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Evolutionary patterns in biogeography and host plant association: 'taxonomic conservatism' in Lophopidae (Hemiptera, Fulgoromorpha)

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Abstract. The association between the Lophopidae (Hemiptera, Fulgoromorpha) and their host plants was studied within a phylogenetic framework. Host plant use was optimized on Lophopidae phylogeny and the most parsimonious hypothesis is presented. This hypothesis describes the evolution of host plant use by the Lophopidae, and postulates the ancestral plant family used. This scenario is discussed within the biogeographical evolutionary context of the fulgoromorphan families, and is corroborated by information from both insect and host plant fossils. The association of the Lophopidae and their host plants is made by comparing the angiosperms and Lophopidae phylogenies, demonstrating at this level of comparison that the insects show 'taxonomic conservatism' for their host plants.

Introduction

The planthoppers (Hemiptera, Fulgoromorpha) constitute a large group of phytophagous insects. Between seventeen and nineteen families are recognized commonly (O'Brien, 2002; Szwedo *et al*., 2004). All species suck fluids from leaves, stems, roots or fungal hyphae (O'Brien & Wilson, 1985; Wilson *et al*., 1994). Adults and nymphs of the family Lophopidae, which contains thirty-seven genera and around 130 described species (Soulier-Perkins, 1998), are found above the ground on their host plants (Wilson, 1987; Wilson *et al*., 1994), feeding on phloem, with 71% of published records from monocotyledonous plants (Wilson *et al*., 1994). Available host records show that most species are either monophagous (43%) or oligophagous (43%) as adults, and even more specialized as nymphs with 67% monophagous (Wilson *et al*., 1994). The morphology-based phylogeny shows that this family is a monophyletic lineage once the genera *Silvanana* and *Hesticus* are removed (Soulier-Perkins, 2001).

An optimization of host plant use performed on the phylogeny of phytophagans provides information about the feeding habits of the ancestor of the group. Such optimization provides hypotheses for the taxa for which no information on the host plant are actually available, and aids future collecting of Lophopidae by providing information on their potential host plants.

As synthesized in Brooks & McLennan (1991, 2002), some main models of co-evolution between host plants and phytophagous insects have been defined, such as the resource or phylogenetic tracking model, which is a special case of colonization and new resource exploitation. The classical 'evolutionary arms race' model of Ehrlich & Raven (1964) involves mutual association and modification between host plants and insects. Allopatric co-speciation (California model), in which a mutual association between plant and insect is observed without mutual modification, forms a null hypothesis for co-evolution (Brooks & McLennan, 2002). We ask whether either model corresponds to a co-evolutionary process between the phytophagous insects and their host plants. A comparison of the insects and the angiosperm phylogenetic hypotheses allows a better understanding of the evolution of phytophagous insect and host plant interactions, and helps to determine whether a particular co-evolutionary model can be applied

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to the insects' host plant relationships. Although no phylogenetic pattern alone can identify unambiguously a model of evolution (Brooks & McLennan, 2002), it can be used to test/reject incompatible or incongruent scenarios.

Materials and methods

Host plants

Host plant information on the Lophopidae (Table 1) has been compiled from the first author's personal observations in the field, literature data and from labels of specimens examined from various collections: Muséum National d'Histoire Naturelle (MNHN), Paris, France; Institut Royal des Sciences Naturelles de Belgique (RIScNB), Brussels, Belgium; Bishop Museum, Honolulu, Hawaii; Lois O'Brien collection, A & M University, Tallahassee, Florida, U.S.A.

Phylogenies

The Lophophidae phylogeny used was proposed by Soulier-Perkins (2001) and is the only one available. It is based on seventy-three morphological characters and contains thirty-four genera out of the known thirty-eight. The angiosperm phylogeny is taken from Angiosperm Phylogeny Group (APG) II (2003).

Optimization of attributes

The question of including against excluding characters of interest from the analysis is central to phylogenetic tests of

Table 1. List of families on which the Lophopidae feed.

Genus	Family of host plant	Source	Plants named in source
Acarna	Arecaceae	Label J.L. Gressitt col. (Bishop Museum)	*Calamus*, palm
Buxtoniella	Pandanaceae,	Muir (1927)	*Freycinetia* sp.
	Arecaceae	Labels O.H. Swezey col. (Bishop Museum)	*Pandanus*, *Clinostigma*
Clonaspe	Arecaceae,	Labels J.L. Gressitt col. (Bishop Museum)	*Heliconia*, palm, ginger
	Zingiberaceae		
Elasmoscelis	Poaceae,	Label written by O'Brien	Grass
	Rubiaceae,	Wilson *et al.* (1994) from Synave (1962)	*Canthium*,
	Fabaceae,		*Lonchocarpus laxiflorus*,
	Bignoniaceae		*Kigelia aethiopia*
Jugoda	Arecaceae	Label J.L. Gressitt col. (Bishop Museum)	Palm, rattan, *Calamus*
Lophops	Poaceae	Label written by H. Synave (MNHN)	[Sur graminée] graminoids
		Personal observation	On sugarcane
		Wilson *et al.* (1994)	*Saccharum officinarum*
		Kirkaldy (1906)	Sugarcane and grasses
Maana	Arecaceae	Label paratype (Bishop Museum)	Slender leaf of rattan
Magia	Arecaceae	Personal observation	*Archontophoenix alexandrae*
Megacarna	Musaceae	Label J.L. Gressitt col. (Bishop Museum)	Banana
Onycta	Arecaceae	Label J.L. Gressitt col. (Bishop Museum)	Palm
Painella	Arecaceae	On label written by L. O'Brien	Coconuts
		Wilson (1988); Stapley (1978)	Coconut palm
Pitambara	Poaceae	Melichar (1915); Distant (1906)	*Bambusa*
		Label J.L. Gressitt col. (Bishop Museum)	Bamboo
Pyrilla	Poaceae	Kumarasinghe (1996); Fennah (1963)	Sugarcane
Sarebasa	Poaceae	Label J.L. Gressitt col. (Bishop Museum)	Bamboo
Serida	Poaceae	Label leg J.M. Ouin (RIScNB)	[Canne à sucre] sugarcane
Virgilia	Arecaceae	Zelazny & Pacumbaba (1982)	Coconut palm
Zophiuma	Arecaceae	Wilson et al. (1994); Smith (1980)	*Cocos nucifera*

evolutionary models (Grandcolas *et al.*, 2001). In this case, host plant use and its chemical or behavioural cues are known imperfectly and their introduction as characters into the insect phylogeny is inappropriate; thus, we optimized host plants as an attribute on the already reconstructed phylogeny (as often performed for exploratory data on habitats; for example, Desutter-Grandcolas, 1997). Mapping host plants onto the Lophopidae phylogeny was performed using the program MacClade (Maddison & Maddison, 2002) to provide the most parsimonious hypothesis, which was then tested for coherence against available palaeontological data for host plants and Lophopidae.

Comparison of trees

An option could have been to compare insect and plant trees with either Brooks parsimony analysis (BPA) or Page's algorithms (Brooks & McLennan, 2002; Page, 2003), but, as shown from recent controversies (Siddall & Perkins, 2003; Brooks *et al.*, 2004), none of these algorithms provides an accurate account of evolutionary events including both possible extinctions and/or duplications. However, TreeFitter 1.0 (Ronquist, 1995) provides some co-evolutionary statistics and allows the testing of the hypothesis of a congruent pattern between phylogenies: is the number of events hypothesized when comparing our trees larger than when the Lophopidae tree is randomly generated? This program allows an assignment of different costs to each of the four co-phylogenetic events: co-speciation (C), host-switching (H), duplication (D) and sorting or extinction of the phytophagous lineage (S). As some Lophopidae feed on more than one host plant, the solution suggested by Page & Charleston (undated) for the 'widespread parasites' is applied.

Results and discussion

Host plants (Table 1)

Four Lophopidae genera, *Zophiuma*, *Pyrilla*, *Virgilia* and *Painella*, are recognized as pests. The genus *Pyrilla* has an economic impact (Kumarasinghe, 1996) on sugarcane production in Asia and India, attacking rice if sugarcane is unavailable (Wilson & Claridge, 1991). Within the five species of *Zophiuma*, *Z. lobulata* Ghauri, 1967 was noted as a pest on coconut trees in Papua New Guinea and caused bronzing of fronds, reduction in yield, marked stunting of growth and occasionally the death of young palms (Smith, 1980). A similar disorder to coconut trees in the Solomon Islands, associated with the presence of *Painella simmondsi* Muir, 1931, was reported by Stapley (1978) (cited in Wilson, 1988). In the Philippines, *Virgilia luzonensis* Baker, 1925 feeds and breeds on palms (Zelazny & Pacumbaba, 1982). These host plant records are confirmed as these insects are involved in plant damage, and the records, as such, have been numerously validated. For the genera *Lophops* and *Magia*, the first author observed specimens feeding during a field trip in Australia. The genus *Lophops* was observed on sugarcane. The genus *Magia*, which is endemic to Australia, is frequently found on the leaves of *Archontophoenix alexandrae* (F. Muell) H. Wendl. & Drude, an Arecaceae species, growing in the central to northern coastal rainforest of Queensland.

Scenario: Lophopidae host plant choice optimization (Fig. 1)

Which host plant was the ancestor of the Lophopidae feeding on? The actual host plants of the taxa, where these data are available, were mapped on the insect phylogeny, optimized and the most parsimonious hypothesis (Fig. 1) retained. According to this, the ancestor of the family was feeding on Arecaceae (Arecales) (two steps) rather than on Poaceae (Poales) or Musaceae (Zingiberales), for which three steps are required. Two changes in the family's host plants are observed. The ancestor of *Megacarna* (one species) switched from the Arecaceae to Musaceae. Another host plant switch was observed for the ancestor of the Sarebasa$^+$ group, which left the Arecaceae for the Poaceae. This switch appears to have been profitable, permitting an important radiation resulting in eleven genera (*Sarebasa*, *Lacusa*, *Elasmoscelis*, *Pitambara*, *Podoschtroumpfa*, *Paracorethrura*, *Acothrura*, *Serida*, *Corethrura*, *Lophops* and *Pyrilla*) and a total of fifty-six described species.

Test: confrontation of the scenario with biogeographical events and fossils

A geographical scenario describing the evolution of the Lophopidae (Soulier-Perkins, 2000) presents the origin of this family at around 65 million years ago (Ma) somewhere in South-east Asia. Their distribution extended northwards where they migrated across the Bering land bridge into North America during the Palaeocene. The only fossil presenting some characteristics of the Lophopidae, *Scoparidea nebulosa* Cockerell, 1920 (Szwedo *et al.*, 2004), was found in the Rocky Mountains and is dated at 53–34 Ma. Concerning the host plants and, especially, the Arecaceae, the oldest fossils known for that family are from the Late Cretaceous (80 Ma). Considering these fossils and their age, it is coherent to postulate that the ancestor of the Lophopidae was feeding on Arecaceae.

The clade Sarebasa$^+$, containing the eleven genera that feed on Poaceae, is found in Asia from India to Japan with a distribution extending east to the Solomon Islands and south to Australia. Two of these eleven genera, *Elasmoscelis* and *Lophops*, are also found in Africa. The typical grass spikelet (basic unit of the inflorescence) fossils appear around the Palaeocene–Eocene boundary at 55 Ma (Crepet & Feldman, 1991), and dinosaur coprolites suggest that Poaceae were present on the Indian continent during the latest Cretaceous (Prasad *et al.*, 2005). The graminoid clade originated in east Gondwana according to Bremer (2002),

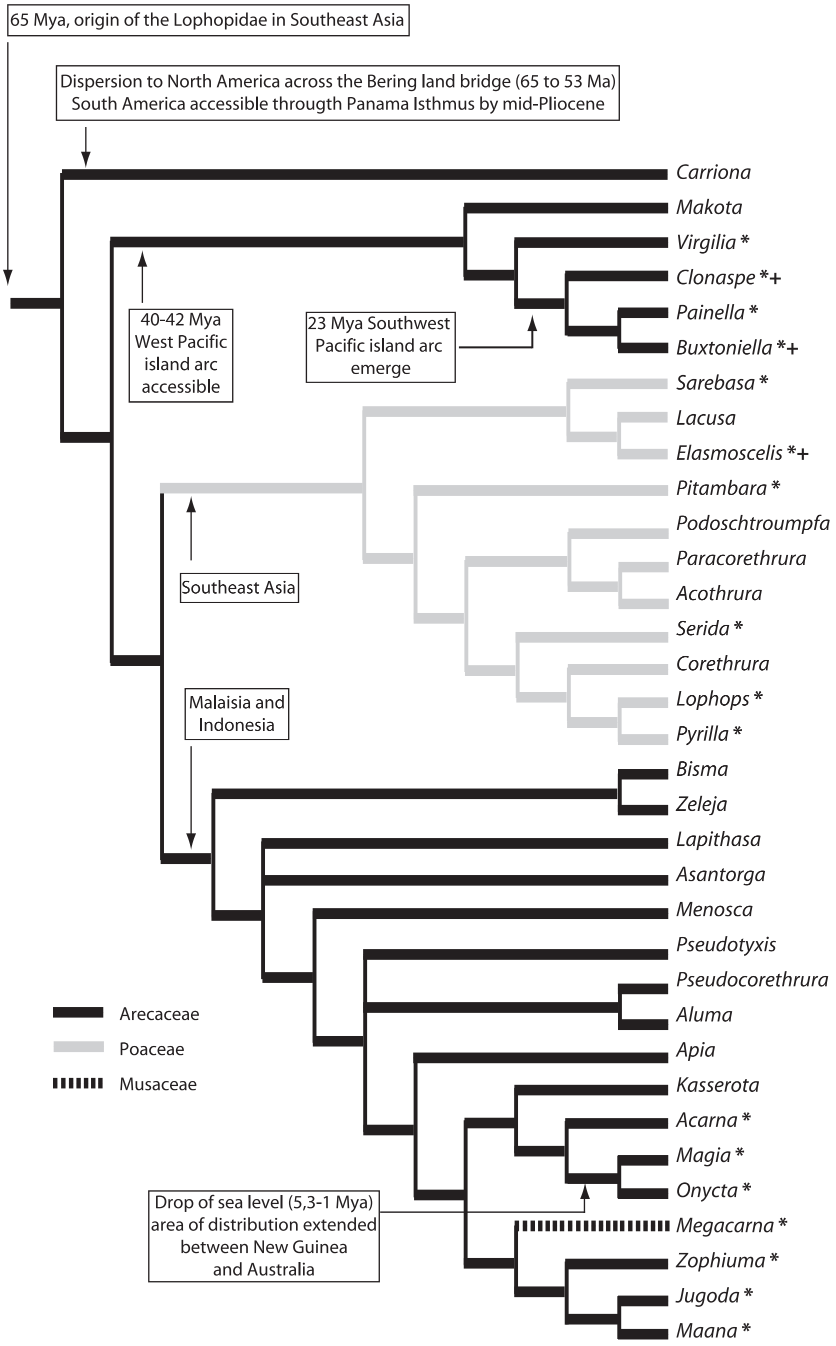

Fig. 1. Scenario hypothesis concerning the evolution of host plants for the Lophopidae. The shortest hypothesis found is with an ancestor feeding on Arecaceae. *Genera for which host plant information is available. +Genera feeding on more than one family. The historical biogeographical information was extracted from Soulier-Perkins (2000).

and the palynology shows that the first Poaceae did not appear in Africa before the mid-Eocene (42 Ma) (Van der Hammen, 1983). The switch of host plant from Arecaceae to Poaceae for the ancestor of these eleven genera is again plausible. The ancestors of *Elasmoscelis* and *Lophops* apparently extended their distributions into Africa, and may have followed the expansion of the savannah on this continent during the Miocene (around 23 Ma), as hypothesized by Soulier-Perkins (2000).

Some families, such as the Musaceae and Zingiberaceae, that are today more or less restricted to Indo-Malaysia, tropical Africa and/or the New World tropics, were widespread in the Eocene and Oligocene (Renner *et al.*, 2001). The oldest records for the Pandanaceae are some microfossils from the upper Cretaceous, and fossil fruits from the Eocene. The host plant family already existed when the ancestor of *Megacarna* started to feed on the Musaceae. The genera *Buxtoniella* and *Clonaspe*, optimized as feeding on Arecaceae, seemingly expanded their resources by colonizing the families Pandanaceae and Zingiberaceae, respectively.

What kind of relationships between the Lophopidae and their host plants?

When we compare now the Lophopidae and angiosperm phylogenies (Fig. 2), can we observe any congruence between them? At this level of detail for the phylogenies, no pattern of co-speciation can be checked, but a degree of 'taxonomic conservatism' (Janz *et al*., 2001; Kergoat *et al*., 2005) in host plant association is clearly visible, i.e. phylogenetically related lophopid species occur on related host plants.

Using TreeFitter, the following results are obtained with the default setting ($C = 0$, $D = 0$, $S = 1$ and $H = 2$): $P = 0.0019$ for 10 000 permutations. The phylogenies fit each other more than expected by chance alone. Lowering the cost of host-switching from $H = 2$ to $H = 1$, the cost decreases from twelve to six with $P = 0.001$. The fit between the two phylogenies shows that the overall cost remains significantly lower than expected by chance. This is still valid when applying the Fitch optimization ($C = 20\,000$, $D = 0$, $S = 20\,000$ and $H = 1$): $P = 0.0004$ with a cost of six. Here, duplications and host-switching are the events involved, with the duplication events corroborating the taxonomic conservatism observed at this level of comparison.

When comparing two phylogenies, the details of the relationships that can be observed between them depend on the choice of terminal taxa. Here, the terminal taxa are generic for the insects and of family or order level for the plants. Many genera of Lophopidae are monospecific or contain only a few species, but the terminal taxa used in the plant phylogeny contain numerous species and, in particular, the two families most frequently used as host plants by the Lophopidae: the Arecaceae and Poaceae contain around 2600 and 10 000 species, respectively. More information on the host species and more detailed phylogenies for the Poaceae and Arecaceae will clarify the details regarding the relationships between the phytophagous insects and their host plants. It will be akin to using a 'magnifying glass': some relationships that appeared previously as taxonomic conservatism will be more detailed, and the type of association between phytophagous insects and host plants may become clearer for the period of time in which their association evolved. However, despite this imbalance between the levels of hierarchy in the insects and plants under study, no problem of temporality or chronological conflict was observed after the analysis of our data.

The Lophopidae are strongly linked to the monocots. Observed switches between host plants are rare, and remain within this lineage and between families that are closely related: from Arecaceae to Poaceae and from Arecaceae to Musaceae. Only the genus *Elasmoscelis* seems to feed on the dicotyledonous families Rubiaceae, Fabaceae and Bignoniaceae. Although, in the literature, this genus is generally associated with these families, when we return to the original observations of Synave (1962), these families appear only as plants from which *Elasmoscelis* was swept. However, if *Elasmoscelis* is using these dicotyledonous families, it represents a recent extension of resources for this group. It would be interesting to document further this genus and, according to a phylogenetic framework at the species level, verify whether the Asian and African taxa of this genus present the same host plant spectrum.

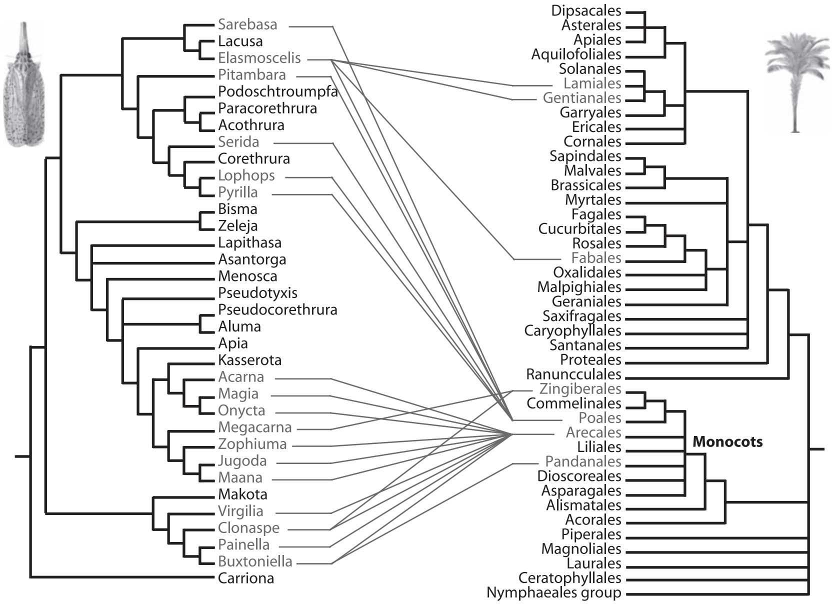

Fig. 2. Phylogeny of the Lophopidae (extracted from Soulier-Perkins, 2001) and the angiosperms (extracted from Angiosperm Phylogeny Group (APG) II, 2003) and links between insects and their host plants.

Conclusion

The Lophopidae present 'taxonomic conservatism'. This observation does not allow us to reject the hypothesis that some strong association or even co-evolution exists between Lophopidae and their host plants. It seems that the ancestor of this family was feeding on Arecaceae, like many of the observed living species, but, for one major clade, its ancestor switched to another monocot family, the Poaceae. The genera of this clade show a successful adaptation and radiation. This clade is represented by fifty-six species; nearly half of the described species and six of the eleven genera are widely distributed. Two may even have followed the development of the savannah in Africa. One genus, *Elasmoscelis*, is polyphagous and feeds on some Poaceae, but also on some dicotyledons (Rubiaceae, Fabaceae, Bignoniaceae). Here, the phylogenetic constraint seems to have loosened to allow the genus to feed on unrelated host plants.

The test of scenario opens up further research: for the genera for which the host plants are unknown, we now know that there is more chance of finding them on certain plant families than others. As the ancestor of the Lophopidae was feeding on Arecaceae, this could indicate its sister group that remains unknown. The same can be said for the genus *Carriona*, the only South American Lophopidae, and for which no ecoethological data are yet known.

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