22

Phylogenetic analysis of pseudomyrmecine ants associated with domatia-bearing plants

Philip S. Ward

Introduction

The close relationship between domatia-bearing plants and certain ants has long held the attention of naturalists and raised questions about the nature and origin of such interactions (Belt 1874; Müller 1876; Ule 1906; Spruce 1908; Bequaert 1922; Wheeler 1942; recent reviews in Benson 1985; Huxley 1986; Jolivet 1986). Tropical arboreal ants of the subfamily Pseudo-myrmecinae are especially prone to involvement in intimate associations with plants, and their behaviour in defence of the plant is often quite apparent, at least to sting-vulnerable observers. Indeed, studies on pseudomyrmecines inhabiting swollen-thorn acacias in Central America and *Barteria* (Passifloraceae) in Africa have provided some of the best evidence of the mutualistic nature of such ant–plant interactions (Janzen 1966, 1972).

Despite these ecological studies, we remain rather ignorant about the origin and evolution of associations between ants and domatia-bearing plants. This may be partly because we have focused too narrowly on a few specific cases, and ignored the wider ecological and historical context in which they are enmeshed. There is increasing recognition of the need for broad based comparative studies of ant–plant mutualisms (Davidson *et al.*, 1989; McKey 1989; Longino Chapter 19, this volume; Davidson and Fisher Chapter 20, this volume); yet the cloud of taxonomic uncertainty hanging over the ant–plant interactants continues to impede research on a large geographical and phylogenetic scale.

In this chapter I adopt a taxonomic–historical approach to the problem of pseudomyrmecine–plant interactions, by probing the phylogenetic rela-tionships of the obligate plant-ants and their non-specialist relatives. The resulting inferences about phylogeny provide a framework upon which the known ant–plant associations and other comparative natural history can be mapped. This admittedly myrmecocentric approach permits us to consider such questions as:

1. How many times have domatia-inhabiting ants evolved in the Pseudomyr-mecinae?

2. Have obligate plant-ants expanded or altered their range of plant associations over evolutionary time?
3. Is there any correspondence between the phylogenetic histories of the ants and their plant partners?
4. What are the pre-conditions for, and consequences of, the evolution of obligate associations with plants?

The Pseudomyrmecinae are a diverse group of ants, containing an estimated 250–300 species, of which a considerable number are poorly known or undescribed. The results of the phylogenetic analyses presented here must be considered tentative and coarse-scaled. Details of relationships within certain difficult sections (e.g. the *Pseudomyrmex sericeus* group) cannot be clarified at this stage. Nevertheless, the results do reveal certain general patterns which are unlikely to be altered by changes in taxonomic detail.

Phylogenetic relationships among the Pseudomyrmecinae

Ongoing systematic research on the Pseudomyrmecinae (Ward 1989*b*, 1990) supports the recognition of three genera: *Pseudomyrmex* (New World; 150–200 species), *Tetraponera* (Palaeotropical; approximately 100 species), and *Myrcidris* (Neotropical, monotypic). I also recognize several major species groups within each of the two principal genera. The African 'satellite' genera *Viticicola* (for *V. tessmanni*) and *Pachysima* (for *P. aethiops* and *P. latifrons*) have recently been formally put into synonymy with the genus *Tetraponera* (Ward 1990). For a first assessment of phylogenetic relationships 50 pseudomyrmecine species were chosen, representing all three genera and all major species groups, and a systematic survey of character variation among these taxa was undertaken. This resulted in a set of 125 morphological characters (both binary and discrete multi-state), of which 66 are male-based and 59 are derived from queen and worker morphology. The characters involve aspects of shape, size, colour, sculpture, and pilosity, of various structural features including male genitalia; biological attributes of the ants (e.g. plant associations) were specifically excluded. The full data matrix (50 taxa by 125 characters) is given in Appendix 22. 1. Undescribed species of pseudomyrmecines are referred to by code numbers (e.g. *Pseudomyrmex* sp. PSW-02).

David Swofford's (1985) PAUP program (version 2.4.1) was employed to search for the most parsimonious tree(s) consistent with this data set, using the options MULPARS, SWAP = GLOBAL, and three different ADDSEQ conditions. *Myrcidris* was used as an outgroup to root the tree since recent studies (Ward 1990) indicate that *Pseudomyrmex* and *Tetraponera* are more closely related to one another than to this third genus. When the data set produced a large number of equally parsimonious trees, a

strict consensus tree (Rohlf 1982) of all such minimum-length trees was calculated.
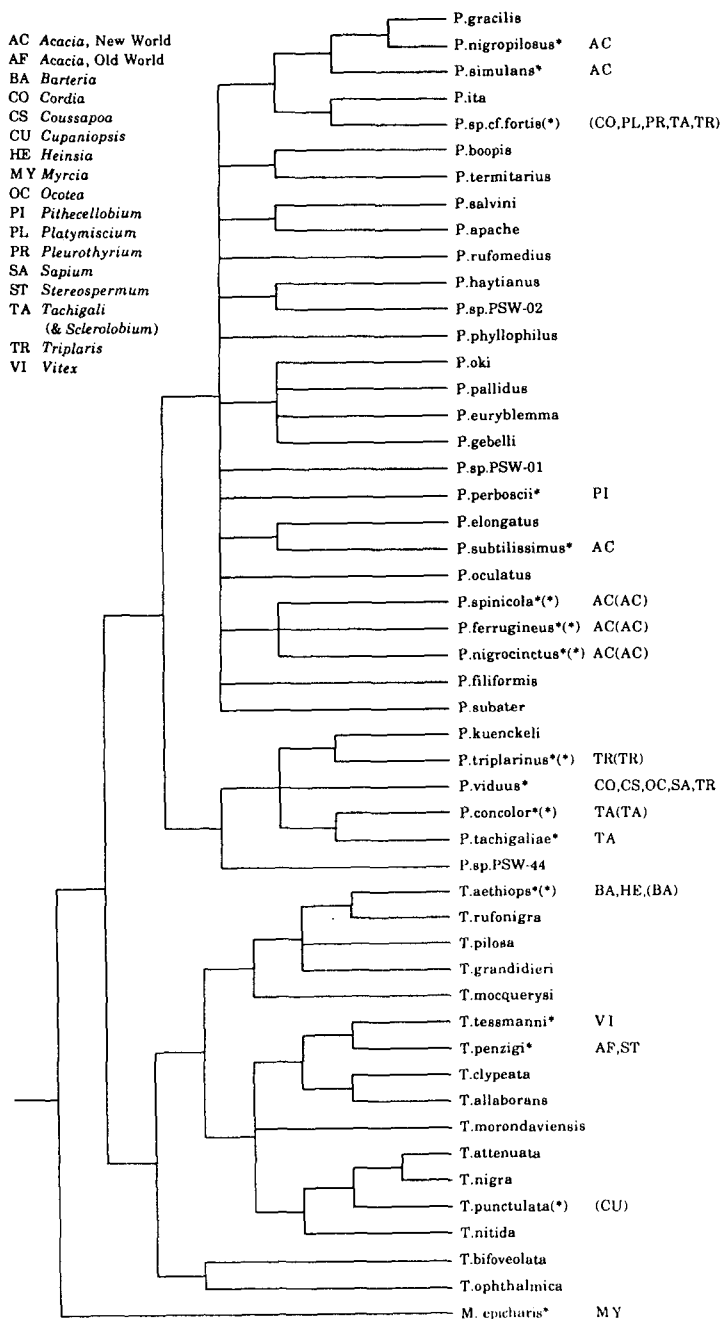
The result of these calculations (Fig. 22. 1) depicts the inferred phylogenetic relationships between the 50 representative species of Pseudomyrmecinae. This strict consensus tree shows only the groupings common to all of the 154 equally parsimonious trees (length 543, consistency index 0.343) generated by PAUP. Despite the lack of resolution in parts of the tree, there is enough overall structure to indicate that obligate plant-ants have arisen a number of times throughout the subfamily and are not confined to one or two lineages.

Nesting behaviour and plant associations of pseudomyrmecine ants

Most species of pseudomyrmecine ants nest in dead stems of woody and herbaceous plants, usually in cavities which have been at least partially excavated by other insects. Although they may exhibit habitat preferences, these species are nest-site generalists, inhabiting dead hollow twigs and branches opportunistically. A minority of pseudomyrmecines live only in specialized live plant cavities (domatia), which are intrinsically hollow or which can be easily excavated by the ants. Of the approximately 230 species of Pseudomyrmecinae (described and undescribed) known to me, at least 37 (16 per cent) appear to be obligate plant-ants (Table 22. 1). Undoubtedly, additional species of pseudomyrmecines have yet to be discovered so that the total number of species probably lies in the region of 250–300; but the percentage of known plant specialists is not likely to change markedly. Before focusing on these obligate plant-ants, however, it is worth noting that some generalist pseudomyrmecines will also nest facultatively in domatia (Table 22. 1) or in insect-bored cavities in *live* parts of non-myrmecophytes (Table 22. 2). Some of the latter cases may provide insight into the origins of more intimate ant–plant associations. In fact, where details of natural history are sparse, it may be difficult to determine the status of the plant and its relationship to the ants. More information is needed, for example, on the interaction between *Stereospermum* (Bignoniaceae) and *Tetraponera penzigi* in Africa (Penzig 1894), and on the association between *Acacia caven* and various ants, in South America (Wheeler 1942).

Information on plant associates and other relevant natural history was compiled from the primary literature, museum records, colleagues, and the results of my own field work in the neotropics, Madagascar, South-east Asia, and Australia. The known obligate plant associations have been plotted on the terminal branches of the cladogram (Fig. 22. 1).

A review of the pseudomyrmecine plant-ants on a case by case basis reveals some interesting patterns and permits us to estimate the minimum number of times that domatia-inhabiting ants have originated in this subfamily. Starting at the top of the tree (Fig. 22. 1), and referring to the

AC *Acacia*, New World
AF *Acacia*, Old World
BA *Barteria*
CO *Cordia*
CS *Coussapoa*
CU *Cupaniopsis*
HE *Heinsia*
MY *Myrcia*
OC *Ocotea*
PI *Pithecellobium*
PL *Platymiscium*
PR *Pleurothyrium*
SA *Sapium*
ST *Stereospermum*
TA *Tachigali*
     (& *Sclerolobium*)
TR *Triplaris*
VI *Vitex*

P.gracilis
P.nigropilosus*   AC
P.simulans*   AC
P.ita
P.sp.cf.fortis(*)   (CO,PL,PR,TA,TR)
P.boopis
P.termitarius
P.salvini
P.apache
P.rufomedius
P.haytianus
P.sp.PSW-02
P.phyllophilus
P.oki
P.pallidus
P.euryblemma
P.gebelli
P.sp.PSW-01
P.perboscii*   PI
P.elongatus
P.subtilissimus*   AC
P.oculatus
P.spinicola*(*)   AC(AC)
P.ferrugineus*(*)   AC(AC)
P.nigrocinctus*(*)   AC(AC)
P.filiformis
P.subater
P.kuenckeli
P.triplarinus*(*)   TR(TR)
P.viduus*   CO,CS,OC,SA,TR
P.concolor*(*)   TA(TA)
P.tachigaliae*   TA
P.sp.PSW-44
T.aethiops*(*)   BA,HE,(BA)
T.rufonigra
T.pilosa
T.grandidieri
T.mocquerysi
T.tessmanni*   VI
T.penzigi*   AF,ST
T.clypeata
T.allaborans
T.morondaviensis
T.attenuata
T.nigra
T.punctulata(*)   (CU)
T.nitida
T.bifoveolata
T.ophthalmica
M. epicharis*   MY

Fig. 22.1. Estimated phylogenetic relationships between 50 representative species of pseudomyrmecine ants. This is a strict consensus tree of 154 equally parsimonious trees generated by PAUP. (Data set given in Appendix 22.1.) Obligate plant-ants are designated by an asterisk, and their plant associates are given. Information in parentheses refers to other (one or more) closely related species of obligate plant-ants

information in Table 22. 1, we find the following. In the *Pseudomyrmex gracilis* group (Kempf 1958; Ward 1989*b*), represented in the cladistic analysis by *P. gracilis*, *P. nigropilosus*, and *P. simulans*, there are two obligate plant-ants (*P. nigropilosus*, *P. simulans*), both associated with swollen-thorn acacias of Central America. Since these two are not sister species and since most of the remaining members of the *P. gracilis* group (20 or more species) are generalist twig-nesters, *P. nigropilosus* and *P. simulans* probably represent two independent origins of specialization on acacia. Moreover, *P. nigropilosus* is a non-protective 'parasite' of the ant–acacia system (Janzen 1975).

Next comes the taxonomically difficult *Pseudomyrmex sericeus* group, represented on the cladogram by *P. ita* and *P.*sp.cf.*fortis*. Although the *P. sericeus* group as a whole is distinctive, and almost certainly monophyletic (diagnosis in Ward 1989*b*), the relationships and species limits within the group are quite unclear. As a result it is difficult to hazard a guess about how many times plant-ants have arisen. There appear to be eight or more species of obligate plant-ants in this group (out of about 15 species in total), showing a tendency to be associated with *Tachigali* and *Sclerolobium* (Caesalpiniaceae), but also recorded from domatia of *Cordia* (Boraginaceae), *Triplaris* (Polygonaceae), *Pleurothyrium* (Lauraceae), and *Platymiscium* (Papilionaceae). At least two species (*P. pictus*, *P. rubiginosus*) occupy more than one plant genus. This looks like a group in which plant switching and secondary colonization of ant-plants have occurred several times. Most, if not all, of the species are aggressive plant defenders, however, and do not appear to be opportunistic parasites like *P. nigropilosus*.

Pseudomyrmex perboscii is a taxonomically isolated and distinctive species, which (at least in northern Colombia and Venezuela) occupies live branches of the mimosoid legume, *Pithecellobium saman* (Benth.) Lyons (= *Albizia saman*) (Mimosaceae) (Ward 1989*b*). Since the ant ranges from Mexico to Bolivia and Brazil, it probably inhabits other ant-plants. Ducke's (1925) record of a *Pseudomyrmex* sp. from *Inga cinnamomea* Spruce, ex Benth. (Mimosaceae) might refer to this species.

Pseudomyrmex subtilissimus is a small timid species, known only from a few collections on swollen-thorn acacias, where it is apparently able to co-exist with aggressive acacia-ants (*P. ferrugineus* group). The latter group, represented on the cladogram by *P. spinicola*, *P. ferrugineus*, and *P. nigrocinctus*, is well defined and undoubtedly monophyletic. Its distribution is co-extensive with that of the swollen-thorn acacias (Mexico to northern Colombia). A brief diagnosis of the group and of the commoner species is given in Ward (1989*b*). Janzen's (1967) detailed experimental study of the ant–acacia interaction (using *P. ferrugineus* and *Acacia cornigera*) demonstrated that the ants provide essential protection against herbivores and competing plants. In many parts of Central America several species of acacia and acacia-ant co-occur, with no specificity of pairing. Moreover, the

Table 22.1. Pseudomyrmecine ants recorded from live plant domatia. Principal sources: Bequaert (1922), Wheeler (1942), Janzen (1966, 1972), Hocking (1970), Benson (1985), Huxley (1986), McKey (1984), personal observations. Plants associated with *Pseudomyrmex* and *Myrcidris* are New World taxa; those associated with *Tetraponera* are from the Ethiopian (ET) and Australian (AU) regions. st = swollen-thorn *Acacia* of Central America and northern South America.

Genus/species group	Species	Plant(s)	Obligate plant-ant?	Coccoidea in cavities?
Pseudomyrmex ferrugineus group	*ferrugineus* and 8 other spp.	*Acacia* (st)	Y	N
P. gracilis group	*nigropilosus*	*Acacia* (st)	Y	N
	simulans	*Acacia* (st)	Y	N
	gracilis complex (2+ spp.)	*Acacia* (st)	N	N
	gracilis complex (1 sp.?)	*Cordia, Triplaris*	N	Y
	sp. PSW-35	*Tachigali*	?	Y
P. oculatus group	*elongatus*	*Cecropia, Cordia, Pithecellobium,* and *Triplaris*	N	?
P. pallens group	*urbanus*	*Cordia*	N	Y
	sp. PSW-03	*Cecropia, Inga*	?	?

Group	Species	Plant(s)		
P. sericeus group	*ita*	*Acacia* (st)	N	N
	sericeus complex (2+ spp.)	*Triplaris*	?	Y
	sericeus complex (2+ spp.)	*Cordia*	Y	Y
	sericeus complex (4+ spp.)	*Tachigali, Sclerolobium,* and *Platymiscium*	Y	Y
	sericeus complex (1 sp.)	*Pterocarpus*	?	?
	pictus	*Tachigali, Platymiscium*	Y	Y
	rubiginosus	*Triplaris, Pleurothyrium*	Y	Y
P. subtilissimus group	*subtilissimus*	*Acacia* (st)	Y	N
P. tenuis group	*boopis*	*Cordia*	N	?
	tenuis	*Patima*	N	N
P. viduus group	*viduus*	*Triplaris, Sapium, Coussapoa, Cordia,* and *Ocotea*	Y	Y
	triplarinus complex (4+ spp.)	*Triplaris*	Y	Y
	concolor complex (5+ spp.)	*Tachigali*	Y	Y
	kuenckeli	*Acacia* (st)	N	N
Pseudomyrmex	*perboscii*	*Pithecellobium*	Y	Y
Tetraponera	*aethiops, latifrons*	*Barteria, Heinsia* (ET)	Y	Y
	tessmanni	*Vitex* (ET)	Y	N
	penzigi	*Acacia, Stereospermum* (ET)	Y[a]	Y[b]
	sp. PSW-77	*Cupaniopsis* (AU)	Y	Y
Myrcidris	*epicharis*	*Myrcia*	Y	Y

[a] Possibly facultative.
[b] In *Stereospermum*; coccoid association in *Acacia* less certain.

Table 22.2. Pseudomyrmecine species recorded nesting in live stems or thorns, apparently excavated by other insects. Most, if not all, of these species are generalist twig-nesters.

Species		Plant(s)	Coccoidea in cavities?	Source
Pseudomyrmex	*acanthobius*	*Acacia caven*	?	Wheeler (1942)
	boopis	*Lantana*	N	Ward (unpublished work)
	gracilis (s.l.)	*Acacia caven*	?	Museum specimens
	tenuis	*Witheringia*	N	Longino (personal communication)
	urbanus	*Tecoma*	Y	Santschi (1936), Ward (1989*b*)
	sp. cf. *fortis*	*Avicennia germinans*	Y	Ward (unpublished work)
Tetraponera	*grandidieri*	*Ixora, Leea, Rhus*	N	Ward (unpublished work)
	hysterica	*Albizia*	N	Ward (unpublished work)
	punctulata	*Eucalyptus, Avicennia*	Y	Ward (unpublished work)
	rufonigra	*Sonneratia*	N	Ward (unpublished work)

swollen-thorn acacias apparently represent several independent lines of evolution towards a myrmecophytic habit (Janzen 1966, 1974*a*). Thus, here there is not expected to be any clear pattern of co-speciation between the ants and plants.

The *Pseudomyrmex viduus* group (previously known as the *P. latinodus* group; see Ward 1989*b*) contains an intriguing set of species, of which five representative taxa were chosen for cladistic analysis (*P. kuenckeli*, *P. triplarinus*, *P. concolor*, *P. tachigaliae*, and *P. viduus*). Of these, *P. kuenckeli* is not an obligate plant-ant, and the cladogram suggests that it has secondarily reverted to more generalized nesting habits. If confirmed by an in-depth phylogenetic analysis of the *P. viduus* group this would represent the only known case of such a reversal. The remaining members (10 or more species) of the *P. viduus* group are all obligate plant-ants, with the *P. concolor* complex specialized on *Tachigali* (Caesalpiniaceae) and the *P. triplarinus* complex confined to *Triplaris* (Polygonaceae). Perhaps most interesting of all is *P. viduus*, an obligate plant-ant whose recorded hosts include plants from five genera in as many families: *Cordia* (Boraginaceae), *Coussapoa* (Moraceae), *Ocotea* (Lauraceae), *Sapium* (Euphorbiaceae), and *Triplaris* (Polygonaceae). It is unclear whether such flexibility is ancestral or derived. In the majority of cladograms produced by PAUP, *P. viduus* is positioned as an outgroup to the remaining members of its species group. This would suggest that association with *Triplaris* (if not additional plants) is part of the ground plan of the *P. viduus* group, with one lineage subsequently remaining on *Triplaris*, and another switching to *Tachigali*.

In the Old World genus *Tetraponera*, *T. aethiops* and its sister species, *T. latifrons*, inhabit and protect small trees in the genus *Barteria* (Passifloraceae) in equatorial West Africa (Janzen 1972). *Tetraponera aethiops* has also been recorded from live stems of the rubiaceous plant, *Heinsia myrmoecia* (Stitz 1910; Schnell and Grout de Beaufort 1966).

Two other Afrotropical species, *Tetraponera tessmanni* (associated with *Vitex*) and *T. penzigi* (associated predominantly with whistling-thorn *Acacia*), appear as sister groups in the cladistic analysis; however they probably represent independent origins of the domatia-inhabiting trait, since there are a number of species more closely related to *T. penzigi* (e.g. *T. liengmei*, *T. gerdae*) which are apparently generalist twig-nesters. Even the status of *T. penzigi* as an obligate plant-ant is uncertain (Bequaert 1922). It is not the most common ant in the whistling-thorn acacias, that role being taken by *Crematogaster* (Hocking 1970), and it has been recorded from live stems of an unrelated plant, *Stereospermum dentatum* (Bignoniaceae) (Penzig 1894).

An undescribed species of *Tetraponera* (*T.*sp.PSW-77), allied to *T. punctulata*, occupies live terminal branches of *Cupaniopsis anacardioides* (Sapindaceae) in south-east Queensland (Ward, unpublished work). The plant has a much wider geographical range than the ant, indicating that this

represents an ant mutualism in the early stages of development (see further discussion below).

Finally, *Myrcidris* contains a single described species *M. epicharis* (Ward 1990), discovered by W. W. Benson, which lives in swollen terminal stems of *Myrcia* sp. (Myrtaceae), an Amazonian understorey tree. This curious ant, possesses some morphological features apparently ancestral to all other pseudomyrmecines and, at the same time, a number of unique and strongly derived (autapomorphous) traits, suggesting that the mutualism may be quite old.

In summary, obligate domatia-inhabiting ants appear to have evolved at least 12 times in the Pseudomyrmecinae. Three groups of plant-ants, all from the New World, have undergone considerable diversification: the *P. ferrugineus* group, on swollen-thorn acacias; the *P. viduus* group, principally on *Triplaris* and *Tachigali*; and a section of the *P. sericeus* group, on *Cordia*, *Tachigali*, *Triplaris*, and other plants. None of these three groups is particularly closely related to the other (Fig. 22. 1). The remaining pseudomyrmecine plant-ants occur in small, independent groups of one or two species. From the plant point of view, the majority of pseudomyrmecines associated with *Acacia*, *Tachigali*, and *Triplaris* form monophyletic groups (the *P. ferrugineus* group, *P. concolor* complex, and *P. triplarinus* complex, respectively), while the remaining species in each assemblage are (with the exception of *P. viduus*) not closely related to these three majority groups, and presumably represent secondary colonizers. In the case of *Tachigali*, the 'secondary group' comprises several species in the *P. sericeus* group, whose diversity and geograpical range suggest that they may have been involved with the *Tachigali* mutualism since its early stages.

These patterns emerge from a pairing of the data in Table 22. 1 with the results of a cladistic analysis of 50 representative taxa (Fig. 22. 1). Given the preliminary nature of this analysis, it is worth inquiring whether the observed patterns continue to hold up with other, slightly less parsimonious trees. I examined about 440 trees of slightly greater length (544 to 549 steps) than the set of most parsimonious trees (543 steps), by sub-optimizing PAUP's performance (using the SWAP and ADDSEQ options). Although differing in details, these trees showed substantial agreement with the set of most parsimonious trees with respect to the major groupings shown in Fig. 22. 1. Perhaps the most noteworthy difference was that the *P. viduus* group appeared as paraphyletic or polyphyletic in a minority of cases. None of the slightly less parsimonious trees altered the major conclusions of:

1. multiple origination of plant-ants;
2. monophyly of the majority of species associated with each of the major ant-plants;
3. the general lack of a close relationship between these majority groups and the remaining group of ants found on the same plants.

The observation of considerable host-plant diversity within some groups of plant-ants also remains valid; and of course the same observation continues to apply to certain species (such as *P. viduus*), regardless of the outcome of phylogenetic inference.

Discussion

Patterns of association

These findings confirm the view that pseudomyrmecine ants have repeatedly developed obligate associations with domatia-bearing plants. The number of origins is not likely to be a simple function of the number of times that the myrmecophytes have evolved, however. This is because there is considerable evidence of plant switching and secondary colonization of pre-existing ant-plants. This is suggested by the occurrence of two or more pseudomyrmecine lineages on *Acacia*, *Triplaris*, and *Tachigali*; by the diversity of plants associated with some groups of plant-ants (*P. sericeus* group, *P. viduus* group); and by the existence of *intraspecific* variation in host-plant choice. Thus, about one-quarter of the 37 obligate plant-ants listed in Table 22. 1 occupy more than one plant genus, sometimes (e.g. *P. viduus*, *P. rubiginosus*, *T. aethiops*, *T. penzigi*) in widely different plant families. These observations belie the notion of a close correspondence between ant and plant phylo-genies. This is true even for the close association between acacia-ants (*P. fer-rugineus* group) and their plants, ostensibly a classic example of co-evolution in the strict sense, and yet one which is diffuse enough to preclude a clear pattern of co-speciation (Janzen 1966, 1974*a*). Diffuse co-evolution is even more likely for the pseudomyrmecine–*Tachigali* system, and that involving *Triplaris*, in which there has evidently been a period of co-participation by the *P. viduus* and *P. sericeus* groups. In some regions of South America ants of the genus *Azteca* are also part of the contemporary guilds on *Triplaris* and *Tachigali*.

Of course, where the present-day assemblage of ants associated with a particular myrmecophyte is taxonomically diverse, it may be difficult (if not impossible) to ascertain with certainty which lineage(s) was involved in the original development of the interaction. In the case of New World *Cordia* and African *Acacia*, ants other than pseudomyrmecines (*Azteca* and *Crematogaster*, respectively) are the predominant inhabitants; but whether the pseudomyrmecines are secondary arrivals or early associates which have been competitively pushed aside cannot be easily determined. Some evidence could be adduced from the geographical ranges of the ants and plants, the morphological fit between ants and domatia, and the behaviour of colony-founding queens; but without a much more thorough knowledge of the historical biogeography of the ant and plant the evidence would remain circumstantial in nature.

Origins of pseudomyrmecine–plant relationships

What factors have predisposed pseudomyrmecines to become obligate plant-ants? Janzen (1966) lists a number of potentially important traits of which arboreal nesting, a tendency to glean foliage for small pieces of organic matter, and the possession of a well-developed sting, seem particularly significant. The pseudomyrmecine sting sheath and lancets are both barbed (the latter are not smooth, as claimed by Janzen (1966)). Although most generalist twig-nesters sting reluctantly and only in defence, a few Old World species can be aggressive (e.g. *T. rufonigra*, *T. difficilis*, *T. morondaviensis*).

A closer look at the nesting habits of pseudomyrmecines provides further insight into the evolution of specialist plant-ants. As noted previously, a number of generalist pseudomyrmecines have been recorded nesting opportunistically in plant domatia (Table 22. 1), illustrating the potential for secondary colonization. A clue to the primary origin of ant–myrmecophyte associations lies in the tendency of some pseudomyrmecine ants to occupy the *live* stems or thorns of unspecialized plants, in cavities excavated by beetle or lepidopteran larvae. Examples are given in Table 22. 2; these involve 10 species of Pseudomyrmecinae, most of which are known to nest in dead stems of woody plants also. This phenomenon has probably been under reported, both for pseudomyrmecines and for other ants (J. T. Longino, personal communication). Of particular interest are two cases (involving *Pseudomyrmex* sp.cf. *fortis* and *Tetraponera punctulata*) in which the ants have been observed tending scales (Coccidae) inside the insect-bored cavities. Colonies of *Pseudomyrmex* sp.cf.*fortis*, which occupy live, excavated branches of *Avicennia* in northern Colombia and tend scales of the genus *Cryptostigma*, have more aggressive workers than those of a sympatric relative, *P. ita*, nesting in dead twigs. A member of the *P. sericeus* complex, *P.*sp.cf.*fortis*, closely resembles species which have been collected in *Cordia* and *Triplaris*. The Australian species, *Tetraponera punctulata*, typically occupies dead branches but it will occasionally nest in live stems of *Avicennia* and *Eucalyptus* with coccids (?*Coccus* sp., and an undescribed species in, or near, *Cryptostigma*). *Tetraponera punctulata* is closely related to the obligate plant-ant, *T.*sp.PSW-77, which keeps *Cryptostigma* in hollow stems of *Cupaniopsis anacardioides*. A related phenomenon has been reported from Malaysia: an undescribed species of *Tetraponera* in the *T. attenuata* complex (*T.*sp.PSW-80) inhabits live hollow internodes of a bamboo, *Gigantochloa ligulata* (Poaceae), and maintains scale insects in the nest (D. Kovac, personal communication).

Nearly all pseudomyrmecines which are obligate plant-ants tend scale insects (principally Coccidae and Pseudococcidae) in their domatia (see Table 22. 1). The only exceptions are, (i) species living in swollen-thorn acacias of Central America, where alternative trophic rewards are available in the form of Beltian bodies and extrafloral nectar, and (ii) *T. tessmanni*, a

Vitex (Verbenaceae) inhabitant, for which there is an indication that workers obtain nutrients directly from plant tissue (Bailey 1922*b*). There is evidence that ants which keep scales in their domatia not only harvest the honeydew but also periodically consume the scales themselves, thus obtaining both carbohydrates and protein (Bailey 1923; Wheeler 1942; Janzen 1972; Carroll and Janzen 1973; Schremmer 1984).

It seems probable that scale insects (Coccoidea), especially those prone to reside in protected crevices or cavities, have been crucial to the inception of most pseudomyrmecine–plant mutualisms, because they provide the trophic resource which draws the ants into a closer relationship with a potential myrmecophyte. If ant activity does not provide a consistent benefit to the plant, the relationship may develop no further than that permitted by the presence of twig-boring insect larvae. However, if ant occupancy confers a net gain in fitness on the plant, despite the cost of maintaining scales, and if the plant possesses the necessary structural features, it may be able to encourage ant inhabitation by developing, or elaborating upon, pithy swellings (McKey 1989). This would allow the ants to escape dependency on twig-boring insects, and (by pre-emption) lower the frequency of the latter. Such a dependency on the activity of insect larvae which bore live or dead stems is, incidentally, very common among generalist pseudomyrmecines and other twig-nesting ants. It is conceivable that the removal of this dependency in the early stages of a pseudomyrmecine–plant relationship does not even require special development in the plant. Consider the *Tetraponera–Cupaniopsis–Cryptostigma* system mentioned previously. The ant, whose workers and queens excavate the pithy terminal stems in which brood and coccids are kept, appears restricted to a limited area in south-east Queensland, yet the plants here are not manifestly different in stem morphology from those found without ants throughout the plant's wide range in eastern and northern Australia. It is not at all obvious that the plant is 'in control' and using homopterans to lure the ants into a close partnership (cf. Janzen 1979; Beattie 1985). Rather, we may be observing the consequences of selection on ants, particularly colony-founding queens, to circumvent reliance on stem-borers while establishing nest sites suitable for coccids. Of course, such a system is ripe for mutually beneficial elaboration by both the ant and plant, and for exploitation by other species of ants and plants in the same community. The association between *Pseudomyrmex perboscii* and *Pithecellobium saman* may represent a slightly later stage in this process, involving additional species of plants in parts of the ant's range.

The evolutionary scenario developed above is applicable to other ants which keep scales in domatia. In New Guinea rainforests, for example, where myrmecophytism appears to be relatively recent, ants of the genera *Iridomyrmex*, *Crematogaster*, and *Podomyrma* can be found in association with *Cryptostigma* scales, both in understorey myrmecophytes, such as *Myristica* (Myristicaceae), and in insect-bored twigs of unspecialized plants (P. S.

Ward, unpublished work). J. T. Longino (personal communication) has made similar observations on ant–coccoid associations involving the New World ant genera *Azteca*, *Myrmelachista*, and *Zacryptocerus*, and has reached similar conclusions about their importance in the development of ant–plant relationships. Benson (1985) suggested a role for homopterans (scales and membracids) in the evolution of so-called secondary domatia (leaf pouches). The argument put forward here is that Coccoidea have been equally important in the origin of many primary domatia (fistulose stems, swollen petioles, etc.), and that the process involves interactions between four classes of participants: ants, plants, scales, and stem-borers (Fig. 22. 2). A major unknown factor is the specificity of the scale insects to particular plants or ants.
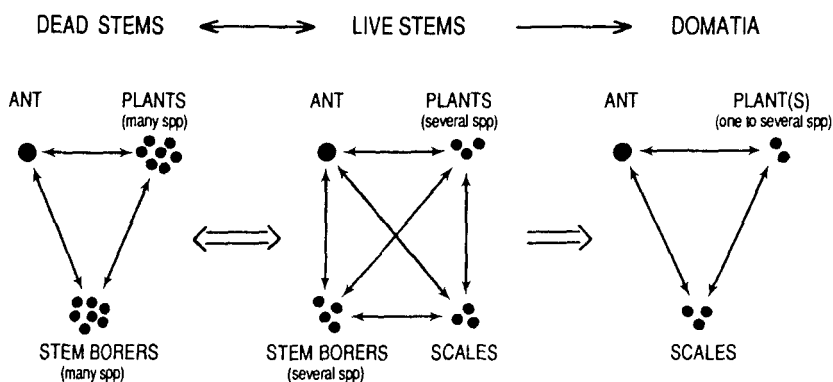
Fig. 22.2. Postulated transition in nesting behaviour of pseudomyrmecine ants, from occupancy of dead twigs to inhabitation of domatia, illustrating the involvement of scale insects (Coccoidea) and stem-boring insects. The process is depicted for a single species or lineage of ants.

Characteristics of obligate plant-ants

Finally, what are the morphological and behavioural consequences of ant–plant specialization in the Pseudomyrmecinae? Domatia-inhabiting species tend to display a series of morphological traits including small eyes, reduced palpal segmentation, short, broad petiolar segments, and hypertrophied metapleural glands (the last two features are not exhibited by the acacia-ants). The significance of some of these traits is obscure; but the enlarged metapleural glands probably reflect the increased importance of antibiotic control of pathogens in the nest environment of plant domatia. This accords with reports (e.g. Bailey 1922; Wheeler 1942) of accumulations of debris, faecal matter, and fungi in the domatia of some rainforest plants; and it is con-sistent with the absence of notably enlarged metapleural glands in acacia-ants, whose nest conditions appear to be cleaner and drier.

Behavioural convergences of pseudomyrmecine plant-ants include extended foraging activity on the plant surface, increased aggressiveness, and a tendency to prune alien vegetation encroaching on the ant-plant (Janzen 1966, 1972; Davidson *et al.* 1988). Polygyny and large colony size have been cited as specialized traits of acacia-ants (Janzen 1966), but they are neither peculiar to, nor characteristic of, pseudomyrmecine plant-ants, also being found in some generalist twig-nesting species (Ward 1989*a*, unpublished work), although not in the extreme form shown by one or two species of acacia-ants.

For the most part pseudomyrmecines which have become ant-plant specialists appear locked into this life history mode. One possible exception is *P. kuenckeli* which may be derived from a *Triplaris*-inhabiting lineage (see above), but this needs confirmation. While such reversals are rare or absent, some plant-ants retain considerable flexibility by inhabiting a range of myrmecophytes. Studies on these species, particularly on geographical variation in plant use and on competitive interactions with other ants in the same myrmecophyte guilds, promise to provide insight into the factors influencing specialization in plant-ants.

Conclusions

Phylogenetic analysis of the Pseudomyrmecinae indicates that obligate plant-ants, which comprise almost 20 per cent of the estimated 250–300 extant species in the subfamily, have arisen at least twelve times. The lack of species-specific pairing, the existence of two or more ant clades on the major ant-plants (*Acacia*, *Triplaris*, and *Tachigali*), and the diversity of ant-plants associated with some groups (and even single species) of ants, all point to a pattern of 'diffuse co-evolution' in pseudomyrmecine–plant associations. There is evidence of both secondary colonization of ant-plants by twig-nesting generalists and of plant switching by obligate plant-ants. The latter process may involve the adoption of new host plants in quite different families, judging by the intraspecific variation in plant use exhibited by some ants. In other words, both ants and plants have been able to exploit pre-existing mutualisms.

The arboreal nesting habits and foraging behaviour of pseudomyrmecines have pre-adapted them to develop close relationships with plants. In many cases their propensity to tend and defend scales (Coccoidea) has probably aided the transition from occasional inhabitation of live, insect-bored stems to more specialized interactions with plants. Studies of incipient ant–myrmecophyte associations (e.g. that involving *Tetraponera* and *Cupaniopsis*) and of obligate plant-ants, such as *Pseudomyrmex viduus*, which maintain a considerable latitude of host plant choice, should prove to be particularly illuminating of the selective forces propelling or arresting such ant–plant mutualisms.

Appendix 22.1

	1	11	21	31	41	51
P.gracilis	0101000141	0200000000	1000100001	1002002112	0310000012	1001010200
P.nigropilosus	0101000141	0200000000	1000100001	1002002111	0310000012	0001013200
P.simulans	0101000141	0200000000	1000100001	1000002111	0310000012	0001010000
P.ita	0101000151	0200000000	1000100001	1010001101	0320000003	0012020000
P.sp.cf.fortis	0101000151	0210000000	1000100001	1010001111	0310000003	0012020000
P.boopis	0101110131	0200000000	1000100001	1010002112	0310000012	0011012000
P.termitarius	0101110131	0200000000	1000100001	1010002112	0310000012	0001012000
P.salvini	0101110131	0200000000	1000100001	1010002111	0310000012	0001013300
P.rufomedius	0101110131	0200000000	1000100001	1000002012	0200200112	0001013001
P.apache	0100110131	0200000000	1000100001	1010001111	0210000012	0001013300
P.haytianus	2100110131	0201000000	1100100001	1010001111	0310000002	0001011200
P.phyllophilus	0101110121	0200000000	1000100001	1000001111	0310000012	0001012000
P.sp.PSW-02	2100110131	0221000000	1100100001	1000002112	0310000012	0001010000
P.oki	1100110131	0211000000	1100100001	1000001101	0310000003	1001012201
P.sp.PSW-01	1100110131	0211000001	1100110001	1010001101	0320000003	1001010200
P.pallidus	1100110121	0211000000	1100100001	1010001111	0310000002	0001013301
P.euryblemma	2100110121	0211000000	1100100001	1010001111	0310000003	1001012301
P.perboscii	1101110231	0200000000	1000100001	1010002101	0210010013	1001013400
P.gebelli	1101110121	0211000000	1100100001	1010002112	0310000012	0001013401
P.kuenckeli	0101110131	0200000000	1000000001	1002002013	0201210111	1013012400
P.triplarinus	1101110131	0200000100	1000000001	1002002012	0201210102	0012012500
P.viduus	1101110131	0211000000	1000100001	1002001011	0210110003	0012012500
P.concolor	1101110121	0221000000	1000000001	1002001011	0201210002	0012023500
P.tachigaliae	1111010141	0211000610	1100000001	1000001011	0200100002	0012012500
P.spinicola	0101110131	0221000000	1100000001	1000001121	0210010012	0001012200
P.ferrugineus	0101010131	0211000000	1000100001	1000001111	0210100002	0001012000
P.nigrocinctus	0101110131	0211000000	1000100001	1000001121	0210100002	0001013200
P.filiformis	1100110131	0210000000	1000100001	1000001111	0310000002	1001013400
P.subater	1100110121	0211000000	1000000001	1000001111	0310000002	0011012500
P.sp.PSW-44	1100110121	0211000000	1000100001	1002001011	0210110012	0012012500
P.elongatus	1001110131	0201000000	1000100001	1000000111	0320000003	1012012000
P.oculatus	0100110121	0201000000	1000100001	1001001111	0310000012	1012012000
P.subtilissimus	0101110121	0201000000	1000110001	1010000110	0320000003	2001013000
T.aethiops	2010291112	1000110200	0001000000	0010003012	1102220211	0002120300
T.mocquerysi	1021991103	1000140000	0000000101	0001102011	1211221112	0001010100
T.pilosa	2010291112	1000100200	0001000000	0010002011	1211121112	0001010100
T.rufonigra	0109211023	1000100210	0001000000	0002003011	1101221211	0001103200
T.grandidieri	0019291012	1000130000	0000000001	0010002021	1101222211	0101003110
T.bifoveolata	1119191013	1200100000	0000000101	1000011011	1212221002	0001013100
T.ophthalmica	0109191013	1200100000	0000000101	1010010021	1211221002	0000003100
T.tessmanni	1000111122	1031000010	0000000211	1010100001	1002220202	0112113400
T.penzigi	1009291012	1100100010	0000000211	0010101011	1102320102	0012110100
T.clypeata	1021991203	1100100000	0010000211	0010100011	1101221202	0100012310
T.morondaviensis	1109191013	1000101000	0000000201	0000101021	1101221202	0001012300
T.allaborans	2021991202	1100120000	0010000201	1010001011	1201221102	0100000410
T.attenuata	1010291112	1100110310	0000000201	0101001021	1101221211	0200000500
T.nigra	1010291112	1100110410	0000000101	0101001021	1101221212	0201010300
T.nitida	2000191113	1000110000	0000000200	0110001001	1211220002	0101010400
T.punctulata	1009291013	1100110510	0000000201	0100001011	1201221103	0001010500
M. epicharis*	2009290010	0211000000	0000001000	0000000001	1201220003	0011013400

Erratum

p. 350 Caption to Appendix 22.1

Pseudomyrmecine data set analysed by PAUP. Characters 1–59 are derived from worker and queen morphology; the remaining characters are based on males, principally male genitalia. Characters 10, 16, 18, 57, 58, 73 and 76 were treated as unordered. A '9' indicates character state unknown or inapplicable. A complete list of the characters and character

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61          71          81          91          101         111         121
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1111111100  000010100   0000000000  0010000010  0021000000  0000001100  01100
1111111100  000010100   0000000000  0010000010  0021000000  0000001100  01100
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1011111000  000010110   0000000000  0000000010  0021000010  0000000100  01100
1011011000  000010100   0000000000  0000000010  0021000100  0000000000  01100
1011011000  000010100   0000010000  0000000010  0021000100  0000000000  01100
1011111100  001010100   0100010000  0000000010  0021000000  0100000100  01100
1111101100  001010101   0000000000  0000000010  0021010010  0000000100  09100
1011111100  000010100   0100010000  0000000010  0021000000  0000000100  01100
1011111100  000010100   0000010000  0100000020  0021000999  9999901000  09100
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1011111000  000010100   0000000010  0000000010  0021000000  0000000100  01100
1011111100  001010100   0000000010  0000000010  0021000001  0000000100  01100
1011111000  000010100   0000000010  0001000010  0021000000  1000000100  09100
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1011111000  002011100   0000000000  0000000000  0021100000  0000000100  00100
1001111000  000010000   0000100000  0000010000  0021100000  0000001000  00100
1011111100  000012100   0000000000  0000111000  0012101000  0000001000  00100
1011110000  000010100   0000000000  0000000000  0021100000  0000100101  00100
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1011111100  100012100   0000010000  0000111000  0022101000  0000300100  00100
0011111000  001000100   0000000000  0000000000  0001000000  0000010000  00000
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Acknowledgements