



# Adaptive radiation of gall-inducing insects

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## Summary

The adaptive radiation of four taxa of gall-inducing insects is compared: sawflies (Hymenoptera: Tenthredinidae), oak gall wasps (Hymenoptera: Cynipidae), aphids (Homoptera: Aphididae), and gall midges (Diptera: Cecidomyiidae). The sawflies, with only three genera but many species per genus, colonized many adaptive zones. Many sibling species have been recently recognized. Such characteristics suggest a dynamic evolutionary state of radiation. Innovations in the substrates used for oviposition by sawflies, probably involving ovipositional accidents, have enabled evolution from free-feeding ancestors into diverse gall types and galling sites – from leaf edge to leaf lamina, leaf midrib, petiole, bud, and stem. Host shifting among species of willows (*Salix*) has been extensive and opportunistic. The oak gall wasps, like the sawflies, colonized many adaptive zones, in terms of galling sites on the plant and diverse gall types. The gall wasps include large genera, and use a geographically widespread host-plant genus rich in species, with largely opportunistic colonization of new hosts. The gall-inducing aphids on *Pistacia* in Israel show radiation into many adaptive zones, with different gall types and galling sites on the host plant, even though the radiation is much less extensive than in sawflies and gall wasps. A major limiting factor in this smaller radiation appears to be the low richness of *Pistacia* species and the host specificity of the galling aphids to this plant genus. The gall midges are similar to the sawflies and gall wasps with many large genera. Their radiation is much greater than in the related fungus-feeding midges, indicating the importance of a rich host flora for insect radiation. The study of adaptive radiation in gall-inducing insect taxa offers many opportunities for comparative studies in evolutionary biology.

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## Zusammenfassung

Es wird die adaptive Radiation bei vier Taxa von gallbildenden Insekten verglichen: Blattwespen (Hymenoptera: Tenthredinidae), Gallwespen (Hymenoptera: Cynipidae), Blattläuse (Homoptera: Aphididae) und Gallmücken (Diptera: Cecidomyiidae). Die Blattwespen mit nur drei Gattungen aber vielen Arten pro Gattung besiedeln viele adaptive Zonen. Viele nah verwandte Arten wurden in letzter Zeit erkannt. Solche

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Charakteristika lassen eine dynamische Phase der Radiation vermuten. Innovationen bei den Substraten, die für die Eiablage bei den Blattwespen genutzt werden, möglicherweise unter Einbeziehung von Eiablagefehlern, ermöglichten eine Evolution von frei fressenden Vorfahren zu diversen Gallentypen und Gallenorten – von der Blattkante bis zur Blattfläche, die Mittelrippen der Blätter, Blüten, Knospen und Stängel. Wirtswechsel zwischen Weidenarten (*Salix*) fanden häufig und opportunistisch statt. Die Gallwespen erschlossen wie die Blattwespen viele adaptive Zonen in Bezug auf die Gallenorte auf der Pflanze und die verschiedenen Gallentypen. Die Gallwespen schließen große Gattungen ein, nutzen eine geografische weit verbreitete artenreiche Wirtspflanzengattung und zeigen eine weitgehend opportunistische Besiedlung von neuen Wirten. Die gallinduzierenden Blattläuse auf *Pistacia* in Israel zeigen eine Radiation in viele adaptive Zonen, mit verschiedenen Gallentypen und Gallenorten auf den Wirtspflanzen, auch wenn die Radiation wesentlich geringer ausfällt als bei Blattwespen und Gallwespen. Ein wichtiger begrenzender Faktor für diese geringere Radiation scheint die geringe Vielfalt der *Pistacia*-Arten und die Wirtsspezifität der gallbildenden Blattläuse hinsichtlich dieser Pflanzengattung zu sein. Die Gallmücken haben ähnlich wie die Blattwespen und Gallwespen viele große Gattungen. Ihre Radiation ist wesentlich größer als die bei den verwandten pilzfressenden Mücken und weist auf die Wichtigkeit einer reichen Wirtsflora für die Radiation hin. Die Untersuchung der adaptiven Radiation bei gallinduzierenden Insektentaxa bietet viele Möglichkeiten für vergleichende Untersuchungen in der Evolutionsbiologie.

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## Introduction

“Galls are abnormal [= atypical] growths formed from tissues of a plant or other host, due to the parasitic activity of another organism” (Redfern & Shirley, 2002, p. 207). Many groups of gall-inducing insects include genera with many species, suggesting that speciation has been rapid, without morphological changes extensive enough to justify placement in different genera. Indeed, sibling species are common and classification has been problematic and challenging in many cases. The species in large genera also attack many different plant species and plant parts, indicating shifts into different kinds of ecological niches or adaptive zones. Therefore, gall-inducing insects illustrate adaptive radiation: “relatively rapid evolutionary divergence of members of a single phyletic line into a series of rather different niches or adaptive zones” (Price, 1996, p. 419). Depending upon the routes of speciation, we may consider adaptive zones to be different plant taxa, or different modules of plants. In the latter case, these could be leaf-gall inducers in one adaptive zone and stem-gall inducers in another.

The subject of adaptive radiation involves almost all of the evolutionary biology of any taxon, including gall-inducers. We need to know host-plant relationships of the gall-inducers, insect behavior in relation to hosts, and their preferences for certain plant conditions and modules. We would like to know, as best we can, the process

of radiation in the host-plant taxa and in the gall-inducers; processes of speciation, host-plant selection, and some biogeographical and palaeontological insights may well be useful and interesting. In fact, this field becomes a fascinating blend of investigations, almost without end for any particular taxon, and on which we have only a very incomplete understanding for any group of gall-inducing insects.

In this paper I will review our current understanding of the adaptive radiation of gall-inducing sawflies (Hymenoptera: Tenthredinidae), and then examine the extent to which other groups conform to, or diverge from, the patterns observed in sawflies. The last overview of adaptive radiation in sawflies appeared over 10 years ago (Price & Roininen 1993), with considerably greater knowledge having been developed since then.

## Gall-inducing sawflies

For any description of adaptive radiation of a taxon, one would expect to know how many species are extant and the resources they exploit. As with most gall-inducing insects, this information is not available for sawflies. Phylogenetic hypotheses are in their infancy and modern systematic techniques are continuously revealing new species (e.g. Kopelke, 1999, Nyman, 2002; Nyman, Widmer, & Roininen, 2000). It is clear that many more species exist than are presently described, and many

sibling species exist, each on a different host-plant species. Only detailed biological knowledge will enable full reckoning of the species present today. For example, Liston (1995) listed 58 species of gall-inducing sawflies in Europe in the family Tenthredinidae, subfamily Nematinae (Nematini), the only group to show extensive radiation among the gall-inducing sawflies. But, within four years, Kopelke (1999) estimated that there were 103 species in Europe, with 18 new species described by the author. Only three genera are represented in this radiation, with members of each genus inducing characteristic galls: *Phyllocolpa* forming leaf folds and rolls; *Pontania* inducing closed galls on leaves; and *Euura* initiating galls on stems, petioles, midribs of leaves, and buds. All species are restricted to host plants in the family Salicaceae, with most on willows (*Salix*), and a few on poplars (*Populus*).

A phylogenetic hypothesis by Nyman et al. (2000) shows a derivation of the group from free-feeding nematine sawflies to leaf folders and rollers in the genus *Phyllocolpa*, then to leaf galls in the genus *Pontania*, and finally stem, bud and petiole galls in the genus *Euura*, the most derived genus. Given that the genera are spread across many host-plant species, it is clear in this case that new sawfly genera are associated with new adaptive zones, and after the formation of each genus, sawfly species have spread extensively across many host-plant species. With this hypothesis in mind, the processes involved with the adaptive radiation of the group can be envisaged.

## The process of adaptive radiation

The phylogenetic hypothesis by Nyman reinforced earlier hypotheses by Roininen (1991) and Price (1992), independently proposed, that the radiation progressed as a series of oviposition mistakes when females laid eggs and induced galls on shoot tips during the differentiation of stems, leaves, and buds. At this stage of shoot elongation, all module types are within 1 or 2 mm of each other, so errors in the placement of eggs are likely. First an egg pouch of a free-feeding sawfly could be made at the leaf edge, causing the leaf to fold under slightly. The larva emerging in the fold may have survived well and given rise to a new leaf-folding lineage: the genus *Phyllocolpa*. Most of the gall inducers are univoltine, ovipositing early in the season, with the chance that reproductive isolation from the nematine stock would result from allochronic phenology on the same host plant.

Alternatively, reproductive isolation would result from an ovipositional mistake coupled with a host shift and sympatric speciation, as envisioned by Bush (1975). Once a species of *Phyllocolpa* had evolved, then colonization of new host willows proceeded, no doubt, with host shifts resulting in speciation events. A new adaptive zone of leaf folding had been colonized.

In the lineage of leaf-folding sawflies, an innovation involving a larger swelling in the leaf, induced by the ovipositing sawfly could have occurred. The swelling formed a closed gall, and the sawflies evolved into the genus *Pontania*. Members of this genus then spread onto many willow species, and the process, no doubt, continued. *Pontania* species tended to oviposit through a leaf vein or midrib, stimulating gall growth on the leaf lamina by a vein, so a small shift in oviposition could have easily stimulated gall growth on the midrib itself, or the petiole, bud or stem. In each novel adaptive zone colonized, by what is now regarded as the genus *Euura*, speciation by host shifting would expand each lineage. The lineage would be characterized by a particular gall type, with each sawfly species colonizing a different willow species.

Host shifting and speciation in each sawfly genus appears to have been opportunistic, based on the ecological possibilities provided by the proximity of willow species in the field. There is no evidence of co-speciation, or congruence, of willows and sawflies, and evidently little concordance among phylogenies of the willows and the galling sawflies (Nyman, 2000). However, the oviposition stimulants for two species of sawfly are known, each responds to a particular phenolic glucoside which is in relatively high concentration in the host plant (Kolehmainen, Roininen, Julkunen-Tiitto, & Tahvanainen, 1994; Roininen, Price, Julkunen-Tiitto, Tahvanainen, & Ikonen, 1999). Given that phenolic glucosides are common to many willows, with the blends changing from one willow species to another, it is easy to imagine ovipositional errors and host shifts among willows with similar ecology and phenolic glucoside blends, or with similarities in at least one critical glucoside which acts as an ovipositional stimulant.

Probably another major factor in the radiation of the gall-inducing sawflies is the rapid growth of willow plants in moist environments, and especially the shrubby growth of so many species. Shrubs continually develop new shoots from basal meristems, so that rapidly-growing juvenile shoots are usually present each year. These are favored by gall-inducing sawflies, and many free-feeding species as well. Modules are large on juvenile shoots,

ovipositional stimulants are more concentrated, and meristems are more active than on mature shoots, providing favorable resources for oviposition and survival of progeny (reviewed by Price, 2003). In the Eurasian biogeographic realm, shrubs have been colonized by galling sawflies as much as trees, and indeed the highest numbers of galling sawfly species per willow host species are observed on shrubs rather than trees. This is probably because the lack of apical dominance in shrubs results in fresh, juvenile, vigorous growth being available for each annual generation of sawflies. Trees, having apical dominance, grow ever more mature, and physiological aging results in shortening and reduced vigor of shoots.

Willows are excellent colonizing, pioneer species, and where soil disturbance is extensive, a patchwork of young willows provides ideal habitat for the many gall-inducing sawflies that utilize them. Rapid growth of willow shrubs, and their adaptation to wet sites, makes them excellent colonizers of moist mineral soil. Their light, wind-borne seeds colonize vacant ground rapidly, often being the first arrivals of new sand bars on glacial rivers. New willow stands are rapidly colonized by sawflies, for example on the Tanana River in Alaska (Price, Roininen, & Carr, 1997). These northern glacial rivers no doubt provide similar environments to those left by receding glaciers during the Pleistocene, and willows repeatedly show peak abundance of pollen and plant fragments in palaeobiological studies of vegetation following the most recent glaciations (Price et al., 1997).

Another essential feature for extensive adaptive radiation of insect herbivores is that the plant taxa that can be utilized are rich in species. Skvortsov (1999) covered 137 species of willows for Eurasia, and in North America there are over 120 species. The poplars have also provided a few hosts for galling sawflies. All willow species are woody, with either a shrub or tree growth form, so that essentially the same kinds of resources are available for colonization in each species, whether they are large trees up to 35 m tall or small shrubs less than 10 cm tall. The full range of sizes is exploited by gall-inducing sawflies, with about 170 species recorded in the Holarctic outside China, but possibly 450 species when all are discovered (Roininen, Nyman, & Zinovjev, 2005). The estimated number of species per genus is, for *Phyllocolpa*, 35–80 species, *Pontania*, 80–230 species, and *Euura*, 40–100 species.

Willows appear to hybridize freely, with many polyploid species, and much active evolution and speciation appears to have occurred during and after Pleistocene times. All this provides an arena

of changing and expanding resources available for colonization by sawflies. With secondary compounds commonly represented by arrays of phenolic glucosides, many of them shared among species, it would be relatively easy for sawflies to shift hosts. In the cool and wet areas after glaciation, both willows and sawflies were no doubt in active states of speciation and adaptive radiation (cf. Price & Roininen, 1993).

### Adaptive radiation in other gall-inducing taxa

Where phylogenetic hypotheses have been developed for gall-inducing insect taxa, it is relatively easy to compare them with the sawflies. We can ask a series of questions as a basis of comparison. (1) Is the host-plant taxon rich or poor in species? (2) Are genera of gall-inducers large or small? (3) Have substantially different kinds of ecological niches been colonized, resulting in adaptive radiation? (4) Is there evidence of co-speciation of host-plant and gall-inducing insect taxa, or has colonization of host-plant species been opportunistic based on ecological association of host plants?

### The gall wasps

The oak gall wasps (Hymenoptera: Cynipidae) have been well studied, and the group has been reviewed recently (Stone & Cook, 1998; Stone & Schönrogge, 2003; Stone, Schönrogge, Atkinson, Bellido, & Pujade-Villar, 2002). Phylogenetic analyses have been published. The questions above are readily answerable based on these sources. Hosts of the oak gall wasps, the genus *Quercus* (Fagaceae), are numerous – over 600 species world wide – and grow in diverse habitats. A rich host-plant flora exists on which cynipids can radiate. Cynipid genera can be large: about 1000 species are distributed in 41 genera, with a mean of 24 species per genus. Some genera are very large, with 300 species in *Andricus*, 150 species in *Callirhytis*, and 100 species in *Neuroterus*. (Some of these taxa are, no doubt, polyphyletic as in large taxa of Cecidomyiidae. However, this does not diminish the argument that follows). Hence, indications are that speciation has been very extensive without developing major differences in wasp morphology. Many kinds of ecological niches have been colonized – stems, leaves, buds, twigs, catkins, acorns and acorn cups, and roots. As one example, most of these sites are exploited by one genus alone – *Andricus* – a genus with great diversity in gall

morphology as well, including spiny galls, multi-ocular galls, resinous galls, entire galls and deeply cut or hairy galls. The diversity of niches used by *Andricus*, and other genera, suggests that the gall wasp radiation differs from the sawflies because many gall types and locations on the host plant occur in a single genus, whereas in the sawflies a genus is restricted to species inducing one gall type, say leaf-edge folders, or leaf lamina galls, or stem galls (but including midribs, petioles, and buds).

Is there evidence of co-speciation of oaks and cynipids? I am not aware of any cladograms of oaks that have been directly compared with those of cynipids, but I suspect that concordance would be very weak or absent. The likely scenario is that cynipids radiated after the oaks (Graham Stone, personal communication). Those cynipid species with host alternation can clearly utilize more than one *Quercus* host species and these hosts are in different sections of the genus (Stone et al., 2002), so there can be no tracking of host divergence by cynipid divergence in this particular and rare case. Indeed, the hosts utilized by these heteroecious species are more similar ecologically than phylogenetically, indicating, as in the sawflies, that host shifting has been opportunistic based on proximity of host species in similar habitats.

For the gall-inducing sawflies and the gall wasps on oaks, we can conclude that comparable adaptive radiation has occurred. Although willow and oak hosts are very different in their ecology and biogeography, the presence of large plant genera, coupled with a lineage of well-adapted gall inducers, appears to result in spectacular radiation. These radiations have occurred on continents, not oceanic archipelagoes but, no doubt, host-plant species exist in their own island groups in space and time, such that continental archipelagoes of species, intermixed with more complex archipelagoes of species within genera, create a hotbed of evolutionary opportunities. (See also Shorthouse et al., 2005, this issue.)

### Gall-inducing aphids

In contrast to the sawflies and oak gall wasps, galling aphids (Hemiptera: Aphididae: Pemphiginae: Fordini) on the host-plant genus *Pistacia* (Anacardiaceae), the wild pistachios, have evolved into several small genera, suggesting rapid generic evolution but slow speciation perhaps. A phylogenetic hypothesis by Inbar, Wink, and Wool (2004) covers 14 species in eight genera or more, or about 1.75 species per genus. And yet gall morphology is

“remarkably different” (Inbar et al., 2004, p. 505). At least six different types of gall are induced, with some supporting many thousands of aphids, such as the horn-shaped gall of *Baizongia pistaciae* which can be 20 cm long. The radiation has been on three *Pistacia* species, so host-plant richness is low. Aphid genera are small, but major shifts in gall morphology and ecological niche have occurred: (1) pea galls (mid-vein, open leaf galls); (2) margin galls (unsealed leaf-margin galls); (3) bag galls (unsealed galls covering most of the leaf surface); (4) spherical galls (sealed on the underside of leaflets); (5) bud galls (large sealed galls formed on main vein but eventually preempting resources from the entire bud). This type can be divided into “banana galls” and “cauliflower galls”, each formed by a different genus of aphid on a different species of host. The authors suggest that the evolution of gall position has been towards galling sites with stronger sinks for nutrients, permitting larger galls, and many more individuals per gall. This pattern is comparable to the sawfly phylogeny, moving from open leaf-edge galls to stems, petioles, and buds, which are more central to the vascular system of the host. “Frequent host shifts” were probably involved in the radiation of the *Pistacia* aphids (Inbar et al., 2004, p. 504), no doubt facilitated by *Pistacia* species having similar ecological requirements.

We should enquire whether the radiations of the galling aphids and the sawflies differ in relation to genus and species formation, or whether the systematics differ in their categorization of genera and the degree to which species should differ to be placed in different genera. This subject is beyond the scope of this chapter, but, as in any discussion of adaptive radiation, real understanding and comparative scenarios will emerge only when common criteria for genera are generally agreed upon and employed. Use of the same kinds of DNA sequences in cladogram construction for different taxa would no doubt help to resolve the issue of genus status. (See also Wool, 2005, this issue.)

### Gall midges

The gall midges (Diptera: Cecidomyiidae) is one of the largest families of insects, with many gall-inducing species. This family provides valuable comparative information on the evolution of primitive groups and the more derived gall-inducing subfamilies (Gagné, 1989). Among the primitive fungus-feeding subfamilies “genera are distinct, species-poor, and widespread, indicating a long evolutionary history ...” (Gagné, 1989, p. 36).

“Many species also are widespread, an indication of great age” (Gagné, 1989, p. 34). Among these primitive groups, the subfamily Lestrimiinae contains about 370 described species worldwide, and the Porricondylinae about 475 described species worldwide. In contrast, the third and youngest subfamily of cecidomyiids, the Cecidomyiinae, which contains the gall inducers, includes about 3850 described species worldwide, with many awaiting discovery and description. “Most of these cecidomyiids are narrowly adapted and synchronized to their hosts” (Gagné, 1989, p. 37, see also Yukawa, 2000). Many genera are large: *Rhopalomyia*, 126 species; *Asphondylia*, 247 species; *Lestodiplosis*, 175 species. Some genera are “catchalls”, such as *Dasineura* and *Contarinia*, suggesting that even at the generic level divergence has been relatively weak and recent, so that genera are less distinct than in the more primitive groups. Thus, we may conclude that the primitive fungus feeders have had a “plodding” evolutionary history with gradual divergence of lineages, while the plant-feeding clades with gall-inducing genera have demonstrated explosive adaptive radiation. The comparison illustrates a strong case for the generation of much biodiversity of plant-feeding lineages specific to host species, with a very rich flora of host-plant taxa on which to radiate (cf. Price, 2002). Roskam (1985) showed strong relationships between the number of plant species per plant family, and the number of cecidomyiids recorded on that family. On woody plants the relationship accounted for 66%, and on herbaceous plants 63% of the variation in gall midge species number. These results suggest that the size of the host-plant taxon is the most important factor in determining the extent of adaptive radiation in gall midges.

The radiation in the plant-associated Cecidomyiidae appears, again, to be largely opportunistic. Species of gall-inducer within a genus can be found on many host genera and even many families of host plants, as for example in the genus *Dasineura* (Gagné, 1989; Roskam & Zandee, 1992), and *Asphondylia* (Gagné, 1989, 1994). Overall, gall-inducing cecidomyiids have successfully colonized a phenomenal range of host-plant families: 85 plant families in the Neotropics, and 89 families in North America. This indicates a remarkable capacity for host shifting across plant genera and families resulting in a very rich flora on which adaptive radiation can develop. Galls may form on buds, leaves, stems, flowers, fruits, and seeds, and many types of galls may be generated even by a single genus of cecidomyiid, such as *Rhopalomyia*. Hence, diversification of gall-inducing midge species

includes use of new plant species, new plant modules, and new gall forms.

## Other gall-inducing taxa

Expanding this examination of adaptive radiation to other taxa of gall-inducing insects would be rewarding. The gall-inducing aphids include three families; Adelgidae, Phylloxeridae, and Aphididae (Wool, 2004), while only one tribe of aphids, Fordini, has been discussed in this paper. The related gall-inducing psyllids (Psylloidea, including several families) is another interesting group, which are host specific and mainly feeding on dicotyledonous angiosperms (Hodkinson, 1984). The Coccoidea include eight families with gall-inducing species (Beardsley, 1984; Gullan & Kosztarab, 1997). There are about 300 species of gall-inducing thrips on which enough biological data are available for comparative studies (Mound, 1994; Crespi, Carmean, & Chapman, 1997). Then there are the gall-inducing fruit flies (Diptera: Tephritidae) with about 200 described species (Freidberg, 1984). However, current evidence suggests that patterns in these groups are not radically different from those discussed in this paper, and that the conclusions to follow are generally relevant to gall-inducing taxa.

## Natural enemies

Gall-inducing species support rich faunas of natural enemies, including predators, inquilines and parasitoids. Many of these are specific to their galling host. Therefore, as plant lineages radiate, followed by gall-inducing lineages, so will the third trophic level of natural enemies. Abrahamson, Blair Eubanks, and Morehead (2003) named this cascading effect *sequential radiation*, or the “escalation of biodiversity up the trophic system” (p. 781). Host-plant goldenrod species (*Solidago*: Asteraceae) have speciated, resulting in divergence of gall-forming tephritid flies and moths, followed by divergence of natural enemies (Abrahamson et al., 2003; Blair, Abrahamson, Jackman, & Tyrrell, 2005; Nason, Heard, & Williams, 2002). The adaptive radiation of plants and gall-inducers is extended up the trophic system. While these processes must be exceedingly common, they are inadequately studied, but no doubt contribute significantly to increases in biodiversity.

## Radiation in non-galling insects

There appears to be no justification for thinking that the adaptive radiation of gall-inducing taxa is

different from other taxa with species largely specific to a single host-plant species. Ross (1962) noted the existence of three species flocks of *Erythroneura* cicadellid leafhoppers on woody plants, totalling about 500 species in the one genus, likely by “sympatric species fission by a host transfer mechanism” (p. 188). The evidence suggests that host shifting was opportunistic, based on ecological proximity among species in the eastern deciduous forest of North America rather than close phylogenetic relationships among host plants and insects. A similar conclusion was reached by Berlocher and Bush (1982), studying *Rhagoletis* non-galling fruit flies: “There is little congruence between the phylogeny of *Rhagoletis* and the representative host-plant phylogeny ...” (pp. 143–144).

## Conclusions

Each adaptive radiation of a gall-inducing taxon of insects is unique. However, there are some similarities and differences among groups worth noting, and questions have been raised.

1. Genuine adaptive radiation has occurred in all gall-inducing groups considered, sawflies, oak gall wasps, aphids, and gall midges. Varied adaptive zones have been colonized in each group, involving markedly different plant modules utilized and gall architecture.

2. Within gall-inducing taxa, large genera occur frequently and sibling species are common, suggesting rapid speciation without extensive differentiation. The impression is that gall-inducing groups are in a dynamic evolutionary state.

3. The high specificity of gall-inducing species, their intimate parasitic life style on plant hosts, and the unique gall structure of each species, has resulted in extensive adaptive radiation rather than an evolutionary dead end (cf. Inbar et al., 2004; Price, 1980).

4. In two groups, sawflies and aphids, in which phylogenetic hypotheses are developed, trends indicate evolution of the galling habit at the periphery of the plant – open galls on leaves – moving toward stronger sinks of resources, such as buds and stems. Cynipids seem to have oviposited into buds over much of their evolutionary history, which results in utilization of highly active meristematic tissue and strong sinks (see Shorthouse et al. 2005, this issue). Trends in cecidomyiid phylogeny are not sufficiently resolved and will be interesting to work out.

5. The question of the equivalence of species and genera across the gall-inducing groups is worth

considerable attention if we are to develop a strong comparative approach to the adaptive radiation of galling species in general. For example, are genera of sawflies as different as genera of other groups, both morphologically and genetically? Should the few genera of sawflies be further subdivided into more narrowly defined taxa? Some groups of leaf-gallers appear to be much more genetically divergent than others, as well as the stem and bud gallers (cf. Nyman et al., 2000). This large variation in genetic divergence among species is also evident in *Andricus* clades of the cynipid gall wasps (cf. Stone and Schönrogge, 2003).

Studying the adaptive radiation of gall-inducing insects will become increasingly interesting as phylogenetic hypotheses are developed and refined. Because the resources utilized by gall-inducers are so discrete and easily recognized, the understanding of the processes of adaptive radiation can be advanced rapidly, with important contributions to be made to evolutionary biology. The long debate on the adaptive significance of the gall-inducing habit (e.g. Cornell, 1983; Price, Fernandes, & Waring, 1987; Stone & Schönrogge, 2003) will be more efficiently adjudicated as more taxa are compared. The importance of the bottom-up effects of the plant resources will be better appreciated, when both taxonomic relatedness of host plants and the quality of individual plants utilized by the gall-inducers are well understood. Further, the extended effects of host plant and galling insect radiations on the carnivorous trophic level will become of great interest in the study of biodiversity. Uniting the subjects of behavior, ecology and evolution, the study of the adaptive radiation of gall-inducing insects will, no doubt, remain fascinating, challenging and instructive for decades to come.

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