

Biology and adaptive radiation in the gall-inducing Cecidomyiidae (Insecta Diptera) and Calophyidae (Insecta Hemiptera) on *Mangifera indica* (Anacardiaceae) in the Indian subcontinent

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Received 9 July 2008, accepted 25 November 2008

Out of the nearly 250 species of plant-feeding arthropods that utilize *Mangifera indica*, about 25 gall midge species (Diptera Cecidomyiidae) (mostly species of *Procontarinia* Kieffer & Cecconi 1906) and one psyllid species (*Apsylla cistellata* (Buckton 1893), Hemiptera Calophyidae) are the known gall-inducing taxa. Almost all of these gall midges induce galls on leaves, whereas the psyllid induces galls on axillary vegetative buds. The *M. indica*-associated species of *Procontarinia* do not show any striking level of shifts either between organs within *M. indica* or between other Indian anacardiaceous taxa such as *Anacardium*, *Buchanania*, *Lannea*, *Holigarna*, *Pistacia*, and *Semecarpus*, which, in fact, host several other species of Cecidomyiidae and Calophyidae. Given that galls induced by a suspected gall-midge species on the fossil leaves of an ancestral taxon of *Mangifera indica* from the Upper Palaeocene sediments of north-eastern India exist, the lack of radiation from leaves either to other organs of *M. indica* or to other anacardiaceous extant taxa suggests that neither the feeding behaviour nor the larval salivary physiology of species of *Procontarinia* has changed over time. The reason for such a conservative behaviour could be either the lack of resistance-breaking genes in the *M. indica*-associated *Procontarinia* complex or the abundance of populations of *M. indica*. A provisional reconstruction of the relationships among the extant *M. indica*-infesting gall-inducing Cecidomyiidae reveals that an extremely modest level of radiation in the leaf-gall-inducing species has occurred from those species that induce structurally simple galls to those that induce structurally complex galls. Because *M. indica* is an evergreen, polyaxial species, with new leaf flushes available almost throughout the year, and thus offering a continuous nutritional supply, the radiation and diversification of gall midges could have been restricted. In addition, the diverse, geographically localized

varieties of *M. indica* with different types of secondary chemicals (e.g., xanthenes and flavanols) may have also imposed a selection pressure on the radiation of gall midges; for instance, mangiferin, the principal secondary chemical present in *M. indica*, possibly acts as an attractant to the Cecidomyiidae and *Apsylla cistellata* and has, consequently, restricted their diversification. We speculate that the gall midges may have progressed conservatively specializing along the host-plant lines, because of the need for precise timing and for minimizing competitive interactions with other parasitic, predatory, and inquiline arthropods, from the time of original host colonization. Available data on the gall-inducing species of the *Procontarinia* complex on the leaves of *M. indica* indicates that both the location and structure of galls generally agree with the patterns evident in other groups of gall-inducing insects, which induce galls of similar morphology, suggesting pathways of *Procontarinia* phylogeny. Galls of different morphologies occur concurrently, mostly on the leaves of *M. indica*, and such an occurrence needs to be explored to establish the origin of multiple species of *Procontarinia*. In the context of *M. indica*-associated gall midges, only *Procontarinia mangiferae* lives both on stems and leaves of *M. indica*, indicating a critical step in *Procontarinia* speciation, through reproductive isolation involving phenological separation. Different species of *Procontarinia* occur on the same host tree and on the same leaf, but how different populations of gall-midge taxa partition their resources effectively and reduce inter-specific competition remain as questions. Effective utilization of the host plant and consequent speciation in the *Procontarinia* complex have resulted from the condition that continuously blossoming individual trees of *M. indica* are available throughout extensive landscapes. But apart from these speculative propositions, a need for empirical studies on the phylogeny and interactions between *Procontarinia* (and related genera) and *M. indica* exists. In Calophyidae, *Apsylla* Crawford 1912 did not speciate on *M. indica*; this may also be true for the three species of *Calophya* Löw 1879 associated with *M. indica*. Due to insufficient information this proposition remains unverified.

KEY WORDS: adaptive radiation, biogeography, Calophyidae, Cecidomyiidae, gall-inducing taxa, host shifts, Indian subcontinent, *Mangifera indica*.

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INTRODUCTION:
HOST SHIFTS AND ADAPTIVE RADIATION IN A GLOBAL CONTEXT

Among insects, gall-inducing ability is mostly confined to Thysanoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, and Hymenoptera. Within these orders, the ability to induce galls often does not occur uniformly in all species. Gall-bearing plants also do not exhibit any discernible pattern because galls induced by closely related species develop on plants belonging to unrelated families. In the temperate latitudes, most of the insect-induced galls occur on species of Fagaceae, Salicaceae, Convolvulaceae, Malvaceae, Capparidaceae, Rosaceae, Asteraceae, and Euphorbiaceae (MEYER 1987). In the tropical (and subtropical) world, species of Fabaceae, Moraceae, Lauraceae, Myrtaceae, Combretaceae, Dipterocarpaceae, Anacardiaceae, and Asteraceae bear the greatest numbers (DOCTERS VAN LEEUWEN-REIJNVAAN & DOCTERS VAN LEEUWEN 1926, MANI 1964, RAMAN et al. 2005a).

Richness of gall-inducing insects in a global context is estimated at about 133,000 species (ESPÍRITO-SANTO & FERNANDES 2007). Gall-inducing insects are highly evolved groups with sophisticated biology and physiology that enable them to utilize their host plants more efficiently and resourcefully than their non-gall-inducing relatives (RAMAN et al. 2005b, SCHAEFER et al. 2005, SHORTHOUSE et al. 2005). Although a majority of the gall-inducing insects are restricted to particular plant species, and even to particular plant organs (ABRAHAMSON et al. 1998, RAMAN et al. 2005a), some of the insect taxa induce galls on plant species closely related to their preferred hosts (RAMAN 1996, 2007a; RAMAN et al. 1996; GAGNÉ 2004; WOOL 2005). Within Cecidomyiidae, for example, most gall-inducing gall midges are either monophagous or narrowly oligophagous (GAGNÉ 2004); however, several species of *Asphondyliina* and *Schizomyiina* have been found, in recent years, to be polyphagous (YUKAWA et al. 2003; UECHI et al. 2002, 2004; TOKUDA et al. 2005).

Host shifts in naturally occurring gall-inducing tephritid populations of North America and Europe have been explained by the evolution of sympatric host races — due to changes either in the preference in feeding and/or oviposition sites or by developing ‘new’ physiological adaptations to new host plants or through assortative mating (ABRAHAMSON & WEIS 1997, KORNEYEV et al. 2005). Differences in the temporally regulated flowering and leafing phenologies in susceptible host plants could also be playing a role in isolating gall-inducing insect populations, thus enabling divergence and diversification by genetic drift (STONE et al. 2001). The general understanding, as of now, is that host shifts and radiation in gall-inducing insects are more complex in non-gall-inducing insects. Such complexity is attributed to (i) composite relationships of gall-inducing insects with plants and (ii) the

spread of gall-inducing insects through different biogeographical realms, mainly influenced by the abundance and variety of plant species.

Relationships of gall-inducing insects with plants

The occurrence of sibling species in Tenthredinidae (Hymenoptera) is well recognized today, with each sibling species occurring on a different host species and a majority inducing galls on different species of *Salix* (Salicaceae) and a minority on species of *Populus* (Salicaceae) in Europe (KOPELKE 1999). The gall-inducing habit in the Tenthredinidae originated from the free-living nematine sawflies, firstly evolving into those that could either fold or roll leaves (e.g., *Phyllocolpa* Benson 1960), subsequently into species that induced galls on leaves (e.g., *Pontania* A. Costa 1859), and finally into species that induced galls on stems (e.g., *Euura* Newman 1837) (NYMAN et al. 2000). These sawfly genera occur on different species of *Salix* indicating that the newly diversified sawfly genera invaded new adaptive zones and after their establishment, each species has radiated on to many other plant species. At least some species of large genera of gall-inducing insects are capable of colonizing diverse plant species and invading new plant organs, indicating shifts into varied ecological niches and adaptive zones (PRICE 1996, 2005; ROININEN et al. 2005). The nematine sawflies also seem to have undergone host shifts between unrelated species of *Salix* (NYMAN et al. 2000, 2006), in contrast to the strong patterns of gall-inducing insect — plant co-speciation demonstrated in the interactions between figs and figwasps (RØNSTED et al. 2005) and thrips and acacias (MCLEISH et al. 2007a).

Insect spread mediated by abundance and richness of plant species

The Beesoniidae (Coccoidea) that include taxa with unusual coccoid behaviours illustrate how the abundance and variety of host-plant species in different biogeographical regions influences radiation in insects. Among the described species of Beesoniidae, *Beesonia dipterocarpi* Green 1926 and *B. shoreae* Takagi 1995 are associated with *Dipterocarpus tuberculatus* and *Shorea curtisii* (both Dipterocarpaceae) in tropical Asia (Myanmar [Burma] and Singapore), respectively, whereas *B. napiformis* (Kuwana 1914) and *B. brevipes* Takagi 1987 are always associated with different species of *Quercus*, *Castanopsis*, *Lithocarpus* (all belonging to Fagaceae) in temperate Asia (China, Japan, and higher elevations of Nepal). Other species of tropical Beesoniidae, *Gallacoccus secundus* Beardsley 1971, *G. anthonyae* Beardsley 1971, *G. spinigalla* Takagi 2001, *G. heckrothi* Takagi 2001, *G. longisetosus* Takagi 2005, *Mangalorea hopeae* Takagi 1992, *Echinogalla pustulata* Takagi 2001, and *Danumococcus parashoreae* Takagi & Hodgson 2005 are associated with particular species of *Hopea*, *Shorea*, and *Parashorea* (Dipterocarpaceae) in tropical southern and south-eastern Asia (TAKAGI 1987, 1995, 2001; GULLAN et al. 2005). Based on the predominant disposition of the Beesoniidae to Dipterocarpaceae in tropical Asia, TAKAGI (2007) proposes that the Beesoniidae have

primarily evolved with Dipterocarpaceae in the tropics and their association with temperate Fagaceae is a secondarily evolved trait, consequent to their diversification from tropical Asia into temperate eastern Asia. Beesoniidae diversification seems to have been strongly influenced by the richness of species in Dipterocarpaceae (ca 650 species in 17 genera) in tropical Asia and Fagaceae (ca 900 species in eight genera throughout the world, and nearly 700 species in temperate Asia) in temperate Asia, similar to the pattern of diversification of Eriococcidae (Hemiptera Coccoidea) on highly speciose *Eucalyptus* in Australia (L.G. COOK & GULLAN 2004). The diversification patterns in the Beesoniidae and Eriococcidae are supported by the apparency theory (FEENY 1976, STRONG et al. 1984).

A pattern of repetitive shifts to new host taxa with subsequent speciation occurs in Aphalaroidinae (Hemiptera Psylloidea). In the Old World, Aphalaroidinae is represented by *Pachyparia* Loginova 1967 and *Yangus* Fang 1990 with several species of non-gall-inducing species associated with Fabaceae. In the New World, *Aphalaroida* Crawford 1914 and *Prosopidopsylla* Burckhardt 1987 are the non-gall-inducing taxa associated with Fabaceae. *Ehrendorferiana* Burckhardt 2005, *Freysuila* Aleman 1887, *Panisopelma* Enderlein 1910, *Russelliana* Tuthill 1959, *Sphinia* Blanchard 1852, *Telmopsylla* Hodkins 1992, and *Zonopelma* Burckhardt 1987 include, so far as known, non-gall-inducing species associated with several unrelated plant families, and only *Baccharopelma* Burckhardt, Espírito-Santo, Fernandes & Malenovský 2004 associated with *Baccharis* (Asteraceae) and *Connectopelma* Šulc 1914 with Rhamnaceae are the gall-inducing taxa (BURCKHARDT 2005a).

In summary, host shifts, and subsequent speciation, among the gall-inducing insects occur because of host-plant traits (e.g., host-plant chemistry), competitive interactions of the gall inducer selecting the 'best' host resources, and the potential for escape from natural enemies (ABRAHAMSON et al. 1994). Yet, it is hard to list reasons why specific host shifts happen, especially because host shifts are of common occurrence only among related plants. Co-speciation and patterns of host shifting have been shown in gall-inducing species of *Kladothrips* Froggatt 1906 (Thysanoptera Phlaeothripidae) on species of *Acacia* (Mimosaceae) in Australia (MCLEISH et al. 2007b). Further, PRICE'S (2005) commentary on the patterns of adaptive radiation among gall-inducing sawflies of North America, cynipid gall wasps of Europe, gall midges of Japan, and aphids of the Middle-East could be useful in considering these enigmatic issues.

DISTRIBUTION OF GALL-INDUCING INSECTS IN THE INDIAN SUBCONTINENT

Gall-inducing ability among the known insects of the Indian subcontinent is found in the Thysanoptera, Hemiptera, Diptera, and Hymenoptera (MANI 1973, 2000; RAMAN 2007a, 2007b), and in relatively few species in the Lepidoptera and Coleoptera, a pattern that matches the global pattern (DREGER-JAUFFRET & SHORTHOUSE 1992, ESPÍRITO-SANTO & FERNANDES 2007,

MENDONÇA 2007). Within these orders, gall-inducing taxa are confined to either particular families or particular subfamilies. For example, among the gall-inducing Psylloidea of the Indian subcontinent, Triozidae dominates with nearly 25 recognized species on plants belonging to Combretaceae, Ebenaceae, Ericaceae, Euphorbiaceae, Lauraceae, Moraceae, Myrtaceae, Sabiaceae, Salicaceae, and Urticaceae (YANG & RAMAN 2007). In general, in the Indian subcontinent, dicotyledons host a majority of gall-inducing insects. Among the remainder of vascular plants, only *Pinus* and *Picea* (Pinaceae) from the Himalaya, *Gnetum ula* (Gnetaceae) in peninsular India (MANI 2000), and a few species of grasses (MANI 1973, GAGNÉ 1985, GROVER 1988) bear galls induced by either Hemiptera or Diptera (Cecidomyiidae). In terms of numbers, galls occur unevenly in Fabaceae, followed by Moraceae, Lauraceae, Combretaceae, Anacardiaceae, and Cucurbitaceae. Asteraceae host the highest number of gall-inducing insect species, whereas Fagaceae, Salicaceae, Convolvulaceae, Malvaceae, Capparidaceae, Rosaceae, and Euphorbiaceae, which bear galls in temperate parts of the world, do not host gall-inducing insect species in comparable numbers (MANI 2000). A caveat, however, remains that several insects and gall-bearing plants have not been determined taxonomically (RAMAN 2007b).

The distribution of gall-inducing insects in the Indian subcontinent shows various peculiarities. Gall-inducing aphids, cynipids, and sawflies appear to be restricted to the Himalayan slopes (28-33°N), whereas gall-inducing thrips and coccids occur only in tropical peninsular India (8-23°N; 73-85°E) (RAMAN 2007a). Although no gall-inducing psyllids have been recorded from the Indian Himalaya (MANI 2000), gall-inducing *Cecidopsylla schimae* Kieffer 1905 and a few species of Triozidae associated with *Symplocos* have been found in Nepalese Himalaya (D. BURCKHARDT unpublished data). *Triozia jambolanae* Crawford 1917 (Hemiptera Triozidae) that induces protruding globular galls on the leaves of *Syzygium cumini* (Myrtaceae) (MATHUR 1975, KANDASAMY 1986, RAMAN et al. 1996) occurs throughout India, irrespective of variations in latitudinal and longitudinal gradients, although its life-history traits (e.g., number of generations per year) varies between the populations that occur in humid, warm peninsular India (RAMAN 1991) and in the non-humid, cold Himalayan foothills (MATHUR 1935, 1946). In contrast, the sea-urchin shaped galls on *Hopea ponga* (Dipterocarpaceae) induced by *Mangalorea hopeae* Takagi 1992 (Hemiptera Beesoniidae) occur only along the western coast of the peninsula (10-20°N) (RAMAN & TAKAGI 1992). Several other species of gall inducers occur only in specific biogeographical subregions: a majority of gall-inducing insects in peninsular India is endemic to this region; however, some of them in the central-Indian plateau have been documented to display morphological affinities to elements of the Afrotropical and Mediterranean biogeographical regions (MANI 2000). On the contrary, those in the western and north-western Himalaya include a high proportion of European and central-Asian elements (MANI 2000). Although the channeling effect of the Himalaya on monsoon currents and the topographic peculiarity of the peninsula explain the oddities in the distribution of gall-susceptible flora and gall-inducing insects in India (RAMAN 2007b), why gall-inducing sawflies, cynipids, and aphids occur only along

the Himalayan slopes and why most of the gall-inducing thrips and coccids occur only in the tropical stretches of peninsular India are unanswered questions (RAMAN 2007a).

MANGIFERA INDICA, CECIDOMYIIDAE, AND CALOPHYIDAE

Mangifera indica

The family Anacardiaceae, to which *Mangifera* belongs, includes ca 850 species in 73 genera (BOMPARD & SCHNELL 1997) grouped under Anacardiaceae, Spondiadeae, Semecarpeae, Rhoeeae, and Dobineae (PELL 2004). Most species of Anacardiaceae are confined to the tropics and their species diversity is particularly high in Malesia (MUKHERJEE 1997) — the phylogeographic region between the southern Malay Peninsula and eastern New Guinea. Anacardiaceae is estimated to have originated in the Palaeocene (65-55 mya) (PRAKASH 1965, MULLER 1984) in Gondwana (GENTRY 1982). Among the extant Anacardiaceae, a variety of perennial plant forms exist, and all species include a characteristic endowment of latex and resins, besides a range of simple and complex phenols and esters (CORTHOUT et al. 1992, 1994; GALVEZ et al. 1992; VIANA et al. 1997; AGUILAR-ORTIGOZA et al. 2003). Certain species of Anacardiaceae contain methyl gallic acid, gallic acid, a methyl ester of 3,4,5-trihydroxybenzoic acid, and 5-(12-heptadecenyl)-resorcinol (an anti-microbial compound) (COJOCARU et al. 1986, SAXENA et al. 1994), and β -ocimene (an anti-insectan compound) (CHEN & WIEMER 1984). Mangiferin, a phenolic glucoside, is a key compound in *M. indica* (NOTT & ROBERTS 1967).

Almost 70 valid species exist within *Mangifera* in tropical Asia — its native range — and these species occur up to 30° North of the Equator and from 80 to 160° East (BOMPARD & SCHNELL 1997). Upper Palaeocene leaf impressions from Assam (north-eastern India; 26°09'-26°15'N; 91°46'-91°77'E) indicate that an ancestor of *M. indica* (*Eomangiferophyllum damalgiensis*) existed and subsequently spread to south-eastern Asia in the Eocene (MEHROTRA et al. 1998). Modern *Mangifera* includes *M. andamanica*, *M. khasiana*, and *M. sylvatica*, which are endemic to north-eastern India and the Andaman Islands (6-14°N; 92-94°E), in addition to the ubiquitous and extensively cultivated *M. indica* (MUKHERJEE & CHANDRA 1983). The land bordered by Assam, Myanmar (Burma), and Bangladesh (Chittagong Hill tract) is considered to be the epicentre of *M. indica*, although currently this taxon has extended to the tip of the Malay Peninsula (IYER & DEGANI 1997). Within the Indian subcontinent, more than 1000 established varieties exist (PANDIT et al. 2007; referred to as 'cultivars'), and a majority of these varieties have evolved through natural hybridization between *M. indica* and *M. sylvatica*, with at least 350 of them being propagated for fruits (MORTON 1987). Considerable variation in the levels of damage and degree of susceptibility to arthropods and microbial-disease agents exists among varieties of *M. indica* (IYER 1991). For example, an undescribed *Mangifera* variety from Tripura (India; 23°50'-23°84'N; 91°17'-91°28'E) is considered resistant to 'mango malformation' pur-

portedly vectored by *Eriophyes mangiferae* (Sayed 1946) (*Aceria mangiferae* Sayed 1946, Acarina Eriophyoidea) (SHARMA & CHOUDHURY 1976).

Nearly 250 species of plant-feeding arthropods utilize different organs of *M. indica* throughout the world (PEÑA & MOHYUDDIN 1997), of which 26 species in the Indian subcontinent are confirmed gall inducers (Table 1). In addition to *Apsylla cistellata* (Buckton 1893) (Hemiptera Psylloidea Calophyidae) for which gall induction is well documented (G. SINGH 2003), three species of *Calophya* Löw 1879 (*Calophya brevicornis* (Crawford 1919), *C. maculata* (Mathur 1975), and *C. mangiferae* Burckhardt & Basset 2000; Hemiptera Psylloidea Calophyidae) are also associated with *M. indica* (SRIVASTAVA 1997), although no details on their gall-inducing ability are available. Gall-induction ability is known from all South-American species developing on *Schinus* (Anacardiaceae) (BURCKHARDT & BASSET 2000) and is likely to occur in other species of *Calophya*. Within the Cecidomyiidae associated with *M. indica*, only *Procontarinia mangiferae* (Felt 1911) and '*Oligotrophus mangiferae* Kieffer 1909 induce galls on stems. The other established species of *M. indica*-infesting Lasiopteridi induce galls on flowers, and the taxa belonging to Cecidomyiidi induce galls of different morphologies on leaves. *Procontarinia mangiferae* was reported by MANI in 1959 as a gall inducer on the stems of *M. indica*, but the same species was reported as a gall inducer on the leaves of *M. indica* by GROVER in 1962. Among the psylloids associated with *M. indica*, *Apsylla cistellata* induces fir-cone like galls on vegetative, axillary shoot buds (Figs 1-2) (MATHUR 1975, RAMAN 2007a).

Table 1.
Indian Anacardiaceae hosting gall-inducing insects¹.

Host plant taxon	Gall-inducer taxon	Gall-bearing organ
SEMECARPEAE²		
<i>Holigarna arnottiana</i>	Cecidomyiidae (Diptera)	
	Cecidomyiinae	
	Undescribed species ²	leaf
<i>Semecarpus anacardium</i>	Cecidomyiinae	
	Undescribed species ²	leaf
	Psyllidae ³ (Hemiptera)	
	Undescribed species	leaf
SPONDIADAEAE²		
<i>Lannea coromandelica</i>	Cecidomyiidae (Diptera)	
	Cecidomyiinae: Cecidomyiidi	
	<i>Odinadiplosis odinae</i> Mani 1935	leaf

(continued)

Table 1. (continued)

Host plant taxon	Gall-inducer taxon	Gall-bearing organ
<i>Spondias mangiferae</i>	Calophyidae (Hemiptera)	
	Calophyinae	
	<i>Calophya spondiasae</i> (Crawford 1915) [<i>Pauropsylla spondiasae</i> Crawford 1915]	leaf
ANACARDIEAE ²		
<i>Buchanania lanzan</i>	Calophyidae (Hemiptera)	
	Calophyinae	
	<i>Calophya longispiculata</i> (Mathur 1975) [<i>Microceropsylla longispiculata</i> (Mathur 1975); <i>Pauropsylla longispiculata</i> Mathur 1975]	leaf
<i>Mangifera indica</i>	Cecidomyiidae (Diptera)	
	Cecidomyiinae: Cecidomyiidi: Cecidomyiini	
	<i>Procontarinia</i> sp.	leaf
	<i>P. allahabadensis</i> (Grover 1962)	leaf
	<i>P. amraeomyia</i> (Rao 1950)	leaf
	<i>P. biharana</i> (Felt 1916)	leaf
	<i>P. brunneigallicola</i> (Rao 1950)	leaf
	<i>P. echinogalliperda</i> (Mani 1947)	leaf
	<i>P. keshopurensis</i> (Rao 1952)	leaf
	<i>P. mangiferae</i> (Felt 1911)	leaf, stem
	<i>P. mangifoliae</i> (Grover 1965)	leaf
	<i>P. matteiana</i> Keiffer & Cecconi 1906	leaf
	<i>P. tenuispatha</i> (Kieffer 1909)	leaf
	<i>P. viridigallicola</i> (Rao 1950)	leaf
	Cecidomyiinae: Lasiopteridi: Lasiopterini	
	<i>Lasioptera mangiflorae</i> (Grover 1968) [<i>Meunieriella mangiflorae</i> Grover 1968]	flower
	Cecidomyiinae: Lasiopteridi: Dasineurini	
<i>Dasineura amaramanjarae</i> (Grover 1964)	flower	
<i>Gephyraulus indica</i> (Grover & Prasad 1965)	flower	
<i>Gephyraulus mangiferae</i> (Felt 1927)	flower	

(continued)

Table 1. (continued)

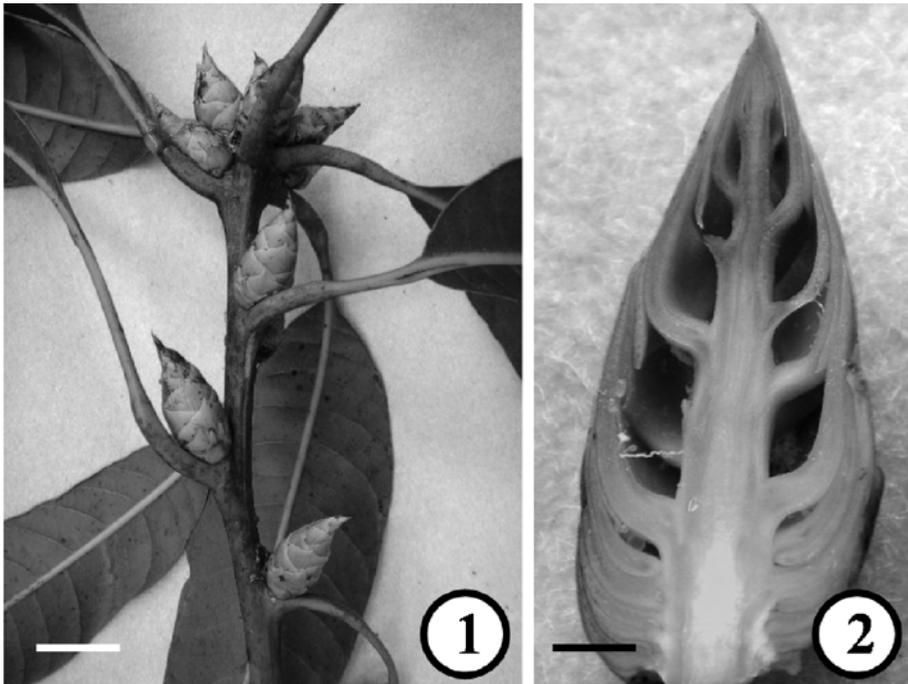
Host plant taxon	Gall-inducer taxon	Gall-bearing organ
	Cecidomyiinae: Unplaced	
	<i>Oligotrophus mangiferae</i> Kieffer 1909	stem
	Cecidomyiinae	
	Undescribed species ² : A, B, C, D, E, F, G, H ⁴	leaf
	Calophyidae (Hemiptera)	
	Apsyllinae	
	<i>Apsylla cistellata</i> Buckton 1896	vegetative bud
	Calophyinae	
	<i>Calophya brevicornis</i> (Crawford 1919) ^{5,6}	leaf
	[<i>Microceropsylla brevicornis</i> (Crawford 1919), <i>Pauropsylla brevicornis</i> Crawford 1919]	
	<i>C. maculata</i> (Mathur 1975) ⁶	leaf
	[<i>Microceropsylla maculata</i> (Mathur 1975), <i>Pauropsylla maculata</i> Mathur 1975]	
	<i>C. mangiferae</i> Burckhardt & Bassett 2000 ⁶	leaf
	[<i>Pauropsylla nigra</i> Crawford 1919]	
RHOEAE ²		
<i>Pistacia integerrima</i>	Aphididae (Hemiptera)	
	Fordini	
	<i>Baizongia pistaciae</i> (Linnaeus 1767) ⁷	leaf
<i>Pistacia khinjuk</i>	Aphididae (Hemiptera)	
	Undescribed species ³	leaf
<i>Rhus semialata</i>	Psyllidae (Hemiptera)	
	Undescribed species ³	leaf
Indeterminate species	Psyllidae (Hemiptera)	
	Undescribed species ²	leaf

¹ Synonyms in parentheses. ² After SUSAN K. PELL (2004). ³ According to MANI (2000). ⁴ MANI (2000) lists eight undescribed species (suspected *Procontarinia*, Cecidomyiidae) and because they induce galls of distinct morphologies, for an easy understanding, they have been tentatively designated 'A'-H'. ⁵ BUCKTON (1893) refers to this as *Pauropsylla brevicornis* (the mango-shoot psylla); now recognized as *Calophya brevicornis* (BURCKHARDT & BASSETT 2000). ⁶ Three species of *Calophya* are associated with mango: *C. brevicornis*, *C. maculata* and *C. mangiferae*. *C. mangiferae* is a replacement name for *C. nigra* [Crawford 1919] nec. *C. nigra* Kuwayama 1908. *C. nigra* occurs on a species of *Phellodendron* (Sapindales Rutaceae) in eastern Asia. ⁷ MANI (2000: 111) lists this species as *Dasia aedificator* (Buckton 1893), a misspelling of *Pemphigus aedificator* Buckton 1893. *P. aedificator* is in addition a junior subjective synonym of *Baizongia pistaciae*.

In the above context of *M. indica* infesting gall-inducing cecidomyiids and psylloids in India, in this paper, we discuss patterns of adaptive radiation considering the potential factors that mediate the choice and restriction of the insects to specific organs of *M. indica*.

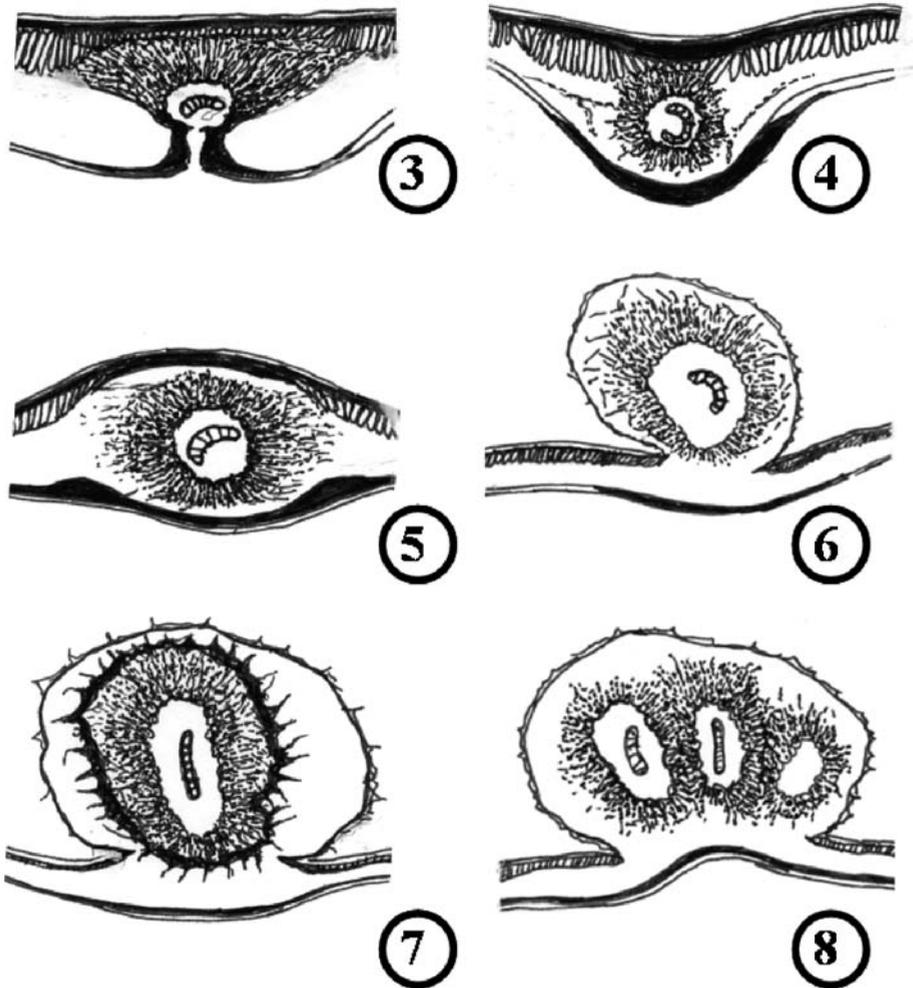
Cecidomyiidae

The gall midges known to infest different taxa of Anacardiaceae belong to the Cecidomyiinae and most of them utilize *Mangifera indica* (Anacardiaceae) (Table 1). Evidence of a Palaeocene gall-inducing cecidomyiid (SRIVASTAVA et al. 2000) on the leaves of *Eomangiferophyllum damalgiensis*, the ancestor of *Mangifera indica* (MEHROTRA et al. 1998), indicates that radiation of *Procontarinia* Kieffer & Cecconi 1906 (Cecidomyiini) on *M. indica* has progressed conservatively, with most of them continuing to utilize only the leaves. The 25 extant species and the extinct Palaeocene gall-midge species may share a common ancestor. The extant species associated with *M. indica* exhibit only subtle variations in their gall shapes, overall patterns of tissue differentiation, nature of dehiscence at maturity, location on either



Figs 1-2. — Galls induced by *Apsylla cistellata* (courtesy: Dr Bijan K. Das, Bidhan Chandra Krishi Viswavidyalaya, Kalyani, West Bengal, India). Fig. 1: Fir-cone like galls in leaf axils (scale bar = 1 cm). Fig. 2: A vertically slit gall showing nymphs and nymphal chambers (scale bar = 10 mm).

the upper or the lower sides of leaves, and numbers of larval chambers (VIJAYA PARTHASARATHY 1991, MANI 2000) (Figs 3-8).



Figs 3-8. — Vertical-sectional diagrams of representative mature galls induced by species of *Procontarinia* on *M. indica* (not to scale). Stippled area surrounding the larva = nutritive tissue; black area = sclerenchyma (adapted from MANI 2000; with permission from Raju Primlani, Editor, Science Publishers, New Hampshire, USA). Fig. 3: Hypophyllous, plano-convex, green gall induced by *Procontarinia biharana*. Fig. 4: Hypophyllous, green gall induced by *P. mangifoliae*. Fig. 5: Spindle-shaped, green gall expressed evenly on both sides of the leaf induced by *P. matteiana*. Fig. 6: Epiphyllous, parenchymatous, brown gall induced by *P. tenuispatha*. Fig. 7: Epiphyllous, green gall induced by *P. allahabadensis* (sclerenchyma surrounds the nutritive tissue). Fig. 8: Epiphyllous, brown, gall induced by *P. viridigallicola* (more than one larval chamber occurs within one gall).

- In terms of geographical distribution of the *M. indica*-infesting species:
- the leaf-infesting *Procontarinia allahabadensis* (Grover 1962), *P. amraeomyia* (Rao 1950), *P. brunneigallicola* (Rao 1950), *P. echinogal-liperda* (Mani 1947), *P. keshopurensis* (Rao 1952), and *P. viridigallicola* (Rao 1950), the flower-infesting *Lasioptera mangiflorae* (Grover 1968), *Dasineura amaramanjarae* (Grover 1964), and *Gephyraulus indica* (Grover & Prasad 1965) remain restricted to the humid and subtropical Northern Indian plains (Indo-Gangetic plains);
 - the leaf-infesting *P. mangifoliae* (Grover 1965) and *P. tenuispatha* (Kieffer 1909), the flower-infesting *Gephyraulus mangiferae* (Felt 1927), the stem-infesting *Oligotrophus mangiferae* Kieffer 1909, and the stem- and leaf-infesting *P. mangiferae* (Felt 1911) remain restricted to the humid, subtropical and tropical wet-dry climate of central India;
 - the leaf-infesting undescribed species of *Procontarinia* remain restricted to the tropical, wet-dry climate of western peninsular India and the semi-arid eastern peninsular India;
 - the leaf-gall inducing *P. biharana* (Felt 1916) and *P. matteiana* Kieffer & Cecconi 1906 occur throughout India.

The two undescribed species of gall midges that induce galls on the leaves of *Holigarna arnottiana* and *Semecarpus anacardium* (Semecarpeae), and *Odinadiplosis odinae* Mani 1935 that induces galls on the leaves of *Lanea coromandelica* (Spondiadeae) occur only in tropical, wet-dry peninsular India (13°09'N; 80°27'E).

Procontarinia matteiana and *P. mangiferae* are the two taxa that have spread extensively, mostly by human activity to the Neotropical (Guadeloupe, Brazil, and West Indies) and Afrotropical (Kenya, South Africa) and Indo-Malayan (Java, Indonesia) biogeographical regions, from their original north-eastern Indian bioregion. The spread of these species must have occurred along with the spread of *M. indica*, which is cultivated extensively for commercial purposes (DE VILLIERS 1998). Yet, both species do not occur on any plant other than *M. indica*, either within Anacardiaceae or within other families of Sapindales (sensu ANGIOSPERM PHYLOGENY GROUP 2003).

Procontarinia matteiana Kieffer & Cecconi 1906

Among the various *M. indica*-infesting Cecidomyiidae, only *P. matteiana* shows a relatively extensive distribution, irrespective of the subtle metabolic variations in different varieties of *M. indica* (IYER & SUBRAMAN-YAM 1993); *P. matteiana* induces galls of similar morphology on various susceptible varieties of *M. indica* that exist throughout the Indian subcontinent, although levels of susceptibility among the different varieties vary (from 75% susceptibility in the variety 'Alphonso' to 20% susceptibility in the variety 'Benisan', JHALA et al. 1987). Varied levels of susceptibility of *M. indica* varieties to *P. matteiana* infestation have also been recorded in southern India (SATHIANANTHAM et al. 1973, RAO et al. 1991) and in South Africa (SCHOEMAN et al. 1996). Among the varieties of *M. indica* populations tested

in South Africa for *P. matteiana* infestation, the varieties 'Keitt', 'Kent', and 'Irwin' are only partly susceptible, and these varieties manifest aborted galls, most likely because of secondary resistance in these varieties causing mortality of early-instar larvae (GITHURE et al. 1998).

The biology of *P. matteiana* in two *M. indica*-growing bioregions ([i] Indo-Gangetic plains, India, 25-27°N; [ii] South Africa 24-26°N) offers insights into its abilities to adapt to local climatic conditions and to demonstrate different behaviours, similar to the behaviour shown in gall-inducing *Andricus kollari* (Hartig 1843) (Hymenoptera Cynipidae) introduced into south-western Britain in the 19th century, now spread throughout the British Isles (SCHÖNROGGE et al. 1999). The Indian populations of *P. matteiana* complete three generations per year; the first batch of adults emerges from the diapausing larvae of the preceding year in March. The first-generation larvae show a highly variable developmental period: some emerge as adults in July, others in October. A subsequent emergence also occurs in October from the first and second generation larvae of the same year. Leaf flushes in *M. indica* occur in March, July, and October each year and adult emergence coincides with these events. The larval period in the Indian populations of *P. matteiana* varies from 2 to 12 months in larvae emerging from the same egg cluster (R.L. GUPTA 1952). The rhythmic emergence of adults coinciding with new leaf flushes of *M. indica* is considered by R.L. GUPTA (1952) as a mechanism to overcome genetic disadvantages. In the South-African populations of *P. matteiana*, two generations per year occur, one in February-March, and the other in October-November. The October-November generation coincides with the commencement of the wet season, which synchronizes with the emergence of new leaf flushes in *M. indica*. Adult midges oviposit on young leaves and galls attain maturity in approximately 90 days (BOTHÁ & KOTZÉ 1987).

Although many of the behavioural traits are similar between the Indian and South-African populations of *P. matteiana*, the striking similarity is in the incidence of two generations per year, in February-March and in October-November each year, notwithstanding the fact that the locations are at identical latitudinal coordinates. The incidence of extended larval periods and delayed adult emergence in one of the three annual generations in the Indian populations of *P. matteiana* is the point to be investigated in exploring explanations for such behaviour.

Procontarinia mangiferae (Felt 1911)

Only *P. mangiferae* (*Rabdophaga mangiferae* Mani 1938; *Erosomyia indica* Grover & Prasad 1966) is capable of living on inflorescences and vegetative shoots, including both young stems and leaves (PRASAD & GROVER 1976). Most of the established species of Cecidomyiidi that induce galls on *M. indica* are currently assigned to *Procontarinia* (Cecidomyiini), but '*Oligotrophus*' *mangiferae* (Cecidomyiinae), a stem-gall inducing taxon, remains unplaced within Cecidomyiidae (GAGNÉ 2004). Among the several gall-inducing taxa associated with *M. indica*, the behaviour of *P. mangiferae* appears striking, since it demonstrates subtle radiation by being able to infest more

than one organ on the same plant; whether gall induction on leaves preceded gall induction on stems is hard to infer presently with the available data. The ability of insects with liquid-ingesting, sucking mouthparts to switch from leaf (an appendicular organ) to stem (an axial organ) or vice versa is a critical step in the evolution of herbivory, primarily because of the quantities and diversity of secondary metabolites in leaves and stems (MULLIN 1986, SCHLUTER 2000). *Procontarinia mangiferae*'s ability to infest both stems and leaves is probably regulated by weather patterns, so that successive generations of *P. mangiferae* proceed to utilize the available host tissues, either tender foliage or tender stem tissue, at an appropriate developmental stage to respond to the gall-induction stimulus. Such a behaviour among gall-inducing insects with sucking mouthparts is documented (ANANTHAKRISHNAN & RAMAN 1989).

Gephyraulus species

The flower-infesting species (*Lasioptera mangiflorae* [Lasiopterini], *Dasineura amaramanjarae*, *Gephyraulus mangiferae*, and *G. indica* [Dasineurini]) belong to Lasiopteridi (GAGNÉ 2004). Because most species of *Gephyraulus* RübSaamen 1916 (*Paragephyraulus* Solinas 1982) occur in flowers of different species of Palearctic Brassicaceae (SOLINAS 1982), the incidence of *G. mangiferae* and *G. indica* in the flowers of *M. indica* (GAGNÉ & ETIENNE 2006) is surprising. Among gall-inducing *Asphondylia* Loew 1850 (Diptera Cecidomyiidae) on *Larrea tridentata* (Chenopodiaceae) and *Andricus* Hartig 1840 (Hymenoptera Cynipidae) on oaks (*Quercus*, *Cerris*, Fagaceae), radiation between organs within the same host taxon is more frequent than shifts between different taxa (J.M. COOK et al. 2002, JOY & CRESPI 2007). However, the biology of Coniferales-infesting, non-gall-inducing *Cinara* spp. (Hemiptera Aphidoidea) indicates that feeding-site fidelity is more critical in speciation than host-plant fidelity (FAVRET & VOEGTLIN 2004).

Impact of natural enemies

In addition to the explanation that gall-inducing insects inhabit a highly specialized habitat, viz., the gall, for nutrition, another opinion is that a gall is an 'enemy-free' space protecting the inducing insect from predators and parasitoids (PRICE et al. 1987). However, evidence shows that gall-inducing insects are susceptible to heavier levels of parasitization than their non-gall-inducing relatives (HAWKINS et al. 1997). A strong selection pressure for achieving a greater level of 'protection' (e.g., greater level of hardness and thickness of gall walls) prevails on any gall-inducing taxon (STONE & SCHÖNRÖGGE 2003) to reduce the vulnerability of their offspring to parasitoids and predators. By depositing multiple eggs at the same host location, multi-chambered galls develop and such a development is also considered as an evolved trait among some gall-inducing insects (STONE et al. 2002).

Association of parasitic Hymenoptera with gall midges that induce galls on species of Sapindales and related orders in tropical landscapes (e.g.,

FERRAZ & MONTEIRO 2003) and how these parasitoids and other associated arthropods influence the evolution of gall-inducing gall midges are well known (see PRICE 2005, ROSKAM 2005, YUKAWA & ROHFRTSCH 2005). However, little is known about the arthropod community associated with different gall-inducing Cecidomyiidae living on species of Anacardiaceae, except for extremely limited information on the parasitic Hymenoptera associated with galls induced by *P. matteiana* (YADAV 1978, AUSTIN 1984, BOUČEK 1986, SANKARAN & MJENI 1986) and *P. mangiferae* (GROVER 1986). Information on predatory arthropods associated with gall-inducing insects of Anacardiaceae is also limited to a few generalist Formicidae (Hymenoptera) in the Indian subcontinent (PEÑA et al. 1998) and two generalist Miridae (Heteroptera) in the Caribbean (WHITWELL 1993).

Calophyidae

Among the Indian Anacardiaceae-infesting psyllids, *M. indica* (Anacardiaceae) hosts four species, whereas *Semecarpus anacardium* (Semecarpeae), *Spondias mangiferae* (Spondiadeae), *Buchanania lanzan* (Anacardiaceae), and *Rhus semialata* (Rhoaceae) host one species each (Table 1). Among the *M. indica*-infesting psyllids, gall induction is confirmed only in *Apsylla cistellata*, whereas gall-inducing behaviour in *Calophya brevicornis*, *C. maculata*, and *C. mangiferae* is unknown, although all the South-American species of *Calophya* associated with *Schinus* (Anacardiaceae) are confirmed gall inducers (BURCKHARDT & BASSET 2000).

Apsylla cistellata (Buckton 1893)

Apsylla cistellata is the sole member of Apsyllinae within Calophyidae (WHITE & HODKINSON 1985). Biological investigations on *A. cistellata* mostly from the northern plains of India [22-28°N; 76-92°E] have been several (e.g., MATHUR 1946; S.M. SINGH 1954, 1959, 1960; PRASAD 1957; K.M. GUPTA & HAQ 1958; G. SINGH et al. 1975; G. SINGH & MISRA 1978; AHSAN 1983; MONOBRULLAH et al. 1998; G. SINGH 2003). Gravid females lay 75-150 eggs/leaf in March-April. According to S.M. SINGH (1954: 563) "... the eggs are partly embedded and white in colour", and according to G. SINGH & MISRA (1978: 15) "... the female insect inserts the eggs in the midrib of the leaf at emergence of new flush in March-April in two parallel rows ... The freshly laid eggs are whitish translucent oval in shape with its tip partly exposed, which is characteristic". Eggs hatch either in mid-September or early October, approximately 200 days after oviposition; nymphal period includes five instars (six according to MONOBRULLAH et al. [1998], which is erroneous), and the development into adults takes about 140 days. Gravid females never oviposit on the leaves of seedlings; they prefer tender leaves of mature plants ready to bear flowers and fruits (G. SINGH 2003).

The first-instar nymph's feeding action 'triggers' gall development, although the first-instar nymph, without proper egg hatch, remains part-

ly within the egg shell and feeds on the same leaf where the adult female oviposited (G. SINGH et al. 1975). Almost every one who studied these galls and the psylloid indicates that galls develop through the modification of vegetative axillary buds as the first-instar nymphs feed on the leaves and only the second-instar nymphs migrate to the already-organized galls. The feeding effect of multiple neonate nymphs (from an egg cluster of 75-150/leaf) possibly induces the modification of adjacent vegetative buds into galls (referred as 'embryos' by G. SINGH 2000, 2003), in an approximate period of 30 days. An increase in endogenous auxin levels and a decrease in total phenols and contents of auxin precursors (e.g., tyrosine and tryptophan) in the buds of *M. indica* that have developed into galls have been demonstrated (G. SINGH 2000); a distinct correlation between age of flowering and gall incidence is also indicated (G. SINGH 2003).

The key message that emerges is that the young nymphal stages ('first-instar nymphs' according to G. SINGH & MISRA (1978); 'embryonic stages' according to G. SINGH (2000, 2003)) of *A. cistellata* feed on the leaf, where the eggs were deposited, and stimulate gall development at a site farther away, viz., the vegetative axillary bud, by translocating a chemical 'stimulus'. Such a behaviour is unusual among the gall-inducing psylloids (BURCKHARDT 2005b), but is analogous to what has been reported in *Adelges cooleyi* (Gillette 1907) (Hemiptera Aphidoidea Adelgidae) that induces galls on the vegetative buds of the hybrid interior spruce (*Picea glauca* × *P. engelmannii*), where a dose-dependent chemical stimulus is transported over long distances from the point where the gall-founding female settled (SOPOW et al. 2003). In spite of an apparent similarity, in the bud galls of *M. indica*, the first-instar nymphs of *A. cistellata* are the purported gall inducers, whereas in the bud galls of *Picea glauca* × *P. engelmannii*, adult females of *A. cooleyi* induce galls. While long-distance transport of a chemical stimulus has been demonstrated in the galls of *A. cooleyi*, the question raised by PRASAD (1957), whether *A. cistellata* plays a vectorial role in transmitting a microbe (e.g., virus), which could be stimulating gall development (see CORNELL 1983), merits investigation, given that many psylloids are established vectors of plant pathogens (AUBERT 1987, WEINTRAUB & BEANLAND 2006).

Apsylla cistellata is confined to the Indo-Gangetic Plains and lower valleys of the Himalaya (20°-34°N; 77°-85°E; G. SINGH 2003); however, KANDASAMY (1986) has reported its incidence in the Shevaroy Hills (11°46'-11°78'N; 78°12'-78°20'E; 700-1200 m a.s.l.) in humid, tropical peninsular India, which has not been verified subsequently. Although *M. indica* is being grown extensively in several warm parts of the world, *A. cistellata* is not known to occur in any geographical area other than the northern plains of the Indian subcontinent (including parts of Pakistan, Bangladesh, and Nepal). A possible reason for the localized incidence of *A. cistellata* is an annual rainfall of more than 1100 mm and a difference of more than 30 °C between the highest maximum and lowest minimum temperatures (G. SINGH 2003). Nonetheless, a recent USDA plant quarantine report identifies *A. cistellata* as a potential risk to *M. indica* populations in USA (USDA 2006). Polyembryonic varieties of *M. indica* in Indian conditions exhibit resistance to *A. cistellata*, whereas the monoembryonic varieties do not (KUMAR 1990). A list referring

to field screening of diverse Indian varieties of *M. indica* against *A. cistellata* infestation is available (KUMAR 1988, G. SINGH 2003).

Due to several autapomorphic characters (e.g., complex metathoracic pleuron, OUVARD et al. 2002) *Apsylla cistellata*'s current position in Calophytidae (Hemiptera Psylloidea) is not supported strongly.

DISCUSSION: REASONS FOR CONSERVATISM AMONG THE CECIDOMYIIDAE AND CALOPHYIDAE ASSOCIATED WITH *MANGIFERA INDICA*

Reproductive isolation and temporal isolation drive radiation in plant-feeding insects. Reproductive isolation progresses through ecological specialization of insect species on specific plant species or feeding on the same host and at the same time, but in different places (CAILLAUD & VIA 2000). Temporal isolation, on the other hand, progresses through mechanisms determined by host plants with varying phenologies such that adults from populations on different plant species may mature and mate at different times (GROMAN & PELLMYR 2000) or on different parts of the same plant (J.M. COOK et al. 2002, JOY & CRESPI 2007). Reproductive isolation, determined by prezygotic isolation, associated with fidelity of mating on a specific host plant (BERLOCHER 2000), leads to formation of host-plant races with moderate levels of reproductive isolation diversifying into independent species (ABRAHAMSON et al. 2001, DRÈS & MALLET 2002). Examples illustrating these patterns of radiation involving rapid shifts to related plant taxa are amply evident among gall-inducing eulophids (Chalcidoidea Eulophidae) (WITHERS et al. 2000, RAMAN & WITHERS 2003, MENDEL et al. 2004, YANG et al. 2004, LA SALLE 2005). Host shifts, although not as striking and as 'rapid' as in the Eulophidae, occur in other gall-inducing Hymenoptera, such as the Agaonidae (J.M. COOK et al. 2002, J.M. COOK & RASPLUS 2003) and Cynipidae (ROKAS et al. 2003). In spite of being speciose, adaptive radiation in the Oriental and eastern Palearctic species of Cecidomyiidae has been demonstrated only in Asphondyliini (UECHI et al. 2002, 2004; YUKAWA et al. 2003; TOKUDA et al. 2005). The *M. indica*-associated *Procontarinia*, within the limits of available evidence (RAMAN 2007b), does not show any striking level of shifts either between organs within *M. indica* or between related taxa such as *Anacardium*, *Buchanania*, *Lannea*, *Holigarna*, *Pistacia*, *Semecarpus* in Indian Anacardiaceae, all of which serve as hosts to species of Cecidomyiidae other than *Procontarinia*. Because shifts to a different plant species require adaptation to distinctly varied characteristics in the host plant (e.g., morphology, chemistry, and phenology), the shifts within a specific plant taxon from one organ to another need not necessarily involve adaptation of that magnitude. J.M. COOK et al. (2002) have demonstrated that shifts within plant lineages are more common than shifts between plant lineages and suggested that shifts between organs within a plant are less challenging, given that the host genotype is the same. But the key point is that the proteomics of these plant organs can be different (THIELLEMENT et al. 2000, HOCHHOLDINGER et al. 2006), which points to and underscores the ability of gall inducers to adapt

to the local host proteomics. In alignment with this possibility, we consider that *M. indica*-associated *Procontarinia* have remained conservative, lacking either the ability or the need to adapt to host proteomics. Moreover, the lack of radiation from leaves to other organs of *M. indica* indicates that neither the feeding behaviour nor the salivary physiology of the respective gall-midge species has changed substantially over time. What could be the possible reasons for such a conservative diversification of *M. indica*-associated gall midges? Conservative diversification in *Procontarinia* appears to reflect the pattern of radiation of *M. indica* within the Indian subcontinent. A recent inter-simple sequence repeat marker study of 60 Indian and non-Indian *M. indica* varieties has shown that the *M. indica* varieties from Australia, USA, Israel, Taiwan, and Thailand cluster into distinctly separate groups from the group that would include the Indian *M. indica* varieties, indicating a distinct genetic divergence between the Indian and non-Indian varieties (PANDIT et al. 2007). In the context of *Procontarinia*, the genetic divergence of the non-Indian *M. indica* varieties is reflected in *P. matteiana* infestation behaviour in South Africa, because the North American (Florida) varieties 'Keitt', 'Kent', and 'Irwin' grown in South Africa manifest only aborted galls consequent to *P. matteiana* feeding, indicating partial susceptibility to the cecidomyiid. *Procontarinia matteiana* infestation behaviour in India manifests in well-developed galls of identical morphology on the different Indian varieties of *M. indica* (SATHIANANTHAM et al. 1973, JHALA et al. 1987, RAO et al. 1991).

Either the possible absence of resistance-breaking genes within the *Procontarinia* complex associated with *M. indica* or the ability of *M. indica* populations to restrict gene flow between specific gall-midge populations is the reason for the conservative diversification among gall-inducing Cecidomyiidae, because, broadly, host-plant regulated impediments on the breeding behaviours influence the radiation of gall-inducing insects (MARTINEZ et al. 2005). Given that no phylogenetic data on *M. indica*-infesting gall-midge populations are currently available, a tangible reconstruction of patterns of phenotypic plasticity among them, which may have taken place over time, is not possible. Nonetheless, a reasonable speculation would be that some level of radiation of leaf-gall inducing species has occurred among the Cecidomyiidae from those species that induce structurally simple galls (e.g., those induced by *P. matteiana*) to structurally complex galls (e.g., those induced by *P. echinogalliperda*) (VIJAYA PARTHASARATHY 1991, MANI 2000), although no established phylogenetic study currently exists in support of this contention. Concrete evidence explaining the polarity of such transformations is also currently unavailable, except for a reconstruction of gall phylogeny based on the anatomy of galls (from a 'structurally simple' pit gall to structurally complex, multi-chambered, sclerenchyma-including galls) induced by different species of *Procontarinia* Kieffer & Cecconi 1906 (MANI 2000). Moreover, the level of relationships of *Procontarinia* with other cecidomyiid genera is currently unknown. The name, originally given to this genus by KIEFFER & CECCONI (1906), implies that *Procontarinia* is related to *Contarinia* Rondani 1860, which is far from certain, and needs to be assessed using genetic tools.

Within the Anacardiaceae of the Indian subcontinent, *Holigarna arnotiana* and *Semecarpus anacardium* (Semecarpeae), *Lannea coromandelica* and

Spondias mangiferae (Spondiadeae), *Buchanania lanzan* and *Mangifera indica* (Anacardiaceae), and *Pistacia integerrima*, *Pistacia khinjuk*, and *Rhus semialata* (Rhoeeae) bear galls mostly induced by species of Cecidomyiidae (Diptera) and a few by those of Calophyidae and Aphididae (Hemiptera). The following comment of SUSAN PELL (pers. comm., e-mail, 2 November 2007) on the current understanding of the phylogeny of Anacardiaceae needs to be factored while examining the patterns of radiation in gall-inducing taxa on anacardiaceous taxa: "Within Anacardiaceae, *Mangifera* comes out in a clade that consists of members of Anacardiaceae, which include *Anacardium*, *Bouea*, *Fegimanra*, *Gluta*, besides *Mangifera*. *Mangifera* is sister to *Bouea*, but the taxa *Androtium* and *Swintonia* from Anacardiaceae as well as numerous Asian genera that could be more closely related to *Mangifera* need to be factored at this point. *Buchanania* does not come out in the clade of other Anacardiaceae members. *Lannea* is in a clade of Spondioideae that is one of the earlier branches in the phylogeny and totally unrelated to the tribe Anacardiaceae clade; *Pistacia* and *Rhus* are in the large Anacardiaceae clade of which the tribe Anacardiaceae clade is a member, although *Pistacia* and *Rhus* are far removed from this clade. *Semecarpus* could be closely related to the Anacardiaceae clade". The PELL comment explains, to a reasonable extent, the patterns that occur within Anacardiaceae; for example, why all the Cecidomyiini (*Procontarinia* spp.) have remained tied to *Mangifera indica* and have not radiated to the Indian species of *Buchanania*, which match the distribution of *M. indica* in the subtropical moist to wet-dry tropical India (DUKE 2001). *Buchanania lanzan*, however, hosts *Calophya longispiculata* (Mathur 1975) a gall-inducing species.

Because *M. indica* is an evergreen, polyaxial species, new flushes of foliage are available almost throughout the year; moreover, the leaf flushes emerge synchronously, with single-leaf longevity of 4-5 years. Because of the unusually long leaf longevity, canopies of *M. indica* remain dense (SEARLE et al. 1995) and therefore also maintain high carbon assimilation efficiency. Populations of *M. indica* are available in high numbers in places wherever it is raised as a commercial plant. For example, in the Indian subcontinent alone, nearly 1.2 million ha of land area is under cultivation of *M. indica* (NEGI 2000). Plentiful availability of *M. indica*, the most preferred host, could have also restricted the diversification of gall midges, although we do not know whether this might apply on a geological time-scale, because we do not know the historical changes in the distributions of *M. indica* populations.

Diverse geographically localized varieties of *M. indica* with different types of secondary chemicals such as xanthenes and flavanols (JOHN et al. 1999, LITZ & GÓMEZ-LIM 2004) could be exerting multiple selection pressures on the radiation of gall midges. Mangiferin, a phenolic glucoside (a glycoxanthone), is known to be occurring in 96 natural orders of flowering plants (dicotyledons — 60; monocotyledons — 36). In Anacardiaceae it is known only in *M. indica* and *M. zeylanica* (RICHARDSON 1983, JENSEN & SCHRIPEMA 2002) and not in any other plant families in Sapindales (sensu ANGIOSPERM PHYLOGENY GROUP 2003). Mangiferin in *M. indica* (NOTT & ROBERTS 1967) possibly plays a role in attracting oviposition by Cecidomyiidae. The point of comparison here is that phenolic glucosides in the leaves of *Salix* have been implicated

to stimulate oviposition by gall-inducing *Euura lasiolepis* Smith 1968 (Hymenoptera Tenthredinidae) (ROININEN et al. 1999). Although gall-inducing sawflies are biologically different to gall-inducing gall midges, whether mangiferin — a component of *M. indica* volatiles — could play a role in restricting gall-midge populations from seeking new host plants needs to be solved.

The present understanding is that the Cecidomyiidae have evolved specializing along host-plant lines (GAGNÉ 1994), because of the need for precise timing and for minimizing interactions with the parasitic, predatory, and inquilinous arthropods, from the time they colonize their host plants. Exclusion from a rigorous competition for resources, in contrast to what is evident in many of the gall-inducing Cynipoidea (STONE et al. 2002) has either disabled or retarded radiation, because the environment has remained not only 'stable', but also 'secure'.

Documented information on the gall-inducing species of the *Procontarinia* complex on the leaves of *M. indica* indicates that both the location and structure of galls generally agree with the patterns evident in other groups of gall-inducing insects, in which related species induce similar types of galls (cf. STERN 1995, CRESPI & WOROBAY 1998, STONE & COOK 1998, NYMAN et al. 2000).

Discussing the phylogeny of the gall-midge subtribe Baldratiina (Diptera Cecidomyiidae) that induce galls on several species of Chenopodiaceae, DORCHIN et al. (2004) indicated that multi-chambered galls on stems constituted the ancestral state in Baldratiina and the single-/multi-chambered galls on the blade evolved from the inconspicuous galls induced on the midrib; they suggested that host shifts among different species of Chenopodiaceae occurred before new gall types evolved. In the context of *M. indica* gall midges, only *P. mangiferae* occurs both on stems and leaves and the critical point is that no shift to another plant species is known, although what needs to be recognized is that shifting to different parts of the same plant species (e.g., from leaf to stem) could be a step towards speciation, through reproductive isolation involving phenological separation (FERDY et al. 2002). The gall-inducing species of *Procontarinia* occur on the same host tree and on the same leaf, but how populations of different gall midge taxa partition their resources effectively and reduce inter-specific competition are questions remaining to be answered.

In the specific context of Cecidomyiidae-*M. indica* interactions, the effective utilization of the host plant and consequent speciation in the *Procontarinia* complex has possibly resulted from the fact that individual trees of *M. indica* had been available throughout extensive landscapes and continuously blossoming, but probably only since mango cultivation began. While *Apsylla* Crawford 1912 did not speciate on *M. indica* and this may be true with *Calophya*. For testing this hypothesis more information is necessary on *Calophya brevicornis*, *C. maculata*, and *C. mangiferae*, such as distribution, gall-inducing ability, sites of eggs and nymphs on *M. indica* as well as the phylogenetic relationships.

Apart from these speculations, empirical studies on the phylogeny and interactions of *Procontarinia* and related genera, and *Apsylla cistellata* and other Calophyidae taxa associated with *M. indica* are necessary investigating the taxonomy of the involved groups extensively and intensively. Experimen-

tal studies characterizing and measuring the ovipositional preference and larval performance need to be carried out. Possibly cryptic species of *M. indica*-infesting gall midges and psylloids occur and therefore experiments assaying reproductive isolation in different geographic localities are also necessary, especially in populations where differences in preference and performance possibly exist. These arguments could be true, although not to the same extent, with other groups of gall-inducing insects in the Indian subcontinent.

ACKNOWLEDGEMENTS

We thank Raymond Gagné (USDA, Washington DC, USA), Peter Price (Northern Arizona University, Flagstaff, Arizona, USA), Graham Stone (The University of Edinburgh, Edinburgh, Scotland), Sagrario Gámez-Virués and Johannes Bauer (The University of Sydney, Orange, NSW, Australia), Suresh Govindaraghavan (Lipa Pharmaceuticals, Minto, NSW, Australia), and Ashwini Kumar Srivastava (Birbal Sahni Institute of Palaeobotany, Lucknow, India) for reviewing the pre-final draft and for offering insightful comments. We also thank the three anonymous reviewers for their useful comments.

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