species were abundant along mountain streams or in other humid locations during the dry season (February until April; Table 3). They could be encountered on waterside vegetation, on wet stones, or on leaves partly submerged in streams. *Felderimyia* and *Ptilona* (Fig. 4B–D) were the only tephritids being commonly encountered on bamboo culms even in the hot season. However, two *Felderimyia* specimens and seven *Ptilona* specimens were also found on wet leaves near streams.

Adults of Gastrozonini and Acanthonevrini were sighted feeding on liquids oozing from bamboo cuts or injuries (shoots or mature culms) or on birds or bat feces. Some Gastrozonini were also found on rotting fruits, and adults of several species dabbed with their proboscis on plant juices adhering to the cloth of the collecting net, on sweat adhering to hands, backpacks, clothing, notebooks, or net handles, especially during the dry season in Thailand. Acanthonevrini were observed dabbing with their proboscis on the surface of mature bamboo culms covered with microbial or fungal or epiphytic growth and on rotting logs. Both Gastrozonini and Acanthonevrini imbibed water from rain drops or dew on leaves or from wet stones and leaves immersed in mountain streams, especially during the dry season (Table 3).

Gastrozonini, Acanthonevrini, and many other insects regularly licked on exudates from extrafloral nectaries situated on the culm sheaths of bamboo shoots in Malaysia and Thailand (Figs. 2 and 3E). Resident tephritids defended such extrafloral nectaries against conspecifics or other approaching invertebrates. Aggressive behavior included displays such as synchronous and asynchronous wing supination (sensu White et al. 1999), and forward darting movements of the body with legs remaining in place (as described for species of the genus *Blepharoneura* by Condon and Norrbom [2000]), accompanied by rapid opening and closing of the wings.

Mating. Our behavioral observations for Gastrozonini and Acanthonevrini are fragmentary. Mating was observed for three species of Gastrozonini: *T. vittigera*, *Enicoptera gigantea* Enderlein and *Chaetellipsis maculosa* Hancock and Drew. *T. vittigera* regularly copulated on freshly cut shoots and shoot stumps (Fig. 3B). *E. gigantea* was also observed to mate on young cut shoots lying on the ground (Fig. 3C). During an observational session on 10 August 1998, between 1705 and 1924 hours, a male standing on a cut shoot mounted two females 33 times. The male copulated at least five times with one female and 13 times with the other. The remaining 15 mountings could not be attributed to a particular female. Several mountings were brief and can be considered failed attempts. The females appeared to reject copulation attempts by tilting their ovipositor upwards to prevent intromis-

Table 3. Feeding sites of Gastrozonini and Acanthonevrini flies

Species	Cut shoots	Cuts in culms	Bamboo nectaries	Rotting logs	Rotting fruits	Feces	Sweat	Net cloth	Wet substrate
Gastrozonini									
Acroceratitis bilineata	x	x	x			x	x		
Acroceratitis ceratitina	x					x		x	
Acroceratitis distincta	x		x			x	x	x	x
Acroceratitis hardyi	x	x	x				x	x	
Acroceratitis histrionica	x							x	
Acroceratitis incompleta	x						x	x	x
Acroceratitis nigrifacies	x	x	x					x	
Acroceratitis septemmaculata	x	x						x	x
Acrotaeniostola fuscinotum			x						
Acrotaeniostola longicauda			x						x
Acrotaeniostola quinaria			x						
Acrotaeniostola sp. n. aff. *quinaria*	x								
Anoplomus rufipes	x							x	
Carpophthorella sookae	x								
Carpophthorella cf. *capillata*	x								
Chaetellipsis bivittata	x		x						
Chaetellipsis maculosa	x	x	x						
Chaetellipsis paradoxa	x		x						
Cyrtostola limbata	x	x	x	x		x	x	x	x
Enicoptera gigantea	x	x	x			x			
Enicoptera sumatrana	x								
Gastrozona fasciventris	x		x	x			x	x	x
Gastrozona balioptera									x
Gastrozona selangorensis	x								
Ichneumonopsis sp. n.	x								
Paraxarnuta anephelobasis	x	x					x	x	x
Paraxarnuta extorris	x	x				x	x		
Paraxarnuta sp.	x								
Taeniostola vittigera	x	x	x				x	x	x
Xanthorrachis annandalei	x		x				x		x
Acanthonevrini									
Felderimyia flavipennis		x	x						
Felderimyia fuscipennis	x	x	x	x					x
Felderimyia gombakensis	x	x	x	x					x
Kambangania ypsilon	x		x						
Langatia setinerva	x	x							
Ptilona confinis	x	x		x					x
Ptilona conformis		x							
Rioxoptilona dunlopi	x		x						
Rioxoptilona gravelyi	x								
Rioxoptilona hemileina	x								
Rioxoptilona ochropleura	x								
Rioxoptilona soluta				x					x
Rioxoptilona vaga	x								x
Themara cf. *hirtipes*	x	x	x	x		x			x
Themara cf. *maculipennis*	x		x						

The flies were feeding on sap of injured shoots and old bamboo culms as well as on plant juices adhering to the cloth of the collecting net (="net cloth").

In northern Thailand, the bamboo tephritids gathered along streams and imbibed water from wet leaves or stones (="wet substrate").

sion. This behavior was observed on other occasions as well. In one case the above-mentioned male reacted to such behavior by grasping the female's ovipositor with its forelegs and shaking it. Finally, the female accepted copulation.

For other Gastrozonini such as *G. fasciventris* or *Chaetellipsis* spp., males were rarely seen on cut shoots (Table 2). On one occasion, a *C. maculosa* male was tracked for ≈40 min on a cut shoot, repeatedly courting females and attempting to grasp them. The females fought the male off or did not react to its courtship in four out of six attempts. The male only managed to mount a female twice and stayed there <1 min. An insertion of the male copulatory organ could not be observed. On a picture of the courting male, it can be

seen that it bore a drop of liquid at the tip of its abdomen.

For the Acanthonevrini, mating was observed in *Felderimyia, Ptilona,* and *Rioxoptilona.* In *F. gombakensis, F. fuscipennis,* and *F. flavipennis* courtship and mating took place on upright mature bamboo culms. In all cases the male produced a white froth ("nuptial gift") from its proboscis before the arrival of females (Dohm et al. 2008). *F. fuscipennis* and *F. gombakensis* males were observed walking up and down the bamboo culm in the vicinity of the white froth. They added froth material from time to time and remained at the same location for the whole day. The male courted an approaching female with fast opening and closing of its wings (enantion sensu Headrick and Goeden 1994).
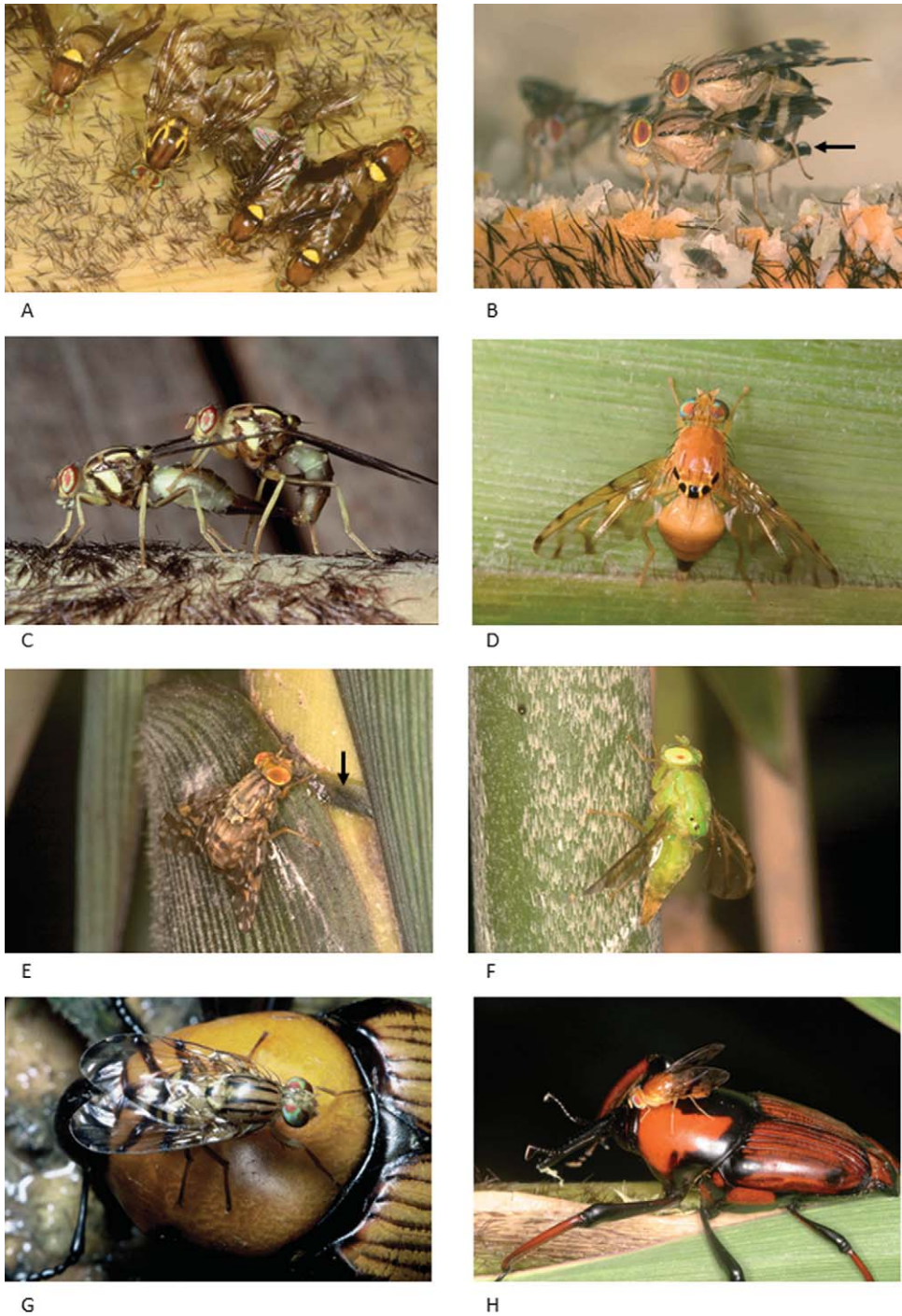
Fig. 3. Gastrozonini developing in dead or living bamboo shoots in Thailand and Malaysia: (A) *Chaetellipsis paradoxa* Bezzi (entirely yellow scutellum) and *G. fasciventris* (centrally blackish scutellum) on dead shoot lying on the ground. (B) *T. vittigera* copulating on freshly cut shoot stump, note the drop of liquid at the tip of the female's abdomen (arrow). (C) *E. gigantea* copulating on a freshly felled bamboo shoot. (D) *A. septemmaculata* female ovipositing under the edge of a culm sheath. (E) *A. distincta* dabbing at the green bamboo extrafloral nectary (arrow). (F) *X. annandalei* resting on a thin bamboo shoot. (G) *C. limbata* waiting on the back of a female beetle *Cyrtotrachelus* sp. (Malaysia). (H) *P. anephelobasis* waiting on the back of *Cyrtotrachelus* sp. (Thailand; figures G and H rotated clockwise through 90°).
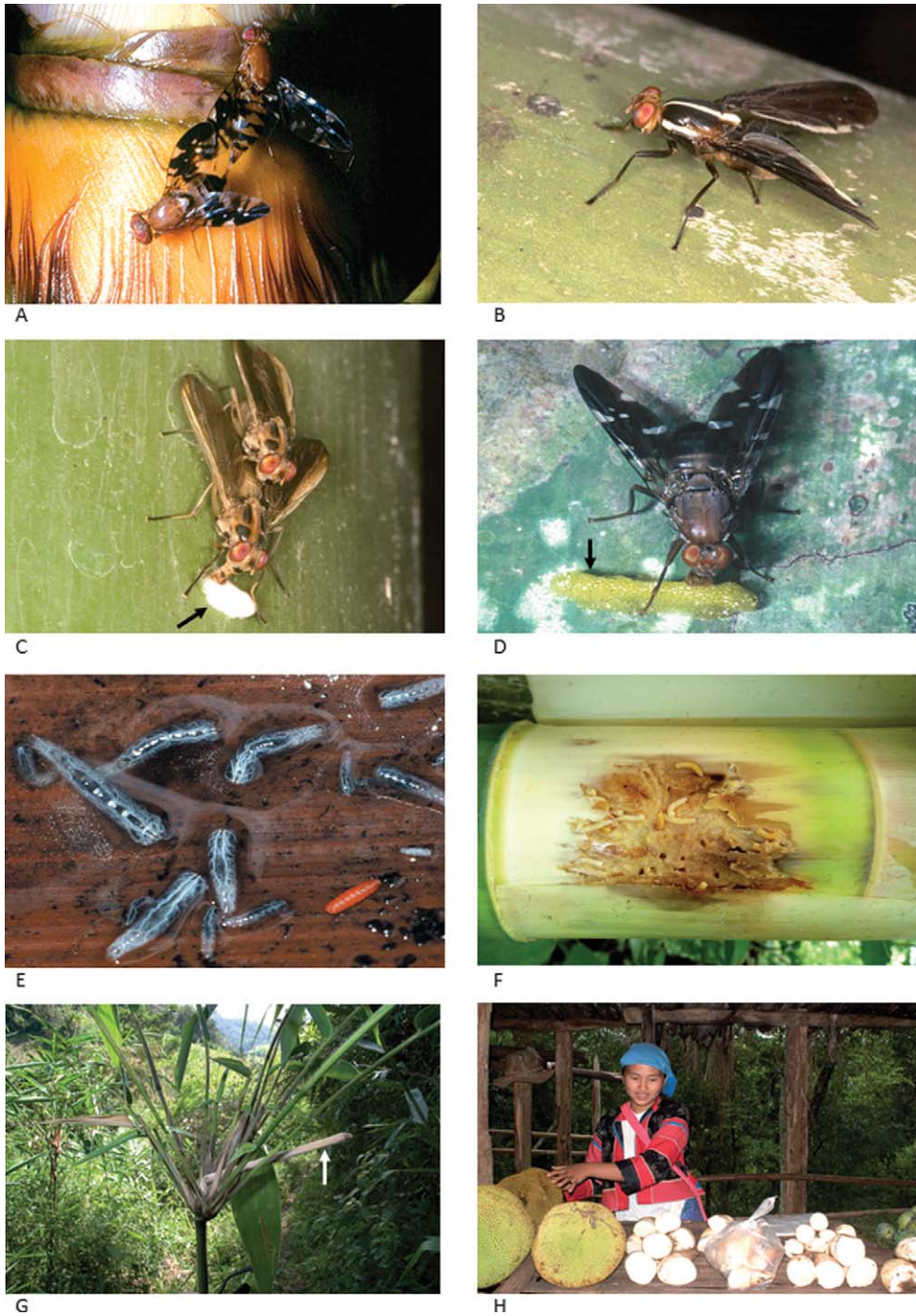
Fig. 4. Acanthonevrini developing in bamboo, Gastrozonini and Acanthonevrini larvae, bamboo damages caused by bamboo tephritids, and bamboo usage: (A) *R. dunlopi* mating on an upright bamboo shoot. (B) *F. fuscipennis* resting on a mature bamboo culm. (C) Female of *F. gombakensis* feeding on the white "nuptial gift" (arrow) during copulation. (D) *P. confinis* male preparing a greenish, elongate nuptial gift (arrow). (E) Semiaquatic larvae of *P. confinis* found in the internode cavity of a dead bamboo culm. (F) Larvae of *A. septemmaculata* feeding on the wall of a bamboo shoot (culm sheath removed). (G) Bamboo shoot damaged by the larva of *I. burmensis*. The dead bamboo internode containing the larva is dangling at the tip of the bamboo culm (arrow). The apical internodes of the shoot have already fallen down. (H) Lahu woman selling shoots of *Dendrocalamus* sp. (right, jackfruit to the left) at a roadside stall in north Thailand. Females of *Gastrozona* and *Chaetellipsis* were ovipositing on these shoots.

However, the female only managed to feed on the white froth for longer during copulation (Fig. 4C). If the female refused to mate, the male chased it away.

Ptilona displayed a similar mating behavior, but mating occurred on dead bamboo culms. A male of *Ptilona* sp. from Sabah, Borneo, was observed producing a white froth mass on a living culm (P. D., unpublished data), and a male of *Ptilona confinis* (Walker) from the Malay Peninsula created an elongated and greenish froth mass on a dead culm (D. K., unpublished data, see Fig. 4D). Some *Ptilona* cf. *confinis* copulated on dead bamboo culms, but there was no evidence of froth masses in the surroundings. Sometimes a drop of a liquid was present at the tip of the abdomen in *P. confinis.*

Mating of *R. dunlopi* was observed on three occasions. In Thailand, *R. dunlopi* mated on the underside of a leaf near a freshly felled bamboo shoot, which was cut to pieces. In Malaysia, *R. dunlopi* mated under a leaf near a freshly cut older shoot and on one occasion on the tip of an upright shoot (Fig. 4A). In the latter case, the male had already dismounted, but the couple's genitalia were still joined. These two flies disengaged when caught, but resumed copulation in the vial. During the following 2 h, still in the vial, the couple switched from the back-to-back position in which they were encountered initially to mounting and back several times. No transfer of a nuptial gift was observed for this species.

Egg Laying (Table 4). *Microhabitats A and B—Cut Bamboo Shoots Lying on the Ground or Placed in an Upright Position.* Several species in the genera *Acroceratitis, Carpophthorella, Chaetellipsis, Enicoptera, Gastrozona, Taeniostola,* and *Rioxoptilona* were observed ovipositing on cut shoots. Females usually inserted their flat aculei under the edge of a protective culm sheath. However, they also exploited injuries to shoots (cuts, etc.) for egg laying. Several females of the same or different species used the same spots concomitantly for egg laying. Females of *Acroceratitis bilineata* (Meijere), *C. maculosa,* and *G. fasciventris* were observed dragging their ovipositor after egg laying.

Carpophthorella sookae Chua females, which were rarely encountered in the field, were observed laying eggs in a freshly cut bamboo stump in western Malaysia, while *Carpophthorella* cf. *capillata* (Bezzi) oviposited on a freshly cut bamboo shoot of *D. giganteus* in Sabah. Some species of *Acroceratitis,* such as *A. bilineata, Acroceratitis nigrifacies* Meijere, and *Acroceratitis septemmaculata* Hardy (Fig. 3D), occasionally oviposited on cut shoots. On one occasion, *A. bilineata* was observed laying eggs under sheaths of an older cut shoot. Other Gastrozonini, which were rarely encountered on cut shoots, that is, *Acrotaeniostola* and *Paraxarnuta* spp., were never observed laying eggs in this substrate.

Acanthonevrini preferred older decaying shoots for oviposition. In *Rioxoptilona* spp., oviposition attempts were observed in cut shoots, which had been lying on the ground for more than 5 d (see Table 2). Egg laying was also observed in older cut shoots placed in an upright position (*Rioxoptilona hemileina* (Hering) and *R. dunlopi*).

In the laboratory, several Gastrozonini (*C. sookae, C. maculosa, Chaetellipsis bivittata* (Hardy), *G. fasciventris,* and *T. vittigera*) oviposited on shoots cut into pieces, and the resulting offspring were successfully bred to the adult stage. *A. nigrifacies* was observed to lay eggs, but no larvae developed. *A. bilineata* only laid eggs in 1 out of 11 trials. In Acanthonevrini, a single female of *F. fuscipennis* was reared. *R. ochropleura* appeared to oviposit, but failed to produce larvae.

Microhabitats C, D, and E—Thick or Thin Upright Bamboo Shoots. Several species of *Acroceratitis, Cyrtostola, Paraxarnuta, Taeniostola,* and *Rioxoptilona* were observed laying eggs on upright shoots. Females of *T. vittigera* oviposited under sheaths or into 2-d-old cuts made with a parang. *A. septemmaculata, Acroceratitis distincta* (Zia), and *E. gigantea* also laid eggs under sheaths of upright shoots. Eggs of *E. gigantea* collected in the field were reared to adulthood. *Rioxoptilona* spp. were the only Acanthonevrini to lay eggs in upright shoots. *R. hemileina* and *R. dunlopi* were observed to lay eggs under sheaths of a shoot that had been injured with a parang.

Gastrozonini belonging to *Cyrtostola* and *Paraxarnuta* oviposited into egg-laying punctures produced by weevils of the genus *Cyrtotrachelus. Cyrtotrachelus* females bored holes with their proboscis ≈20–30 cm below the apex of a shoot. The flies usually remained on the back of the beetle until the hole was finished and then laid their eggs concomitantly with the beetle. *Cyrtotrachelus* laid eggs between overlapping culm sheaths close to the surface (Kovac 2005). Consequently, the freshly hatched beetle larva had to penetrate the bamboo wall to reach the internode cavity. *Paraxarnuta anephelobasis* Hardy and the associated *Cyrtotrachelus* species were observed laying eggs in the daytime, while *C. limbata* and the associated *Cyrtotrachelus* species were active during the night (Kovac and Azarae 1994, Kovac 2005).

Females of *F. gombakensis* laid their eggs in the lower region of older shoots (Fig. 2). Eggs were placed under culm sheaths near entry holes created by larvae of leaf beetles of the genus *Lasiochila.* In one case, eggs were laid in the *Lasiochila* bore-dust adhering to the culm surface, and on another occasion a female probed a *Lasiochila*-hole with its ovipositor, but the duration was probably too short for oviposition. One female was observed laying eggs under a sheath on a stump of a shoot that had a hole, most probably made by *Tetraponera* sp. (Formicidae: Pseudomyrmecinae), but larvae did not develop from these eggs. Another female was observed ovipositing under sheaths and into cuts made into a young shoot with a parang.

Microhabitats F and G—Mature or Dead Bamboo Culms. F. fuscipennis oviposited on mature culms under the rotting remains of a culm sheath still adhering to the bamboo surface (one observation). Oviposition by *Ptilona* spp. was observed on freshly prepared "experimental internodes" (see "Materials and Methods") in felled mature culms. Females oviposited under re-

Table 4. Larval microhabitats (A–G), oviposition sites, and host species of bamboo-breeding Gastrozonini and Acanthonevrini investigated in the present study

Tephritid species	A: Dead or felled shoot	B: Dead or felled upright shoot	C: Erect shoot, apical part	D: Erect shoot, lower part	E: Thin shoot or side branch	F: Mature bamboo culm	G: Rotting bamboo culm	Oviposition site	Bamboo species, M, Malaysia; T, Thailand	References
Acroceratitis bilineata	Wall tissue, inner side of sheaths	—	Eggs below sheath	—	—	—	—	Below sheath	*G. scortechinii* (M)	Hancock and Drew 1999, present study
Acroceratitis distincta	Wall tissue, internode cavity	—	—	—	Wall tissue, internode cavity	—	—	Below sheath	*M. compactiflorus* (T), *D. strictus* (T), *B. polymorpha* (T)	Allwood et al 1999, present study
Acroceratitis hardyi	Wall tissue, inner side of sheaths	—	—	Wall tissue next to sheath	—	—	—	Below sheath?	*G. scortechinii* (M) *D. pendulus* (M)	Present study
Acroceratitis histrionica	—	—	—	Wall tissue next to sheath	—	—	—	Below sheath	*D. strictus* (T)	Present study
Acroceratitis incompleta	Wall tissue, internode cavity	Wall tissue, internode cavity	Wall tissue, internode cavity	—	—	—	—	Below sheath?	*B. polymorpha* (T), *Dendrocalamus* sp. (T), *M. compactiflorus* (T)	Present study
Acroceratitis nigrifacies	Wall tissue, inner side of sheaths	—	Wall tissue	—	—	—	—	Below sheath	*G. scortechinii* (M)	Present study
Acroceratitis septemmaculata	—	Wall tissue next to sheath	Wall tissue next to sheath	—	—	—	—	Below sheath	*D. strictus* (T)	Present study
Acrotaeniostola longicauda	Wall tissue	—	Wall tissue	—	—	—	—	?	*Dendrocalamus* sp. (T)	Present study
Acrotaeniostola n. sp. aff. *quinaria*	—	—	Wall tissue	—	Wall tissue, internode cavity	—	—	?	*M. compactiflorus* (T)	Present study
Carpophthorella cf. *capillata*	Wall tissue?	—	—	—	—	—	—	In cuts	*D. giganteus* (M, Sabah)	Hancock and Drew 1999, present study
Carpophthorella sookae	Wall tissue	—	—	—	—	—	—	Inner walls and cut surface of bamboo shoot stumps	*G. scortechinii* (M)	Chua 2003, present study
Chaetellipsis bicittata	Wall tissue	—	—	—	—	—	—	Below sheath?, in cut tissue	*G. scortechinii* (M)	Allwood et al. 1999, present study
Chaetellipsis maculosa	Wall tissue	—	—	—	—	—	—	Below sheath?, in cut tissue	*G. scortechinii* (M) *S. grande* (M)	Hancock and Drew 1999, present study
Cyrtostola limbata	—	—	Wall tissue, internode cavity	—	—	—	—	Oviposition holes of *Cyrtotrachelus* spp. (Coleoptera)	*G. scortechinii* (M), *D. strictus* (T), *C. pergracile* (T), *B. polymorpha* (T)	Kovac and Azarae 1994, present study
Enicoptera gigantea	Wall tissue	Wall tissue	Wall tissue, internode cavity	—	—	—	—	Below sheath	*G. scortechinii* (M)	Hancock and Drew 1999, present study
Enicoptera cf. *sumatrana*	Wall tissue	—	—	—	—	—	—	Below sheath?	*D. pendulus* (M)	Present study
Gastrozona fasciventris	Wall tissue	—	—	—	—	—	—	Below sheath, in cuts	*G. scortechinii* (M), *D. giganteus* (M), *S. grande* (M), *B. polymorpha* (T), *C. pergracile* (T), *D. tuldoides* (T)	Allwood et. al 1999, present study
Gastrozona selangorensis	Wall tissue	—	—	—	—	—	—	Below sheath?, in cuts?	*S. grande* (M)	Chua 2003, present study
Ichneumonopsis burmensis	—	—	—	—	Pith of internode cavity	—	—	Below sheath?	*M. compactiflorus* (T)	Kovac et al. 2013

Table 4. Continued

Tephritid species	A: Dead or felled shoot	B: Dead or felled upright shoot	C: Erect shoot, apical part	D: Erect shoot, lower part	E: Thin shoot or side branch	F: Mature bamboo culm	C: Rotting bamboo culm	Oviposition site	Bamboo species, M, Malaysia; T, Thailand	References
Parataxaruta anephlebobasis	—	—	Wall tissue, internode cavity	—	—	—	—	Oviposition holes of *Cyrtotrachelus* spp. (Coleoptera)	*C. pergracile* (T), *M. compactiflorus* (T), *B. polymorpha* (T)	Kovac 2005
Taeniostola vittigera	Wall tissue	—	Eggs below sheath	—	—	—	—	Below sheath, in cuts	*G. scortechinii* (M)	Allwood et al. 1999, present study
Xanthorrachis annandelei	—	—	—	—	Internode cavity	—	—	Below sheath	*D. strictus* (T)	Allwood et al. 1999, present study
Felderimyia fuscipennis	—	—	—	—	—	? Internode cavity	—	Under decaying sheath	*G. scortechinii* (M) *C. pergracile* (T)	Present study
Felderimyia gombakensis	—	—	—	Internode cavity	—	Internode cavity	—	Below sheath, in cuts, near entrance holes of *Lasiochila* spp.(Coleoptera)	*G. scortechinii* (M), *C. pergracile* (T)	Dohm et al. 2008
Langatia setinerva	Internode cavity	—	—	—	—	—	—	?	*G. scortechinii* (M)	Dohm et al. 2008
Ptilona confinis	—	—	—	—	—	—	Internode cavity	Under remains of sheaths, in cracks of bamboo wall, near insect holes	*G. scortechinii* (M) *S.* cf. *grande* (M)	Hancock and Drew 1994, Kovac and Streit 1996, Dohm et al. 2008, Kovac et al. 2010, present study
Ptilona cf. *conformis*	—	—	—	—	—	—	Internode cavity	Under remains of sheaths, in cracks or crevices of bamboo wall	*G. scortechinii* (M) *S.* cf *grande* (M)	Present study
Rioxoptilona dunlopi	?	Wall tissue	Wall tissue	—	—	—	—	Below sheath?	*C. pergracile* (T), *D. tuldoides* (M)	Allwood et al. 1999; present study
Rioxoptilona graelpi		Wall tissue		—	—	—	—		*C. pergracile* (T)	Present study
Rioxoptilona hemileina	Wall tissue	Wall tissue	Wall tissue	—	—	—	—	Below sheath	*B. polymorpha* (T), *Dendrocalamus* sp. (T)	Present study
Rioxoptilona ochropleura	Wall tissue	-	Wall tissue, internode cavity	—	—	—	—	Below sheath?	*D. giganteus* (M), *G. scortechinii* (M)	Present study
Rioxoptilona vaga	Wall tissue	Wall tissue	Wall tissue	—	—	—	—	Below sheath	*G. scortechinii* (M) *D. pendulus* (M), *Dendrocalamus* sp. (T), *B. polymorpha* (T)	Hancock and Drew 1995, present study

References mainly refer to the overview of Allwood et al. 1999 as well as more recent publications.

Table 5. Duration of puparial stages and total developmental times of bamboo tephritids

Species	Puparial stage (d)				Total developmental time (d)			
	Min.	Max	Mean	n	Min.	Max	Mean	n
Acroceratitis hardyi	10	10	10	1	20	26	21.7	11
Acroceratitis bilineata	9	10	9.8	79	21	33	24.1	78
Acroceratitis nigrifacies	10	11	10.2	5	21	30	25.8	6
Carpophthorella sookae	8	10	9.2	122	16	25	18.1	122
Chaetellipsis bivittata	8	9	8.4	8	15	21	17.5	13
Chaetellipsis maculosa	9	10	9.5	20	16	38	26.7	49
Cyrtostola limbata	15	17	15.8	7	—	—	—	—
Enicoptera gigantea	11	17	14.2	53	30	58	35.6	19
Felderimyia fuscipennis	—	—	—	—	43	43	43	1
Felderimyia gombakensis	13	16	14.9	26	—	—	—	—
Gastrozona fasciventris	8	13	11.2	371	24	49	32.5	418
Gastrozona selangorensis	—	—	—	—	40	41	40.3	3
Langatia setinerva	18	18	18	1	—	—	—	—
Ptilona confinis	10	21	15.3	18	31	34	32.4	5
Ptilona conformis	11	13	12.3	3	—	—	—	—
Rioxoptilona ochropleura	13	15	14.2	6	40	45	42.5	2
Rioxoptilona vaga	12	14	12.7	50	25	44	33	65
Taeniostola vittigera	10	11	10.6	5	24	26	24.8	5

The data combine results from breeding experiments and incubation of field-collected material.

Data presented are the min., max., and mean developmental time in days and the number of specimens investigated.

mains of sheaths or in small cracks near the nodes of the culms.

Immature Biology, Larval Development. The larvae of most Gastrozonini and Acanthonevrini developed during the rainy season, when bamboo shoots were available. Young larvae were usually pale creamy, whereas older larvae were either pale or their color changed to orange, yellow, green, or purple. Most larvae jumped frequently at the end of the last larval stage, while others such as *F. gombakensis* rarely jumped, and *Ichneumonopsis burmensis* Hardy did not jump at all (Kovac et al. 2013). For most species, several to many larvae per internode were found, but for *I. burmensis* and *Xanthorrachis annandalei* Bezzi each colonized internode was inhabited by a single larva.

Our data on larval development of the bamboo-inhabiting Gastrozonini and Acanthonevrini are fragmentary and mostly originate from the breeding experiments in which field-captured females were transferred to boxes containing pieces of young bamboo shoots for egg laying. Five out of 15 tested species of Gastrozonini were bred to the adult stage using this method. The duration of larval development was between 5 and 17 d: *C. sookae* (5 and 6 d), *C. bivittata* (8 and 11 d), *C. maculosa* (5, 10, 14, and 17 d), *G. fasciventris* (8 and 11 d), and *T. vittigera* ($\approx$13 d).

The length of the puparial stage could be determined for 10 species of Gastrozonini and six species of Acanthonevrini. For Gastrozonini, it lasted between 8 and 17 d, and for Acanthonevrini between 11 and 21 d. Our data combine results from breeding experiments and incubation of field-collected material (see Table 5).

We also calculated the duration of total developmental time for several species from the assumed time of egg laying, that is, from the beginning of a breeding experiment, the collection of freshly laid eggs in the field, or time of cutting of the shoot. Thus, we esti-

mated a total approximate developmental time of between 15 and 58 d for the Gastrozonini (10 species) and between 25 and 45 d for the Acanthonevrini (three species; see Table 5).

Larval Microhabitats (Table 4). *Microhabitat A— Felled Bamboo Shoot.* Thirteen Gastrozonini and three Acanthonevrini species were reared from larvae found in felled shoots lying on the ground. The shoots were either felled or had toppled owing to natural causes. In the first case, we assume that oviposition took place after cutting; in the latter case, larvae could have started development in an upright shoot. The larvae reared to the adult stage belonged to *Acroceratitis*, *Carpophthorella* (breeding experiment), *Chaetellipsis*, *Enicoptera*, *Gastrozona*, *Taeniostola* (breeding experiment), *Rioxoptilona*, and *Langatia*. Larvae of one to several species developed more or less simultaneously in one shoot, feeding in the soft bamboo tissue and the small node cavities, until the bamboo tissue turned into a foul-smelling mush. Three species—*E. gigantea*, *A. nigrifacies*, and *R. vaga*—were also bred from eggs collected on stumps of felled shoots.

Chaetellipsis and *Gastrozona* were exclusively found in dead shoots lying on the ground. They fed on the softer material of the shoot tip, where they were found in large accumulations, turning the substrate into liquefied sludge. Species belonging to other genera occurred in cut shoots as well as in other bamboo microhabitats. For example, *A. distincta* was usually found in thin upright bamboo shoots in Thailand; however, in one case we reared this species from a thin cut bamboo shoot. At that time of the year (end of November, after the rainy season), the common *Chaetellipsis* and *Gastrozona* species were not seen on the shoots.

In contrast to the species mentioned above, larvae of *L. setinerva* were found in the cavity of an already elongated internode at the base of an older felled

shoot (single observation). They were semiaquatic and stayed close to the water surface.

Microhabitat B—Dead Upright Bamboo Shoot Found in the Field (a) or Cut Shoot Placed in an Upright Position (b). (a) In several cases, we found dead young shoots that showed no signs of damage by *Cyrtotrachelus* or other organisms. These shoots were relatively dry and hard and contained larvae of *R. dunlopi, Rioxoptilona gravelyi* (Munro), and *R. vaga,* mining between the bamboo wall and the sheaths. Two puparia of *E. gigantea* were found in a container with the remains of such a shoot.

(b) Felled bamboo shoots placed in an upright position yielded *A. septemmaculata, Acroceratitis incompleta* Hardy, and *R. hemileina.* The larvae fed in the bamboo wall protected by the surrounding culm sheaths (*A. septemmaculata* close to the bamboo surface, Fig. 4F).

Microhabitat C—Upright Bamboo Shoots, Upper Part, Entirely Covered by Overlapping Culm Sheaths. Larvae were usually found in shoots that had been injured by *Cyrtotrachelus* (a) or otherwise damaged (b). (a) *C. limbata* and *P. anephelobasis* developed in internodes, which were infested by a (usually single) beetle larva of the weevil genus *Cyrtotrachelus.* Larvae remained in those internodes, which were interconnected through the perforations caused by the beetle larva. The tephritid larvae fed on the bamboo tissue of the wall or on material which had been digested or crushed by the beetle larva. Tephritid larvae ready for pupation abandoned the shoot through the exit hole made by the beetle larva. In rare cases ($n > 3$), a single specimen of *P. anephelobasis* pupated in the damaged bamboo shoots, while the other 8–10 larvae left the internode. The shoot or only the apical part of a shoot (in higher or older shoots) died off owing to the damage caused by the beetle larva. Dead *Cyrtotrachelus* shoots of *C. pergracile* remained in the upright position and were colonized by *R. dunlopi* and *R. gravelyi* after the beetle larva had left.

(b) The apical parts of upright bamboo shoots damaged by unknown natural causes or by cuts made with a parang yielded several bamboo tephritids: *A. incompleta, A. nigrifacies, A. septemmaculata* (Fig. 4F), *Acrotaeniostola longicauda* Wang, *E. gigantea, T. vittigera* (eggs found behind sheath), *R. dunlopi,* and *R. hemileina.* One shoot that was basally damaged by an organism yielded *R. hemileina.* Larvae were found in the bamboo tissue or in small internode cavities.

Larvae of *A. septemmaculata* were also found in shoots showing no apparent damage ($n \geq 5$). They stayed between the apex (Microhabitat C) and basal area of the shoot (Microhabitat D). In this intermediate zone, the internodes were elongated but had not yet reached the final length, and thus the sheaths were overlapping to some extent. Larvae were orange and fed on bamboo tissue close to the surface, protected by the surrounding sheaths.

Microhabitat D—Lower Part of Upright, Intact Bamboo Shoot, in Which the Internodes Are Elongated and Only Partly Covered by the Culm Sheaths. In this microhabitat, we found the larvae of *Acroceratitis histri-*

onica (Meijere). The larvae were whitish and fed on the surface of the basal part of the internode in the area close to a latent branch bud protected by the culm sheath. The surface of the bamboo was harder than the surface of the internodes eaten by *A. septemmaculata.*

Larvae of *F. gombakensis* were found in the same type of internodes as *A. septemmaculata,* that is, in those which were elongated and still enveloped by a sheath. These whitish tephritid larvae inhabited the internode cavities and were semiaquatic. To enter the internodes, *F. gombakensis* larvae used perforations created by leaf beetle larvae of *Lasiochila goryi* (Guerin) (Malaysia) and *Estigmena* Hope sp. (Thailand; D. K., unpublished data). They remained close to the water surface, but some also advanced into drier parts of the internode or deeper into the water. They are also capable of floating with their posterior spiracles attached to the water surface and to swim erratically through powerful bending of their bodies. These highly active larvae grazed on the walls of the internode or collected material from the water surface. They left the internodes for pupation through exit holes created by the leaf beetle larvae (Dohm et al. 2008).

Microhabitat E—Thin Bamboo Shoot of Small Bamboo Species or Side Branch of Large Bamboo Species. In Thailand, larvae of four Gastrozonini were found in thin shoots of the small bamboo species *M. compactiflorus.* The cavity of the internode at the apex of the shoot was inhabited by a single green-colored larva of *X. annandalei* ($n \geq 15$). Larvae of *I. burmensis* occurred about four to six internodes below the apex ($n \geq 40$). A single *Ichneumonopsis* larva fed on the white pith found inside the internode cavity and caused characteristic damage patterns (Kovac et al. 2013; Fig. 4G). Internodes located below *I. burmensis*-internodes were occasionally infested by *A. distincta* ($n \geq 10$). Every *A. distincta* internode was inhabited by ≈10–15 *A. distincta* larvae. In one case, an internode contained larvae of both *A. distincta* and *Acrotaeniostola* n. sp. aff. *quinaria.* Two of the species found in thin bamboo shoots, *X. annandalei* and *A. distincta,* also developed in growing buds or lateral branches of the large bamboo species *D. strictus* (Fig. 2). The thickness of the dead apical shoots killed by the species mentioned above was ≈1–2 cm.

Microhabitat F—Mature, Old Bamboo Culm. In Malaysia and Thailand, we found larvae in mature upright bamboo culms, and these could not be reared to the adult stage. The larvae were large and whitish and remained near the water surface or sometimes crawled into the water all the way to the bottom of the internode. They probably belonged to *F. fuscipennis* or *F. flavipennis.*

Microhabitat G—Felled or Fallen Mature Bamboo Culms. In cavities of fallen or felled bamboo culms, we detected larvae of two *Ptilona* species, *P. confinis* (Fig. 4E) and *P. conformis* Zia. The larvae were semiaquatic and behaved similarly to larvae of *F. gombakensis.* They entered internodes through holes created by various organisms (leaf beetles, long-horn beetles, and

woodpeckers) or through cracks in the bamboo wall. On one occasion at least three *Ptilona* females laid eggs on a bamboo culm containing experimental internodes (see "Materials and Methods"). Females oviposited under remains of sheaths or in small cracks near the nodes. Because it was the end of a prolonged dry period in February 2002 (Ulu Gombak), the internode cavities were dry. Two days after oviposition it rained, the cavities filled up with water, and the *Ptilona* larvae hatched. Oviposition behavior like this on an experimental internode was observed at least in one more case.

Discussion

Adult biology (feeding, mating, and egg laying), seasonal history, larval microhabitats, and the potential economic impact of bamboo-breeding tephritids are discussed below. Our results reveal the extraordinary diversity (at least 31 species) of tephritids exploiting a single resource (bamboo), as well as the extraordinary diversity of behavioral repertoires and life history strategies used by these species. As highlighted by Sivinski et al. (2000), studying the natural history of little known groups within the Tephritoidea can shed light on the evolutionary patterns of a group for which our knowledge is based on only a handful of species of economic importance.

Adult Biology. Bamboo tephritids were usually encountered on living or dead shoots (Gastrozonini and Acanthonevrini) or on upright or dead culms (Acanthonevrini). Both groups were observed feeding on the liquid emanating from injured shoots or culms, on exudates from extrafloral nectaries, or on feces, but there were differences between the two groups. Gastrozonini fed on plant liquids adhering to the collecting net, on rotting fruits, and on sweat, whereas Acanthonevrini preferred feeding on rotting logs (Table 3).

Cut bamboo shoots were attractive to the Tephritidae as oviposition sites, but many Gastrozonini (e.g., *Paraxarnuta* spp.) and Acanthonevrini (e.g., *Ptilona* spp.) visited them exclusively for feeding. This was also true for other Acanthonevrini such as *Themara* spp., which develop in dead wood, or *Adrama* spp., which develop in fruits with hard texture. Even *Bactrocera* spp. were occasionally observed on cut shoots. Acanthonevrini developing in bamboo (*F. gombakensis* and *Ptilona* spp.) were occasionally observed on rotting logs (Table 3). These patterns indicate that the attraction of tephritids to cut shoots cannot be taken as indicative of a host association with bamboo, and that the sole unequivocal criterion by which to establish host association is that of finding the larvae of a certain species in the host tissue.

We only observed Gastrozonini of the genera *Chaetellipsis*, *Enicoptera*, and *Taeniostola* mating on their breeding substrates; males approached the females from behind and mounted them without any apparent courtship displays. Sometimes Gastrozonini males or females, for example, *C. maculosa* or *T. vittigera* (Fig. 3B), carried a drop of liquid at the tip of their abdomen during mating. A hypothesis to test is that such drops contain pheromones or volatiles that could act as aphrodisiacs. Extracting these volatiles and testing female response to them could contribute in elucidating its function. Multiple matings were common, as is the case in the Acanthonevrini (Kovac et al. 2010) and several other Tephritidae (Sivinski et al. 2000). These patterns are normally found in species that exhibit resource defense mating systems (Headrick and Goeden 1994), a fact that future in-depth studies are expected to confirm. In some other Gastrozonini such as *Acroceratitis*, *Chaetellipsis*, and *Gastrozona*, only females were encountered on cut shoots. These and other Gastrozonini perhaps mate near bamboo stands on the underside of leaves, as we observed in *R. dunlopi*.

In the Acanthonevrini genera *Felderimyia* and *Ptilona*, courtship behavior was complex and comprised the transfer of a viscous secretion from the males to the females ("nuptial gift") (Dohm et al. 2008, Kovac et al. 2010). The secretion is apparently produced by the salivary glands of the male and was placed on the surface of mature, upright bamboo culms. The nuptial gift appears to be a concentrated nutritional resource attractive to females that is monopolized by the males to increase an individual's chances of mating (Kovac et al. 2010). The function of the nuptial gift may be to attract females, to overcome the female's tendency to resist or take flight, to facilitate coupling, or to maximize ejaculate transfer (Kovac et al. 2010). Alternatively, females could be using the secretion as a component of courtship to evaluate male condition. To elucidate the function of these secretions, it would be interesting to examine their nutritional content and the effect of consumption on female fitness (e.g., fecundity, fertility, and longevity; see Freidberg 1982).

Typically, Gastrozonini and Acanthonevrini laid their eggs by pushing their flat aculei below the edges of culm sheaths (Fig. 3D). However, they also readily oviposited in injuries. The oviposition sites were often species-specific. For example, females of *A. histrionica* always oviposited below the sheaths of elongated shoot internodes (Fig. 2). Ovipostition of Gastrozonini was only observed on fresh shoots, while Acanthonevrini were observed ovipositing in shoots that were dead for several days.

Gastrozonini females belonging to various species often laid their eggs concomitantly in the same injury in the bamboo shoot. During collective egg laying, they did not appear to interfere with each other, although agonistic interactions had been witnessed among adults in other situations, such as when feeding on extrafloral nectaries. Although dragging of the ovipositor after egg laying in a manner resembling host marking (Prokopy 1972), was observed for females of several species (e.g., *A. bilineata*, *C. maculosa*, and *G. fasciventris*), the size and abundance of bamboo shoots indicate a low level of resource competition, suggesting that such behavior should be considered as cleaning of the ovipositor rather than as host marking, as suggested by Fitt (1984) for *Bactrocera.* Another

hypothesis is that collective egg laying could have evolved if collective feeding of a large number of larvae produces chemical changes in the shoot that deactivate chemical defensive compounds (e.g., cyanide) or generate a more nutritional medium.

Bamboo sheaths are tough and cannot be pierced by the ovipositor of Gastrozonini or Acanthonevrini. Consequently, after hatching, the larvae of these taxa relied on injuries inflicted on the bamboo to reach its edible tissues, especially in the apical parts of thick shoots of the genera *Bambusa*, *Dendrocalamus*, and *Gigantochloa*, which are protected by many overlapping culm sheaths. Two tephritid species, *C. limbata* and *P. anephelobasis* (and perhaps other *Paraxarnuta* species), have evolved specialized behavioral repertoires to overcome the hardness of such culm sheaths. Females of these species remained on the back of a *Cyrtotrachelus* female until it had bored its egg-laying puncture and thereafter both the weevil and the fly laid their eggs into this puncture. *Cyrtostola* and *Paraxarnuta* appear to have been selected to be on the spot during the egg laying of the beetle, because the beetle puncture is closed after a short time (2 h in *G. scortechinii*; Kovac 2005), owing to the rapid growth of the shoot, which causes the sheaths to move in relation to each other.

The feeding damage caused by *Cyrtotrachelus* was much more conspicuous than the egg-laying punctures, because the continued growth of the shoot during the long feeding process led to extensive tearing of the coarse culm sheath into individual fibers (Kovac and Azarae 1994). Nevertheless, larvae of *Cyrtostola* or *Paraxarnuta* have never been found in the feeding scars. They were always associated with beetle larvae. The benefit of this association may be that the beetle larva creates the entrance hole into the internode cavity and that the feeding activities of the beetle larva produce good developmental conditions for larvae, by breaking down, digesting, or introducing bacteria that promote rotting in bamboo tissues. Finally, the beetle larva also prepares an exit hole from the shoot.

It is not yet known how flies discriminate between sexes and between feeding and egg-laying *Cyrtotrachelus* females. Flies were observed on the dorsum of the weevil before oviposition, dabbing their proboscis onto the weevil's pronotum and elytra. It is possible that cuticular chemical cues allow the flies to determine the sex and reproductive status of the weevil. Differences in the composition of cuticular hydrocarbons depend among other things on age, sex (Tregenza et al. 2000), and mating status (Everaerts et al. 2010).

In summary, our studies have unraveled a wealth of adult behavioral repertoires for courtship and mating, and an especially rich array of adult egg-laying preferences. It is likely that the evolution of the former is tightly linked to the latter, as has been found for other phytophagous Tephritidae (Headrick and Goeden 1994). The documentation of these patterns will undoubtedly contribute to acquiring a more robust understanding of their evolution.

Seasonal History. Larvae of bamboo tephritids developed when bamboo shoots were available, that is, mainly during the rainy season although for some species, larval development extended into the dry season (Dohm et al. 2008, Kovac et al. 2013).

Larvae usually hatched shortly after egg laying. In *P. confinis*, we observed that females deposited their eggs in dry internode cavities. Because the larvae are semiaquatic and need water-filled internodes for development, in this case egg hatching may be triggered by rain or water availability.

The period from egg laying to emergence of flies lasted ≈3–5 wk in Gastrozonini (10 species) and 4–6 wk in most Acanthonevrini (three species). This may indicate that Acanthonevrini developing in older shoots or in hard bamboo substrates in internode cavities require longer periods for development than the Gastrozonini, which develop in soft nutrient-rich shoot substrates.

The studied tephritid larvae usually left the substrate and pupated in the soil. This is to be expected when the larval habitat is short lived. Dead bamboo shoots laying on the ground decompose after 2–3 wk. In upright dry shoots or rotting bamboo culms, which may be present for many weeks or months, the majority of larvae abandoned the substrate. However, individual larvae of *Ptilona* and *Paraxarnuta* spp. pupated in the internodes. Larvae of *I. burmensis* were an exception, because they always pupated in the internode where they had been feeding. Their pupae remained in the tip of the bamboo culm for 4–5 mo despite high temperatures during the dry season (Kovac et al. 2013).

Most bamboo tephritids apparently spent their time in the adult stage between shoot growing seasons. Adult *P. anephelobasis* were collected in Thailand during most of the year. At the end of the shoot-growing season, adults dispersed to various habitats and could only be found in low numbers. In northern Thailand, many species gathered along streams during the dry season (mid-February until April) and returned to the bamboo stands at the beginning of the rainy season.

Different bamboo species produced shoots at different times of the rainy season. Thus, both in Malaysia and Thailand, shoots were available for ≈6 mo of the year. Thin shoots were present for a longer time period. Because immature development of bamboo tephritids took ≈3–6 wk, and most species were able to use shoots of different species (see Table 4 and compare with data presented in Allwood et al. [1999]), we assume that many bamboo tephritids are multivoltine.

Regarding other Tephritidae, seasonality is governed by the availability of suitable resources for larval development (Aluja et al. 1996). Seasonal patterns in species inhabiting temperate regions are characterized by the occurrence of obligate or facultative diapause (Denlinger 2002), while tropical tephritids exhibit strategies such as aestivation, and reproductive diapause (Aluja et al. 2000). Examining adult longevity among bamboo tephritids could contribute to the general understanding of life history patterns in tropical insects.

Larval Microhabitat Associations. Our study shows that larvae of Gastrozonini mainly feed on the shoot meristem or other soft tissue of living or dead shoots. The meristem is located at the shoot apex, at the base of the developing internodes and in the buds or tips of lateral branches. In our opinion, the main restriction for using this food source is the tough culm sheaths, especially if there is much overlapping. Therefore, we have classified the bamboo microhabitats inhabited by different guilds of tephritids according to the life stages of the bamboo and the degree of protection offered by the culm sheaths.

Most species of bamboo tephritids investigated in the current study were bred from dead shoots lying on the ground (Table 4). Either oviposition took place directly into the tissue or the larvae penetrated the shoot through injured surfaces or soft parts. Other insects developing in this habitat, especially beetles, also contributed in making the substrate available to tephritid larvae.

Chaetellipsis spp. and *Gastrozona* spp. are probably confined to fallen shoots lying on the ground, while other Gastrozonini developed in both cut and upright shoots. However, some of the species found in fallen shoots may have begun development in upright shoots. Gastrozonini always developed in freshly cut shoots, whereas *Rioxoptilona* used older, more fibrous, dead shoots lying on the ground. Some *Rioxoptilona* species seemed to prefer dead upright shoots, which were dry and hard.

Tephritids attacking upright thick shoots required the presence of injury to the sheaths to infest the shoots. Injury could result from falling branches, from animals (wild boars, elephants, and woodpeckers), from human activity or tunnels created by beetle larvae to reach the internode cavity.

In the basal area of taller bamboo shoots, the internodes were fairly elongated and the sheaths overlapped just a little or only covered the basal part of the corresponding internode. In such internodes, the females could lay their eggs under the edge of a sheath. The freshly hatched larvae were able to squeeze themselves through between the sheath and the bamboo surface and reach the soft base of the internode. Larvae of some species, for example *A. septemmaculata*, may even be able to squeeze between sheaths overlapping to some extent.

In thin bamboo shoots and lateral branches of bamboo stems, the apical part of the shoot was enveloped by just a few sheaths, and these were softer than in thick shoots of large species. In such shoots, there was a clear zonation in host plant utilization. At the apex, larvae of *Xanthorrachis* were able to squeeze between several overlapping relatively soft sheaths and developed in the apical internode. In the fifth to sixth internode below the apex, where the sheaths covered just part of the internode, the larva of *I. burmensis* was found (Kovac et al. 2013). Further down, larvae of *A. distincta* were common and sometimes co-occurred with *Acrotaeniostola* n. sp. aff. *quinaria*. All these larvae developed in internode cavities. Internodes infested by *Xanthorrachis* and *Ichneumonopsis* contained only a single larva per internode, while in *Acroceratitis* and *Acrotaeniostola* several larvae developed in a single internode.

Rioxoptilona was the only Acanthonevrini genus breeding in the tissue of bamboo shoots, while the larvae of other Acanthonevrini genera developed inside internode cavities: *F. gombakensis* in basal internodes of older shoots, *Ptilona* spp. in internodes of decaying bamboo culms, and *L. setinerva* was found in basal internodes of a felled older shoot. The larvae of these other Acanthonevrini were semiaquatic and scraped material from the wet bamboo internode wall or collected it from the water surface.

The larval habitat of *F. fuscipennis* and *F. flavipennis* is not yet known. We bred *F. fuscipennis* from shoot material in our breeding experiments, but this breeding yielded only one specimen. This indicates that freshly cut bamboo shoots are not the appropriate substrate for the development of this species. We have strong evidence that at least *F. fuscipennis* breeds in internodes of mature culms, because adults were always sighted in this habitat; a female was observed laying eggs on the surface of an upright culm; and we collected large tephritid larvae from cavities of old upright bamboo culms (*F. fuscipennis* is one of the largest tephritids developing in bamboo). However, we were unable to rear any flies from these larvae.

Likewise, the breeding substrate of *L. setinerva* is still unclear. We found larvae of this species only once in internodes of a felled shoot. Because the adults of *L. setinerva* are common on fallen mature bamboo culms, they may actually develop in them, like *Ptilona*.

Larvae of *F. gombakensis* searched for entrance holes made by the leaf beetle *Lasiochila* or other Cassidinae (Chrysomelidae) to enter the internode cavity. Likewise, larvae of *Ptilona* penetrated the bamboo walls by using holes made by leaf beetles or other organisms (longhorn beetles, woodpeckers, etc.), or cracks in the wall. Acanthonevrini living in other habitats were also dependent on insect holes or cracks for entering the substrate, for example, larvae of *Rioxa* and *Themara* use holes created by bark beetles (Kovac et al. 2010).

Bamboo-breeding tephritids, at least those belonging to Phytalmiinae, are probably descendants of wood-inhabiting saprophagous tephritids, which have evolved in several evolutionary lines. Phytalmiinae primarily feed on decaying plant material and several species develop in decaying wood, such as the members of Phytalmiini or the Acanthonevrini genera *Rioxa, Themara,* and possibly others (see Kovac et al. 2010).

Despite the fact that bamboo does not appear to be a limited resource in south–east Asian forests, we found repeated evidence of ecological niche partitioning among bamboo tephritids. Closer examination of larval feeding modes and interspecific competition might shed some light on the underlying causes of bamboo tephritid diversity, which appears to have undergone significant radiation in South East Asia.

Potential Economic Impact of Bamboo Flies. Although bamboo is an important renewable resource,

used as food (shoots), for construction, parquet flooring, production of furniture, paper, and many other purposes, we have only scarce information on tephritids as pests in bamboo plantations. To date, with the exception of *I. burmensis* (Kovac et al. 2013), bamboo tephritids have only been identified as secondary pests.

White and Elson–Harris (1992) in their compilation, only cite *Acroceratitis striata* (Froggatt) (Sri Lanka), *Acroceratitis plumosa* Hendel, and *G. fasciventris* (Taiwan) as pests of bamboos of commercial value.

Chang et al. (2001) trapped tephritids in bamboo cultivation areas near Taipei, Taiwan, using colored sticky traps. They collected four dominant species: *A. plumosa*, *G. fasciventris*, *Euphranta chrysopila* Hendel, and *Ptilona persimilis* Hendel. They stated that the larvae of *A. plumosa* and *G. fasciventris* only feed on cut bamboo or bamboo shoots as decomposers and are therefore not economically important. They also mention that *A. plumosa* and *G. fasciventris* are no threat to bamboo shoots after the harvest, because shoots are regularly harvested in the early morning when the flies are not yet active.

Our findings suggest that Acanthonevrini represent the lowest potential risk for shoots or culms. Species of *Rioxoptilona* spp. and maybe *L. setinerva* infest shoots that are already in an advanced stage of decay. Other Acanthonevrini infest water-filled internode cavities of decaying culms (*Ptilona* spp.), live older shoots (*F. gombakensis*), and perhaps live culms (*F. flavipennis* and *F. fuscipennis*). All these species are dependent on other organisms for access into the plant. Their larvae feed on fine particulate material scraped from the bamboo wall or acquired from water surfaces, and there is no identifiable damage which can be attributed to them. Besides, they are only part of a complex community living in such internodes and breaking them down (Kovac 1998, Kovac and Streit 1996).

The majority of the Gastrozonini investigated in the current study were secondary pests that developed in freshly cut shoots (e.g., *Chaetellipsis* and *Gastrozona*). They were not able to infest shoots harvested for consumption, because such shoots are for the most part still buried in the ground and well protected by the culm sheaths. However, *Gastrozona* and *Chaetellipsis* oviposited on harvested shoots for sale at roadside stands (Fig. 4H).

Some Gastrozonini developed in living shoots with damaged sheaths (e.g., *Enicoptera*). These species may induce distortions in the growing bamboo, similar to those caused by some other insects, but in our case we cut the shoots to rear the larvae before such distortions could become apparent. The fact that we bred many Gastrozonini from damaged living shoots suggests that in commercial plantations in which machinery is used, inadvertent mechanical damage inflicted on shoots could lure the flies and facilitate egg laying.

In contrast to the above, some species of *Acroceratitis*, *Acrotaeniostola*, *Ichneumonopsis*, *Xanthorrachis*, and possibly some other genera, can be considered as primary pests of bamboo. They are able to penetrate into the internodes of older bamboo shoots. *A. distincta*, as well as *Acrotaeniostola*, *Ichneumonopsis*, and *Xanthorrachis*, infested thin shoots near the apex. *Xanthorrachis* destroyed only the tip of the thin shoot, while *A. distincta*, *Acrotaeniostola* n. sp. aff. *quinaria* and *I. burmensis* destroyed several apical internodes, which fell down to the ground. The fallen off apical internodes were up to 1–2 cm thick. The lower part of the bamboo shoot remained alive and undamaged. In contrast, larvae of *A. histrionica* infested thick internodes in the basal part of older bamboo shoots, slightly damaging the exterior surface at the base of the internodes but not affecting the growth of the bamboo culm.

To date, our data suggest that tephritid larvae may render harvested bamboo shoots unfit for human consumption, increase the damage to living shoots caused by other organisms, or destroy the thin apical parts or side branches of bamboo shoots. The economic damage caused by these flies, however, may not be substantial.

Acknowledgments

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