# Chapter 11
# Reversal of Mutualism

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## 11.1 How Do Mutualisms Break Down?

A major goal in the study of mutualism is to understand how co-operation is maintained when mutualism may potentially turn into parasitism. As detailed in Chap. 8, certain mutualisms feature host sanction or partner choice mechanisms that help stabilize cooperation by decreasing the fitness of noncooperative individuals. For example, in obligate pollination mutualisms, plants selectively abscise flowers that contain high numbers of pollinator eggs relative to the amount of pollen deposited, thereby punishing individuals that impose heavy egg loads or those that do not pollinate (Pellmyr and Huth 1994; Addicott and Bao 1999; Goto et al. 2010; Jandér and Herre 2010; Jandér et al. 2012).

Although mechanisms such as host sanctions may promote the stability of mutualisms, phylogenetic analyses of mutualist lineages often indicate that nonmutualistic taxa are nested within ancestrally mutualistic lineages (Pellmyr et al. 1996a; Hibbett et al. 2000; Bidartondo and Bruns 2001; Lutzoni et al. 2001; Culley et al. 2002; Als et al. 2004), suggesting that mechanisms promoting stability over ecological timescales may be decoupled from those shaping macroevolutionary patterns. Mutualisms may break down either as the result of (1) mutualism reversal, whereby mutualists become parasites of the original mutualism, or (2) mutualism dissolution, whereby mutualists evolve alternative life histories and live independently of the original partners. Early theoretical models emphasized the likelihood of the former process, but examples of parasites that evolved from mutualists are rare. Such parasites include mycoheterotrophic plants that evolved from photosynthetic ancestors, and derived fig wasps and yucca moths

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that consume fig/yucca seeds without pollinating the plants (Pellmyr et al. 1996a; Machado et al. 2001; Peng et al. 2008; Heraty et al. 2013). The rarity of mutualism reversal either suggests that parasite evolution is constrained in most mutualisms by mechanisms such as sanctions, or that parasites arise frequently but are evolutionarily short-lived.

Mutualism dissolution, by contrast, is much more widespread than reversals (Sachs and Simms 2006). For example, plants have repeatedly abandoned partnerships with animal pollinators, shifting to wind- or self-pollination (Culley et al. 2002). Also, various lineages of mycorrhizal fungi have reverted to saprotrophic lifestyles and live independently of plant hosts (Hibbett et al. 2000). The shift to free-living status may be common because, over evolutionary time, the cost–benefit aspect of the mutualism becomes unfavorable as partners become difficult to encounter due, for example, to decoupled biogeographical history (Pellissier et al. 2012; Espíndola et al. 2014), or the benefits gained from mutualistic partners become easily accessible in the environment, as exemplified by plants that abandon nutritional symbioses with mycorrhizal fungi or nitrogen-fixing bacteria in rich soils (Sachs and Simms 2006).

This chapter focuses on the natural history and process of mutualism reversal in the *Epicephala* moth lineage. As detailed in Chap. 6, one such reversal involves the clade of *Epicephala* moths that shifted onto herbaceous *Phyllanthus* and lost pollination behavior. Because their host plants normally attain a 100% fruit set via pollination by abundant ants that forage for nectar (Chap. 6), the benefit moths gain (seeds) is freely accessible without any need for the moths to pay the associated cost (pollination). Another case is the *Epicephala* moths on plants of the *Phyllanthus reticulatus* species complex in Taiwan. A close investigation resulted in a finding of six *Epicephala* species, of which three were mutualists and three were derived parasites. The latter did not provide benefits to the plants because they induced gall formation on flowers/buds without producing any seeds. This chapter details the natural history and evolutionary history of the six *Epicephala* species associated with plants of the *Phyllanthus reticulatus* species complex in Taiwan and suggests the possibility that the presence of a third-party partner (braconid wasps) may help explain the evolution of mutualism reversal in *Epicephala*.

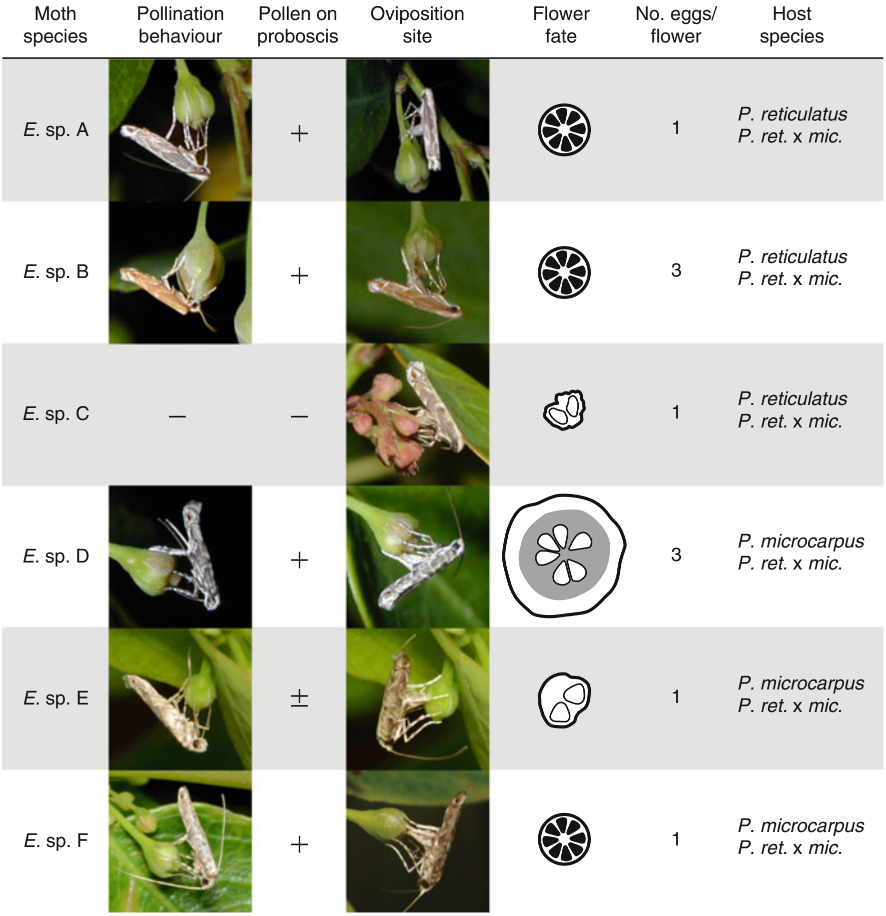
## 11.2 *Phyllanthus reticulatus* Species Complex and Associated *Epicephala* in Taiwan

*Phyllanthus reticulatus* is a shrub that is common along roadsides and forest edges in the tropical regions of Asia. Although long treated as a single species, the shrub has recently been split into two species, *P. reticulatus* and *P. microcarpus*, based on several distinct morphological and ecological characteristics (Luo et al. 2011a). Both species occur throughout our study sites in Taiwan, but in many of the populations that we studied, the plants showed intermediate characteristics

**Fig. 11.1** Plants of the *Phyllanthus reticulatus* species complex and associated insects. (**a**) The habit of *Phyllanthus reticulatus* along roadside in Taiwan. (**b**) Male flower of *P*. *reticulatus*. (**c**) Female flower of *P*. *reticulatus*. (**d**) Fruit of *P*. *reticulatus*. (**e**), Tough galls (arrows) induced by *Epicephala* sp. C. (**f**) Swollen galls induced by *E*. sp. D. (**g**) Knobbed galls induced by *E*. sp. E. (**h**) Normally developing fruits (*upward arrows*) and swollen galls (*downward arrows*) occurring on the same branch. Note the size difference. (**i**) Cross sections of a normal fruit (*upper left*), tough gall (*lower left*) and swollen gall (*right*) depicted to the same scale. Only a fraction of the seeds are destroyed by *Epicephala* larva in normal fruits, whereas galled ovules are entirely destroyed by moth larvae. Two locules are galled in the tough gall shown, one of which contains an *Epicephala* larva. All nine locules of the swollen galls had been galled. (**j**) Oviposition marks (*arrows*) left by *E*. sp. D on immature swollen galls. (**k**) Longitudinal section of a fully developed swollen gall with an irregularly developed ovule containing a larva of *E*. sp. D (*black arrow*) and undeveloped ovules (*white arrows*). Note the airspace around the infested ovule. (**l**) A braconid wasp ovipositing in a swollen gall. (**m**) An eulophid wasp resting on a tough gall produced by *E*. sp. C

suggestive of hybridization, which rendered distinctions between the two species obscure. Here it is considered that the plants belong (only) to the *Phyllanthus reticulatus* species complex; individual species names and putative hybrid status are mentioned only where appropriate.

Plants of the *P. reticulatus* species complex produce separate, small, inconspicuous male and female flowers on leaf axils (Fig. 11.1). Flowering and fruiting occur



| Moth species | Pollination behaviour | Pollen on proboscis | Oviposition site | Flower fate | No. eggs/ flower | Host species |
|---|---|---|---|---|---|---|
| *E.* sp. A | | + | | | 1 | *P. reticulatus*<br>*P. ret.* x *mic.* |
| *E.* sp. B | | + | | | 3 | *P. reticulatus*<br>*P. ret.* x *mic.* |
| *E.* sp. C | – | – | | | 1 | *P. reticulatus*<br>*P. ret.* x *mic.* |
| *E.* sp. D | | + | | | 3 | *P. microcarpus*<br>*P. ret.* x *mic.* |
| *E.* sp. E | | ± | | | 1 | *P. microcarpus*<br>*P. ret.* x *mic.* |
| *E.* sp. F | | + | | | 1 | *P. microcarpus*<br>*P. ret.* x *mic.* |

**Fig. 11.2** The six *Epicephala* moth species co-occurring on plants of the *Phyllanthus reticulatus* species complex in Taiwan. Plus (+) and minus (–) symbols indicate presence and absence, respectively. Some ovipositing females of *Epicephala* sp. E do not carry pollen on the proboscis (hence "±" under "Pollen on proboscis"). *Epicephala* sp. A, B, and F produce normal fruits containing viable seeds (drawn as filled ovules under "Flower fate"), whereas *E.* sp. C, D, and E induce galls that contain non-viable galled ovules (drawn as open ovules). Shaded areas inside galls indicate internal airspace. Fruits and galls are drawn proportional to their actual sizes. A putative hybrid between *P. reticulatus* and *P. microcarpus* is indicated as *P. ret.* × *P. mic.* under "Host species". Reproduced from Kawakita et al. (2015)

throughout the year, and *Epicephala* moths emerge many times each year. The fleshy fruits contain 12–20 ovules, of which roughly half are consumed by a single pollinator larva. Although previous chapters suggested that these plants are pollinated by species-specific *Epicephala* moth species (e.g., Chap. 6), detailed observation of moth behavior, genital morphology, and COI sequences indicated that six distinct species are associated with the plants of the *P. reticulatus* species complex in Taiwan.

***Epicephala* sp. A** is a pollinator that actively pollinates flowers and lays eggs in female flower pedicels (Fig. 11.2). Oviposition occurs only once on each flower. Pollinated flowers develop into normal fruits (Fig. 11.1), and a single larva consumes some of the developing seeds. ***Epicephala* sp. B**, the least common of the six species, is also a pollinator that produces normal fruits. It actively pollinates, and lays eggs superficially on the upper wall of the ovary (Fig. 11.2). This behavior is usually repeated three times on a single flower, and three eggs per flower are thus laid per visit by each moth. ***Epicephala* sp. C** is a parasite that induces a tough gall with a dented surface (hereafter, tough gall) on female flower buds (Fig. 11.1). None of the moths observed exhibited any pollinating behavior, and laid eggs in young female buds (Fig. 11.2), which eventually developed into tough galls. Ovipositing females do not carry pollen. ***Epicephala* sp. D** is also a parasite that induces a swollen gall (with an internal airspace) that is distinctly larger than a normal fruit (hereafter, swollen gall). Notably, this species has pollination behavior similar to that of the pollinator species (Fig. 11.2). The eggs are superficially laid on the upper ovary wall of the female flower. Ovipositing females carry abundant pollen on the proboscises, indicating that they had collected pollen on male flowers. Pollination and oviposition occur three times on each visit to a single flower. Infested flowers develop into swollen galls with internal airspaces (Fig. 11.1) within which ovules containing moth larvae develop into masses of endospermlike tissue that lack the features of normally produced seeds (e.g., a seed coat). Such irregular ovules are entirely consumed by the larvae of *E.* sp. D; thus, although whether the irregularly developed ovules retain the germination ability has not been tested, the presence of *E.* sp. D is clearly not beneficial to the plant. Ovules that are not attacked by moth larvae inside the swollen gall remain undeveloped (Fig. 11.1). ***Epicephala* sp. E** is (similarly) a parasite that induces a gall with a weakly knobbed surface that is similar in size to a normal fruit (hereafter, knobbed gall). Adults also display the pollination behavior (Fig. 11.2). However, ovipositing moths sometimes do not carry pollen, suggesting that pollen collection may be occasionally omitted in this species. Oviposition occurs once per visit, and infested flowers develop into galls containing irregularly developed ovules typical of those induced by *E.* sp. D, but lacking the internal airspace. ***Epicephala* sp. F** is a pollinator that lays eggs into the apical stigmatic pits of female flowers (Fig. 11.2). Only one egg is laid per visit.

Analysis of COI sequences identified six distinct clades (Fig. 11.3) that corresponded perfectly with the observed differences in adult behavior, genital morphology, and the characteristics of the fruits/galls from which adults were reared. In mainland China, there are three additional *Epicephala* species associated with plants of the *P. reticulatus* species complex (Li and Yang 2015), although the

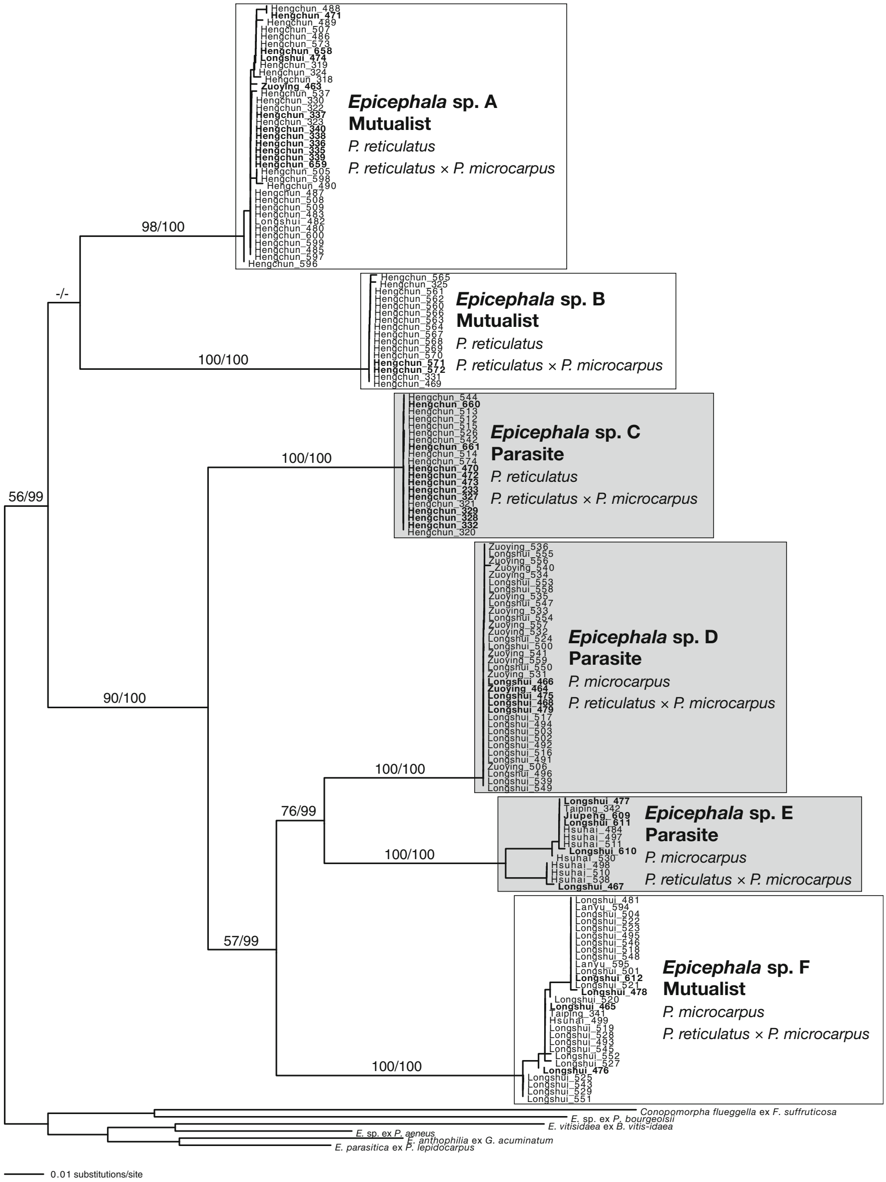


**Fig. 11.3** Phylogeny of 174 *Epicephala* moths collected from plants of the *Phyllanthus reticulatus* species complex based on COI gene sequences. The numbers above branches are maximum-likelihood bootstrap values followed by the Bayesian posterior probabilities. Individual moths are labelled with locality name followed by unique numbers. Individuals for which oviposition behavior was observed in the field are indicated in bold. Parasitic species are shaded in grey. The taxonomy of the host with which each species is associated is shown

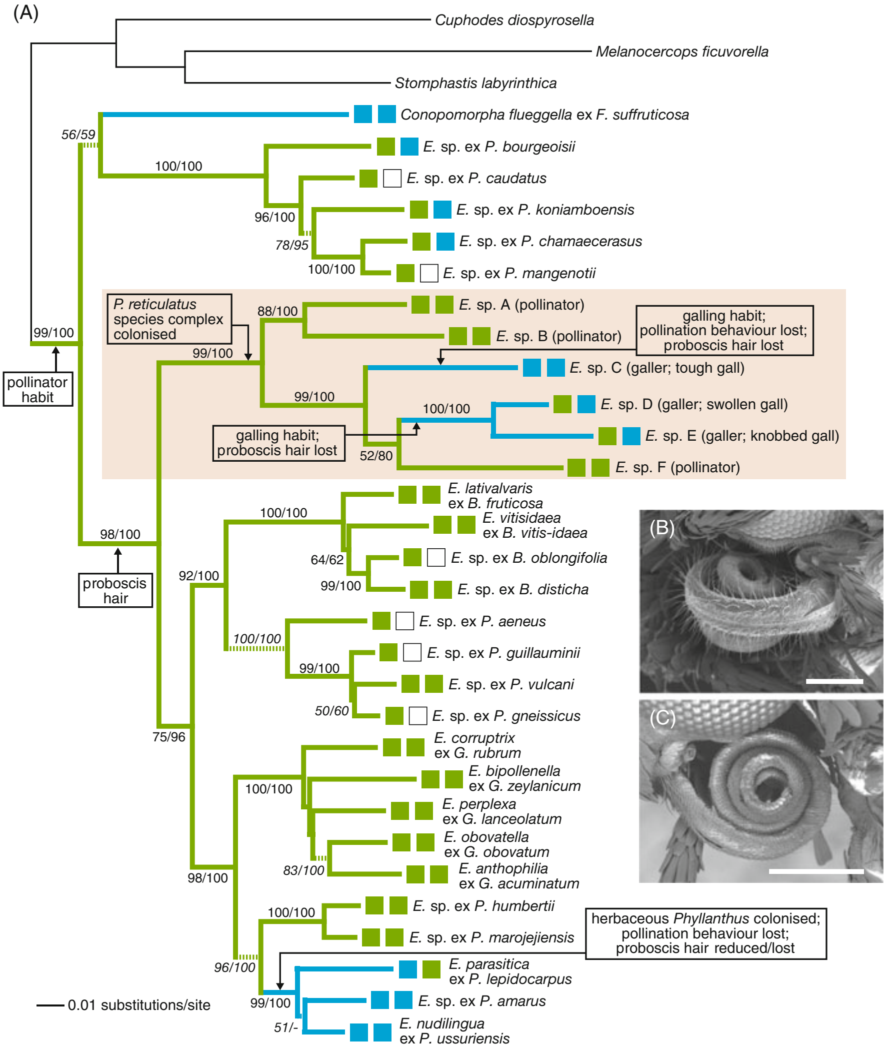


**Fig. 11.4** Reversal of mutualism in *Epicephala*. (**a**) Maximum-likelihood phylogeny of the genus *Epicephala* based on combined data from the COI, ArgK, and EF1α genes. Numbers at the branches are the maximum-likelihood bootstrap values followed by the Bayesian posterior probabilities. Nodes unsupported upon individual gene analysis are indicated as hatched lines, with support values in italics. The monophyletic clade containing the six species associated with plants of the *Phyllanthus reticulatus* species complex is highlighted in the shaded box. Mutualistic and parasitic lineages are coloured green and blue, respectively. Boxes located to the left of the terminal taxon names indicate the presence/absence of pollination behaviour (*left*; present when *green*) and hairs on the proboscis (*right*; present when *green*; *open boxes* indicate missing data). Major evolutionary events are indicated in boxed notes. Genus abbreviations are: *E.*, *Epicephala*; *F.*, *Flueggea*; *P.*, *Phyllanthus*; *B.*, *Breynia*; and *G.*, *Glochidion*. (**b**) Scanning electron micrograph (SEM) of female proboscises of *Epicephala* sp. A (pollinator). (**c**) SEM of female proboscises of and *E.* sp. D (galler). Reproduced from Kawakita et al. (2015)

larval ecology of these species has not yet been studied in detail. Because plants of the *P. reticulatus* species complex is distributed throughout tropical Asia and Africa, it is likely that numerous more species with varying adult and larval ecology will be found throughout the range.

Phylogenetic analysis of *Epicephala* and *Conopomorpha flueggella* associated with a broad diversity of Phyllantheae plants indicated that the six species associated with the *P. reticulatus* species complex were monophyletic, and that the parasitic species were derived from pollinating ancestors (Fig. 11.4a). It is unclear whether mutualism reversal occurred only once, or many times, within the clade, because the level of statistical support at internal nodes was low (Fig. 11.4a). Reversion to parasitism also occurred in a clade of *Epicephala* moths associated with the weed *Phyllanthus*, as previously reported (Chap. 6). The nonpollinating *Conopomorpha flueggella* associated with *Flueggea suffruticosa* is embedded within *Epicephala* in this tree. However, it is not clear if this represents another case of mutualism reversal, because of low statistical support at the basal nodes (Fig. 11.4a). Female proboscis sensilla that are characteristic of the core *Epicephala* clade (Chap. 5) were absent in the three gall-forming *Epicephala* species found in the present study (Fig. 11.4b, c), indicating that the sensilla were lost as the galling habit evolved.

## 11.3 Third-Party Partner of the Mutualism

Because variation in gall traits, or in the galling habit in general, may be caused by selection imposed by natural enemies (Stone and Schönrogge 2003; Bailey et al. 2009), we hypothesized that galling in *Epicephala* evolved as a defense against a specialist parasitoid, rather than as a response to a shift in the cost–benefit balance

**Table 11.1** Intensity of parasitism by braconid and eulophid wasps on *Epicephala* sp. A (pollinator) and E. sp. C (gall maker)

| | Fruit (*E*. sp. A) | Gall (*E*. sp. C) | Significance[a] |
|---|---|---|---|
| Selectivity of wasp oviposition | | | |
| Natural abundance | 282 | 258 | |
| Braconid ovipositions | 27 | 1[b] | $P < 0.001$ |
| Eulophid ovipositions | 1 | 25 | $P < 0.001$ |
| Parasitism rate | | | |
| Number examined | 176 | 189 | |
| Fruit/gall with braconid | 31 | 2 | $P < 0.001$ |
| Fruit/gall with eulophid | 1 | 95 | $P < 0.001$ |

Data are based on fruit/gall samples collected from six *Phyllanthus reticulatus* individuals at the Hengchun population, Taiwan

[a] Significance based on Fisher's exact test

[b] A single wasp alighted on the gall and attempted oviposition but failed to pierce ovipositors through gall wall

of the interaction of the moth with plants. This hypothesis was tested using two *Epicephala* species: those that induce tough galls and those that induce swollen galls. These species were chosen because both gall types were abundant at the study sites, and because the defensive functions of these gall traits were relatively straightforward in both species.

The most prevalent natural enemies of *Epicephala* larvae are specialized *Bracon* wasps associated with most *Epicephala* species studied to date. The wasps insert their ovipositors into fruits/galls containing later-instar *Epicephala* larvae and lay single eggs on the body surface of a moth larva. The wasp larvae develop by consuming the moth larvae externally, and emerge as adults from the fruits/galls. Gall toughness may render it impossible for the piercing wasp ovipositor to penetrate the gall wall, whereas the internal airspace of the swollen gall may increase the distance between the gall surface and *Epicephala* larvae inside galled ovules, rendering the wasp ovipositor too short for effective oviposition.

Field observation of wasp oviposition on tough galls produced by *E*. sp. C, and subsequent dissection of the galls, indicated that the braconid wasp seldom attacked the larvae of *E*. sp. C (Table 11.1). In only one instance did we observe the braconid attempting to oviposit on the tough gall, but the wasp failed to pierce the gall wall. Rather, *E*. sp. C moths were regularly infested by a eulophid, *Aprostocetus* sp. (Fig. 11.1), which was far less abundant on *E*. sp. A that produces normal fruits. *Aprostocetus* wasps thus far have not been found from *Epicephala* species associated with plants other than those of the *P. reticulatus* species complex. Braconid ovipositions into tough galls occurred significantly less frequently, and those by eulophids occurred significantly more frequently than expected by consideration of the natural abundances of fruits and galls (Table 11.1). The same pattern was observed when actual parasitism levels (by braconids and eulophids) inside galls and fruits were evaluated (Table 11.1).

In contrast, *E*. sp. D, which induces a swollen gall, was susceptible to braconid attack (Fig. 11.1). However, this species was more likely to escape braconid parasitism when larger galls were infected. Overall gall size increased as more ovules were infested in each flower (Fig. 11.5), indicating that gall size was dependent on the number of moth larvae infesting the gall. In turn, the number of ovules infested per gall did not affect the size of infested ovules per se, indicating that the increase in overall gall size was not due to increase in the size of infested ovules but was solely attributable to an increase in the volume of the internal airspace. In addition, galls containing parasitized moth larvae were smaller than those with intact moth larvae only (Fig. 11.5), suggesting that larval induction of gall development ceases as moth larvae become parasitized. Thus, the number of infested ovules per gall is a better proxy of the gall size at which braconid ovipositions occur. Logistic regression of the parasitism rate (the proportion of moth larvae parasitized per gall) on the number of infested ovules (a proxy for gall size) showed that the parasitism level decreased as more larvae infested the gall, and hence, as galls became larger (Fig. 11.5).

Phylogenetic analysis of the *Bracon* COI sequences suggested that the wasps reared from fruits and galls of plants in the *P. reticulatus* species complex group

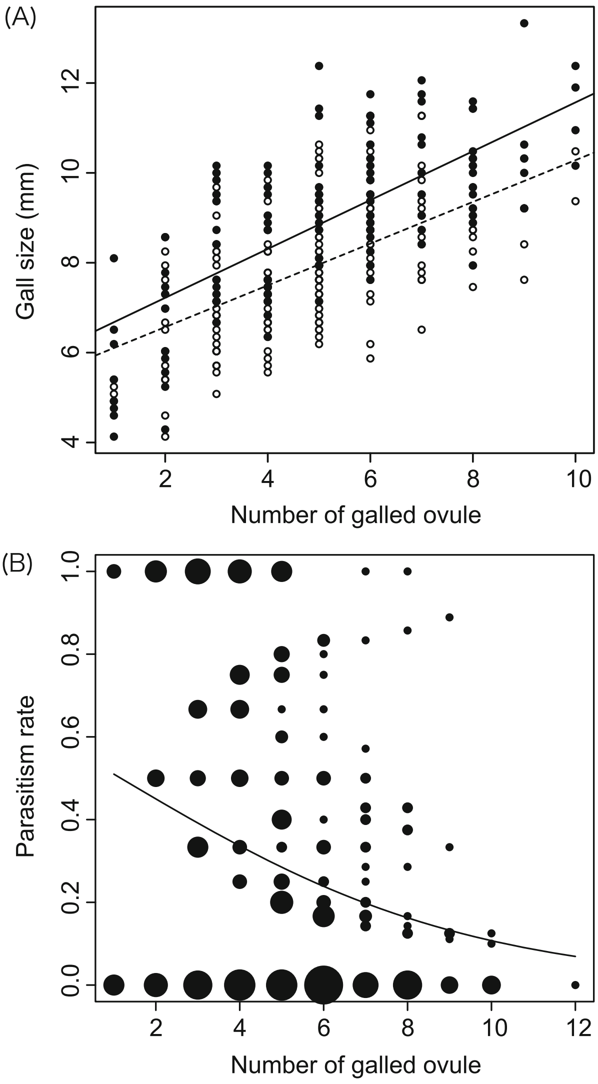


**Fig. 11.5** Variation in the size of swollen galls and braconid oviposition success. (**a**) Relationship between the number of infested ovules per gall and overall gall size (N = 348). White and black circles indicate galls with and without parasitized moth larvae. (**b**) Logistic regression of the proportions of parasitized moth larvae on infested ovule numbers per gall (N = 380). The area of each circle is proportional to the sample size. Reproduced from Kawakita et al. (2015)

into two separate clades (Fig. 11.6). There was a clear difference in the pattern of dorsal markings on the thorax and abdomen of male wasps between the two clades (Fig. 11.6), suggesting that each clade represents distinct species. The first species contained wasps reared from tough galls produced by *E*. sp. C and fruits of *P*. *microcarpus* produced by *E*. sp. F. The second species contained wasps reared from fruits of *P*. *reticulatus* produced by *E*. sp. A and swollen galls produced by *E*. sp. C (Fig. 11.6). There was no support from the COI phylogeny that these two *Bracon* species are sister to each other (Fig. 11.6).

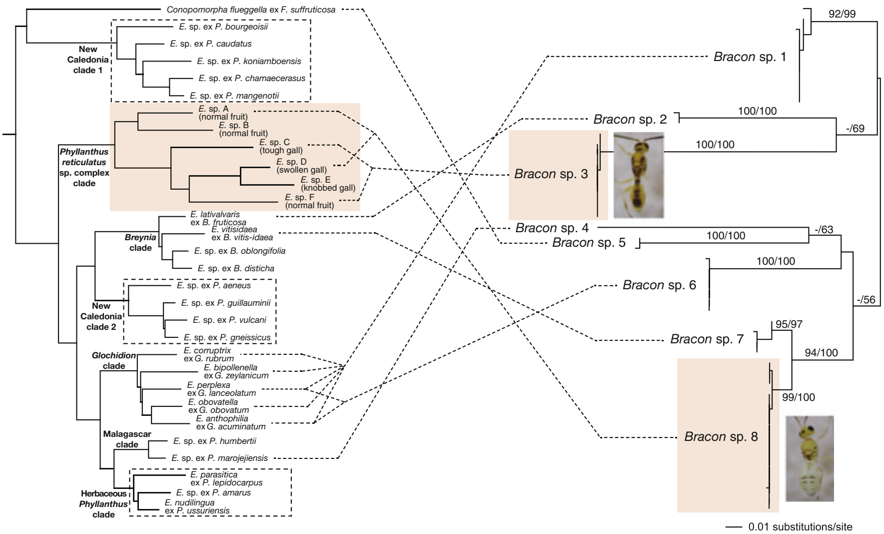


**Fig. 11.6** Phylogeny of 49 *Bracon* wasps (*right*) based on COI gene sequences and their associations with *Epicephala* moth hosts. The wasps were divided into eight distinct clades, which are considered as species. The numbers above the branches are the maximum-likelihood bootstrap values followed by the Bayesian posterior probabilities (given only for nodes above species level). Hatched lines connect each wasp species with its host *Epicephala* species. The two *Bracon* species that attack *Epicephala* associated with plants of the *Phyllanthus reticulatus* species complex (sp. 3 and sp. 8) can be distinguished based on the markings on the dorsal surface of thorax and abdomen in the males: the former possesses dark markings at the centre of first to sixth metasomal terga (T1–T6), both sides of the propodeum and areas around the wing base, whereas the latter possesses only light markings on T3–T6 that are intermitted centrally by non-pigmented area and no mesosomal markings as in sp. 3 (photos). Although *Bracon* wasps are prevalent among *Epicephala* moths, they are absent from *Epicephala* that colonized New Caledonia and those associated with herbaceous *Phyllanthus* (indicated by hatched boxes). Islands and herbaceous host may have provided *Epicephala* moths with enemy-free space. Reproduced from Kawakita et al. (2015)

## 11.4 Third-Party Partner as a Driver of Mutualism Reversal

Examples of parasites evolving from mutualistic ancestors offer opportunities to study the circumstances under which such evolution occurs, but documented examples of mutualism reversals are still limited (Pellmyr et al. 1996a; Machado et al. 2001; Peng et al. 2008). As detailed in this chapter, the Phyllantheae–*Epicephala* association offers an exciting opportunity to study mechanisms underlying the shift to parasitism because parasitic *Epicephala* arose multiple times in the history of the mutualism (Fig. 11.4).

Nevertheless, identifying the cause of the mutualism reversal found in the three galler *Epicephala* species is not straightforward. One possibility is that galling afforded a more cost-effective means of gaining resources than pollinating.

However, the parasitic *E.* sp. D and sp. E both retain pollination behavior in addition to investing in the chemical substances that induce the galls, indicating that the cost paid by gallers is not substantially lower, if it is lower at all, than that paid by the mutualistic ancestors. Alternatively, galling may improve the nutritional value of larval food, or allow the moths to circumvent selective flower abscission, and thereby increase larval survival. However, nutritional improvement or flower retention does not comprehensively explain some features of the galls, such as toughness or presence of airspace inside the gall.

We hypothesize that the mutualism reversal evident in the present study is a by-product of an adaptation made by *Epicephala* moths to escape braconid parasitism. Proof that galling is an effective defense mechanism requires a comparison of mortality between gallers and nongalling ancestors at the time when galling evolved; such analysis is impossible using long-established extant galler lineages. Nevertheless, the patterns of parasitism experienced by the galler species studied are consistent with the possibility that galling initially evolved as a defense, as often assumed in the case of galls produced by many other insects (Stone and Schönrogge 2003; Bailey et al. 2009). For example, *E.* sp. C, bearing tough galls, is virtually free of braconid parasitism, whereas *E.* sp. D, with swollen galls, experiences higher survival when the galls have a larger internal airspace. Presently, neither species necessarily experiences lower parasitism than closely related mutualist species (overall parasitism rates are 41.7% ($n = 240$) and 27.7% ($n = 1724$) for the parasitic *E.* sp. C and D, respectively, and 22.5% ($n = 151$) for the mutualist *E.* sp. A, calculated based on the original data used for Table 11.1 and Fig. 11.5), probably because enough time has elapsed for the parasitoid community to adapt to gallers. For example, *E.* sp. C is presently attacked by a eulophid wasp, and *E.* sp. D continues to suffer high-level braconid parasitism, possibly because the wasp ovipositor coevolved (became longer) with increasing gall size. Escape from parasitoid attack by gall induction may be a common evolutionary trajectory in *Epicephala* because similar galls are produced by *Epicephala* moths associated with *Glochidion obovatum* in Japan (Chap. 5) and *Phyllanthus* in Madagascar, both distantly related to the *Epicephala* species associated with plants of the *P. reticulatus* species complex (Chap. 5).

It is still unclear why *E.* sp. D and sp. E retain pollination behavior despite development of a galling ability. One possibility is that although pollination is unnecessary, the behavior cannot be easily lost because it is tightly integrated into the sequence of *Epicephala* oviposition. This was suggested by the observation that some individuals of *E.* sp. E did not have pollen on the proboscis, that they sometimes oviposited in buds, and that proboscis hairs were absent in both species. These findings indicate that selection toward pollen transport was relaxed. Unlike pollination behavior, however, proboscis hair may be a labile character that can be quickly lost after galling evolves. In any case, the evolution of galling did not eliminate the cost of pollination behavior. Whether proboscis hairs are associated with substantial costs (e.g., impeding of feeding) remains to be determined. The proboscis constitutes less than 0.3% of moth body mass, and the microscopic structures evident on the surface thereof are unlikely to be costly, at least energetically (also see Pellmyr 1997 for a discussion of the similarly small structural cost of the pollen-manipulating appendages of yucca moths).

Some mutualism theories suggest that long-term persistence of mutualisms is facilitated by mechanisms that stabilize the cost–benefit ratios of the interacting partners (Sachs et al. 2004). However, this study leads to a hypothesis that factors extrinsic to the mutualism can have large effects on the evolutionary fate of mutualisms, regardless of whether the pairwise interaction continues to favor cooperation. In the present study system, derived parasitic *Epicephala* species are able to coexist stably with related mutualistic *Epicephala* species on a single host. However, if parasitic species limit the persistence of mutualist populations via processes such as resource competition or reproductive interference, it is possible that mutualism collapses solely via a process unrelated to the cost–benefit balance of the interaction. Our study thus highlights the need to explore how factors extrinsic to a mutualism may shape the macroevolutionary dynamics of that mutualism; such work will improve our understanding of mutualism stability.