The evolution of inquilinism, host-plant use and mitochondrial substitution rates in *Tamalia* gall aphids

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Abstract

We used mitochondrial DNA data to infer phylogenies for 28 samples of gall-inducing *Tamalia* aphids from 12 host-plant species, and for 17 samples of *Tamalia inquilinus*, aphid 'inquilines' that obligately inhabit galls of the gall inducers and do not form their own galls. Our phylogenetic analyses indicate that the inquilines are monophyletic and closely related to their host aphids. *Tamalia coweni* aphids from different host plants were, with one exception, very closely related to one another. By contrast, the *T. inquilinus* aphids were strongly genetically differentiated among most of their host plants. Comparison of branch lengths between the *T. coweni* clade and the *T. inquilinus* clade indicates that the *T. inquilinus* lineage evolves 2.5–3 times faster for the cytochrome oxidase I gene. These results demonstrate that: (1) *Tamalia* inquilines originated from their gall-inducing hosts, (2) communal (multi-female) gall induction apparently facilitated the origin of inquilinism, (3) diversification of the inquilines has involved rapid speciation along host-plant lines, or the rapid evolution of host-plant races, and (4) the inquilines have undergone accelerated molecular evolution relative to their hosts, probably due to reduced effective population sizes. Our findings provide insight into the behavioural causes and evolutionary consequences of transitions from resource generation to resource exploitation.

Introduction

Understanding how different groups of insects and other organisms have diversified requires the recognition of convergent patterns that connect particular aspects of the biology of the group to their evolutionary dynamics (e.g. Mitter *et al.*, 1988; Farrell & Mitter, 1990; Mitter & Farrell, 1991; Gaston *et al.*, 1992). For example, most cases of cospeciation between phytophagous insects and their host plants, or between phytophagous insects and their enemies, involve relatively intimate ecological interactions, such as specialized plant chemistry (e.g. Farrell & Mitter, 1998), obligate mutualism or parasitism (Herre *et al.*, 1996; Machado *et al.*, 1996; Ikino *et al.*, 2001; Lopez-Vaamonde *et al.*, 2001), gall induction (Ronquist & Nylin, 1990; Burckhardt & Basset, 2000) and a high degree of specialization to a particular host (e.g. Roderick, 1997; Roderick & Metz, 1997; Ikino *et al.*, 2001). By contrast, frequent expansion and contraction of host-plant ranges is apparently more common in insect groups that exhibit less complex forms of ecological interaction (e.g. Janz & Nylin, 1998; Jones, 2001). The evolution of 'host-races', forms exhibiting partial genetic differentiation among host-plant species (Abrahamson *et al.*, 1994; Bush & Smith, 1997; Drès & Mallett, 2002), appears to represent one of the main routes to diversification in phytophagous insects. However, the circumstances that give rise to host races, rather than a single panmictic and polyphagous species, are as yet poorly understood (Berlocher & Feder, 2002; Drès & Mallett, 2002).

Diversification often involves transitions into new adaptive zones. Such transitions take place rarely, due to the magnitude of the evolutionary change required,

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but their macroevolutionary consequences are large because adaptive radiation will commonly ensue (Mitter *et al*., 1988; Price & Roininen, 1993; Schluter, 2000). One of the more common forms of transition is the adoption of an obligately parasitic or inquiline lifestyle. Transitions to parasitism (which involves harm to the host) or inquilinism (which, by our definition here, does not) may coincide with speciation events or, alternatively, may entail direct anagenetic transformation. Evidence from some taxa suggests that this type of transition can be facilitated by host-plant shifts (Akimoto, 1988a,b, 1989; Pellmyr *et al*., 1996) and a close evolutionary relationship to the exploited form (e.g. Carpenter *et al*., 1993; Lowe & Crozier, 1997), or it may involve sympatric speciation (Buschinger, 1990; Bourke & Franks, 1991). Moreover, the adoption of parasitism may result in accelerated rates of molecular evolution, perhaps due to reduced effective population sizes (Dowton & Austin, 1995; Page *et al*., 1998; Castro *et al*., 2002), and it may engender bursts of speciation and diversification (Price, 1980). Additional case studies that combine phylogenetic with ecological and behavioural information are required, however, before convergent patterns in the causes and consequences of such transitions can be identified.

The purpose of this paper is to analyse the diversification of *Tamalia* galling aphids and their non-galling inquilines, in relation to their patterns of host-plant use. To do so, we use molecular-phylogenetic information on the gallers and inquilines collected from the different host-plant species of *Arctostaphylos, Comarostaphylis* and *Arbutus* that each of them inhabits. In particular, we address two main questions. First, what is the evolutionary relationship between the host aphids and their inquilines, and how did the inquilines originate? Secondly, how have the hosts and inquilines each diversified in host-plant use, and do they constitute a small number of polyphagous species, or a larger number of monophagous species or host-plant races?

Methods

Life history of *Tamalia* aphids

The genus *Tamalia* Baker (Tribe Phyllaphidini, Subfamily Drepanosiphinae, Family Aphididae, Order Homoptera) comprises four described species and at least three undescribed species, all in North America and primarily in xeric or boreal habitats (Remaudière & Remaudière, 1997; Miller & Sharkey, 2000; Von Dohlen & Moran, 2000). All known host plants are of the subfamily Arbuteae, family Ericaceae. All described *Tamalia* are found on *Arctostaphylos* spp.; one novel species studied here is reported from *Arbutus* and another is from *Comarostaphylis*. These constitute the first records of *Tamalia* from any genus other than *Arctostaphylos*. Inquiline *Tamalia* are so far known only from galls on *Arctostaphylos* spp.

Tamalia coweni

The life history of *T. coweni* has been described for populations at the contact zone of the host plants *Arctostaphylos viscida* and *A. patula* in the Sierra Nevada, California (Miller, 1998a)(Fig. 1). On *A. viscida*, the stem mother aphid emerges from the overwintering egg between late April and early June to initiate a gall. During initiation, the gall is open and vulnerable to intrusion; we refer to this stage as the early-phase gall (Mani, 1964). Stem mothers readily share gall space communally and tolerate the heterospecific *T. inquilinus* (Miller, 1998a,b; Miller & Sharkey, 2000). In the trophic-phase gall, the stem mother continues to induce growth and closure of the gall tissue around her. The stem mother produces a series of offspring parthenogenetically, including males, mating females and, when conditions are favourable, winged parthenogenetic females (Fig. 1). Subsequently, the now mature-phase gall dries and splits open, allowing release of the offspring, all of which complete their fourth and final moult outside the gall before dispersing aerially. Males and mating females, both of which are winged, then disperse and mate elsewhere, typically over the tops of the host plant; thus, a degree of spatial reproductive isolation is achieved and may suppress gene flow among different host-plant populations. The life cycle is completed by July to early August with the oviposition of overwintering eggs by the mating female.

The life cycle of *T. coweni* on *A. patula* differs from that on *A. viscida* in two important respects: (1) it is delayed a full month, so that stem mothers appear in late May and the life cycle is completed by late August–September; (2) on *A. patula*, the tissue susceptible to gall induction is more widely distributed on the host plant, with the result that stem mothers more commonly produce an additional generation of dispersers and gall-inducers on *A. patula*. Despite the phenological difference between *T. coweni* life cycles on these two host plants, limited gene flow may occur between *A. viscida* and *A. patula*, as winged females emerging from galls readily larviposit on non-natal host plants under experimental conditions (D. Miller, unpublished data).

Tamalia inquilinus

The life history of *T. inquilinus* (Miller & Sharkey, 2000) is incompletely known, but first-instar stem mothers can invade galls of *T. coweni* during both the early and mature phases of gall growth (Fig. 1). In this respect, the window of opportunity available to inquilines is narrower than that of gall-inducers, which can induce galls as long as suitable host-plant tissues are still growing. Mature-phase galls support higher numbers of inquilines than do early or trophic-phase galls. Inquilines begin parthenogenetic reproduction upon reaching adulthood in the host gall. The great majority of offspring produced are

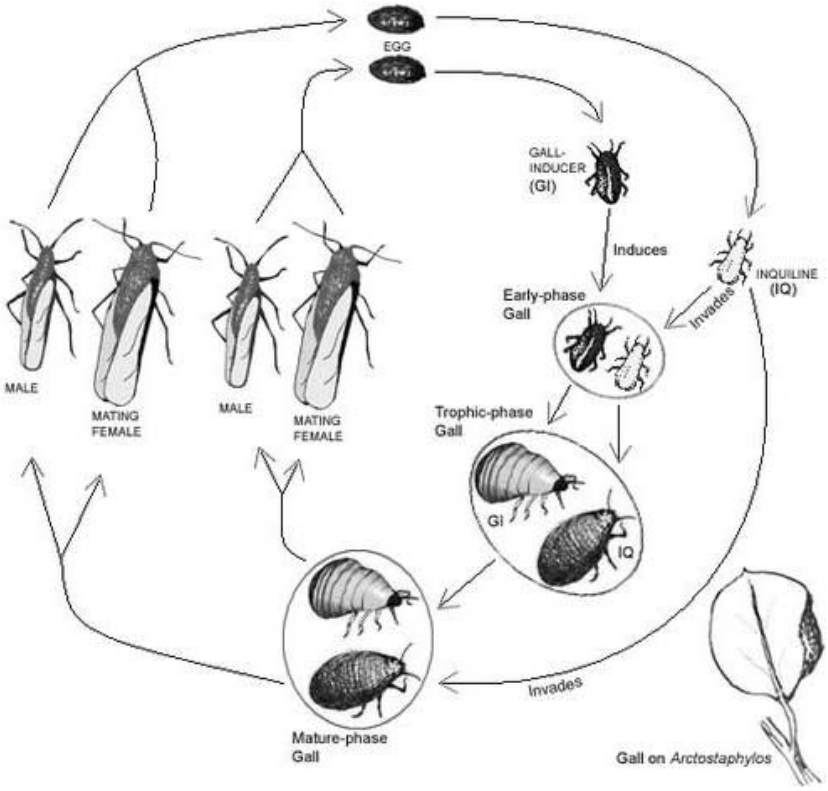

Fig. 1 Life histories for *Tamalia coweni* and *T. inquilinus*. Life cycles are drawn in parallel, with *T. coweni* on the inside and *T. inquilinus* on the outside of the diagram. In *T. coweni*, the stem mother induces a gall on the host plant, manzanita (*Arctostaphylos* spp.), before producing males and mating females, which disperse and mate after emerging from the gall to complete the cycle. The inquiline can enter the host gall at either the early or mature phases of gall elaboration, to reproduce alongside the host aphid, yielding males and mating females.

males and mating females, but winged asexual females occasionally appear as well. As winged females are relatively rare, *T. inquilinus* may achieve substantially less dispersal than does *T. coweni*. Inquilines can persist in mature-phase galls well after the gall-inducers have completed their life cycle. Like the host aphids, male and mating female inquilines are both winged and presumably disperse aerially before mating, probably in the vicinity of the host plant.

Collection

Tamalia coweni gall-forming aphids and their inquilines *T. inquilinus* were collected from 10 species of *Arctostaphylos*, one species was collected from *Comarostaphylis diversifolia*, and one species was collected from *Arbutus arizonica* (Table 1). Our sampling scheme involved collection of *T. coweni* and *T. inquilinus* from as many host plants as possible, and, for each host plant, from several different, far-removed localities (Fig. 2). This scheme allowed us to assess the independent roles of host-plant use and geographical separation on aphid phylogenetic and phylogeographic relationships.

DNA isolation, PCR and sequencing

Aphids were crushed with a sterilized glass pipette and suspended in 0.9 mL Lifton buffer (0.2 M sucrose, 0.05 M EDTA, 0.1 M Tris, 0.5% SDS). DNA was extracted with phenol-chloroform and 70% ethanol precipitation. PCR was performed using combinations of the mitochondrial cytochrome oxidase I (COI) primers S1718 and A2191 (Simon *et al*., 1994). PCR product was processed using exonuclease I and shrimp alkaline phosphatase to digest single-stranded DNA and inactivate free nucleotide. Big Dye Cycle Sequencing was used to sequence a fragment 452–493 bp long.

Phylogenetic analyses

We used maximum likelihood (ML) analysis, maximum parsimony (MP) analysis and neighbour joining (NS) to infer phylogenies for *Tamalia*. Pea aphid (*Acyrthosiphon pisum*) and wheat aphid (*Schizaphis graminum*)(family Aphididae) were used as outgroups.

Prior to ML analysis, we used MODELTEST (Posada & Crandall, 1998, 2001) to infer the best model of nucleotide substitution. We conducted ML analysis, MP analysis (heuristic searching with multiple random-addition replicates and tree bisection-reconection (TBR) branch swapping) and NJ (under a Kimura two-parameter model) in PAUP4.0b10 (Swofford, 2002). For likelihood analyses, phylogenies were also inferred using Mr Bayes 2.01 (Huelsenbeck & Ronquist, 2002), which allows assessment of phylogeny robustness using *a posteriori* probabilities. In our Bayesian analysis, we

Table 1 Aphid samples used for generating the phylogenies based on mtDNA sequences. See Fig. 2 for geographical locations of collection sites.

Host plant	Aphid species	Fig. 2 location	Collection site
Gall-inducers			
Arbutus arizonica	*Tamalia morani*	8	Santa Catalina Mts, AZ
Comarostaphylis diversifolia	*Tamalia cruzensis*	17	Santa Cruz Island, CA
Arctostaphylos glandulosa3	*Tamalia coweni*	24	Mt Tamalpais, CA
Arctostaphylos glandulosa1	*Tamalia coweni*	37	Santa Monica Mts, CA
Arctostaphylos glauca1	*Tamalia sp. nov.*	30	San Bernardino Mts, CA
Arctostaphylos glauca4	*Tamalia sp. nov.*	33	San Gabriel Mts, CA
Arctostaphylos glauca2	*Tamalia sp. nov.*	45	Potrero, CA
Arctostaphylos insularis1	*Tamalia coweni*	46	Santa Cruz Island, CA
Arctostaphylos patula8	*Tamalia coweni*	2	Pea Vine Ridge, Sierra Nevada, CA
Arctostaphylos patula1	*Tamalia coweni*	6	Blodgett Forest, Sierra Nevada, CA
Arctostaphylos patula6	*Tamalia coweni*	25	Sierra Buttes, CA
Arctostaphylos patula5	*Tamalia coweni*	29	Trinity Alps, CA
Arctostaphylos patula4	*Tamalia coweni*	32	Santa Rosa Mts, CA
Arctostaphylos pringlei4	*Tamalia dicksoni*	14	San Bernardino Mts, CA
Arctostaphylos pungens1	*Tamalia coweni*	13	Santa Catalina Mts, AZ
Arctostaphylos pungens6	*Tamalia coweni*	19	Cuyacama Mts, CA
Arctostaphylos pungens2	*Tamalia coweni*	27	New York Mts, CA
Arctostaphylos pungens4	*Tamalia coweni*	39	Laguna Mts, CA
Arctostaphylos tomentosa1	*Tamalia coweni*	18	Montara Mt, CA
Arctostaphylos tomentosa2	*Tamalia coweni*	21	Montara Mt, CA
Arctostaphylos uva-ursi	*Tamalia coweni*	34	Indiana Dunes Lakeshore
Arctostaphylos viridissima1	*Tamalia coweni*	40	Santa Cruz Island, CA
Arctostaphylos viscida3	*Tamalia coweni*	3	Blodgett Forest, Sierra Nevada, CA
Arctostaphylos viscida6	*Tamalia coweni*	9	Pea Vine Ridge, Sierra Nevada, CA
Arctostaphylos viscida1	*Tamalia coweni*	11	American River Forks, CA
Arctostaphylos viscida4	*Tamalia coweni*	36	Ione, CA
Arctostaphylos viscida8	*Tamalia coweni*	42	S. Fork American River, CA
Arctostaphylos viscida10	*Tamalia coweni*	44	Quincy, CA
Inquilines			
Arctostaphylos glandulosa2	*Tamalia inquilinus*	10	Santa Monica Mts, CA
Arctostaphylos glandulosa4	*Tamalia inquilinus*	22	Mt Tamalpais, CA
Arctostaphylos glauca3	*Tamalia sp. nov.*	15	San Bernardino Mts, CA
Arctostaphylos glauca5	*Tamalia sp. nov.*	47	San Gabriel Mts, CA
Arctostaphylos patula9	*Tamalia inquilinus*	12	Pea Vine Ridge, Sierra Nevada, CA
Arctostaphylos patula7	*Tamalia inquilinus*	20	Sierra Buttes, CA
Arctostaphylos patula2	*Tamalia inquilinus*	26	Blodgett Forest, Sierra Nevada, CA
Arctostaphylos patula3	*Tamalia inquilinus*	28	Santa Rosa Mts, CA
Arctostaphylos pringlei3	*Tamalia sp. nov .*	35	Santa Rosa Mts, CA
Arctostaphylos pungens7	*Tamalia inquilinus*	4	Cuyacama Mts, CA
Arctostaphylos pungens5	*Tamalia inquilinus*	16	Laguna Mts, CA
Arctostaphylos pungens3	*Tamalia inquilinus*	31	New York Mts, CA
Arctostaphylos viscida2	*Tamalia inquilinus*	1	Blodgett Forest, Sierra Nevada, CA
Arctostaphylos viscida7	*Tamalia inquilinus*	7	Pea Vine Ridge, Sierra Nevada, CA
Arctostaphylos viscida5	*Tamalia inquilinus*	38	Ione, CA
Arctostaphylos viscida9	*Tamalia inquilinus*	41	S. Fork American River, CA
Arctostaphylos viscida11	*Tamalia inquilinus*	43	Quincy, CA

used 33 000 trees inferred after stabilization of the likelihood for our *a posteriori* distribution, from which a 50% majority rule tree was constructed. We also tested the validity of a molecular clock, by comparing the likelihood of the best tree to the likelihood of a clock-constrained tree with the same topology.

For NJ analysis, we evaluated phylogeny robustness using 500 bootstrap replicates. MP bootstrapping was not computationally feasible due to the presence of very similar sequences for numerous samples.

As many of our samples were intraspecific, such that ancestral haplotypes may be extant, we also inferred haplotype networks using TCS (Templeton-Crandall-Sing) networks (Clement *et al.*, 2000), whereby statistical parsimony is used (Templeton *et al.*, 1992) to infer relationships between closely related haplotypes. Statistical parsimony analysis utilizes information in identical as well as differing base pairs, under a model where changes are assumed independent and equally likely at different sites.

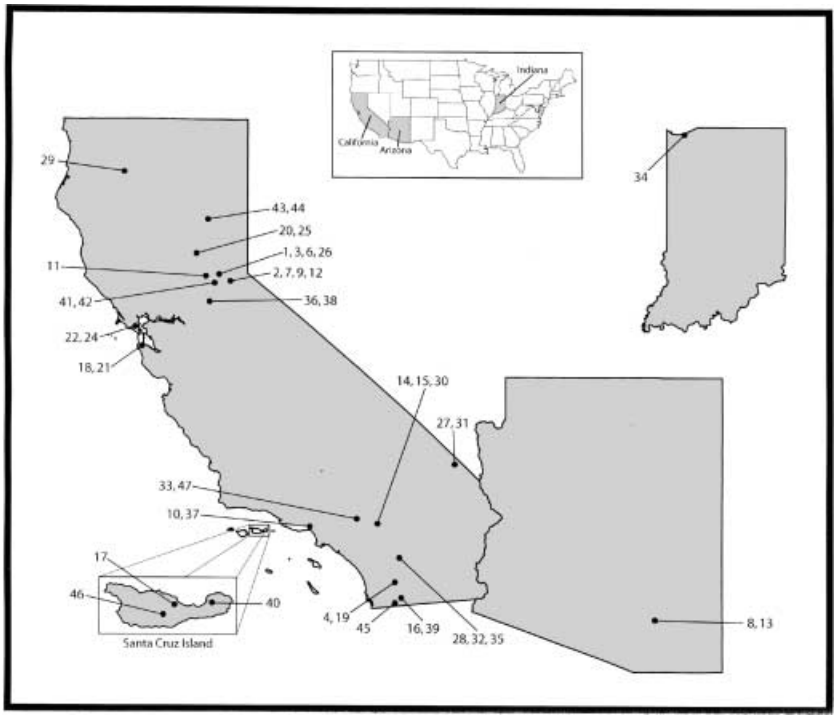

Fig. 2 Collection sites for *Tamalia* aphids. Numbers correspond to samples listed in Table 1.

Results

Data set

The full data set comprised 452–493 base pairs for 45 samples, of which 25 were *T. coweni*, 17 were *T. inquilinus*, and there was one each of *T. dicksoni*, *T. cruzensis*, and *T. morani*. Of these 45 samples, there were nine cases of identical haplotypes (described below). Within the in group, 61 characters were parsimony-informative, most of which (50) were third codon positions. Distances within the in group ranged from 0 to 9.2%.

Phylogenetic analyses

Maximum-likelihood analysis yielded two best trees (-ln likelihood 1902.52) (Fig. 3a,b). In both of these trees, the genus *Tamalia* was monophyletic, the galler *T. coweni* was paraphyletic with respect to the galler *T. dicksoni*, and the inquiline *T. inquilinus* was monophyletic and formed the sister-group to (*T. coweni* + *T. dicksoni*). These three species on *Arctostaphylos* thus formed a monophyletic group. *Tamalia cruzensis* on *C. diversifolia* was sister-taxon to (*T. coweni* + *T. dicksoni* + *T. inquilinus*) and *T. morani* on *Arbutus arizonica* was basal to the other *Tamalia*.

Bayesian-ML analysis (Fig. 4) demonstrated strong support (100%) for the monophyly of *Tamalia*, for the monophyly of (*T. coweni* + *T. dicksoni*)(84%) and for the monophyly of *T. inquilinus* (98%). However, by this analysis the relationships of these two groups with *T. cruzensis* and *T. morani* were unclear. The main intraspecific pattern exhibited by this analysis was a striking asymmetry in the degrees of support for the monophyly of *T. coweni* vs. *T. inquilinus* collected from different host plants. Thus, there was strong support for the monophyly of *T. inquilinus* on *A. viscida, A. pungens* and *A. glauca*, and for two monophyletic groups (although polyphyly overall) on *A. patula*; there was also strong support for monophyly of the *T. inquilinus* on *A. glandulosa* and *A. pringlei*. By contrast, *T. coweni* from different host plants exhibited strong support for monophyly (97%) only on *A. glauca*, although three of the four samples from *A. patula* were also monophyletic. This asymmetry in resolution and support between the gallers and their inquilines was not due to the presence of gallers from four host plants (*A. tomentosa, A. viridissima, A. insularis* and *A. uva-ursi*) that were not represented among the inquilines; when the samples from these plants were omitted, degrees of resolution and support in *T. coweni* remained similar (results not shown).

Maximum parsimony analysis on the full data set was not computationally feasible due to the presence of identical haplotypes in *T. coweni* on *A. viscida* (five identical haplotypes), *A. glauca* (two identical), on *A. patula, A. pungens* and *A. insularis* (one identical, on all three plant species), and in *T. inquilinus* on *A. viscida* (four identical). As a result, we ran the analysis after pruning the data set such that it contained no identical haplotypes for a given aphid species on a given host plant

Fig. 3 Two best maximum-likelihood trees for *Tamalia* aphids. Taxon designation indicate: Species: 'c' = *T. coweni*, 'i' = *T. inquilinus*, 'Td' = *T. dicksoni*; Host plant: 'Arct' = *Arctostaphylos*, 'Com' = *Comarostaphylis*, 'Arb' = *Arbutus*, followed by species name of host plant; Number = specimen number, corresponding to numbers in Table 1 and Fig. 2.

(i.e. we removed four of the *T. coweni* on *A. viscida*, one of the *T. coweni* on *A. glauca* and three of the *T. inquilinus* on *A. viscida*). Parsimony analysis of this reduced data set yielded 15 866 trees of length 231, and a strict consensus of these trees (Fig. 5) was similar to the ML trees, in that it showed (1) monophyly of *T. inquilinus*, (2) paraphyly of *T. coweni* with respect to *T. dicksoni*, (3) a basal position within the genus for *T. morani* on *Arbutus*, (4) good resolution among the *T. inquilinus* from *A. pungens, A. glauca, A. viscida*, and two monophyletic groups comprising *A. patula*, and (5) a relative lack of resolution for *T. coweni* from different host plants, in that only the samples from *A. glauca* were monophyletic on their host plant.

The NJ tree (Fig. 6) was very similar in topology to the ML trees. The main differences between the NJ tree and the ML trees were that in the NJ tree, *T. cruzensis* from *C. diversifolia* was sister-taxon to *T. coweni* and *T. dicksoni*, and the two *T. coweni* from *A. tomentosa* were monophyletic. Bootstrapping under NJ revealed the same general patterns as found in the ML Bayesian analysis, with strong support for: (1) monophyly of *Tamalia*, (2) monophyly of (*T. coweni* + *T. dicksoni*), (3) monophyly of *T. inquilinus*, (4) a basal position of *T. morani* on *Arbutus* within the genus, and (5) monophyly of *T. inquilinus* on each of the plants *A. viscida, A. pungens* and *A. glauca*, and for two clades on *A. patula*, but for *T. coweni* only the haplotypes from *A. glauca* forming a clear monophyletic group.

Statistical parsimony analysis also showed extremely different patterns of association between molecular-genetic relatedness and host-plant use for *T. coweni* vs. *T. inquilinus* (Fig. 7). Thus, for *T. coweni* and *T. dicksoni*, many pairs of haplotypes collected from different *Arctostaphylos* species were separated by only a single mutational step (e.g. *viscida* and *patula, patula* and *pringlei, patula* and *glandulosa, viscida* and *uva-ursi*) and there was only slight apparent evidence for clustering of haplotypes by host plant, for *T. coweni* on *A. tomentosa, A. patula, A. glauca* and *A. glandulosa*. By contrast, the *T. inquilinus* haplotypes formed four networks that were separated by more steps than the statistical parsimony limit. Three of these networks contained haplotypes from a single host plant, and in the fourth, largest network, haplotypes from *A. pungens* clustered together, and the haplotype on *A. viscida* was separated from haplotypes on other plants by at least nine steps. Indeed, only the two haplotypes of *T. inquilinus* on *A. glandulosa* and *A. pringlei* that were separated by two steps provided any evidence against

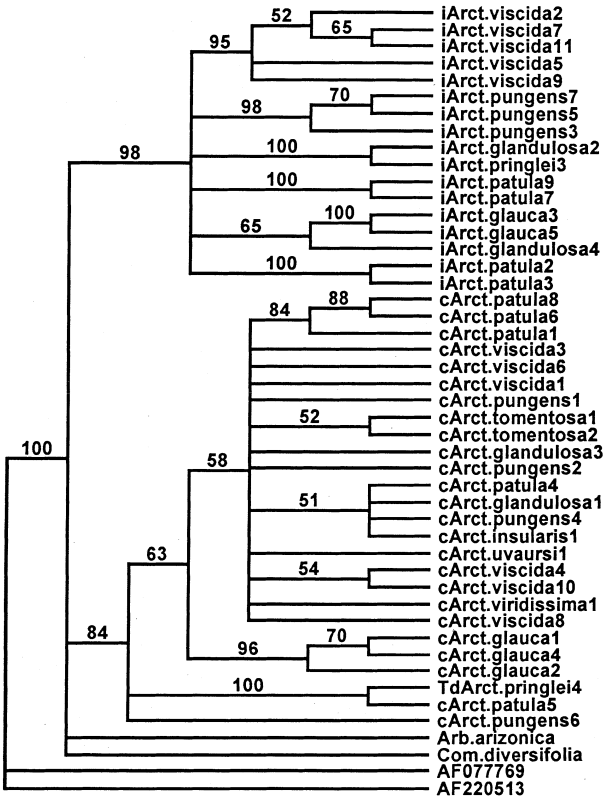

Fig. 4 Bayesian maximum-likelihood majority rule tree, inferred from 33 000 *a posteriori* trees after convergence to a stable likelihood.

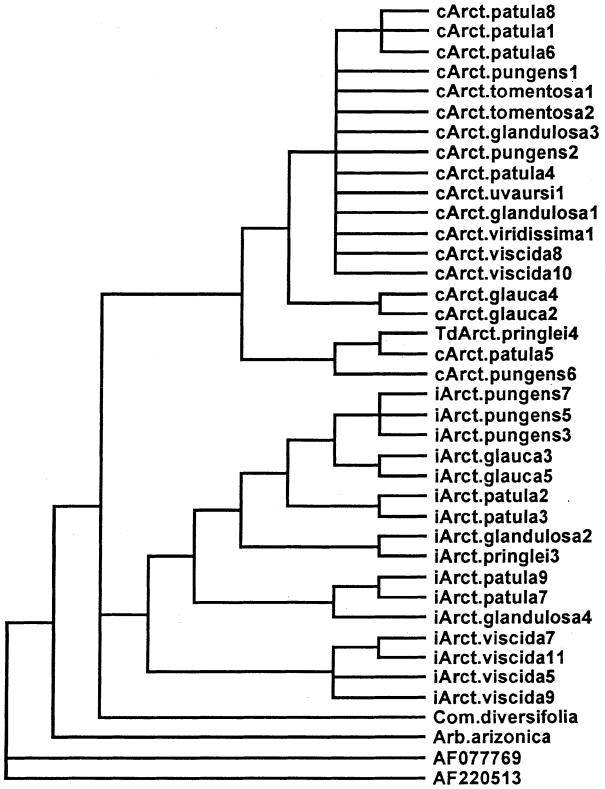

Fig. 5 Strict consensus maximum parsimony tree. Taxon designations are described in legend to Fig. 3.

strong genetic differentiation by host plant in this species.

A molecular clock was strongly rejected for the in-group (-2 ln likelihood difference = 279.5, d.f. = 35, $P < 0.001$, identical haplotypes excluded). This rate variation was apparently due to an accelerated rate of molecular evolution in *T. inquilinus* compared with *T. coweni*: the branch lengths (internodes) within the *T. inquilinus* clade were 2.5–3 times longer on average than the branch lengths within *T. coweni*, and this difference was significant using patristic distances, NJ distances, and for one of the two best ML trees using ML branch lengths (Table 2).

Discussion

Evolutionary origin of inquilines

What is the evolutionary relationship between the host aphids and their inquilines, and how did the inquilines originate? Our ML, MP and NJ phylogenies provide strong support for the monophyly of *Tamalia*, the monophyly of (*T. cruzensis* + *T. coweni* + *T. dicksoni* + *T. inquilinus*), and the monophyly of *T. inquilinus*. Moreover, the ML tree supports a sister-taxon relationship between *T. inquilinus* and their *T. coweni* hosts, although this relationship was not strongly supported by the Bayesian majority-rule trees, nor by the NJ tree, which put *T. cruzensis* as sister-taxon to *T. coweni* and (*T. coweni* + *T. cruzensis*) as the sister-group to *T. inquilinus*. These analyses show that the inquilines evolved once, from a gall-inducing *Tamalia* ancestor, and subsequently underwent their remarkable radiation primarily along host-plant lines.

Based on the natural history of *Tamalia* aphids, there are two possible routes to the origin of inquilinism: (1) interspecific colonization or (2) intraspecific divergence. By the interspecific colonization hypothesis, one species of gall-inducing aphid that exhibited communal galling gave rise to two species, presumably on different host plants. Upon recontact, one of the species began to colonize galls of the other, but it did not form galls on this plant, either because it arrived too late in leaf development (caused by differences in host-plant phenology), or because it was unable or prohibitively costly to form galls (e.g. caused by differences in host-plant physiology). This host-shifting, colonizing species then evolved obligate inquilinism as a consequence of selection for specialization as a gall invader, and via specialization to its newly adopted host plant.

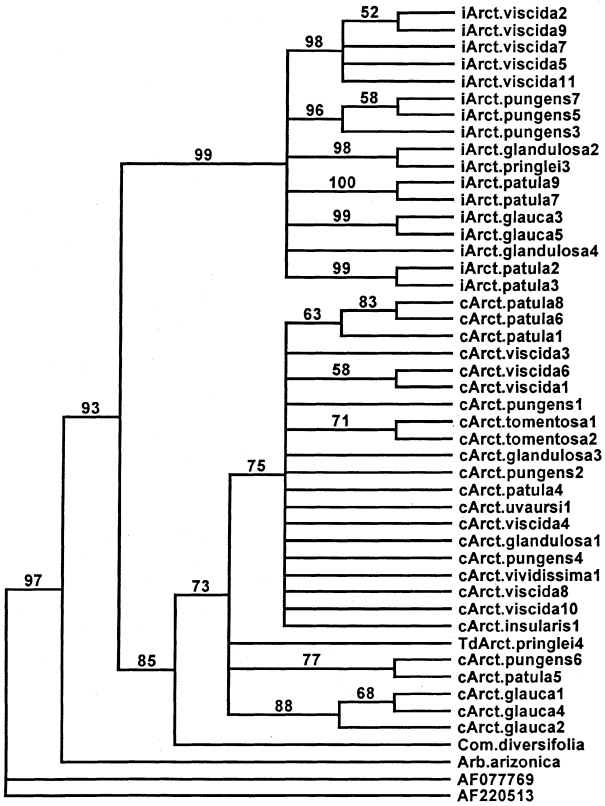

Fig. 6 Neighbour-joining bootstrap tree. Taxon designations are described in legend to Fig. 3.

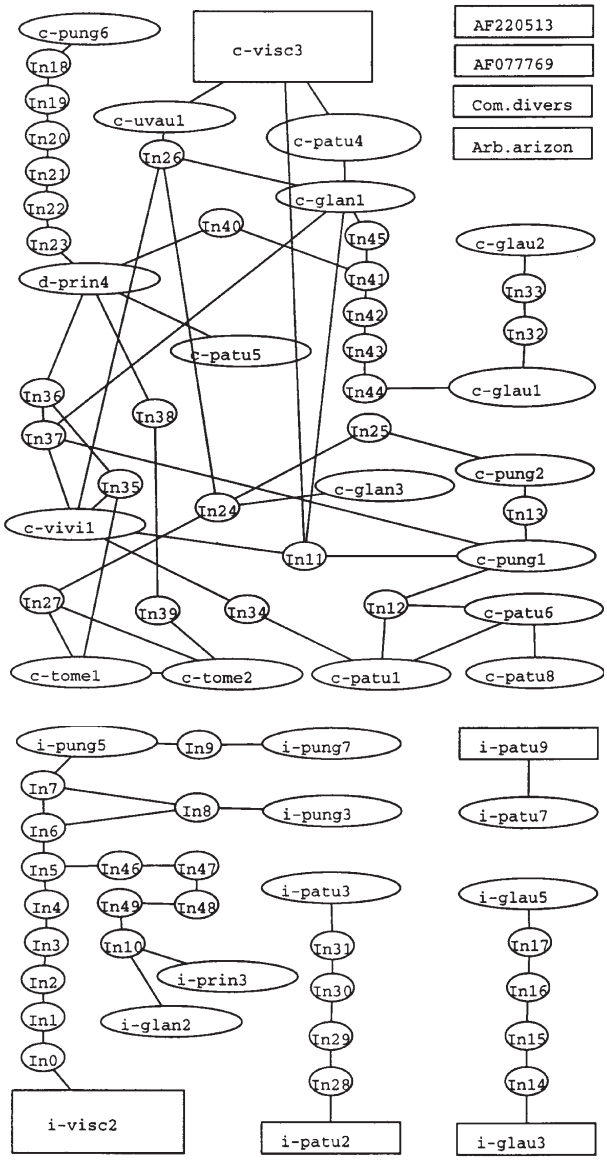

Fig. 7 TCS network. Taxon designations are described in legend to Fig. 3 and circles containing 'In' refer to inferred intermediate haplotypes. Separated subnetworks or taxa differ by greater than the statistical parsimony limit of nine steps.

There are three main lines of evidence consistent with the interspecific colonization hypothesis. First, in both *Eriosoma* aphids (Akimoto, 1988a,b, 1989) and *Yucca* moths (Pellmyr *et al*., 1996), obligate invaders or cheaters have also originated in conjunction with host-plant shifts by closely related species (see also Després & Jaeger, 1999, for a case of parasitism arising without a host shift). These parallel cases suggest that host-plant shifting may often facilitate the origin of new life-history modes in phytophagous insects, perhaps because the host-insect species have few evolved defences against the nascent inquiline or cheater (i.e. it is invading 'defence-free space')(Crespi & Abbot, 1999), and because a shift to a new host plant will engender a period of strong divergent selection, capable of leading to major life-history alteration (e.g. Price & Willson, 1976; Berlocher & Feder, 2002). Secondly, the origin of inquilines was inferred to have taken place near to the time of the split between *Tamalia* on *Comarostaphylis* and those on *Arctostaphylos*, such that it may have involved a host shift between these aphids on different plant genera, which would be expected to involve stronger selective effects than a within-genus switch. Thirdly, *Tamalia* host plants differ substantially in phenology (Munz, 1974), as do *T. coweni* and *T. inquilinus*, which suggests that, as in other cases of speciation among phytophagous insects (Butlin, 1990; Wood *et al*., 1990; Knerer, 1991; Feder *et al*., 1993; Pellmyr *et al*., 1996; Romstock-Völkl, 1997; Dixon, 1998; Lin & Wood, 2002), changes in life-cycle timing may often drive the origin of reproductive isolation.

By the intraspecific divergence hypothesis, host-plant shifting was not involved in the origin of the inquilines. Instead, they evolved sympatrically with their hosts via facultative intraspecific inquilinism (i.e. communal galling) being transformed into obligate intraspecific inquilinism and finally obligate interspecific inquilinism.

Table 2 Comparisons of branch lengths (internodes) between the *Tamalia coweni* clade and the *T. inquilinus* clade. Maximum-likelihood (ML) distances were used for the two best ML trees, patristic distances (numbers of inferred steps) were used for maximum parsimony (MP) trees and neighbour-joining (NJ) distances were used for the NJ trees. Results were qualitatively the same as regards significance values for a larger sample of the other equally parsimonious MP trees. Identical haplotypes were excluded prior to these analyses, and terminal tip branch lengths were not included in the calculations because some were undefined or of zero length.

	Maximum likelihood mean ± SE (N)		Maximum parsimony mean ± SE (N)		Neighbour joining mean ± SE (N)
	ML tree 1	ML tree 2	MP tree 1	MP tree 2	
T. coweni	0.005 ± 0.001 (17)	0.005 ± 0.001 (18)	1.71 ± 0.34 (17)	1.82 ± 0.37 (17)	0.002 ± 0.00034 (26)
T. inquilinus	0.013 ± 0.004 (14)	0.012 ± 0.004 (14)	4.46 ± 0.95 (13)	4.21 ± 0.86 (14)	0.006 ± 0.001 (16)
Z (Mann–Whitney *U*-test)	2.58	1.79	2.44	2.31	2.23
P	0.0098	0.074	0.015	0.021	0.026

This hypothesis is formally similar to the ideas proposed for the sympatric origin of parasitic and inquiline ant species (Wilson, 1971; Buschinger, 1986, 1990; Bourke & Franks, 1991; see also West-Eberhard, 1986), and it entails the same difficulty in that the social, ecological or phenological bases for the necessarily strong assortative mating and divergent selection have yet to be clearly demonstrated. However, such a mode of speciation might be feasible if intraspecific inquilines were selected to emerge at ever-later dates in the season, such that they appeared after gall-makers had mated and so were temporally reproductively isolated with a concomitant loss of the ability to cause galls. Consistent with this hypothesis, inquilines are more abundant late in the season when galls are mature or abandoned. However, on some host plants, such as *A. glauca*, the gall-inducers and inquilines frequently co-occur early in the season, which argues against a phenological shift unless this overlap in life history, or use of such host plants, evolved after the inquilines arose.

By both the interspecific colonization hypothesis and the intraspecific divergence hypothesis, the habit of communal galling serves as a crucial pre-adaptation to inquilinism. Communal intraspecific gall habitation creates conditions favouring inquilinism because, unlike in other galling insects that exhibit extreme aggression among foundresses (Whitham, 1979; Crespi, 1992; Ngakan & Yukawa, 1996; Akimoto & Yamaguchi, 1997), *Tamalia* foundresses tolerate one another within their newly forming gall. Indeed, both intraspecific communal galling, and non-aggressive interspecific cohabitation of hosts and inquilines, are known in aphids only from this genus. Analogously, the presence of larvae from multiple females in the communal galls formed by some other gall-forming insects may also have facilitated the evolution of interspecific inquilinism (Ronquist, 1994; Yang & Mitter, 1994; Ronquist & Liljeblad, 2001; Stone *et al.*, 2002; Yang *et al.*, 2001).

The above-mentioned ideas could be tested further via: (1) conducting experimental, interspecific host-plant switches, to determine if *T. coweni* that arrive relatively late at a host plant are more likely to act as intraspecific inquilines, or, apparently, interspecific inquilines in the case of *A. glauca* vs. other *Arctostaphylos* species, (2) quantification of phenological overlap between *T. coweni* and *T. inquilinus* on different *Arctostaphylos* species, and (3) testing the sympatric speciation scenario using methods outlined in Berlocher & Feder (2002). Such tests should improve our understanding of one of the most important types of life-history transitions in insects and other animals, from resource generation to exploitation.

Host-plant specificity of gallers and inquilines

Our phylogenetic analyses indicate that the gall-inducing species *T. coweni* is substantially less differentiated by host-plant than its inquiline *T. inquilinus*. Thus, for *T. coweni* only the samples from *A. glauca* formed a strongly supported monophyletic group. Although the samples from *A. viscida, A. tomentosa*, and from three of the four samples from *A. patula*, were each monophyletic on the host plant, bootstrap or Bayesian support was weak for these nodes, and the TCS network showed that all of the samples were only one to three mutational steps away from samples on a different host plant. Moreover, field experiments demonstrate that *T. coweni* winged females from *A. patula* will larviposit on *A. viscida*, and *vice versa* (D. Miller, unpublished data), which also is consistent with oligophagy, or very weak differentiation, between *T. coweni* on plants other than *A. glauca*.

In contrast to the general lack of strong host-plant association in *T. coweni*, for *T. inquilinus* the samples from *A. glauca, A. pungens* and *A. viscida* were each clearly monophyletic on their host plant, and the four samples from *A. patula* formed two separate monophyletic groups of two. Indeed, the only evidence for deviation from strict host-plant specificity in these inquilines is the polyphyly of the two samples from *A. glandulosa*, and the observation that one sample from *A. glandulosa* was only two mutational steps away from a sample from *A. pringlei* in the TCS network.

The degree of mitochondrial divergence between host-plant associated groups of *T. inquilinus* was over 2% in all

cases, which is consistent with an absence of gene flow between them and possible sibling species status. Similarly, for *T. coweni*, the divergences between samples on *A. glauca*, and samples from all of the other *Arctostaphylos* host plants, were all over 1.5%, which is also consistent with sibling species status. Further testing of hypotheses concerning sibling species vs. host race or polyphagous status requires data on gene flow, the genetic basis of adaptation, or mating experiments (Berlocher & Feder, 2002; Ferguson, 2002). Whatever the results of such studies, our data show conclusively that *T. inquilinus* shows a substantially higher degree of mitochondrial differentiation along host-plant lines than does its host aphid *T. coweni*. Given the close ecological similarities between these two species, comparison between the two clades comprising them should help in elucidating the conditions under which specificity of insects to host plants evolves. Indeed, these and clades of other phytophagous insects showing variable degrees of host-plant-associated differentiation (e.g. Roininen *et al*., 1993; Downie *et al*., 2001; Nyman, 2002) should provide especially useful systems for analysing the processes leading to speciation.

We propose three non-exclusive hypotheses to help explain the higher degree of host-plant differentiation in *T. inquilinus* than in *T. coweni*. First, rates of gene flow may be lower among populations of *T. inquilinus*, because winged asexual females of this species are rare and the primary mode of dispersal in this species is via the sexual generation at the end of the growing season. By contrast, in *T. coweni* both winged females and sexual aphids are common and can disperse. Moreover, *T. coweni* may be under stronger selection to disperse, because these aphids need find only an appropriate host plant to gall, whereas *T. inquilinus* must find a host plant that is already occupied by the gall-inducers. Under these conditions, staying in the same patch of the host plant, which has supported *T. coweni* in the previous generation, may be strongly favoured.

Secondly, inquilines, like parasites, should exhibit smaller population sizes due to their reliance on resources created by their hosts (Dowton & Austin, 1995; Page *et al*., 1998; Castro *et al*., 2002). Such small population sizes should engender enhanced founder effects, and stronger demic structure leading to local population subdivision. This hypothesis predicts higher rates of molecular evolution in *T. inquilinus* than in *T. coweni*, which is supported by our molecular-clock analyses and by comparisons of branch lengths (Table 2).

These data, together with previous studies (Dowton & Austin, 1995; Castro *et al*., 2002), show that faster molecular-evolutionary rates in parasites or inquilines, than in hosts, occur across a broad range of insect taxa, which implies that such rate differences and their causes are of general importance to the evolution of such systems. In *T. inquilinus*, a hypothesis of lower effective population size leading to accelerated mtDNA substitution rates could be tested more directly using phylogeny-based coalescent methods (e.g. Beerli & Felsenstein, 2001), or by measuring gene diversity at codominant loci.

The above mentioned hypotheses involve more local genetic differentiation in *T. inquilinus* than in *T. coweni*, which would not necessarily occur among host-plant species unless there were selection for host-plant specialization. A third hypothesis for the higher levels of specialization in *T. inquilinus* is that they are more closely adapted to specific host-plant species, physiologically, morphologically, behaviourally or phenologically. The main differences between *T. coweni* and *T. inquilinus* relevant to their host plants involve life cycle phenology: most important, *T. inquilinus* females have a narrower window of opportunity to establish themselves within galls, such that shifting between host plants that differ in their timing of leaf production may be considerably more difficult. Phenological effects are also implicated in the differentiation of both *T. coweni* and *T. inquilinus* on *A. glauca*, as this host plant exhibits earlier flowering (December–March), and presumably earlier leaf flushes, than *A. glandulosa* (January–April), *A. viscida* and *A. pringlei* (Febuary–April) or *A. patula* (April–June) (Munz, 1974).

The evolution of host races in other insects is, in general, marked by a relatively intimate association between the insects and the plant, involving galling, internal feeding by larvae, tight synchronization of life cycles, tendency to feed on a single host plant, and mating and oviposition on the host (Berlocher & Feder, 2002; Drès & Mallett, 2002). As inquilines, *T. inquilinus* are subject to such host-related selection not only from their gall-inducing *T. coweni* hosts, but also from their host plants. As a result, they are expected to exhibit a higher level of host-related adaptation, which should lead more readily to specialization (Jaenike, 1990; Whitlock, 1996; Kawecki, 1998; Berlocher & Feder, 2002; Nosil *et al*., 2002; see also Kindlemann & Dixon, 1994; Guldemond & Mackenzie, 1994; Mackenzie & Guldemond, 1994; Dixon, 1998 on the evolution of specialization in aphids).

Diversification of *Tamalia* on Arbutoideae

Although the gall-inducing *Tamalia* on *Arctostaphylos* do not exhibit strong host-plant specificity, there is a notable pattern in *Tamalia* host-plant use at the genus level. Thus, *T. morani*, the most-basal species, is found on *Arbutus*, and *T. cruzensis*, which is sister-taxon to the species on *Arctostaphylos*-inhabiting species (*T. coweni* + *T. inquilinus* + *T. dicksoni*) in the ML trees, is found on *Comarostaphylis*. This higher-level phylogenetic pattern in aphid host-plant use matches the phylogeny of the plant genera: *Arbutus* is inferred as basal and *Comarostaphylis* is sister-taxon to *Arctostaphylos* (Hileman *et al*., 2001). This coincident pattern would support cospeciation at the plant genus level if the ages of the relevant inferred cospeciation events were similar for the aphids and

plants. According to Hileman *et al*. (2001), fossil data indicate that the genus *Arbutus* is in the order of 100–240 million years old, but the presence of this genus in North America may be much more recent (as late as about 20 million years ago), and the genera *Arctostaphylos* and *Comarostaphylis*, which were derived from within the genus *Arbutus*, are no younger than about 15 million years old. *Tamalia morani* on *Arbutus* has diverged a maximum of 9.5% from other *Tamalia*, which corresponds to roughly 10 million years under an insect COI clock (Brower, 1994; Juan *et al*., 1995, 1996), and *T. cruzensis* from *Comarostaphylis* has diverged a maximum of 7.2% from *Tamalia* on *Arctostaphylos*, which corresponds to roughly 5 million years. Taken together, this evidence suggests that unless the genus *Tamalia* has an unusually slow rate of mtDNA evolution, it is too recent to have cospeciated with their host plants, at least not at the genus level. Instead, this genus may initially have colonized *Arbutus*, presumably host-shifting from some other plant, and later shifted to *Arctostaphylos* and *Comarostaphylis* that were already extant in western North America. This hypothesis can be tested further by collecting and sequencing *Tamalia* from other species of *Arbutus, Comarostaphylis* and *Arctostaphylos*, which may drive their inferred date of origin back to a time more compatible with the evolutionary chronology of their host plants. By contrast, the possibility remains that *T. inquilinus* is cospeciating with its *Arctostaphylos* hosts, as they have both apparently diversified primarily over the past several million years. Testing this idea will require more complete and robust phylogenies for both the plants and the *T. inquilinus* aphids.

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