



# Ecology and radiation of galling aphids (*Tamalia*; Hemiptera: Aphididae) on their host plants (Ericaceae)

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## KEYWORDS

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*Comarostaphylis*

## Summary

At least two species of aphid, *Tamalia coweni* and *Tamalia dicksoni* (Hemiptera: Aphididae) induce galls on the leaves of *Arctostaphylos* spp. shrubs (Ericaceae). These galls are frequently inhabited by at least one species of congeneric inquiline. The inquiline clade has branched off from the gall-inducing clade and appears to be radiating rapidly on different host-plants, in contrast to the gall inducers. This striking pattern may offer insight into the factors driving speciation. Three key innovations present ecological opportunities for *Tamalia* gall-inducers and inquilines: (1) the induction of galls not only on leaf margins, but also on leaf midribs and inflorescences, both of which are novel host plant organs for *Tamalia*. (2) Gall-induction on well-armed host plants, otherwise protected with dense and viscous pubescence. (3) The origin of the inquiline habit in congeneric *Tamalia* aphids is a shift into a novel adaptive zone. Inquiline *Tamalia* exploit gall-inducers by competing successfully within the gall. They may have specialized along host-plant lines because of the critical need for precise timing with the plant during the gall invasion process.

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## Zusammenfassung

Mindestens zwei Röhrenlausarten *Tamalia coweni* und *Tamalia dicksoni* (Hemiptera; Aphididae) induzieren Gallen auf den Blättern von *Arctostaphylos* spp.-Sträuchern (Ericaceae). Diese Gallen werden regelmäßig von mindestens einer Art von kongenerischen Inquilinen bewohnt. Dieser Inquilinenstamm zweigt von dem gallinduzierenden Stamm ab und scheint im Gegensatz zu den Gallinduzierern eine schnelle Radiation auf verschiedene Wirtspflanzen zu machen. Dieses auffällige Muster könnte Einsicht in die Faktoren bieten, welche die Artbildung voran treiben. Drei Schlüsselinnovationen bieten ökologische Chancen für *Tamalia*-Gallinduzierer und

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–Inquilinen: (1) Die Induktion von Gallen nicht nur an den Blatträndern, sondern auch an den Mittelrippen der Blätter und den Infloreszenzen, die beide neue Wirtspflanzenorgane für *Tamalia* darstellen. (2) Galleninduktion auf stark bewehrten Wirtspflanzen, die durch dichte und klebrige Behaarung geschützt sind. (3) Der Ursprung der inquilinen Verhaltensweise bei kongenerischen *Tamalia*-Blattläusen ist ein Übergang in neue adaptive Zonen. Inquiline *Tamalia* nutzen Gallinduzierer aus, indem sie erfolgreich innerhalb der Galle mit ihnen konkurrieren. Sie könnten sich, aufgrund der kritischen Notwendigkeit für eine präzise Zeitabstimmung auf die Pflanze während des Invasionsprozesses in die Galle, auf Wirtspflanzen-Linien spezialisiert haben.

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## Introduction

Galling aphids hold much potential as model phytophagous insect systems of adaptive radiation. Like other gall-inducing insect taxa, galling aphids are diverse, numbering at least 10% of the total of about 4400 described aphids (Forrest, 1987; Wool, 2004). Yet, a great deal remains to be learned about their taxonomy, ecology and phylogenetic relationships with their host plants.

The known gall-inducing *Tamalia* aphids (Hemiptera: Aphididae) comprise four described species, *Tamalia coweni* (Cockerell), *Tamalia dicksoni* Remaudière and Stroyan, *Tamalia keltoni* Richards and *Tamalia pallida* Richards, and one closely related inquiline species or species complex, *Tamalia inquilinus* Miller. All species have complex life histories coordinated with host plant phenology. All known host plants of *Tamalia* are in the allied genera *Arctostaphylos*, *Arbutus* and *Comarostaphylis* in the subfamily Arbutoideae (Ericaceae). The radiation of *Arctostaphylos* is associated with the great heterogeneity in microclimate, soils, and fire regimes found in Western North America (Markos, Hileman, Vasey, & Parker, 1998): the diverse ecology of these plants appears to be the driving force behind radiation in both gall-inducers and their inquilines. It is noteworthy that inquilines appear to be radiating significantly more rapidly than gall-inducers. The inquiline habit constitutes a key innovation, with the result that *Tamalia* gall-inducers and *Tamalia* inquilines have undergone a form of sequential radiation, as has been observed in other galling insects (Abrahamson, Blair, Eubanks, & Morehead, 2003). Unlike the sequential radiation of unrelated organisms described by Abrahamson et al. however, the *Tamalia* gall-inducer/inquiline system does not involve an escalation of biodiversity up trophic levels. *Tamalia* inquilines compete for resources with gall-inducers, rather than attack them directly.

My purpose in this paper is to outline the ecology of *Tamalia* aphids on their host plants in light of

their potential as model systems of adaptive radiation. I focus on three innovations observed in the *Tamalia* system, any of which may facilitate adaptive radiation in this genus: the induction of galls on novel host plant organs, the exploitation of host plants apparently well-protected with pubescence, and the evolution of inquilinism in *Tamalia* in association with host-plant specialization.

## Materials and methods

### Systematics and distribution of *Tamalia* host plants and aphids

#### The host plants

The Arbutoideae are a rich flora, numbering in excess of 87 species, over half of which are in the genus *Arctostaphylos* (Hileman, Vasey, & Parker, 2001). All Arbutoideae are woody plants ranging in size from prostrate vine-like forms to large shrubs or small trees. What little information we have of the ecology and evolution of *Tamalia* aphids has been obtained largely from their association with *Arctostaphylos*, probably because this plant genus occurs primarily in the California floristic province (Markos, Hileman, Vasey, & Parker, 1998; the other two genera now known to sustain *Tamalia* have a neotropical center of distribution). Although at least 32 *Arctostaphylos* are known host plants for *Tamalia* spp., a significant number of *Arctostaphylos* are narrow endemics, their range restricted by edaphic or topographic features (Wells, 2000). Because wide-ranging host plant taxa are associated with adaptive radiation in phytophagous insects (Strong, Lawton, & Southwood, 1984), highly localized host plants are unlikely to be important in driving species richness in incipient or extant *Tamalia* spp. Hybridization is common in *Arctostaphylos* (Schierenbeck, Stebbins, & Patterson, 1992; Wells, 2000), and can enhance diversification rates in host plants and, by extension, in phytophagous insects (Nuismer & Thompson, 2001).

Essig (1915) had probably overlooked some *Arctostaphylos* when he wrote that “no *Arctostaphylos* I know of is immune to the galling effects of *Tamalia*,” but a sizeable number of *Arctostaphylos* species, and very probably of *Comarostaphylis* and *Arbutus* species, indeed sustain galls. There are no comprehensive lists of *Tamalia* host plant records, but Miller (unpublished), and Andres and Connor (unpublished) maintain some records. Additional sources include the mention of an unidentified galling insect on *Arbutus xalapensis* HBK in Mexico, quite possibly *Tamalia* (Ezcurra, Gómez, & Becerra, 1987), as well as herbarium specimens, some of which include clearly recognizable examples of *Tamalia* galls.

### The aphids

*Tamalia* may represent an entirely independent origin of the galling habit: depending on the taxonomic authority, they are placed either in their own subfamily or within the large and diverse family Aphididae. The unique biology of *Tamalia* includes an alate (winged) sexual female stage and strict monophagy (no host alternation): all other galling-aphid taxa are host-alternating or secondarily monophagous (Wool, 2004). Because of its singular anatomy and life history attributes, Remaudière and Stroyan (1984) considered the genus *Tamalia* sufficiently distinct to be placed in a monotypic subfamily, Tamaliinae. By all accounts, *Tamalia* bear no close affinity to the families or subfamilies comprising the vast majority of galling aphids: Hormaphididae, Pemphigidae, Adelgidae and Phylloxeridae (Foster & Northcott, 1994; Von Dohlen & Moran, 2000).

The North American distribution of species of *Tamalia* and their host plants fits well with the global pattern in galling insect diversity. Richness of galling insects appears greatest in warm temperate climates such as the Mediterranean, which is characterized by scleromorphic vegetation (Price, 2003). Only about five species of *Tamalia* are listed in the literature, but another three additional distinct entities await description, including two on the novel host plant genera *Arbutus* and *Comarostaphylis*. There is good evidence of additional host races or sibling species on *Arctostaphylos* (Miller & Crespi, 2003).

## Results and discussion

### Life history and ecology of gall-inducers and their inquiline

#### Gall-inducers

All known species of *Tamalia* develop within galls. As is true of most galling aphids (Wool, 2004),

*Tamalia* spp. are cyclically parthenogenetic: a series of clonal generations appears during the growing season, and terminates with a single sexual generation produced in anticipation of dormancy. Unlike other known genera of galling aphids, *Tamalia* spp. are monophagous rather than host-alternating. A representative sequence of life history stages occurs in populations of the gall-inducer *T. coweni*, the best known member of the genus (Miller, 1998a). In *T. coweni*, the fundatrix (stem mother) and third generation aphids (referred to as foundresses) induce galls. Stem mothers and foundresses are wingless and generally remain within the gall, alternating with winged individuals, which disperse from the galls. In the final, sexual generation, both males and mating females are winged and disperse before mating and oviposition. As is generally true of aphids, the life history of *T. coweni* is plastic and adaptable: aphid clones can respond to host plant and seasonal heterogeneity by varying the number of parthenogenetic stages, as well as the sex allocation in the sexual generation (Moran, 1992; Miller, 1998a; Miller & Avilés, 2000).

Three characteristics of the *Tamalia* life history are noteworthy in a phylogenetic context. First, two or more females of both gall-inducing generations frequently co-occupy galls, although this results in significantly lowered per capita fitness (Miller, 1998b). Such communal associations were found in galls on all species of host plants examined by the author; thus the gall-sharing behavior appears to be a plesiomorphic character. Gall-sharing contrasts sharply with the highly territorial behavior displayed by stem mothers in nearly all other galling aphids (Aoki & Makino, 1982; Moran, 1993; Whitham, 1979). Whether close relatedness among co-foundresses is important as a driving force in gall sharing is unknown. Second, on certain *Arctostaphylos* host plants, *Tamalia* inquiline invade and co-occupy galls with gall-inducers, creating a remarkable pattern of radiation (see below). Third, on at least one *Arctostaphylos*, *T. coweni* is capable of inducing three types of gall on two distinct organs of the host plant.

#### Inquiline *Tamalia*

The recently described *T. inquilinus* specializes in exploiting gall-inducing congeners (Miller & Sharkey, 2000). Newer evidence suggests that *T. inquilinus* was derived from gall-inducing *Tamalia*, and comprises a complex of host races or sibling species (Miller & Crespi, 2003). Like gall-inducers, inquilines coordinate their life cycle closely with host plant phenology, because inquilines must rely on precise timing for gaining entrance to galls.

Inquiline stem mothers hatch from sexually derived eggs during leaf flush as do the gall-inducing stem mothers. Inquilines and gall-inducers presumably respond to the same environmental cues for hatching. First-instar inquilines invade incipient unsealed galls of the host aphid. Once within the gall, they complete their development and begin producing daughters viviparously. Like the *T. coweni* gall-inducers, at least some daughters bear wing buds; when mature, these individuals disperse from the gall and produce a second generation of wingless gall-invaders. Unlike *T. coweni*, a number of inquiline daughters remain wingless and disperse from their natal galls – as immatures or as adults – apparently in search of additional galls locally for invasion (Miller, 2004). The second generation of wingless gall-invaders give rise to sexual females and males, both of which are winged. This fourth and final generation of the season disperse from the galls, before they mate and oviposit, thus completing the life cycle.

Inquilines and gall-inducers apparently do not engage in agonistic interactions. Indeed, gall-inducer tolerance for sharing gall space appears to facilitate intrusion by inquilines, and the inquilines themselves will readily group within galls (Miller, 2004). There is no evidence that inquilines increase gall-inducer mortality, but inquilines are strong competitors and can significantly depress the reproductive output of gall-inducers in mixed-species galls (Miller, 2004). Consequently, it remains a puzzle why selection has not favored discrimination against inquilines by gall inducers.

Inquilines can invade galls not only in their incipient stages, but also after the galls have matured and re-opened, often following the emergence of winged offspring of gall-inducers. Inquilines can successfully occupy, develop and reproduce within old, abandoned galls apparently no longer suitable for gall-inducers, thus resulting in temporal niche partitioning between the two forms. The ecology of inquilinism in open galls involves additional risks of desiccation and predation; as a correlate, the inquilines are more sclerotized and pubescent than gall-inducers. Experiments confirm that inquilines are indeed significantly more resistant to desiccation and to predators (Miller, 2004).

### Key innovations in *Tamalia* aphids and their role in potential adaptive zones

Under-exploited resources may be regarded as ecological opportunities which become available when key innovations arise in a lineage; in this

sense, ecological opportunity is a precondition for adaptive radiation (Schluter, 2000). I present here three examples of ecological opportunity: two are exceptional life history attributes in *Tamalia* gall-inducers; the third embodies a hypothesis for the origins of *Tamalia* inquilines.

#### Novel galling sites

In some California populations of *Arctostaphylos patula* E. Greene, the fundatrices of *T. coweni* induce the first generation of galls on leaf margins (the typical galling site in *Tamalia* spp.), but they may also attack the leaf midrib. In the same populations, a second generation of gall-inducer causes distinct spherical galls on *A. patula* inflorescence bracts: these have been referred to as flower bud galls (Miller, 1998a). This exploitation of a novel host plant organ, and the change of gall morphology, constitute a shift to a new ecological niche, as has been documented in galling aphids on *Pistacia* (Inbar, Wink, & Wool, 2004). The apparent entry into a new adaptive zone is consistent with the hypothesis on the adaptive radiation of galling sawflies (Nyman, Roininen, & Vuorinen, 1998; Price, 2003). One advantage of this shift in niche may be increased enemy-free space (Jeffries & Lawton, 1984): flower bud galls contain significantly lower mean numbers of arthropod associates – most of which are predators – than do leaf-margin galls (Miller, 1998a). The dense packing of galls on *A. patula* inflorescences is correlated with significantly higher rates of communal galling; thus, host plant architecture may mediate sociality in these insects. Gall induction appears to destroy the viability of *A. patula* inflorescences, and numerous *Tamalia* galls may reduce the numbers of seed set, lowering host plant fitness (Miller, unpublished).

#### Viscous and pubescent host plants

Besides viscosity, glandular hairs (trichomes) on host plants can be an important element in the ecology of phytophagous insects (Strong et al., 1984). Reciprocal transplant trials of gall-inducers in sympatric populations of *A. patula* and *Arctostaphylos viscida* C. Parry resulted in galls on inflorescences of *A. patula* but not *A. viscida*. Apparently, the highly viscous *A. viscida* inflorescences entrapped *Tamalia* foundresses and they died before establishing galls (Miller, unpublished data). In a survey of folivorous insects on 26 species of *Arctostaphylos*, Andres and Connor (2003) examined the effects of pubescence on the abundance of insects in several guilds. They found an inverse relationship between pubescence length and the abundance of sap-sucking insects, including *Tamalia* aphids. It was suggested that pubescence

may impede *Tamalia* stem mothers from moving over or probing plant tissues during the establishment of galls (Andres & Connor, 2003). An exception to this attractive hypothesis is *T. dicksoni* on *Arctostaphylos pringlei* in southern California. Remaudière and Stroyan (1984) in the original description of *T. dicksoni* did not specify its host plant beyond identifying it as *Arctostaphylos* sp. I have collected and identified *T. dicksoni* from galls on *A. pringlei drupacea*, an unusually viscous and pubescent plant, in the San Bernardino and Santa Rosa mountains of southern California. Indeed, this is the only *Arctostaphylos* I have examined which is pubescent inside the galls as well as throughout the foliage and younger stems. That *T. dicksoni* occurs (perhaps even specializes) on *A. pringlei* would seem counter to the Andres/Connor hypothesis. *T. dicksoni* possesses exceptionally long mouthparts and legs. These apparently are modifications enabling the exploitation of this otherwise well defended host plant, and may constitute a key innovation facilitating its invasion of a novel adaptive zone.

#### Inquilinism in *Tamalia*

The adoption of inquilinism and subsequent radiation in the *T. inquilinus* clade constitutes a shift into a novel adaptive zone. It presents a striking pattern of differential evolutionary rates between inquilines and gall-inducers. Recent evidence from mtDNA sequence analysis indicates that *Tamalia* inquilines constitute a monophyletic clade, which originated from gall-inducing *Tamalia* and which diversified rapidly along host-plant lines (Miller & Crespi, 2003). At least four lineages of *Tamalia* inquilines show 2% divergence or more in the cytochrome oxidase I (COI) region of mtDNA among host plant species, indicating the strong possibility of host race formation or sibling species status. Thus, *Tamalia* inquilines may be co-speciating with their host plants, as both clades have diversified comparatively rapidly beginning only in the Pleistocene (Hileman et al., 2001; Miller & Crespi, 2003). This is noteworthy, as parallel cladogenesis or co-speciation between phytophagous insects and their host plants appears the exception rather than the rule (Crespi, Morris, & Mound, 2004; Nyman, Widmer, & Roininen, 2000). By contrast, phylogenetic analysis of gall-inducers from the same set of host plants indicated very little differentiation along host-plant lines; hence, gall-inducers appear to have diversified relatively slowly. That gall-inducers, but not inquilines, show opportunistic use of host plants is perhaps surprising, since aphid gall induction is an intricate

process typically associated with great host plant specificity, at least locally (Wool, 1984).

Two hypotheses explaining greater levels of host plant specificity in inquilines (as compared to gall-inducers) are: (1) phenological constraints may be more critical for inquilines, since the window of opportunity for gall invasion is narrower than that for gall induction; (2) relatively low rates of dispersal may be favored for inquilines, since staying in the same host plant patch may facilitate locating suitable galls to invade.

#### Biogeographic origins of Arbutoideae and *Tamalia* aphids

The available phylogenetic evidence suggests that the ancestor of *Tamalia* gall-inducers first arose on *Arbutus*, followed by a shift to *Comarostaphylis* and *Arctostaphylos*, and that the inquiline *Tamalia* clade appeared in conjunction with the shift to *Arctostaphylos* (Miller & Crespi, 2003). Thus the higher-level phylogenetic pattern of the aphids is concordant with that of the three host plant genera as outlined by Hileman et al. (2001). Interestingly, the host plant genera *Arctostaphylos* and *Arbutus* are Holarctic, but *Tamalia* spp. appear restricted to the New World, which suggests their comparatively recent origin. Cockerell, in his original description of *Phyllaphis* (now *Tamalia*) *coweni* on *Arctostaphylos uva-ursi* (L.) Sprengel in Colorado, first noted the absence of *T. coweni* on *A. uva-ursi* in Europe (Cockerell, 1905). Of 11 species of *Arbutus*, 3 of which are Palearctic, only New World *Arbutus* are host to galls of *Tamalia* spp. However, DNA sequence data suggest that *Arbutus* is paraphyletic, with North American *Arbutus* sister to the rest of Arbutoideae. According to the Madrean-Tethyan hypothesis for the origins of North American/Mediterranean disjunct flora, a continuous, scleromorphic flora ranging from North America to the Mediterranean Basin existed at least until the Paleogene/Neogene boundary circa 25 MYA, after which the widening Atlantic Ocean separated these global regions (Hileman et al., 2001). If *Tamalia* indeed originated on the ancestral New World *Arbutus* lineage, we might expect its extant distribution to be Holarctic, but its apparent absence in the Old World suggests a more recent origin. Estimates of the antiquity of *Tamalia* based on a molecular clock from the COI mtDNA region indicate a divergence time of about 10 million years for the lowermost branch of the clade, far less than would be expected had *Tamalia* appeared before the Paleogene/Neogene boundary (Miller & Crespi, 2003). By contrast, Von Dohlen and Moran (2000)

used mitochondrial ribosomal DNA sequence data to show that most extant aphid tribes diversified by the early Tertiary. They placed *Tamalia* sister to other genera in the tribe Phyllaphidini, which would pre-date the Paleogene/Neogene boundary, even though this is not well supported in their phylogeny. A more robust phylogeny of *Tamalia* spp. on additional host plants in the Arbutoideae is needed before firm conclusions can be drawn about the biogeographic origins of these taxa.

## Conclusion

*Tamalia* gall-inducing aphids and their inquiline present great potential for investigating the ecology of radiation. It is premature to conclude that their pattern of diversification constitutes *adaptive* radiation, as illustrated by Darwin's finches and Hawaiian silverswords (Schluter, 2000), but the patterns observed here satisfy Schluter's four criteria for this process. Two criteria in particular seem well-supported: first, the *Tamalia* clade clearly constitutes a monophyletic group; and second, the inquiline clade has radiated quite rapidly along host-plant lines, resulting in a complex of host races or sibling species. The two other criteria – a demonstrated phenotype-environment correlation and trait utility – await careful investigation. One possibility of testing for these criteria might involve reciprocal transplanting experiments between *Tamalia* inquilines from different species of host plants. Another could involve careful documentation of the relative timing of gall induction and gall invasion by inquilines across host plants from different putative host races. Finally, careful examination of galling activities on additional host plant organs and pubescent host plant species may well yield further evidence of adaptive radiation in this remarkable genus of phytophagous insects, giving us a more general understanding of the origins and driving forces of biodiversity.

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