

Seed-beetles in the age of the molecule: recent advances on systematics and host-plant association patterns

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Abstract. Our understanding of the evolution of host-plant associations in phytophagous insects has greatly benefited from the recent and continuous development of molecular phylogenetics studies. It was also the case for seed-beetles (Coleoptera: Chrysomelidae: Bruchinae), as numerous studies based on molecular phylogenetics were published on this group in the last ten years. In this paper, we have used a supertree approach to reconstruct the phylogenetic relationships of nearly 200 species of seed-beetles. The resulting phylogenetic framework was used to investigate their systematics and host-plant association patterns. This supertree provides an interesting overview of the current state of knowledge in bruchine phylogenetic relationships and also underlines the likely paraphyletic condition of numerous bruchine groups. Regarding the evolution of host-plant associations, our analyses recover a clear trend toward conservatism in host-plant use at distinct taxonomic levels.

Keywords. Bruchinae, character optimizations, evolution, host-plant associations, molecular phylogenetics, taxonomy, phytophagous insect, secondary compounds, species groups, supertrees, systematics.

1. Introduction

With species estimates ranging between 1,300 (Borowiec 1987) and 3,500 species (Jolivet *et al.* 1988), seed-beetles account for a minority of the estimated 135,000 known species of phytophagous beetles (Lawrence 1982). This group is nevertheless

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particularly important because it includes numerous species of economic importance, which infest numerous crop species throughout the world (Southgate 1979; Delobel & Tran 1993; Kingsolver 2004). Several species are also used in biological control programs of invasive plants (Syrett *et al.* 1999; Redmon *et al.* 2000; Radford *et al.* 2001; Kingsolver 2004).

Since the work of Spinola (1843), seed-beetles have been traditionally considered as a separate family (*i.e.* family Bruchidae), related to the Chrysomelidae (Lacordaire 1845). This prevailing view was almost unchallenged till the mid 1990s (but see Böving & Craighead 1931; Crowson 1953), when it became a matter of heated debates, especially in the newsletter *Chrysomela* (see Kingsolver 1995; Reid 1996; Verma & Saxena 1996; Duckett 1997; Lingafelter & Pakaluk 1997; Schmitt 1998). The strongest argument for demoting the Bruchidae was the fact that they share a well-supported sister-group relationship with the subfamily Sagrinae of the Chrysomelidae. This placement was suggested based on either morphological (Crowson 1946; Monrós 1955; Borowiec 1987; Reid 1995) or molecular (Farrell 1998; Duckett *et al.* 2003; Farrell & Sequeira 2004; Gómez-Zurita *et al.* 2007) evidence. While retaining the use of a familial rank for seed-beetles is convenient because it provides taxonomic stability, it does not reflect the assumed phylogenetic relationships (Riley *et al.* 2002). In this review, we have considered seed-beetles as a subfamily of the Chrysomelidae to reflect our current state of knowledge in the systematics of Coleoptera. The resulting subfamily Bruchinae consists of approximately 64 genera grouped into six tribes (Amblycerini, Bruchini, Eubaptini, Kytorhinini, Pachymerini and Rhaebini; hence formerly considered as subfamilies) (Kergoat 2004). According to Johnson (1989), about 80% of the species are assigned to the tribe Bruchini; the remaining species are mostly found in the tribes Amblycerini and Pachymerini (10% and 9% respectively). The tribes Eubaptini, Kytorhinini and Rhaebini are both monogeneric with respectively four, 15 and six species (Borowiec 1987; Lopatin & Chikatunov 2000).

Seed-beetles are found in all continents except Antarctica, and are more diverse in tropical regions (Southgate 1979). A clear biogeographical pattern is indicated by the distribution of the known genera that are found either in the Nearctic and Neotropical regions or in the Afrotropic, Australasia, Indomalaya and Palearctic regions, with the exception of the genus *Kytorhinus* (Lukjanovitch & Ter-Minassian 1957). The present distribution of the latter genus (15 species are found in the Palearctic whereas a single species is found in the Nearctic) is probably linked to the Early-Mid Tertiary fragmentation of the temperate forest that extended throughout the Northern hemisphere (Sanmartín *et al.* 2001). Recent molecular clock calibrations (Farrell 1998; Kergoat *et al.* 2005a) suggest that the general disjoint biogeographic pattern in seed-beetles is likely not Gondwanan in origin, and that bruchines started their diversification in the Late Cretaceous, consistent with the proposal of Borowiec (1987). Unfortunately, further investigations on this issue (*i.e.*, through the acquisition of more precise time estimates) are currently limited by the scarcity of reliable fossil records for the subfamily (Poinar Jr. 1999).

The latter are only constituted by several representatives of the tribe Pachymerini, the oldest one being *Mesopachymerus antiqua* Poinar Jr., 2005 (Pachymerini: Pachymerina), recovered from Cretaceous Canadian amber (approximately 79 mya; Poinar Jr. 2005). More recent specimens include an undescribed member of the subtribe Caryopemina found in British Columbia shales (approximately 52-54.5 mya; Archibald & Mathewes 2000), a new species of *Caryobruchus* (Pachymerini: Pachymerina) found in Dominican amber (approximately 15-45 mya; Poinar Jr. 1999), and several species of the extinct genus *Oligobruchus* (Pachymerini: Caryopemina) recovered from Florissant shales (approximately 35 mya; Kingsolver 1965). Evidence of bruchine predation was also found on fossil seeds, as in the case of the damaged mimosoid seeds found in Mahenge shales and mudstones (approximately 46 mya; P. Herendeen unpublished).

Bruchines are especially notorious for their obligate seed-feeding habit (hence their common name of 'seed-beetles'), with only one species, *Bruchidius cinerascens*, known to feed on another host-tissue (*B. cinerascens* larvae develop into stems of Apiaceae; see Hoffman 1945; Delobel & Delobel 2003). Though this group is not a particularly speciose or conspicuous one, it constitutes an interesting model to study the evolution of host-plant associations (Johnson, 1981a; Jermy & Szentesi 2003; Kergoat *et al.* 2004). Unfortunately, for many species, host-plant records are missing or doubtful (mostly because of misidentification issues; Johnson *et al.* 2004). Moreover, the old bruchine literature is literally plagued by hundreds of records that require thorough examination (*e.g.*, Zacher 1952a, 1952b). As underlined by Kingsolver (1990), it is only with the work of researchers from the monographic period (1962-present) that numerous and reliable (*i.e.*, based on rearing of pods collected in the field) records are currently available. Accurate records indicate that seed-beetles are associated with over 30 plant families (Johnson 1981a, 1989). However, this apparent diversity in host-use must not obscure the fact that most species (especially in the species-rich tribe Bruchini) exhibit a strong preference for the plants belonging to the family Leguminosae (Johnson 1970, 1981a, 1989). A critical examination of the abundant host-plant data from the literature also reveals a high level of dietary specialization at the species level: according to Johnson (1989) more than 80% of bruchine species are only associated with one to three species of plants. The latter finding is consistent with the widely accepted hypothesis that internal feeders (*i.e.*, stem borers, wood borers and seed feeders) are generally more specialized than concealed or external feeders (Gaston *et al.* 1992; Bernays & Chapman 1994; Anderson 1995; Denno *et al.* 1995; Bucheli *et al.* 2002; Marvaldi *et al.* 2002).

Several explanatory hypotheses have been proposed while compiling reports on the evolution of host-plant associations in seed-beetles. In 1957, Lukjanovitch & Ter-Minassian described the evolution of bruchines as "a process of divergence, with adaptations toward feeding on distinct species of angiospermous plants": therefore, related species of beetles are expected to be associated with related species of plants. A similar pattern, defined as 'adaptive radiation', was later proposed

by Johnson (1989) to describe the evolution of host-plant association in the genus *Acanthoscelides* (Bruchini: Acanthoscelidina). In this large genus, morphologically related species (belonging to the same taxonomic groups) usually develop on similar host-plant genera or subfamilies. To explain this trend, Johnson made the assumption that during the course of evolution of *Acanthoscelides*, shifts toward unrelated host-plant groups were followed by subsequent diversifications of the insect groups that specialize on them. Coevolution, in which the insects and their host-plants experience reciprocal selective responses (the so-called ‘arm-race’; Ehrlich & Raven 1964), was also advocated to explain the observed patterns of host-plant associations in bruchines (Janzen 1969; Center & Johnson 1974). However, this hypothesis was later questioned, even by some of its first proponents (Janzen 1980a; Johnson, 1990), because of the inadequacy of correlative studies to demonstrate coevolutionary processes (Spencer 1988). Another hypothesis, referred as sequential evolution, was proposed by Jermy (1976, 1984) to describe the evolution of bruchines (see also Jermy & Szentesi 2003). In opposition to the coevolution theory, the sequential evolution model predicts that the insects do not influence the evolution of plants, because they do not exercise a significant selective pressure. Under this scheme, seed-beetles are supposed to have undergone their diversification on host-plant groups that were already diversified (a similar pattern was advocated for other members of the family Chrysomelidae in the study of Gómez-Zurita *et al.* 2007).

Without robust historical frameworks, it was virtually impossible to estimate the relevancy of all these hypotheses at the time they were made. A turning point was reached in the late 90s when studies on bruchines benefited from a regain of interest with the burst of molecular analyses (Silvain & Delobel 1998): in the last ten years, numerous studies on bruchines based on molecular phylogenetics were published (*e.g.*, Morse & Farrell 2005; Tuda *et al.* 2006). In this paper we propose to use a supertree approach to perform a meta-analysis based on the results of these previous studies. It will provide us with an opportunity to investigate several taxonomic and systematics issues (*e.g.*, the monophyletic condition of specific groups). The resulting phylogenetic framework will also allow us to examine the evolution of host-plant associations in bruchines through the use of character optimization methods.

2. Methods

2.1. Supertree analyses

The principle of the supertree method reconstruction is to combine trees resulting from separate analyses of distinct data sets into a single and larger supertree. Several methods for supertree reconstruction have been developed (Sanderson *et al.* 1998; Bininda-Emonds *et al.* 2002; Bininda-Emonds 2004; Wilkinson *et al.* 2005), with the most commonly used method being a global optimization method: the

Matrix Representation using Parsimony (MRP; Baum 1992; Ragan 1992). In the MRP method, all source trees are converted into binary matrix representations and the resulting MRP matrix is then analyzed under parsimony to reconstruct a single (or more) most-parsimonious supertree. Among the other methods of supertree reconstruction, the Modified MinCut (MMC) algorithm of Sempel and Steel (Page 2002) is worth citing because of its ability to compute large supertrees in polynomial times. This method is based on a 'divide and conquer' approach (Page 2002). It uses a graphical network representation to combine the information of each input tree. In this graph each node corresponds to a leaf, and two nodes are connected if the two corresponding leaves are nested in at least one of the input trees. The MMC algorithm seeks to find the supertree that agrees with the maximum number of compatible nestings by performing minimum cuts on the graph. In an iterative process, subgraphs are disconnected from the original graph, and the components of the corresponding subgraphs are grouped in the output supertree. One of the advantages of this method is that the MMC algorithm ensures that uncontradicted relationships in the input trees are present in the output supertree (Page 2002).

Preliminary analyses were run using these two methods, as implemented in the program Rainbow version 1.3 (Chen *et al.* 2004). Though a more intensive use of the various methods of supertree building was conceivable, we have chosen to use only two methods to focus on the topic of bruchine evolution. MRP analyses were conducted using heuristic searches of 100 replicates with the Tree Bisection Reconnection (TBR) option and a 'Maxtree' setting of 1000. In all analyses *Pachymerus cardo* (Pachymerini: Pachymerina) was used as outgroup, because of its likely basal status (Kergoat *et al.* 2007b).

2.2. Source trees

A total of 15 phylogenetic trees from nine studies (Silvain & Delobel 1998; Kergoat & Silvain 2004; Kergoat *et al.* 2004, 2005a, 2005b; Morse & Farrell 2005; Tuda *et al.* 2006; Kergoat *et al.* 2007a, 2007b) were used to build a supertree including 196 species from 20 genera (Table 1). In this study, we have followed the taxonomic treatment of Borowiec (1987) that merges together the subtribes Acanthoscelidina and Bruchidina sensu Bridwell (1946). When necessary, the names of species were updated to take into account recent revisional studies (Anton & Delobel 2004; Delobel 2004; Johnson *et al.* 2004; Delobel 2006a, 2006b, 2007). Specimens assigned to the poorly defined genus *Tuberculobruchus* (Borowiec 1987; Anton 1999; Delobel 2006a) were treated as members of genus *Bruchidius* following Kergoat *et al.* (2007a). The more recent studies were used to discuss current taxonomic groups (*e.g.*, Johnson *et al.* 2004 for *Caryedon*; Kergoat *et al.* 2007b for *Bruchus*), especially in the large genus *Bruchidius* (Anton & Delobel 2003; Delobel *et al.* 2004; Delobel 2006a; Delobel & Delobel 2006). To deal with the presence of multiple phylogenetic hypotheses in a single study (*e.g.*, due to the use of distinct inference methods or

data sets), the source trees belonging to the same study were downweighted by a number equal to the total number of phylogenetic hypotheses of the study (Table 2). The program Mesquite version 1.12 (Maddison & Maddison 2006) was used to reconstruct each source tree.

Taxon	host-plant groups*		sampled in **
Amblycerini: Amblycerina			
<i>Spermophagus</i> Schoenherr, 1833 – Old World			
<i>Sp. sp.</i>	(no reliable host records)		c
<i>Zabrotes</i> Horn, 1885 – New World			
<i>Za. subfasciatus</i> (Boheman, 1833)	Leg. Papilionoideae	Cicereae Phaseoleae	g
Bruchini: Acanthoscelidina			
<i>Acanthoscelides</i> Schilsky, 1905 – New World			
<i>Ac. anoditus</i> Johnson, 1983	Mal. Malvoideae	Malveae	d
<i>Ac. argillaceus</i> (Sharp, 1885)	Leg. Papilionoideae	Phaseoleae	d
<i>Ac. biustulus</i> (Fall, 1910)	Leg. Papilionoideae	Desmodieae	d
<i>Ac. clandestinus</i> (Motschulsky, 1974)	Leg. Papilionoideae	Phaseoleae	d
<i>Ac. cuernavaca</i> Johnson, 1983	Leg. Papilionoideae	Desmodieae	d
<i>Ac. desmodicola</i> Johnson, 1983	Leg. Papilionoideae	Desmodieae	d
<i>Ac. desmoditus</i> Johnson, 1983	Leg. Papilionoideae	Desmodieae	d
<i>Ac. flavescens</i> (Fahraeus, 1839)	Leg. Papilionoideae	Phaseoleae	d
<i>Ac. guazumae</i> Johnson & Kingsolver, 1971	Mal. Byttnerioideae	Theobromeae	d
<i>Ac. isla</i> Johnson, 1983	Leg. Papilionoideae	Phaseoleae	d
<i>Ac. macrophthalmus</i> (Schaeffer, 1907)	Leg. Mimosoideae	'basal mimosoids'	d
<i>Ac. malvastrumicis</i> Johnson, 1983	Mal. Malvoideae	Malveae	d
<i>Ac. mazatlan</i> Johnson, 1983	Leg. Papilionoideae	Desmodieae	d
<i>Ac. mexicanus</i> (Sharp, 1885)	Leg. Mimosoideae	'basal mimosoids'	d
<i>Ac. mundulus</i> (Sharp, 1885)	Leg. Papilionoideae	Aeschynomeneae	d
<i>Ac. oblongoguttatus</i> (Fahraeus, 1839)	Leg. Mimosoideae	'basal mimosoids'	d
<i>Ac. obtectus</i> (Say, 1831)	Leg. Papilionoideae	Phaseoleae	b,d
<i>Ac. obvelatus</i> Bridwell, 1942	Leg. Papilionoideae	Phaseoleae	d
<i>Ac. palmasola</i> Johnson, 1983	Leg. Papilionoideae	Phaseoleae	d
<i>Ac. puellus</i> (Sharp, 1885)	Leg. Papilionoideae	Phaseoleae	d
<i>Ac. sanblas</i> Johnson, 1983	Mal. Grewioideae		d
<i>Ac. sanfordi</i> Johnson, 1983	Leg. Papilionoideae	Phaseoleae	d
<i>Ac. styliifer</i> (Sharp, 1885)	Leg. Papilionoideae	Desmodieae	d
<i>Ac. taboga</i> Johnson, 1983	Leg. Papilionoideae	Phaseoleae	d

Table 1. Taxon sampling.



Taxon	host-plant groups*		sampled in **
<i>Ac. zonensis</i> Johnson, 1983	Leg. Papilionoideae	Phaseoleae	d
<i>Algarobius</i> Bridwell, 1946 – New World			
<i>Al. prosopis</i> (LeConte, 1858)	Leg. Mimosoideae	'basal mimosoids'	b,d
<i>Bruchidius</i> Schilsky, 1905 – Old World			
<i>Bi. albizziarum</i> (Decelle, 1958)	Leg. Mimosoideae	'derived mimosoids'	b,d,e,h
<i>Bi. auratopubens</i> Delobel, 2007	Leg. Mimosoideae	'derived mimosoids'	b,d,e,h
<i>Bi. aureus</i> Arora, 1977	Leg. Mimosoideae	'derived mimosoids'	h
<i>Bi. aurivillii</i> (Blanc, 1889)	Leg. Mimosoideae	'basal mimosoids'	b,d,e
<i>Bi. babaulti</i> (Pic, 1921)	Leg. Mimosoideae	'basal mimosoids'	b,e,h
<i>Bi. badjii</i> Delobel, 2006 ¹	Leg. Caesalpinioideae	Cassieae	b,d,e,h
<i>Bi. bernardi</i> Delobel & Anton, 2004	Leg. Papilionoideae	Galegeae	b,d
<i>Bi. biguttatus</i> (Olivier, 1795)	Cis.		b,c
<i>Bi. bimaculatus</i> (Olivier, 1795)	Leg. Papilionoideae	Trifolieae	b,c,d
<i>Bi. cadei</i> Delobel, 2007	Leg. Mimosoideae	'derived mimosoids'	b,d,e,h
<i>Bi. calabrensis</i> (Blanchard, 1844) ²	Leg. Papilionoideae	Trifolieae	b,c,d
<i>Bi. campylacanthae</i> Delobel, 2007	Leg. Mimosoideae	'derived mimosoids'	b,d,e,h
<i>Bi. caninus</i> (Kraatz, 1869)	Leg. Papilionoideae	Galegeae	b,c,d
<i>Bi. centromaculatus</i> (Allard, 1868)	Leg. Mimosoideae	'basal mimosoids'	b,d,e
<i>Bi. chloroticus</i> (Dalm., 1833)	Leg. Papilionoideae	Robinieae	b,d,e,h
<i>Bi. cinerascens</i> (Gyllenhal, 1833)	Api.		c
<i>Bi. dichrostachydis</i> Delobel & Anton, 2003	Leg. Mimosoideae	'basal mimosoids'	b,d,h
<i>Bi. dispar</i> (Gyllenhal, 1833)	Leg. Papilionoideae	Trifolieae	b,c,d
<i>Bi. elnairensis</i> (Pic, 1921)	Leg. Mimosoideae	'basal mimosoids'	b,d,e
<i>Bi. flavovirens</i> Arora, 1977	Leg. Mimosoideae	'derived mimosoids'	h
<i>Bi. fulvicornis</i> (Motschulsky, 1874)	Leg. Papilionoideae	Trifolieae	b,c,d
<i>Bi. fulvus</i> (Allard, 1883)	Leg. Papilionoideae	Galegeae	e
<i>Bi. grandemaculatus</i> (Pic, 1933)	Leg. Mimosoideae	'basal mimosoids'	d
<i>Bi. holosericeus</i> (Schonherr, 1832)	(no reliable host records)		b
<i>Bi. incarnatus</i> (Boheman, 1833)	Leg. Papilionoideae	Vicieae	b,d,e
<i>Bi. ivorensis</i> Delobel, 2007 ³	Leg. Papilionoideae	Desmodieae	e
<i>Bi. lerui</i> Delobel, 2006 ⁴	Leg. Caesalpinioideae	Caesalpinieae	e,h
<i>Bi. lineatopygus</i> (Pic, 1924)	Leg. Papilionoideae	Indigofereae	b,d,e
<i>Bi. lineolatus</i> Arora, 1977	Leg. Mimosoideae	'derived mimosoids'	h
<i>Bi. lividimanus</i> (Gyllenhal, 1833)	Leg. Papilionoideae	Genisteae	b,c,d
<i>Bi. marginalis</i> (Fabricius, 1776)	Leg. Papilionoideae	Galegeae	b,c,d
<i>Bi. nanus</i> (Germar, 1824)	Leg. Papilionoideae	Trifolieae	b,c,d
<i>Bi. natalensis</i> (Pic, 1903)	Leg. Mimosoideae	'basal mimosoids'	b,d,e,h

Table 1 [CONTINUED].



Taxon	host-plant groups*		sampled in **
<i>Bi. nianingensis</i> (Delobel, 2006) ⁵	Leg. Papilionoideae	Milletieae	b,d,e
<i>Bi. nodieri</i> (Pic, 1943)	Leg. Papilionoideae	Indigofereae	e
<i>Bi. pauper</i> (Boheman, 1829)	Leg. Papilionoideae	Loteae	c,d
<i>Bi. picipes</i> (Germar, 1824)	Leg. Papilionoideae	Trifolieae	b,c,d
<i>Bi. poecilus</i> (Germar, 1824)	Leg. Papilionoideae	Galegeae	b,d
<i>Bi. pusillus</i> (Germar, 1824)	Leg. Papilionoideae	Loteae	b,c,d
<i>Bi. pygidiopictus</i> Delobel, 2007	Leg. Mimosoideae	'derived mimosoids'	b,d,e,h
<i>Bi. pygmaeus</i> (Boheman, 1833)	Leg. Papilionoideae	Trifolieae	b,c,d
<i>Bi. quadrisignatus</i> (Fahraeus, 1871)	Leg. Mimosoideae	'derived mimosoids'	b,e,h
<i>Bi. quinqueguttatus</i> (Olivier, 1795)	(no reliable host records)		d
<i>Bi. raddianae</i> Anton & Delobel, 2003	Leg. Mimosoideae	'basal mimosoids'	b,d,e
<i>Bi. rubicundus</i> (Fahraeus, 1839)	Leg. Mimosoideae	'derived mimosoids'	b,d,e,h
<i>Bi. rubiginosus</i> (Desbrochers, 1869)	Leg. Papilionoideae	Genisteae	d
<i>Bi. saundersi</i> (Jekel, 1855)	Leg. Mimosoideae	'derived mimosoids'	h
<i>Bi. saudicus</i> Decelle, 1979	Leg. Mimosoideae	'basal mimosoids'	e
<i>Bi. securiger</i> Delobel & Anton, 2003	Leg. Mimosoideae	'basal mimosoids'	e
<i>Bi. seminarius</i> (L., 1767)	Leg. Papilionoideae	Loteae	b,c,d
<i>Bi. sericatus</i> (Germar, 1824)	Leg. Papilionoideae	Trifolieae	b,c,d
<i>Bi. silaceus</i> (Fahraeus, 1839)	Leg. Mimosoideae	'derived mimosoids'	b,e,h
<i>Bi. sinaitus</i> (K. Daniel, 1907)	Leg. Mimosoideae	'basal mimosoids'	b,e,h
<i>Bi. sparsemaculatus</i> (Pic, 1913)	Leg. Mimosoideae	'derived mimosoids'	h
<i>Bi. submaculatus</i> (Fahraeus, 1839)	Leg. Mimosoideae	'derived mimosoids'	b,d,e,h
<i>Bi. subuniformis</i> (Fahraeus, 1839)	Leg. Mimosoideae	'derived mimosoids'	b,e,h
<i>Bi. terrenus</i> (Sharp, 1886)	Leg. Mimosoideae	'derived mimosoids'	h
<i>Bi. trifolii</i> (Motschulsky, 1874)	Leg. Papilionoideae	Trifolieae	b,c,d
<i>Bi. tuberculatus</i> (Hochhuth, 1874)	(no reliable host records)		d
<i>Bi. uberatus</i> (Fahraeus, 1895)	Leg. Mimosoideae	'basal mimosoids'	b,d,e
<i>Bi. unicolor</i> (Olivier, 1795)	Leg. Papilionoideae	Hedysereae	b,c
<i>Bi. urbanus</i> (Sharp, 1885)	Leg. Mimosoideae	'derived mimosoids'	h
<i>Bi. varius</i> (Olivier, 1795)	Leg. Papilionoideae	Trifolieae	b,c,d
<i>Bi. villosus</i> (Fabricius, 1792)	Leg. Papilionoideae	Genisteae	b,c,d
<i>Bi. sp. KE01</i>	Leg. Mimosoideae	'derived mimosoids'	e,h
<i>Bi. sp. KE02</i>	Leg. Mimosoideae	'derived mimosoids'	e,h
<i>Bi. sp. KE03</i>	Leg. Mimosoideae	'basal mimosoids'	e
<i>Bi. sp. KE04</i>	Leg. Mimosoideae	'basal mimosoids'	e,h
<i>Bi. sp. KE05</i>	Leg. Mimosoideae	'basal mimosoids'	e,h
<i>Bi. sp. KE06</i>	Leg. Mimosoideae	'basal mimosoids'	e
<i>Bi. sp. KE07</i>	Leg. Mimosoideae	'basal mimosoids'	e,h

Table 1 [CONTINUED].



Taxon	host-plant groups*		sampled in **
<i>Bi. sp. KE08</i>	Leg. Mimosoideae	'basal mimosoids'	e,h
<i>Bi. sp. KE09</i>	Leg. Mimosoideae	'derived mimosoids'	e,h
<i>Bi. sp. KE11</i>	Leg. Papilionoideae	Indigofereae	e
<i>Bi. sp. KE12</i>	Leg. Papilionoideae	Indigofereae	e
<i>Bi. sp. KE13</i>	Leg. Papilionoideae	Indigofereae	e
<i>Bi. sp. SE01</i>	Leg. Papilionoideae	Aeschynomeneae	e
<i>Callosobruchus</i> Pic, 1902 – Old World			
<i>Cal. analis</i> (Fabricius, 1781)	Leg. Papilionoideae	Phaseoleae	g
<i>Cal. chinensis</i> (Linnaeus, 1758)	Leg. Papilionoideae	Phaseoleae	b,d,e,g
<i>Cal. dolichosi</i> (Gyllenhal, 1839)	Leg. Papilionoideae	Phaseoleae	g
<i>Cal. imitator</i> Kingsolver, 1999	Leg. Papilionoideae	Phaseoleae	g
<i>Cal. latealbus</i> (Pic, 1926)	Leg. Papilionoideae	Phaseoleae	g
<i>Cal. maculatus</i> (Fabricius, 1775)	Leg. Papilionoideae	Phaseoleae	a,b,d,e,g
<i>Cal. nigripennis</i> (Allard, 1895)	Leg. Papilionoideae	Phaseoleae	g
<i>Cal. phaseoli</i> (Gyllenhal, 1833)	Leg. Papilionoideae	Phaseoleae	b,d,e,g
<i>Cal. pulcher</i> (Pic, 1922)	Leg. Papilionoideae	Phaseoleae	g
<i>Cal. rhodesianus</i> (Pic, 1902)	Leg. Papilionoideae	Phaseoleae	g
<i>Cal. semigriseus</i> (Motschulsky, 1874)	Leg. Papilionoideae	Phaseoleae	g
<i>Cal. subinnotatus</i> (Pic, 1914)	Leg. Papilionoideae	Phaseoleae	b,d,e,g
<i>Cal. theobromae</i> (Linnaeus, 1767)	Leg. Papilionoideae	Phaseoleae	g
<i>Cal. utidai</i> Tuda, 2003	Leg. Papilionoideae	Phaseoleae	g
<i>Conicobruchus</i> Decelle, 1951 – Old World			
<i>Co. albopubens</i> (Pic, 1921)	Leg. Papilionoideae	Indigofereae	e
<i>Co. strangulatus</i> (Fahraeus, 1839)	Leg. Papilionoideae	Crotalariaeae	b,d,e
<i>Decellebruchus</i> – Old World			
<i>De. atrolineatus</i> (Pic, 1921)	Leg. Papilionoideae	Phaseoleae	d,e
<i>Gibbobruchus</i> Pic, 1913 – New World			
<i>Gi. sp.</i>	Leg. Caesalpinioideae	Cercideae	b,d,e,h
<i>Kingsolverius</i> Borowiec, 1987 – Old World			
<i>Ki. gibicollis</i> Borowiec, 1987	(no reliable host records)		b
<i>Megabruchidius</i> Borowiec, 1987 – Old World			
<i>Meg. tonkineus</i> (Pic, 1904)	Leg. Caesalpinioideae	Caesalpinieae	b
<i>Merobruchus</i> (Bridwell, 1946) – New World			
<i>Mer. insolitus</i> (Sharp, 1885)	Leg. Mimosoideae	'derived mimosoids'	f
<i>Mer. placidus</i> (Horn, 1873)	Leg. Mimosoideae	'basal mimosoids'	d
<i>Paleoacanthoscelides</i> Borowiec, 1985 – Old World			

Table 1 [CONTINUED].



Taxon	host-plant groups*		sampled in **
<i>Pa. gilvus</i> (Gyllenhal, 1839)	Leg.	Papilionoideae Hedysereae	c
<i>Penthobruchus</i> Kingsolver, 1973 – New World			
<i>Pe. germaini</i> (Pic 1894)	Leg.	Caesalpinioideae Caesalpinieae	b
<i>Pseudopachymerina</i> Zacher, 1952 – New World			
<i>Ps. spinipes</i> (Erichson, 1834)	Leg.	Mimosoideae ‘basal mimosoids’	b
<i>Sennius</i> Bridwell, 1946 – New World			
<i>Se. breveapicalis</i> (Pic, 1922)	Leg.	Caesalpinioideae Cassieae	f
<i>Se. morosus</i> (Sharp, 1885)	Leg.	Caesalpinioideae Cassieae	f
<i>Stator</i> Bridwell, 1946 – New World			
<i>St. aegrotus</i> (Sharp, 1885)	Leg.	Mimosoideae ‘derived mimosoids’	f
<i>St. beali</i> Johnson, 1963	Leg.	Mimosoideae ‘derived mimosoids’	f
<i>St. bottimeri</i> Kingsolver, 1972	Leg.	Mimosoideae ‘basal mimosoids’	f
<i>St. cereanus</i> (Pic, 1930)	Leg.	Mimosoideae ‘derived mimosoids’	f
<i>St. chalcodermus</i> Kingsolver, 1972	Leg.	Mimosoideae ‘derived mimosoids’	f
<i>St. chihuahua</i> Johnson & Kingsolver, 1976	Leg.	Mimosoideae ‘derived mimosoids’	f
<i>St. furcatus</i> Johnson & Kingsolver, 1989	Leg.	Mimosoideae ‘basal mimosoids’	f
	Leg.	Mimosoideae ‘derived mimosoids’	
<i>St. generalis</i> Johnson & Kingsolver, 1976	Leg.	Mimosoideae ‘derived mimosoids’	f
<i>St. limbatus</i> (Horn, 1873)	Leg.	Caesalpinioideae Caesalpinieae	f
	Leg.	Mimosoideae ‘basal mimosoids’	
	Leg.	Mimosoideae ‘derived mimosoids’	
<i>St. maculatopygus</i> (Pic, 1930)	Leg.	Mimosoideae ‘derived mimosoids’	f
<i>St. mexicanus</i> Bottimer, 1973	Leg.	Mimosoideae ‘basal mimosoids’	f
<i>St. monachus</i> (Sharp, 1885)	Leg.	Mimosoideae ‘derived mimosoids’	f
<i>St. pacarae</i> Johnson & Kingsolver, 1989	Leg.	Mimosoideae ‘derived mimosoids’	f
<i>St. pruininus</i> (Horn, 1873)	Leg.	Mimosoideae ‘derived mimosoids’	f
	Leg.	Mimosoideae ‘basal mimosoids’	
	Leg.	Papilionoideae Robinieae	
<i>St. pygidialis</i> (Schaeffer, 1907)	Leg.	Mimosoideae ‘derived mimosoids’	f
<i>St. sordidus</i> (Horn, 1873)	Leg.	Mimosoideae ‘basal mimosoids’	f
	Leg.	Mimosoideae ‘derived mimosoids’	
<i>St. subaeneus</i> (Schaeffer, 1907)	Leg.	Mimosoideae ‘basal mimosoids’	f
<i>St. testudinarius</i> (Erichson, 1847)	Leg.	Mimosoideae ‘basal mimosoids’	f
	Leg.	Mimosoideae ‘derived mimosoids’	
<i>St. tigrensis</i> (Pic, 1938)	Leg.	Mimosoideae ‘basal mimosoids’	f
	Leg.	Mimosoideae ‘derived mimosoids’	
<i>St. trisignatus</i> (Sharp, 1885)	Leg.	Mimosoideae ‘derived mimosoids’	f

Table 1 [CONTINUED].



Taxon	host-plant groups*		sampled in **
<i>St. vachelliae</i> Bottimer, 1973	Leg. Mimosoideae	'basal mimosoids'	f
<i>St. vittatithorax</i> (Pic, 1930)	Leg. Mimosoideae	'basal mimosoids'	f
	Leg. Mimosoideae	'derived mimosoids'	
Bruchini: Bruchina			
<i>Bruchus</i> Linnaeus, 1767 – Old World			
<i>Bu. affinis</i> Frölich, 1799	Leg. Papilionoideae	Vicieae	b,c,i
<i>Bu. altaicus</i> Fahraeus, 1839	Leg. Papilionoideae	Vicieae	i
<i>Bu. atomarius</i> (Linnaeus, 1761)	Leg. Papilionoideae	Vicieae	i
<i>Bu. brachialis</i> Fahraeus, 1839	Leg. Papilionoideae	Vicieae	c,i
<i>Bu. brisouti</i> Kraatz, 1868	(no reliable host records)		i
<i>Bu. canariensis</i> Decelle, 1975	(no reliable host records)		i
<i>Bu. dentipes</i> (Baudi, 1886) ⁶	Leg. Papilionoideae	Vicieae	b,c,i
<i>Bu. emarginatus</i> Allard, 1868	Leg. Papilionoideae	Vicieae	i
<i>Bu. griseomaculatus</i> Gyllenhal, 1833	Leg. Papilionoideae	Vicieae	i
<i>Bu. hamatus</i> Miller, 1881	Leg. Papilionoideae	Vicieae	i
<i>Bu. laticollis</i> Boheman, 1833	Leg. Papilionoideae	Vicieae	c,i
<i>Bu. lentis</i> Frölich, 1799	Leg. Papilionoideae	Vicieae	i
<i>Bu. libanensis</i> Zampetti, 1993	Leg. Papilionoideae	Vicieae	i
<i>Bu. loti</i> Paykull, 1800	Leg. Papilionoideae	Vicieae	b,c,i
<i>Bu. luteicornis</i> Illiger, 1794	Leg. Papilionoideae	Vicieae	c,i
<i>Bu. occidentalis</i> Luk. & Ter-Min., 1957	Leg. Papilionoideae	Vicieae	b,i
<i>Bu. pisorum</i> (Linnaeus, 1758)	Leg. Papilionoideae	Vicieae	i
<i>Bu. rufimanus</i> Boheman, 1833	Leg. Papilionoideae	Vicieae	c,f,i
<i>Bu. rufipes</i> Herbst, 1783	Leg. Papilionoideae	Vicieae	c,i
<i>Bu. sibiricus</i> Germar, 1824	(no reliable host records)		i
<i>Bu. signaticornis</i> Gyllenhal, 1833	Leg. Papilionoideae	Vicieae	i
<i>Bu. tristiculus</i> Fahraeus, 1839	Leg. Papilionoideae	Vicieae	c,i
<i>Bu. tristis</i> Boheman, 1833	Leg. Papilionoideae	Vicieae	c,i
<i>Bu. venustus</i> Fahraeus, 1839	Leg. Papilionoideae	Vicieae	i
<i>Bu. viciae</i> Olivier, 1795	Leg. Papilionoideae	Vicieae	c,i
Pachymerini: Caryedontina			
<i>Caryedon</i> Schoenherr, 1823 – Old World			
<i>Car. acaciae</i> Gyllenhal, 1833	Leg. Mimosoideae	'basal mimosoids'	a
<i>Car. abdominalis</i> Anton & Delobel, 2004 ⁷	Leg. Mimosoideae	'derived mimosoids'	a
<i>Car. albonotatus</i> (Pic, 1898) ⁸	Leg. Mimosoideae	'basal mimosoids'	a
<i>Car. crampeli</i> (Pic, 1924)	Leg. Caesalpinioideae	Cassieae	a

Table 1 [CONTINUED].



Taxon	host-plant groups*	sampled in **
	Leg. Caesalpinioideae	Cercideae
	Leg. Mimosoideae	'basal mimosoids'
<i>Car. dialii</i> Decelle, 1973	Leg. Caesalpinioideae	Cassieae
<i>Car. fathalae</i> Delobel, 1997	Com.	a
<i>Car. femoralis</i> Anton & Delobel, 2004 ⁹	Leg. Mimosoideae	'basal mimosoids'
<i>Car. fuliginosum</i> Prevet, 1965	Com.	a
<i>Car. furcatus</i> Anton & Delobel, 2004 ¹⁰	Leg. Mimosoideae	'derived mimosoids'
<i>Car. immaculatum</i> Prevet, 1965	Com.	a
<i>Car. longipennis</i> (Pic, 1898) ¹¹	Com.	a
<i>Car. lunatus</i> Prevet, 1965 ¹²	Com.	a
<i>Car. macropterae</i> Delobel, 1997	Com.	a
<i>Car. nongoniermai</i> Anton & Delobel, 2004 ¹³	Leg. Mimosoideae	'basal mimosoids'
<i>Car. pallidus</i> (Olivier, 1790)	Leg. Caesalpinioideae	Cassieae
<i>Car. serratus</i> (Olivier, 1790)	Leg. Caesalpinioideae	Cassieae
	Leg. Caesalpinioideae	Cercideae
	Leg. Caesalpinioideae	Detarieae
Pachymerini: Pachymerina		
<i>Pachymerus</i> Thunberg, 1805 – New World		
<i>Pa. cardo</i> (Fahraeus, 1839)	Are.	b,c,d,e,h

* the following abbreviations were used: Apiaceae (Api.); Arecaceae (Are.); Cistaceae (Cis.); Combretaceae (Com.); Leguminosae (Leg.); Malvaceae (Mal.)

** the following abbreviations were used: Silvain & Delobel 1998 (a); Kergoat & Silvain 2004 (b); Kergoat *et al.* 2004 (c); Kergoat *et al.* 2005a (d); Kergoat *et al.* 2005b (e); Morse & Farrell 2005 (f); Tuda *et al.* 2006 (g); Kergoat *et al.* 2007a (h); Kergoat *et al.* 2007b (i)

1 recorded as *Bi. dialii* Decelle, 1973 in Kergoat & Silvain 2004; Kergoat *et al.* 2005a, 2005b

2 recorded as *Bi. varipictus* (Motschulsky, 1874) in Kergoat *et al.* 2004, 2005a; Kergoat & Silvain 2004

3 recorded as *Bi. sp. KE14* in Kergoat *et al.* 2005b

4 recorded as *Bi. sp. KE10* in Kergoat *et al.* 2005b

5 recorded as *Bi. niokolobaensis* (Decelle, 1969) in Kergoat & Silvain 2004; Kergoat *et al.* 2005a, 2005b

6 recorded as *Bi. atomarius* (Linnaeus, 1761) in Kergoat *et al.* 2004; Kergoat & Silvain 2004

7 recorded as *Car. excavatus auct.* in Silvain & Delobel 1998

8 recorded as *Car. albonotatum* Prevet in Silvain & Delobel 1998

9 recorded as *Car. longispinosus auct.* in Silvain & Delobel 1998

10 recorded as *Car. mauritanicus auct.* in Silvain & Delobel 1998

11 recorded as *Car. longipennis* Prevet in Silvain & Delobel 1998

12 recorded as *Car. lunatum* Prevet in Silvain & Delobel 1998

13 recorded as *Car. sahelicus auct.* in Silvain & Delobel 1998

Table 1 [CONTINUED].

Source	Inference method	Number of taxa	Data set information	Weight in the supertree analysis
Silvain & Delobel 1998	Maximum likelihood	17	12S	0.33333
	Parsimony	17	morphol.	0.33333
	Parsimony	17	12S, morphol.	0.33333
Kergoat <i>et al.</i> 2004	Bayesian inference	32	12S, Cytb, CO1	0.33333
	Maximum likelihood	32	12S, Cytb, CO1	0.33333
	Parsimony	32	12S, Cytb, CO1	0.33333
Kergoat & Silvain 2004	Bayesian inference	65	12S, Cytb, CO1, 28S	0.50000
	Parsimony	65	12S, Cytb, CO1, 28S	0.50000
Kergoat <i>et al.</i> 2005a	Bayesian inference	76	12S, Cytb, CO1	1.00000
Kergoat <i>et al.</i> 2005b	Bayesian inference	53	12S, Cytb, CO1, 28S	1.00000
Morse & Farrell 2005**	Bayesian inference	26	CO1, EF1a	0.50000
	Parsimony	26	CO1, EF1a	0.50000
Tuda <i>et al.</i> 2006	Bayesian inference	16	CO1, CO2	1.00000
Kergoat <i>et al.</i> 2007a	Bayesian inference	33	12S, Cytb, CO1, 28S	1.00000
Kergoat <i>et al.</i> 2007b	Bayesian inference	29	12S, Cytb, CO1, 28S	0.50000
	Parsimony	29	12S, Cytb, CO1, 28S	0.50000

* the following abbreviations were used: (i) – for mitochondrial genes – 12S rRNA (12S), cytochrome b (Cytb), cytochrome c oxidase subunit I (COI), cytochrome c oxidase subunit II (COII); (ii) – for nuclear genes – domain D2-D3 of the 28S rDNA (28S), elongation factor 1-alpha (EF1a); (iii) morphological data (morphol.).

** pruned trees were used in order to only have one specimen per species.

Table 2. Tree sampling.

2.3. Host-plant associations

A review of the literature of bruchine host-plant associations was conducted to identify reliable host records in 188 species out of the 196 species of our data set (see also Table 1 for a list of the corresponding host-plant groups). Doubtful or imprecise records were discarded following Kergoat *et al.* 2005a and Kergoat *et al.* 2007b. Systematics and host-plant names from the literature were systematically checked, and updated if necessary, by using the International Legume Database and Information Services database (ILDIS 2007 <http://www.ildis.org>) or the Germplasm Resources Information Network (GRIN 2007; <http://www.ars-grin.gov/cgi-bin/npgs/html/index.pl>).

2.4. Character optimizations

Based on the results of the preliminary supertree analyses, a pruned supertree was reconstructed by removing the eight taxa without known or reliable host-plant

records. The resulting phylogenetic framework was then used to perform distinct character optimizations of bruchine host-plant associations. These analyses were conducted under the parsimony criterion. To carry out the corresponding analyses the Mesquite software was preferred over other programs, because it allows a partial treatment of multiple associations under parsimony (see López-Vaamonde *et al.* 2003 for a discussion on the issue of the treatment of multiple associations). To better describe the limits of host-plant associations in bruchines, host-plant data were hierarchically categorized using three distinct taxonomic ranks (*i.e.*, family, subfamily, tribe) and analyzed accordingly (three distinct character optimizations were thus performed). The four species with more than two distinct character states for a given taxonomic rank (*i.e.*, *Stator limbatus*; *St. pruininus*; *Caryedon crampeli* and *Car. serratus*) were treated as ambiguous data in the corresponding analyses. In order to take into account the likely paraphyletic status of the tribe Acaciae (Maslin *et al.* 2003), we have defined new categories at the tribe level: (i) Ingeae and members of the genera *Acacia* (formerly genus *Acacia* subgen. *Phyllodineae*), *Acaciella* (formerly genus *Acacia* subgen. *Aculeiferum* Sec. *Filicinae*), *Mariosousa* (formerly genus *Acacia* subgen. *Aculeiferum* *Acacia coulteri* group) and *Senegalia* (formerly genus *Acacia* subgen. *Aculeiferum*) were placed in a so called ‘derived mimosoid’ group; (ii) Mimoseae, Parkieae and members of the genus *Vachellia* (formerly genus *Acacia* subgen. *Acacia*) were placed in a so-called ‘basal mimosoid’ group. For four host-plant groups (*i.e.*, Arecaceae, Cistaceae, Combretaceae and Malvaceae), the taxonomic information below the family level was missing; nonetheless, this does not affect the results of the corresponding character optimizations.

Finally, Permutation Tail Probability tests (PTP; Faith & Cranston 1991), as implemented in PAUP* (Swofford 2003), were performed in a complementary way to quantify how conservative the pattern of host-plant associations was. The various character states were randomized across the tips the phylogeny 1,000 times to generate a frequency distribution of minimum steps (multiple associations were treated as missing data). This distribution was then compared to the minimum number of steps observed.

3. Results

3.1. Supertree analyses

The MRP supertree analysis yielded puzzling topologies with all genera found paraphyletic and randomly dispersed throughout the trees. For instance, the presumably monophyletic genera *Bruchus* (according to seven source trees) and *Caryedon* (according to the three source trees) are both recovered scattered in seven distinct groups in the MRP trees. Given the rather high average fit value of the MRP trees (85.0%), these discrepancies were unexpected; they were surprising because the corresponding groupings were never found in any of the source trees. In addition,

they are in strong contradiction with morphological evidence. By contrast, the MMC supertree analysis results in a supertree (see Plates 6 and 7) whose overall topology is more in agreement with the groupings suggested by the source trees (average fit of 91.5%). We hypothesize that the discrepancies between the two approaches could be partially explained by the limited level of taxon overlapping between all source trees, with the MMC approach being likely less sensitive to this issue because the MMC algorithm has the desirable property of retaining more of the information shared by the input trees (*i.e.*, the uncontradicted relationships *sensu* Page, 2002). Since our use of a supertree approach was first motivated by the possibility of summarizing and discussing the results of previous studies, we have thus chosen to only focus on the results based on the MMC supertree.

The resulting phylogenetic framework provides an interesting overview of the current state of knowledge in bruchine phylogenetic relationships. It also constitutes a useful framework to investigate current taxonomic groups (the latter, when known, are figured on Plates 6 and 7). A clear biogeographical pattern is recovered (see also Plates 6 and 7), in which almost all species distributed in the Afrotropic, Indomalaya and Palearctic regions are distributed in two distinct clades. Within these species, the majority of Palearctic species are also distributed in two distinct clades: (i) the first gathers *Paleoacanthoscelides gilvus* (subtribe Acanthoscelidina) and all the members of the genus *Bruchus* (subtribe Bruchina); (ii) the second gathers 19 *Bruchidius* species from five taxonomic groups.

The basal part of the supertree is not resolved. As a result, no evidence is found for the monophyly of the three sampled tribes (*i.e.*, Amblycerini, Bruchini and Pachymerini). At the subtribe level, the tribe Acanthoscelidina also appears as paraphyletic. At the genus level, the two largest genera (*i.e.*, *Acanthoscelides* and *Bruchidius*), which are respectively represented by 25 and 78 species, appear paraphyletic (Kergoat & Silvain, 2004; Kergoat *et al.*, 2005a). Two other genera (*Conicobruchus* and *Merobruchus*), which are only represented by two species, are also found paraphyletic in the supertree reconstruction. By contrast, five genera appear monophyletic in the supertree analysis: *Bruchus* (represented by 25 species), *Callosobruchus* (represented by 14 species), *Caryedon* (represented by 16 species), *Senniuis* (represented by two species) and *Stator* (represented by 22 species). No conclusions could be drawn on the status of the remaining 11 genera because they were only represented by single species.

The results of the supertree analyses provide us with an opportunity to assess whether extant bruchine taxonomic groups correspond to monophyletic groups or not (only the groups represented by more than one species in the supertree were investigated). In *Acanthoscelides*, only one group is found monophyletic (*Ac. aequalis* group) whereas the remaining groups are found paraphyletic (*Ac. flavescens*, *Ac. mexicanus*, *Ac. obtectus*, *Ac. pertinax* and *Ac. puellus* groups) (*sensu* Johnson 1989). In *Bruchidius*, out of nine taxonomic groups (Anton & Delobel 2003; Delobel *et al.* 2004; Delobel 2006a; Delobel & Delobel 2006), seven appear monophyletic (*Bi. astragali*, *Bi. bimaculatus*, *Bi. fovelolatus*, *Bi. pauper*,

Bi. seminarius, *Bi. serraticornis* and *Bi. villosus* groups) whereas the remaining groups are recovered as paraphyletic (*Bi. centromaculatus* and *Bi. rubicundus* groups). In *Bruchus*, out of six taxonomic groups (sensu Borowiec 1988; Kergoat *et al.* 2007b), five appear monophyletic (*Bu. affinis*, *Bu. atomarius*, *Bu. pisorum*, *Bu. rufipes* and *Bu. tristis* groups) whereas one group is recovered paraphyletic (*Bu. brachialis* group). In *Callosobruchus*, the seven members of the *Cal. chinensis* group (sensu Anton 2000; Tuda 2003) (*Cal. chinensis*, *Cal. dolichosi*, *Cal. nigripennis*, *Cal. pulcher*, *Cal. semigriseus*, *Cal. theobromae* and *Cal. utidai*) are recovered monophyletic. In *Caryedon*, the three taxonomic groups (sensu Johnson *et al.* 2004; *Car. acaciae*, *Car. longipennis* and *Car. serratus* groups) that include more than one species appear paraphyletic.

3.2. Character optimizations

A far from random pattern in the evolution of host-plant use is revealed by the character optimizations, with two major trends being discernible at the host-plant subfamily and tribe level.

First, with the few exceptions noted below, it appears that each of the sampled bruchine species is only associated with a set of closely related plants. This marked dietary specialization can be easily visualized in the three character optimizations of host-plant evolution (Plates 6 and 7): most species are coded by using a sole character state (hence they are only associated with a single host-plant group). At the family level, no species is known to develop in plants belonging to distinct plant families: more than 93% of the sampled species exclusively develop into Leguminosae seeds whereas the remaining species are exclusively associated with one of the four other plant families. At least for our data set, feeding on Leguminosae appears as a primitive condition. However, the nature of the ancestral host-plant group remains uncertain, because the presumably most basal species for this study, *Pachymerus cardo*, develops on palm trees (Arecaceae): therefore, pending a denser sampling of Pachymerini and the inclusion of representatives from the tribe Rhaebini (which is exclusively restricted to Zygophyllaceae; Lukjanovitch & Ter-Minassian 1957; Borowiec 1987) no further conclusions can be reasonably made. High degree of dietary specialization was also observed at the subfamily level, as only two species (out of 188), *Caryedon crampeli* and *Sator pruininus*, were associated with plants belonging to two distinct subfamilies. Similarly, at the tribe level, only nine species (seven members of the genus *Sator* and two members of the genus *Caryedon*) are known to develop in plants belonging to two (or more) distinct tribes.

A second trend, hereby referred to as ‘taxonomic conservatism in host-plant use’, is revealed by the character optimizations. In this evolutionary pattern, closely related insect species (and their common ancestors) are found associated with phylogenetically related plants: host-plant shifts are constrained and seldom occur between unrelated plant groups (*e.g.*, between plants that belong to distinct

families). As a result, entire clades are sometimes associated with plants belonging to the same botanical subfamily or tribe. For example, all *Callosobruchus* species are found associated with members of the tribe Phaseoleae whereas all *Bruchus* species appear associated with members of the tribe Viciae. For our data set this trend is also supported by the finding of a strong phylogenetic structure between the insect phylogeny and the nature of host-plant associations, as indicated by the results of the PTP tests ($P < 0.01$ whatever taxonomic levels considered: family, subfamily or tribe). At the family level, only six independent shifts from Leguminosae toward three other plant families (Apiaceae, Cistaceae and Combretaceae) are indicated by the character optimizations. Below the family level, a more dynamic pattern is suggested by the character optimizations, with multiple independent shifts and reversals. At the subfamily level, the character optimizations suggest that feeding on Mimosoideae was the primitive condition for the legume feeders. Interestingly, this trend is not irreversible since secondary shifts from Papilionoideae toward Mimosoideae are also found on two occurrences (*i.e.*, in a large clade of Palearctic *Bruchidius* and in a clade that groups together *Merobruchus placidus* and several *Acanthoscelides*). At the tribe level, multiple independent shifts are often recovered: for instance, the tribe Phaseoleae was colonized three times by members of three genera (*Acanthoscelides*, *Callosobruchus* and *Decellebruchus*) whereas basal mimosoids were independently colonized on six occurrences (by representatives of seven genera).

4. Discussion

4.1. Biogeography

In the supertree analysis, large group of species do cluster according to their geographical origin (either Afrotropic, Indomalaya and Palearctic regions or Nearctic and Neotropical regions). Both molecular and fossil evidence suggest that this vicariant pattern of distribution is better explained by a Cretaceous origin of seed-beetles, followed by dispersal through the various land bridges that have connected the Palearctic region with the Nearctic region between the Cretaceous and the beginning of the Tertiary (Kergoat *et al.* 2005a; Poinar Jr. 2005). However, the issue of knowing whether the bruchines originate from the Afrotropic, Indomalaya and Palearctic regions or the Nearctic and Neotropical regions remains unclear. As underlined by Poinar Jr. (2005), the present fossil record argues for the latter hypothesis. This hypothesis is also partially supported by the phylogenetic pattern that is recovered in our analyses, in which most species from the Afrotropic, Indomalaya and Palearctic regions are found in a more derived position. On the other hand, the complete lack of fossil records for the tribe Rhaebini, which is presumably one, if not the most, primitive bruchine tribe (Borowiec 1987; Kingsolver 2004), is problematic because this tribe is presently found only in Asia Minor and Israel (Lopatin

& Chikatunov 2000): the question of whether the present distribution is a good reflection of the past distribution of the Rhaebini remains unanswered.

4.2. *Bruchine systematics*

The supertree composition reflects the fact that most past molecular phylogenetics studies on bruchines have been focused on the tribe Bruchini, represented by 177 species from 16 genera. By contrast, the tribe Amblycerini is only represented by two species from two genera whereas the tribe Pachymerini is represented by 17 species from two genera. In absence of a more representative sampling, it is not possible to determine whether these three tribes are paraphyletic or not. Regarding the sampled subtribes, the finding of a paraphyletic subtribe Acanthoscelidina is well supported by the placement of the members of the genus *Bruchus* (that alone constitutes the subtribe Bruchina) within the Acanthoscelidina. Yet, little can be reported on the status of the subtribes Amblycerina, Caryedontina and Pachymerina because of their respective limited sampling.

Unsurprisingly, the genera that are supposedly poorly defined appear paraphyletic in the supertree analysis. It is especially the case for the genera *Acanthoscelides* and *Bruchidius* (Kergoat *et al.* 2005a), which aggregate most of the Acanthoscelidina species that fail to be affiliated to better-circumscribed genera (Borowiec 1987; Kergoat & Silvain 2004; Kingsolver 2004). In a similar way, the polyphyletic nature of the genus *Conicobruchus* was quite expected because of the equivocal definition of this genus that was separated from *Bruchidius* on the basis of a sole character: the concave shape of the sides of the pronotum (Borowiec 1987). The fact that both *Conicobruchus* and the related *Bruchidius* species (in molecular phylogenetics analyses) share a similar type of male genitalia argues for a complete revision of this genus. Though a paraphyletic genus *Merobruchus* was also recovered in the supertree, its status certainly needs further investigation (Kingsolver 2002) because the basal placement of *Me. insolitus* (in relation to *Me. placidus*) is likely to be biased due to its use as an outgroup in the study of Morse & Farrell (2005). In addition both species are underrepresented in the source trees (Table 1). With regard to the five genera that appear monophyletic in the supertree analysis (*i.e.*, *Bruchus*, *Callosobruchus*, *Caryedon*, *Senniuis* and *Stator*) little can be said of the status of the genus *Senniuis*, represented by two species only. The four other genera whose monophyly was recovered correspond to well-defined genera (see Borowiec 1987 for details); hence their apparent monophyly appears consistent with the information based on morphology.

The examination of the supertree reveals that nearly half (10 out of 25) of the taxonomic groups that are represented by more than one species are recovered paraphyletic (or polyphyletic). This finding clearly underlines the need for more studies to clarify the systematics of Bruchinae. In *Bruchus*, two recent studies have already permitted to clarify the status of the *Bu. rufipes* group, by transferring *Bu. griseomaculatus* to a group of its own (Kergoat *et al.* 2007b; Kergoat &

Alvarez 2008). Further investigations are required to precise the condition of the *Bu. brachialis* group, whose paraphyletic status is not statistically supported by available molecular analyses (Kergoat *et al.* 2007b). In *Bruchidius*, all European species groups are recovered monophyletic, in agreement with the recent revisional work of Delobel & Delobel (2006). To complete this study we hereby assign *Bi. mulsanti* (Brisout, 1863) to the *Bi. villosus* group. The latter group (that also includes *Bi. lividimanus*, *Bi. rufisurus* (Allard, 1883) and *Bi. villosus*) is morphologically characterized by an internal sac that includes dense groups of thin spicules; in this group all species whose biology is known are exclusively associated with plants from the tribe Genisteae (Delobel & Delobel 2003, 2005, 2006). The newly defined *Bi. seminarius* group (*Bi. seminarius* group *s.s.* in Delobel & Delobel 2006) is constituted by eight species that are morphologically characterized by an internal sac with specific denticles (see also Anton 1998); in this group all species whose biology is known are exclusively associated with plants from the tribe Loteae (Delobel & Delobel 2003, 2005, 2006). The 11 members of the *Bi. rubicundus* group are embedded within a clade that groups together 30 species in the supertree. This large clade also includes five species formerly assigned to the genus *Tuberculobruchus* by Decelle (1951), seven Asian species that are not currently assigned to any taxonomic group and seven species that have not been identified yet. All these species are morphologically homogeneous and share a similar type of morphological type of male genitalia (see Delobel 2006a for details). They are also well characterized by their diet specialization (they are exclusively associated with Mimosoideae, with the exception of a few species; Delobel 2006a). To clarify and better circumscribe the *Bi. rubicundus* group, we propose assigning the former members of the genus *Tuberculobruchus* (*Bi. albizziarum*, *Bi. babaulti*, *Bi. natalensis*, *Bi. silaceus* and *Bi. subuniformis*) and the seven Asian species (*Bi. aureus*, *Bi. flavovirens*, *Bi. lineolatus*, *Bi. saundersi*, *Bi. sparsemaculatus*, *Bi. terrenus* and *Bi. urbanus*) to the *Bi. rubicundus* group. Further studies will be necessary to better circumscribe this taxonomic group, in order to include the numerous other species (that are not represented in the present study) that are clearly related to this group (*e.g.*, *Bi. biloboscutus* Pic, 1947; see Delobel 2006a). In a similar way, we assign *Bi. saudicus* and *Bi. uberatus* to the *Bi. centromaculatus* group: these two species possess the same type of male genitalia and are also strictly associated with a similar set of host-plants (they only develop on genus *Vachellia*). In *Caryedon*, the three taxonomic groups that are represented by more than one species all appear paraphyletic. The latter finding suggests that the main criterion that has been used to define the various *Caryedon* species group (*i.e.*, the pattern of pubescence; Johnson *et al.* 2004) needs to be carefully assessed in future studies. Altogether, these results clearly argue for an increased use of male genitalia structures in studies on bruchine taxonomy and systematics, especially when defining or revising taxonomic groups.

Several likely artefactual results were recovered by the MMC approach, especially in some clades that mix together Afrotropic, Indomalaya and Palearctic species with Nearctic and Neotropical species. For instance, the placement of four

Bruchidius species (*Bi. grandemaculatus*, *Bi. quinqueguttatus*, *Bi. rubiginosus* and *Bi. tuberculatus*) within a large clade of Nearctic and Neotropical species appears unlikely (Plate 6). *Bruchidius grandemaculatus* is known for being closely related to members of the *Bi. centromaculatus* group (Kergoat *et al.* 2005a). The three other species are also affiliated to other Palearctic *Bruchidius* species groups (*Bi. serraticornis* group and *Bi. tuberculatus* group; Lukjanovitch & Ter-Minassian 1957; Kergoat *et al.* 2005a; Delobel & Delobel 2006). It is also the case for the two Nearctic and Neotropical species (*Acanthoscelides obtectus* and *Algarobius prosopis*). *Algarobius prosopis* is related to members of the genus *Acanthoscelides* whereas *Ac. obtectus* appears as the sister species of *Ac. obvelatus* (Alvarez *et al.* 2004; Kergoat *et al.* 2005a); the doubtful placement of *Ac. obtectus* in the MMC supertree can be likely accounted for by the fact that this species was used as an outgroup in the study of Tuda *et al.* (2006). Another doubtful result corresponds to the split of a presumably monophyletic group (Kergoat *et al.* 2005b; Kergoat *et al.* 2007c) into two distinct groups (the first gathers *Co. albopubens*, *Bi. nodieri*, *Bi. sp. KE11*, *Bi. sp. KE12* and *Bi. sp. KE13*; the second gathers *Co. strangulatus* and *Bi. lineatopygus*). All these species are also morphologically homogeneous and well characterized by the nature of their host-plant associations, as they only develop on Crotalariaeae and Indigofereae.

4.3. Evolution of host-plant associations

In this study, a clear trend toward conservatism in host-plant use was unravelled for nearly 200 bruchine species: overall, this evolutionary tendency best fits with the proposals of Lukjanovitch & Ter-Minassian (1957) and Johnson (1989). It is also consistent with the results of recent studies that have recovered similar patterns in other chrysomelid groups (see Gómez-Zurita *et al.* 2000; Gómez-Zurita, this volume). Since our perception of this phenomenon is still limited by the incomplete sampling of many bruchine groups we can assume that an even more marked pattern will be recovered using a more comprehensive data set. For instance, numerous genera, that are absent or very poorly sampled in our analyses, are known for their marked dietary specialization (Borowiec 1987): for instance the genus *Senniis* is restricted to the tribe Cassieae of the Caesalpinioideae (Johnson 1980); in a similar way species in the genus *Mimosestes* are mostly associated with basal mimosoids (Johnson 1987; Johnson & Siemens 1996). It is thus tempting to hypothesize that the entire subfamily shares a similar level of conservatism in the evolution of host-plant associations. Finer-scale studies may also reveal unexpected and interesting findings, as in the case of a recent study on the genus *Bruchus* that has indicated a trend toward conservatism in host-plant use at the plant genus and subgenus level (Kergoat *et al.* 2007b). Similarly, in two clades of *Callosobruchus*, conservatism in host-use was found below the tribe level, in relation with an adaptation to distinct climatic conditions: one clade is associated with young beans from the subtribe

Cajaninae in humid areas whereas the other clade is associated with the subtribe Phaseolinae in arid environments (Tuda *et al.* 2005; Tuda *et al.* 2006).

Among the various factors that have likely driven the evolutionary trajectory of seed-beetle groups by constraining their host-plant range, plant chemistry is likely one of the most important because it influences not only the host selection (Jermy & Szentesi 1978; Annis & O’Keeffe 1984; Huignard *et al.* 1990; N’Diaye & Labeyrie 1990) but also the host-suitability (Janzen *et al.* 1977; Janzen 1980b; Birch *et al.* 1986; Bleiler & Rosenthal 1988; Gatehouse *et al.* 1990; Siemens *et al.* 1991; Huignard *et al.* 1996; Kergoat *et al.* 2005b). Since chemically similar host plants are often closely related (*e.g.*, see the review of Bisby *et al.* 1994 for the Leguminosae; but see also Van Wyk 2003), we can assume that the females will preferentially oviposit on phylogenetically related host-plants, hence accounting for the marked dietary specialization and conservatism in host-plant use. Regarding host-suitability, numerous studies have shown that seed toxic metabolites act as a very effective defence against seed-beetles (see previous references), leading the latter to specialize and develop specific detoxification abilities (Bleiler & Rosenthal 1988; Rosenthal 1990; Zhu-Salzman *et al.* 2003; Moon *et al.* 2004). The resulting specializations likely involve evolutionary trade-offs (*sensu* Cornell and Hawkins 2003) that constrain seed-beetle groups to feed on restricted set of plants that share similar toxic metabolites (Kergoat *et al.* 2005a, 2007b). Having said that, our character optimizations have also underlined the fact that seed-beetles have retained the possibility to shift toward unrelated hosts, and further diversify on them. In relation with this issue, several field studies have reported that ovipositions sometimes occurred on plants that are not part of the usual host-range of the species (Johnson & Siemens 1991; Delobel *et al.* 1995; Delobel & Delobel 2005). According to the same authors, these oviposition mistakes are not uncommon and may have promoted the adaptation to new hosts (through expansion of host-range) during the course of the diversification of seed-beetles, especially in species with weak discrimination abilities (Delobel *et al.* 1995). These shifts toward chemically dissimilar host-plants have also likely involved the development of several ‘key innovations’ (*e.g.*, new detoxification abilities) to circumvent extant plant defences (Kergoat *et al.* 2005a, 2005b).

Pending further studies, our understanding of the influence of other factors (*e.g.*, behavioural factors, geographic distribution, genetic constraints or phenology of host-plants) on the evolution of host-plant associations in bruchines is still limited. For instance, the issue of potential niches being unexploited and permanently vacant remains unanswered. Janzen (1980b) made a report on the fact that numerous plants in Costa Rica were not preyed upon by bruchines, despite the fact that they were phylogenetically related to plants attacked by seed-beetles. Szentesi *et al.* (1996) made similar observations on the *Bruchus* species associated with *Vicia* whereas Delobel & Delobel (2006) stressed that *Bruchidius* feeding on *Cytisus* were unable to develop on *Ulex* despite the fact that both plant genera belong to the same tribe, share most secondary compounds, and have a similar phenology. Several studies have also underlined the possible influence of behavioural adaptations

on the pattern of host-plant associations. Johnson (1981b) was the first to report the fact that numerous bruchine species are clustered within three distinct oviposition guilds: (i) the species that oviposit on seed pods only; (ii) the species that oviposit only on mature seeds in pod on plants; (iii) the species that oviposit only on mature seeds on ground. Interestingly, the strong influence of the associated oviposition behaviours on the evolution of host-plant associations was recently demonstrated in a study on the genus *Stator* (Morse & Farrell, 2005). Similarly, another recent study (Delobel & Delobel 2006) has revealed that distinct lineages of *Bruchidius* associated with *Trifolium* seeds (Trifolieae) present very specific behavioural adaptations that allow them to exploit resources that are usually not exploitable by most bruchine species (*i.e.*, very small or subterranean seeds). All these recent findings clearly indicate that considerable work is required in the future to better understand the evolution of host-plant associations in bruchines.

Acknowledgements

The authors wish to thank G. Poinar Jr. for the reprint of his study on *M. antiqua*. This paper was greatly improved by the thoughtful comments made by M. Schmitt, J. Gómez-Zurita and one anonymous referee.

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Plate 6. Supertree resulting from the MMC analysis of 15 source trees. The monophyletic or paraphyletic condition of the taxonomic groups that are represented by more than one species is indicated either by black (for monophyletic groups) or grey (for paraphyletic groups) sidebars. Higher taxonomic ranks (tribes and subtribes) are also indicated on the right of the figure. Information on the biogeographical regions of the sampled species is also indicated by several arrows.





